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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 r-selected in that it produces fewer seeds, but each, being a nut, have more energy reserves, and are more likely to produce a viable adult than do the other conifer seeds (Tomback, 1982). In the most stressful condition the other species primarily establish when facilitated by the presence of *P. albicaulis*, which protects them from desiccation, provides a moisture source by trapping snow, and may enrich the soil with finer sediment, all by changing wind effects (Resler and Fonstad, 2009; Holtmeier and Broll, 2010). While those conditions could also favor a seedling of *P. albicaulis*, they apparently are not locations favored for seed caches by *N. columbiana*; thus the mutualism is unbalanced, but how strongly is uncertain. None of these species is clearly a superior competitor at treeline in that none eliminate any other once they have become established. At alpine treeline sites the lifespans of the tree species are greater than the time since the Little Ice Age, and so their mortality rates are not well known, but none are short-lived. *P. albicaulis* appears to be the pioneer because of its association with Clark's nutcracker, while *A. lasiocarpa* and *P. engelmannii* take advantage of facilitation that is not so available to *P. albicaulis* itself, possibly because of the special conditions for its seed dispersal and caching. This alteration of prototypical C–S–R relations by a plant-animal interaction may not be uncommon. Johnson and Adkisson (1985) revealed the relationship between *Fagus grandifolia* (Fagaceae) and *Cyanocitta cristata* (Corvidae) in the upper midwest after wondering how apparently K-selected beech persisted in increasingly fragmented forest remnants. Other plant–animal interactions may also add dimensions to the C–S–R framework (e.g., Chaneton et al., 2010; Grau et al., 2013; Olofsson et al., 2013).

These species coexist in mature subalpine forests and together are found through the transition into the ecotone with alpine tundra. No gradient from competitive to stress-tolerant species is observed unless one extends the gradient further to valley bottoms where possibly better competitors, not found at higher elevations, may dominate. Thus in the portion of the gradient where the SGH is likely to become important, the strategies differ but are not so clearly differentiated in the C–S–R framework. In the more stressful part of a stress-gradient, relations between two stress-tolerators may be more informative on facilitation that the more extreme C–S–R contrasts.

Thus the prototype species that we simulate do not represent the extremes of gradients of competitors, stress-tolerators, and ruderals in Grime's (1979) classification, but as he noted, many species will be within the C–S–R triangle, not only at its corners. We create a pioneer SP1, similar to *P. albicaulis*, and the beneficiary SP2, similar to *A. lasiocarpa* or *P. engelmannii*, but all are still prototypes and not calibrated with species-specific empirical data. SP1 produces fewer seeds (1/10th) per mature individual than does SP2, but the probability of establishment for any seed is 10 times greater. With these conditions alone, the two species produce equal populations when simulated individually or together, all other factors held equal. To capture the specific condition of facilitation in which the seeds of *A. lasiocarpa* and *P. engelmannii* are more successful when adjacent to *P. albicaulis*, we apply the effects of facilitation more strongly for seedling establishment for SP2 while holding facilitation effects on seed production, growth, and mortality equal for both species.

We define mature as >10 iterations. Although we could combine the probability of establishment and mortality in this period and create new individuals as mature, in our approach the immature individuals hold space and facilitate others, but with less continuity. Mortality and growth are set equal for the two prototypes. We do include growth, and both species are able to expand into adjacent area at a greater rate than they can establish new individuals. We use lateral expansion because prostrate forms are so common in the treeline environment. All processes are simulated stochastically per individual.

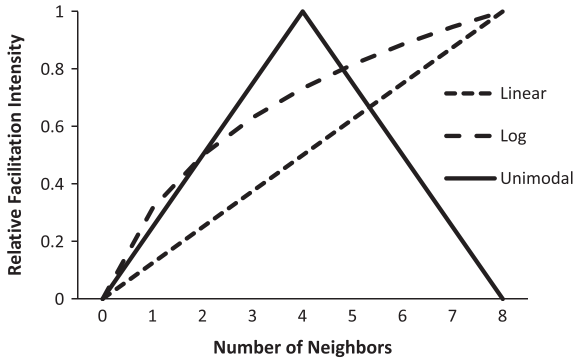

Fig. 1. The intensity of facilitation varies with the number of neighbors in a Moore neighborhood.

