



## A size-gradient hypothesis for alpine treeline ecotones

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**Abstract:** Research on the stress gradient hypothesis recognizes that positive (i.e. facilitative) and negative (i.e. competitive) plant interactions change in intensity and effect relative to abiotic stress experienced on a gradient. Motivated by observations of alpine treeline ecotones, we suggest that this switch in interaction could operate along a gradient of relative size of individual plants. We propose that as neighbors increase in size relative to a focal plant they improve the environment for that plant up to a critical point. After this critical point is surpassed, however, increasing relative size of neighbors will degrade the environment such that the net interaction intensity becomes negative. We developed a conceptual (not site or species specific) individual based model to simulate a single species with recruitment, growth, and mortality dependent on the environment mediated by the relative size of neighbors. Growth and size form a feedback. Simulation results show that the size gradient model produces metrics similar to that of a stress gradient model. Visualizations reveal that the size gradient model produces spatial patterns that are similar to the complex ones observed at alpine treelines. Size-mediated interaction could be a mechanism of the stress gradient hypothesis or it could operate independent of abiotic stress.

**Keywords:** Competition; Ecotone; Environmental gradient; Plant interaction; Stress gradient; Facilitation

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### Introduction

The study of biotic interactions among organisms, and their influence on distribution, abundance, and diversity, is a well-established area in ecology (e.g., Mack and Harper 1977), even for current climate change (e.g., Malanson et al. 1992; Woodward 1992), and remains an active research frontier (Wisz et al. 2013). Because vegetation dynamics are substantially influenced by the spatial attributes of individuals, one key research area is the spatially explicit examination of competition and facilitation among neighboring plants (e.g., Rietkerk et al. 2002). Observational, experimental, and modeling approaches are pursued (Wright et al. 2014; Cowles et al. 2016). At alpine treeline, such feedbacks have been suggested as important controls on spatial pattern and potential dynamics (Wilson and Agnew 1992; Smith et al. 2003; Malanson et al. 2011), and Korner (2016) recently emphasized size a central attribute.

The stress gradient hypothesis (SGH) and the intensive body of work under its umbrella offer an established framework for examining plant-plant interactions by creating linkages between physiological functioning and environment. The SGH contends that the balance of interactions will shift from negative to positive, essentially from competition to facilitation, as stress increases along

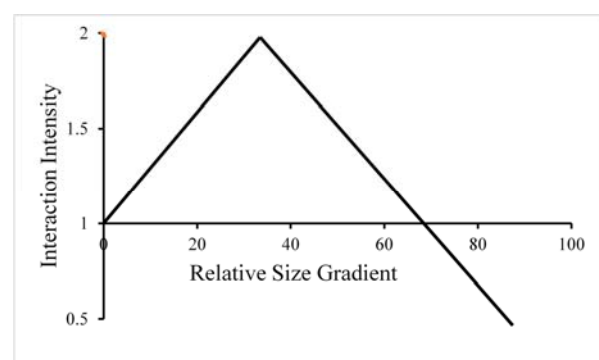
an environmental gradient (Bertness and Callaway 1994; see Maestre et al. 2009; Soliveres et al. 2014; Schöb et al. 2014; inter alia). Facilitation and competition operate simultaneously, and their relative balance can be affected by multiple environmental variables, including but not limited to shading (Schweiger et al. 2015), protection from wind (le Roux and McGeoch 2008), and nutrient availability (Chen et al. 2015).

Butterfield and Callaway (2013), in examining functional traits to address mechanisms, suggested that leaf area could play a significant role in both facilitative responses and effects. But total leaf area is only one aspect of the above-ground structure that could be facilitative, especially with regard to wind, which they did not mention (although Callaway (2007) devoted a section to it). Brathen and Lortie (2016) have demonstrated a facilitative effect of the height of benefactor plants that persists across a stress gradient. However, most of the work on the SGH is not mechanistic with regard to how individuals affect the environment and each other (Michalet and Pugnaire 2016).

