

2015

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.

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Diversity differs among three variations of the stress gradients hypothesis in two representations of niche space

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HIGHLIGHTS

- 3 modes of interaction for the stress gradient hypothesis (SGH) are simulated.
- Hierarchical and separated niche responses on environmental gradients are represented.
- Positive interactions increase coexistence through greater source-sink dynamics.
- SGH effects increase coexistence by the separation of facilitation and competition.
- Among the 3 SGH modes coexistence decreases variably with environmental change.

ARTICLE INFO

Article history:

Received 5 March 2015

Received in revised form

28 July 2015

Accepted 17 August 2015

Available online 29 August 2015

Key words:

Agent-based simulation

Climate change

Coexistence

Competition

Facilitation

ABSTRACT

How does the stress-gradient hypothesis affect coexistence in relation to established theory? For two orthogonal stress gradients, a spatially explicit agent based simulation is used to project diversity for simple competitive and facilitative interactions and for three variations of the stress-gradient hypothesis: intraspecific and interspecific competitive and facilitative interactions are a function of the abiotic environment; interactions are relative to species-specific fitness along gradients; or interaction is fixed by species regardless of the abiotic environment. Simulations are run with two orthogonal environmental gradients for two representations of niche. Facilitation can increase diversity by maintaining larger source populations and thus higher establishment rates and sink populations. With species hierarchically related in niche space, the simulations show that positive interactions and changing interactions along a stress gradient maintain greater diversity through intraspecific competition that is effective where dominance would occur and through facilitation where stress is high. A changing environment that favors some species and harms others decreases diversity in the hierarchical cases, where poor competitors most likely subject to interspecific interaction respond most strongly. Diversity outcomes differ among the three stress gradient variations because the intensity of interactions differs across the environmental gradients, not because of change in the environment.

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1. Introduction

Global change has ignited renewed interest in questions of the distribution and abundance of species, particularly of range limits (e.g., Henry et al., 2013; Tingley et al., 2014). For example, the development of mechanistic species distribution models aims to add process-based, rather than simply correlative, dimensions to widely used techniques (e.g., Merow et al., 2011). These approaches, however, still have a weak theoretical foundation in that they are primarily based on the realized niche with recent attempts to approximate a fundamental niche based on a single or few

dimensions or by adding additional, but still realized, niche dimensions. HilleRisLambers et al. (2012) have argued that more fundamental theory would improve the body of research on response to global change (cf. Adler et al., 2012). An area where theory has developed in relation to species distributions is work on the stress gradient hypothesis (SGH; He and Bertness, 2014) because global warming may change stress in marginal environments (e.g., Ohse et al., 2012) and responses will be affected by interactions (Brooker et al., 2007). My purpose is to examine how global change could affect species coexistence with differing conceptualizations of the stress gradient hypothesis and of the fundamental niche, aspects of species interactions and environmental constraints recently identified as needing further elucidation (Kraft et al., 2015). By unpacking the theory in simulations,

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potential outcomes can better be anticipated, or more rigorous hypotheses drawn for empirical testing, and species distribution models connected with theory (cf. [Godsoe et al., 2015](#)).

The SGH holds that the relative importance or intensity of individual and species competitive and facilitative effects vary inversely along environmental gradients of stress ([Bertness and Callaway, 1994](#)). The direct and indirect mechanistic interactions (e.g., shading, [Schweiger et al., 2015](#); nutrient availability, [Chen et al., 2015](#)) are qualitatively the same, but their effect on individuals varies with the abiotic environment. The hypothesis was developed further by [Brooker and Callaghan \(1998\)](#), [Maestre et al. \(2009\)](#), and [He et al. \(2013\)](#). The SGH may be linked to neighbor dependent selection ([Vasseur et al., 2011](#)) in maintaining diversity. The SGH has been described as a community effect ([Gross et al., 2010](#)), which probably applies best when plants affect the microclimate in similar ways, but it is possible that the change in interaction along a stress gradient differs individually for every species ([Lortie and Turkington, 2008](#); [Soliveres et al., 2011](#); [Cranston et al., 2012](#)) illustrated a cross-scale effect. Given that individuals influence the environment and others organisms in multiple ways (e.g., shade and wind, [Baumeister and Callaway, 2006](#); trophic effects, [Van der Putten, 2009](#); shade and water uptake, [Prevosto et al., 2012](#); see [Filazzola and Lortie, 2014](#) and [McIntire and Fajardo, 2014](#) for typologies), alternative stress gradient concepts are expected (cf. [Michalet et al., 2015a](#)), and extreme environments may overwhelm interactions ([Michalet et al., 2014a](#)).

Here I examine the SGH realized in three ways, which I call variations: environmental stress effects, species–individual stress effects, and fixed-species effects (“effects” because these are variations in the way the processes work). For environmental stress effects (ESE) the interactions among individuals depend on where they are on the stress gradient regardless of species identity or fitness, with the gradient from negative to positive interaction strength directly correlated with the environmental gradient; this approach is most similar to that of [Chen et al. \(2009\)](#) and [Droz and Pekalski \(2013\)](#). As simulated by [Malanson and Resler \(2015\)](#), different tree species on a mountain slope may be competitors or facilitators depending on the environment because they interact by modifying the microclimate (but even these interactions may be asymmetrical). For its second variation, the species–individual (SIE), the interaction strength would vary from positive to negative with its fitness along an environmental gradient. Thus each species would have individuals with more stress, i.e., those in an environment in which they are less fit, having facilitative interactions while those with less stress would be competitive. This variation is derived from the individual strain interpretation of the SGH ([Gross et al., 2010](#); [Soliveres and Maestre, 2014](#)), which is species specific but emphasizes effects on individuals. In the third variation, the fixed-species effect (FSE), the interactions depend on the species with some always competitive and others always facilitative and others in between; this approach follows [Travis et al. \(2005\)](#), and the result is seen as a stress gradient because the distribution of the species along the gradient is correlated with their interaction process and perhaps their functional traits ([Soliveres et al., 2015](#); [Zhang and Zhao, 2015](#)). [Soliveres et al. \(2011\)](#) argued that facilitation observed on stress gradients was a characteristic of individual species, not communities, but it applies at least to similar physiognomies (cf. [Gross et al., 2010](#)). For alpine environments studied in the SGH context (e.g., [Dvorsky et al., 2013](#)), cushion plants might always facilitate but their beneficiaries always compete; the interaction is completely asymmetrical. Overall, the model developed here is not specific to any system, but is guided by stress gradient work for mountain plants by [Callaway \(1998\)](#), [Choler et al. \(2001\)](#), and [Michalet et al. \(2014b\)](#)

and by observations of patterns at alpine treeline (e.g., [Resler et al., 2014](#)) and in alpine tundra ([Rose and Malanson, 2012](#)).