2.2. Facilitation scenarios

Here we represent facilitation intensity (FI) as a function of stress under six facilitation scenarios. First, in baseline runs, we simulate facilitation without regard to the stress gradient but with three neighborhood functions for intensity: changing linearly, logarithmically, or unimodally with the number of neighbors (up to eight) as shown in Fig. 1 (labeled BL, BLog, and BX). We modify the unimodal function of Zeng and Malanson (2006). Although they used a Gaussian function, we think that gives too little weight to the first neighbor. For the baseline runs, we set the value so that FI for the average neighborhood would be 0.1 across the entire grid. Second, to represent the stress gradient, we modify FI so that it is zero at the low stress end of the gradient and doubled (0.2) at the high stress end. We repeat the three neighborhood functions (labeled GL, GLog, GX). The average possible FI is always equal. Given observations of establishment patterns at alpine treeline (e.g., Maher et al., 2005; Resler et al., 2005), the range of FI up to 0.2 is conservative and we do not have physiological data for calibration. We did not move the mode of the unimodal function or explore thresholds (cf. Xiao et al., 2009) or temporal variation in stress (Bulleri et al., 2014; Wright et al., 2014).

2.3. Spatial environment

We represent space as a 500×100 grid of cells. Only one individual can occupy any cell at a time. We represent a stress gradient as its inverse, which we refer to as site quality (SQ). On the long axis of the grid (rows) the gradient of site quality is as follows:

$$SQ = (1 - \text{row\#}/500) * 0.5 \qquad (1)$$

and thus runs from 0.5 to 0 (i.e., the stress increases from 0.5 to 1); we only simulate one-half of a 0–1 range because all the difference occurs where stress is high. The grid wraps at its lateral edges both ends of the rows are also adjacent. The space is thus a cylinder of 100-cell circumference and 500-cell length. SQ captures the environmental gradient from the plant's-eye-view, and thus avoids complications of nonlinear responses to real environmental variables. Facilitation, based on number of trees in the neighborhood is added to site quality, based on the location on the gradient, and their sum (SQ+FI) used in Monte Carlo simulation of population processes (Section 2.4). We also simulated the processes for the same landscape without any facilitation, i.e., as a function of original site quality.

2.4. Population dynamics

We initialize the simulation with an approximately equal number of individuals of SP1 and SP2 ($\sim$775 each) (among 50,000 cells) by stochastically assigning trees as a function of SQ. We then simulated the spatial coverage, and thus populations, of SP1 and SP2, by stochastically stepping through the processes of plant population ecology. First, we calculate the number of seeds per extant adult that could arrive on any cell of the grid:

$$\#\text{Seeds} = \text{SeedProb}_{Sp} * (\text{SQ} + \text{FI}) \quad (2)$$

where $\text{SeedProb}_{SP1} = 0.01$ and $\text{SeedProb}_{SP2} = 0.05$. For seeds landing on an empty grid cell, establishment probability is computed as follows:

$$P_{\text{estab}} = \text{Estab}_{\text{Sp}} * (\text{SQ} + \text{FI}) \quad (3)$$

where $\text{Estab}_{\text{SP1}} = 0.002$ and $\text{Estab}_{\text{SP2}} = 0.0004$. For both SP1 and SP2, the probability of an individual growing a branch into any adjacent cell is computed as follows:

$$P_{\text{grow}} = .05 * (\text{SQ} + \text{FI}) \quad (4)$$

The mortality rate is the same for both SP1 and SP2, but differs with age (higher when <10):

$$P_{\text{die}} = \text{MortalProb}_{\text{Age}} * (\text{SQ} + \text{FI}) \quad (5)$$

where $\text{MortalProb} < 10 = 0.01$ and $\text{MortalProb} > 10 = 0.10$. Death of a branch is a singular event, but if the original stem dies its branches die simultaneously. Whether an event is executed is determined stochastically by comparing the probability to a random number.

