Lupinus breweri is competitive, not facilitative, in a subalpine habitat

Zachary M. Devereux¹, Elyse A. Fitzsimons², Brittney Martinez³, Maya Nagaraj⁴

¹University of California, Los Angeles; ²University of California, Berkeley; ³University of California, Irvine; ⁴University of California, Davis

ABSTRACT

The direction and strength of species interactions within communities often depend on environmental conditions. Interactions in plant communities can be influenced by additional factors, like symbiotic rhizobia, which can cause their host plants to have imbalanced impacts on other community members. We studied the effects of a nitrogen fixing legume, Lupinus breweri, on community productivity and richness in a semi-arid sagebrush steppe habitat in the White Mountains, CA. We found that species richness was greater in plots containing lupines. Additionally, percent vegetative cover tended to be higher and plants were larger in the absence of lupines. This suggests that Lupinus breweri engages in more competitive than facilitative interactions in this habitat despite the relatively high environmental stress level. Our study considers lupines on the community level, demonstrating the complexity of interactions that is not reflected in otherwise similar pairwise studies.

Keywords: competition, facilitation, environmental stress, Lupinus, subalpine

INTRODUCTION

The spectrum of species interactions ranges from competition, which decreases the fitness of both sides, through facilitation, which increases one player’s fitness, to mutualism, which benefits both species involved. The direction and strength of interactions can vary due to differences in abiotic stressors: negative interactions like competition often occur when environmental stress is low, while facilitation and other positive interactions occur when environmental stress is high (Callaway and Walker 1997, Callaway et al. 2002). Interactions within the same species pairs or communities can change due to spatial variation across environmental gradients and temporal variation between and within seasons (Callaway 1998, Kikvidze et al. 2006, Pugnaire and Luque 2001).

Plant interactions are particularly interesting because community composition and environmental factors vary across individual species’ ranges, altering the types of interactions in which they are involved (Soliveres and Maestre 2014, Brooker and Callaghan 1998). In addition, plant community interactions can involve
belowground associations with root symbionts like mycorrhizae and rhizobia. Mycorrhizae, symbiotic associations between fungi and plant roots, can be mutualistic, commensal, or parasitic to the plant host depending on soil nutrient levels (Johnson et al. 1997). Mycorrhizal fungi increase their host’s ability to absorb limited resources like phosphorus in exchange for photosynthate. However, the fungi may become parasitic if soil phosphate levels are high (Koide and Elliott 1989). Rhizobia, a group of root-infecting bacteria including those in the genus *Rhizobium*, range from mutualistic to parasitic as well. Some rhizobia convert atmospheric nitrogen into molecules that their hosts can use in exchange for photosynthate, while others fix little or no nitrogen but still take carbon products from their hosts (Denison and Kiers 2004).

Most rhizobia are mutualistic, including the bacteria that form nodules on the roots of lupines and other legumes (Stewart 1967). Due to their associations with rhizobia, lupines can grow in nitrogen-limited soils and even increase local nitrogen levels (del Moral and Bliss 1993, Morris and Wood 1989). Because they increase available nitrogen, they also have the potential to facilitate other plant species. Lupines primarily increase local nitrogen levels through deposition of nitrogen-rich leaf litter (Palaniappan et al. 1979). Although lupines drop leaves throughout their lives, they release much greater quantities of fixed nitrogen after senescence and during decomposition, and dead lupines may encourage more recruitment than live lupines (del Moral and Bliss 1993, Maron and Connors 1996). Thus, living and especially dead lupines can aid the growth of other plants by fertilizing surrounding soil.

While lupines can facilitate other species, they are also strong competitors that can inhibit neighbor productivity and recruitment (Morris and Wood 1989, Goergen and Chambers 2012). Because of this combination of negative and positive effects as well as the variation in responses between different neighbor species, it can be difficult to predict the net effect of lupines on the entire surrounding plant community. Indeed, most studies on facilitation and inhibition by lupines have focused on how they affect only a few species instead of overall community health and richness. However, species interactions rarely occur between isolated pairs of species, but occur more often within complex communities that cannot be disentangled (Soliveres and Maestre 2014). Studying interaction on a community-wide scale instead of between individual species can increase our understanding of how communities are structured and how changes in diversity could impact the entire system. (Brooker et al. 2008, Soliveres and Maestre 2014).