I examine altered diversity as the outcome of interactions on a stress gradient. While diversity has been discussed for such interactions ([Molofsky and Bever, 2002](#); [Michalet et al., 2006](#); [Gross, 2008](#); [Cavieres and Badano, 2009](#); [Cavieres et al., 2014](#); [McIntire and Fajardo, 2014](#); [Schöb et al., 2014a](#); [Soliveres et al., 2015](#)), more linkage to process is needed ([Soliveres and Maestre, 2014](#)); e.g., [Diaz-Sierra et al. \(2010\)](#) used a mechanistic model to examine conditions for coexistence with facilitation on environmental gradients. Given the gradient from competition to facilitation on an environmental gradient, expected outcomes might be greater coexistence where competition creates negative density dependence (a primary theoretical, biotic explanation for species coexistence; cf. [Adler et al., 2012](#)) as long as the negative effects do not cause extinctions, and sharper boundaries among species where facilitation creates a positive feedback switch (sensu [Wilson and Agnew, 1992](#)) (at least intra-physiognomic) but may allow coexistence at a different scale where allowing more existence increases diversity ([Schöb et al., 2014a](#)); additionally, interspecific positive interactions can be a form of negative density dependence ([Schöb et al., 2013](#)). These diversity effects are now beginning to be explored (e.g., [Schöb et al., 2014b](#)) given the impetus of climate change.

Diversity on environmental gradients will depend fundamentally on species adaptations to the environment and each other as developed in niche theory. While theory on species coexistence on environmental gradients extends back at least to [Gleason \(1926\)](#) and was more formalized by [Hutchinson \(1957\)](#) and [MacArthur, \(1972\)](#), *inter alia*, it has been revitalized by explicit development of thought on species interactions and coexistence (e.g., [Chesson, 2000](#); [Wilson, 2011](#)) and related critiques ([Siepielski and McPeck, 2010](#)). Here, two fundamental niche representations are taken from [Keddy \(1989\)](#). The [MacArthur \(1972\)](#), *inter alia* – derived representation has distributions with separate modes on a niche axis or environmental gradient ([Fig. 1A](#)). Following [Connell \(1980\)](#) and [Keddy \(1989\)](#) called this representation the “ghost of competition past.” His alternative hierarchical niche representation

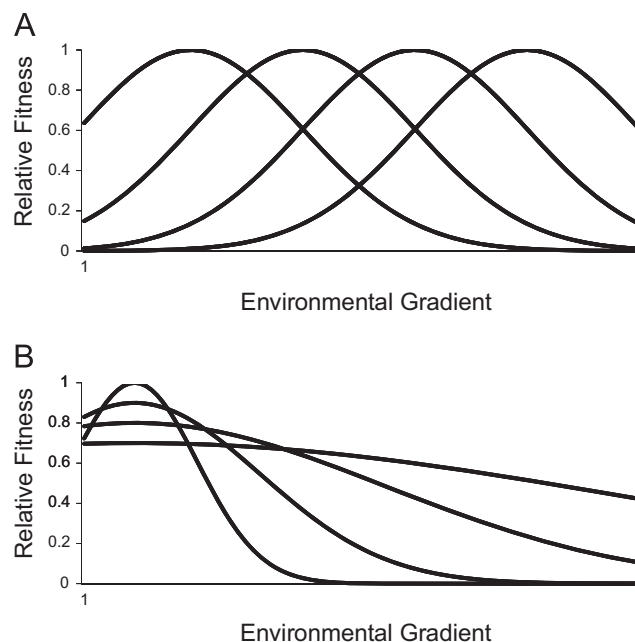


Fig. 1. Two representations of species in niche space: (A) Ghost and (B) hierarchical, after [Connell \(1980\)](#) and [Keddy \(1989\)](#). In the simulations, 16 species are represented on two orthogonal environmental gradients.

places the mode of fitness for all species at the high productivity or low stress end of the gradient, but with lower modes and broader distributions for species lower in the hierarchy (Fig. 1B). These two concepts are contrasted here as the ghost and hierarchical niche representations and capture existing adaptations to the environment and other species; earlier simulations with this contrast have shown differences in response times and in local coexistence (Malanson et al., 1992; Malanson, 1997).

Following, Section 2 develops the logic for the simulations, including the combinations of parameters and expected outcomes. Section 3 describes the simulation model with the relevant equations, and Section 4 presents the results in tables and figures. Section 5 discusses the results in terms of the differences in concepts of the stress gradient hypothesis in light of theory on species diversity.

2. Model rationale

The processes to be compared are competition, facilitation, and their combination in the SGH. These processes are implemented in an agent-based simulation on a spatially explicit framework so that individuals affect only their immediate neighbors (cf. Travis et al., 2005). The three possible expressions of the SGH are examined in two possible representations of niche space. To provide context, I also examine simulations with competition and facilitation only. I also add a change in environment to represent a kind of climate change; change in stress may affect the outcomes of interactions (Brooker et al., 2007; HilleRisLambers et al., 2013; Singer et al., 2013). I hypothesize that the species-specific version of the SGH will allow greater coexistence because every species will experience some degree of negative density dependence. Further, climate change that increases stress for some species while decreasing it for others should reduce coexistence in all three variations of stress gradient if it sharpens the transition between species experiencing competition vs. facilitation in the environmental stress gradient case or if it reduces existence per se of any species in any variation; a transient period of increasing coexistence may result from simple nonequilibrium between establishment and mortality.