Up to this point SP1 and SP2 should have equal outcomes, with 5 times as many seeds produced by SP2 but with 1/5th the establishment rate of SP1. These balanced values of the control parameters are simplifications of those derived for *P. albicaulis* and *A. lasiocarpa* for a model examining responses to climate change (Smith-McKenna et al., 2014); varying those by ±10% produced changes in the populations of $<10\%$. Then we create the distinct difference that captures the unbalanced mutualism between SP1 and SP2: for establishment probability we double the intensity of facilitation for SP2 (Eq. (3) becomes $P_{\text{estab}} = \text{Estab}_2{}^*(\text{SQ} + (\text{FI}^*2))$).

We run the simulation for 100 iterations – shorter than the number of years since the end of the Little Ice Age and the lifespans of the observed species; the model does not reach equilibrium, but with facilitation longer runs would fill the entire space with trees. We run 20 replications of each scenario and present averaged results (coefficients of variation are typically 0.01–0.02 and we do not present the variance), except for the maps, which are chosen from single runs. Although the order of the species in each replication matters little, we switched it for half. The model is available in the NetLogo community library at http://ccl.northwestern.edu/netlogo/models/community/index.cgi.

3. Analyses and results

We examined key indicators of the difference between the scenario and control simulations. Over the course of the iterations we examined (1) the populations of SP1 and SP2; (2) the average position of all individuals of SP1 and SP2 on the stress gradient (the average row of the grid); (3) the number of edges, across which facilitation and subsequent establishment or growth occur; (4) the average potential, which we define as the sum of all facilitation divided by the number of empty cells on the grid; and (5) the net number of new occupied cells, by establishment and growth minus mortality, per iteration.

As in other models, the stress gradient scenarios result in larger populations of both species relative to the controls in all three facilitation neighborhood realizations (e.g., Fig. 2). The difference between stress gradient facilitation and control facilitation is greater than between the latter and no facilitation at all. Here we examine the spatial effects and transient dynamics.

3.1. Even facilitation vs stress gradient facilitation

The stress gradient function produces farther average advances into the area of higher stress than does the control (Fig. 3). Because the initial population is widely scattered, mortality reduces the average position of the populations on the grid during the first half of the simulation runs, but not so greatly with the stress gradient facilitation because the individuals in the more stressful part of the gradient have a higher relative effect in improving their neighborhood. For edges, the number rises as the populations develop but then falls as small patches coalesce (less with no facilitation because the limits of the grid are not approached) (Fig. 4). The rise is faster with stress gradient facilitation as a result of faster population increase. The facilitation potential increases in the early stages of the simulations, but declines (for the linear NI) because more individuals have neighbors, up to eight, and exert less and less facilitation on empty cells. Potential has a larger relative difference between the control and stress gradient facilitation than any other measure (Fig. 5)

3.2. Neighborhood intensity functions

Differences among the neighborhood intensity scenarios are also seen in populations of both species (Fig. 6). Differences in spatial outcomes, such as mean position on the gradient and edge density, and the change in the potential created by facilitation, are more pronounced. The unimodal intensity function creates distinctly larger patches higher on the stress gradient than do the others.

