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Ubiquitous germination among common perennial species in response to facilitated and unfacilitated microhabitats

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ABSTRACT

We present results from a study that examines species-specific facilitation of germination in an arid perennial community. This system suffered 64% adult mortality and the local extinction of two common species as a consequence of drought that occurred between 1999 and 2004. *Ambrosia dumosa*, *Larrea tridentata*, and *Tetracoccus hallii* are included as candidate benefactor species based on their high abundance and broad distribution at the study site. Using complementary field and greenhouse experiments, we measured the effects of facilitation, light and nitrogen on germination of four species common to the region, *L. tridentata*, *A. dumosa*, *Sphaeralcea ambigua* and *Eriogonum fasciculatum*.

Our results show that benefactor species do not uniquely influence germination. Species-specific effects among beneficiaries largely explained differences in percent germination in the field, and the interaction between beneficiary species and microhabitat was significant for only one species. *E. fasciculatum* consistently showed significantly higher germination than more abundant species and showed reduced germination in the interspace. In the greenhouse, germination responses differed at each light level, beneficiaries responding most uniquely at full light. These results refine expectations from previous studies of facilitation at this site by showing that facilitation does not strongly enhance germination.

1. Introduction

Chronic drought in the US Southwest has caused high mortality of woody species in many arid and semiarid plant communities (Bowers, 2005; Hamerlynck and McAuliffe, 2008; Miriti et al., 2007). One consequence of this mortality is a reduction in the number of benefactors, which are plants that provide safe-sites for early establishment. Benefactors provide increased moisture and nutrients, (Flores and Jurado, 2003; Schlesinger and Pilmanis, 1998; Schlesinger et al., 1996) and decreased light intensity (Franco and Nobel, 1988) that enhance early survival and growth of beneficiary species. Interactions between benefactors and beneficiaries are dynamic and influenced by environmental conditions (Yu et al., 2009; Seifan et al., 2010; Luzuriaga et al., 2012). Benefactors may compete with seedlings for below-ground resources (e.g. Walker et al., 2001; Schenk and Mahall 2002) or reduce light availability for establishing seedlings (Seifan et al., 2010). The relationship between environmental severity and frequency or relevance of facilitation is an active, but as yet unresolved area of ecological research (see Soliveres et al., 2015 for a recent review). For arid species that rely on facilitated establishment (Flores and Jurado, 2003), benefactor loss may threaten or preclude novel recruitment (McAuliffe and Hamerlynck, 2010; Tiedemann and Klemmedson, 1986). This threat is exacerbated if mortality is biased towards species that facilitate a large number of beneficiary species.

Benefactor species identity can influence patterns of recruitment among beneficiary species. Species-level variation influences the reliance of beneficiaries on benefactors (Castro and Gómez, 2002; Padilla and Pugnaire, 2009), and the patterns of mortality among beneficiary species (Callaway, 1998; de la Cruz et al., 2008; Miriti et al., 2007, 1998; Padilla and Pugnaire, 2009). The effectiveness of facilitation can vary with the canopy architecture of benefactors, which affects microhabitats through litter trapping and moisture directed to the understory through stem flow (De Soyza et al., 1997; Tromble, 1988), or heterogeneity of soil resources under benefactor canopies, which determines small-scale distributions of beneficiary establishment (López-Pintor et al.,

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2003) and survival (Castro and Gómez, 2002; Walker et al., 2001). The relative importance of species-specific variation becomes apparent when multiple benefactor species are examined.

In deserts, where adaptations for long-range or directed dispersal are rare (Ellner and Shmida, 1981), the spatial distribution of benefactors can limit the efficacy of facilitation as a driver of biodiversity. Seeds must arrive at suitable host sites suggesting that species abundance and distribution affects the likelihood that a given species plays a benefactor role (Yoshihara et al., 2010). Similarly, because the responses of seeds and seedlings to individual adult species influence seedling performance, the distribution and abundance of benefactors can determine the rate of recovery and species composition of a community after a disturbance event. Studies that examine benefactor roles are commonly targeted to species that have significant and apparently positive associations with juveniles of one or many species (e.g. Schlesinger et al., 1996; Schenk and Mahall 2002). Species that are not recognized as benefactors may not necessarily lack sufficient resources to support germination and early survival, but dispersal to those canopies is limited. Drought mortality imposes changes in the distribution of potential benefactors and increases the importance of understanding variation in the ability of different species to facilitate juvenile establishment. Also, the quality of facilitation among survivors may be reduced in response to reduced canopy volume and litter inputs. Disparities among common benefactor species will influence species composition during drought recovery.

