



Shrub seedling survival under climate change – Comparing natural and experimental rainfall gradients



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ABSTRACT

Predicting responses of plant communities to environmental changes is a key challenge in ecology. Here we examined climate-related mechanisms regulating seedling dynamics of a common Mediterranean shrub. Our objective was to analyze effects of water availability on seedling survival and to determine whether geographical gradients can serve as proxy for predicting local climate change effects. We conducted a field experiment along a natural rainfall gradient with additional long-term rainfall manipulations at a Mediterranean site, enabling the investigation of the relative importance of biotic and abiotic factors on seedling dynamics. Along the natural and artificial rainfall gradient seedling survival increased with increasing soil water availability. However, seedling survival at the Mediterranean site yielded a clear trend of decreasing seedling survival with artificially increasing aridity whereas at the dry end of the geographical gradient seedling survival was relatively high. We attribute this pattern to biotic interactions, which appeared less negative at the dry end. These findings indicate that ignoring biotic interactions is misleading when predicting shifts in the distribution of species under climate change and that because of the complex interplay between abiotic and biotic factors, environmental gradients can be poor proxies for predicting the response of plant species to climate change.

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1. Introduction

Understanding and predicting the responses of plants to environmental modifications such as climate changes represents a major challenge for ecologists (Krebs, 2009). One of the practical problems encountered by researchers is the relatively long temporal scale required to observe changes in nature (Fukami and Wardle, 2005). To overcome this problem, natural gradients that vary in their climatic conditions are often used as a proxy for the temporal changes in climate (Fukami and Wardle, 2005; Sternberg et al., 2011). For example, natural rainfall gradients provide a useful framework to analyze changes in species distribution in systems driven by water availability (Holzapfel et al., 2006; Sternberg et al., 2011). However, the response of plant species growing along natural gradients may vary depending on the amount of time the

community was exposed to the particular climate conditions and to the relative contribution of other local environmental factors (Dunne et al., 2004; Fukami and Wardle, 2005; Sternberg et al., 2011). These shortcomings highlight the importance of combining experimental and correlative approaches when studying the potential effects of climate change (see also Fukami and Wardle, 2005). To the best of our knowledge, only few studies compared in situ manipulations of the limiting factor with correlations along an associated environmental gradient (e.g. Dunne et al., 2004; Liancourt et al., 2012). With this study, we attempted to fill this gap by monitoring seedling responses of a dominant shrub to climate change in a water-limited system using both a steep rainfall gradient and rainfall manipulations.

Early plant life stages are considered vulnerable to environmental alterations (Fay and Schultz, 2009; Howard and Goldberg, 2001) and particularly to climate changes (Gómez-Aparicio et al., 2005). Seedling survival depends on a narrow spatial and temporal window ("safe site") created by specific environmental conditions (sensu Harper et al., 1961). Seedling survival determines plant

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population dynamics, persistence and expansion (Kitajima and Fenner, 2002) and is therefore considered a bottleneck in many ecosystems, especially those characterized by extreme climatic conditions (Leck et al., 2008). The impact of survival success in the plant's early stages is especially large for long-lived, woody plant species, because small seedlings do not yet exhibit the robustness of adult plants that may protect them from drought, high temperatures, or competition with larger or faster developing neighbors (Matías et al., 2011; Mendoza et al., 2009). In dry regions, several studies have shown that water availability was the main limiting factor for seedling establishment (e.g. Padilla and Pugnaire, 2007), while after establishment, seedlings appeared to be less affected by abiotic and biotic factors (Davis et al., 1999; van Aken, 2000).

The contribution of climatic factors to early survival of plants is not limited to direct effects on the plant's demographic processes through an impact on abiotic resources, but can also be detected through alterations of the density and biomass of the entire community (Holzapfel et al., 2006; Seifan et al., 2010; Sternberg et al., 1999). If these alterations are species-specific, climatic changes will be associated with modifications of biotic interactions, whose direction (positive vs. negative) and intensity depend on the abiotic environment (Bertness and Callaway, 1994; Brooker et al., 2008). In the specific case of the potential indirect effect of climate on shrub seedling dynamics in a water limited system, we need to take into account the potential effects of two groups of neighbors: the herbaceous species and the adult shrubs. Herbaceous neighbors often have a faster growth rate relative to shrub and other woody seedlings (Sánchez-Gómez et al., 2006). This may indicate that the herbaceous neighbors can utilize abiotic resources more efficiently and may intensify competition for the limiting factors (McLaren et al., 2004; Vilà and Sardans, 1999). On the other hand, because of their faster growth rate, herbaceous neighbors may ameliorate habitat conditions, e.g. by providing shade which decreases evapotranspiration and buffers high temperatures (Holmgren et al., 1997). Adult shrubs are known to play an important role in water-limited systems as well, because they may influence seedling establishment success through alterations of microclimatic conditions, including the improvement of soil moisture, soil nutrients, temperature and light availability (Gómez-Aparicio et al., 2005; Pugnaire et al., 1996, 2004). On the other hand, adult shrubs can also negatively influence seedling establishment, especially by decreasing light availability to the seedlings growing in the shrub understory (Reisman-Berman, 2007; Seligman and Henkin, 2002).