The mean position of the populations on the gradient start high, but well short of the midway point, because the initial allocation of seedlings is a direct function of the gradient of site

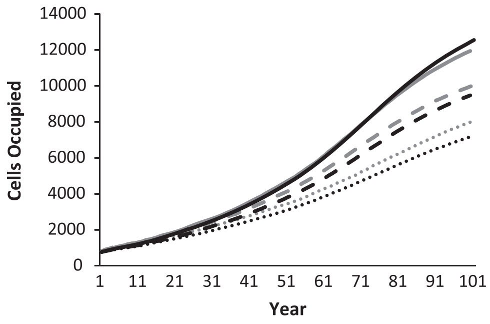

Fig. 2. The population dynamics of SP1 and SP2 differ among no-facilitation (NoF), baseline linear facilitation (BL), and stress-gradient linear facilitation (GL) simulations. Only the linear neighborhood intensity functions are shown.

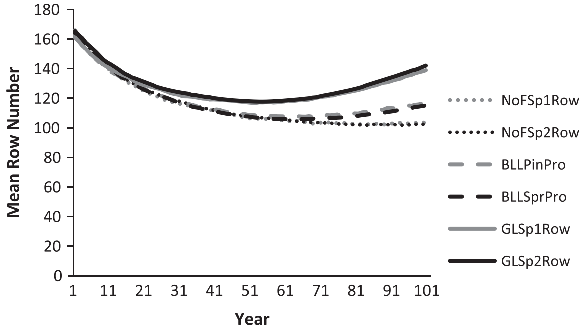

Fig. 3. For SP1 and SP2, the mean position of their populations on the gradient are more advanced with the stress-gradient facilitation model (GL) than the baseline facilitation (BL) or no facilitation models. Only the linear neighborhood intensity functions are shown.

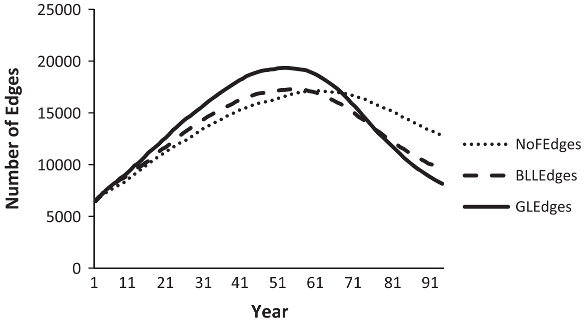

Fig. 4. The number of edges between occupied and empty cells differs in their transient dynamics between the no facilitation (NoF), baseline facilitation (BL), and the stress-gradient (GL) facilitation models, although the latter two are similar at the end of the iterations. Only the linear neighborhood intensity functions are shown.

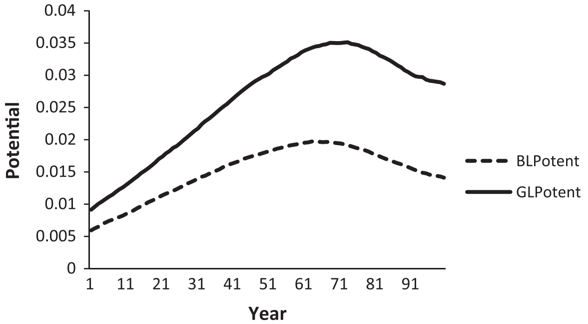

Fig. 5. The potentials (the sum of all facilitation in empty cells divided by the total number of empty cells) differ between the baseline facilitation (BL) model and the stress-gradient facilitation (GL) model. Only the linear neighborhood intensity functions are shown. With no facilitation there is no potential.

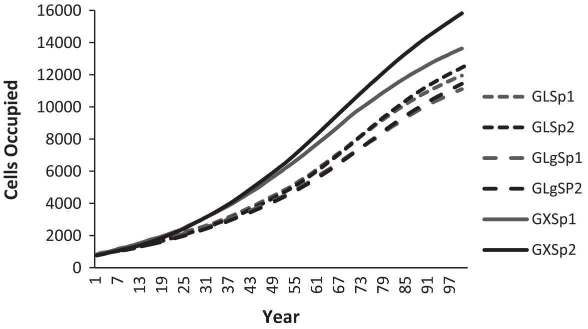

Fig. 6. The population dynamics of SP1 and SP2 differ among the linear (GL), logarithmic (GLog), and unimodal (GX) neighborhood functions of facilitation. Only the stress-gradient facilitation models are shown.

quality (SQ) and the numbers should decrease linearly (Fig. 7). This position declines as establishment success and survival are improved by the facilitation of the greater numbers in the higher quality area of the grid. The decline reverses when most of the lower grid is filled, and additional population growth occurs as the two species advance along the gradient, changing it through facilitation as they establish and grow.

