



Diversity differs among three variations of the stress gradient 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.

Published by Elsevier Ltd.

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 individualistically 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

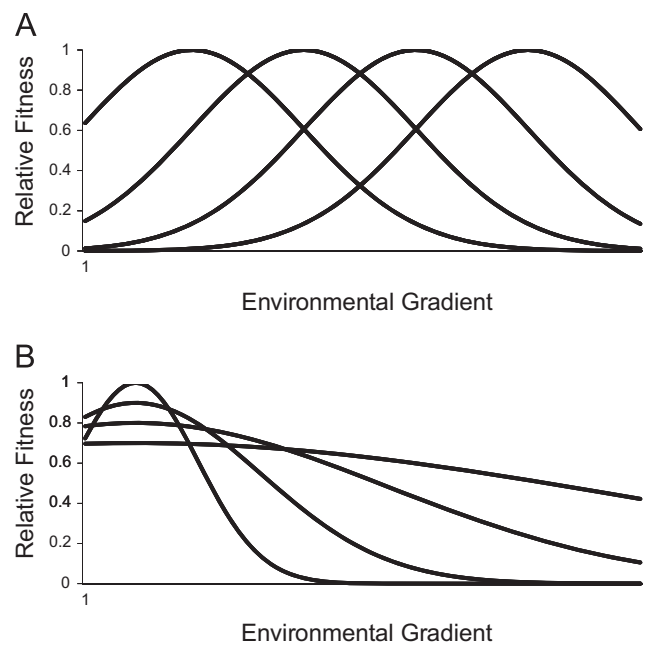


Fig. 1. Two representations of species in niche space: (A) Ghost and (B) hierarchical, after [Connell \(1980\)](#) and [Keddy \(1989\)](#). In the simulations, 16 species are represented on two orthogonal environmental gradients.

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