To date, it is virtually unknown how the direction and intensity of such biotic interactions will change under a new climate. However, because many studies have shown that abiotic stress (e.g. decreasing rainfall) strongly affects the nature of biotic interactions, it is highly relevant to monitor plant–plant interactions when studying climate change. Therefore, the objective of our study was to determine whether changes in the interaction between a dominant perennial shrub and its herbaceous neighbors along a natural rainfall gradient can serve as proxy for predicting in-situ climate change effects. For this purpose, we artificially manipulated rainfall availability in accordance to regional climate change scenarios and monitored the establishment success of a common shrub in relation to herbaceous neighbors and adult shrub presence. These observations were compared to the shrub establishment success along a geographical rainfall gradient which served as spatial control for climate change scenarios (Sternberg et al., 2011). We predicted that shrub seedling survival will decrease with increasing site aridity and with experimental drought. If shrub seedling survival along a natural and artificial rainfall gradient is indeed similar, it will support the use of geographical gradients as proxy for temporal change in climate. In

addition, because of the potential change in biotic interactions with climatic conditions, we predicted that the presence of adult shrubs or herbaceous neighbors will have a positive effect on shrub seedling survival with either naturally or manipulative decreased rainfall.

2. Material and methods

We conducted our study within the Mediterranean shrubland in Israel. Eastern Mediterranean scrub formations are characterized by highly heterogeneous plant communities and diverse environmental conditions distributed over a small geographical area (Danin, 1992). In Israel, this vegetation formation is found along a steep rainfall gradient across a small spatial distance ranging from 900 mm mean annual precipitation in the north to 250 mm in the south (Danin, 1992), which is accompanied by an increasing temporal variability with decreasing rainfall (Nahal, 1981). This combination offered a unique possibility for investigating climate change effects on the structure and functioning of ecosystems. Our study was conducted at three sites along the natural climatic aridity gradient (183 km; see: “2.2 Geographical gradient”), and was compared to rainfall manipulation outcomes at the central site for testing potential climate change scenarios (see: “2.1 Climate change manipulations”).

2.1. Climate change manipulations

The central study site was located in the Judean Mountains (N 31°42', E 35°03'). It is characterized by Mediterranean climate with an average annual rainfall of 540 mm. At this site we used experimental long-term rainfall manipulations (12 years) evaluating two potential scenarios that were based on predicted climatic changes for the region: 30% decrease and 30% increase in total annual rainfall. The increased rainfall scenario was achieved by adding irrigation with drizzle sprinklers at the end of each rainfall event higher of 5 mm. Decreased rainfall was simulated by fixed rainout shelters (Yahdjian and Sala, 2002). Rainout shelters were made from metal frames (2.5 m mean height), with u-shaped plastic bands intercepting 30% of rainfall. Excess water was drained into gutters leading away from the experimental plots. Wind movement was not impeded as sides of the rainout shelters were open, additionally minimizing microclimatic differences under and outside the shelter (Fay et al., 2000). This method enabled us to manipulate only rainfall amount, while maintaining natural timing, frequency and intervals of rainfall (Sternberg et al., 2011). Five plots of 10 m × 25 m were set for each treatment and randomly located at the site. From here on we will refer to the treatments as irrigation, control and drought. For more detailed description of the experimental design see Sternberg et al. (2011).

While designing the experiment, our aim was to cover the uncertainty of global climate models and thus included artificially increased and decreased rainfall, in accordance with the available models and predictions for the region (Ben-Gai et al., 1998). However, during the course of the study high-resolution models became available, predicting a decrease in annual rainfall by 10–30% in the next decades (Smiatek et al., 2011). Therefore, while both treatments provide mechanistic information about the response of shrub seedlings to changes in rainfall, the drought treatment better mimics future climate change scenarios in the region.