Differences in edge density and in the potential created by facilitation are greatest for the unimodal expression, wherein edge density peaks earlier (Figs. 8 and 9). Although the difference in the number of edges is small, it results in large relative differences in potential facilitation and its effects. Examining the relationship between the potential for establishment and growth created by facilitation and their rates (as seen in the change in cells occupied), the effect of feedback in a spatially extended system is seen in the time lag between the creation of the potential and the peak rate of new cells being occupied by the species (Fig. 10). Although the potential could be fulfilled in the next iteration, because we include growth the population dynamics always depend on the past and potential that was created at any one time lasts until the cell is

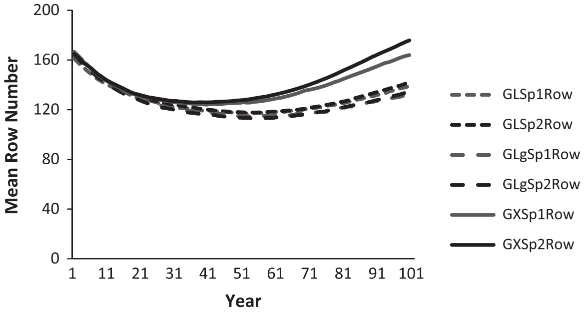

Fig. 7. The mean position of SP1 and SP2 along the gradient for the linear (GL), logarithmic (GLog), and unimodal (GX) neighborhood functions of facilitation. Only the stress-gradient facilitation models are shown.

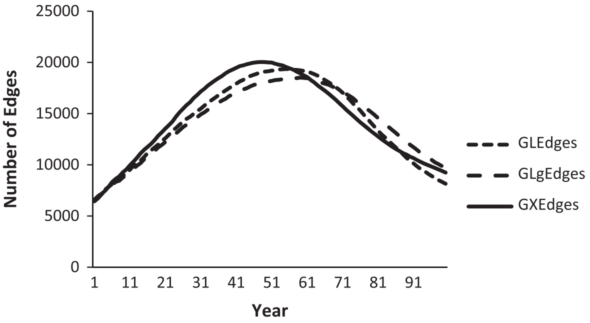

Fig. 8. The number of edges differs in transient dynamics among the linear (GL), logarithmic (GLog), and unimodal (GX) neighborhood functions of facilitation. Only the stress-gradient facilitation models are shown.

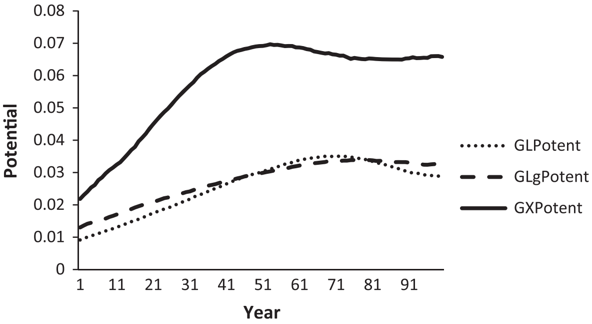

Fig. 9. The additional potential contributed by facilitation among the linear, logarithmic, and unimodal neighborhood functions of facilitation. Only the stress-gradient facilitation models are shown.

