Effects of extreme drought on plant community dynamics and ecosystem function in a Mediterranean shrubland

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by

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Abstract

Climate change scenarios predict an increase in the frequency of extreme climatic events. In the eastern Mediterranean region, an increase in frequency, intensity and duration of droughts is predicted. We used rain-out shelters to simulate drought by a 66% reduction in annual rainfall to answer following questions: What are the effects of extreme drought on net primary production of an annual plant community in a Mediterranean shrublands? How do annual plant communities in Mediterranean shrublands respond to extreme drought, in terms of changes in their species composition, species richness, species diversity and plant functional traits?

Above ground primary production as well as soil nitrogen content were significantly reduced by drought, while below ground production remained mostly stable. Consequently, the shoot:root ratio was significantly reduced by drought, indicating increased community resource allocation to root production at the expense of shoots. Species showed a wide range of different and often contrasting species-specific trait responses to extreme drought, with some increasing specific leaf area (SLA) while others decreasing it under drought. In addition, significant community compositional and structural changes were observed. Extreme drought seems to increase species diversity and evenness, likely due to release from competition with dominant species Brachypodium distachyon. We predict this effect to be counter-balanced by low biomass production and species abundance as extreme drought persists, eventually lowering future ecosystem primary productivity. We may further see drought adapted species become more abundant at the expense of drought intolerant species, altering plant dominance patterns and community structure. We conclude that extreme drought at the studied Mediterranean shrubland had a profound impact at all ecological scales, from the ecosystem level down to individual plant species.
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Introduction

Climate change is predicted to affect the Mediterranean basin by increasing the frequency, duration and severity of droughts, along with prolonged dry spells and intensification of summer heat waves (Lelieveld et al. 2012; Lionello et al. 2014; Spinoni et al. 2014). A steady decrease in annual precipitation, as well as a shortening of the wet season have already been observed in the eastern Mediterranean region (Shohami et al. 2011; Ziv et al. 2014). Vegetation in the eastern Mediterranean region has supported human settlements for thousands of years, providing genetic resources for some of the world’s most important crop species, grazing pastures for livestock and non-material ecosystem services such as natural landscapes and recreation (Blondel 2006; Fleischer & Sternberg 2006; Nadel et al. 2012; Snir et al. 2015). It is therefore essential to study the effects of the aforementioned increase in the frequency and intensity of droughts on ecosystem productivity and plant community composition and function. Extreme climatic events and changes in precipitation patterns have been shown to have profound implications for vegetation (Gutschick & BassiriRad 2003; Liu et al. 2015; Barbeta et al. 2015; Rita et al. 2016) and ecosystem functioning (Fay et al. 2003; Yahdjian & Sala 2006; Miranda et al. 2009). In order to understand and predict these implications it is necessary to define what constitutes an extreme climate event for a given ecosystem, an issue discussed in detail in the Background chapter.

In the eastern Mediterranean, water is the primary limiting resource for plant growth and ecosystem function, but in some occasions natural ecosystems have shown high resistance to changes in rainfall regimes (Miranda et al. 2011; Tielbörger et al. 2014; Estiarte et al. 2016). For example, Tielbörger et al. (2014) conducted a nine year rainfall manipulation experiment along an aridity gradient in Israel, where 30% rainfall was either added or subtracted from experimental plots. They found that these treatments
had little to no effect on natural plant communities, indicating either that the ecosystem is highly resistant to change, or that the change induced by the manipulation was not extreme enough. Knapp et al. (2015) analyzed 1,614 long-term (100 year) precipitation records from around the world in order to find what distinguished extreme dry and extreme wet years from average ones. They found that for arid ecosystems (mean annual rainfall <500 mm), extreme dry years (10% driest years of the historic record) had 60% less rainfall than average, whereas extreme wet years (wettest 10%) had 150% more than average. However, for mesic ecosystems (mean annual rainfall >1000 mm) extreme dry years had 30% less rainfall than average, whereas extreme wet years had 40% more than average. Thus, the more arid an ecosystem is, the greater the deviation from average needs to be for it to be considered as an extreme event.

Studies on the effects of climate change on vegetation typically focus on one or more of the following ecological scales:

1) **Ecosystem level**: Studies at this level measure the overall productivity of the ecosystem as expressed by annual or seasonal above and below ground biomass production. In addition, biogeochemical cycles are studied, including input and output of carbon and nitrogen, and carbon sequestration (Knapp & Smith 2001; Zhou et al. 2009; Beier et al. 2009; Tielbörger et al. 2014). For example, it is widely agree upon that above ground net primary productivity (ANPP) is positively correlated with precipitation (Knapp & Smith 2001; Wu et al. 2011), although different plant functional groups may respond differently (Gherardi & Sala 2015).

2) **Community level**: Research at this level focuses on plant community structure and composition, using species abundance and presence/absence data to quantify the richness and diversity of the community. Species can also be separated into functional groups (e.g. grasses, legumes, forbs, etc.) based on the species’ similar functional responses and strategies (Lloret et al. 2004; Kreyling et al. 2008; Jiménez-Alfaro et al. 2014; Rysavy et al. 2016). Observations of changes in
plant communities range from reduction of species richness and diversity (Lloret et al. 2004) and a gain of abundance of rare species (Gherardi & Sala 2015), to modifications of interspecific interactions induced by drought (Rysavy et al. 2016).

3) Individual level: At the level of a single plant, numerous plant traits have been studied, ranging from morphological and reproductive to phenological and ecological traits. Several frameworks have been developed concerning which plant traits are the most relevant in determining plant ecological strategies and their responses to disturbance and environmental change (Westoby 1998; Lavorel & Garnier 2002; Westoby & Wright 2006; Díaz et al. 2015). While many studies have been done on the relationship of plant traits and climate, few have tested for changes in important traits such as specific leaf area (SLA) and plant height as direct result of precipitation manipulation (Von Arx et al. 2012; Jung et al. 2014).
**Research Questions**

- What are the effects of extreme drought on above and below ground net primary production (ANPP and BNPP respectively), of annual plants in Mediterranean shrublands?
- How do annual plant communities in Mediterranean shrublands respond to extreme drought in terms of changes in their composition, species richness and species diversity?
- Do annual plant species traits change due to extreme drought conditions, and in case positive into what direction?