The three variations of the SGH, environmental stress effects (ESE), species–individual effects (SIE), and fixed-species effects (FSE), are evaluated; the first two of these in both the ghost and hierarchical representations of the fundamental niche, and the third only for the hierarchical representation, on which it depends. For the ESE, with a given environmental/stress gradient from 0 to 1, the effect of neighbors is strongly competitive at the low stress end, nil in the middle, and strongly facilitative at the high stress end. For the SIE each species has the gradient from competitive to facilitative effect proportional to its fitness, as shown in Fig. 1. In the FSE, for the hierarchical niche representation only, each species has a fixed effect dependent on its position in the hierarchy, grading from fully competitive to nil to fully facilitative. For the five combinations of stress gradient hypothesis and niche representations, global change is added as a change in stress. The combinations are shown in Table 1.

As generally predicted by coexistence theory, I expect that negative interactions alone, i.e., competition, will result in higher coexistence, and positive interactions alone will result in the lowest coexistence (noting that the interactions are partly interspecific and partly intraspecific). Because all three variations of the stress gradient hypothesis have some degree of both negative and positive interactions, I expect that the resulting amount of coexistence will be between the two extremes. Furthermore, I expect that the effects of changing the climate will be similar between the ghost and hierarchical niche representations in the relative

Table 1

The combinations that were simulated of representations of niche, climate change, species interactions (with the three variations of the stress gradient hypothesis), and the codes used in figures.

Niche Representation	Climate Change	Interaction Variation	Code
	No	Negative	GNN
		Positive	GNP
		{ Environmental stress	GNESE
		Species–individual	GNSIE
Ghost	Yes	Fixed species	GNFSE
		Negative	GCN
		Positive	GCP
		{ Environmental stress	GCESE
	No	Species–individual	GCSIE
		Fixed species	GCFSE
		Negative	HNN
		Positive	HNP
	Yes	{ Environmental stress	HNESE
		Species–individual	HNSIE
		Fixed species	HNFSE
Hierarchy	Yes	Negative	HCN
		Positive	HCP
		{ Environmental stress	HCESE
		Species–individual	HCSIE
	No	Fixed species	HCFSE

changes in coexistence, and the change in climate per se should not change the order of coexistence among the variations of the stress gradient hypothesis. If these expectations are not met, the patterns should reveal particulars of how positive vs. negative interactions change with environmental variability.

3. Model development

A model was derived from the spatially explicit agent based simulation presented by Malanson and Resler (2015). Their basic grid had a single environmental gradient, two species, and the hierarchical niche representation to examine specific neighborhood effects of the stress gradient hypothesis; here I use the same approach but examine more basic theory in more dimensions, and to have a tool for easy visualization of the spatial patterns produced (cf. Jia et al., 2011). Additional information on the parameters is given in Table 2; subscripts used are: s, species; xy, grid coordinates.

3.1. Initiation

The environmental gradients and the species niche representations are developed on a 100×100 grid of cells. For the ghost niche cases, the environmental gradients run linearly 0–1 as rows or columns, both originating at (0,0) – the lower left corner of the grid. For the hierarchical niche cases the two gradients originate at (0,0) and (99,0): at the lower left and right corners of the grid. In both niche cases the environmental gradients are orthogonal; while this work is focused on theoretical relations, orthogonal gradients, such as for energy and water, could exist at various scales (e.g., latitude \times continentality). Interpretation of multiple niche axes is fraught (Trisos et al., 2014), but multiple gradients exist (Mod et al., 2014) and two orthogonal gradients are interpretable. The grid is not wrapped horizontally, as was that of Malanson and Resler (2015). An edge effect is created either way,

Table 2
Summary of the simulation model calculations.

Parameter	Value	Explanation
σ^2	400 for the Ghost representation; 250–32,000 for the 8 species in each hierarchy for the Hierarchical representation	Chosen so that all species coexist through the simulation runs without climate change
K	the condition that reproduction or growth cannot occur in cells with > 4 individuals	Based on Rose and Malanson (2012)
r	.0001 for the ghost case, varies .0001 to .0002 across the 8 species of the two groups in the hierarchical case (higher for less competitive species).	With 10,000 cells, $P=1$ Increases for species that cannot supersede others and with higher d
d	1 for the ghost case; the inverse of r for the hierarchical cases	Fit so that the probability of reproduction is balanced by the probability of mortality
N_s	Number of individuals of a species on the grid	Used with r as the basis for establishment

and wrapping would slightly increase the coexistence of species in a local neighborhood – the primary metric of this study.

Sixteen species niches are each represented for the ghost niche case by two dimensional Gaussian functions

$$S_{sxy} = e^{-(x-mx)^2/2\sigma^2 + (y-my)^2/2\sigma^2}$$

where for each species, x and y are the grid coordinates and mx and my are the coordinates of their modes, which are evenly spaced across the grid from 20,20 to 80,80; σ^2 is the variance, here 400. For the hierarchical niche, half of the 16 species have their modes near the origin points of the two environmental gradients ((10,10); (89,10)); these produce two orthogonal gradients with eight species on each (Sp1 – Sp8 and Sp9 – Sp16, respectively). The most competitive species has a height of 1 and a standard deviation of 10. Each successive species decreases in its height by 5% and increases in standard deviation geometrically; e.g., written out for species 1, 2, and 8

$$S_{1xy} = e^{-(x-10)^2/250 + (y-10)^2/250}$$

$$S_{2xy} = .95 e^{-(x-10)^2/500 + (y-10)^2/500}$$

$$S_{8xy} = .65 e^{-(x-89)^2/32000 + (y-89)^2/32000}$$

and repeated for Sp9–Sp16.