2.2. Geographical gradient

Two additional sites were established north (Galilee Mountains, N 33°0', E 35°14') and south (northern Negev desert,

N 31°23', E 34°54') of the central study site. Climatic conditions are considered mesic Mediterranean in the northern site and semi-arid in the southern site (Harel et al., 2011). All sites are located on southern slopes of calcareous bedrock at similar elevations. The three sites share a similar Mediterranean climate, characterized by mild, rainy winters and hot, dry summers, and have similar mean annual temperatures (17.0–19.1 °C). However, they differ in the average annual rainfall which varies between 780 mm in the North, 540 mm in the central site, and 300 mm in the South. The main growing season (November–April) is closely linked with the temporal distribution of rainfall. For further information about the sites see Appendix 1, Holzapfel et al. (2006) and Sternberg et al. (2011). Experimental sites were left uncultivated for approximately 50 years, but were under moderate grazing by cattle at the northern site and sheep and goat at the intermediate and southern site.

The study was conducted over a two year period. Rainfall in the two consecutive years (season 2009/10 and 2010/11) was 251 and 178 mm at the southern site, 533 and 357 mm at the central and 832 and 711 mm at the northern site, respectively.

2.3. Study species

The thorny dwarf shrub *Sarcopoterium spinosum* (L.) Spach (Rosaceae) was the focal species of this research. We chose this species because of its dominant appearance at all three sites along the natural rainfall gradient (see also Appendix 1). *S. spinosum*, 30–60 cm in height, grows mainly on infertile, shallow soils in association with secondary succession and grazing systems (Litav and Orshan, 1971; Litav et al., 1963). Seedlings develop taproots, reaching up to 40 cm, which remain dominant (approx. 2–4 years) until adventitious roots are formed (Litav and Orshan, 1971). During this stage, the seedlings are very sensitive to drought and competition from neighbor plants (Litav et al., 1963). All three experimental sites are dominated by genera belonging to the family of the Poaceae and Asteraceae. Additionally, Brassicaceae is a dominant family at the semi-arid site whereas genera of the Fabaceae increased in their abundance towards the wet end of the natural rainfall gradient (Appendix 1).

2.4. Environmental measurements

In order to obtain a more complete understanding of the relative importance of abiotic conditions in controlling the dynamics of shrub seedling establishment we measured soil moisture and light availability, which are among the main factors affecting shrub seedling success (Matías et al., 2011; Seifan et al., 2010), as well as soil temperature and biomass of the annual neighboring community.

Soil moisture, soil temperature and light availability were measured once towards the end of the vegetative growth (around May). Soil moisture was measured gravimetrically for each treatment and microhabitat (0–5 cm depth; $n = 15$ per treatment). Soil temperature and light intensity were recorded for each quadrat and habitat. Soil temperature at a depth of 5 cm was measured at noon, using a digital thermometer. Simultaneous measurements of light intensity 5 cm above ground were carried out using a lux meter. For measuring aboveground biomass of the surrounding annual community, we harvested three quadrats (20×20 cm) in the open space between shrubs in each plot and treatment at the peak of biomass production. Overall, there were 75 quadrats of biomass samples, which were oven dried to constant weight at 75 °C, and weighed.

2.5. Seedling survival monitoring

Seedling survival was monitored at each site along the geographical gradient and within the rainfall manipulations. Approximately 2–3 months after the main germination event and after no further germination was observed, seedlings were marked with unique identifiers. In order to cover the major source of small-scale heterogeneity, seedlings growing in the open space between shrubs and under the shrub canopy of *S. spinosum* were marked (Holzapfel et al., 2006; Seifan et al., 2010). To fully characterize the range of variability in seedling survival processes across space and time, 200 seedlings in each treatment combinations and habitats were marked (a total of 2000 seedlings). At the time of the census, *S. spinosum* seedlings had cotyledons and one to three leaves. The presence of cotyledons was a reliable indicator for the seedlings to have germinated in the current season. Seedlings were examined again after the first initial rains of the following season (November–December), and characterized as either dead or alive.