Here, we suggest that a gradient of neighbor relative sizes can capture one mechanism by which interactions change along a stress gradient. The effects of an individual plant on its neighborhood might shift from facilitative to competitive as its size increases. Specifically, we define 'size' here as above-ground biomass or correlates thereof (which includes Butterfield and Callaway's (2013) identification of leaf area as a facilitating functional trait and Brathen and Lortie's (2016) use of shrub height). At this point we focus on above-ground size, and below-ground interactions may differ even in the same plants (Sthultz 2007). Our objective is to examine whether a switch in interaction (e.g. from competitive to facilitative) resulting from a change in the *relative size* of individual plants produces the population metrics and spatial patterns seen for a stress gradient switch in model comparisons. We include a feedback mechanism through growth. Others have addressed size as a factor in a SGH analysis, but emphasized community biomass or the ontogenetic stage of the beneficiary of facilitation (Xiao et al. 2009; le Roux et al. 2013). Plant size, of course, may depend on the environment, the identification of stress gradient interactions may follow

observation of size differences, and size is the obvious factor in some studies of the SGH. However, a focus on relative size provides a more mechanistic hypothesis in which a physiological process – growth – is at the center of feedback with plant – plant interactions and may be independent of stress. More generally, relative size is a known factor in plant interactions (e.g., Miriti 2006; Xiao et al. 2006; Luo and Chen 2011).

We propose that as relative plant size theoretically increases from zero, facilitation will increase to some intermediate point; beyond this size, the competitive processes begin to cancel out the benefits (Schwinning and Weiner 1998) so that interaction becomes negative (Figure 1). At this point we focus on above-ground size and our reasoning is based on general observations at alpine treelines. Alpine treelines seem to be a useful model for examining a size gradient hypothesis because they are a clear stress gradient ecotone over which size changes significantly and positive feedback (i.e., self-facilitation) is recognized as a common process (Wilson and Agnew 1992; Malanson et al. 2011). From our work and that of others at alpine treeline, we suggest that as plants grow they increasingly reduce wind and evapotranspirative stress, capture snow that becomes late-summer soil moisture in an otherwise dry environment, increase the accumulation of fine sediment and organic matter in the soil, and reduce the impact of UV radiation and of night sky exposure and cold temperature photoinhibition (Germino and Smith 1999; Resler et al. 2005;



**Figure 1** The proposed size model. The relative size of neighbors is the sum of the size of up to eight neighbors divided by the size of the focal individual. The feedback intensity is used as a multiplier for growth and in Monte Carlo simulation of recruitment and mortality. If the focal individual is larger than the neighbors, the relative size is  $<1$  with minimal effect.

Holtmeier and Broll 2010; Malanson et al. 2011). All of these effects facilitate the recruitment and growth of other individuals. At some point, however, larger neighbors may increase snow to the point where the growing season is shorter (Ettinger et al. 2011), the shade cast by a tree is competition for light, larger canopies can have lower leaf temperatures than nearby tundra (Körner 2016), and perhaps more importantly, shade maintains colder soil temperatures under the canopy than are found in nearby tundra, which is the primary limiting factor for treelines at global scale (Körner 1998). These indirect effects on the neighborhood depend on the relative sizes of the plants; similar processes may operate in other environments (cf. Wang et al. 2015).

Although spatially explicit models of facilitation have addressed the size of the neighborhood per se (Jia et al. 2011; Lin et al. 2012), individual size has been incorporated by (Buenau et al. 2012), and Weiner et al. (2001) linked the two. Bittebiere et al. (2012) illustrated the complexity of modeling plant-plant interactions, and concluded that simple models could be appropriately realistic. The model we develop is meant to be as simple as possible, thus several caveats are needed:

- what is important about “size” and at what relative sizes would a change between interactions occur will vary among systems (and absolute rather than relative size may matter); here, we present a conceptual level model with arbitrary parameters;
- size does not add fully mechanistic processes to the stress gradient hypothesis, and the specific interaction (whether above- or belowground and how it affects growth, for example in carbon balance versus carbon allocation) will vary among systems.

Further assessment of the importance of size could be addressed with current empirical data, but we leave that to those who developed those field data.

We expect that the projections of a size gradient model will be similar to those of a stress gradient model except with respect to spatial patterns; spatial relations will differ in that immediate neighbors should differ more in comparative size in the size gradient model because the hypothesis leads to divergence with small plants facilitating larger ones that in turn

competitively suppress them (e.g., McAuliffe 1984, for saguaro cacti; Jia et al. 2011, in simulations; Nakagawa et al. 2015, fir-based simulations). Further, spatial pattern differs because the feedbacks from size are indirectly linked to position on the gradient.