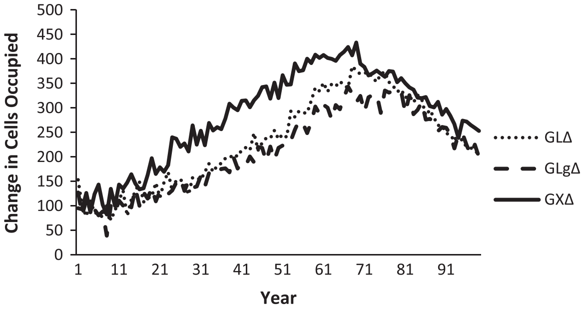

Fig. 10. The total net population (establishment and growth minus mortality) dynamics differ among the linear, logarithmic, and unimodal neighborhood functions of facilitation. Only the stress-gradient facilitation models are shown.

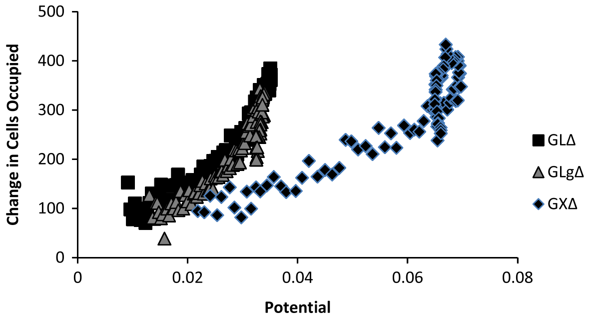

Fig. 11. The relationship between the total net population (establishment and growth minus mortality) and the potential (the sum of all facilitation in empty cells divided by the total number of empty cells) at each iteration differs among the linear, logarithmic, and unimodal neighborhood expressions of facilitation. Both increase through ~2/3 of the iterations, after which they decline – creating a loop for the unimodal neighborhood model. Only the stress-gradient facilitation models are shown.

occupied (or the individual/s that created it die). Biplots of new cell occupancy and facilitation potential show not only a correlation but also track the relationship through time (Fig. 11).

For most variables, the differences between the outcomes with or without the stress gradient and among the alternative intensity formulations are similar, but the combination of the stress gradient and unimodal formulations stands out. The spatial patterns created can be seen in visualizations of the grid at the last iteration of the simulations. The unimodal expression has distinct patches (Fig. 12).

4. Discussion

The results depend on the selection of the range of facilitation being 0–0.2 for the average neighborhood. Given that a reduction in the possible facilitation would approach the no-facilitation result, at some point of weak facilitation a stress gradient could not be detected as different from uniform facilitation. Inability to detect a difference could also occur if the range in which it matters, here in the range of site quality 0.25–0, was spatially compressed to fewer cells.

Other variants would be to change the mode of the unimodal function along the gradient or introduce thresholds (e.g., Xiao et al., 2009); such variations could affect the details but probably not the general results (cf. Zeng et al., 2007).

The models that represent the SGH not only produce results that differ in the dynamics of the two species, they also produce different spatial patterns. In all comparisons, the spatial patterns with the stress gradient produce more distinct large patches in the area of the gradient beyond the contiguous area occupied by SP1 and SP2. This effect is seen, in part, in the number of edges that exist at any time. Although this number is similar for all simulations at the end of the period because the dynamics are slowing as less area with higher site quality is available, the transient change indicates that the stress gradient condition allows more complex patterns to develop (in the linear and diatonic cases, earlier) than without facilitation as a function of stress.

