



## Tansley review

# Community Response to Extreme Drought (CRED): a framework for drought-induced shifts in plant–plant interactions

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## Summary

As climate changes, many regions of the world are projected to experience more intense droughts, which can drive changes in plant community composition through a variety of mechanisms. During drought, community composition can respond directly to resource limitation, but biotic interactions modify the availability of these resources. Here, we develop the Community Response to Extreme Drought framework (CRED), which organizes the temporal progression of mechanisms and plant–plant interactions that may lead to community changes during and after a drought. The CRED framework applies some principles of the stress gradient hypothesis (SGH), which proposes that the balance between competition and facilitation changes with increasing stress. The CRED framework suggests that net biotic interactions (NBI), the relative frequency and intensity of facilitative (+) and competitive (–) interactions between plants, will change temporally, becoming more positive under increasing drought stress and more negative as drought stress decreases. Furthermore, we suggest that rewetting rates affect the rate of resource amelioration, specifically water and nitrogen, altering productivity responses and the intensity and importance of NBI, all of which will influence drought-induced compositional changes. System-specific variables and the intensity of drought influence the strength of these interactions, and ultimately the system's resistance and resilience to drought.

## I. Introduction

### 1. Current research on drought-induced plant community reordering

Climate change is creating new abiotic and biotic conditions in many terrestrial ecosystems, inducing community shifts that alter

ecosystem structure and function (Smith, 2011; Zeppel *et al.*, 2014). Many regions are expected to experience increases in the frequency and/or magnitude of droughts and in regions where drought intensification does not occur, increased precipitation variability may lead to more frequent dry periods (IPCC, 2013; Knapp *et al.*, 2015b; Martínez-Vilalta & Lloret, 2016). Episodic disturbances such as droughts are anticipated to cause more rapid

and lasting effects on plant communities than more gradual but chronic changes, such as rises in atmospheric CO<sub>2</sub> or decreases in mean annual precipitation (MAP) (Dukes *et al.*, 2005; Smith *et al.*, 2009; Kardol *et al.*, 2010; Smith, 2011; IPCC, 2013; Hoover *et al.*, 2014; Knapp *et al.*, 2015b). While abiotic stressors caused by drought drive community change, plant–plant interactions influence community-level responses to drought by mediating the effects of these stressors (Grant *et al.*, 2014).

Studies examining changes in community composition following drought often focus on species richness, but few address the mechanisms of abundance change (species re-ordering, Smith, 2011) and species turnover through time (Magurran, 2016). Focusing solely on richness can mask biologically important changes in species composition, which can have lasting legacy effects on plant communities, potentially affecting post-drought recovery and responses to future drought conditions (Smith, 2011; Sala *et al.*, 2012). For example, Hoover *et al.* (2014) found that species richness was not altered by drought; however, the system shifted from a grass–forb co-dominated community to a grass-dominated community. Concurrent environmental stressors, such as drought, may cause communities to cross thresholds that delay or prevent recovery (Smith *et al.*, 2009; Smith, 2011; Schwalm *et al.*, 2017; Harrison *et al.*, 2018). The underlying mechanisms for changes in community composition may be physiological or may act at the community level through alterations to plant–plant interactions that guide the direction of succession after drought (Bazzaz, 1990; Harrison *et al.*, 2018).

Drought-induced vegetation shifts have been captured in paleohistorical records as well as contemporary observational and experimental studies across a variety of biomes (Martínez-Vilalta & Lloret, 2016). While these studies have furthered our understanding of drought-induced community reorganization, each has limitations. Paleorecords, such as pollen in sediment cores, describe the existence of vegetation changes at centennial scales, but their temporal resolutions are commonly too coarse to be ecologically informative (Martínez-Vilalta & Lloret, 2016). Experimental droughts provide important information about community change at finer timescales; however, they rarely observe the community for extended periods of time and do not mimic important aspects of natural drought, such as increased vapor pressure deficit (VPD) and high heat conditions (De Boeck & Verbeeck, 2011; Novick *et al.*, 2016).

Observational studies that explore historical, natural droughts provide insight into the temporal trends of community reordering both during and after drought. These studies allow us to observe changes at fine temporal scales that are ecologically relevant and include abiotic conditions that are difficult to simulate. In Table 1, we highlight several studies in herbaceous systems, which typically respond more rapidly to environmental change than systems dominated by longer-living species, for example forests. In these examples, plant communities shifted substantially and composition stabilization took several years. These studies demonstrate variability in response times in similar community types, providing evidence that resistance and resilience of community composition varies depending on drought severity and the biotic and abiotic characteristics of the system (Lloret *et al.*, 2012).

The mechanisms for the temporal evolution of community drought responses are not fully understood, but biotic interactions are increasingly recognized as potentially important drivers of community composition (Brooker, 2006; Brooker *et al.*, 2008; He *et al.*, 2013; HilleRisLambers *et al.*, 2013). Previous studies examining the roles of biotic interactions and community composition have focused on interactions between trophic levels, such as herbivory (Johnson *et al.*, 2011; Lee *et al.*, 2014), while the role of plant–plant interactions, notably facilitation, have been largely ignored.

## 2. The role of plant–plant interactions in shaping communities

Competition is the most studied biotic interaction both within and between species, but fewer studies explore the balance between competition and facilitation (Michalet & Pugnaire, 2016). While the concept of facilitation, positive interactions among species, was originally proposed over a century ago (Clements, 1916), the introduction of the stress-gradient hypothesis (SGH; Bertness & Callaway, 1994; Callaway & Walker, 1997) led to heightened interest in the topic (Brooker, 2006; Michalet & Pugnaire, 2016). The SGH proposes competitive interactions are more prevalent and intense under low-stress conditions, while facilitative interactions are more frequent under high-stress conditions (Callaway & Walker, 1997). Refinements to the SGH acknowledge that the intensity and importance of facilitation may be highest under moderate stress and may decrease or even collapse under severe conditions (Michalet *et al.*, 2006, 2014a; Maestre *et al.*, 2009; Castanho *et al.*, 2015).

Empirical studies and meta-analyses have found support for the SGH (Lortie & Callaway, 2006; Seifan *et al.*, 2010b; Ariza & Tielbörger, 2011; Dohn *et al.*, 2013; He *et al.*, 2013; Michalet *et al.*, 2014b; Ziffer-Berger *et al.*, 2014; Lopez *et al.*, 2016) and evidence contradicting the SGH (Tielbörger & Kadmon, 2000; Maestre *et al.*, 2005; Bu *et al.*, 2013; Butterfield *et al.*, 2016), which have led to refinements of the model (Butterfield *et al.*, 2016). A meta-analysis by He *et al.* (2013) found increasing stress led to shifts towards facilitation or decreased competition across climates and ecosystems, although the strength of facilitation was system-dependent, and few studies have examined tropical dry forests and rainforests.

Despite evidence for increased facilitation under increasing stress, the vast majority of plant–plant interaction studies still focus on competition (Michalet & Pugnaire, 2016). Generally, the literature on facilitation is dominated by variations in interactions along environmental gradients (Michalet & Pugnaire, 2016). Few studies have explored plant–plant interactions across time (Biswas & Wagner, 2014), as they apply to drought stress (Resco de Dios *et al.*, 2014), or under more favorable conditions (Grant *et al.*, 2014). Even fewer studies have explored plant–plant interactions as water stress decreases after drought (Resco de Dios *et al.*, 2014).

Stress tolerance and competition for resources are often considered the primary determinants of compositional change in response to drought (Michalet & Pugnaire, 2016). Competition is a negative response that hinders growth or survival of other plants

**Table 1** Papers quantifying the response and recovery of herbaceous communities experiencing naturally occurring droughts.