Initially, individuals of species are distributed on each cell with a probability equal to S_{sxy} so that these populations are overly abundant, but they adjust to an equilibrium quickly. Test runs on the grids as described produced 16 distinct patches in the ghost niche case and two patterns of distinct concentric rings grading away from the modes into indistinction in the hierarchical niche case. The simulation is run for 300 iterations, with 30 repetitions for each variation.

3.2. Processes

Equations for reproduction, growth, and death are given in terms of the probabilities, P , used in the Monte Carlo simulations, with competition–colonization tradeoffs. In both the ghost and the niche instantiations, species occupy cells in two ways, by ubiquitous dispersal across the grid and by growth into the eight adjacent cells.

3.2.1. Reproduction

Each cell (x,y) with fewer than 5 occupants (the condition K , a limit based on point observations by [Rose and Malanson \(2012\)](#)) has a probability of adding each species proportional to the number of extant individuals of the species on the grid (N_s) and the niche function for that species on that cell, including the effects of interactions

$$P(R_{sxy}|K) = rN_s Q_{sxy}$$

where the reproductive rate r is 0.0001 in the ghost niche case (i.e., all species disperse equally); in the hierarchical niche case the reproductive rate increases as competitive ability decreases (from 0.0001 to ~0.0002 across 8 species on each gradient), but less competitive species cannot establish on a cell already occupied by any more competitive species; Q_{sxy} is explained below as the niche function as modified by interactions and climate change. In the hierarchical case the order in which species are computed is from the highest to lowest reproductive rate, alternating between the two gradients, with the order of the gradients randomly chosen at each iteration. For the ghost niche representation, the order starts at opposite ends of the grid and randomly switches each iteration.

3.2.2. Growth

Individuals can expand into adjacent cells with fewer than 5 occupants. This probability is computed for each extant individual as proportional to the niche function plus interaction of that species on the target cell. In the hierarchical case species can grow only onto cells that are not occupied by any superior competitor.

$$P(G_s|K) = Q_{sxy}$$

The order of growth is the inverse of that used for reproduction and the switch is computed in the same way.

3.2.3. Mortality

Individuals die with probability proportional to their niche function for the cell they occupy in the ghost case.

$$P(D_s) = d/Q_{sxy}$$

where a mortality rate $d=1$. In the hierarchical case, species of higher competitive ability die at a lower rate, d =the inverse of their establishment rate.

3.2.4. Interactions

Interaction occurs locally. For competition or facilitation alone the species niche functions of each species for each cell are decremented or incremented proportional to the number of individuals, n on the cell and the surrounding eight cells, counting the numbers of the focal species, i.e., the conspecifics, as 1.5 in order to represent the greater intensity of intraspecific interaction (no precise relative numbers are common, but see [Forrester et al., 2011](#)). The spatial effects of positive and negative interactions are treated as equal, and a different approach would probably affect the results (cf. [Tewksbury and Lloyd, 2001](#); [Rietkerk et al., 2002](#); [Svejcar et al., 2015](#)). The value subtracted or added is a linear function ([Le Roux and McGeoch, 2010](#); [Malanson and Resler, 2015](#) have examined other shapes) set so that it would be 0.2 with 45 conspecific neighbors and 0.15 for 45 others (45 would be the maximum, 5, in each cell) (see [Fajardo and McIntire, 2011](#) for intraspecific facilitation)

$$I_{sxy} = 0.0022n + 0.05$$

where n is the number of neighbors counted. The value of 0.2 is chosen as a conservative estimate of the effects of interaction as 20% of the range of a possible niche function (cf. Hart and Marshall, 2013), and giving the first neighbor a larger effect with the positive intercept is intuitive.

3.2.5. Variation dependent interaction

I_{sxy} is multiplied so that it ranges from -0.2 to 0.2

$$Ev_{sxy} = I_{sxy} * Gv$$

where v is the variation in the SGH and Gv is the function of the environment (ESE variation), individual (SIE variation), or species (FSE variation). For ESE, the function varies linearly over the range of the environment computed in the initialization, with 0 at the midpoint of the environmental gradient

$$GESE = -1 + ((1 - (\sqrt{(x^2 + y^2)/d}))*2)$$

where d is 100 or 140 in the ghost and hierarchical representations, respectively, to relativize to the length of the environmental gradient (length or width of the grid in the former and diagonally across it in the latter).

For SIE, the neighbor effect is multiplied so that it ranges from -0.2 to 0.2 given the niche function of the species on that cell in the range, with 0 at $1/2$ of the species optimum niche function.

$$GISIE = -1 + ((1 - S_{sxy})*2)$$

For the third variation, FSE, the effect ranges from -0.2 to 0.2 for the eight species along each of the two hierarchies, with an increment of 0.05 between each species; e.g.:

$$GIFSE, Sp1 = -0.2$$

$$GIFSE, Sp16 = 0.2$$

For simple competition and facilitation, G is -1 or 1 , respectively. The interaction effect is relative to the environment, not a proportion of it, and so remains 'intensity' rather than "importance" as defined by Brooker et al. (2005) (cf. Welden and Slauson, 1986; Maestre et al., 2009).

3.2.6. Climate change

To include the effects of climate change, I change the niche functions of the species, as represented in Fig. 1 (climate change can be visualized as raising or lowering these representations) for both the ghost and hierarchical cases. Species relative fitness (S_{sxy}) increases or decreases up to 0.002 in each iteration during iterations 101–200 (up to 1.0 or down to 0.0 at the limit); they increase/decrease for $1/2$ the species so that the individuals experience climate change as advantageous or deleterious according to their position in the environmental space. In the ghost cases, the grid is halved, with the species in the upper half (Sp1–Sp8) experiencing the improved climate. For the hierarchical case the division is between the two gradients, with the computation

$$C_{xy} = .002 - .001 * \sqrt{(\text{column}^2 + \text{row}^2)/140}$$

where C_{xy} is a fraction added to the species in the first hierarchy (Sp1–Sp8, with the peak near the lower left of the grid) or subtracted from the other (Sp9–Sp16, with the peak near the lower right of the grid), with the relative fitness changing most at these corners (140 is the distance diagonally across the grid). For use in the Monte Carlo computations above, the competition and facilitation, the value calculated for each species on each cell is added (it may be negative), respectively, to its niche function

$$Q_{sxy} = S_{sxy} + E_{sxy} + C_{xy}$$

3.3. Metrics and caveats

Given the aim of exploring the effects on diversity, I derived a spatially explicit metric related to species richness: the average number of different species on each cell and its eight immediate neighbors, \bar{a} . This metric represents local coexistence. In addition to \bar{a} , I calculated Simpson's index ($1-\lambda$) to capture regional diversity at the full scale of the grid. Michalet et al. (2015b) showed that local processes of facilitation could affect regional diversity. I refer to \bar{a} and to Simpson's index specifically, and to diversity as a general result. I averaged each metric for the 30 replicated simulations. I did not test for statistical differences; White et al. (2014) have shown why tests would be inadvisable.