Facilitation is a spatial feedback, and so the neighborhood expression of its effects will determine the spatial patterns that develop and dynamics such as the advance of species into new territory. Droz and Pekalski (2013) examined some of the consequences of spatial arrangement of individuals for competition and facilitation for light and water resources. In our three expressions, the linear effect with no stress gradient is least differentiated from the model with no facilitation. The populations of SP1 and SP2 and their mean position on the grid all increase from the linear, to logarithmic, to unimodal forms of neighborhood intensity. The linear form has relatively weak intensity until a cell is nearly surrounded by neighbors; this instance is probably rare because patches expand at their outer edges, and it would have less effect on the mean position of the population because it would never be at a leading edge. The difference between the logarithmic and unimodal forms indicates that the slightly increased intensity of the former for a single neighbor, which means that a single individual would affect its eight neighbors more strongly, is outweighed by the increased intensity for three and four neighbors in the latter expression. Although individuals establishing beyond the contiguous area occupied by SP1 and SP2 would seem to drive the spatial advance of the species along the gradient, it is the patches and irregular edges that create the more important instances of facilitation and so where feedback intensity is strongest with 3 or 4 neighbors, the dynamics are most differentiated.

Spatially explicit systems with feedbacks that propagate across space are the locus for our understanding of self-organized complexity (Levin, 2005; Meron, 2012). In our simulations, we do not see a gradual thinning of the population along the environmental gradient, just as we do not see such a gradual thinning at alpine or arctic treelines. Instead, the spatial feedbacks lead to the organization of patches, and the spatial characteristics of the patches – their edges and perforations – affect the dynamics of the populations. Where Martinez-Garcia et al. (2013) reported on nonlinear interactions over distance, we examine nonlinear interactions around a neighborhood, and both models produce what they term the "non-homogenous patterns characteristic of realistic situations" – for an ecotone. While the unimodal feedback increased patchiness, observed alpine treelines in the Rocky Mountains do not match this pattern closely, but there wind, which we did not model, creates elongated patches by adding direction to the intensity of feedback (Alftine and Malanson, 2004). Without an external driver, patches would develop more as our unimodal model indicates.

The particular imbalance in facilitation embodied in out model could also have more specific forms. We assumed that the establishment of Sp2 would be facilitated by neighbors of SP1 or Sp2, but Sp1 would not be so enhanced because its dispersal agent would not place seeds with such neighbors as often (as we assume that *N. columbiana* would not cache the seeds of *P. albicaulis* next to other trees as often, while the wind-dispersed *A. lasiocarpa* or *P. engelmannii* would be dropped there). The behavior of a seed-caching bird is more complex than our simulation captures, and where they cache seeds relative to seedlings, saplings, trees, or other environmental features could alter spatial outcomes.

The unbalanced facilitation would seem to give an advantage to Sp2 in our simulations, in which the number of seeds X establishment probability, and other population processes, are equal. The assumption that advantages are somehow balanced in C–S–R dimensions in order for coexistence at equilibrium (cf. Grime, 1979) may not apply far along a stress gradient (in a forest-tundra ecotone). Balanced coexistence might evolve for interactions in the more populous and extensive areas of less stress (lower on mountain slopes), but not be balanced at the margins. Populations in the ecotone are usually sinks, producing little viable seed, and not contributing to the evolution of the species or to strategies. Moreover, ecotones may be transient, with constant change as range boundaries spatially fluctuate with climatic change.

As Brooker et al. (2007) noted, biotic interactions will affect species responses to a changing climate, and the SGH will be important near species range limits as in ecotones (e.g., D'Odorico et al., 2013). While we do not change the climate (here, site quality) in this version of our model, wherein the spatial dynamics are driven by the species population processes and interactions, the way in which facilitation is expressed in a spatial neighborhood will affect any ecotone response to climate change.