Authors	Location and system	Drought conditions			Compositional change		
		Duration (yr)	Recovery (yr)	Definition	Greatest change	During drought	After drought
Stampfli & Zeiter (2004)	Mesobromion Grassland; Negrentino, Switzerland MAP: c. 1300 mm	3	9	Centennial max number of days with < 10 mm of rain	After	No shift in relative cover of grasses and forbs	Grasses decreased for 4 yr following drought. Forbs replaced grasses. System stabilized 4 yr after drought
Tilman (1996) (also see Tilman & El Haddi, 1992)	Grassland (old fields of varying ages and native prairie); Minnesota, USA MAP: 815 mm	2	6	3 <sup>rd</sup> worst drought of the past 150 yr	During	Relative abundance Grasses: C <sub>4</sub> increased; C <sub>3</sub> declined. Legumes declined slightly	Relative abundance C <sub>4</sub> and C <sub>3</sub> grasses returned to predrought levels after 6 yr. Legumes increased; still rare
Rondeau <i>et al.</i> (2013)	Short grass steppe; Colorado, USA MAP: 302 mm	2	7	2002: Worst drought in > 100 yr 2003: 60% below average	Both	Shrubs: Total cover decreased slightly, all species declined equally Grasses: Total cover decreased dramatically; subdominant species becomes dominant Drought 1: Dominant grass reduced dramatically, subdominant grass decreased slightly. Drought 2: Dominant grass decreased, subdominant grass became dominant Drought 1: S. <i>scoparium</i> decreased 98% while a formerly rare more xeric grass increased Drought 2: Only slight changes	Shrubs: Total cover 38% higher; driven by 59% increase in one species Grasses: Total cover did not recover, subdominant species maintained new dominance
Albertson & Tomanek (1965)	Short grass community; Kansas, USA MAP: 582 mm	Two droughts: 7 and 5	Two recovery periods: 10 and 4	Annual precipitation considerably below average	Both	Recovery 1: Cover of both species fluctuated and did not stabilize. Recovery 2: Dominance switch from 2 <sup>nd</sup> drought persists, but community continued to fluctuate	Recovery 1: Cover of both species fluctuated and did not stabilize. Recovery 2: Dominance switch from 2 <sup>nd</sup> drought persists, but community continued to fluctuate
	<i>Schizachyrium scoparium</i> dominated community; Kansas, USA MAP: 582 mm				Both	Recovery 1: S. <i>scoparium</i> increased; three co-dominant grasses Recovery 2: S. <i>scoparium</i> rebounds to predrought 1 levels, one of other co-dominants persists, other declines Recovery 1: One of the initial co-dominants recovers, the new co-dominants decrease but not to predrought levels Recovery 2: Grass that increased in recovery 1 continues to increase, and the two new grasses stabilize at intermediate levels	
	<i>S. scoparium</i> and <i>Andropogon gerardii</i> co-dominated community; Kansas, USA MAP: 582 mm				Both (no change after 2 <sup>nd</sup> drought)	Drought 1: Initial co-dominant grasses decrease and are replaced by different co-dominants Drought 2: No dramatic change	

within the community, whereas stress tolerance is an individual's ability to buffer against stress and involves physiological responses to drought (Harper, 1977). While there are many physiological responses to drought (e.g. stomatal closure), these tend to be species-specific and can manifest as facilitative mechanisms for neighboring plants (Holmgren *et al.*, 1997; Volaire, 2018).

Facilitation can protect communities against drought through habitat modification, resource enhancement, provision of a refuge from predators and competitors, and recruitment enhancement (Fig. 1; Stachowicz, 2001; Brooker *et al.*, 2008; Michalet & Pugnaire, 2016). While competition and stress tolerance clearly play important roles in community reorganization, facilitation may also have a strong influence. Thus, frameworks for community-level drought responses across time should incorporate facilitative plant–plant interactions, as stress levels change continuously and often dramatically during and after drought.

## II. The Community Response To Extreme Drought (CRED) framework

Measures of ecosystem function, such as above-ground net primary productivity (ANPP), often respond rapidly to the onset of extreme drought and recover rapidly (Tilman & El Haddi, 1992; Hoover *et al.*, 2014; Stuart-Haëntjens *et al.*, 2018). Conversely, plant community reordering can persist for years following an extreme drought (e.g. Table 1; Suarez & Kitzberger, 2008; Lloret & Granzow-de la Cerda, 2013), suggesting that community-level effects may be better indicators of drought severity (Smith, 2011). Altered plant–plant interactions may play an important role in driving community dynamics and species coexistence during and following drought (Lloret & Granzow-de la Cerda, 2013; Grant *et al.*, 2014).

Recent research has shown that plant–plant interactions can shift towards facilitation not only in locations with permanently harsh climates, but also during and after episodic drought in a variety of settings (Table 2; Brooker *et al.*, 2008; Lloret *et al.*, 2012; He *et al.*, 2013; Michalet & Pugnaire, 2016). Here, we propose the Community Response to Extreme Drought (CRED) framework, which transfers some of the spatial concepts from the SGH to the temporal progression of drought. CRED explores plant–plant interactions as water stress increases during drought and decreases through recovery and suggests how these interactions may influence community reorganization and stabilization after drought (Fig. 2).

### 1. Assumptions and definitions

In CRED, the general term *net biotic interactions* (NBI) refers to the balance between interactions, as facilitation and competition occur simultaneously within a community (Callaway & Walker, 1997). NBI can shift along a continuum from net negative (competitive) to net positive (facilitative). The SGH initially proposed that the 'frequency' of interactions changes under stressful conditions; however, frequency does not necessarily translate into the 'intensity' of interactions and only qualitatively addresses the 'importance' of interactions (Welden & Slauson, 1986; Brooker *et al.*, 2005; Maestre *et al.*, 2009; Seifan *et al.*, 2010a). 'Intensity' describes the absolute impact of interactions on plants, whereas

'importance' describes the effects of neighbors on a plant in relation to abiotic factors. This distinction between 'intensity' and 'importance' allows for the differentiation between biotic and abiotic drivers of community change, respectively (Welden & Slauson, 1986; Brooker *et al.*, 2005; Maestre *et al.*, 2009; Seifan *et al.*, 2010a).

Drought can be defined from multiple viewpoints, so we define drought from two perspectives: meteorological, 'a prolonged absence or marked deficiency of precipitation' (IPCC, 2013), and ecological, an episodic deficiency in water availability that pushes ecosystems beyond their threshold of vulnerability and, in plants, results in the continuous loss of water through transpiration until stomatal shutdown (Jaleel *et al.*, 2009; Hao & Singh, 2015; Crausbay *et al.*, 2017). Prolonged meteorological drought will eventually elicit physiological responses of plants to water limitation, and this indication of drought stress marks the onset of ecological drought. In CRED, we only consider droughts that qualify as extreme climatic events (ECEs; *sensu* Smith, 2011); that is, events that result in changed community composition.

Time in CRED is a relative measure, as plant communities can respond to extreme drought in time frames of weeks or months (Jung *et al.*, 2014), or years (e.g. Table 1). While time frames vary, the reference period is considered to be the typical generation time of the dominant species, including its persistence in the seed bank (Lloret *et al.*, 2012; Martínez-Vilalta & Lloret, 2016). If there is a shift in vegetation, we would expect an abrupt change in the abundance of species or plant functional types (PFTs), for example grasses, forbs and trees, exceeding the range of natural temporal variability (Lloret *et al.*, 2012; Hoover *et al.*, 2014).

We use the term *relative community change* (RCC) to illustrate the degree of compositional change arising through changes in abundance, extirpation and/or immigration. RCC can be visualized, or measured, as the distance between two communities in multivariate space, and is a generalizable way to describe temporal variation in community composition (Avolio *et al.*, 2015).

Resistance is the capacity of the system to withstand change during extreme drought, and resilience is the degree to which the system recovers to its initial composition (Stuart-Haëntjens *et al.*, 2018). In the theoretical communities used for this framework, both communities have the same resistance (A in Fig. 2a) and resilience (E in Fig. 2a) to drought, but the trajectory of community change is different (B–D in Fig. 2a), where one community experiences most of the change during drought (dotted line in Fig. 2a; e.g. Tilman, 1996) and the other experiences most of the change after drought (solid line in Fig. 2a; e.g. Stampfli & Zeiter, 2004). For systems that are highly resistant, we expect a longer lag time between the onset of ecological drought and changes in the relative abundance of species (i.e. a greater distance of solid line A in Fig. 2a). In practice, the onset of ecological drought is rarely recorded; therefore, resistance can also be considered from the start of the meteorological drought (dashed line A in Fig. 2a).

### 2. Shifting from meteorological to ecological drought

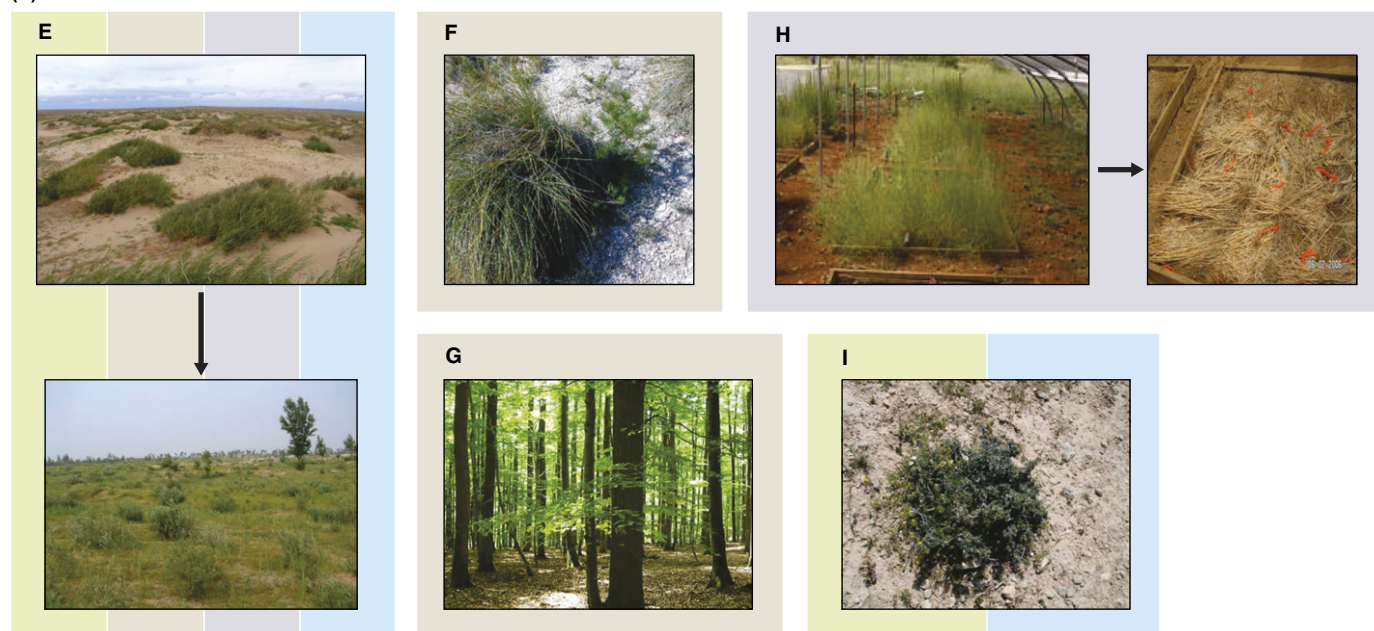
At the onset of meteorological drought, soil water content (SWC) begins to decline, but plants are not drought stressed. During this