**Research Hypotheses**

- ANPP and BNPP will be significantly reduced as a response to increased limiting of resources imposed by drought.
- Drought will induce lower shoot:root ratios due to higher root investment in water uptake.
- Extreme drought will lead to lower species richness and diversity, and a significant change in community composition.
- Extreme drought will promote plants with lower SLA and leaf area.
- Extreme drought will significantly lower adult canopy height and seed mass.
- Extreme drought will increase plant investments in leaf construction leading to a reduction in leaf nitrogen content.
Background

Climate change in the Eastern Mediterranean region

Global climate change is predicted to intensify the global water cycle (Huntington 2006). This intensification is likely to cause major shifts in precipitation patterns worldwide, increasing annual precipitation amounts in the mid to high latitudes and decreasing them in the sub-tropics regions (IPCC 2014). Furthermore, an increase in the frequency and intensity of extreme events is expected so that for instance, individual thunderstorms produce more intense precipitation events and droughts become more prolonged and extreme (Trenberth 2011). In the Mediterranean region, an increase in the incidence number, duration and severity of droughts, along with prolonged dry spells, intensification of summer heat waves and a drop in annual precipitation are predicted (Lelieveld et al. 2012). In addition, a shortening of winter along with warming of spring, summer and autumn will have major impacts on terrestrial ecosystems and human activities (Giannakopoulos et al. 2009). These types of changes in the Mediterranean region are likely to have profound effects on native ecosystems. These were evident in a semiarid Mediterranean plant community in Spain where a delay in the beginning of rainfall season induced a decrease in aboveground productivity, number of individuals, and mean individual ANPP (Miranda et al. 2009). Additionally, strong changes in temperature during different seasons were reported to affect plant phenological timing in Mediterranean ecosystems (Gordo & Sanz 2010). Persistent drought has caused a general decrease in the number of seedlings in a Mediterranean shrubland (Lloret et al. 2009). As plant evolution has been found to be shaped by extreme events, the aforementioned effects are likely to intensify (Gutschick & BassiriRad 2003; Knapp et al. 2008). Prolonged droughts and higher temperatures are likely to increase the frequency of fires in the Mediterranean basin (Luis et al. 2001; Mouillot et al. 2002) and, accompanied with extreme heat waves, can increase irrigation demand by crops that are already on the limit of their temperature tolerance (Olesen & Bindi 2002). The Mediterranean basin has been recognized as one of the global biodiversity hotspots deserving extensive conservation efforts, but it is also one of the most threatened (Myers et al. 2000; Hoekstra et al. 2005). Human development, habitat loss and eminent climate change exert enormous pressures on natural ecosystems, making studies on their responses to climate extremes all the more pressing.
Extreme climatic events

An extreme event was defined by the Board on Atmospheric Sciences and Climate (2016) as: “a weather or climate event that is rare at a particular place (and, sometimes, time of year) including, for example, heat waves, cold waves, heavy rains, periods of drought and flooding, and severe storms. Definitions of what is rare vary, but an extreme weather event would normally be as rare as or rarer than a particular percentile (e.g., 1st, 5th, 10th, 90th, 95th, 99th) of a probability density function, estimated from observations expressed as departures from daily or monthly means”. This definition however, is problematic since an event can be deemed extreme from a statistical perspective, but not for the specific organism or ecosystem considered (Gutschick & BassiriRad 2003; Smith 2011). It is therefore more useful for the purpose of estimating the effects of future climate change on plant individuals and communities, to use a different definition of extremity. Smith et al. (2011) defined an extreme climatic event as “an episode or occurrence in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability”. Thus it is not enough for a climatic event to be statistically extreme, it must also evoke responses beyond the individual or population level, including the re-ordering of key or common species in the community, widespread species loss and/or invasion by novel species, with subsequent large and potentially persistent effects on ecosystem structure and function (Smith 2011).
Hierarchical responses to extreme climatic events

In this study we have taken a hierarchical approach to estimate the effects of extreme drought on a Mediterranean shrubland. A conceptual framework for ecosystem response to chronic resource alterations, has been previously formulated by Smith et al. (2009). In their hierarchical-response framework, they suggest first looking for responses to stress at the individual plant level. Then, as extreme conditions persist, a reordering of the community is expected as a result of some species being favored by changing conditions at the expense of others. Eventually, the community might become susceptible to invasion of exotic species more suited to the new environmental conditions. We have chosen to adopt this framework and measure three hierarchical levels: ecosystem, community and individual level. Following is a description of these levels and the properties measured in each, as well as an account of previously observed effects of climate change.

Ecosystem level

Net primary productivity (NPP) has been thoroughly studied as an ecosystem parameter, that influences, and is influenced by species biodiversity and composition, thus being an important indicator of ecosystem function and structure (Loreau et al. 2001; Hooper, Chapin III, Ewel, et al. 2005). NPP can be divided into above and below ground primary production (ANPP and BNPP respectively), with ANPP being generally more studied because of the technical difficulties of measuring BNPP (Hui & Jackson 2003). ANPP is generally positively correlated with mean annual precipitation (MAP) in grasslands (Sala et al. 1988; Knapp & Smith 2001), while the relationship between BNPP and MAP remains largely unexplored (Hui & Jackson 2003). BNPP is known to represent a significant portion of total NPP. Therefore, including it in studies of ecosystem productivity will provide a much deeper and more complete picture of net primary production (Jackson et al. 1996; Hui & Jackson 2003).

Soil nutrients are an additional ecosystem property to be considered. For example, plant growth in many natural and semi-natural terrestrial ecosystems is limited by soil nitrogen (N) content. Further, some ecosystems are characterized by strong competition for soil N between plants and soil communities of fungi and bacteria (Larsen et al. 2011). N is heavily influenced by climatic conditions such as precipitation and temperature, thus it is a valuable indicator of ecosystems’ response to environmental factors (Emmett et al. 2004; Sardans et al. 2008; Larsen et al. 2011). Generally, soil N content and cycling
has been observed to increase with increasing soil water availability and increasing temperatures (Sardans et al. 2008; Liu et al. 2009; Larsen et al. 2011). Since N is a limiting factor in Mediterranean systems (Fernández et al. 2006), it is pertinent to estimating the response and function of this nutrient at our specific studied ecosystem.