## 1 Methods

We developed a spatially explicit agent based model using NetLogo (Wilensky 1999) to examine whether a switch in interaction (i.e., between facilitative and competitive) based on the relative size of individual plants can produce the patterns seen at an alpine treeline in comparison to a switch based on the stress gradient. This type of model is able to include neighbor interactions and produce visual output for interpretation. We created a grid of  $1000 \times 50$  cells; the grid is wrapped as a cylinder to eliminate edge effects. The grid has a linear environmental gradient,  $E_y$ , 1-0 across the rows,  $y$ . We model the dynamics of a single species. Each cell of the grid can be occupied by one individual, and to initialize model runs all cells can be occupied by an individual  $j$  with a probability proportional to  $E_y$  and with random variation between 0.5 and 100 for its age and size. This is an abstract model meant to explore the relative size concept and is not tied to a specific place or species. The parameters are chosen to reduce dimensions, in which individuals have unit growth and unit reproduction, balanced by mortality, per iteration, all else being equal.

Interaction intensity is examined in three treatments: none; the SGH based on the number of neighbors and the environmental gradient; and based on relative size. The stress gradient version is computed as a logarithmic increase with the number of neighbors: multiplied by a gradient from 0.5 to 2 across the length of the grid:

$$d = \text{number of neighbors}$$

$$I_{\text{stress}} = 0.26 + 0.333 \ln d \times (2 - 1.5E_y)$$

No feedback occurs if  $d = 0$ . The size-mediated version is

$$d = S_n / S_f$$

$$I_{\text{size}} | d < 33.333 = 1 + 0.0333d$$

$$I_{\text{size}} | d > 33.333 = 2.75 - 0.0225d$$

where  $S_n$  is the sum of the sizes of the eight neighbors and  $S_f$  is the size of the focal individual;

for empty cells the intensity for recruitment is calculated with  $S_f = 1$  interaction intensities less than 0.5 or greater than 2 are reset to these limits (Figure 1).  $E_y$  of each cell is multiplied by the interaction intensities  $I_{stress}$  or  $I_{size}$  for each cell at each iteration.  $I_{stress}$  or  $I_{size}$  become  $I_j$  for each individual  $j$  in the simulations.

The parameter values for the stress relationship are from the logarithmic increase in facilitation with number of neighbors modified by the stress gradient used by Malanson and Resler (2015); which is the logically conservative choice of greater interaction intensity with the first neighbors than with additional ones. The parameter values for the size function are arbitrarily set as multipliers with limits to double or halve the effects of the environment; the sum of neighbor sizes at which the effects begin to reverse (the point-of-reversal at 33.333 is the peak in Figure 1) is an arbitrary number but set so that it is about 1/2 of the mean sizes and 1/3 of the maximum sizes seen in the simulations (with size increments being in units of 1/iteration). We examine the sensitivity of this parameter by using the point of reversal at 16.666 and 50 and adjusting the slopes accordingly. The dynamics of the population are simulated over 500 iterations of recruitment, growth, and death as Monte Carlo processes:

Recruitment only occurs on empty cells, with probability a function of the size of the entire population, the environment of the row, and the effect of neighbors

$$P(R_j) = rN \times (E_y I_j)$$

where  $N$  is 1/2 the current population and  $r$  is 0.00002, so that the maximum population, with all cells occupied, would have a  $rN = 0.5$ ; The rate for recruitment and, below, for mortality, is set at half of the value of the environment (including interaction) based on the logic that recruitment and mortality are relatively rare, and these balance each other.

We compute the increase in size proportional to environment times intensity:

$$\Delta S_f = E_y I_j - 0.002 S_f E_y I_j$$

so that the smallest individual on a site of perfect environment would increase by ~ 1 unit of mass.

Mortality is simulated as

$$P(M_j) = 0.1 E_y I_j$$

The metrics of analysis here are the total population; the mean biomass of the individuals;

the number of edges as an indicator of spatial pattern; the sum of the interaction intensity across the grid (here  $I_j - 1$  for all cells), labeled the Force; and the size of each individual relative to the size of its neighbors, as an indicator of spatial relations; all averaged over 30 replications. Standard deviations are computed to illustrate model run consistency, recognizing White et al.'s (2014) argument against statistical tests applied to simulation results.

