



Shrub-annual facilitation complexes mediate insect community structure in arid environments



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ARTICLE INFO

Article history:

Received 20 October 2015

Received in revised form

31 May 2016

Accepted 16 June 2016

Keywords:

Facilitation

Indirect interactions

Insect

Larrea tridentata

Mojave desert

Pollinator

ABSTRACT

In dryland systems, shrubs often increase the productivity, abundance, and diversity of understory plants, however these positive interactions can also scale to other trophic levels. The facilitative effect of *Larrea tridentata* was hypothesized to extend beyond plants to the local insect community in the Mojave Desert. Pan traps were placed under shrubs and in open microsites to test the following predictions: 1) shrub-annual facilitation complexes increase insect abundance, richness, and diversity; and 2) specific insect families or functional groups respond to the shrub-annual facilitation complex more strongly due to increased resources. Abundance, richness, and diversity of the insect communities associated with shrubs were significantly greater in shrub compared to open microsites. The families Sphecidae, Formicidae, Bradynobaenidae and Lauxaniidae were positively associated with shrubs while Scarabaeidae was associated with open microsites. However, there was no difference in the relative abundances of major functional groups, suggesting that the primary pollinators for this ecosystem are not sensitive to differences in floral resources at this scale. This study demonstrates that shrubs facilitate local insect communities and supports the hypothesis that plant-plant facilitation can extend to other trophic levels. Management of desert shrubs is thus an effective means to enhance many components of insect biodiversity.

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1. Introduction

Positive interactions between shrubs and understory plants have important impacts on plant communities. Well established evidence demonstrates that the frequency of positive plant interactions is relatively common and that these positive effects have important implications for community dynamics (Michalet et al., 2014). However, there are also many important research gaps and opportunities within this field, such as decoupling the specific mechanisms of facilitation by shrubs (Filazzola and Lortie, 2014), identifying direct versus indirect interactions (Michalet et al., 2015; Sotomayor and Lortie, 2015), and exploring the importance of positive interactions to other trophic levels or groups of species (Schleuning et al., 2015). It has been proposed that multiple trophic levels can be tightly coupled and supported by abundant, generalist plant species, including many species of shrubs (Verdú and Valiente-Banuet, 2008). In arid areas, shrubs can frequently act as

benefactors to other plant species through many mechanisms including ameliorating abiotic stress by providing things such as shade and shelter from wind, increasing access to water and other resources, and providing protection from herbivores (Pugnaire et al., 2011). Many shrub species have been shown to increase understory plant abundance and diversity and shrubs can also collectively maintain ecosystem function within a region (Pugnaire et al., 2011). Consequently, shrubs can act as foundation species by maintaining biodiversity and preventing extinctions within the community matrix (Verdú and Valiente-Banuet, 2008).

Insects and pollinators are also important participants in community dynamics including the maintenance of ecosystem services. The positive effects of benefactor plants can extend to specific insect and pollinator communities (e.g. cushion plants, see: Molina-Montenegro et al., 2006; Molenda et al., 2012) linking different sets of species integral to ecosystem function. For instance, benefactor plants can increase pollination rates for beneficiary plants, increasing their reproductive output (Feldman et al., 2004; Sieber et al., 2011). These plants and their beneficiary species may facilitate insects directly by providing food resources and ameliorating harsh abiotic conditions, or indirectly by providing access to

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resources through the facilitation of the beneficiary plant community. To date, these relationships have been studied predominantly using cushion plants in alpine environments (Molina-Montenegro et al., 2006; Molenda et al., 2012). Facilitation by shrubs in particular is frequent in other high-stress ecosystems such as deserts (Pugnaire et al., 2011; He et al., 2013), but the connection between benefactor shrubs, the facilitation of insects, and/or the pollination of the understory plants has not been investigated. The study of this shrub-annual facilitation complex—whereby the combined resources and protection offered by the benefactor shrub and the beneficiary plants in the understory attracts insects such as pollinators—is a novel and unstudied concept that is likely important to many desert ecosystems. Thus, it is important to resolve whether the facilitation patterns commonly detected between benefactor plants and their beneficiaries, also positively influences local insect and pollinator communities.

Here, we examined the hypothesis that plant facilitation by the desert shrub species, *Larrea tridentata*, positively influences the insect community by ameliorating abiotic conditions (e.g. high temperatures) and increasing resource availability (e.g. vegetative resources). The following predictions were tested in the Mojave Desert for the proposed facilitation pathway: (i) *L. tridentata* and its associated annual plants increase insect relative abundance, richness, and diversity, and (ii) The response by the insect community to the *L. tridentata* shrub-annual facilitation complex is family and functional group specific. Pollinators should respond most strongly due to increased understory annual plant densities (a proxy for floral resources) in shrub microsites. In summary, we explore the idea that *L. tridentata* can provide islands of resources for insects, including pollinators, in desert ecosystems.