Community level

Changes in community composition and species abundance as a result of extreme events, can eventually alter the function of a community (Smith et al. 2009). Ecosystems’ response to extinction or invasion will be determined at least as much by which species and functional traits are lost and remain behind, as by how many species are lost. As a predictor of ecosystem properties, community composition is at least as important as species or functional richness alone (Hooper, Chapin III, Ewel, et al. 2005). The effects of climate change, specifically drought on community composition and structure, have already been observed across many ecosystems including Mediterranean shrublands (Lloret et al. 2009), high mountain communities (Jiménez-Alfaro et al. 2014), temperate grasslands (Kreyling et al. 2008; Cantarel et al. 2013) and deserts (Báez et al. 2013). Responses of community composition and structure are highly varied and site dependent. For instance, Cantarel et al. (2013) reported a steady decline in the fraction of grasses in the annual ANPP after four years of experimental drought, and Rysavy et al. (2016) showed that neighbor presence imposed a stronger negative effect on the survival of shrub seedlings due to competition intensity, which seemed to increase with drought. However, community changes are not always induced by experimental drought, as it needs to cross an ecosystem specific threshold (Tielbörger et al. 2014; Knapp et al. 2016).

Individual level

Plant traits have long been used for the purpose of predicting and explaining plants’ responses to biotic and abiotic environment. Grime’s C-S-R plant trait scheme (Grime 1974), defined plants based on their respective ecological strategy schemes (Competitors, Stress-tolerants and Ruderals), while more recently Westoby (1998) suggested a complementary version using specific plant traits, the L-H-S scheme (L - specific leaf area SLA, H - height of the plant’s canopy at maturity and S – seed mass). Díaz et al.
(2016) recently published the global spectrum of plant form and function, showing that most of the variation in the world’s plants traits can be explained by six traits (adult plant height, stem specific density, leaf size expressed as leaf area, leaf mass per area, leaf nitrogen content per unit mass, and diaspore mass) forming two main axes of variation representing plant size and the acquisitive-conservative continuum. This trend of attempting to understand plants’ functions and responses using plant traits, was accompanied by numerous studies on the connection between changes in plant traits induced by environmental change (Lavorel & Garnier 2002; Flombaum & Sala 2012). Studies in this field may focus on a single trait and its variation across environmental gradients and treatments (Poorter et al. 2009; Scheepens et al. 2010), or on mean trait values of whole communities and their responses to shifts in abiotic conditions (Jung et al. 2010; Sandel et al. 2010a). These studies often produce contrasting results, for instance SLA was found to increase (Moolman et al. 1996; Poorter et al. 2009) or decrease (Fernández et al. 2002; Thorne & Frank 2009) under experimental drought. Other studies have reported contrasting responses within communities, as different species reacted by changing their traits in different directions (Sandel et al. 2010a; Jung et al. 2014). It is therefore difficult to predict how individual plants will respond to future climatic changes, and more research is required in many different ecosystems and climatic scenarios.

We selected plant traits with the aim of reflecting plant strategies in response to environmental changes (Lavorel & Garnier 2002; Diaz et al. 2004; May et al. 2013; Díaz et al. 2015). The plant traits selected were (for full descriptions see Pérez-Harguindeguy et al. 2013 and Díaz et al., 2016):

1) **Specific leaf area (SLA)** - the one-sided area of a fresh leaf, divided by its dry mass. This trait differentiates between “conservative” species with physically robust, low SLA leaves with high construction costs per unit leaf area and long expected leaf lifespan (and thus duration of photosynthetic income) and “acquisitive” species with tender, low-cost high SLA leaves, and short leaf lifespan. SLA relates the area of light interception to leaf biomass, being an expression of how much carbon is invested per unit of light-intercepting area, and thus reflecting a trade-off between construction cost and longevity of lamina.

2) **Leaf area** - defined as the one-sided or projected area of an individual leaf, expressed in mm$^2$. Interspecific variation in leaf area has been variously related to climatic variation, geology, altitude and latitude, where heat stress, cold stress, drought stress, nutrient stress and high-radiation stress all tend to select for relatively small leaves.
3) **Adult canopy height** - the shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level, expressed in meters. It is associated with growth form, position of the species in the vertical light gradient of the vegetation, competitive vigor, reproductive size, whole-plant fecundity, potential lifespan, and whether a species is able to establish and attain reproductive size between two disturbance events.

4) **Seed mass** - mass of an average seed of a species, expressed in mg. Seed mass is composed of two parts:

   1) Establishment – the mass of the embryo and the mass of the reserve tissue both determine survival upon arriving at a new site.

   2) Dispersal and defense - the diaspore mass and structure determine the distance and mode of dispersal, as well as whether the seed will be exposed to predation.

Seed mass arranges species along a dimension describing the trade-off between seedling competitiveness and survival on the one hand, and dispersal and colonization ability on the other. Large seeds tend to help the young seedling to survive and establish in the face of environmental hazards (e.g. deep shade, drought, herbivory). Smaller seeds can be produced in larger numbers with the reproductive effort. Smaller seeds also tend to be buried deeper in the soil, particularly if their shape is close to spherical, which aids their longevity in seed banks.

5) **Leaf nitrogen content (LNC)** - leaf nitrogen content per unit of leaf dry mass. Directly related to photosynthesis and respiration, as the majority of leaf nitrogen is found in metabolically active proteins. LNC reflects a trade-off between, on the one hand, two different costs that increase with higher LNC (to acquire N, and potentially suffer more herbivory) and, on the other hand, the greater photosynthetic potential that higher LNC allows.
Methods

Precipitation manipulation experiments

One of the approaches for studying the effects of changes in precipitation patterns on terrestrial ecosystems, is through rainfall manipulation experiments (Beier et al. 2012). These experiments attempt to simulate changes in water availability by either adding or subtracting rainfall inputs artificially. These include changes in absolute annual precipitation amounts (Tielbörger et al. 2014), or changes to the frequency of precipitation events by predetermined artificial watering regimes (Miranda et al. 2009). Rainfall reduction experiments are usually done by constructing rainout shelters that exclude a predetermined percentage of natural rainfall, thus simulating drought over a selected experimental plot (Yahdjian & Sala 2002). As many experiments are done with different protocols, techniques and measurements, it is necessary to construct a large-scale comparative experimental framework, conducting coordinated drought experiments across many different ecosystems worldwide in order for it to be possible to compare among different experimental sites (Fraser et al. 2013). To achieve this goal, a new multi-site International Drought Experiment (IDE) was established using a common design and standardized protocol measurements. The present study has joined this initiative by including the Mediterranean shrublands ecosystem, generally underrepresented in rainfall manipulation experiments (Wu et al. 2011; Beier et al. 2012).