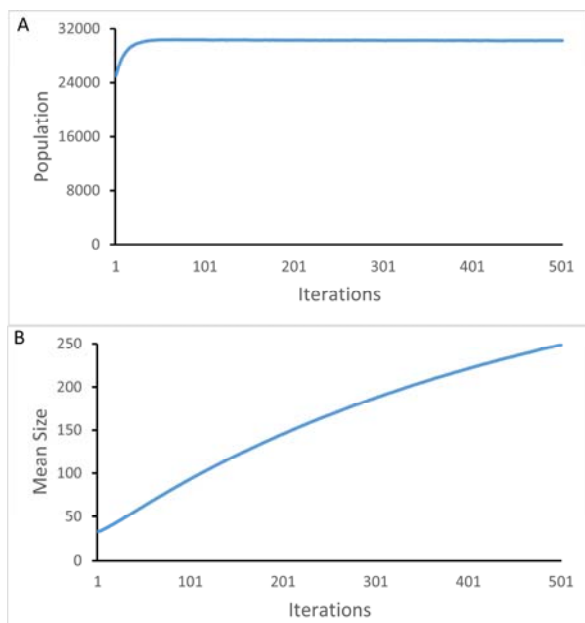
## 2 Results

Changing the relative size-at-reversal parameter by 50% results in changes in populations and mean sizes less than 10% in sensitivity tests (Table 1). Given that the other parameters in the model aim toward nondimensionalization, for the purpose of introducing this conceptual model we do not present further analysis of the parameter space. Major parameters equilibrate long before 500 iterations with the exception of size, which increases approximately linearly through this period (Figure 2); nonequilibrium size is acceptable for our purposes because the change is the same among all trials.

**Table 1** Differences in simulation outcomes for 30 replicate runs with the relative size-at-reversal (the peak difference in sizes, when the facilitation doubles the environmental value; see Figure 1) set at small (16.67) medium (33.33) and high (50) points on the relative size gradient, all for the size gradient model.

	Population	Mean Size
Small	27771±86	245.6±0.46
Medium	30269±76	246.7±0.68
Large	31530±75	248.6±0.97

The three simulated treatments or interaction hypotheses (none, stress, and size) produce small differences in the metrics examined (Table 2). The populations are approximately 1.3% lower with the size gradient than with the stress gradient, though the mean size of individuals for the size gradient is 25% greater than that of the stress gradient. This difference exists because the stress gradient maintains more individuals than does the size gradient in the high stress environment but they grow slowly. The Force (sum of interaction intensity across the grid) is increased 6% for the



**Figure 2** The dynamics of the system are shown for the population and mean size of the individuals. Mean size does not equilibrate until 3000 iterations, but the transient dynamics are the same for all scenarios.

**Table 2** Mean ( $\pm$  standard deviation) values of the metrics recorded at the end of 500 iterations of the simulations models for the cases with no feedback, the size gradient model, and the relative size gradient model.

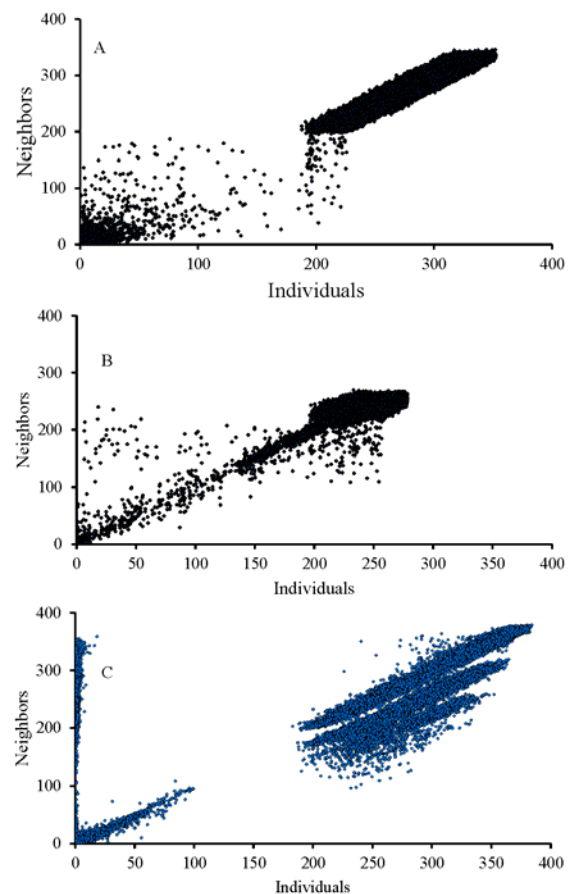
	None	Stress	Size
Population	30810 $\pm$ 49	34036 $\pm$ 50	30269 $\pm$ 76
Mean Size	225 $\pm$ .36	225 $\pm$ .30	247 $\pm$ .68
Force	NA	-1804 $\pm$ 52	4270 $\pm$ 63
Edges	6054 $\pm$ 82	1340 $\pm$ 69	12929 $\pm$ 156
Neighborhood	7.99 $\pm$ .05	8.60 $\pm$ .01	20.48 $\pm$ .38