(a)

A Habitat modification	B Resource enhancement	C Refuge from predators and competitors	D Recruitment enhancement
<ul style="list-style-type: none"> <li>• Reduce thermal stress (shade)</li> <li>• Reduce wind stress</li> <li>• Nurse plants               <ul style="list-style-type: none"> <li>- Reduce soil erosion and improve soil texture</li> <li>- Create better conditions for root growth</li> <li>- Create microhabitats for seed germination and seedling recruitment</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• Reduce SWC loss (shade)</li> <li>• Resource sharing through mycorrhizal networks</li> <li>• Alter resource use               <ul style="list-style-type: none"> <li>- Species-specific responses to drought</li> <li>- Mortality</li> </ul> </li> <li>• Hydraulic redistribution</li> <li>• Nurse plants/'fertility islands'               <ul style="list-style-type: none"> <li>- Increase nutrient availability (e.g. N and P)</li> <li>- Increase SWC</li> <li>- Reduce evapotranspiration</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• Deter predators               <ul style="list-style-type: none"> <li>- Presence of a plant resistant to herbivores (non-palatable), lowers herbivory</li> </ul> </li> <li>• One species suppresses a species' competitors</li> <li>• Mortality               <ul style="list-style-type: none"> <li>- Reduce plant density</li> <li>- Competitor release (e.g. mortality of dominant species)</li> </ul> </li> </ul>	<ul style="list-style-type: none"> <li>• Plant interactions including animal facilitation (i.e. shrub-plant-animal or shrub-animal-plant interactions)               <ul style="list-style-type: none"> <li>- see Lortie <i>et al.</i> (2016)</li> </ul> </li> <li>• Seed trapping (shrubs)</li> <li>• Herbivore protection</li> <li>• Magnet pollination</li> </ul>

(b)



**Fig. 1** (a) Potential facilitative mechanisms that occur within plant communities (Stachowicz, 2001; Brooker *et al.*, 2008; Lortie *et al.*, 2016; Michalet & Pugnaire, 2016). (A) Habitat modification, one individual or species alters local environmental conditions (green shading). This can be a physical barrier, where a plant (or species) protects their neighbors from stresses, such as heat and wind. A plant (or species) can also alter environmental conditions. (B) Individuals or species can also enhance resource availability by improving abiotic conditions, such as soil water content (SWC) and plant available nitrogen (N) and/or phosphorus (P) (brown shading). Resource availability can also be improved for other species indirectly when another species or plant is no longer taking up resources. This can occur through mortality or through species responses to drought, such as reduced water uptake in isohydric species. (C) Individuals (or species) can also provide refuge from predators or competitors simply by being present (purple shading). (D) Recruitment enhancement can facilitate the community, particularly during the recovery phase (blue shading). (b) Pictures providing examples of empirical evidence for the outlined facilitative mechanisms (A–D). The letters (A–D) next to each picture's description correspond to the mechanisms outlined above. (E) The top picture is of a shifting sand dune, and the bottom picture is of a restored sand dune using remnant shrub canopies of *Caragana microphylla* and *Salix gordejewii* in a semi-arid region of China. These shrubs acted as nurse plants/'islands of fertility', using at least one of the strategies in all four types of facilitative mechanisms (A–D; photo from Zhao *et al.*, 2007). (F) Adult individuals of tussock grass, *Stipa tenacissima*, facilitated saplings of *Pinus halapensis* in a semi-arid steppe in Spain by improving soil quality and through microclimate amelioration (B; Maestre *et al.*, 2003; photo from Brooker *et al.*, 2008). (G) In southern Germany, *Fagus sylvatica* was more resistant and resilient to drought stress when *Quercus petraea* were present compared to monoculture, which was probably caused by hydraulic redistribution of water from *Q. petraea* (B; photo from Hans Pretzsch; Pretzsch *et al.*, 2013). (H) The photo on the left shows live grasses, *Heteropogon contortus*, which are normally competitors of the shrub, *Prosopis velutina*. The photo on the right shows dead grass canopies, which acted as strong facilitators for *P. velutina* saplings (labeled with orange tape) (C; photo from Victor Resco de Dios; Resco de Dios *et al.*, 2014). (I) *Gymnocarpus decander* facilitated annual vegetation in a semi-arid environment in Jordan through protection from browsing and drought (A, D; photo from Pierre Liancourt; Brooker *et al.*, 2008).

phase, the NBI is negative, as plants compete for limiting resources at normal rates and water stress remains low. As the meteorological drought continues, SWC declines to a point at which plants begin

to respond physiologically and ecological drought begins, indicated by time zero in Fig. 2. As plants become increasingly drought-stressed, we hypothesize that NBI will shift from competitive to

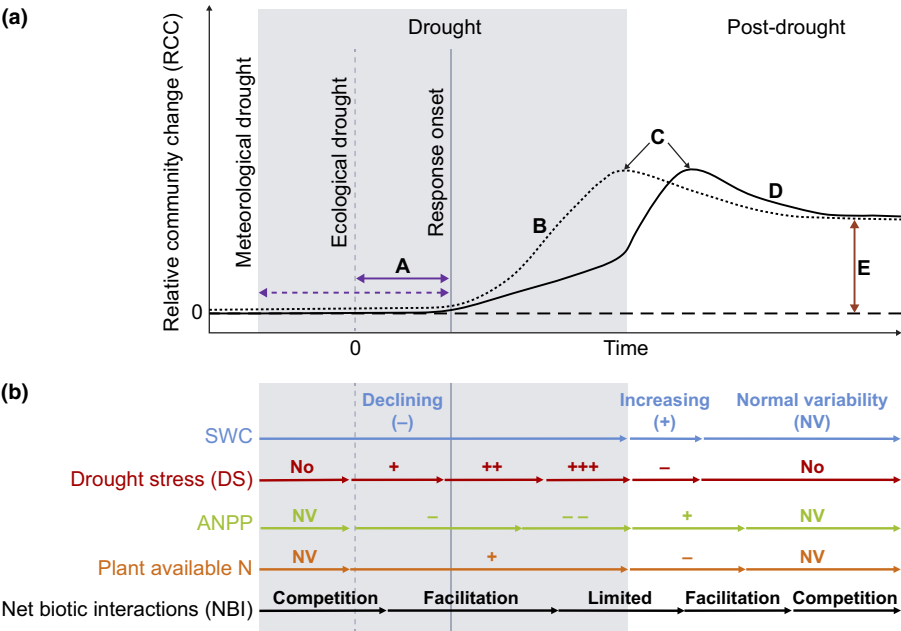
**Table 2** Studies exploring plant–plant interactions in relation to drought.