2.6. Data analysis

In order to analyze differences in seedling survival we compared the effect of both water availability and habitat (open space vs. shrub understory) on seedling survival in two different models: one representing the experimental climate change conditions within the central (Mediterranean) site (drought, control and irrigation) and the other the geographical gradient (which covered three climatic zones: semi-arid, Mediterranean and mesic Mediterranean). The potential effect of these factors on seedling survival was analyzed using generalized linear models (GLM) with a binomial distribution and a logit-link function. The effect of water availability and habitat on the local abiotic conditions (soil moisture, light availability and soil temperature) were tested using a GLM with a normal distribution and identity link. To evaluate the effect of the annual neighbor community, we adopted Lauenroth and Sala (1992) approach. We constructed the relationship between the annual plant above-ground biomass and precipitation and use it as a proxy for the rain use efficiency of the neighboring plants (see also Cherwin and Knapp, 2012; Ruppert et al., 2012). We further analyzed using GLM models (with a binomial distribution and logit-link function) the relationship between the shrub seedlings and the estimated annual community biomass, generated from the biomass–rainfall relationship.

Post-hoc comparisons, with the least significant differences multiple comparison method, were conducted when significant main effects or interactions were detected. All analyses were performed using SPSS 19.

3. Results

3.1. Environmental measurements

Extremely low seedling survival (0.2%) in the first year of the experiment prevented us from performing any statistical tests. Therefore, within the scope of this article we present and discuss only data from the second year of the experiment.

No significant differences in soil moisture were found between the rainfall manipulations in the Mediterranean site ($\chi^2_2 = 1.27$, $p = 0.53$; Fig. 1A). Light intensity in the open space decreased with increasing water input, with a significant difference among the driest and the two other treatments ($\chi^2_2 = 7.93$, $p = 0.019$; Fig. 1B). Soil temperature showed a similar decreasing trend with irrigation, but the results were not significant. Adult shrub presence positively affected soil moisture in the

