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Shrubs facilitate pine colonization by controlling seed predation in dry Mediterranean dwarf shrublands

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ABSTRACT

Spatial association between pine recruitment and shrubs is widely observed in dry environments and often associated with physical facilitation provided by the shrub, alleviating seedling drought stress. However, shrubs may also facilitate recruitment by sheltering seeds from granivores. In this study we investigated the influence of shrub-related microsites on post-dispersal pine seed survival in dry Mediterranean shrubland. We present a novel approach investigating the survival of single seeds in the context of long-distance wind dispersal. In four dry shrubland sites of central Israel, we placed seeds of *Pinus halepensis* in different microsites associated with *Sarcopoterium spinosum* shrubs: under canopy, at two margins and in between shrubs. We monitored the seed persistence monthly, replacing seeds removed by granivores. We also compared seed survival in burned vs. unburned areas. Logistic regression showed that seeds placed under shrubs had significantly higher survival rates than elsewhere. In unburned sites survival was higher than in burned sites and remained higher under shrub canopies. We show that these effects were substantial by considering the length of the season through which seeds need to persist. We conclude that shrubs constitute an important facilitator for *Pinus halepensis* colonization in dry shrubland through their positive effect on seed survival.

1. Introduction

The phenomenon of pine expansion through dispersal of seeds from forested into unforested landscapes is increasingly observed worldwide (Améztegui et al., 2010; Curt et al., 2003; Pellerin and Lavoie, 2003; Richardson et al., 1994a). This phenomenon has been reported from many parts of the world, specifically in the southern hemisphere, where pines are not native and their expansion is considered as a human-related process with potentially undesired ecological consequences (Falleiros et al., 2011; Richardson et al., 1994b; Simberloff et al., 2010).

It is widely accepted that the extent of colonization reflects a dynamic balance between propagule pressure, i.e. seed flow into the focal area (Hufbauer et al., 2013) and the system resistance to colonization determined by the availability of physically suitable establishment microsites i.e., safe sites (Crawley, 2000) as well as by biotic agents influencing colonizer survival and development (Levine et al., 2004a). Two major determinants of biotic resistance to colonization are seed predation and competition with resident vegetation (Maron and Vilà, 2001). Yet, very little is known about the interaction between these two factors, since they have usually been considered separately. The effect of resident vegetation structure on colonization of new species has commonly been considered in the context of competition and facilitation (Levine et al., 2004b), but has rarely been explored as a possible factor mediating the extent of seed predation and/or herbivory, creating refuges from seed consumers (Stutz et al., 2015). Such a perspective on the role of resident vegetation may provide new understandings with regard to spatial patterns of colonization processes.

In xeric environments, spatial association between pine seedlings and resident shrub patches or other perennial plants has been reported previously in the context of colonization and regeneration (Gasque and García-Fayos, 2004; Sheffer et al., 2014) This association is most commonly attributed to physical facilitation i.e., amelioration of abiotic conditions within the nurse microenvironment (Holmgren et al., 1997) and to the shrubs' function

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as seed traps (Bullock and Moy, 2004; Giladi et al., 2013). To our knowledge, studies addressing the possibility that shrub patches influence the spatial arrangement of tree seedlings through their effect on seed predation (Pinheiro and Ganade, 2007; Russell and Schupp, 1998) are lacking for wind-dispersed colonizer species. Understanding this interaction may provide new insights with regard to the role of trophic interactions for influencing plant community assembly processes. Furthermore, it may contribute to the management of shrublands under risk of undesired pine encroachment.

Pine colonization and encroachment into habitats of high conservation value are particularly alarming (Richardson, 1998). In Israel, the expansion of the wind dispersed *Pinus halepensis* from plantations into adjacent natural landscapes is widespread and commonly observed in areas extending beyond the forest margins (Sheffer, 2012). Although *Pinus halepensis* is native to Israel (Nahal, 1962), its rapid expansion is considered to be human related due to the extensive use of this species for afforestation as well as the spread of high-severity fires from plantations into natural unforested areas (Lavi et al., 2005; Osem et al., 2011; Sheffer, 2012). Pine colonization has become a major source of concern among rangeland managers, specifically when it occurs in dwarf shrublands (batha) of the semi-arid transition zone between mesic and xeric vegetation (Lavi et al., 2005; Waitz, 2013) which are recognized in Israel as endangered habitats of particularly high biodiversity and conservation value (Blank, 2012).