Authors	Natural system (✓) or number of species in experimental community	Natural drought	Removal experiment	Seeds planted	Assessment of facilitation	During drought	After drought (yr)	Observed mechanisms
During drought								
Cipriotti <i>et al.</i> (2008)	✓			✓	Seedling success	✓		Facilitative role of adult plants on grass seedlings during drought
Grant <i>et al.</i> (2014)	5				Individual and community biomass	✓		Positive effect on all species except the legume during drought due to release from competition
Jentsch <i>et al.</i> (2011)	2–4				Productivity	✓		Drought induced complementary plant–plant interactions; increase in facilitative and competitive effects, species-specific
Khan <i>et al.</i> (2014)	3				Productivity	✓		No facilitation of community productivity under drought; species-specific facilitation from legumes under climate manipulations
Kitzberger <i>et al.</i> (2000)	✓	✓			Seedling success	✓		Establishment of species requires nurse shrubs during years with substantial drought stress
Mariotte <i>et al.</i> (2013)	✓		✓		Productivity			Presence of subordinates facilitated regrowth of dominant and transient neighbors during drought
Resco de Dios <i>et al.</i> (2014)	✓			✓	Seedling success	✓		Drought positive effect on woody plant recruitment through mortality of competitive grasses—passive facilitation
Sthultz <i>et al.</i> (2007)	✓	✓			Growth and survival of juveniles	✓		Positive effects on juvenile tree survival and growth in high-stress sites with shrub cover; opposite effect in low-stress sites
After drought								
del Cacho & Lloret (2012)	✓	✓			Seedling success		4	Drought-induced canopy dieback increased establishment of woody species; pioneer shrubs facilitate establishment of late-successional species
Lloret & Granzow-de la Cerda (2013)	✓	✓			Plant growth juveniles		4	Juveniles less damaged beneath dense vegetation canopy during drought; post-drought growth higher in juveniles in open spaces
During and after drought								
Koyama & Tsuyuzaki (2013)	✓	✓			Seedling success	✓	2	Severe drought facilitative effect decreased for several species; collapse of facilitation under severe conditions; variation in seedling response suggests species-specific traits

Table 2 (Continued).

Authors	Natural system (✓) or number of species in experimental community	Natural drought	Removal experiment	Seeds planted	Assessment of facilitation	During drought	After drought (yr)	Observed mechanisms
Pretzsch <i>et al.</i> (2013)	✓	✓			Annual basal area of trees	✓	27/8	Species-specific facilitation in mixed stands (oak positive effect on beech); temporal example of stress gradient hypothesis (SGH)
Seifan <i>et al.</i> (2010b)	✓		✓		Seedling success	✓	1	Positive effect of drought on shrub seedling establishment (competitive release from annuals)
Tielborger & Kadmon (2000)	✓	✓			Demographic responses of four annual species	✓	2	Shrubs limited emergence and reproduction of understorey plants during drought; facilitation increased following drought

Studies that did not define drought as it relates to the system's climate were excluded.



**Fig. 2** (a) Conceptual framework for plant community responses to extreme drought. Relative community change (RCC), the degree of compositional change, which can be visualized, or measured, as the distance between two communities in multivariate space. RCC is a generalizable way to describe temporal variation in community composition. RCC includes, but is not limited to, species reordering, shift in dominance, extinction and immigration. In this framework, we differentiate between two drought definitions: meteorological drought (i.e. a prolonged and abnormal moisture deficiency), and ecological drought (i.e. plants exhibit physiological responses to drought stress (DS)). The gray area indicates that the community is experiencing a meteorological drought. At time = 0, plants start to respond to the drought at an individual level (physiological, mortality). The time between individual- to community-level response (A) depends on a specific system's ability to resist drought stress. The purple lines indicate the two ways that resistance can be viewed, either from the start of the ecological drought (solid line) or from the start of the meteorological drought (dashed line). Resistance is the capacity of the system to withstand change during extreme drought (Stuart-Haëntjens *et al.*, 2018). The rate of RCC (B) is system-dependent, here illustrated by a fast-responding (dotted line) and slow-responding (solid line) system. Furthermore, the timing of peak community change (C) may vary between systems and can occur during or after the drought. Similarly, the rate and magnitude of post-drought recovery (D) are system-dependent and vary with the rewetting scenario (see also Fig. 4). The community finally stabilizes at a state similar to predrought or may experience lasting changes in composition (E) depending on the community's resilience, the degree to which the system recovers to its initial composition (Stuart-Haëntjens *et al.*, 2018). A highly resilient community will have a lower RCC value (i.e. a shorter distance of E). (b) Temporal trajectories and stages of five key drivers for RCC: soil water content (SWC), drought stress (DS), above-ground net primary productivity (ANPP), plant available nitrogen (N) and net biotic interaction (NBI). NBI refers to the balance between plant–plant interactions, as facilitation (+) and competition (–) occur simultaneously within a community. See main text for details on the influence of each driver.

facilitative (Fig. 2b). The intensity of competition will probably relax because of mortality and differential use of resources (Michalet *et al.*, 2006), which could increase the importance of physiological responses and lead to stronger relative facilitation.

Plant functional traits (hereafter traits) such as growth forms, life histories, life stage, physiological characteristics and origin, can provide insight into the strength and nature of plant interactions in low stress conditions (He *et al.*, 2013). For example, in low stress conditions, grasses and herbs are often highly competitive, whereas trees exhibit strong facilitative mechanisms. As conditions become highly stressful, regardless of traits or magnitude of competitive responses, plants typically show decreasing competition and increasing facilitation (He *et al.*, 2013).

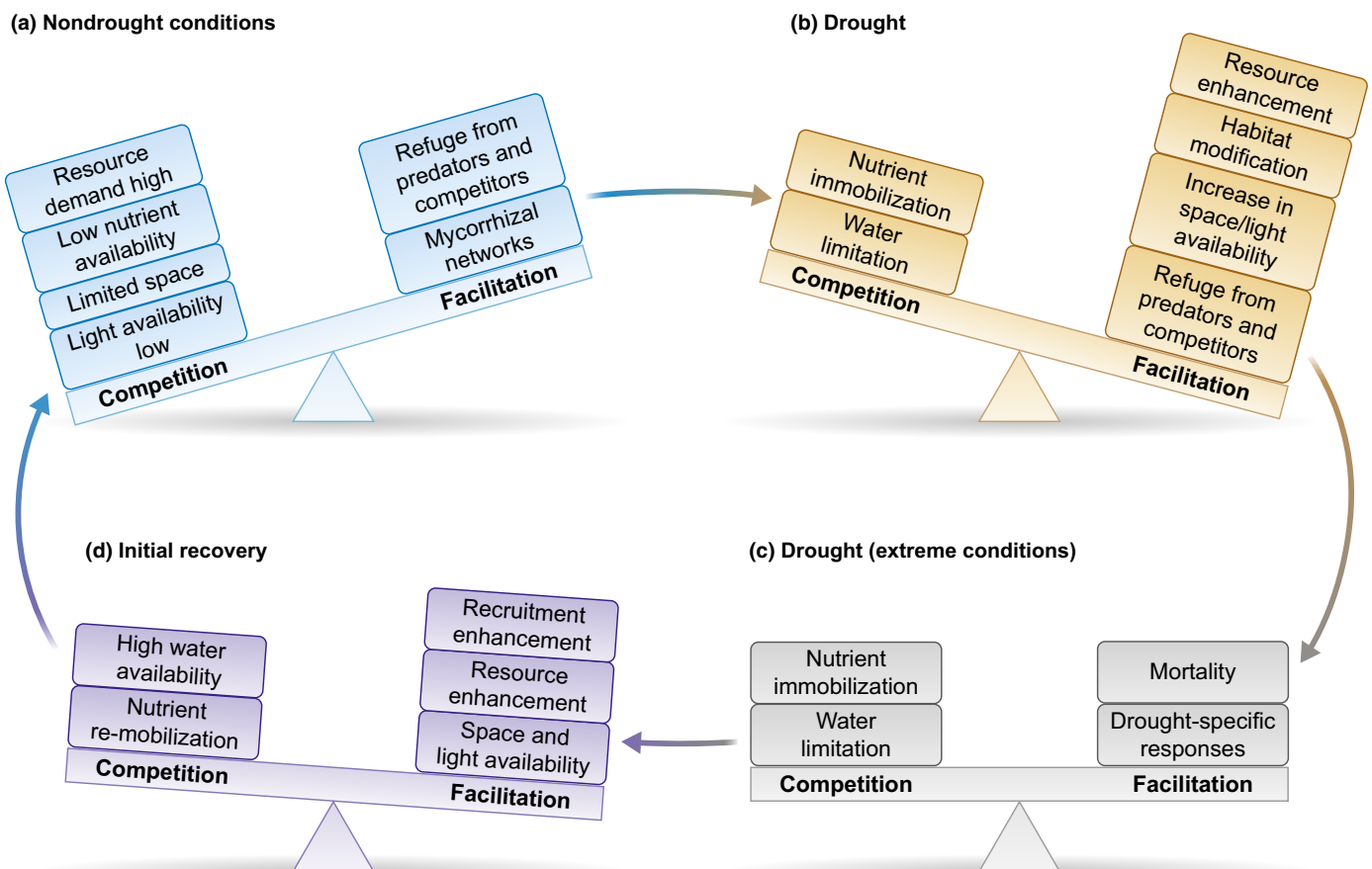
While changes to plant–plant interactions are system-dependent, we expect facilitative mechanisms to increase in intensity and importance during drought, particularly resource enhancement, habitat modification, increase in space/light availability, refuge from predators and competitors (Figs 1a (A–D), 3b). As mortality increases and growth decreases, we expect competitive release. We anticipate that these facilitative mechanisms will outweigh competition for resources. Reductions in competition can manifest as indirect facilitation when species-specific responses to drought leave behind resources for other species (Fig. 1b). For

example, isohydric behavior has been observed in  $C_4$  grasses, temperate hardwoods and other species of gymnosperms, where plants reduce water consumption and growth in the early phases of drought stress, leaving behind unused resources for anisohydric plants (McDowell *et al.*, 2008; Pretzsch *et al.*, 2013).