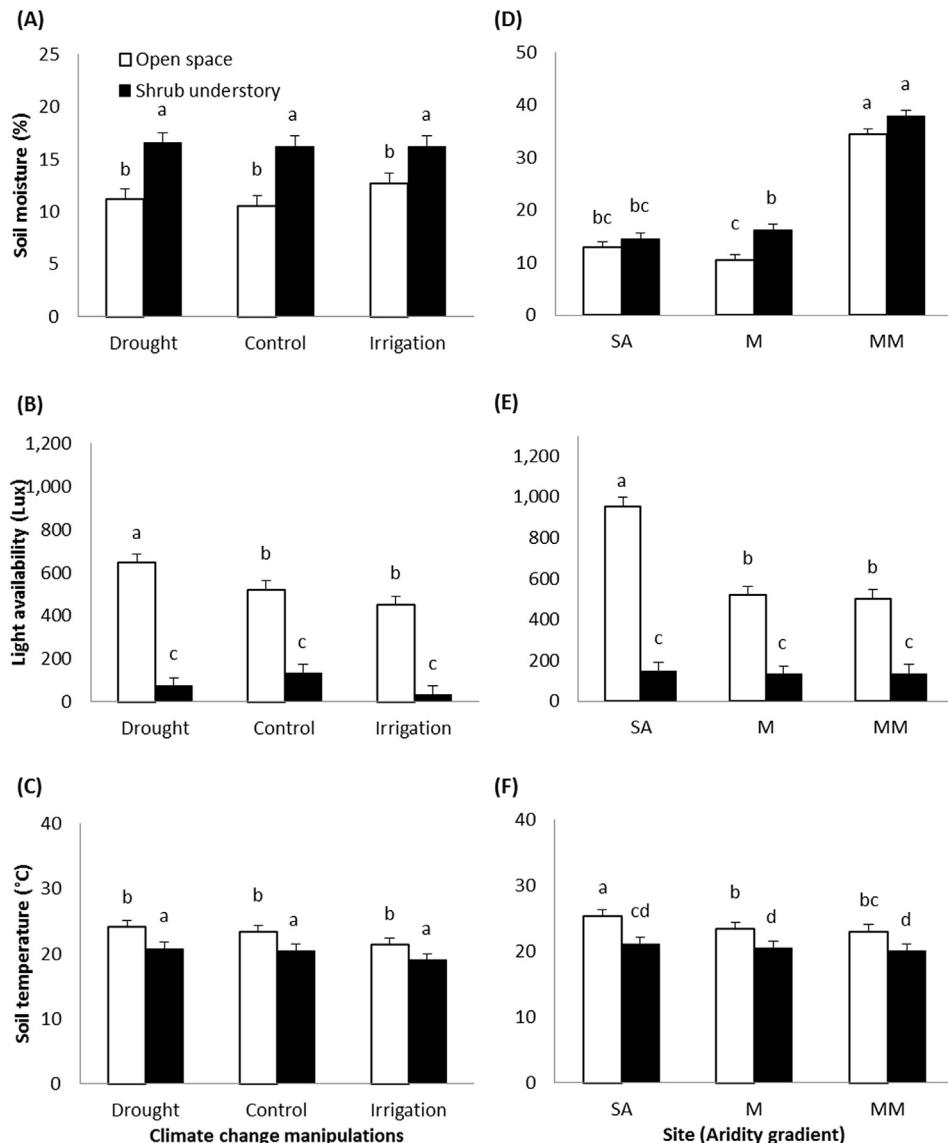


Fig. 1. Abiotic conditions in the three climate change manipulations (drought, control and irrigation) and the three sites indicating semi-arid (SA), Mediterranean (M) and mesic Mediterranean (MM) conditions for the two microhabitats (open space vs. shrub understory) ($\bar{X} \pm 1SE$). Letters represent significantly different groups ($p < 0.05$). A) & D) soil moisture (%); B) & E) light intensity (Lux); C) & F) soil temperature ($^{\circ}\text{C}$).

understory ($\chi_1^2 = 25.1, p < 0.001$; Fig. 1A), while light intensity and temperature were always significantly lower in the shrub understory ($\chi_1^2 = 61.02, p < 0.001$; Fig. 1B and $\chi_1^2 = 21, p < 0.001$; Fig. 1C, light intensity and temperature, respectively), regardless of irrigation treatment.

Soil moisture along the geographical gradient increased significantly with increasing rainfall ($\chi_2^2 = 94.02, p < 0.001$, Fig. 1D). Light intensity in the open space was significantly higher at the semi-arid, compared to the Mediterranean and mesic Mediterranean site ($\chi_2^2 = 18.63, p < 0.001$; Fig. 1E). Soil temperature followed a similar trend with a significant decrease from the semi-arid to the mesic Mediterranean site ($\chi_2^2 = 12.12, p = 0.002$; Fig. 1F). In all three sites, soil moisture was higher in the shrub understory ($\chi_2^2 = 14.48, p < 0.001$; Fig. 1D) while light availability ($\chi_1^2 = 63.42, p < 0.001$; Fig. 1E) and soil temperature were lower ($\chi_1^2 = 39.09, p < 0.001$; Fig. 1F).

Although the soil moisture measurements showed no significant differences between the rainfall manipulations, the annual neighbor

community significantly increased with increasing water availability ($F_{1,15} = 7.53, p = 0.017$; Fig. 2A). The biomass of the annual neighbor community also increased along the geographical gradient, but with a steeper response ($F_{1,15} = 103.58, p < 0.001$; Fig. 2A).

3.2. Survival

In the Mediterranean study site where irrigation manipulations were conducted, mean seedling survival was $2.6 \pm 0.77\%$. Seedling survival increased significantly with increasing water input ($\chi_2^2 = 14.97, p < 0.001$; Fig. 3A). Shrubs had a positive effect on survival in all treatments ($\chi_1^2 = 4.31, p = 0.038$) with no significant interaction with treatment and habitat ($\chi_2^2 = 1.02, p = 0.6$). Interestingly, shrub survival showed a significant positive response to increase in annual neighbor biomass ($\chi_1^2 = 7.11, p = 0.008$; Fig. 2B).

Along the geographical gradient, overall mean seedling survival was $10.2 \pm 1.2\%$ and varied significantly among the three sites