size gradient relative to the stress gradient. The size gradient becomes negative for individuals, only for high asymmetry between large and small individuals, and thus overall positive interactions are the net result. A difference in spatial pattern is apparent between the two interactions, with the number of edges 5.7 times higher in the size gradient. The local variation in sizes is the greatest difference between the stress and size models, with the size model resulting in greater (5.6 times) local contrasts. This difference can also be seen visually; Figure 3 shows that while most neighborhoods are similar, the size gradient model (C) has a number of small individuals with very large neighbors that do not occur in the other models, and the linear features indicate more structured spatial relations.

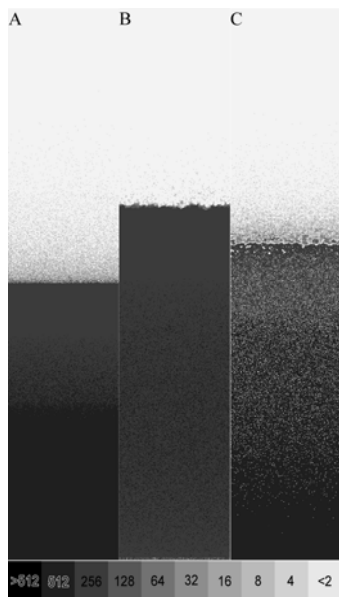
Visual examination of the three treatment scenarios (Figure 4a-c) reveals both similarities

and differences in model output. In all three models a somewhat abrupt transition from occupied to unoccupied cells occurs. Without interaction (Figure 4a), the transition is lower than on the stress gradient (i.e., lower stress, higher habitat quality), at the point where initial habitat quality is 0.498 (row 502). In the stress gradient model (Figure 4b), the transition is higher on the gradient, where the initial habitat quality is 0.358 (row 642; at higher stress, as with higher elevation at a treeline ecotone). The size gradient model transitions where the initial habitat quality is 0.429 (row 570), between the other two on the gradient since the lack of positive interactions restricts presence in the higher stress environment (as apparent in the no interactions model), whereas the stress gradient model facilitation covaries positively with stress and so presence can advance along the gradient.

Furthermore, spatial patterns differ in



**Figure 3** The average size of neighbors plotted against the average size of each individual at the end of a simulation run for A) no feedback, B) stress gradient and C) size gradient models.



**Figure 4** The pattern at the end of the simulation for the cases with A) no feedback, B) the stress gradient, and C) the size gradient modes.

abruptness among the three models. Without interaction (Figure 4a) the transition is less abrupt, with the occupancy of cells per row gradually declining along the gradient beyond the last row of complete occupancy. The transition is most abrupt for the stress gradient model (Figure 4b), with few individuals in scattered patches beyond the last complete row. The size gradient model (Figure 3c) has three notable features of pattern. First, there is a long gradual transition of scattered unoccupied cells from low on the stress gradient that do not simply coalesce into emptiness; second, there is a sharp but irregular line of empty cells across the grid at the center of the zone of transition that represents the last fairly contiguous band of larger trees across the grid; and third, a zone of distinct patches of variable size exists before occupancy gradually thins out at higher stress.

### 3 Discussion

When the interaction of individuals is affected by the environment indirectly, through the size of their neighbors, model results are similar to those where the effects change directly with a stress gradient for populations and mean sizes, but differ in aspects of spatial pattern and relations. The spatial patterns in Figure 4 are superficially similar, but the metrics of the number of edges and the

relative sizes of neighbors differ. Greater spatial variability is created by the size gradient model. The reasons for the similarity in populations but differences in spatial patterns and relations are the result of the feedbacks in the models. The stress model creates a feedback in the size of populations by increasing the habitat quality in the area of high stress – in fact multiplied by stress – when an individual recruits there. The feedback persists regardless of size. Thus the ecotone in the stress model is farther along the stress gradient and is relatively abrupt. While the size model also maintains the population in moderate stress levels, because individuals of different size can suppress neighbors more edges exist, and because neighbors can have opposite feedback effects on each other more local variance in size exists.

