SPECIAL FEATURE
FACILITATION IN PLANT COMMUNITIES

Effects of facilitation on community stability and dynamics: synthesis and future directions

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Summary

1. New insights into the mechanisms and outcomes of facilitation have led to important advances in our understanding of ecological patterns and processes. However, the effects of facilitation on non-successional community dynamics have yet to be developed into a general theory.

2. By synthesizing spatial and temporal relationships between biotic interactions and environmental severity, a new model of facilitation-driven community dynamics is presented that applies to any facilitative mechanism related to abiotic stress or resource limitation.

3. In general, facilitation tends to stabilize community dynamics in moderately severe environments, due to a buffering effect of increased facilitation during more severe periods and enhanced competitive effects in milder conditions. In contrast, a strong negative relationship between environmental severity and facilitative strength in highly severe environments leads to a destabilizing effect of facilitation on community dynamics.

4. If only mature plants have significant facilitative effects, developmental lags may be introduced that decouple environmental fluctuations and community dynamics, decreasing the effects of facilitation on community stability. Additionally, dual regulation of facilitation by environmental and demographic factors decouples abundance from climate and produces periodic local extinctions. In general, the interplay of facilitation and competition produce highly variable dynamics in moderate-severity environments, whereas qualitatively similar results were found in high-severity environments regardless of facilitative mechanism or model parameters.

5. Additional variation in community dynamics can be explained by the combination of effect and response functional traits of species within a community. The relative abundance and proportion of species within a community falling into one of four different effect and response categories provide an effective framework for predicting responses to climatic variation and biotic interactions.

6. *Synthesis.* Facilitation either increases or decreases community stability in predictable ways as a function of empirically identifiable environmental gradients. Effects of developmental lags, complex controls of facilitative mechanisms and species' functional traits explain additional variation in community dynamics that can be applied to a broad array of ecosystems in which facilitation occurs.

Key-words: alpine, arid, competition, functional traits, mutalism, nurse plant, salt marsh, stress

Introduction

Temporal patterns in plant communities and the factors that regulate those dynamics have been fundamental concerns of biologists for some time. Many models have been developed to understand and predict population dynamics, but with the exception of several models of mutualisms (e.g. Holland, DeAngelis & Schultz 2004) most have focused on negative interactions such as predation (e.g. Polis & Strong 1996) and competition (e.g. Tilman 1985). While we have gained much insight into the relevant parameters and behaviours in predatory and competitive systems through both theoretical and

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empirical research (Deangelis & Waterhouse 1987), dynamics generated by positive interactions within the same trophic level (i.e. facilitation) have not been thoroughly addressed theoretically (but see Travis, Brooker & Dytham 2005), nor have many empirical studies focused explicitly on temporal patterns in systems where facilitation is a predominant form of interaction (but see Armas & Pugnaire 2005; Miriti 2007; Butterfield *et al.,* in press). To advance our understanding of the effects of facilitation on population and community dynamics, existing information must be synthesized and predictive models developed to guide future research (Brooker *et al.* 2008).

The outcome of biotic interactions is often strongly influenced by variation in the abiotic environment, and within a given habitat environmental conditions can vary dramatically through time, influencing the outcome of biotic interactions and driving community dynamics (Ernest, Brown & Parmenter 2000; Tilman, Reich & Knops 2006). Likewise, the intensity and importance of biotic interactions vary spatially among habitats along gradients of environmental stress or resource availability (Callaway & Walker 1997; Goldberg & Novoplansky 1997), hereafter referred to as 'environmental severity' *sensu* Brooker *et al.* (2008). The importance of competitive interactions generally declines with environmental severity, whereas facilitation is most apparent and influential in moderate to high-severity environments (Bertness & Callaway 1994; Callaway *et al.* 2002; Travis *et al.* 2006; Callaway 2007). Assessing the relative effects of competition and facilitation on community dynamics is not, however, a simple matter of comparing observed temporal patterns in sites with different levels of environmental severity. Empirical assessment of facilitation-driven dynamics is impossible without corresponding spatial data of seedling establishment to determine the strength and temporal variation in facilitation (Miriti 2007; Butterfield *et al.,* in press). An additional complication is that potential dynamics generated by positive feedbacks via facilitation are difficult to differentiate from abiotically driven fluctuations in abundance observed in chronically low-productivity environments (Holmgren *et al.* 2006). Likewise, temporal interactions between facilitative effects and environmental conditions can be significant, such that static spatial predictions of biotic interactions do not reveal the true variation in competitive and facilitative outcomes (Tielbörger & Kadmon 2000; but see Holzapfel *et al.* 2006). These two factors – differentiating temporal pattern from process, and modulation of biotic interactions by environmental conditions – are the keys to assessing controls on plant community dynamics in severe environments.

A sufficient number of empirical experiments and observations now exist to develop predictive models of facilitation-driven dynamics. While few in number, studies that measure the sign and magnitude of biotic interactions through multiple years have provided insightful results. Increasing environmental severity in some communities causes a shift from competition toward facilitation (Greenlee & Callaway 1996), whereas the opposite occurs in other communities (Tielbörger & Kadmon 2000). This suggests that the relationship between environmental severity and facilitation is unimodal (hump-shaped) and is supported by temporally static studies across spatial gradients in environmental severity (Maestre & Cortina 2004; Michalet *et al.* 2006). This congruence of spatial and temporal variation in interaction outcomes is an important step in unifying theories of facilitation and points out the importance of understanding the range of spatial and temporal variation in environmental conditions within a study. While the unimodal relationship between facilitation and environmental severity is relatively consistent at certain scales (M. Holmgren & M. Scheffer, unpublished data), environmental severity is relative to the stress tolerance and resource use adaptations of species, such that some species within a community may exhibit different facilitative responses to environmental variation (Maestre *et al.* 2009) and entire communities may be restricted to a narrow range of the unimodal facilitation–severity curve (Butterfield *et al.,* in press). In addition to the complexity introduced by local adaptation and species specificity in short-term experiments (Maestre, Vallardes & Reynolds 2005), studies conducted at broader temporal scales have revealed other factors that alter the effects of interaction intensity and environmental fluctuations on dynamics. Many interactions are highly dependent upon the ontogenetic stage of the interacting individuals (Miriti 2006), which can generate time lags in facilitative effects and responses. Facilitation may also be a function of the size or quality of benefactors rather than simply their abundance, and therefore be regulated by both demographic and environmental factors. For example, plant cover is influenced by both variation in environmental conditions and number of individuals, and this dual regulation of facilitation can lead to unique dynamics that either buffer or amplify environmental variation (Butterfield *et al.,* in press). While complex, the basic patterns generated by facilitation can be explained by the manner in which plants modulate environmental fluctuations within the microenvironment that they occupy, with additional variation relatable to particular facilitative mechanisms and species-specific characteristics.

