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Spatial patterns provide support for the stress-gradient hypothesis over a range-wide aridity gradient

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ABSTRACT

We examined variations in the relative importance of facilitation vs. competition, in light of the Stress-Gradient Hypothesis (SGH) by assessing plant interactions along an aridity gradient over biogeographic scales. We surveyed the relationship between a shrub species (*Artemisia tridentata*) and pine seedlings (*Pinus monophylla*) across the Great Basin and the Mojave Desert, USA, encompassing the entire range of *P. monophylla*. Using 69 sites we evaluated the spatial association between *P. monophylla* seedlings and *A. tridentata* shrubs, quantified with an electivity index, and implemented multiple regression analysis on the effects of macro- and micro-environmental factors: precipitation, temperature, monsoonality index, topography, substrate and litter cover. We identified annual precipitation as a main factor, which was negatively related to shrub-seedling association. Additionally, shrub-seedling association was stronger in the hot- than in the cold-desert, and was negatively related to litter cover. Effects of monsoonality, summer temperature, and bedrock type were not significant. We also considered nonlinear functional forms of a precipitation–electivity relationship, but the negative linear model proved most predictive. Our observations match SGH predictions. Studying the role of interspecific interactions in shaping species range shifts may lead to improved predictions of distribution ranges and changes in dryland vegetation under global change scenarios.

1. Introduction

Facilitation in natural plant communities has been characterized as an important but under-developed topic of study (Brooker and Callaway, 2009; Brooker et al., 2008; Bruno et al., 2003). Research over the past decade has shown that the ecological role of facilitation can vary along gradients of resource availability and abiotic stress (Holmgren and Scheffer, 2010; Lortie and Callaway, 2006; Maestre et al., 2006, 2009; Michalet, 2006). The stress-gradient hypothesis (SGH) is a widely supported unifying paradigm (He et al., 2013) which suggests that the importance of interplant positive interactions (i.e., facilitation) increases along gradients of increasing abiotic stress and, correspondingly, the importance of negative interactions (i.e., competition) decreases (Bertness and Callaway, 1994). Accordingly, one would expect to find evidence of the SGH by observing the net balance between competitive and facilitative interactions over a species' range. This is because the biogeographic ranges of species usually lie along environmental gradients, and their boundaries are often influenced by abiotic stress (Normand et al., 2009) and competitive interactions (Sexton et al., 2009). Given that stress gradients at the scale of a species' range are often strongly linked to climate, the use of the SGH may be extended from discussion of patterns of interspecific interactions to predictive models of species distribution in the context of climate change. Thus, the SGH is inherently a question of biogeographic scope. However to date only few studies have addressed the SGH over extensive portions of a focal species' range (Armas et al., 2011; Cavieres et al., 2006; Dohn et al., 2012; Schöb et al., 2013; Soliveres et al., 2011). For this reason there is a need to critically examine the SGH over broader spatial scales, and the present study attempted to fill this gap. In contrast to previous studies, which are mainly based on an experimental approach of examining plant interactions through controlled manipulations (Armas and Pugnaire, 2005; Callaway et al., 2002; Chambers, 2001; Gómez-Aparicio et al., 2005; Maestre and Cortina, 2004), or alternatively observational approaches comparing different species in

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different systems (Holzapfel et al., 2006; Kikvidze et al., 2005, 2011), we aimed to detect plant interactions between two focal species, *in situ*, with the goal of describing the functional form of the variation of inter-specific plant interactions along abiotic stress gradients, over a biogeographic scale.

Whereas the SGH generally predicts a positive linear relationship between abiotic stress level and the relative importance of facilitation, Maestre and Cortina (2004) as well as Michalet (2006) proposed that under certain circumstances nonlinear relationships, such as unimodal or asymptotic ones might be expected. Michalet (2006) and Maestre et al. (2009) further hypothesized that the functional form of the relative importance of facilitation might not only depend on the stress level, but rather might also depend on multiple additional factors, including the nature of the stress factors, the life history of the target species and ontogenetic stage.

We conducted our study in a water-limited system by assessing the pair-wise relationship between mature shrubs and tree seedlings across the entire geographic range of the tree species. We carried out an extensive field study of the single-leaf pinyon pine (*Pinus monophylla* Torr. and Frém.) as a model species, focusing on the importance of facilitation during its early establishment phase. *P. monophylla* has already been characterized as relying on facilitation for early establishment (Chambers, 2001; Chambers et al., 1999), and it co-occurs throughout its range with its facilitating shrub, the polymorphic species *Artemisia tridentata* Nutt. (sagebrush) (Durant McArthur and Welch, 1982).