Study site

The study site is found in the Judean Hills area in Israel, situated on a south facing slope near Matta (31°42’ N, 35° 3’E; 600m above sea level, mean annual precipitation 540 mm). The site is located on Terra Rossa soil developed over hard limestone bedrock, and experiences a typical Mediterranean type climate with a mean annual rainfall of 540 mm and an average temperature of 17.7°C. Soil moisture field capacity on site is 40%, with a wilting point of 25% (Sternberg, unpublished data). The area is characterized by a Mediterranean shrubland dominated by the dwarf-shrub Sarcopoterium spinosum, interspersed by herbaceous vegetation. Annuals cover up to 90% of the open areas and include approximately 80% of all plant species (Tielbörger et al. 2014). Annual precipitation amounts during the experiment were 900 mm in 2014/15 and 575 mm in 2015/16.
Experimental setup

The site was established in September 2014, as an adjunct to the long-term experimental site located in the area (Sternberg et al. 2011). The 2014–’15 rainfall season was considered as a baseline zero-year for monitoring the vegetation before rainfall manipulations were applied. Ten 5 m × 5 m plots where randomly selected and marked in December 2014. In September 2015, before the onset of the second rainfall season, rainout shelters were constructed in half of the plots in a pair-wise randomized block design. Trenches were dug uphill from shelters to minimize downhill runoff. The randomized block design was established with the purpose of addressing the high spatial heterogeneity of the study area. Rainout shelters were covered by transparent plastic strips which cover 66% of the roof area, thus simulating a 66% decrease in rainfall amount. This amount was chosen according to long term (65 years) records of rainfall amounts in the area, and the driest 1% of years were found to have 60% less annual rainfall than

Figure 1 - Matta study site.
average (following the International Drought Experiment (IDE) protocol, see also http://wp.natsci.colostate.edu/droughtnet/ and Knapp et al. 2015). Three soil moisture and two temperature sensors (STE and EC-TM - probes for measuring water content and temperature and EC-5 Volumetric Water Content sensors by Decagon) were installed in two plots at 10 cm soil depth.
**Sampling**

**Above and below-ground biomass production, species composition and species diversity sampling**

In April 2015 (peak of flowering season) all plant species present in each plot were identified and recorded. Additionally, plant, rock and bare ground cover at each plot were visually estimated. Five 25 cm x 25 cm iron quadrats were randomly placed on the ground just outside the limit of each of the plots (around 30-40 cm), and all vegetation was harvested down to the soil surface. Plants were stored in paper bags and brought to the lab for identification and counting. Soil was sampled with a soil corer (15 cm depth x 5.3 cm wide) and placed in plastic bags and marked. In March 2016 (peak ANPP), above ground biomass was harvested within the plots, and embedded and external root ingrowth cores (see below) were removed for further analysis in the lab. Plant species present in each plot were recorded again as in April 2015. All above ground samples (2015 and 2016) were sorted by species, dried in an oven at 80°C for 48 hours and weighed. In 2016, the number of individuals per species at each sampled quadrat was counted. Soil samples were collected from embedded and external root ingrowth cores, dried in the same manner as above and then sieved through metal sieves with a decreasing aperture size for roots, which were then oven dried again and weighed. Fine grained soil collected from the finest sieve (125 µm), was dripped with HCl solution to extract inorganic carbon (Bisutti et al. 2004), and then analyzed using a CHNS Elemental Analyzer. Soil and organic carbon (OC), total nitrogen (N) and OC/N ratios were obtained.

In order to measure below-ground primary production we used two methods: First, four mesh root ingrowth cores (22 cm depth by 6 cm width composed of a plastic mesh with 0.5 cm aperture size), were inserted into previously dug 20 cm deep holes (around maximum soil depth in the area), in each plot (Fig.3). Embedded mesh root ingrowth cores were then filled with local soil collected from an adjacent area to the study site and a thin layer of topsoil (2-5 cm) was placed on top of them to renew the
presence of soil seed bank and plant litter. Second, three pipes (PVC pipes, 33 cm long with a diameter of 10.6 cm, hereafter external root ingrowth cores) were placed upright at each plot, also filled with local soil from the surrounding area, and a thin layer of topsoil was placed on their surface as done with the embedded cores. They were then covered with a black shading net to prevent overheating of the pipes (Fig. 4). The two root ingrowth core methods were used in order to overcome the pros and cons of each method in estimating below-ground productivity. Mesh root ingrowth cores embedded in the soil, represent a more whole picture of ecosystem productivity since they allow conditions most similar to the surrounding soil, competition between plants in and outside of the core and permit the flow of resources and soil organisms. However, it is impossible to distinguish between roots originating inside and outside the core, therefore BNPP measurement could be inaccurate. External root ingrowth cores

Figure 3 - Embedded mesh root growth core placement in the field.
on the other hand have the advantage of being an isolated environment, containing a miniature version of the community, thus biomass data can be more reliable here.

Figure 4 - External root growth cores before placement (top), after placement and covering before the onset of winter (bottom left) and in peak growing season at the time of harvesting (bottom right).
Plant traits measurements

The plant traits selected were: specific leaf area (SLA) adult canopy height, seed mass, leaf carbon and nitrogen content, and C/N ratios. We classified the sampled plant species into four plant functional groups which represented dominant growth forms at the study site and possibly different resource allocation traits, and thus could be used as indicators of functional change. The functional groups considered were: annual grasses (17 spp. 10% of total), annual composites (21 spp. 12% of total), annual legumes (32 spp. 19% of total) and annual forbs (50 spp. 30% of total) that represented the rest of the annual species. Eight dominant species of different plant functional groups were selected. The chosen species were:

1) Annual grasses - Aegilops peregrina, Brachypodium distachyon

2) Annual composites - Urospermum picroides

3) Annual legumes - Onobrychis squarrosa

4) Annual forbs - Stachys neurocalycina, Anagallis arvensis, Lomelosia palaestina, Linum pubescens

Plant traits were measured in the field and in the lab following the protocols and methods established by Pérez-Harguindeguy et al. 2013.

Leaf traits and seed mass

Three adult individuals from each species were randomly selected in each plot, and from each three healthy leaves that were exposed to maximum sunlight were harvested. Leaves were then stored in cool and moist conditions until they were scanned in the lab (Pérez-Harguindeguy et al. 2013). Leaf area was
estimated using Leafarea software (A. P. Askew, University of Sheffield, UK, downloadable from the Nucléo DiverSus toolbox), which processed an image produced using a desktop scanner. Leaves were then dried for 48 hours in an oven at 80°C and weighed. Leaf nitrogen and carbon content was obtained for Brachypodium distachyon, Urospermum picroides and Lomelosia palaestina by grinding the oven-dried samples and analyzing them with a CHNS Elemental Analyzer. In May 2016 seeds were collected from the selected species then counted and weighed. Single seed mass was calculated by dividing total weight of seeds by their number.