The goal of this paper is to present a general model of facilitation-driven community dynamics that is generally applicable across facilitative mechanisms and the biomes in which facilitation is a persistent form of interaction. By synthesizing existing small-scale experiments and observations, the model presented here can be extrapolated to population and community-level dynamics. Empirical research conducted at broader temporal scales is also used to develop slightly more complex models that incorporate developmental lags and demographic regulation of facilitative mechanisms, accompanied with a discussion of the circumstances under which these models may be more or less relevant. Finally, I discuss the effects of interspecific variation in facilitative and competitive effect and response traits, and how these characteristics might influence overall community stability and dynamics. The focus of this study is on ecosystems in which facilitation is a persistent and important form of biotic interaction (e.g. arid, alpine and salt marsh ecosystems, etc.), in contrast to successional processes (Gómez Aparicio 2009). The community dynamics of these low productivity, severe environments are not well understood relative to more productive systems, and must be assessed within a unique framework that incorporates facilitation.

## Conceptual and mathematical models

INTEGRATING SPATIAL AND TEMPORAL ENVIRONMENTAL VARIATION

Facilitation and competition primarily influence community dynamics by modulating environmental stresses and resource availability, which are ultimately controlled by external abiotic factors. To assess the effects of biotic interactions on community dynamics, the fitness of plants in the presence versus absence of a neighbour can be compared under varying environmental conditions. This reveals the relationship between spatial and temporal variation in environmental conditions and target plant fitness (e.g. growth, survival, reproduction) in both the presence and absence of neighbours, with the latter serving as a useful null model against which to compare the outcomes of biotic interactions. The relationship between target plant fitness, biotic interactions and environmental conditions can then be extrapolated to population and community-level behaviour.

In this model, individual fitness in the absence of a neighbour increases exponentially with decreasing environmental severity, eventually reaching a plateau at which there is no benefit of an additional unit of resource or decline in stress. In the presence of a neighbour, the gross competitive and facilitative effects combine to determine the net neighbour effect on a target plant. In the model, competition for one or more resources exponentially increases in intensity with decreasing environmental severity, potentially reaching a plateau in very low-severity environments. This is supported by both empirical (Goldberg *et al.* 1999) and other theoretical models (Grime 1977). In contrast, the intensity of facilitation is modelled as being unimodally related to environmental severity, with the strongest impact in relatively severe environments (Fig. 1a). As discussed below, the full range of this unimodal curve is not observed in all environments, but regardless of the mechanism by which plants ameliorate environmental severity there has to be some set of environmental conditions in which that amelioration is optimal, with reduced ameliorative effects in more or less severe environments. Evidence suggests that plants in many of the most extreme alpine environments approach or reach just beyond this optimal buffering ability (Callaway

et al. 2002), whereas perennial plants in the Sonoran Desert lie beyond this optimum (Butterfield *et al.*, in press). Of course, facilitation is clearly an important determinant of community structure in the latter case (McAuliffe 1988; Tewksbury & Lloyd 2001), but may become weak in particularly dry years or in extremely arid areas (i.e. importance versus intensity *sensu* Welden & Slauson 1986). Studies in sites that contrast in aridity indicate that semi-arid to arid environments may lie along the entire range of the environmental severity gradient represented in this model (Pugnaire & Luque 2001; Maestre & Cortina 2004; Holzapfel *et al.* 2006), although facilitation does tend to increase with environmental severity in most studies. However, real communities are represented by points along the full range of the severity gradient presented in this model, and thus the dynamics generated by this model at these different points will be applicable to specific habitats and communities. While different mechanisms of facilitation clearly influence where communities lie along this gradient, if the concept of 'environmental severity' is treated as relative to the species occupying that environment then contrasting systems can be understood within a general context of the balance between competition and facilitation.

The fitness curve of a target plant in the presence of a neighbour is determined by combining the facilitation and competition curves, then adding this net neighbour effect to the fitness curve of an isolated plant. In this model, the fitness curve therefore increases rapidly with declining severity in the most extreme environments, but begins to level off in less severe environments (Fig. 1b). While varying in skewness and kurtosis across species and ecosystems (see Community Dynamics below), the net concave relationship between fitness and environmental severity in the presence of a neighbour may be broadly applicable for many facilitative mechanisms (M. Holmgren & M. Scheffer, unpublished data). Although a seemingly minor change to other representations of the relationship between neighbour effects and environmental severity, assessing absolute fitness rather than relative fitness is a new approach that is essential for determining the effects of facilitation and competition on population dynamics. As the objective of most facilitation studies has been to identify the sign and magnitude of neighbour effects, performance in the absence of a neighbour is used as
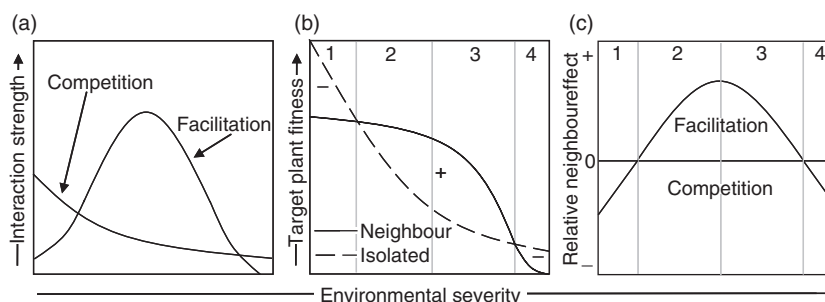

