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Neighborhood functions alter unbalanced facilitation on a stress gradient

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HIGHLIGHTS

- Stress gradient correlated facilitation (SGCF) boosts edges and mean facilitation.
- SGCF increases populations in the area of higher stress.
- SGCF increases the beneficiary species relative to even facilitation.
- Unimodal functions of facilitation for neighbor density magnify all above effects.
- Unimodal functions of SGCF may be important in ecotones with patchy patterns.

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ABSTRACT

The stress-gradient hypothesis states that individual and species competitive and facilitative effects change in relative importance or intensity along environmental gradients of stress. The importance of the number of facilitators in the neighborhood of a potential beneficiary has not been explored. Evenly distributed and stress-correlated facilitation and the increase in the intensity of facilitation with neighbors as linear, logarithmic, and unimodal functions is simulated for two hypothetical species, both of which improve the local environment. The mutualism is unbalanced in that the establishment of one species is enhanced by neighbors more than the other. Compared to no facilitation or evenly distributed facilitation, the stress gradient produces more edges in the spatially advancing population, more overall intensity of facilitation, and more individuals further advanced into the area of higher stress; the more enhanced species has increased population relative to the other – to the point where they are equal. Among three neighborhood functions, little difference exists in outcomes between the linear and logarithmic functions, but the unimodal function, which shifts peak facilitation intensity to fewer neighbors, increases the above state variables more than the differences between the even and stress gradient facilitation scenarios; the population of the beneficiary species exceeds that of the other. Different neighborhood functions change the effects of spatial pattern on the biological outcome. The unbalanced mutualism may be important where additional species alter the basic interaction in the high stress area of the environmental gradient, such as ecotones where the spatial pattern becomes central to facilitation.

1. Introduction

The stress gradient hypothesis (SGH), which has dominated research on facilitation during the last two decades (Brooker et al., 2008), proposes that relative frequency or importance of competitive and facilitative interactions among organisms vary inversely along environmental stress gradients (Bertness and Callaway, 1994). Facilitation, according to SGH, is predicted to be more common in communities experiencing high abiotic stress, whereas competition would theoretically dominate under low stress. The hypothesis was developed by Bertness and Callaway (1994) (cf. Brooker and Callaghan, 1998) and elucidated for alpine plants by Callaway et al. (2002) and Michalet et al. (2014) and, more extensively, by He et al. (2013).

Though beginning as a general conceptual model, it has subsequently inspired extensive field research and model development,

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results of which have contributed to fundamental increases in our understanding of the relative importance of positive and negative interactions among plants under varying abiotic conditions. These increases have been in the elucidation of interspecific relations, notably contrasting competitive versus stress-tolerant species (usually sensu the competitor–stress tolerant–ruderal (C–S–R)) scheme of Grime (1979) (cf. Liancourt et al., 2005), although the principle applies to intraspecific relations as well. Furthermore, the SGH varies in applicability under different, and sometimes unpredictable, abiotic contexts. For example, in extremely constrained environments, Michalet et al. (2006) proposed that plant facilitation decreased or ceased. Change in the form of the interactions between species and among stress factors along a gradient have been shown to affect the facilitation/competition outcome (Choler et al., 2001; Kawai and Tokeshi, 2007). However, as modified by Michalet et al. (2006) and others (Michalet, 2007, Maestre et al., 2009), it now is a leading stimulus in ecology (e.g., Brooker et al., 2008; Holmgren and Scheffer, 2010; Malkinson and Katja Tielbörger, 2010; Michalet et al., 2014).

The modeling of competition and facilitation on a stress gradient is a subset of theoretical models addressing species interactions in spatially heterogeneous environments. The general approach was pioneered by Shigesada et al. (1979) and later generally described by Kareiva (1990). The analysis of facilitation per se is part of that work that examines mutualistic interactions. While theoretical models have examined most aspects of mutualism, some spatial constraints are unexplored.

Brooker et al. (2005) and Maestre et al. (2009) have argued that intensity of interactions is a significant aspect of the stress-gradient hypothesis, but the dependence of facilitation intensity on the number of facilitators in the neighborhood has not been part of the discussion, although Droz and Pekalski (2013) considered spatial arrangement. Interaction effects or intensity are usually modeled as a binary function of neighbor presence (e.g., Travis et al. 2005, 2006, wherein the neighbor is co-located on a dual-lattice) or assumed to be a linear function of number of neighbors (e.g., Chen et al., 2009; Xiao et al., 2009). Addressing facilitation but the not the SGH, Zeng and Malanson (2006) modeled the effect of neighbors on the probability of establishment at a point as a quasi-Gaussian function. Thus for the eight neighbors of a Moore neighborhood of 3×3 cells, facilitation increased from none at no neighbors, to a maximum at 4, and back to none at 8 neighbors. They assumed that the positive effects of facilitation would begin to be canceled out by the competitive effects of crowding at the higher densities. For their alpine treeline example, they reasoned that effects such as increased water available from the trapping of snow by neighbors would be reduced at high densities by the shorter growing seasons caused by too much trapped snow; other facilitative effects, such as reduced wind-induced desiccation, would level off while competitive effects, such as shading would not. Here we focus on the number of facilitators in the neighborhood on a stress-gradient.