All of the patterns seen in Figure 4 could approximate some of the alpine treeline ecotones of the western USA, which are quite variable. Most have relatively abrupt boundaries, however, which is the basis for building on the positive feedback switch proposed by Wilson and Agnew (1992). The stress gradient model produces abrupt boundaries, and appears to be more realistic in that regard than the no-interaction model. However, the size gradient model replicates some features of alpine treeline ecotones not seen in the stress gradient model. For example, in many cases upright trees end abruptly and patches of dwarf trees and/or krummholz are scattered in a zone above this possible ‘timberline’ in contrast to a smooth and gradual transition of larger to smaller to dwarf to krummholz growth forms with a continuous canopy (Holtmeier 2009); this pattern has been attributed to a combination of abiotic heterogeneity and positive feedback in biotic interactions (e.g., Malanson et al. 2002; Butler et al. 2004; Malanson et al. 2011; Smith-McKenna et al. 2014; Bourgeron et al. 2015; Pyatt et al. 2016). The empty line across the grid separating the zone of larger trees (with empty space as also seen in montane forest) may not be as visually striking on mountainsides as it appears in Figure 4c, but something similar does exist. We do not model tundra here, nor the intermediate sized and sometimes prostrate shrub forms, such as willows, sometimes associated with treeline ecotones.

A size-mediated effects model still represents an initial step toward adding more mechanistic

explanation to the stress gradient hypothesis. Cairns (2005) already took such a step by assessing size and canopy structure for alpine treeline krummholz and dwarf trees using a version of the physiologically based –BGC model group. In that model, dwarf trees had higher carbon balance output than krummholz for typical leaf area indices, but within-canopy variation in thermal regime did not make a difference for either canopy type.

The size gradient model introduces a specific feedback mechanism that allows a change from facilitation to competition as the relative sizes of the plants diverge. For the response of alpine treelines, Korner (2016) recently emphasized the role of size on feedbacks, but did not specify a gradient. Our model introduces a single functional trait, but from a different perspective than most of the functional traits commonly discussed for plant species. Most work on functional traits is about the traits as indicators of the functions within individuals (e.g., Butterfield and Callaway 2013). Our perspective is on the function of altering the abiotic environment of a neighborhood (cf. Smith et al. 2003); some commonly used traits, such as canopy height, will have either type of function for alpine treelines, but differentiating the two will be important in assessing their role in plant community response to climate change (cf. Heikkinen et al. 2006).

#### 4 Conclusion

A size gradient is one possible process of the stress gradient hypothesis (and it ignores some

details, such as reciprocal costs, sensu Schöb et al. 2014, or the breakdown of facilitation at extreme stress, as in Michalet et al. 2014). Although size responds to stress, and as modeled here size differences are a phenomenon of the SGH, it could also act without a stress gradient (and could, for example, be a process of succession). A consideration of a size gradient hypothesis will lead to new empirical work to define the inflection point at which relative sizes change the direction of the interaction. The role of size could also be a way in which the change from facilitation to competition with increasing stress is a change in the identity of species that are always facilitators or always competitors (as in one variation examined by Malanson, 2015) if this function is based on size alone. We advance this project with caution because the mediation of the SGH, essentially an abiotic pathway of plant-plant interactions, could be confounded with direct biotic interactions and we temporarily ignore ontogenetic state (cf. Miriti 2006). However, while we developed our model based on experience at alpine treeline, a relative size gradient could mediate the SGH in other environments.