Fig. 1. Spatial and temporal variation in biotic interactions and target plant fitness. (a) The effect of environmental severity on the strength of competitive and facilitative interactions. (b) Absolute target plant fitness in the presence and absence of a neighbour along an environmental severity gradient. Zones 1 through 4 represent low, moderate, high, and extreme-severity environments, respectively, as those terms are used in the text. (c) Relative target plant fitness in the presence of a neighbour along an environmental severity gradient.

a reference for assessing neighbour effects (e.g. Maestre, Vallardes & Reynolds 2005) and is essentially used as a covariate to account for variation in environmental severity (Fig. 1c). This method of standardizing by the performance of isolated plants obscures the true temporal relationship between climatic and microenvironmental conditions in the presence or absence of a neighbour.

Measuring relative fitness does, however, play an important role in identifying the location of real populations and communities along gradients of environmental severity. The likely effects of environmental conditions on population dynamics can be experimentally or observationally determined by calculating (i) the net effect of a neighbour and (ii) how that effect varies in time. In what will hereafter be referred to as 'low-severity' environments, average net neighbour effects are negative but are positively correlated with environmental severity in time. In other words, a stressful year results in a shift toward facilitation, and a productive year shifts toward stronger competition. Similarly, 'moderate-severity' environments are defined as those in which net neighbour effect is still positively correlated with environmental severity in time, but the average effect is positive. 'High' and 'extreme-severity' environments exhibit negative relationships between net neighbour effect and environmental severity in time, with positive and negative average net neighbour effects respectively (Fig. 1b, c). Of course, a population, community or study may cover two or more of these zones depending on the range of temporal variation in environmental severity, which reinforces the importance of considering gradient length (Lortie & Callaway 2006) and non-linear regression models (Maestre & Cortina 2004; Callaway 2007) in tests of the original or modified Stress Gradient Hypothesis (Bertness & Callaway 1994; Brooker *et al.* 2008). In addition, the gradient of interest can span from local to regional scales, as variation in environmental conditions can be nearly as great within a landscape as across a biome (Körner 2003). This method of identifying the degree of environmental severity is very useful in that it does not subjectively identify an environment as severe or not, but is in fact tied to ecological processes that are relative to species' adaptations to their environment. This also makes it possible to directly relate real populations and communities to theoretical predictions of the model presented here.

Within a community, many species may only maintain a viable population along a certain portion of the environmental severity gradient experienced in time within a given habitat, restricting the shape of the species-specific relationship between net neighbour effect and environmental severity (Liancourt, Callaway & Michalet 2005). This means that many species will be obligate beneficiaries (i.e. they cannot survive without a neighbour or 'benefactor') within some or all of their distribution, whereas they may be facultative beneficiaries in the less severe parts of their distribution. For example, a species with low stress tolerance (Species A, Fig. 2a) may only be able to survive next to a benefactor in a habitat where a more stress-tolerant species (Species B) may be able to persist in the absence of a neighbour (point X, Fig. 2a). This supports earlier predictions suggesting that the relative stress tolerance or com-
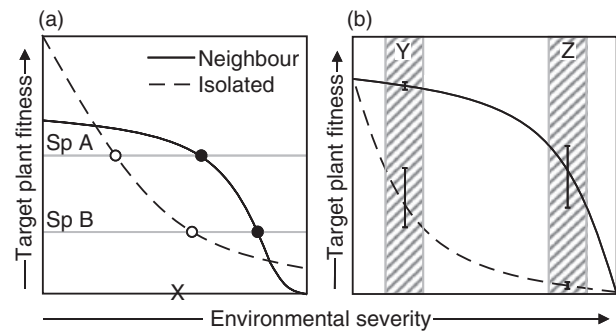
Fig. 2. Effects of mean and variance in environmental severity on target plant fitness. (a) Depending on stress tolerance or resource requirements, species may be either obligate (species A) or facultative (species B) beneficiaries in the same habitat. The grey lines are zero-net growth isoclines (ZNGI), with environments that are less severe than those where the ZNGI crosses the isolated plant fitness curve (○) permitting facultative facilitation, and those in more severe environments necessitating obligate facilitation. Environments that are more severe than the point where the ZNGI crosses the fitness curve in the presence of a neighbour (•) are unsuitable for that species, even with a neighbour. (b) Temporal variation in fitness in moderately severe habitats (Y) is greater in the absence of a neighbour, whereas the opposite is true in highly severe habitats (Z). The breadth of the cross-hatched bars represents the range of temporal variation in environmental severity within a habitat.

petitive ability of a species would determine the shape of its relationship between net neighbour effect and environmental severity (Michalet *et al.* 2006; Maestre *et al.* 2009), which would be the case if different species are restricted to different ranges of the potential fitness curves.

Regardless of the facilitative response, the manner in which existing plants modulate fluctuations in environmental severity follows directly from the net neighbour effect curves and largely determines the effect of facilitation on community dynamics. In high-severity environments, temporal variation in environmental severity is amplified beneath plant canopies relative to bare microsites, thereby producing greater temporal fitness variation in the presence of neighbours (Fig. 2b, habitat Z). However, as the net neighbour effect declines moving into moderately severe environments, temporal fluctuations in environmental conditions are strongly buffered, leading to greater stability of target plant fitness in time (Fig. 2b, habitat Y). Thus, depending on the mean and range of environmental conditions within a habitat relative to the stress tolerance and resource requirements of the species present, facilitation can either stabilize or destabilize community dynamics. This is true when compared with either a null model of density-independent fitness or to a strictly competitive model. With this information in mind, it is possible to assess the effects of facilitation on population and community dynamics.