Assuming facilitation affects neighbors, it is expressed across edges and to a limited distance, and so its spatial expression and the resulting spatial pattern are linked in a feedback loop. Spatial feedbacks are at the core of many interactions among individuals, and thus central to self-organized complexity in ecology (cf. Levin, 2005), and are particularly important at boundaries, such as ecotones, where local scale feedbacks can determine the population dynamics and larger scale change (or stability) in biogeography (e.g., Loehle et al. 1996; Milne et al., 1996; Li, 2002; D'Odorico et al., 2013; Olofsson et al., 2013).

Here, we refine the conceptual SGH with regard to neighborhood facets of facilitation intensity in a complex system. Our model is developed from studies of climate change, although we do not change the climate herein, and complements insights of Brooker (2010), Addison et al. (2013), and Singer et al. (2013). Our current model is more concerned with spatial patterns and feedbacks, and is more informed by the work of Brooker et al. (2007), Martinez-Garcia et al. (2013), and Bulleri et al. (2014), among others, who considered the range of spatial structures generated. For example, Brooker et al. (2007) found that spatial patterns affected dynamics through competition for space, and Chen et al. (2009) concluded that patterns can simultaneously be indicators of self-organizing dynamics. Like Chen et al. (2009), we use a single lattice model so that species use space exclusively at any time (cf. Travis et al., 2006).

To address differences in the neighborhood expression of facilitation, we create a simulation with two prototype species on a grid of cells with an environmental gradient. We examine three neighborhood functions: linear and logarithmic increases in facilitation with neighbors and a unimodal pattern that modifies Zeng and Malanson's (2006) quasi-Gaussian function.

2. Model design

We simulate the population dynamics of two prototype species on a grid of cells as an abstract representation of an alpine treeline environment. Different scenarios embody alternative representations of facilitation in the stress gradient hypothesis.

2.1. *Prototype species*

Where Travis et al. (2006) simulated mutualists and cheaters, Chen et al. (2009) simulated competitors and stress-tolerators to examine stress gradients, and others have commonly compared competitors and colonizers (e.g., Tilman et al., 1994; Malanson, 2002), here we create a somewhat different pairing. Our model is derived from our work on tree species at alpine treeline ecotones in Rocky Mountains of western North America (e.g., Zeng and Malanson (2006), Resler and Tomback (2008), Resler et al. (2014)). Alpine treeline ecotones reflect a threshold stress gradient for trees at higher elevations, whereby trees are eventually replaced with tundra vegetation (cf. Elliott, 2012). At Rocky Mountain treeline ecotones, the most noticeable combination of species does not follow the abstract pairing seen in other SGH simulations, but may be more representative of pairings where the SGH applies.

Whitebark pine (*Pinus albicaulis*) is high elevation keystone species throughout its range in the western mountains of the United States and Canada (Tomback, 2009). At some alpine treelines whitebark pine is often the pioneer in the advance of tree species into tundra and plays an important role in tree island development through facilitation, thereby shaping treeline vegetation pattern (Resler and Tomback, 2008, Tomback, 2009). It facilitates, and is followed in the development of dwarf tree or krummholz islands, by other conifers, typically *Abies lasiocarpa* and *Picea engelmannii* (e.g. Habeck, 1969; Resler and Tomback, 2008). While these spruce and fir species may alter the environment in a way that could benefit *P. albicaulis*, the mutualism is unbalanced. This imbalance may be explained in part by the particular relationship of *P. albicaulis* with another mutualist – its primary dispersal agent, *Nucifraga columbiana* (Clark's nutcracker; family Corvidae). *N. columbiana* buries caches of seeds of *P. albicaulis* in the alpine treeline ecotone in places such as near rocks and dead trees that appear well-suited to germination because these are the places where burial is easy (Resler et al., 2005) and the birds can relocate the cache (Tomback, 1980). Thus *P. albicaulis* is not simply a colonizer or a stress tolerator in that it has elements of both. It is often the first tree to colonize tundra as trees have moved upslope in the past century, but it is not