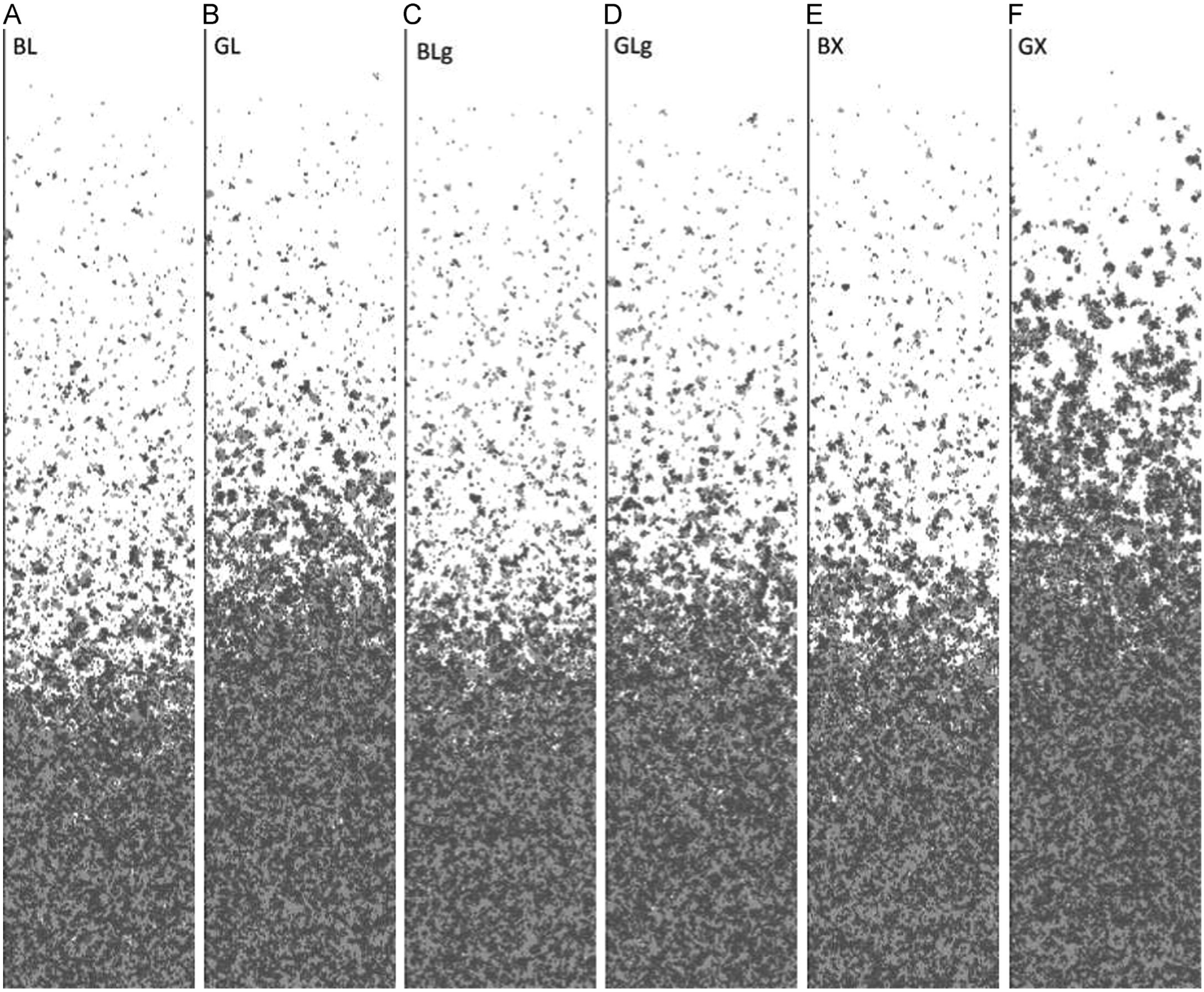

Fig. 12. Spatial realization of single runs of the models for control facilitation and stress-gradient facilitation (B vs G) and for the linear, logarithmic, and unimodal neighborhood functions of facilitation (L, Lg, X). Gray is SP1; black is SP2; tree icons (🌲) are original establishment; branch icons (🌿) are growth.

The spatial patterns are themselves of interest because they may be the best indicators of response to climate change (e.g., Allen and Walsh, 1996; Malanson et al., 2011) and the way in which facilitation on a stress gradient creates patterns can inform interpretation of change, as it occurs, and of its explanatory factors.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2014.10.005.

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