MATHEMATICAL MODEL

Based on the conceptual model outlined above, a mathematical model can be developed to simulate the responses of plant populations and communities to temporal variation in environmental severity that is modulated by competitive and

facilitative interactions. For species i, changes in abundance (N) are modelled as

$$\frac{dN_i}{dt} = r_i N_i \frac{K_i(X) - N_i + \sum_{i=1}^{n} h_i(X)}{K_i(X) + \sum_{i=1}^{n} h_i(X)}, \qquad \text{eqn 1}$$

where r_i is the maximum population growth rate and K is the equilibrium abundance at a given level of environmental severity (X) which is proportional to resource availability or inversely proportional to environmental stress. K varies as a function of X in the following manner

$$K_i(X \leq \varepsilon_i) = \kappa_i \exp\left[-\left(\frac{X - \varepsilon_i}{y_i}\right)^2\right], \quad K_i(X > \varepsilon_i) = \kappa_i, \quad \text{eqn 2}$$

where ε is the saturating resource level or negligible stress level, κ is the maximum fitness in the absence of a neighbour and y is the breadth of environmental conditions in which fitness is responsive to environmental variation.

The net neighbour effect is

$$h_i(X) = f_i(X) - g_i(X) \qquad \text{eqn 3}$$

where the gross facilitative effect is

$$f_i(X) = c_i \exp\left[-\left(\frac{X - \gamma_i}{v_i}\right)^2\right] \qquad \text{eqn 4}$$

with c being the maximum facilitative effect, γ the level of X at which $f(X) = c$, and υ is the breadth of environmental conditions in which gross facilitation occurs. The gross competitive effect

$$g_i(X \leq \delta_i) = d_i \exp\left[-\left(\frac{X - \delta_i}{w_i}\right)^2\right], \quad g_i(X > \delta_i) = d_i \qquad \text{eqn 5}$$

is subtracted from the gross facilitative effect to determine the net neighbour effect. The maximum competitive effect is d, which is achieved at levels of $X \geq \delta$. The range of environmental conditions in which competition varies is w.

In the simulations below, X is a Gaussian random driving variable with a defined mean and variance. Note that time is rescaled to the demographic rates of the populations in the community such that time is relative to the dynamics generated by the simulations. In other words, low frequency (i.e. decadal or centennial) temporal variation in X will drive the dynamics of long-lived species in much the same way that high frequency (i.e. annual) variation will influence the dynamics of ephemerals.

Additional variations on this model (see below for discussion) include time lags in facilitative effects and dual regulation of an intermediary facilitative mechanism. Time lags are incorporated into the above model by substituting $h_i(X_{t-\tau})$ for $h_i(X)$, where τ is the length of the developmental lag in relevant time units. For the dual regulation model, the term $M_i(X)$ is incorporated in the following manner

$$\frac{dN_i}{dt} = r_i N_i \frac{K_i(X) - N_i + \sum_{i=1}^{n} M_i(X) h_i(X)}{K_i(X) + \sum_{i=1}^{n} M_i(X) h_i(X)} \qquad \text{eqn 6}$$

where $M_i(X)$ is the facilitative intermediary that is a function of X and N such that

$$M_i(X) = \alpha(X - \bar{X}) + \beta N_i \qquad \text{eqn 7}$$

where $\bar{X}$ is the mean resource or stress level within a given habitat, and α and β are the effects of the resource (or stress) and density on cover. Environmental effects on cover are via resource limitation or stress that influences productivity of individual plants, whereas increasing the number of plants per unit area (density) can also increase cover independently of the productivity of individual plants.

Results and discussion

POPULATION MODEL

If population or community dynamics are a direct consequence of variation in microenvironmental conditions, the effects of facilitation on dynamics are straightforward. This assumption is justified in communities where biotic responses to environmental change are rapid, as might be expected in relatively fast-growing populations with little dispersal limitation. In moderately severe environments, the counteracting effects of competition and facilitation minimize temporal fluctuations in stress next to a benefactor, thereby minimizing fluctuations in demographic or physiological rates and stabilizing population dynamics (Fig. 3a, top). One caveat is that if a population maintains facultative facilitation dependence, fluctuations in demographic or physiological rates for the subpopulation without neighbours will be greater than that of the beneficiary subpopulation, due to the greater fluctuations in microenvironmental conditions for isolated plants. This subpopulation somewhat reduces the buffering effect of neighbours on overall population stability, but the contribution of the non-beneficiary subpopulation to total population dynamics depends on what proportion of the population they represent, which may vary substantially across biomes. In ecosystems where substantial bare ground is absent, such as many grasslands and herbaceous plant-dominated systems, as well as partially closed-canopy shrublands in semi-arid environments, nearly all individuals will have neighbours, resulting in strong population stabilization near the lower end of the relevant environmental gradient. In contrast, in desert ecosystems where isolated individuals or clumps of plants exist in a matrix of bare ground even at the relatively high end of soil moisture gradients, a large proportion of the population may exist in isolation despite a net positive effect of neighbours, thereby reducing the stabilizing effect of the beneficiary subpopulation. However, regardless of the relative proportion of either subpopulation, the general effect of neighbours within a moderately severe environment will be to stabilize population dynamics.