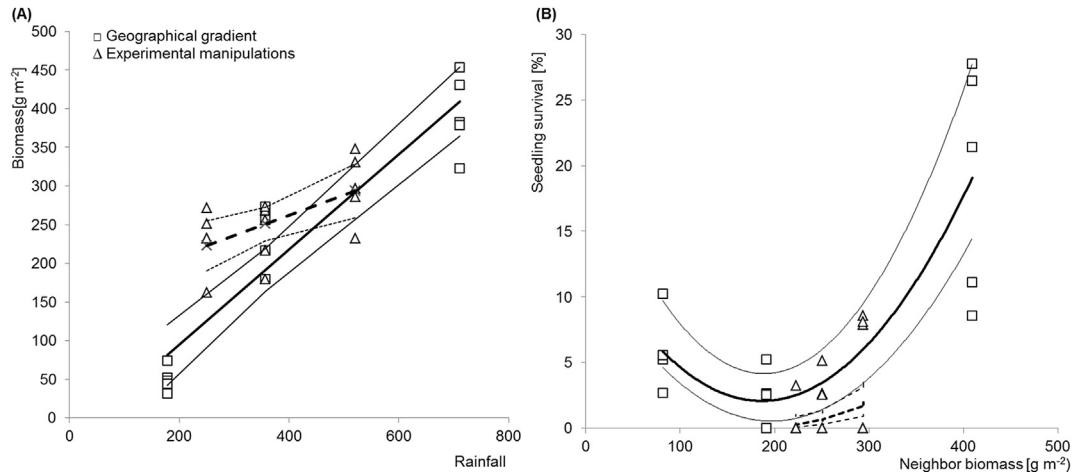


Fig. 2. (A) Relationship between annual rainfall estimation and the annual community above ground biomass. Squares and black lines represent the values, estimated average and confidence intervals along the geographical gradient. Triangles and dashed lines represent the values, estimated average and confidence intervals in relation to the experimental rainfall manipulations. (B) Relationship between the estimated annual community and shrub seedlings survival. Squares and black lines represent the values, estimated average and confidence intervals along the geographical gradient. Triangles and dashed lines represent the values, estimated average and confidence intervals in relation to the experimental rainfall manipulations.

($\chi^2 = 52.86, p < 0.001$). Seedling survival decreased from the semi-arid to the Mediterranean site and increased again towards the mesic Mediterranean site (Fig. 3B). A significant interaction between geographic location and the adult shrub presence ($\chi^2 = 5.98, p = 0.05$) indicated that in the semi-arid site seedling survival in the shrub understory was significantly higher than in the open space. In addition, when comparing seedling survival in the open space along the sites, survival was significantly higher in the northern, mesic Mediterranean site. The effect of the annual neighbor biomass followed the pattern of the geographical location ($\chi^2 = 33.40, p < 0.001$), showing a unimodal response with the lowest seedling survival at the intermediate values of neighbor biomass and an increase in seedlings survival toward either higher or lower neighbor biomass (Fig. 2B).

4. Discussion

Our overall results show that climate gradients are a poor proxy for predicting the response of the studied shrub species to climate

change. In particular, shrub seedling survival showed a different response to neighbor presence along water availability gradient when comparing the local climate manipulations with the natural geographical gradient.

Overall, we supported the working assumption of water as a limiting factor in the study system (García-Fayos et al., 2000; Lloret et al., 2005) when examining the effect of increased water availability (either by additional irrigation or by a higher rainfall regime as measured in the northern, mesic Mediterranean site) on shrub seedling survival. Increased water availability probably alleviated stress levels by adding the most limiting resource and thus boosting survival and establishment success (Davis et al., 1999; Mendoza et al., 2009; Sternberg et al., 1999). In addition to the clear physiological advantage of increased water availability to plant survival, this result has also an ecological importance. Many previous studies and theories, including the stress gradient hypothesis, suggested that the nature of biotic interactions becomes negative with decreased environmental stress (Bertness and Callaway, 1994). Competition