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#### References

- Berger U, Piou C, Schifffers K, Grimm V (2008) Competition among plants: Concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology Evolution and Systematics* 9: 121-135. DOI: 10.1016/j.ppees.2007.11.002
- Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191-193. DOI: 10.1016/0169-5347(94)90088-4
- Bittebierea AK, Monya C, Clémenta B, et al. (2012) Modeling competition between plants using an Individual Based Model: Methods and effects on the growth of two species with contrasted growth forms. *Ecological Modelling* 234(10): 38-50. DOI: 10.1016/j.ecolmodel.2011.05.028
- Brathen KA, Lortie C (2016) A portfolio effect of shrub canopy height on species richness in both stressful and competitive environments. *Functional Ecology* 30: 60-69. DOI: 10.1111/1365-2435.12458
- Buenau KE, Price NN, Nisbet RM (2012) Size dependence facilitation and microhabitats mediate space competition between coral and crustose coralline algae in a spatially explicit model. *Ecological Modelling* 237: 23-33. DOI: 10.1016/j.ecolmodel.2012.04.013
- Butterfield BJ, Callaway RM (2013) A functional comparative approach to facilitation and its context dependence. *Functional Ecology* 27: 907-917. DOI: 10.1111/1365-2435.12019
- Cairns DM (2005) Simulating carbon balance at treeline for krummholz and dwarf tree growth forms. *Ecological Modelling* 187: 314-328. DOI: 10.1016/j.ecolmodel.2005.01.041
- Callaway RM (2007) Positive interactions and interdependence in plant communities. Dordrecht: Springer. p 404. DOI: 10.1007/978-1-4020-6224-7
- Chen JG, Yang Y, Stocklin J, et al. (2015) Soil nutrient availability determines the facilitative effects of cushion