Test runs indicate that increasing the size of the grid, while increasing the standard deviation of the species niche function, produces quantitatively similar results. Changing the neighborhood for a produces qualitatively similar results in the range of 1–4 cell radii, but at larger extents (8 cell radii) dynamics are less and slower; extended radii would have coexistence approach total species richness. Edge effects exist on the simulation grid, but are insignificant in trials with the grid wrapped or not. In a completely different initialization of the grid, with the two environmental gradients distributed as the elevation and slope of fractally built hills on the grid, with variations in their number and smoothness, the results were quantitatively similar to those presented below.

4. Results

4.1. Equilibration

Because the grid is over populated by the initialization (so that the populations adjust to the environment and are not dictated by the initialization), the first 20–30 iterations are not meaningful as the populations equilibrate. After that, change is minimal and selected trials show steady levels through 10,000 iterations. Direct comparisons of the ghost and hierarchical niche representations are not warranted, but how the other factors differ within them can be compared between them.

4.2. Local coexistence and Simpson's index

4.2.1. Direct results

Without climate change, simple negative interactions, which include intraspecific negative density dependence in the feedback, result in higher \bar{a} than do positive interactions in the ghost niche representations, as expected, but this result is weakly reversed in the hierarchical representation and (for Simpson's index this reverse is found weakly in both representations) (Tables 3 and 4). For \bar{a} , the outcomes for the first and second SGH variations, the environmental stress effect and the species–individual stress effect, are greater than those of the simple competition or facilitation scenarios; \bar{a} for the fixed-species effect is between the simple scenarios. Among the three variations on the SGH, the species–individual effect \bar{a} is notably higher in the ghost niche representation but not so for the hierarchical representation. The fixed-species case has the lowest \bar{a} of the three. The results are similar for Simpson's index, showing some correspondence between the two scales.

4.2.2. Results between interactions

The local \bar{a} and regional Simpson's index for the stress gradient cases are not between those of purely negative and positive interactions in both the ghost and hierarchical cases, as might be

Table 3

Mean (standard deviation) of the local coexistence measure (\bar{a}) at the end of 301 iterations across 30 replicated simulation runs for the two representations of niche and the simple and stress gradient variations on interactions – as defined in the text.

Climate	Interaction	Ghost	Hierarchy
No	Competition	1.610(0.019)	3.313(0.077)
No	Facilitation	1.108(0.016)	3.686(0.026)
No	Environmental	1.623(0.021)	3.828(0.059)
No	Species–individual	2.323(0.024)	3.737(0.048)
No	Fixed-species	na	3.567(0.040)
Yes	Competition	1.392(0.019)	2.430(0.023)
Yes	Facilitation	1.561(0.021)	2.841(0.021)
Yes	Environmental	1.440(0.017)	2.910(0.026)
Yes	Species–individual	3.257(0.182)	2.613(0.099)
Yes	Fixed-species	na	2.109(0.014)

Table 4

Mean (standard deviation) of Simpson's index ($1-\lambda$) at the end of 301 iterations across 30 replicated simulation runs for the two representations of niche and the simple and stress gradient variations on interactions – as defined in the text.

Climate	Interaction	Niche Representation	
Change	Variation	Ghost	Hierarchy
No	Competition	0.930(0.000)	0.778(0.005)
No	Facilitation	0.934(0.000)	0.790(0.004)
No	Environmental	0.933(0.000)	0.801(0.003)
No	Species–individual	0.921(0.000)	0.785(0.003)
No	Fixed-species	na	0.778(0.004)
Yes	Competition	0.892(0.001)	0.678(0.001)
Yes	Facilitation	0.900(0.000)	0.716(0.003)
Yes	Environmental	0.909(0.001)	0.704(0.002)
Yes	Species–specific	0.883(0.001)	0.677(0.003)
Yes	Fixed-species	na	0.646(0.001)

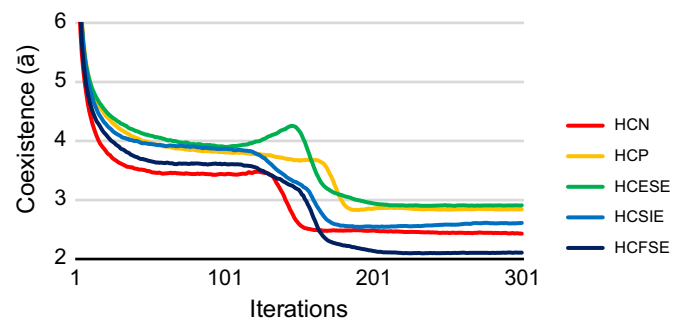


Fig. 2. Trajectories of coexistence among the five scenarios of species interactions: negative (N, competition), positive (P, facilitation), environmental stress effects (ESE), species–individual effects (SIE), and fixed-species effects (FSE) on the hierarchical representation of niche and with climate change (HC). The differences of the stress gradient concepts are explained in the text.

expected for processes that mix the two. The fixed stress gradient case differs markedly from the others. It has lower local and regional effects than the others because the less competitive species therein always have the strongest facilitation. With climate change the pattern is similar among the variations. The effect of climate change per se is to increase \bar{a} for the ghost niche representations for all interactions except simple competition. For the hierarchical representation, climate change decreases \bar{a} in all cases.