Drought-resistant systems, such as those with many drought-tolerant species, will probably maintain net competitive interactions for longer periods during the early stages of a drought. In some cases, the presence of a single species can enhance the drought resistance of a community (Fig. 1). For example, in a removal experiment in a grassland, the presence of a subordinate species facilitated the growth of dominant and transient species in the community during drought, increasing the resistance of the system (Mariotte *et al.*, 2013). These examples demonstrate that plant–plant interactions may be an important factor in determining a community's resistance to drought.

### 3. Onset of community change

As a drought extends over time, we anticipate that more species will reach drought tolerance thresholds (Michalet *et al.*, 2006; Maestre *et al.*, 2009). Thus, we expect that both intra- and interspecific competition will continue to relax, as growth is reduced further and



**Fig. 3** Temporal transitions of net biotic interactions (NBI) through the course of an extreme drought. NBI refers to the balance between plant–plant interactions, as facilitation (+) and competition (–) occur simultaneously within a community. Letters (a–d) correspond to different time periods over the course of an extreme drought. The angle at which the scale is leaning represents the relative importance and/or strength of the plant–plant interaction. The boxes on the scales suggest the potential mechanisms driving the interactions towards either negative, positive or NBI.



mortality increases (B in Fig. 2a). The combined effects of habitat modification, competition release through increases in mortality, reduced competition for available resources and resource modification cause NBI to become more facilitative (Fig. 1a (A–C)). In a savanna, Resco de Dios *et al.* (2014) found that active competition continued under drought conditions when live grasses were present, but once grass canopies died, strong passive facilitation for shrubs occurred because areas with dead grasses had higher SWC than bare soils.

As the meteorological drought persists beyond the point at which NBI shifts from competitive to facilitative, we predict that plants will still experience net facilitative NBI, although the strength of the facilitative interactions may diminish through time as drought intensifies (Michalet *et al.*, 2006; Maestre *et al.*, 2009). As ANPP declines, nitrogen (N) begins to accumulate in the soil as plant and microbial activity decouple and reduced SWC limits the mobility of N (Reichmann *et al.*, 2013; Dijkstra *et al.*, 2015).

Plant interactions are expected to weaken as the drought intensifies, and traits and drought tolerance become the biotic determinants for plant survival, further increasing RCC. Under very extreme droughts, we expect the importance of biotic interactions to be reduced and interactions to be minimal. As proposed in the hump-shaped model for plant–plant interactions (Michalet *et al.*, 2006), if stress levels become extreme enough, facilitative mechanisms may decrease or even collapse; the intensity and importance of facilitation is highest under moderate stress (Michalet *et al.*, 2006, 2014a; Maestre *et al.*, 2009; Castanho *et al.*, 2015). Therefore, in line with the hump-shaped model, if conditions become extreme enough, we hypothesize that NBI will be near zero or may become negative (Figs 3c, 4d: orange line).

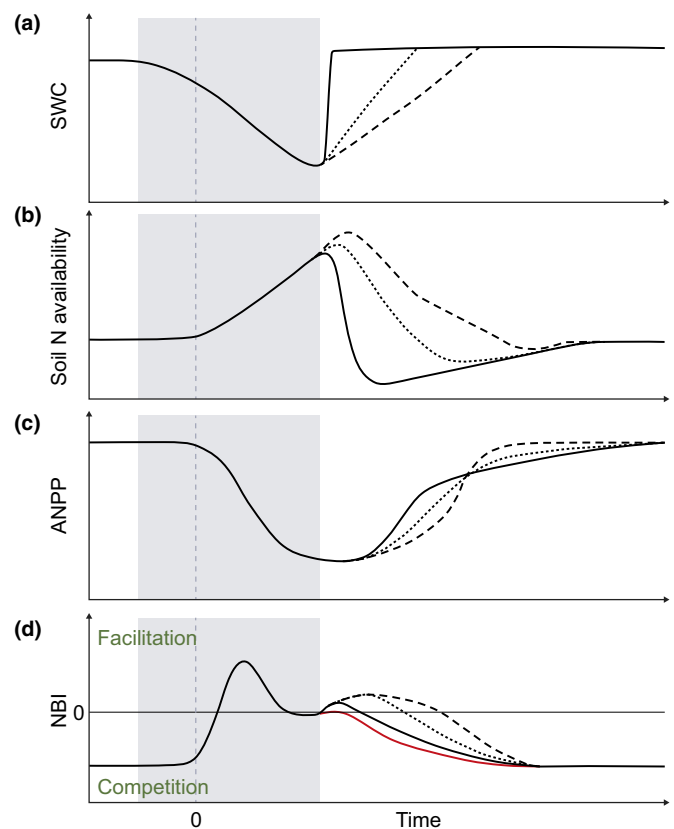
#### 4. Post-drought recovery

We define the end of a meteorological drought as the time at which the SWC rises above the wilting point of the dominant species in the community, which will depend on the nature of rewetting event(s) and site-specific characteristics. Plant communities do not immediately respond to the amelioration of water stress, and the response time of the community will vary, depending on a variety of potential modifiers (D in Fig. 2a; see also Fig. 3 and Table 3). As stress is alleviated, we expect that plant–plant interactions will respond in a manner that is essentially the inverse of the SGH, and facilitative NBI will increase (Fig. 2b), although interactions will probably be weaker than before or during the drought, as competition is ameliorated by both the reduction in competitors and the relatively high resource availability (Figs 3d, 4d). Primary facilitation mechanisms at this stage will differ from those during the drought, including a shift from mechanisms that facilitate survival to those that facilitate growth and recruitment (Fig. 1).

As favorable growth conditions persist, plant competition probably increases, generally resulting from the reduction of available resources through increased N uptake by both plants and microbes, and increased plant growth (Schimel & Bennett, 2004). The rate of N reduction and increase in productivity are likely to depend on the post-drought rewetting rate of the soil (Fierer & Schimel, 2002; Homyak *et al.*, 2018; Fig. 4). As climate, nutrient availability,

productivity and other conditions return to ‘normal’ (i.e. within their previous ranges), compositional changes begin to stabilize.

We consider the community to have stabilized when it maintains normal variability in community composition from year to year with clear dominant and subdominant species, and NBI shifts back to its pre-drought status (E in Fig. 2a). Drought-induced changes to plant composition can result in changes at the community level, through the establishment of a new dominant species or PFT, such as a shift from a grass-dominated community to a forb-dominated community (Stampfli & Zeiter, 2004). These effects can also shift the community to a new ecosystem type, such as from grassland to savanna (Resco de Dios *et al.*, 2014). These types of community changes (i.e. state changes) will probably generate new plant–plant



**Fig. 4** Conceptual diagram showing different post-drought rewetting scenarios, and their hypothesized effects on (a) soil water content (SWC), (b) soil nitrogen (N) availability, and community-level drought recovery as measured by (c) above-ground net primary production (ANPP) and (d) net biotic interactions (NBI). NBI refers to the balance between plant–plant interactions, as facilitation (+) and competition (–) occur simultaneously within a community. Solid lines represent the most rapid rewetting scenario, dotted lines represent the slowest and dashed lines represent an intermediate rewetting rate. The gray box and red line are meant to correspond to those in Fig. 1 and represent the extent of meteorological drought (i.e. a prolonged and abnormal moisture deficiency) and the point at which plants begin to experience measurable physiological drought stress (ecological drought), respectively. Rates of change in each variable are primarily for comparative purposes between rewetting scenarios, as the rates themselves are likely to depend on a multitude of other factors, such as community composition, soil texture and physiography. Similarly, because we aimed to illustrate relative differences in rates of change at various stages of post-drought recovery, time is relative and continuous, but not intended to be linear.