Moving toward more severe environments, the temporal stability of open microenvironments versus those with benefactors shifts. Between moderately and highly severe environments the temporal stability of isolated and benefactor microenvironments is similar, but becomes increasingly variable next to a benefactor in more severe environments while

greatly decreasing in variability in the open. Regardless of the biome or vegetation type, this is accompanied by a shift toward obligate facilitation such that a greater proportion of the population can only persist next to a benefactor and will experience the greater temporal fluctuations in that microenvironment.
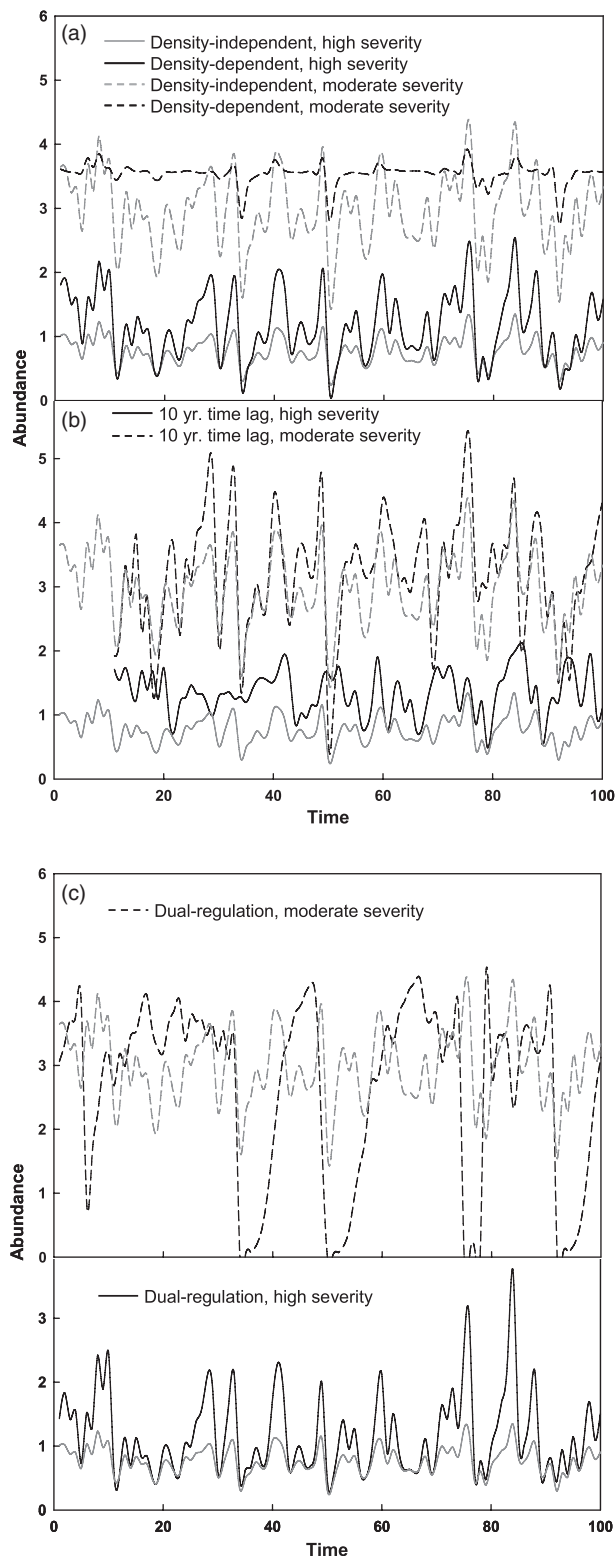
Thus, facilitation destabilizes population dynamics in highly severe environments (Fig. 3a, bottom). Despite shifts in the equilibrium value of fitness metrics (e.g. abundance, reproductive output, survival etc.) in different microenvironments and at different points along a severity gradient, if stability is defined as the coefficient of variation in fitness, then only the slope and shape of the microenvironment–severity gradient relationship are important. The convex shape of the beneficiary curve also means that negative deviations from median abundance will tend to be greater than positive deviations, whereas the opposite is true for non-beneficiary individuals. This is certainly the case in moderately severe environments, however in many high-severity environments mean abundance, productivity, reproductive output, etc. are constrained to be greater than zero. This causes positive deviations to be greater than negative ones simply because an upper limit to fitness or population density is unlikely to be reached in high-severity environments. These positive deviations due to facilitation would also be greater than for an isolated subpopulation, so facilitation would still lead to greater instability than under density-independent (i.e. no effects of facilitation or competition) growth. In summary, despite several caveats facilitation stabilizes dynamics in moderate to low-severity environments, whereas it destabilizes dynamics in high to extreme-severity environments. These patterns should also extend to systems in which nurse objects (e.g. rocks) or facilitation by other species that are fairly static (e.g. perennials facilitating annuals) are the predominant determinants of plant performance, although the absence of demographic feedbacks will somewhat reduce the effects of facilitation exhibited in the population model.

TIME LAG MODEL

So far, this model has included the assumption that the effects of temporal variation in environmental severity have been immediately modulated by a benefactor and that the responses of the beneficiary have also been rapid. If either the facilitative effect or response is slow, population and environmental variation may not be directly correlated. Slow-growing species may take decades to become effective benefactors, thereby introducing a developmental delay that can decouple population

Fig. 3. Simulations of population dynamics under different models but with identical random variation in environmental conditions. Simulations with higher mean abundance are from identical moderately severe environments, and those with lower mean abundance are from identical highly severe environments, *sensu* Fig. 1. (a) Basic population model. (b) Developmental time-lag model with a 10-time step lag period, which is why the first 10 time steps are omitted from the figure. (c) Dual *regulation model, where the facilitative mechanism is regulated by both environmental and demographic controls. The basic population model simulation is used as a reference in (b) and (c). Parameter values are (a)* $\kappa = 10$, $\varepsilon = 20$, $y = 10$, $c = 2$, $\gamma = 7$, $\upsilon = 3$, $d = 5$, $\delta = 30$, $w = 15$, moderate-severity: $\bar{X} = 9$, $\sigma = 2$, high-severity: $\bar{X} = 4$, $\sigma = 2$; (b) same as above with the addition of $\tau = 10$; (c) same as above with the addition of α and $\beta = 0.5$.

and environmental variation, depending on the length of the delay relative to the frequency of environmental variation. The effect of a time lag at any given time depends on both antecedent and current conditions. A mild year in the past may negate a severe current year, or vice versa, thereby reducing the effect of environmental variation on population change. The other possibility is that a mild or severe year in the past may reinforce a current mild or severe year, which would amplify the effect of environmental variation. While this system memory tends to create a relatively unpredictable temporal pattern unless extremely accurate data are collected, there is still a general effect of time lags on stability. Regardless of environmental severity, developmental lags reduce the effects of density dependence leading to greater stability in high-severity environments and lower stability in moderate-severity environments relative to facilitation-driven dynamics without time lags (Fig. 3b, bottom and top, respectively). While stability therefore becomes closer to that of a density-independent or strictly competitive system, the actual dynamics of the population are poorly correlated with environmental variation. This creates a perplexing situation for ecologists or natural resource managers observing such systems if specific predictive models of dynamics are desired. The broader concept of stability is more tractable in this instance, perhaps making the range of variation in abundance a more meaningful metric for study or management. In this case, the potential for facilitative time lags to generate extreme fluctuations in abundance that are unrelated to current environmental conditions and not linearly related to past conditions is an important consideration.