In this study, we focused on the community-level effects of a subalpine lupine species, *Lupinus breweri* (Brewer’s lupine). We examined the impact of *Lupinus breweri* on productivity of dominant functional groups in the community as well as the richness and productivity of all neighboring species, using plant height and vegetative percent cover as proxies. We also compared neighboring plants associated with living and dead lupines, expecting dead lupines to be more facilitative than live. We hypothesized that in a stressful subalpine habitat neighbor productivity and species richness would be higher in the presence of *Lupinus breweri*. Furthermore, we
hypothesized that dead lupines would have a greater positive effect than living lupines on neighbor productivity and richness.

METHODS

2.1 Site Description

Research was conducted at the University of California Natural Reserve System’s White Mountain Research Center from August 1 through 5, 2018. WMRC is located in the White Mountains, east of Bishop, Inyo County, California. The White Mountains are characterized by a cold, semi-arid climate and are dominated primarily by subalpine forests, montane woodlands, and sagebrush steppes, with over 1,000 native plant species.

2.2 Study Species

Our study focused on *Lupinus breweri* (hereafter *L. breweri*), a perennial mat-forming lupine with a deep taproot found in the sagebrush steppe of the White Mountains. It is native to subalpine and alpine habitats on the west coast of the United States. In the White Mountains, *L. breweri* occurs on granitic soil types in open, sunny sagebrush steppe habitats.

2.3 Experimental Design

In order to examine the extent of facilitation or competition between *L. breweri* and its surrounding plant species, we conducted an observational study surveying *L. breweri* at four different study areas. The study areas spanned an elevational gradient of 3084 m to 3205 m and consisted primarily of granitic substrate. Each area was located in sagebrush steppe habitat, although there was some variation in vegetative composition among areas. At each of the four areas, we surveyed five to six different sites. Each site was composed of three plots: a live lupine plot, a dead lupine plot, and a null plot without lupine. Dead lupines had between 40 to 95% tissue death. All three plots in a site were within a short distance of each other. At each area, we randomly selected a starting point, found and surveyed the nearest site, and then randomly selected the subsequent four to five sites.

To assess the effect of *L. breweri* state (live, dead, or null) on surrounding plant species richness and productivity, we took a series of measurements within a circular quadrat with a 0.5 m radius. In null plots, we used the circular quadrat to measure plant percent cover. In live and dead lupine plots, we began by measuring the average diameter of the lupine and only included plots with lupine between 30 to 50 cm in diameter. We then centered the same quadrat on the lupine to measure plant percent cover of the species surrounding the lupine. Finally, to determine the effect of lupine on plant productivity and species richness, we identified all species in the quadrat and haphazardly measured the height of three individuals of each species. If three or fewer individuals of a given species were present, we measured the height of all individuals in the quadrat.

2.4 Statistical Analysis

All statistical analyses were conducted with JMP Pro statistical software v14. We used ANOVAs to test the effect of *L. breweri* state on four responses: plant species richness, neighboring plant percent cover,
and average height of two dominant functional groups, graminoids (grasses, rushes, and sedges) and sagebrush shrubs (Artemisia spp.). In all analyses, site was treated as a random effect. To eliminate bias in percent cover comparisons between lupine and null plots, we removed the lupine from our initial measure with the following formula for corrected percent cover:

\[
\frac{(\text{total plant area} - \text{lupine area})}{(\text{total quadrat area} - \text{lupine area})} \times 100
\]

(where total plant area is defined as quadrat area x measured percent cover).

RESULTS

We surveyed a total of 22 sites with live, dead, and null plots. Plant species richness was greater in live lupine plots than in null plots (N = 22, F = 4.66, P = 0.01; Figure 1). Plant percent cover was marginally lower in plots with live and dead lupine than in null plots (N = 22, F = 2.86, P = 0.07; Figure 2). Graminoids were tallest in null plots (N = 22, F = 4.23, P = 0.02; Figure 3). Artemisia spp. height was not affected by lupine presence (N = 22, F = 0.44, P = 0.64; Figure 4).

Figure 1. Effect of Lupinus breweri on plant species richness. Plant species richness was greatest in plots surrounding a live lupine and lowest in null plots. Plots contained either a lupine with fully alive tissue, a lupine with ≥40% dead or dying tissue, or no lupine. Bars not connected by the same letter are significantly different. Vertical lines represent ±1 SE.

Figure 2. Effect of Lupinus breweri on plant percent cover. Plant percent cover was marginally higher in null plots than in plots with lupine (P = 0.07). Percent cover was determined using a circular quadrat with a 0.5 m radius. Plots contained either a lupine with fully alive tissue, a lupine with ≥40% dead or dying tissue, or no lupine. Vertical lines represent ±1 SE.
Figure 3. Effect of *Lupinus breweri* on average height of graminoids. Graminoid refers to all grasses, rushes, and sedges found in plots. Graminoids were tallest in null plots and shortest in plots with dead lupine. Plots contained either a lupine with fully alive tissue, a lupine with ≥40% dead or dying tissue, or no lupine. Bars not connected by the same letter are significantly different. Vertical lines represent ±1 SE.