Our approach used the level of spatial association between young *P. monophylla* seedlings and mature *A. tridentata* as a surrogate for the relative importance of facilitation (Callaway et al., 1996; Greenlee and Callaway, 1996). We expected that the most fundamental abiotic stress gradient within the geographic range of *P. monophylla* would be that of water availability, which constitutes the main limiting factor for seedling establishment (Chambers, 2001). Accordingly, we projected that water-related environmental factors such as precipitation and temperature regimes would influence the nature of the inter-specific interaction. We tested two alternative hypotheses: (1) that in accordance with the SGH the spatial association between *P. monophylla* and mature *A. tridentata* would increase consistently with increasing water stress, which would indicate the relative importance of facilitation over the entire species range; and (2) that the increasing relative importance of facilitation with increasing water stress would be limited to only a fraction of the water-stress gradient within the species range. In the latter case, asymptotic or unimodal relationship patterns might emerge, corresponding to patterns proposed by Maestre and Cortina (2004).

2. Methods

2.1. Target species

P. monophylla Torr. and Frém. is a long-lived tree species distributed in the U.S. Intermountain West, from southern Idaho to Baja California (Farjon and Styles, 1997; Little, 1971; Fig. 1). Its seeds are dispersed by seed-caching rodents and birds, which cache seeds under and near shrubs, as well as in intershrub open spaces with no clear microsite preference (Vander Wall, 1997). Previous work reported that *P. monophylla* seedlings are more likely to establish under shrub canopies than in intershrub open spaces (Chambers, 2001).

A. tridentata is a widely distributed shrub that occurs throughout most of western North America, from British Columbia to Baja California. It is highly drought resistant, growing in regions with annual rainfall as little as 160 mm (Kolb and Sperry, 1999). It constitutes a major understory component in *P. monophylla* woodlands (West et al., 1978) and has been documented as the primary *P. monophylla* nurse shrub species (Callaway et al., 1996; Chambers, 2001).

2.2. Study area

Our study encompassed the entire distribution range of *P. monophylla* within the semi-arid Intermountain region of the United States (Fig. 1). *P. monophylla* woodland landscapes are typically patchy mosaics of trees, shrubs and bare interspaces, a vegetation formation that is typical of many semi-arid ecosystems (Webster and Maestre, 2004). These woodlands are usually poor in annual species and geophytes, with a shrub dominated understory.

The climatic conditions within the geographic range of *P. monophylla* are highly varied. Annual precipitation ranges from 200 to 700 mm (PRISM, 2010) and varies with both latitude and elevation. The temporal distribution and form of precipitation are also highly variable: most precipitation occurs as snow in the winter season, especially in the western part of the range, with increasing frequency of monsoonal rains towards the eastern part (Adams and Comrie, 1997). Bedrock types are diverse and include plutonic, metamorphic and also various sedimentary rock formations.

2.3. Field survey structure

We designed the field survey to quantify the spatial association between *P. monophylla* seedlings and mature *A. tridentata* shrubs over a broad range of environmental conditions. We designated survey sites by using stratified random sampling throughout the geographic range of the *P. monophylla*. We divided its distribution area (Little, 1971) into three yearly precipitation levels: 250–350 mm, 351–500 mm, and 501–650 mm, and three regions: eastern Central Great Basin, western Central Great Basin (east-west division through the geographical center of Nevada), and Mojave Desert. This allowed us to obtain an equal representation of all parts of the *P. monophylla* range. A total of 69 spatially random survey sites were visited (Fig. 1). In cases where a randomly computer-generated site was inaccessible or lacked any pine recruitment we used the closest suitable location. At each site we randomly selected a reference point and marked the 25 young seedlings closest to the reference point. We laid out a square plot around the selected group of seedlings and therefore the plot size varied according to seedling density. The 69 plots ranged in area from 80 to 155 m^2, with a mean plot area of 105 m^2. We included only established seedlings with distinct juvenile characteristics (glaucous color, short needles) in the survey, and excluded seedlings that lacked these characteristics and those that had recently germinated and lacked bark and branches.

2.4. Site data

We characterized each study site by using the following spatially extrapolated climate variables, obtained from PRISM (PRISM Group, 2010), and used them to form climatic gradients: (1) annual precipitation, to form a gradient of aridity; (2) minimum January temperature, to form a gradient of extreme low temperature; and, (3) maximum July temperature, to form a gradient of extreme high temperature. Additional information relevant to each plot included: (1) bedrock type from Ludington et al. (2005), classified to bedrock types: calcareous and non-calcareous, a property which noticeably affects nutrient availability (Larcher, 2003), (2) "monsoonality index", calculated as the proportion of annual precipitation occurring from July through September (Romme et al., 2009); (3) "topographic position index" (TPI), calculated as the relative