DUAL REGULATION MODEL

Another interesting way indirect positive feedbacks influence dynamics is through the dual regulation of facilitation by both environmental and demographic controls. A good example is benefactor canopy cover, which depends both on the number of benefactors (i.e. density) and variation in environmental conditions (Yahdjian & Sala 2006). If facilitation is a direct consequence of total canopy cover or individual canopy size rather than the number of benefactors, as may often be the case (McAuliffe 1986), then variation in cover will determine variation in facilitative effects. In a desert perennial plant community, Butterfield *et al.* (in press) showed that rapid fluctuations in environmental conditions are buffered because while cover will vary with environmental severity, this variation is also demographically constrained by the number of individuals. However, low-frequency variation in severity (i.e. a period of multiple productive years) is amplified due to positive demographic feedbacks, both with respect to population growth and decline. At high densities, this may also result in temporary decoupling of environmental and population dynamics due to a dominating effect of density on cover. Using a modification to the population model presented above that incorporates dual regulation of facilitation, it is clear that positive feedbacks leading to population peaks only occur in high-severity environments (Fig. 3c). In moderate-severity environments, if environmental and demographic variation contribute to cover

equally dual regulation produces a response lag due to the contribution of density to variation in cover. More strikingly, periodic local extinctions can occur due to negative feedbacks. As with the simple population model, potential increases in abundance are lower than potential declines due to the shape of the net neighbour effect curve – plants cannot ameliorate already benign conditions during favourable periods in moderate-severity environments. This is amplified in the dual regulation model, with negative feedbacks of low density following a highly severe period producing dramatic declines in abundance. Changing the relative strength of environmental versus demographic controls on cover alters these dynamic: increases in the relative effects of either factor decrease the potential for negative feedbacks to produce population crashes, with greater demographic control producing greater positive feedbacks and stronger environmental regulation producing dynamics that approach density independence (results not shown). The complexity of potential outcomes in this model are a simple function of relative control on cover, so understanding the importance of demographics versus environment on plant size can explain a great deal of the variation observed in moderate-severity environments. This dual regulation is likely a predominant mechanism of facilitation across low productivity environments due to the likely overwhelming importance of cover or benefactor size as a determinant of facilitation, although the contribution of benefactor age (i.e. accumulation of beneficiaries over time) versus size is often difficult to distinguish empirically (Tewksbury & Lloyd 2001).

COMMUNITY DYNAMICS: THE IMPORTANCE OF TRAITS AND ONTEGENY

A large proportion of community dynamics may be explained by the population models discussed so far, ignoring species-specific characteristics. However, many communities may exhibit dynamics that deviate from those predicted by the population models due to important interspecific differences in: (i) the shape of the facilitative effect and response curves and (ii) the ontogenetic stage at which facilitation occurs. Species within a community can vary substantially in their facilitative effects (Hutto, McAuliffe & Hogan 1986; Larrea-Alcazar &
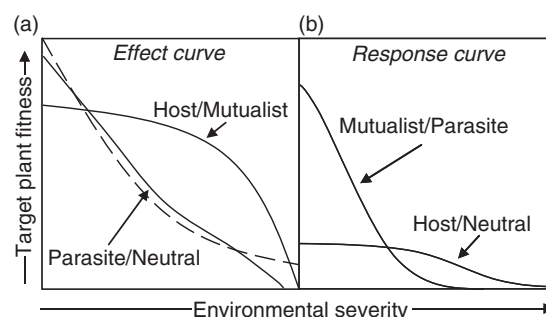
Fig. 4. Effect (a) and response (b) fitness curves of the four facilitative strategies. The fitness curve of an isolated plant (dashed line) is provided as a reference. Strategy terms are those presented in the text.

Soriano 2006), and the distribution of facilitative effect curves across species can also differ dramatically among communities. Likewise, physiological and demographic responsiveness to environmental severity also differs dramatically across species (Grime 1977), producing different response curves (Fig. 4). If the effect and response curves of all species within a community are known, the models presented in this study can be used to predict specific outcomes of community dynamics. However, measuring the effect and response curves for all species of interest may be difficult or impossible. For the sake of generality, understanding the relationships between functional traits and facilitative effects and responses may provide rapid insight into the mechanisms that determine the shape of, and relationship between, effect and response curves (Lavorel & Garnier 2002; Suding *et al.* 2008). Few studies have quantitatively assessed the relationship between traits and facilitative effects and responses, but those that have suggest traits are very important determinants of facilitative interactions (Valiente-Banuet *et al.* 2006). Facilitative effects can be tied to traits such as leaf size (shade), leaf nutrient content (litter and soil fertility) and canopy structure (shade and temperature). Traits related to competitive effects, including water or nutrient use efficiency (resource uptake rates), leaf mass area (nutrient requirements and growth rate), and rooting depth or canopy height (overlap of resource acquisition organs), can also be measured to estimate the net effect curve across species. The response curve will also vary across species based on the relationship between microenvironmental conditions and response traits that are related to stress tolerance and competitive ability in open versus benefactor microenvironments (i.e. seed size, relative growth rate, resource use efficiency, leaf longevity). In many communities there is a strict directionality to facilitative interactions, where mature plants primarily facilitate seedlings. In such cases mature plant effect traits and seedling response traits are those that should be measured to assess facilitative interactions. As mature plant traits are often uncorrelated with seedlings traits (Grime 1977), it is necessary to measure traits at multiple ontogenetic stages if both effects and responses are of interest. The latter represents an important point of emphasis for future empirical research, and also ties the causes and consequences of facilitation into many other processes (e.g. evolution, biogeochemical fluxes) that are directly related to functional traits (McGill *et al.* 2006; Cornwell *et al.* 2008). The challenge and promise of this approach lies in identifying the relevant traits, as well as the manner in which they may be correlated.