**Statistical analyses**

All plant traits and biomass data were normalized via log transformation before any statistical test were performed. N and OC content data were arcsine-transformed prior to analysis. A two way ANOVA for randomized block design was performed on all traits and biomass data with treatment as a fixed effect to determine significant differences between droughted plots and controls. Canonical correspondence analysis (CCA) was used to determine differences in species abundance between treatments. Changes in species composition between treatments, were determined by principal coordinates analysis (PCoA) on presence-absence data. Distance-based redundancy analysis (db-RDA) was calculated and ANOVA was performed on the ordination results.

All statistical analyses were performed using R (R Core Team (2016) and the statistical package JMP 11 (SAS Institute Inc., Cary, USA).
Results

Effects of treatments on soil moisture and temperature

Soil Volumetric Water Content (VWC) was lower under the rainout shelter during the beginning of the rainfall season from October to January 1\(^{st}\) and from March 18\(^{th}\) (peak growing season) until April 18\(^{th}\) (Fig. 5). Soil temperature was on average one degree Celsius warmer under the rainout shelters relative to ambient control. In droughted plots soil moisture increased above wilting point on January 1\(^{st}\) until March 1\(^{st}\). Afterwards soil moisture decreased below wilting point and remained so for the remainder of the growing season.

Effects of drought on biomass production and species abundance

Above-ground as well as total biomass production (ANPP + BNPP) was significantly reduced in drought plots in all harvesting methods used (standard vegetation sampling, embedded mesh and external root ingrowth cores). In addition, an ANCOVA was performed using previous year (2015) biomass production as covariate (F = 0.0036, p > F = 0.95), to control for any production difference between plots that is unrelated to the treatment. The effects of natural site heterogeneity and year to year changes in ANPP were thus found to be insignificant. Richness in random samples explained 24\% of the variance in ANPP in drought plots, and 17\% in control (Fig 6). The relationship between ANPP and species richness was significantly different between treatments in 2016, in contrast to 2015 (before treatment) when the relationship was similar (Fig. 6). Below-ground biomass production showed no significant difference between treatments in embedded mesh root ingrowth cores, but was slightly reduced by drought in external root ingrowth cores. Shoot:root ratio was significantly reduced by drought treatment in embedded mesh and external root ingrowth cores, but mostly due to lower above-ground biomass production while below ground production remained similar (Fig. 7). Embedded mesh ingrowth cores showed a several-fold higher variability compared with external ingrowth cores. The coefficients of
Soil volumetric water content ratio

Figure 5 – Soil volumetric water content for drought plots and control (a), and soil temperature difference (control – drought) between the treatments (in Celsius) (b). These readings refer to annual plants’ growing season only.
Figure 6 – ANPP as a function of species richness in random samples in 2015 (a) and 2016 (b). Drought samples are colored orange and control samples are colored blue. Significance value is denoted by asterisks: ** - $p < 0.01$, and refers to treatment effects.
Figure 7 – Above ground biomass production obtained from random sampling (a), Total, above and below ground biomass production per treatment (C, blue – control, D, brown – drought) per method (b-h) and shoot/root biomass production ratio per treatment per method (i and j). Error bars are standard errors of the means. All p-values for biomass are calculated from two way ANOVA performed on log transformed data, using randomized block design. Significance values are denoted by asterisks: * - p<0.05, ** - p< 0.01, *** - p<0.001.
variance for external cores were 17% and 23% in control and drought respectively, and 39% and 65% in control and drought respectively for embedded mesh cores. Canonical correspondence analysis (CCA) was performed based on individual species biomass and relative abundance data, using Monte Carlo permutations to test for differences between treatments (Fig. 8), with biomass distribution being significantly different (p < 0.05) in drought plots relative to control. A similar result was found for species abundance distribution (p < 0.003). Wilcoxon’s signed-rank test was used on per-species average biomass and average abundance (averaged over plots and then over treatments), with average per-species biomass not showing significant difference between treatments. However, species abundance showed significantly higher values in control plots (p < 0.05) compared with drought plots.

Table 1 – Plot species richness. Each block includes a control + treatment pair, with richness values obtained by a survey performed in both years before harvesting random samples.

<table>
<thead>
<tr>
<th>Block</th>
<th>2016</th>
<th>2015</th>
</tr>
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<td>D</td>
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<tr>
<td>9-10</td>
<td>55</td>
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Figure 8 - Canonical correspondence analysis (CCA) for per-species biomass 2015 (a) and 2016 (b) and per-species abundance CCA 2016 (c). Light blue polygons include control plots, and light brown ones refer to drought plots. Significance values are denoted by asterisks: * - p<0.05, ** - p< 0.01, *** - p<0.001.
Comparing biomass of functional groups, the greatest contribution to the difference between the treatments was attributed to grasses, which had nearly 43% lower biomass production in drought plots compared with control. Forbs did not respond significantly, although compared with the baseline year (2015), grasses surpassed them in biomass production (Fig. 9 a, b). Most of grass biomass came from individuals of *Brachypodium distachyon*, which dominated this functional group in both 2015 and 2016 (Fig. 9).

**Species composition and diversity**

Principal coordinate analysis (PCoA) was done on presence-absence data recorded in the field (converted into Jaccard distance matrix). The ordination showed an overlapping of treatment plots in 2015 (zero year) and complete separation in 2016 following the drought treatment (Fig. 10 a, b respectively). A correlation test was performed on distances in the plot and in the original matrix to confirm correct representation of the ordination plot (Fig. 10 d, c). Subsequently distance-based redundancy analysis

![Figure 9](image_url)

Figure 9 – Above ground biomass production obtained from random sampling per year per functional group (a-b), and biomass of *Brachypodium distachyon* per year in control (blue) and drought (brown) plots. Error bars are standard errors of the means. All p-values for biomass are calculated from two way ANOVA performed on log transformed data, using pair-wise randomized block design. Significance values are denoted by asterisks: * - p<0.05, ** - p<0.01.
Figure 10 – PCoA ordination plots for species presence-absence data from 2015 (a) and 2016 (b) (plot numbers are arbitrary). Correlation tests for distances in plots versus original Jaccard distances for 2015 (c) and 2016 (d). Light blue polygons include control plots, and light brown ones refer to drought plots. Significance values are denoted by asterisks: * - p<0.05, ** - p<0.01, *** - p<0.001.
(db-RDA) was performed with treatment as constraint, with 16% of the variation explained by the treatment. Species composition was found to be significantly different between control and drought plots in 2016 ($p < 0.05$), compared with no significant differences in 2015 (Fig. 11). Rarefaction curves were calculated from the abundance data (Fig. 12). When correcting for sampling efforts by samples, the control treatment curve was higher than the drought treatment curve. However, individual based rarefaction showed the opposite relationship. The individual based rarefaction curve shows that, species richness is gained faster in drought than in control plots but reach saturation quickly and remaining below the control treatment curve. The sample based curve shows the control curve rising faster and remaining above the drought curve. However, using a EcoTest.individual and EcoTest.sample null model tests for rarefaction curves from rareNMtests R package (Cayuela et al. 2015), only the individual based curves were significantly different ($p<0.01$), which is in agreement with absolute plot richness values obtained by the species survey. Thus, extreme drought treatment did not reduce species richness at the plot level (Table 1). Effective Shannon diversity index was calculated and compared for each treatment using the above null model tests, and was found to be significantly higher in drought plots only in individual based rarefaction curves (Fig. 13). Sample based rarefaction showed no significant difference in effective Shannon index between treatments. Pielou’s evenness was significantly higher on droughted plots ($p = 0.03$) relative to control (Figs. 14).