2. Methods

2.1. Shrub species

Larrea tridentata (Zygophyllaceae), commonly known as creosote bush, is a drought-tolerant evergreen shrub species that is one of the most widely distributed plants found in arid areas of the southwestern United States such as the Mojave Desert. *L. tridentata* has been recognized for its ability to facilitate the surrounding annual plant community through various mechanisms (e.g. Suzán et al., 1994; Whitford et al., 1997), despite its intraspecific allelopathic effects. It has bright yellow flowers (<2.5 cm diameter) that bloom between April and May (Porter, 2014), and is predominantly animal pollinated with strong ties to many insect and pollinator communities (Minckley et al., 1999, 2000). More than 120 species of bees (Hurd and Linsley, 1975; Minckley et al., 1999, 2000) have been documented on *L. tridentata*, the second highest species richness recorded of any plant globally after sunflower (*Helianthus annuus*) (Hurd et al., 1980). It is presumed that these insects are using *L. tridentata* for its abundant floral resources though the relative effect of these shrubs on the insect community of understory vegetation has not been contrasted. Thus, *L. tridentata* is a model species for the study of facilitation effects on insect communities in an arid ecosystem.

2.2. Study site

This study was conducted in the Mojave Desert, at Kelso Dunes, California, USA (34°53'37.88"N, 115°42'6.58"W; elevation: 793 m; Appendix A, Fig. A.1). This dune system is surrounded on all sides by mountains and thus is relatively discrete within the Mojave Desert (Sharp, 1966). The Kelso Dunes also support a diverse array of plants and insects (Bowers, 1984), and the surrounding area is dominated by the shrubs *L. tridentata* and *Ambrosia dumosa*

(Bowers, 1984; Lei, 1998). Common native herbs include *Chaenactis fremontii* (Fremont pincushion), *Malacothrix glabrata* (Desert dandelion), *Aliciella leptomeria* (Sand gilia), *Eriophyllum wallacei* (Woolly daisy), *Hesperocallis undulata*, (Desert lily), *Anisocoma acaulis* (Scalebud), *Cryptantha micrantha* and various grasses. Sand is the primary substrate (sand: 78.70 ± 1.29%, silt: 14.89 ± 0.27%, clay: 6.41 ± 1.04%; Lei, 1998), with grains ranging in size from 0.25 to 4 mm in diameter (Sharp, 1966). Soil water content is low, at 0.94 ± 0.05%, and there is little organic matter present (1.12 ± 0.09%) (Lei, 1998). The mean annual precipitation in the area is between 34 and 310 mm year⁻¹ (Urban et al., 2009), and the average daily maximum temperature is 40 °C in July and the minimum is 1 °C in January (1937–2007 records; WRCC 2008).

2.3. Plant selection and insect sampling

A pilot survey was conducted to determine the average size of *L. tridentata* and to compare open and understory microsite diversity within the study site (see Appendix, Fig. B.1). Fifteen shrubs and an adjacent open microsite were randomly selected on parallel transects within the dune scrub. These transects were perpendicular to the independent transects used for insect sampling. In each plot, maximum shrub length, shrub width (perpendicular to maximum length) and shrub height were measured. Understory plant abundance was recorded for each species within a 50 cm quadrat placed on the south side of the shrub, and 2 m away in the adjacent southern open area. The temperature and relative humidity under five randomly selected *L. tridentata* shrub microsites and adjacent paired open microsites were recorded hourly for the period of April 27th to May 2nd using HOBO Pro V2 loggers (Onset Computer Corporation, Bourne, Massachusetts), with the sensor nodes positioned 3 cm above the surface of the sand to mimic the height of pan traps.

Insect samples were collected at Kelso dunes over a nine-day period between April 24th and May 2nd, 2013. Insects were sampled daily using pan traps (approximately 18 cm in diameter) set at ground-level along an east-west axis parallel to Kelso Dunes. Thirty pairs of pan traps were set along two parallel 45 m transects (transects were 10 m apart) with alternating blue, yellow, and white traps approximately every 3 m using the NSERC-CANPOLIN protocol (<http://www.uoguelph.ca/canpolin>). Pan traps were paired so that each replicate had one pan trap under the southern portion of a *L. tridentata* canopy, halfway between the base of the shrub and the drip-line, and within a patch of annual plants. The other pan traps were deployed 2 m south of each paired shrub in an adjacent open microsite, also with annual plants present (see Appendix A; Fig. A2). Open microsites were located two metres from the drip-line of shrubs because this was on average the maximum distance possible without being within a two metre radius of another shrub (Ruttan pers. obs). Pan traps were half-filled with a solution of soapy water prepared by mixing five drops of unscented dish detergent per litre of water (for protocol, see: <http://www.uoguelph.ca/canpolin>). Pan traps were set out by 9:00 a.m. and collected at 5:00 p.m. daily targeting typical peak insect activity (<http://www.uoguelph.ca/canpolin>). All samples were collected on sunny days with no precipitation. Samples were collected from each pan trap replicate and stored in vials of 70% ethanol. Insects were then sorted from samples and identified to the family level for ease of identification using Goulet and Huber (1993) and Borror et al. (1989). Following identification, insects were categorized into their primary functional groups, including pollinators (mostly bees), herbivores, granivores, parasites, nec-tarivores (that contribute only marginally to pollination), and others. Immature instars and non-insect arthropods were not included in these analyses due to the difficulty of identification and

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