By assigning species to one of four simple categories based on their facilitative effects and responses, all of which are found in nature and may coexist within the same community (McAuliffe 1988), functional traits can be tied to community dynamics (Fig. 4). First, a species may have significant facilitative effects but receive little benefit from a neighbour (hereafter a 'host' species). Many of these stress-tolerant species are relatively unresponsive to variation in environmental conditions due to their conservative resource use and acquisition strategy. For a host species facilitative effects of a conspecific or other species within that community only ameliorate environmental conditions that are already suitable or perhaps optimal for such a stress-tolerant species, resulting in no facilitative response. The antithesis of this strategy is to benefit greatly from a neighbour but have a net neutral or negative effect on other individuals ('parasitic' species). This combination of strategies would be expected to arise if competitive and facilitative interactions are a function of a single resource pool or stress, and if there is a trade-off between resource use efficiency and turnover. If competition and facilitation are a function of different niche dimensions, or ontogenetic niche shifts occur, other strategies may be exhibited. Some species may have no facilitative effect coupled with a negligible response ('neutral' species), while others may have both a substantial facilitative effect and response ('mutualist' species). Again, the frequency with which these different strategies occur within or across communities depends on the traits that mediate facilitative and competitive interactions, the degree to which those traits are correlated and on whether or not ontogeny is relevant. A species may also shift from one strategy to another at different points along an environmental severity gradient, as shown in the population model for shifts from facultative to obligate facilitation dependence. The terms used to identify these categories represent the potential form of facilitative interaction that species may undertake as a function of their responses to and effects on environmental conditions. For example, a mutualist species may benefit from a host, but have no reciprocal positive effect since host species are not responsive to environmental amelioration.

Each of these four strategies influences community dynamics in different ways. Host species largely determine the dynamics of the rest of the community if parasites or mutualists are common. As shown in the population model, microenvironmental fluctuations beneath host plants will be dampened in moderately severe environments and amplified in highly severe environments. However, host species are generally less responsive to environmental variation due to their conservative growth strategy, such that variation in parasite or mutualist abundance will be somewhat less than in the population model. This is because while microenvironmental variation may be substantial, the number of host microsites is relatively consistent, reducing the effects of density-dependent demographic feedbacks. It is still possible for host abundance to vary dramatically in some habitats if a secondary disturbance unrelated to facilitative interactions occurs, in which case the abundance of all species within the community would fluctuate dramatically. Nevertheless, a high proportion of host species within a community will tend to stabilize community-level dynamics in moderately severe environments, and destabilize dynamics in highly severe environments.

Mutualist species may also greatly influence community dynamics by amplifying the microenvironmental effects induced by host species, reducing overall community stability in any environment. Mutualist abundance demographically transfers the fluctuations in host microenvironments and the microenvironments beneath mutualists vary as well, thereby demographically and environmentally influencing temporal

variation in resource availability or stress levels. A community with a high proportion of mutualist species will therefore be extremely unstable in highly severe environments due to strong positive feedbacks among species. Parasitic species, on the other hand, simply vary in abundance as a direct function of host or mutualist availability and environmental fluctuations within those microsites. While parasites with strong negative impacts on hosts or mutualists could potentially produce classic oscillatory host–parasite dynamics (Vandermeer 1980), there is little empirical evidence to support this. Finally, neutral species abundance will simply vary with environmental conditions, having no other effects on community dynamics except perhaps through competitive interactions.

The relative proportion of species within a community falling into these four functional groups may depend in large part on the strength and nature of correlations between effect and response traits. The relationships between many functional traits are relatively consistent across plants globally, although variation in ecological and evolutionary selection pressures across biomes and biogeographic regions are significant. Understanding relationships between facilitative effect and response traits provides an ultimate explanation for community assembly and dynamics in severe environments, and while other approaches to understanding effects of facilitation on plant communities may be informative (e.g. incorporating positive covariances in the assessment of biodiversity–stability relationships (Tilman & Lehman 2002)) a trait-based approach provides a deeper understanding of the causes and consequences of facilitation. This framework also provides an important means of predicting the effects of facilitation on community-level responses to climate change (Suding *et al.* 2008).

Conclusions

This paper provides an outline of many of the temporal patterns that can be generated by facilitation, along with the mechanisms that may be responsible. All of these patterns can theoretically be observed within a single community, necessitating empirical observations and experiments that can tease apart and identify the predominant mechanisms of facilitation-driven dynamics. Regardless of this complexity, facilitation research has reached the point where cross-system comparisons have fostered the development of more accurate conceptual models, of which this study is an example. Without the apparently contradictory patterns amassed following the proposition of the original Stress Gradient Hypothesis (e.g. Tielbörger & Kadmon 2000; Maestre, Vallardes & Reynolds 2005; Lortie & Callaway 2006), this model could not have been constructed. Looking forward, several new approaches to studying facilitation are likely to be particularly fruitful. First, testing the predictions of the models presented above, particularly the stabilizing and destabilizing effects of facilitation in moderate and high-severity environments, respectively, should provide great insight into the regulation of plant communities. In particular, measuring absolute rather than relative fitness and how this extends to population and community-level dynamics is a new field ripe for exploration. While patterns were qualitatively similar across models in high-severity environments, the more complex dynamics generated by the interplay between competition and facilitation in moderate-severity environments warrant further exploration. Second, and perhaps most important, the relationship between facilitation and functional traits must be assessed. Functional traits will not only provide greater insight into the assembly and dynamics of communities in which facilitation is prevalent, but also integrate facilitation into more traditional areas of research including competition, evolution and ecosystem processes. While the ever-growing body of empirical evidence for facilitation is undeniable, a greater mechanistic understanding is necessary to fully incorporate the causes and consequences of facilitation into more established realms of ecology and evolution.