![Figure 11](image-url)

**Figure 11** – Constrained Analysis of Principal Coordinates (CAP) or Distance-based redundancy analysis (db-RDA), on species composition in 2015 (a) and 2016 (b). Difference between treatment groups was only significant in 2016. Light blue polygons contain control plots, and light brown ones contain drought plots. Significance values are denoted by asterisks: * - $p<0.05$. 

Figure 12 – Sample-based (a) and individual-based (b) rarefaction curves for control (light blue line) and drought (light brown line) plots.

Figure 13 – Null model tests of significance of effective Shannon index for sample based (a) and individual based (b) rarefaction. The drought curve is represented by the lower curve in the sample based rarefaction (a) and by the higher curve in the individual based rarefaction (b).
Figure 14 – Relative abundance bar plot (log scale) based on 2016 random sampling, for control (blue) and drought (brown) plots (a), and Pielou’s evenness for 2016 (b).
Figure 15 – Relative ANPP bar plot based on 2015 (a) and 2016 (b) random sampling, for control (blue) and drought (brown) plots.
With the exception of *Brachypodium distachyon* and *Linum pubescens*, all studied species were found to be significantly shorter in drought plots compared to control plots. Responses of SLA to drought were mixed with *Aegilops peregrina*, *Lomelosia palaestina* and *Brachypodium distachyon* showing higher values in droughted plots, while *Linum pubescens*, *Stachys neurocalycina* and *Anagallis arvensis* showed opposite results. *Onobrychis squarrosa* and *Urospermum picroides* showed no significant SLA treatment response. Regarding leaf area, several strategies were observed: *Aegilops peregrina*, *Lomelosia palaestina* and *Brachypodium distachyon* increased SLA and leaf area. *Linum pubescens* reduced its SLA and leaf area while *Anagallis arvensis* and *Stachys neurocalycina* reduced their SLA but only slightly increased leaf area (non-significant). *Urospermum picroides* decreased its leaf area under drought, but showed no significant change in SLA. Finally, *Onobrychis squarrosa*, the only legume sampled, showed no effect on leaf traits. Only *Brachypodium distachyon* showed an effect on seed mass, with lower (~15%) values in droughted plots (Table 2). No measureable effect was detected for leaf nitrogen content, but *Lomelosia palaestina* showed a higher C/N ratio in control plots.
<table>
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<tr>
<th>Species</th>
<th>Trait</th>
<th>Control</th>
<th>Drought</th>
<th>p-value</th>
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</thead>
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<td><em>Brachypodium distachyon</em></td>
<td>SLA</td>
<td>18.16±1.80</td>
<td>&lt; 20.70±1.02</td>
<td>0.00162</td>
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<tr>
<td></td>
<td>H</td>
<td>11.25±0.44</td>
<td>≈ 10.41±0.38</td>
<td>0.09478</td>
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<td></td>
<td>LA</td>
<td>116.15±8.86</td>
<td>&lt; 269.84±32.1</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>SM</td>
<td>4.48±0.25</td>
<td>&gt; 3.79±0.13</td>
<td>0.0101</td>
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<tr>
<td><em>Aegilops peregrina</em></td>
<td>SLA</td>
<td>19.23±5.01</td>
<td>&lt; 29.66±13.34</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>15.65±0.4</td>
<td>&gt; 13.34±0.37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>LA</td>
<td>83.3±7.13</td>
<td>≈ 130.57±12.95</td>
<td>0.006372</td>
</tr>
<tr>
<td></td>
<td>SM</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Anagallis arvensis</em></td>
<td>SLA</td>
<td>26.16±3.31</td>
<td>&gt; 15.06±2.18</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>8.23±0.3</td>
<td>&gt; 6.78±0.23</td>
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<tr>
<td></td>
<td>LA</td>
<td>52.04±2.13</td>
<td>≈ 59.04±2.58</td>
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<tr>
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<td>0.37±0.02</td>
<td>≈ 0.37±0.02</td>
<td>0.1636</td>
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<tr>
<td><em>Linum pubescens</em></td>
<td>SLA</td>
<td>25.58±3.28</td>
<td>&gt; 8.11±1.37</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
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<td>18.7±1.66</td>
<td>≈ 15.5±0.71</td>
<td>0.297678</td>
</tr>
<tr>
<td></td>
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<td>67.1±5.62</td>
<td>&lt; 103.61±9.7</td>
<td>0.00135</td>
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<tr>
<td></td>
<td>SM</td>
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<td>0.1619</td>
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<td><em>Lomelosia palaestina</em></td>
<td>SLA</td>
<td>16±1.38</td>
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<td>0.6394</td>
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<td><em>Stachys neurocalycina</em></td>
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<td>18.77±1.48</td>
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<td>&lt;0.001</td>
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<td></td>
<td>H</td>
<td>11.68±0.33</td>
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<tr>
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<tr>
<td></td>
<td>SM</td>
<td>0.71±0.08</td>
<td>≈ 0.75±0.08</td>
<td>0.8133</td>
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<tr>
<td><em>Urospermum picroides</em></td>
<td>SLA</td>
<td>21.86±1.35</td>
<td>≈ 52.01±14.77</td>
<td>0.131</td>
</tr>
<tr>
<td></td>
<td>H</td>
<td>22.01±2.23</td>
<td>&gt; 14.41±0.87</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Table 2 - Trait abbreviations are specific leaf area in mm²/gram (SLA), plant height in cm (H), leaf area in mm² (LA), and seed mass in mg (SM). All p-values are calculated from two way ANOVA performed on log transformed data, using randomized block design. NA - Not available.
The coefficients of variance (CV) of traits of the different species were different between treatments, with some of the species having higher variability under drought while others showing lower variability (Table 3). Additionally, some species showed no difference in CV between treatments.