4.2.3. Transient dynamics

The trajectories reveal differences in the timing of the response to climate change, with a notable delay for the simple facilitation case, and an initial positive response for the ESE variation (Fig. 2). Simpson's index shown a muted, qualitatively similar pattern, but

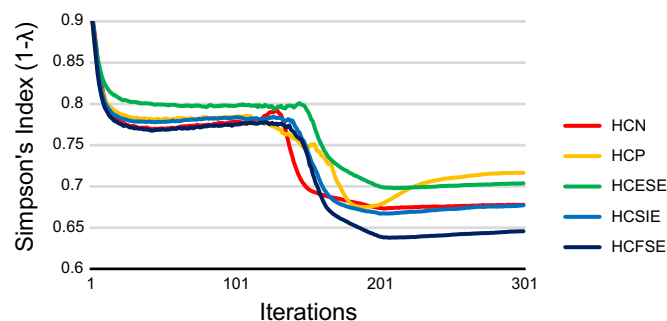


Fig. 3. Trajectories of Simpson's index ($1-\lambda$) among the five scenarios of species interactions: negative (N, competition), positive (P, facilitation), environmental stress effects (ESE), species–individual effects (SIE), and fixed-species effects (FSE) on the hierarchical representation of niche and with climate change (HC). The differences of the stress gradient concepts are explained in the text.

with a more distinct rebound in the simple facilitation case beginning near the end of the period of climate change (Fig. 3). In all cases a short lag in response to climate change is seen because most of the populations are by then in areas with a combination of environment and neighbors that is not marginal (their realized niche), and this lag is longest in the simple facilitation case because the realized niches are reinforced for all in this case. Coexistence increases briefly in the ESE case because climate change allows establishment, and thus expansion, of species for which it is advantageous before those for which it is deleterious start to respond. This process occurs because overall coexistence is higher and species have more individuals in a wider range of the environment.

4.3. Spatial patterns

Visualization can help interpret these results. Fig. 4 shows the pattern of \bar{a} mapped for each cell at year 100 (which remains effectively unchanged if climate does not change) and at year 200, at the end of the period of climate change, for the simple negative and positive interactions and both niche representations. Trivially, the patterns differ between the ghost and hierarchical niche representations as expected. The ghost niche representations show how facilitation leads to the development of the 16 areas dominated by each species with the highest areas of \bar{a} between them in contrast to a greater mix of species for competitive interactions that include negative density dependence. Climate change disrupts the pattern, with the core areas starting to appear for species that experience an improving climate for negative interactions and increasing for positive interactions for the species with improving climate. For the species with deteriorating climate, \bar{a} decreases near the edges with negative interactions because of declining populations, while with positive interactions the climatic change leads to a breakdown of dominance and thus greater coexistence.

4.4. Exemplar species

For the SGH variations the breakdown and increase are more widespread (Fig. 5). For the hierarchical niche representations, concentric rings develop with the highest \bar{a} where all species have their optimum fitness. With climate change, the favored species on the left increase so that the core becomes more diverse while their expansion into the areas formerly dominated by the group to the left leaves this area with lower \bar{a} as some of those species become extinct. Among the SGH variations this effect is greatest for the fixed-species effect.

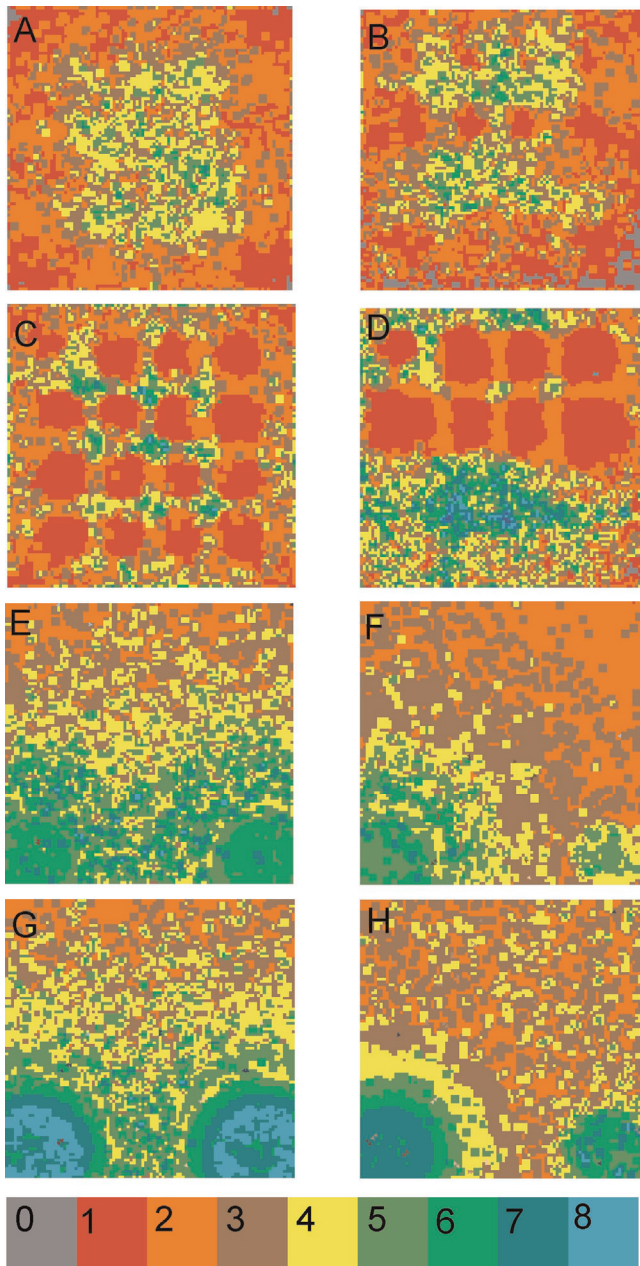


Fig. 4. Contrast in the pattern of local coexistence (a) on the simulation grid for the ghost (A–D) and hierarchical (E–H) niche representations before (left) and after (right) climate change for the simple negative (A and B, E and F) and positive (C and D, G and H) interactions.