**Table 3** Factors influencing community resistance and resilience to drought and related studies.

Potential modifier	Related observational studies
Ecosystem	
1. Precipitation regime (MAP and variability)	Hallett <i>et al.</i> (2014); Michalet <i>et al.</i> (2014b); Ziffer-Berger <i>et al.</i> (2014); Knapp <i>et al.</i> (2015a); Lopez <i>et al.</i> (2016); Stuart-Haëntjens <i>et al.</i> (2018)
2. Ecosystem fertility	Kreyling <i>et al.</i> (2008); Khan <i>et al.</i> (2014); Michalet <i>et al.</i> (2015); Smith <i>et al.</i> (2016)
Soil properties	
1. Texture, depth and infiltration rates	Sala <i>et al.</i> (1988); Buckland <i>et al.</i> (1997); English <i>et al.</i> (2005); Weng & Luo (2008)
2. Plants' roles in infiltration rates	Cipriotti <i>et al.</i> (2008); Marshall <i>et al.</i> (2016)
Environmental conditions contributing to stress	
1. Timescale and intensity of drought	Albertson & Tomanek (1965); Adler & Levine (2007)
2. Vapor pressure deficit	Novick <i>et al.</i> (2016)
3. Heat	Prieto <i>et al.</i> (2009); Dreesen <i>et al.</i> (2014)
4. Disturbance (e.g. fire/grazing)	Prieto <i>et al.</i> (2009); Koerner & Collins (2014)
Landscape	
1. Land use/age	Morecroft <i>et al.</i> (2004); Forey <i>et al.</i> (2009)
2. Heterogeneity	Gitlin <i>et al.</i> (2006); Ovalle <i>et al.</i> (2006)
Plant assemblage	
1. Niche partitioning (resources, predators, time, space)	Sala <i>et al.</i> (1989); Pearson <i>et al.</i> (2003); Nippert & Knapp (2007); Shriver (2017)
a. Diversity (PFT/species)	Tilman (1996); Tilman <i>et al.</i> (2006); Jentsch <i>et al.</i> (2011); Fry <i>et al.</i> (2013)
b. Community composition/species-specific traits	Koyama & Tsuyuzaki (2013); Pretzsch <i>et al.</i> (2013); Grant <i>et al.</i> (2014); Khan <i>et al.</i> (2014)
c. Storage effect	Adler <i>et al.</i> (2006); Peterson <i>et al.</i> (2013)
2. Stability of dominant functional type/species	Kardol <i>et al.</i> (2010); Rondeau <i>et al.</i> (2013); Hoover <i>et al.</i> (2014)
3. Timing of drought (life stage)	Schiffers & Tielbörger (2006); Castanho <i>et al.</i> (2015)
4. Intraspecific trait variability/stress memory	Malyshev <i>et al.</i> (2016); Jung <i>et al.</i> (2014)
5. Lifespan of community/plants	Kreyling <i>et al.</i> (2008); Suarez & Kitzberger (2008); Cleland <i>et al.</i> (2013)
Multi-trophic interactions	Johnson <i>et al.</i> (2011); Lee <i>et al.</i> (2014)

Many of these studies have relevance to more than one of these modifiers.

interactions and could have important implications for ecosystem processes and trophic interactions.

### III. Post-drought rewetting rates: system and community recovery

#### 1. Recovery and the importance of abiotic and biotic conditions

The recovery period immediately following a drought or multiple drought events is a critical time for community reorganization, as exhibited by changes in plant community composition highlighted in the case studies in Table 1. These case studies demonstrate that drought events are often not a singular event, can occur over multiple years, and lapses between drought events can create multiple 'recovery periods' (Albertson & Tomanek, 1965). The exact relevant time period for recovery depends on site-specific variables influencing infiltration rates, such as soil texture, climate and community composition (see Section IV), and on the temporal sequence of drought events, such as frequency, recurrence and lapses between drought events. While specific characteristics of plant taxa can determine their ability to respond to post-drought conditions, variability in resource dynamics will influence which suites of traits are most advantageous, thereby driving compositional changes during the recovery period (Volaire, 2018).

The effects of post-drought rewetting rates on plant–plant interactions and community composition have received relatively

little attention, but many ecosystem processes are heavily reliant on water availability (He & Dijkstra, 2014). Rewetting rates will influence the temporal dynamics of water, nutrient and light availability, plant growth, and, therefore, the dynamics of NBI during community recovery. Nutrient limitation is common in many ecosystems, most frequently in the form of limitations in N or phosphorous (P), or N–P co-limitations (Augusto *et al.*, 2017). We focus on soil N during post-drought rewetting as a result of its mobility in the soil and because it is more directly affected by climatic conditions than P (Augusto *et al.*, 2017).

During a drought, inorganic N typically accumulates in the soil as a result of decreased plant and microbial uptake, despite lower mineralization rates (Evans & Burke, 2013; He & Dijkstra, 2014; Dijkstra *et al.*, 2015). Whether this translates into enhanced productivity or a lag in productivity response depends on whether the community is able to capitalize on the accumulated N, or if this N is lost from the system before plants can benefit (Fig. 3; Yahdjian *et al.*, 2006; Sala *et al.*, 2012). Different rewetting scenarios, through their effects on SWC and soil N, are likely to influence not only the temporal dynamics of plant–plant interactions, but also the relative strength of plant–microbe interactions, affecting community composition, retention of ecosystem N and carbon sequestration (Dijkstra *et al.*, 2015).

#### 2. CRED and resource recovery following drought

We predict that rewetting rates are negatively associated with N availability, through both abiotic mechanisms, such as

volatilization, leaching and resource remobilization, and biotic mechanisms by affecting N demand and the plant community's uptake ability (Fig. 3b). During recovery, maximum water and N availability may occur at different times, and this asynchrony could explain observed lags in the response of ANPP to increases in water availability (Yahdjian *et al.*, 2006).

When dry soils are rewetted, there is an increase in decomposition of organic matter, which may increase N mineralization (He & Dijkstra, 2014). By contrast to the rapid metabolic response of microbes to rewetting, recovery of maximum photosynthetic rates in plants is a slower process. For example, perennial C<sub>4</sub> grasses of a tallgrass prairie did not attain maximum photosynthetic rates for a week or more following drought, despite recovery of leaf water status and stomatal conductance (Heckathorn *et al.*, 1997). Reduced leaf N concentrations can persist for a similarly long time after rewetting (Heckathorn *et al.*, 1997). A result of the differential responses of plants and microbes to rewetting rates is additional N accumulation, which we predict is more prominent under slower rewetting scenarios (Fig. 4b; dotted and dashed lines); this consequently drives the dynamics of NBI during the post-drought period (Fig. 4d).

During rewetting, plant available N is susceptible to loss, which is likely to be exacerbated by faster rewetting (Fig. 4b, solid line; Gordon *et al.*, 2008; Evans & Burke, 2013). Under the faster rewetting scenario, we expect faster initial recovery of ANPP, as photosynthesis and water uptake ability can respond relatively quickly to increased SWC (Heckathorn *et al.*, 1997; Bloor & Bardgett, 2012). However, recovery of N uptake ability is not immediate, and the lag can vary widely across taxa (Franco & Nobel, 1990; Bloor & Bardgett, 2012). Relatively high ANPP early in the recovery period increases above-ground competition for space and light, while low available N increases below-ground competition for N (Wilson & Tilman, 1993). Combined, these processes accelerate the transition back to net competitive plant–plant interactions (Fig. 4d; solid line). As the recovery period progresses following rapid rewetting, reduced N availability probably drives stronger competition belowground and depresses ANPP recovery rates (Fig. 4c; solid line).

Conversely, at slower rewetting rates, we expect soils to retain more inorganic N before and during ANPP recovery, as less leaching is likely to occur (Fig. 4b, dashed and dotted lines; Bloor & Bardgett, 2012). When SWC is limiting for an extended period, we expect slower initial ANPP recovery as water may still limit growth (Fig. 4c, dashed line). We expect competition for above-ground resources (space/light) and plant available N to be relaxed and develop more slowly and for facilitative mechanisms to remain the primary NBI for a longer period of time under slower rewetting scenarios (Fig. 4d, dashed and dotted lines). Gradual rewetting may reduce the competitive advantage of species that respond rapidly to renewed soil water availability by increasing the strength of facilitation during this period and may benefit taxa that use N less efficiently in the longer term (Vinton & Burke, 1995; Evans & Burke, 2013).

### 3. Mechanisms for positive NBI during initial recovery

Many lines of evidence suggest that facilitation plays important roles at times of increasing stress (Lortie & Callaway, 2006;

Cipriotti *et al.*, 2008; Seifan *et al.*, 2010b; Ariza & Tielbörger, 2011; Dohn *et al.*, 2013; Pretzsch *et al.*, 2013; Ziffer-Berger *et al.*, 2014; Lopez *et al.*, 2016); however, studies that examine the role of facilitation as drought stress becomes relaxed are less common (Table 2). We hypothesize that facilitative interactions will be more important than competitive interactions both during and immediately after drought (Figs 1, 3d, 4d). Lloret & Granzow-de la Cerda (2013) found that seedling establishment of dominant shrubs was enhanced following drought and suggested that facilitative interactions may enhance species coexistence and drive community dynamics. The processes in post-drought plant communities are expected to be similar to those identified during early succession, and interactions would lead to the eventual dominance and coexistence of superior competitors (Bazzaz, 1990). Following a severe disturbance such as a drought, forest sites maintain high levels of structural complexity and spatial heterogeneity and retain legacy materials, such as a seed bank (Swanson *et al.*, 2011). In nonforest systems, we might similarly expect recovery to be characterized by high species diversity, including survivors, opportunists and drought-tolerant species, and organic material/structures that can create habitats for surviving and colonizing species (Swanson *et al.*, 2011; Lloret *et al.*, 2012; Harrison *et al.*, 2018).