We measure species variation in facilitation in a post-drought community in the Colorado Desert in southeastern California using field and greenhouse experiments. Between 1999 and 2004, this region experienced exceptional drought conditions (Breshears et al., 2005), resulting in 64% adult shrub mortality (Miriti, 2007). Subsequent reestablishment of species has been slow to nonexistent such that no seedlings have been documented since 2004 (*personal observation*, *Miriti lab*) even after years of above average precipitation (2005, 2010–2011 http://www.epa.gov/climatechange). Although one common species, *Ambrosia dumosa*, is a strong candidate to be a generalist benefactor (*sensu* Verdú and Valiente-Banuet, 2008) due to persistent positive associations with species common at this site (see Miriti et al., 1998; Miriti, 2007), species-specific variation in the ability to provide or benefit from facilitation has not been experimentally examined. If common species are not equally able to facilitate establishment, such unprecedented mortality may disrupt facilitation networks (Verdú and Valiente-Banuet, 2008) and compromise community recovery to pre-drought composition. Drought conditions are projected to increase (Overpeck and Udall, 2010), which could have adverse impacts on community regeneration. Although precipitation is a driving factor of species dynamics in arid systems, dense or intermediate shading by benefactors can ameliorate the effects of drought for establishing seedlings (Carvajal et al., 2014), which increases the importance of benefactors during drought intervals.

To anticipate recovery of this shrub community, we compare the abilities of the three most abundant species, *A. dumosa*, *Larrea tridentata*, and *Tetracoccus hallii*, to facilitate seed germination compared to unvegetated sites. Facilitation studies typically focus on seedling recruitment and survival (see Bonanomi et al., 2011 for a recent review), but we focus on germination because this stage is most sensitive to levels of environmental gradients (Parish and Bazzaz, 1985). Further, persistence of long-lived plants in arid communities is considered to be less dependent on novel germination and largely dependent on persistence of reproductives, thereby reducing the relative importance of recruitment to maintain extant populations (Wiegand et al., 2004). As such, the population-level significance of seed banks is not well-studied for perennials (but see Cao et al., 2014). As a result, it is important to consider that the absence of a perennial seed bank may make perennial species more susceptible to local extinction after disturbance that causes extensive adult mortality. Taken together, examination of the pattern of seed germination in response to facilitation can enhance understanding of the mechanism of persistence in arid perennial communities.

Four species once common to this site prior to the extended drought, *A. dumosa*, *L. tridentata*, *Sphaeralcea ambigua* and *Eriogonum fasciculatum* are used as beneficiary species. These species experienced 2%–100% local mortality during the drought (Miriti et al., 2007). The aims of the current study were 1) to determine species-specific effects of benefactors or their absence on germination, and 2) to determine the influences of light and nitrogen levels associated with the focal benefactor species on germination. Shade and nitrogen are consistent mechanisms of facilitation (see Bonanomi et al., 2011 for a recent review). The results of these experiments are interpreted in light of patterns of species abundance and spatial associations accumulated from more than 20 years of census data collected at the field site (Miriti et al., 1998, 2007; Wright and Howe, 1987). Benefactors that significantly improve early establishment can be managed to enhance recovery of this disturbed plant community.

2. Methods

2.1. Study site

The study site is located in Joshua Tree National Park, CA, near the transition zone between the Mojave and Sonoran Deserts (33°44′50″ N, 115°48′38″ W; elevation 955 m), approximately 1 km west of a 1 ha plot that has been monitored in five year intervals for over 20 years (Miriti et al., 2007, 1998; Wright and Howe, 1987). Plants characteristic of this desert scrub community include *A. dumosa*, *E. fasciculatum*, *L. tridentata*, *Simmondsia chinensis*, *S. ambigua* and *T. hallii* along with cacti, *Opuntia echinocarpa* and *Opuntia ramosissima* and intermittent distributions of the succulent plant, *Yucca schidigera* (Miriti et al., 1998). Soils at this site are characterized as 62.4% sand, 29.8% gravel, 7.8% clay (Wright and Howe, 1987).

At the Twentynine Palms weather station, located 103 km from the study site, the average annual temperature was 21 °C and average annual precipitation totaled 62.3 mm from 2009 to 2012 (National Climatic Data Center). In this region, the largest pulse of rain occurs during the winter, although summer monsoonal rains may occur during July–August. Perennial germination typically occurs in the spring following winter precipitation.

2.2. Benefactor species

Benefactor species were chosen based on their abundance and broad local distribution. *L. tridentata* (D.C.) Coville (creosotebush) and *A. dumosa* (A. Gray) Payne (white bursage) are common among low elevation plant communities throughout US southwestern deserts. In contrast, *T. hallii* Brandegee (Hall's shrubby-spurge) is endemic and rarely found outside of California. The relative abundance of these species at the study site is *A. dumosa* 63%, *T. hallii* 13% and *L. tridentata* 4%. *A. dumosa*, *T. hallii* and *L. tridentata* adults experienced 68%, 58%, and 2% drought mortality, respectively (Miriti et al., 2007). Each of these species presents contrasting canopy morphology and associations with juveniles at the study site.

A. dumosa is drought-deciduous with a low-lying canopy, and reaches heights of 60–90 cm. Several native perennial species show significant positive spatial association with *A. dumosa* at the long-