Part of the development of pattern is the decrease in coexistence in the areas of the grid away from the zones of peak fitness. This decrease is caused by the loss of the poor competitors in the group for which climate change is deleterious, which are replaced by those from the other group. I examine some of these more informative exemplars. In the group for which climate change is advantageous, the two weakest competitors (Sp7–Sp8) increase their populations (Fig. 6), but Sp7 starts with a small population and is able to increase 4–5 fold in the stress gradient variations. Sp8 has less room for change and less difference in response to interaction. The change for these two species indicate that the interaction conditions, with Sp7 bracketed by other species in niche space, have a greater effect on responses than does the environment directly.

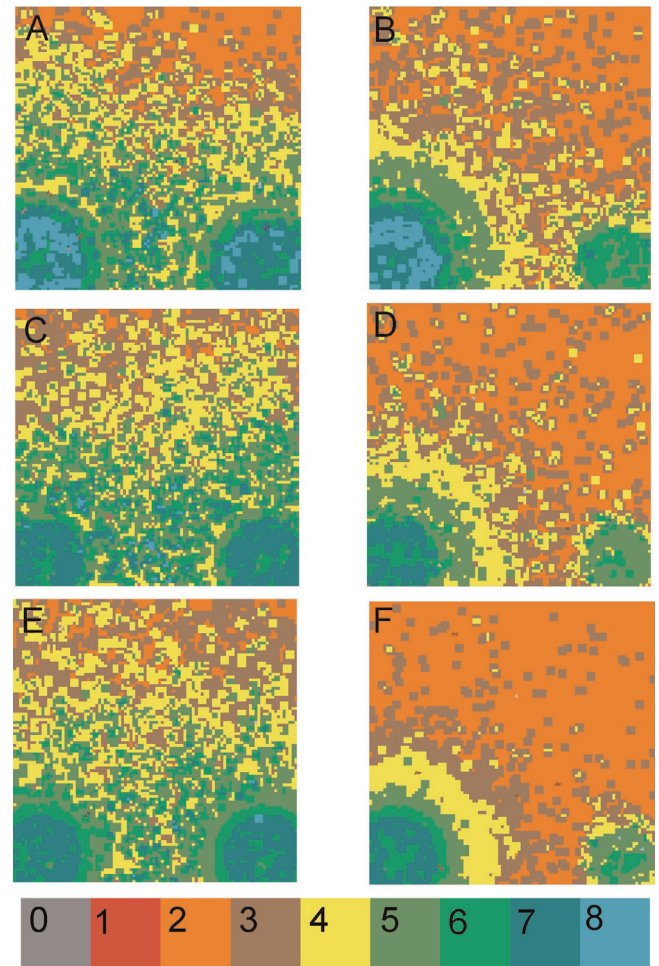


Fig. 5. The pattern of local coexistence (a) on the simulation grid for the hierarchical niche representations and the three stress gradient variations, environmental (ESE; A and B), species–individual (SIE; C and D), and fixed-species (FSE; E and F) before (left) and after (right) climate change.

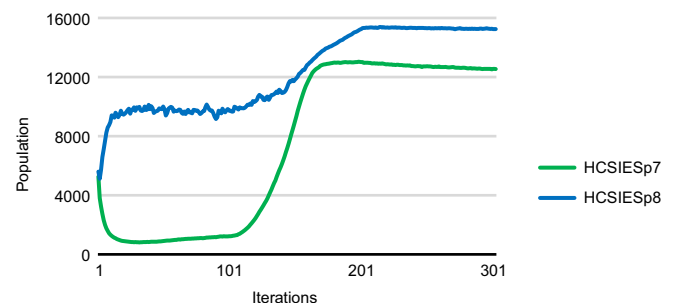


Fig. 6. Trajectories for the populations of Sp7 and Sp8, the two weakest competitors in the hierarchy that experiences an improving climate, with the species–individual variation (SIE) of the SGH.

5. Discussion

Although facilitation can decrease local coexistence and regional diversity relative to negative density dependence for species with different niche optima in environmental space, as expected, it can increase local coexistence when those optima are hierarchically arranged at points. Further increases are found when facilitation and competition both occur along an environmental, or stress, gradient, and differences in outcomes and transient dynamics are seen depending on how the interactions are conceived. As with many simulations, in hindsight some results are

not surprising, but the explication in a model highlights where new thinking or observation will advance ecology. The similar general outcomes for both local coexistence and regional diversity support the findings of [Michalet et al. \(2015b\)](#) linking local processes of interaction with regional diversity patterns. The lesson of the simulation results is that the variations in how the switch in interactions occurs will make a difference in diversity outcomes, and these in turn differ somewhat between how species are adapted to each other and the environment. Among the three variations of the SGH, without climate change the species-individual effects variation has higher diversity than that of environmental stress effects because negative density dependence acts where competitive exclusion is otherwise most likely while facilitation maintains interacting populations where a species might otherwise not persist.

With climate change, the variation of environmental stress effects results in higher diversity because the more marginal populations supported by facilitation adjusted to the species individually or to those that have facilitation just where it is most needed (those that have realized niches in the high stress areas) suffer the greater populations losses. In the ghost niche representation, because species have less overlap on the grid by design the environmental change allows broader niches with more overlap for the species that experience an improving environment while having little effect on those with the opposite environmental change. This response is reduced to the point where α is lower with simple competition, which minimizes niche expansion. In the hierarchical representation, wherein most of the species experiencing environmental improvement have contact with most of the others, α decreases as one group of populations increase while the other decreases, some to extinction. Being well adapted to a particular environment supports diversity with facilitation until the environment changes.

The more specific differences – that diversity increases briefly in the HCP and HCESE simulations – indicate that with simple effects of non-specific facilitation species are able to establish in new areas faster than competition eliminates them in others as their niche shifts across the grid. The difference in the HCFSE case where the pre-climate change diversity is highest and then the decline in α is delayed relative to the others indicates that this variation produces species that have broader realized niches.