Due to limited direct evidence for facilitation following extreme drought, we also include a null hypothesis that NBI will not become positive after drought (Fig. 4d, orange line). In this scenario, facilitative mechanisms still act simultaneously with competitive mechanisms, but net competitive mechanisms are either equal to or greater than net facilitative mechanisms. While this may be the case, we suggest that at least in some systems NBI will lean towards the positive side after a drought. Fig. 3(d) illustrates how this may occur using the facilitative mechanisms outlined in Fig. 1(a (A, B, D)).

Post-drought facilitation may become the dominant interaction following a drought through several mechanisms: species composition (Zhao *et al.*, 2007; Koyama & Tsuyuzaki, 2013), reduced competition (Stampfli & Zeiter, 2004; Suarez & Kitzberger, 2008), enhanced recruitment (Stampfli & Zeiter, 2004; Zhao *et al.*, 2007) and altered resource availability (Dale *et al.*, 2001; Zhao *et al.*, 2007). For example, in a *Sphagnum* peatland, seedling emergence was enhanced near tussocks (Koyama & Tsuyuzaki, 2013). This phenomenon was observed both before and after the drought but collapsed during the drought, providing evidence for recruitment enhancement following drought (Fig. 1a (D)), as well as the collapse of facilitation under extreme drought (also see Fig. 3c).

During the initial phases of recovery, the intensity of competition is relaxed compared to nonstressful conditions (Fig. 3d vs 3a). Drought-induced mortality results in reduced plant densities and therefore reduced competition (Lloret *et al.*, 2012). Plant traits have been linked to facilitative effects, and physical traits related to temperature and water buffering may reduce mortality during ECEs, such as drought. In forests, per-capita soil water availability can increase with mortality, which may promote survival after the drought (Fig. 1a (A); Dale *et al.*, 2001; Lloret *et al.*, 2012). A recent modeling study established a physiologically meaningful metric for hydraulic failure risk for chaparral species in southern California



and species-specific changes in hydraulic risk that could induce shifts in composition (Feng *et al.*, 2017). These types of models may be beneficial for understanding species sensitivity across timescales of rainfall variability to improve our understanding of community responses to drought.

#### IV. Site-specific characteristics influencing community resistance and resilience

While we expect extreme droughts to induce similar shifts in NBI across ecosystems, the timing and rate of change will be affected by the intensity, duration, timing and recurrence of drought, by ecosystem characteristics and by their interaction. These site-specific characteristics driving community resistance and resilience following extreme drought can be highly system-specific and require a deep understanding of the mechanisms driving community composition in a particular system (Knapp *et al.*, 2015a). We present a nonexhaustive overview of these factors (Table 3), which aims to emphasize the most widely recognized and generalizable characteristics influencing community reorganization. In the following sections, we highlight some of the main abiotic and biotic factors thought to influence drought-induced community composition change and system-wide resistance and resilience. We also discuss how ecosystem factors may modify the rate of drying and rewetting within a system and ways plant community composition at the onset of drought may affect the intensity and importance of plant–plant interactions.

##### 1. Ecosystem properties contributing to resistance/resilience and drying/rewetting rates

Physical attributes such as moisture regime and soil characteristics can strongly influence a community's resistance and resilience to drought conditions (Weng & Luo, 2008; Stuart-Haëntjens *et al.*, 2018). Climatic gradients (e.g. MAP) drive spatial variation in richness and composition of plant communities and generate differential sensitivity in responses to drought; systems with a higher MAP generally support higher diversity, which in turn increases community stability (Knapp *et al.*, 2015a). In a synthesis of grassland sites across the USA, Cleland *et al.* (2013) found that species turnover rates were higher in arid systems that had a high proportion of annual species. Hallett *et al.* (2014) suggest that mechanisms behind community stability vary in importance across environmental gradients, and the key driver of stability in sites with high MAP was species richness. Conversely, in systems with high precipitation variability, compensatory dynamics were more important for stability, such that a decline of stress-intolerant species was compensated for by growth of others (Hallett *et al.*, 2014).

A recent meta-analysis found that MAP was a good predictor of resistance to extreme drought in both grasslands and forests and indicated that physiological mechanisms may determine resistance (Stuart-Haëntjens *et al.*, 2018). However, the relationship for resilience to extreme drought with MAP was positive in grasslands and negative in forests, which may be driven by differences in plant residence time, plant architecture and drought strategies. Dry

grasslands may have low resistance and resilience as a result of general water-limitation or greater mortality than mesic systems (Stuart-Haëntjens *et al.*, 2018).

Butterfield *et al.* (2016) found that the difference between soil moisture under shrubs and in gaps decreased along an aridity gradient when long-term averages were considered, contradicting the SGH. However, when extreme years were considered, positive effects of shrubs on soil moisture were greatest at intermediate points along the aridity gradient, which is consistent with the hump-shaped model of plant–plant interactions (Michalet *et al.*, 2006; Holmgren & Scheffer, 2010; Butterfield *et al.*, 2016). These patterns were contingent on soil type, where plants had stronger effects on water availability in coarse soils, whereas physical properties were more important in fine soils (Butterfield *et al.*, 2016).

While few studies have focused on the role of soil texture in modulating the effect of droughts on community composition, Lane *et al.* (1998) found that soil texture affected the proportion of ANPP contributed by different PFTs, demonstrating that soil texture plays a role in community compositional changes. In a semi-arid desert grassland, English *et al.* (2005) found that coarse-textured soils rewetted faster, had lower soil water potential and did not maintain SWC as long as finer soils. Soils with more silt and clay retain more N, in the form of  $\text{NO}_3^-$ , than sandy soils (Gaines & Gaines, 1994). Drought was found to reduce the maximum water-holding capacity of hydric and mesic heathland soils, apparently as a result of changes to soil texture (Sowerby *et al.*, 2008). These findings demonstrate how soil texture could play an important role in SWC and nutrient availability under drought-induced community change, altering resource availability both during drought and under different rewetting scenarios (Fig. 4).

Differences in community structure along precipitation gradients can also impact soil hydraulic properties through the presence of macropores, or soil cavities that can be created by decaying roots. Macropores can increase infiltration capacity and rate and, therefore, speed up soil rewetting. Macropores created by roots depend largely on root architecture (Devitt & Smith, 2002; Marshall *et al.*, 2016). Perennials generally have deeper and thicker roots and an extensive root network compared to annual species, hence creating more macropores than annual species (Marshall *et al.*, 2016). By contrast, some grasses may decrease hydraulic conductivity when roots form thick matting near the soil surface (Archer *et al.*, 2002). Rooting depth, and the ability of roots to penetrate different substrates, can also affect post-drought recovery and community resilience (Lloret *et al.*, 2004). Species also differ in their contributions to soil organic matter which affects nutrient content, water-holding capacity and infiltration rates (Pugnaire *et al.*, 1996, 2004; Michalet *et al.*, 2015).

##### 2. The role of plant community composition in species coexistence and plant–plant interactions

In times of water limitation, community responses are products of species and/or PFT composition and traits, which can strongly filter species within a community (Lloret *et al.*, 2012). Partitioning of available resources can mediate community responses to drought



stress and is affected by the specific plant community composition at the time of drought and by the amount of diversity of the system (Reich, 2014; Felton *et al.*, 2017). Demographic tradeoffs in growth and survival can promote niche partitioning and the distribution of limiting resources during a drought (Shriver, 2017).

Understanding the relationship between traits and the trajectories and strengths of plant–plant interactions may provide insight into the resistance and resilience of a system (Butterfield, 2009; Lloret *et al.*, 2012, 2016; He *et al.*, 2013; Kunstler *et al.*, 2015). Partitioning of resources and species coexistence depends on the composition of PFTs and intraspecific phenotypic plasticity (Nicotra *et al.*, 2010; Reich, 2014). Soil water partitioning can be achieved through utilization of water from different soil layers or greater plasticity in water uptake strategies (Sala *et al.*, 1989; Nippert & Knapp, 2007). Drought can also act as a means to filter out species with traits that are unable to cope with water stress. In grassland ecosystems, species with low resource acquisition strategies tend to be favored, and competitors are more facilitated than stress-tolerant species under water stress, highlighting the importance of understanding traits within a community (Michalet *et al.*, 2006; Grant *et al.*, 2014; Jung *et al.*, 2014). Intraspecific trait variability may also be an important driver in short-term functional responses of plant communities (Jung *et al.*, 2014).

High inter- and intraspecific trait variability in resource acquisition increases niche differentiation and has a role in stabilizing a community (Tilman & El Haddi, 1992; Tilman *et al.*, 2006; Jung *et al.*, 2014). This is particularly true in systems with high PFT diversity as opposed to species diversity, *per se*. With a broad range of water use and resource acquisition strategies, functionally diverse plant communities could be expected to resist changes in community structure (Fry *et al.*, 2013; Jung *et al.*, 2014). Indeed, in a drought study manipulating PFT diversity, temperate grasslands with greater ranges of PFTs were more resistant to changes in key ecosystem processes and vegetative losses than systems with lower diversity (Fry *et al.*, 2013).