Pinus halepensis seeds are highly palatable and consumed by rodents, birds and ants (Broncano et al., 2008; Saracino et al., 2004). Post-dispersal predation rates of *P. halepensis* seeds in the Mediterranean ecoregion of Israel are high, with reported rates of seed loss of 90% within a month (Schiller, 1979), 95% within 12 days (Nathan and Ne'eman, 2004) and nearly 100% within 60 days (Finkel, 2011). However, these rates were all recorded within the trees' dispersal kernels (Nathan and Ne'eman, 2004), where the density of pine seeds is high and the population and behavior of granivores are expected to be highly responsive to the availability of pine seeds (Myster and Pickett, 1993). In areas which are distant from seed sources (i.e. few hundred meters and more), however, the density of pine seeds can be several orders of magnitude lower (Nathan et al., 2000). Thus, in the process of pine colonization (as opposed to within stand recruitment), where the colonized areas are quite distant from seed sources (Lavi et al., 2005; Sheffer et al., 2014), the pine seeds are present in low densities and sporadically distributed in time and space (Nathan and Ne'eman, 2004). In such cases colonizing pine seeds are likely to have a minor effect on seed predator populations and behavior as they do not constitute a key food source.

Very little is known about the extent of pine seed predation in non-forested Mediterranean habitats and about the importance of this factor in controlling long-distance pine colonization (Glazer, 2013). We propose that long distance pine colonization, characterized by sporadic seed distribution, is influenced by resident vegetation structure determining spatial variability in post-dispersal seed predation rates.

The aim of this work was therefore to study the role of shrub-patch microsites in post-dispersal predation of *P. halepensis* seeds colonizing dry Mediterranean dwarf shrublands. Our specific objectives were to examine:

1 The importance of post-dispersal seed predation as a resistance factor in the process of long-distance pine colonization of shrublands.
2 The influence of shrub-related microsites on seed predation rate
3 The influence of shrub cover reduction via fire disturbance on seed predation rate.

2. Methods

2.1. Study sites

The study was carried out in four replicate sites within the low Judean Lowlands (Shephela(region of Central Israel: Beth Shemesh, Zor'a, Shahariyya and Lahav (Fig. 1). The replicate sites represent natural dwarf shrublands dominated (more than 90% of the vegetation cover) by *Sarcopoterium spinosum* (Rosaceae) shrubs typical of Israel's dry Mediterranean zone. Soils in all study sites are bright to brown rendzinas developed on chalk bedrock (Singer, 2007). All sites are subjected to seasonal livestock grazing. The inclination angle of the slopes was ranges from 5° to 20°. Detailed information on each of the study sites is given in Table 1.

2.1.1. Experimental design

In each site, a single experimental plot (25 × 25 m) was located on a south-facing hillslope at least 300 m away from *P. halepensis* plantations. In Zor'a and Shahariya sites two additional plots were assigned representing shrubland areas that were recently burned (2 and 3 years prior to the study, respectively) and shrub cover had been notably reduced by 50% and 40%, respectively.

In each plot 15 distinct shrub patches of *S. spinosum* were randomly selected, maintaining at least 2 m distance between patches. For each shrub patch four camouflaged plastic rings (Diameter 5 cm), fastened to the ground by U-shaped pegs, were placed in four different shrub related microsites: (1) under the shrub, (2) uphill shrub margin, (3) downhill shrub margin and, (4) intershrub space (at least 30 cm away from shrub patch margins). Within each patch, rings were placed at least 50 cm apart to minimize seed density effects. Thus, the distinct shrub patches served as experimental blocks, with each incorporating the four different microsites. In the burned plots (Shahariya and Zor'a) where shrub patches were very small, rings were only placed on shrub patch margins (downhill and uphill) and intershrub spaces. One *P. halepensis* seed was placed on the ground in each ring and the entire experimental setup was surveyed once a month over a 15-month period. Lost seeds were considered consumed by granivores, after having observed in a previous 3-month trial with 15 seeds at each site, that seeds protected from predation by an animal-proof net and by insecticides remain in their place even after strong wind storms and heavy rain events.

New seeds were replaced in all rings every month. Germinated seeds were not treated in this analysis. Altogether, 5400 observations were conducted representing four sites, two fire histories (recently burned and unburned, in two sites only), 15 shrub patches in each plot, and 4 microsites in each patch.

2.1.2. Data analysis

Data were analyzed using logistic regression, in which survival was a nominal binary response variable (survived, not survived). In order to determine the effect of microsite on survival we conducted an analysis with the following independent variables: Microsite (under shrub, uphill margin, downhill margin and intershrub), season (autumn, winter, spring and summer), and the interaction between microsite and season.

In order to determine the effect of vegetation disturbance on seed survival we conducted a logistic regression analysis by different fire histories (burned, unburned) for the relevant sites (Zora, Shahariyya). We then conducted a further analysis to detect the effect of microsite and season on seed survival in burned sites. We used SAS JMP 7.0.1 software for all statistical analyses.