The divergence from expectations leads to three questions:

- How can facilitation lead to lower coexistence in the ghost niche cases but to higher coexistence in the hierarchical niche cases?
- Why does climate change, as simulated, lead to lower coexistence, with abrupt drops in the change period, in the hierarchical stress gradient cases?
- What is important about the differences among the three stress gradient variations?

The ghost cases have many cells where the pairs of species have close to the same niche function levels; for the interior species, at least four and perhaps eight neighbors interact in cells where the response level is high enough for persistence. In these areas negative interactions lead to lower Q_{sxy} values for these cells and thus lower temporary persistence: new individuals that might be short lived but frequently replaced are fewer. Conversely, positive interactions maintain higher levels of these transient individuals. In the hierarchical cases, there are fewer zones of cells that have similar niche values for so many species, as seen in the visualizations. A reason for this result differing from what has been thought in the past is the use of two orthogonal gradients instead of one.

[Schöb et al. \(2014b\)](#) have made a case for facilitation leading to lower fitness for the benefactor. In these simulations, a benefactor

could be harmed by the beneficiaries only through scramble competition. The limit on the number of individuals on a cell means that increasing the probability for any species could then exclude another. However, because the primary beneficiary of facilitation is always a conspecific individual the difference is not within cells but among cells. Local coexistence is calculated for a window of nine cells, and facilitation that creates sharp boundaries can still promote it at this scale by allowing persistence of transient individuals.

The effects of climate change differ between the ghost and hierarchical representations of niche. Coexistence decreases in the latter because the change leads to extinctions that do not occur in the former, where each species has a habitat of peak fitness without a superior competitor. In the hierarchical representations, the species lower in the hierarchies (Sp6–Sp8 and Sp14–Sp16) occupy extensive areas on the grid but with low fitness. When for one hierarchy their reproduction decreases and mortality increases with climate change (Sp14–Sp16), they initially lose individuals and then become extinct. It is the interaction with other species that determines outcomes because the least competitive species is able to maintain a population longer in the low quality environment where it has no competition while its superior competitor goes extinct, even with facilitation, because it is squeezed between two other species. Among variations, the response is most different for the second lowest ranked species. In the hierarchy for which climate improves, Sp7 has different lags in response and an overall greater difference in outcomes with climate change because the change loosens allows more stochastic population increase via scramble competition.

These differences in the transient dynamics among the variations indicate new interactions on the grid. In the environmental case, the initial change in the environment upsets the equilibrium that had been developing and allows a re-mixing of species and thus higher coexistence. In the species-specific variation the change affects all species and so coexistence decreases as some populations decline but there is a slight gain as a new equilibrium is reached. The fixed stress gradient variation allows more coexistence before climate change when the species all coexist across the grid, as determined by the initial conditions (a modeling artifact, but one that implements the assumption that extant species have an extant niche), but with climate change the decrease in coexistence is more severe because all populations of the impacted gradient (Sp9–Sp16) decline as negative interactions are added to the decreasing environmental quality for the competitively dominant species. These simulation results emphasize the relative importance of species interactions in the response to climate change and support the calls for greater attention to theory in this area (i.e., [Adler et al., 2012](#); [HilleRisLambers et al., 2013](#)).

[Wilson \(2011\)](#) identified 12 mechanisms for species coexistence; he classified these into 3 groups: the doubtful, the important, and the unexplored. Here, the important mechanism of alpha-niche differentiation plays a role in the initial conditions of the ghost and hierarchical niche representations. The other three important mechanisms, environmental fluctuation, pest pressure, and spatially explicit allogenic disturbance are not included. The results of simulations here illustrate a mix of what Wilson called “unexplored” mechanisms: interference/dispersal trade-off, spatial mass effect, and aggregation or spatial inertia.

For the ghost niche representation without climate change, Wilson's “important mechanism” of alpha-niche differentiation maintains greater coexistence with negative density dependence because the niches are more clearly ordered and positive feedbacks reinforce spatial divisions. Conversely, negative density dependence blurs otherwise sharper boundaries and allows more coexistence.

Unexpected results in the hierarchical niche representation, with greater coexistence with positive than negative feedback,

occur because the positive effects of species on the environment and their neighbors allow continued persistence in areas of low fitness. This result illustrated the three mechanisms because higher overall dispersal across the grid from extant populations is maintained when overall fitness is indirectly increased by facilitation. A source-to-sink process supports the spatial mass effect maintaining coexistence through numbers of individuals on cells where they have a low probability of persistence (i.e., fugitive coexistence, sensu [Hanski and Zhang, 1986](#)); and the spatial inertia mechanism acts as the positive feedback maintains populations that exclude potential competitors that cannot replace them.

These effects persist until climate change. The negative density dependence is strongest in part of the environmental gradient with high fitness for all species and where otherwise competitive dominance would reduce coexistence, while it is weak where the competitive species have lower fitness. With climate change the reduction in coexistence differs among the variations of the stress gradient hypothesis with their mix of competition and facilitation relative to the change. The fixed-species variation has the greatest reduction because the species with facilitation become extinct in the areas where it had been effective.

These simulations focus on the balance of competitive and facilitative interaction across environmental gradients. The outcomes indicate differences in diversity that results from the particular variations of the processes along gradients defined by the abiotic environment, the species fitness, and combination of the two. While the simulations address abstract environmental gradients, these results can initiate a reconsideration of expectations for general ecological responses to environmental change, and may inform incipient efforts to address the evolution of traits involved in interactions, such as facilitation, at the extremes of a species distribution (cf. [Bronstein, 2009](#); [Soliveres et al., 2015](#)). They also demonstrate that a better theoretical framework is needed to guide efforts to monitor or mitigate the ecological effects of climate change.

Acknowledgments

This research was supported by the US National Science Foundation, award 1121305. This material is based upon work while serving at the National Science Foundation; any opinion, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://doi:10.1016/j.jtbi.2015.08.012>.

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