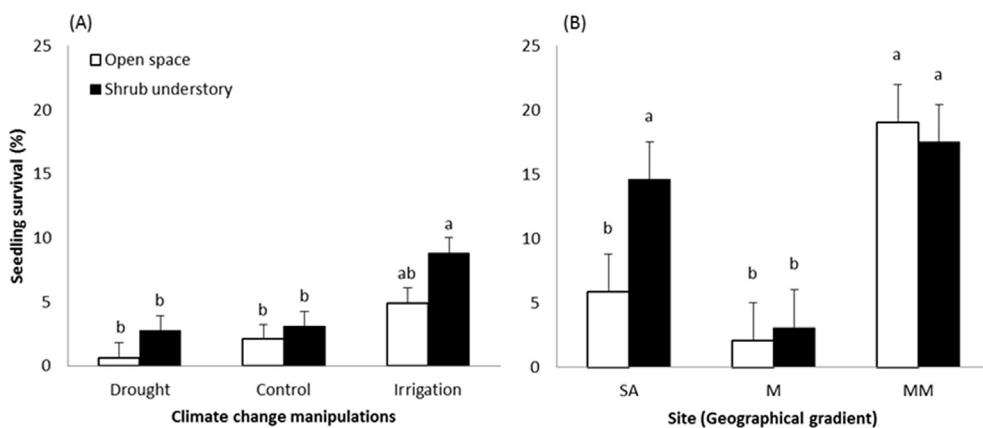


Fig. 3. Seedling survival (A) in the three climate change manipulations (drought, control and irrigation) and two microhabitats (open space vs. shrub understory) at the Mediterranean site and (B) in the three sites indicating semi-arid (SA), Mediterranean (M) and mesic Mediterranean (MM) conditions, and two microhabitats (open space vs. shrub understory) along the geographical gradient ($\bar{X} \pm 1\text{SE}$). Letters represent significantly different groups ($p < 0.05$).

with the immediate neighbors, and particularly with herbaceous ones, was observed with higher water availability in many systems, including the one studied here (Holzapfel et al., 2006; Schiffers and Tielbörger, 2006). Nevertheless, our results indicate that even in a constrained and relatively poor environment as the Mediterranean environment, addition of a limiting resource can exceed the overall requirements of the plant community and allow all the species to have a better performance instead of intensifying their competitive interactions. Moreover, the positive effect of increased water availability on the annual community and on the shrub seedling survival contradicted findings from other dry regions, where the increased herbaceous plant production after a sequence of wet years was utilized to inhibit shrub recruitment (Peters et al., 2012).

The discrepancy between the responses of shrub seedlings to local climate manipulations and to a natural geographical gradient is revealed when taking into account the indirect effects of neighbors. In particular, we detected a change in the role of adult shrubs between the two gradients. The presence of adult shrubs in the semi-arid site provided shrub seedlings with a more favorable microhabitat. These results support previous findings that canopies of woody plants may ameliorate the microenvironment and function as nurse plants for seedlings (Brooker et al., 2008; Callaway, 1995; Gómez-Aparicio et al., 2005). In less harsh conditions, the presence of adult shrubs had no significant effect on shrub seedling survival. Interestingly, this contradicts previous result about the same species, which showed that at least in Mediterranean type sites, the shade provided by the canopy may become a limiting factor for the development of *S. spinosum* seedlings (Reisman-Berman, 2007; Seifan et al., 2010). The discrepancy, as well as the generally low survival rate in the Mediterranean site, may be related to the differences in rainfall between studies. While both Seifan et al. (2010) and our studies were conducted in years with below-average precipitation, drought was much stronger during our current study (rainfall in the two studies were 9% and 34% below average in Seifan et al. (2010) and our study, respectively). It may well be that under more limiting conditions the balance between positive and negative effects of adult shrub canopy was tipped and the overall effect of the shrub presence has shifted from negative to neutral. In combination with the overall positive effect of shrub canopy in drier conditions, the results emphasize the flexibility and sensitivity of biotic interactions to relatively small changes in abiotic conditions.

Unlike the natural geographical gradient, adult shrubs did not serve as nurse plants in the drought manipulation in the central site. Instead, a higher shrub seedling survival in the shrub understory was detected in the high irrigation treatment. This result, which seems counterintuitive at first sight, may be explained by the presence of the annual neighbor component. As expected, the water use efficiency of the annual plants responded positively to increase in water availability (Lauenroth and Sala, 1992). Because shrub seedlings at early stages share resources with their herbaceous neighbors but are often less efficient in resource uptake (McLaren et al., 2004; Vilà and Sardans, 1999), competition might have been intensified in the open space (Davis et al., 1999). In comparison, shrub seedlings which grew in the shrub understory may have been at least partially protected from competition while still enjoying a higher level of water availability (Gómez-Aparicio et al., 2005). Hence we suggest that adult shrub presence had a different role in the natural geographical gradient than in the climate change manipulation. Along the natural gradient, the shrubs had a facilitative role, probably due to amelioration of light and temperature levels,

which was advantageous toward the more stressful end of the gradient. Toward the more productive end of the geographical gradient, both the annual plants and the shrub seedlings increased their water use efficiency, weakening the ameliorating role of the adult shrub. In the experimental manipulation, adult shrubs did not have a direct facilitative role, but they might have provided seedlings with a relative shelter from the more competitive condition outside shrub understory.