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References

Armas, C. & Pugnaire, F.I. (2005) Plant interactions govern population dynamics in a semi-arid plant community. *Journal of Ecology*, **93**, 978–989.

Bertness, M.D. & Callaway, R.M. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Butterfield, B.J., Betancourt, J.L., Turner, R.M. & Briggs, J.M. (in press). Facilitation drives 65 years of vegetation change in the Sonoran Desert. *Ecology*.

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht, The Netherlands.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Deangelis, D.L. & Waterhouse, J.C. (1987) Equilibrium and nonequilibrium concepts in ecological models. *Ecological Monographs*, **57**, 1–21.

Ernest, S.K.M., Brown, J.H. & Parmenter, R.R. (2000) Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos*, **88**, 470–482.

Goldberg, D. & Novoplansky, A. (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology*, **85**, 409–418.

Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.

Gómez-Aparicio, L. (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, **97**, 1202–1214.

Greenlee, J. & Callaway, R.M. (1996) Effects of abiotic sress on the relative importance of interference and facilitation. *The American Naturalist*, **148**, 386–396.

Grime, J.P. (1977) Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Holland, J.N., DeAngelis, D.L. & Schultz, S.T. (2004) Evolutionary stability of mutualism: interspecific population regulation as an evolutionary stable strategy. *Proceedings of the Royal Society of London. Series B*, **271**, 1807–1814.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R. *et al*. (2006) Extreme climatic events shape arid and semiarid ecosystems. *Frontiers in Ecology and the Environment*, **4**, 87–95.

Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J. & Sternberg, M. (2006) Annual plant-shrub interactions along an aridity gradient. *Basic and Applied Ecology*, **7**, 268–279.

Hutto, R.L., McAuliffe, J.R. & Hogan, L. (1986) Distributional associates of the saguaro (*Carnegiea gigantea*). *The Southwestern Naturalist*, **31**, 469–476.

Körner, C. (2003). *Alpine Plant Life*, 2nd edn. Springer-Verlag, Berlin.

Larrea-Alcazar, D.M. & Soriano, P.J. (2006) Spatial associations, size-distance relationships and population structure of two dominant life forms in a semiarid enclave of the Venezuelan Andes. *Plant Ecology*, **186**, 137–149.

Lavorel, S. & Garnier, E. (2002) Predicting change in community composition and ecosystem functioning from plant traits: revisiting the holy grail. *Functional Ecology*, **16**, 545–556.

Liancourt, P., Callaway, R.M. & Michalet, R. (2005) Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology*, **86**, 1611–1618.

Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology*, **94**, 7–16.

Maestre, F.T. & Cortina, J. (2004) Do positive interactions increase with abiotic stress? A test from a semi-arid steppe. *Proceedings of the Royal Society of London. Series B*, **271**, S331–S333.

Maestre, F.T., Vallardes, F. & Reynolds, J.F. (2005) Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, **93**, 748–757.

Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, **97**, 199–205.

McAuliffe, J.R. (1986) Herbivore limited establishment of a sonoran desert tree, *Cercidium microphylum*. *Ecology*, **67**, 276–280.

McAuliffe, J.R. (1988) Markovian dynamics of simple and complex desert plant communities. *The American Naturalist*, **131**, 459–490.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.

Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I., Valiente-Banuet, A. & Callaway, R.M. (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, **9**, 767–773.

Miriti, M.N. (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology*, **94**, 973–979.

Miriti, M.N. (2007) Twenty years of changes in spatial association and community structure among desert perennials. *Ecology*, **88**, 1177–1190.

Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist*, **147**, 813–846.

Pugnaire, F.I. & Luque, M.T. (2001) Change in plant interactions along a gradient of environmental stress. *Oikos*, **93**, 42–49.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Diaz, S., Garnier, E. *et al*. (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, **14**, 1125–1140.

Tewksbury, J.J. & Lloyd, J.D. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, **127**, 425–434.

Tielbörger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology*, **81**, 1544–1553.

Tilman, D. (1985) The resource-ratio hypothesis of plant succession. *The American Naturalist*, **125**, 827–852.

Tilman, D. & Lehman, C. (2002) Biodiversity, composition, and ecosystem processes: theory and concepts. *The Functional Consequences of Biodiversity* (eds A.P. Kinzig, S.W. Pacala & D. Tilman), pp. 9–41. Princeton University Press, Princeton, NJ.

Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, **441**, 629–632.

Travis, J.M.J., Brooker, R.W. & Dytham, C. (2005) The interplay of positive and negative species interactions across and environmental gradient: insights from an individual-based simulation model. *Biology Letters*, **1**, 5–8.

Travis, J.M.J., Brooker, R.W., Clark, E.J. & Dytham, C. (2006) The distribution of positive and negative species interactions across environmental gradients on a dual-lattice model. *Journal of Theoretical Biology*, **241**, 896–902.

Valiente-Banuet, A., Rumebe, A.V., Verdú, M. & Callaway, R.M. (2006) Modern quaternary plant lineages promote diversity through facilitation of ancient tertiary lineages. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 16812–16817.

Vandermeer, J. (1980) Saguaros and nurse trees: a new hypothesis to account for population fluctuations. *The Southwestern Naturalist*, **25**, 357–360.

Welden, C.W. & Slauson, W.L. (1986) The intensity of competition versus its importance: an overlooked distinction and some implications. *The Quarterly Review of Biology*, **61**, 23–44.

Yahdjian, L. & Sala, O.E. (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology*, **87**, 952–962.