**Soil nitrogen and organic carbon**

Soil nitrogen content was significantly reduced by drought treatment, while carbon content increased though not significantly. C/N ratio increased strongly in all plots from 2015 to 2016 (Fig. 16).
Figure 16 – Comparison between soil organic carbon and nitrogen content and C/N ratio in control plots and drought plots in 2015 (blue) and 2016 (brown). Significance values are denoted by asterisks: * - p<0.05, ** - p<0.01, *** - p<0.001.
Discussion

Measurements from soil moisture sensors in the field showed that the effects of the rainout shelters were greatest at the beginning and end of the growing season (end of autumn and spring respectively). This resulted in effectively shortening the growing season, which has been found to have a significant effects on phenological timing of plants, i.e. germination time, flowering, seed and fruit set, etc. (i.e. phenology; Gordo & Sanz 2010) and is one of the expected outcomes of climate change for the region (i.e. shortening of the growing season). For instance, a study in a semi-arid Mediterranean plant community has shown that a delay of the first onset of watering suspended germination, and decreased ANPP, number of individuals, and mean individual ANPP (Miranda et al. 2009). The shelters induced a one degree warming during winter, which potentially increased evapotranspiration and reduced soil water content even further, exacerbating drought stress and reducing plant biomass production (Eatherall 1997; De Boeck et al. 2007). Thus, it is likely that the measured warming in our rainout shelters contributed to increasing soil water deficit enhancing the drought effect.

The effects of extreme drought were evident at the ecosystem level, as ANPP was significantly reduced. This result is not uncommon as several studies have already observed reductions in ANPP caused by extreme drought (Peñuelas et al. 2007; Wu et al. 2011; Byrne et al. 2013). This can be explained in part by delayed germination causing lower recruitment rates or due to a shortening of the wet season (Fay et al. 2003; Walck et al. 2011). The reduction in ANPP in our study was mainly attributed to the dominant annual grass functional group, while annual forbs showed no significant response. The reduction in ANPP of annual grasses can be attributed to the fact that species within this group have relatively shallow roots, while drought mainly affected the upper soil layers as shown in similar studies (Fay et al. 2003; Heitschmidt et al. 2005). Additionally, most of the grass biomass was attributed to the dominant annual grass *Brachypodium distachyon*. Previous studies on this species have shown it to have high phenotypic
plasticity in Mediterranean regions of Israel, a property also expressed in its phenological responses to drought (Aronson et al. 1992). BNPP showed a significant reduction only in the external root ingrowth cores, which could be the result of increased drying of the soil, with no lateral water movement. This result indicates that the drought treatment was significantly more effective in external ingrowth cores, crossing a threshold in significantly reducing BNPP, an effect which was not observed in embedded mesh ingrowth cores. Embedded mesh ingrowth cores had a several-fold higher variability in root mass data relative to external ingrowth cores. This was likely caused by the very high heterogeneity of the study site, whereas external cores were very similar in soil conditions, and were not exposed to biotic interactions as much embedded mesh cores. Thus the reduction in BNPP in external ingrowth cores under drought might be representative of the response to drought excluding both biotic and abiotic interactions present in the field. Embedded mesh ingrowth core hint that *in situ* processes might have a stabilizing effect on BNPP. BNPP has previously shown many different and contrasting responses to drought, from reduction in biomass production (Frank 2007) to BNPP stability across years of experimental drought (Jentsch et al. 2011) to inconsistent responses (Byrne et al. 2013). This diversity of results could be attributed to the fact that these studies were performed in different biomes and climates as well as under different treatment protocols. As the structure and behavior of root systems across biomes is highly diverse, such differences are to be expected (Jackson et al. 1996). A significant reduction in shoot:root ratio under drought was measured in both embedded ingrowth mesh cores and external root ingrowth cores, which resulted in maintaining stable levels of BNPP while ANPP was reduced significantly. Lloret et al. (1999) showed that seedlings in a Mediterranean system had a better chance of surviving the summer drought when they allocated more resources to root growth. It is possible that Mediterranean annual plants, already having among the highest root allocation rates of the different world biomes, have evolved to divert more resources to roots when sensing water stress at the earliest life stages (Jackson et al. 1996). Indeed, annual plants have been previously found to resist drought by accumulating reserves in stems or roots (Chaves
et al. 2002). For example, *Lupinus albus*, a Mediterranean annual plant, responded to a 15 day water shortage by shedding 50% of its leaves while increasing stem dry weight by 55% (Rodrigues et al. 1995). On a global scale, Mokany et al. (2006) found that shoot:root ratio increased significantly with increasing annual precipitation, with shrubland and grasslands having among the lowest ratios, thus indicating a global trend of higher investment in roots in drier habitats.

Soil N was lower on all plots in 2016 compared with 2015 but significantly more in droughted plots, with a reduction of nearly 30% compared with only a little over 14% in control plots. N mineralization has been attributed to microbial and micro fauna activity in the soil, an activity highly sensitive to soil moisture levels (Emmett et al. 2004; Larsen et al. 2011). Thus, the decrease in all plots can be explained by the fact that 2015 was an extremely wet year (nearly 900 mm of rainfall – 66% higher than mean annual rainfall), and 2016, an average one (575 mm). Therefore, N mineralization was naturally lower, an effect which was reinforced by the drought treatment. Interestingly, we found no significant change in soil carbon content, although previous studies have found that soil carbon generally decreases under drought, due to reduced soil moisture which leads to lower plant litter decomposition rates and microbial activity (Borken & Matzner 2009; Bloor & Bardgett 2012). The previous extremely wet and productive year, combined with the measured reduction in soil N can account for the significant increase in soil C/N ratio.