- plants on other plant species at high elevations in the south-eastern Himalayas. *Plant Ecology and Diversity* 8: 199-210. DOI: 10.1080/17550874.2013.872206
- Cowles JM, Wragg PD, Wright AJ, et al. (2016) Shifting grassland plant community structure drives positive interactive effects of warming and diversity on aboveground net primary productivity. *Global Change Biology* 22: 741-749. DOI: 10.1111/gcb.13111
- Germino MJ, Smith WK (1999) Sky exposure, crown architecture, and low-temperature photoinhibition in conifer seedlings at alpine treeline. *Plant Cell and Environment* 22: 407-415. DOI: 10.1046/j.1365-3040.1999.00426.x
- Holtmeier FK, Broll G (2010) Wind as an ecological agent at treelines in North America the Alps and the European subarctic. *Physical Geography* 31: 203-233. DOI: 10.2747/0272-3646.31.3.203
- Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115: 445-459. DOI: 10.1007/s004420050540
- Körner C (2016) When it gets cold, plant size matters – a comment on treeline. *Journal of Vegetation Science* 27: 6-7. DOI: 10.1111/jvs.12366
- Jia X, Dai XF, Shen ZX, et al. (2011) Facilitation can maintain clustered spatial pattern of plant populations during density-dependent mortality: insights from a zone-of-influence model. *Oikos* 120: 472-480. DOI: 10.1111/j.1600-0706.2010.18674.x
- Le Roux PC, McGeoch MA (2008) Spatial variation in plant interactions across a severity gradient in the sub-Antarctic. *Oecologia* 155: 831-844. DOI: 10.1007/s00442-007-0954-1
- Le Roux PC, Shaw JD, Chown SL (2013) Ontogenetic shifts in plant interactions vary with environmental severity and affect population structure. *New Phytologist* 200: 241-250. DOI: 10.1111/nph.12349
- Lin Y, Berger U, Grimm V, Ji QR (2011) Differences between symmetric and asymmetric facilitation matter: exploring the interplay between modes of positive and negative interactions. *Journal of Ecology* 100: 1482-1491. DOI: 10.1111/j.1365-2745.2012.02019.x
- Luo Y, Chen HYH (2011) Competition, species interaction and ageing control tree mortality in boreal forests. *Journal of Ecology* 99: 1470-1480. DOI: 10.1111/j.1365-2745.2011.01882.x
- Mack RN, Harper JL (1977) Interference in dune annuals: spatial pattern and neighbourhood effects. *Journal of Ecology* 65: 345-363. DOI: 10.2307/2259487
- Maestre FT, Callaway RM, Valladares F, Lortie CJ (2009) Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology* 97: 199-205. DOI: 10.1111/j.1365-2745.2008.01476.x
- Malanson GP (2015) Diversity differs among three variations of the stress gradients hypothesis in two representations of niche space. *Journal of Theoretical Biology* 384: 121-130. DOI: 10.1016/j.jtbi.2015.08.012
- Malanson GP, Resler LM (2015) Neighborhood functions alter unbalanced facilitation on a stress gradient. *Journal of Theoretical Biology* 365: 76-83. DOI: 10.1016/j.jtbi.2014.10.005
- Malanson GP, Resler LM, Bader MY, et al. (2011) Mountain treelines: a roadmap for research orientation. *Arctic Antarctic Alpine Research* 43: 167-177. DOI: 10.1657/1938-4246-43.2.167
- McAuliffe JR (1984) Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. *Oecologia* 64: 319-321. DOI: 10.1007/BF00379128
- Michalet R, Pugnaire FI (2016) Facilitation in communities: underlying mechanisms, community and ecosystem implications. *Functional Ecology* 30: 3-9. DOI: 10.1111/1365-2435.12602
- Michalet R, Le Bagousse-Pinguet Y, Maalouf JP, Lortie CJ (2014) Two alternatives to the stress-gradient hypothesis at the edge of life: the collapse of facilitation and the switch from facilitation to competition. *Journal Vegetation Science* 25: 609-613. DOI: 10.1111/jvs.12123
- Miriti MN (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology* 94: 973-979. DOI: 10.1111/j.1365-2745.2006.01138.x
- Nakagawa Y, Yokozawa M, Hara T (2015) Competition among plants can lead to an increase in aggregation of smaller plants around larger ones. *Ecological Modelling* 301: 41-53. DOI: 10.1016/j.ecolmodel.2015.01.014
- Rietkerk M, Boerlijst MC, van Langevelde F, et al. (2002) Self-organization of vegetation in arid ecosystems. *American Naturalist* 160: 524-530. DOI: 10.1086/342078
- Resler LM, Butler DR, Malanson GP (2005) Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography* 26: 112-125. DOI: 10.2747/0272-3646.26.2.112
- Schöb C, Callaway RM, Anthelme F, et al. (2014) The context dependence of beneficiary feedback effects on benefactors in plant facilitation. *New Phytologist* 204: 386-396. DOI: 10.1111/nph.12908
- Schweiger AH, Otieno DO, Kulunge SR, et al. (2015) The Afro-alpine dwarf shrub *Helichrysum citrispinum* favours understorey plants through microclimate amelioration. *Plant Ecology and Diversity* 8: 293-303. DOI: 10.1080/17550874.2015.1014207
- Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113: 447-455. DOI: 10.1007/s004420050397
- Smith TB, Wayne RK, Girman DJ, et al. (1997) A role for ecotones in generating rainforest biodiversity. *Science* 276: 1855-1857
- Soliveres S, Smit C, Maestre FT (2014) Moving forward on facilitation research: response to changing environments and effects on the diversity, functioning and evolution of plant communities. *Biological Reviews* 90: 297-313. DOI: 10.1111/brv.12110
- Sthultz CM, Gehring CA, Whitham TG (2007) Shifts from competition to facilitation between a foundation tree and a pioneer shrub across spatial and temporal scales in a semiarid woodland. *New Phytologist* 173: 135-145. DOI: 10.1111/j.1469-8137.2006.01915.x
- Weiner J, Stoll P, Muller-Landau H, Jasentuliyana A (2001) The effects of density, spatial pattern, and competitive symmetry on size variation in simulated plant populations. *American Naturalist* 158: 438-450. DOI: 10.1086/321988
- White JW, Rassweiler A, Samhuri JF, et al. (2014) Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* 123: 385-388. DOI: 10.1111/j.1600-0706.2013.01073.x
- Wilensky U (1999) NetLogo. <http://ccl.northwestern.edu/netlogo/>. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL USA.
- Wilson JB, Agnew ADQ (1992) Positive feedback switches in plant communities. *Advances in Ecological Research* 23: 263-336 DOI: 10.1016/S0065-2504(08)60149-X
- Wisz MS, Pottier J, Kissling WD, et al. (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15-30. DOI: 10.1111/j.1469-185X.2012.00235.x
- Wright A, Schnitzer SA, Reich PB (2014) Living close to your neighbors: the importance of both competition and facilitation in plant communities. *Ecology* 95: 2213-2223. DOI: 10.1890/13-1855.1
- Xiao S, Chen SY, Wang G (2006) An ESS for the height of a plant population, or an optimal height for an individual? Rethinking game-theoretic models for plant height. *Bulletin of Mathematical Biology* 68: 957-967. DOI: 10.1007/s11538-006-9073-0
- Xiao S, Michalet R, Wang G, Chen SY (2009) The interplay between species' positive and negative interactions shapes the community biomass-species richness relationship. *Oikos* 118: 1342-1348. DOI: 10.1111/j.1600-0706.2009.17588.x