Figure 4. Effect of *Lupinus breweri* on average height of *Artemisia* spp. There was no difference in *Artemisia* spp. height among plots with and without lupine. Plots contained either a lupine with fully alive tissue, a lupine with ≥40% dead or dying tissue, or no lupine. Bars not connected by the same letter are significantly different. Vertical lines represent ±1 SE.

**DISCUSSION**

Given that *L. breweri* is a nitrogen fixing plant, we expected it to improve soil nutrients and have a positive effect on its neighbors in this stressful, nutrient-limited subalpine environment. Contrary to our hypotheses, *L. breweri* did not appear to facilitate growth of surrounding plant species. Although species richness was higher in live lupine plots than null plots, in the context of our other results, this indicates that lupines prevent species from becoming competitively dominant. If *L. breweri* were truly facilitating, one would expect a few species to monopolize the resources provided and grow larger. Instead, we found that species richness was higher and plants were smaller in plots with lupine. Additionally, dead lupines did not have a more positive effect on neighboring plants than live lupines and in some instances seemed to negatively impact neighbors. Therefore, in the abiotic environmental conditions of our study, *L. breweri* appears to be competing with rather than facilitating other plant species.

Other studies have found mixed positive and negative effects of lupines on neighbors. Morris and Wood (1989) discovered that *Lupinus lepidus* (Pacific lupine) reduced recruitment of two perennials during primary succession, but increased the productivity of plants once established. *Lupinus argenteus* (silvery lupine) had varying effects on seedling establishment, survival, and productivity depending on the seedling species and levels of abiotic stress (Goergen and Chambers 2012). On the other hand, we primarily found negative impacts of *L. breweri* on neighboring plants, highlighting its capacity to act as a
competitor rather than facilitator in the abiotic conditions of our study. Perhaps *L. breweri* does not fix enough nitrogen to fertilize the surrounding soil; when we examined the roots of a subsample of *L. breweri* plants, we found limited rhizobial nodulation.

Previous work has shown that dead lupines typically increase usable soil nitrogen by an order of magnitude compared to null plots and provide shelter for significantly more recruitment than live lupines (del Moral and Bliss 1993, Maron 1996). Our results did not indicate that dead lupines provide greater soil benefit to neighbors than live lupines and, as with graminoids, may negatively impact surrounding plants. Given that we did not ourselves kill the dead lupines, we cannot be sure what caused mortality. In Maron and Connor’s (1996) experiment, lupines were killed by the researchers to ensure the surrounding plants were not affected by the instrument of mortality. Thus, in our system it is possible that the cause of lupine mortality was negatively impacting surrounding plant species in the microhabitat, to the extent that it overwhelmed the nitrogen input benefit of the dying lupine tissue. In del Moral and Bliss’ (1993) study, the lupines were completely dead and were no longer potential competitors. We had no completely dead lupines and the living part of the lupine could have been consuming the nutrients from dead tissue. Potentially after more time and complete death of the lupine, we would have found benefits for the neighboring plants.

Our study was confined to a small spatial and temporal scale and nonetheless yielded relevant findings. To provide further context for the stress gradient hypothesis, future studies on the community-level effects of lupines could examine varying levels of environmental stress (Bertness and Callaway 1994, Callaway and Walker 1997). This type of study could test whether lupine interactions become more positive with increasing environmental stress by sampling a greater elevation range or among different soil types. Community responses to changing stress levels could also be examined in manipulation experiments, such as fertilizer additions or lupine removals. Furthermore, if *L. breweri* fixes nitrogen at low rates relative to other lupine species, this study could be repeated in lupine species with more rhizobial nodulation to show whether facilitative interactions increase with greater nitrogen fixing proficiency.

Our findings provide information about community dynamics without the controversy associated with inferring community-level interactions from pairwise data (Soliveres and Maestre 2014). In contrast with most pairwise studies, we did not find any positive effects of *L. breweri* on its neighboring plant species. Because of our unexpected results regarding the role of a lupine in its habitat, we hope our study encourages further research into the effects of nitrogen fixing plants at the community level.

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REFERENCES


SUPPLEMENTARY FIGURES

Figure S1. Live lupine plots.

Figure S2. Dead lupine plots.

Figure S3. Null plots.