Drought stress can alter interactions between PFTs, but these changes are system-specific. Legumes, which often act as complementary or facilitative species under normal or wet conditions, can become competitive in drought conditions (Grant *et al.*, 2014; Khan *et al.*, 2014). Conversely, PFTs that typically confer competitiveness under ideal soil water conditions tend to become more facilitative under drought conditions (Khan *et al.*, 2014). While the resistance of a system is generally greater in systems with high PFT diversity, the dominant species or PFT tends to play an important role in community restructuring. For example, following a natural drought in a mesic grassland, the dominant PFT, grasses, were replaced by forbs (Stampfli & Zeiter, 2004), but in an experimental drought in a similar ecosystem, Hoover *et al.* (2014) found the opposite pattern. These differences are probably the result of the traits of the dominant species, and its interactions with neighboring species.

He *et al.* (2013) found that regardless of traits, or the intensity of an individual's competitive effects or responses, there was consistently a decrease in competition and an increase in facilitation with increasing stress (Fig. 4b). During drought, highly competitive species probably decrease their competitive effects and less

competitive species increase their facilitative effects. Species composition therefore determines the specific mechanisms of plant–plant interactions at play in a community (Fig. 1; He *et al.*, 2013). The intensity and magnitude of these community effects/responses is an important component in the resistance (Fig. 2a, A–B) and resilience (Fig. 2a, D–E) of a community. Modified plant behavior in the form of facilitation may promote recovery (Fig. 4d; Brotherton & Joyce, 2015). For example, delayed recovery of a dominant species may release other species from competition, which can induce change in community dominance (Brotherton & Joyce, 2015).

Following drought, resilience will depend on several mechanisms, but stabilization will probably occur faster under scenarios that minimize mortality (i.e. increase survival) and/or enhance recruitment, particularly in those dominated by long-lived species (Lloret *et al.*, 2012; Martínez-Vilalta & Lloret, 2016). Physiological mechanisms, such as enhanced stress tolerance, and phenotypic plasticity and variability can reduce mortality. Stress tolerance can also be influenced by the historical environmental conditions experienced by a community (Lloret *et al.*, 2012).

Leaf, root and seed traits were found to affect mortality in a Mediterranean shrubland, where plant cover resilience was positively related to higher water use efficiency (WUE) and lower specific leaf area (SLA). Conversely, resistance was characterized by higher SLA and lower WUE (Lloret *et al.*, 2016). Phenotypic plasticity can also reduce mortality (Nicotra *et al.*, 2010; Lloret *et al.*, 2012). This variability can be related to age, where early developmental stages are more sensitive to drought stress than adult stages and can create a major bottleneck in recruitment (Walck *et al.*, 2011; del Cacho & Lloret, 2012).

Resilience to drought will also be impacted by the recruitment ability of the dominant PFT(s). Recruitment can be reduced through low fecundity, self-incompatibility and low genotype diversity, and through increases in seed mortality via processes such as desiccation or seed age (Stampfli & Zeiter, 2008). More frequent and intense droughts may favor long-lived clonally spreading species and reduce populations of species that depend on frequent recruitment from seed (Stampfli & Zeiter, 2008). Positive interactions between adult plants and seedling establishment may occur when the adult plant provides protection and improves abiotic conditions for germination (del Cacho & Lloret, 2012). Recruitment has also been found to be positively related to mortality and seed size in a Mediterranean shrubland (Lloret *et al.*, 2016). Seed bank richness has been found to be lower in drier years, and the total number of established seedlings is negatively influenced by drought (del Cacho & Lloret, 2012; Lloret *et al.*, 2016). These effects are also species-specific and therefore result in changes in species composition within the seedling pool (del Cacho & Lloret, 2012).

## V. Conclusions

ECEs are anticipated to increase in the future, and drought intensification can drive rapid responses at both the ecosystem and the community level. Empirical evidence demonstrates that drought can lead to community reordering, result in changes to

the dominant species or PFT (Hoover *et al.*, 2014), or cause transitions to new ecosystem types (Resco de Dios *et al.*, 2014), and alter important ecosystem functions and processes (Smith, 2011), but the mechanisms behind these changes are still not fully understood. Species turnover can also lead to increases in invasive species and extinction of rare species (Prev  y & Seastedt, 2014; Van Peer *et al.*, 2014). Changes to a plant community are rarely immediate, and community stabilization can take years following an extreme drought (e.g. Table 1).

Many studies discuss mechanisms underlying the relatively slower rates of community stabilization compared to productivity recovery, but few have explicitly explored the mechanisms proposed in CRED, namely the temporal evolution of plant–plant interactions during and after drought. While only a fraction of drought research has explored the role of NBI in community reordering (Table 2), the few studies that have been conducted demonstrate that plant–plant interactions can at least partially explain community changes that result from an extreme drought (Pretzsch *et al.*, 2013; Grant *et al.*, 2014; Resco de Dios *et al.*, 2014). However, these studies did not monitor the community for long enough to detect community stabilization. Plant responses to ECEs are highly variable and idiosyncratic, highlighting the value of long-term monitoring following drought (Lloret *et al.*, 2012). While more extreme climate does not necessarily result in shifts in vegetation, it is likely that as droughts become more frequent and intense more systems will experience compositional changes (Lloret *et al.*, 2012).

Plant communities engage in a complex set of interactions, within and between trophic levels (e.g. herbivory), and species vary dramatically in their interactions with one another and their environment. These interactions can sometimes be categorized or predicted based on plant traits, and taking a functional comparative approach to facilitation could improve our ability to identify general patterns and consequences of positive interactions (Butterfield, 2009; Butterfield & Callaway, 2013; Kunstler *et al.*, 2015). Tests of the hypotheses in the CRED framework could provide relevant information for communities that are sensitive to extreme drought, which could be used to inform management and conservation efforts, maintain ecosystem function and slow species extinctions.

Targeted research into the role of plant–plant interactions in drought responses will provide insight into the mechanisms responsible for changes in community composition and increase our understanding of local adaptation to drought and other factors that contribute to localized extinction under drought intensification. We advocate for the establishment of drought experiments that manipulate neighborhood interactions (Grant *et al.*, 2014) and explore plant–plant interactions during drought and recovery. These experiments should be careful to use standardized definitions and protocols to test plant–plant interactions and use multi-factorial approaches that consider variables such as PFT, traits and diversity (Brooker *et al.*, 2005, 2008; Butterfield, 2009; Seifan *et al.*, 2010a; He *et al.*, 2013). Furthermore, indices for competition and facilitation need to incorporate the relative ‘importance’ and ‘intensity’ of these plant–plant interactions to help differentiate between the abiotic and biotic drivers of community change

(Welden & Slauson, 1986; Brooker *et al.*, 2005; Seifan *et al.*, 2010a).

The CRED framework organizes some of the mechanisms hypothesized to cause drought-induced shifts in community composition. Currently, however, little evidence is available to show how NBI changes over time with drought (see Table 2). Even less is known about how NBI may respond in a shifting climate, as droughts become warmer, and more frequent and intense in some regions. While it might be expected that communities experiencing more frequent droughts would become progressively more resistant/resilient to them, for now this remains an untested hypothesis.

Recently, land-surface models and remotely sensed data have been used to explore recovery of gross primary productivity (GPP) after drought (Schwalm *et al.*, 2017). Model data suggest drought impacts have increased over the 20<sup>th</sup> century, with longer recovery times of GPP following drought, which could lead to a chronic state of incomplete recovery of GPP. Many ecological processes, including species turnover, may act to buffer impacts to GPP in the future, but the effectiveness and timescales on which these processes act relative to new drought regimes is unknown (Schwalm *et al.*, 2017). There are limitations of this study, namely that land-surface models do not represent many relevant dynamic processes of drought impacts and recovery, such as plant mortality (Seneviratne & Ciais, 2017). Regardless, Schwalm *et al.* (2017) highlight an underappreciated dimension of drought impacts on GPP: the timescale of recovery and its relationship to the occurrence of drought events (Seneviratne & Ciais, 2017). These factors will probably be important for community dynamics post-drought as well.







We suggest that the CRED framework will be applicable in some systems that experience more frequent droughts, but the trajectories and intensity/importance of plant–plant interactions may change based on the new community structure, prior baseline climatic conditions and new drought conditions, particularly in relation to droughts that occur during recovery.

Long-term surveys of vegetation responses and multi-site research studies can provide the data needed to identify key characteristics influencing community composition response to drought or other stressors (Smith *et al.*, 2009; Lloret *et al.*, 2012; Fraser *et al.*, 2013; Felton *et al.*, 2017). These coordinated distributed experiments and surveys hold the potential to test some CRED hypotheses and provide further insight into the role of site-specific characteristics that alter the trajectory of NBI during and after drought. These datasets will expand our knowledge of how drought affects plant communities, and how recurrent droughts (some of which may occur during the recovery phase) and changes to recovery timescales will alter the trajectories of future communities.

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