The differences in response of shrub seedlings to local manipulations of water availability relative to their survival along a geographical gradients emphasize the problems encountered in the space for time approach (Dunne et al., 2004; Sternberg et al., 2011). This was indicated not only by the different effect of adult shrubs, but also when comparing the average seedling survival between the drought treatment ($1.7 \pm 0.29\%$) and the semi-arid natural sites ($10.2 \pm 2.48\%$). The higher seedling survival in the semi-arid site may be explained by facilitation by adult shrubs. However, because seedling survival was higher (though not significantly) also in the open space, we suggest that shrub seedlings in the semi-arid site have also acquired some level of local adaptation to the drier conditions (Jump and Peñuelas, 2005), e.g., by having physiological and morphological mechanisms which reduce the negative impacts of drought such as rapid root elongation and/or increasing root size (Padilla and Pugnaire, 2007). In contrast, when water availability changes within a site, seedlings may have less potential to adjust their response to the changing environment and therefore may show a reduced survival with decreasing water availability. This explanation may also be supported by the response of the annual neighbors to rainfall. As expected, we have found a steeper response to water availability along the geographical gradient relative to the local one (Lauenroth and Sala, 1992; Ruppert et al., 2012). While the large changes along geographical gradients may be regarded as directional long-term adaptation, the local (and in our case, experimentally manipulated) response, may be regarded as a relatively short-term, and thus an individual, effect (Smith et al., 2009). In accordance, it may be expected that at the local scale we could only detect a change in the immediate response of the plants to water availability, but did not detect potential shifts in the interactions between shrubs and herbs, which would require longer time periods (Sala et al., 2012).

In summary, this complex interaction among climatic and biotic effects demonstrates the potential dangers in using geographical gradients as unique proxies and highlights the importance of combining both experimental and correlative approaches (see also Fukami and Wardle, 2005). In particular, we showed that the interactions with neighbors may differ significantly between natural gradients and local resource changes. Therefore, our study support previous warnings that sessile organisms, even those with relatively large geographical distribution, may not be able to adapt sufficiently fast (Jump and Peñuelas, 2005). Moreover, we suggest that correlative models are not satisfactory for predicting species changes under climate change and may either over- or underestimate changes in species abundance.

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Appendix 1

Ecosystem type	Location	Avg temp (°C)	Elevation (m a.s.l.)	Avg rainfall (mm)	Soil type	Vegetation description
Semi-arid (N 31°23', E 34°54')	Northern Negev desert	18.4	590	300	Light Brown Rendzina	Dwarf shrubland: 10 % total shrub cover with 70 % <i>S. spinosum</i> , 10 % <i>Thymelaea hirsuta</i> , 6 % <i>Thymus capitatus</i> and 4 % others; 15 % annuals with e.g. <i>Crithopsis delileana</i> , <i>Aegilops peregrina</i> , <i>Brachypodium distachyon</i> , <i>Anagallis arvensis</i> , <i>Daucus sessilifolius</i> , <i>Torilis tenella</i> , <i>Hippocratea unisiliquosa</i> , <i>Hymenocarpos circinnatus</i> , <i>Onobrychis squarrosa</i>
Mediterranean (N 31°42', E 35°03')	Jerusalem Mountains	17.7	620	540	Terra Rossa	Dwarf shrublands: 30 % total shrub cover with 56 % <i>S. spinosum</i> , 23 % <i>Pistacia lentiscus</i> , 10 % <i>Cistus</i> spp. and 1 % others; 60 % annuals with e.g. <i>Avena sterilis</i> , <i>B. distachyon</i> , <i>Hordeum spontaneum</i> , <i>A. arvensis</i> , <i>Plantago</i> spp., <i>Trifolium</i> spp., <i>H. unisiliquosa</i> , <i>H. circinnatus</i> , <i>Onobrychis</i> spp.
Mesic-Mediterranean (N 33°0', E 35°14')	Galilee Mountains	18.1	500	780	Montmorillonitic Terra Rossa	Mediterranean maquis to marrigue: 55 % total shrub cover with 25 % <i>S. spinosum</i> , 37 % <i>Calicotome villosa</i> and 18 % <i>Cistus</i> spp. and 20 % others; 45 % annuals with <i>Catapodium rigidum</i> , <i>Lolium rigidum</i> , <i>B. distachyon</i> , <i>A. arvensis</i> , <i>Plantago</i> spp., <i>Trifolium</i> spp., <i>H. unisiliquosa</i> , <i>H. circinnatus</i> , <i>Onobrychis</i> spp.

Modified from Sternberg et al., 2011; Sternberg unpubl. data.

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