At the community level, extreme drought significantly changed species composition and species diversity. Tielbörger et al. (2014), have previously reported no significant changes in species composition or species diversity after nine consecutive years of experimental drought in a study site adjacent to the current experiment. This was likely due to the fact the 30% reduction in rainfall throughout the experiment was not considered an extreme climatic event by the native plant community (Smith 2011; Knapp et al. 2016). Thus, the current study’s 66% reduction in rainfall was sufficiently extreme to cause a significant change in this ecosystem. The reduction in species diversity and change in species composition have been reported in similar studies in Mediterranean ecosystems (Lloret et al. 2004; Peñuelas et al. 2007;
Báez et al. 2013). As our study site is home to nearly 300 plant species, 163 of which have been sighted in our experimental plots, it is reasonable to assume species will display a wide variety of different possible responses to extreme drought, an assumption confirmed by the difference in trait response observed. Indeed, differences in species-specific biomass production between treatments were varied, with both higher and lower values of biomass production measured in droughted plots. Community evenness was higher in droughted plots, possibly due to the strong dominance of *Brachypodium distachyon* whose abundance and biomass were greatly reduced by the drought treatment. This in turn reduced competitive pressure and allowed other species to increase their relative abundance (Kardol et al. 2010). This change is clearly evident by the steeper slope of ANPP versus species richness in droughted plots (Fig. 6). Because of the increased evenness of droughted plots, increasing richness adds significant amounts of biomass to the total, where as in control plots each species contributes less biomass (Hooper, Chapin III, & Ewel 2005). This increase in evenness might explain why no difference in plot level species richness was found between treatments: Release from competition and an increase in the abundance and biomass of rare species in droughted plots, might counterbalance the loss of species to the extreme conditions induced by the treatment. This coincides with drought individual based rarefaction curves showing higher values of richness and effective Shannon diversity index, indicating higher small scale species diversity in these plots. Observed lower abundance of species under drought, especially *Brachypodium distachyon*, might hint at further future change as the study moves into its second year of extreme drought (Lloret et al. 2004). The rapid gain of species in the individual based rarefaction curve, suggests an additional structural and spatial change. As one counts individuals in drought plots, species richness quickly reaches a maximum, perhaps caused by homogenization of the distribution of species in drought plots, due to reduced competition from the dominant species. All of the above suggests a strong divergence between the treatments, effectively creating two separate communities with different species composition and structure (Spehn et al. 2005).
Five out of the eight sampled species showed significantly shorter plant height under drought, with the remaining three showing non-significant reductions, validating our original hypothesis for shorter plant height under extreme drought. In contrast, the response of SLA measured for these species was highly variable, including higher and lower values under drought with two species showing no significant response. Our original hypothesis was that extreme drought will cause plants to reduce their SLA. Previous theoretical work suggests extreme resource deprivation may cause plants to adopt more conservative strategies associated with lower SLA (Grime 1981; Westoby 1998; Díaz et al. 2015). There is also experimental work showing this to be the case in a variety of climatic conditions (Casper et al. 2001; Fernández et al. 2002; Thorne & Frank 2009). We were surprised to find three species of the total eight sampled, to have significantly higher SLA and leaf area values under drought. The species that showed higher SLA under drought were the grasses *Brachypodium distachyon* and *Aegilops peregrina* and the annual forb *Lomelosia palaestina*. Leaf area responded in a multi-directional manner, confirming or contradicting expectations. This result is rarely found in the literature. One study by Poorter et al. (2009), suggested that perhaps plants raised SLA in order to reach reproductive stage faster, by investing in larger and thinner leaves. This type of large intraspecific trait variability has been reported before by Jung et al. (2014), who suggested that species can combine trait responses in different ways to cope with drought, which can result in a lack of convergent responses of a given trait among species. They further proposed that since trait values can be used as a surrogate for species niche (Violle & Jiang 2009), the intraspecific trait response to drought can vary depending on whether drought moves species closer or away from their ecological optimum (Albert et al. 2010). Albert et al. (2010), proposed that each trait responds to environmental with a species-specific distribution, depending on the individual’s location on the species geographic and environmental range. Assuming bell-shaped curves for the current study’s species, a higher trait variability under drought might indicate a species being pushed outside of it’s optimal niche. Conversely, a species showing lower variability under drought might be closer to it’s ecological optimum.
Sandel et al. (2010) proposed that plant communities might respond to climate change in a two-phased response. In the initial phase, shifts in species abundances within the local species pool, may cause shifts in community mean traits. In the second phase, species immigration and extinction cause trait shifts over longer timescales. They argue that trait shifts in these two phases may often be in opposite directions. However, in our study changes in species composition, richness and diversity had already been observed, thus our studied community responded across multiple ecological scales and quite rapidly.

Conclusions

Extreme drought at the studied Mediterranean shrubland had profound effects at all ecological scales, from the ecosystem level down to individual plant species. Total primary production and individual species abundance were significantly reduced by drought, accompanied by an unexpected increase in species diversity and community evenness. The plant community showed a wide range of different trait responses to extreme drought, possibly contributing to the already observed compositional changes. We can therefore conclude that the applied treatment of 66% reduction in annual rainfall was extreme enough to invoke a significant and multilevel response in this ecosystem, which had shown high resistance in previous studies within a 30% rainfall reduction range (Tielbörger et al. 2014). Future studies aiming at understand responses to extreme drought events, should therefore preferably take into consideration the long term variation in climatic conditions and choose accordingly the suitable precipitation reductions for the considered area, in case that a threshold is searched (Smith 2011; Knapp et al. 2015). In this study we were able to sample a small subset of the species present in our study site for just a few of their traits. Species-specific trait responses to extreme drought are turned out to be unpredictable using current knowledge of the studied community. Collecting a more comprehensive account of plant traits not measured here and expanding sampling into a higher number of species, will allow us to provide a more complete picture of the response of the community as a whole. In addition, for each species selected, a complete profile of
each trait for its geographical and environmental range should be assembled prior to field measurement. Thus, the intraspecific distribution of traits can be used to draw more informed conclusions regarding the effects of the treatment on each trait.

The studied ecosystem showed no significant change in species richness at the ecosystem level. We suggest this may be due to the existence of a large regional species pool at the study site. Out of the 300 species recorded at the adjacent study site over a decade ago, 148 species were identified within the experimental plots in 2015. In 2016, an additional 15 new species out of the 300 were identified. Nevertheless, a clear separation in plant community composition and structure was observed hinting at a likely future divergence between the treatments.

Our results have shown that extreme drought can lead to important changes at different ecological scales in Mediterranean shrublands. We predict that under continued extreme drought, adverse effects will become further evident through a reduction in primary productivity and individual species abundance. This will likely lead to the exclusion of several species currently present at the site, thus lowering species richness and diversity, and changing community dominance relationships.
Bibliography


תקציר

תרגישו שנתייםcliniken חולים עליה בתרדויות ישרותאי קייז'יים. במקראים הם החסינים.מודלים ציבועים על
עליזה בתרדויות, בטעותה במשרור של ברות. מקדה הצהרה בשמהו בسكنא של גוש במקרא עד
ידי המשקעה לשנת, עלון על השאלות הבאות: מהו כתובות של ברות
כקז'יון על היהודים ארסי ונשע ברות הצלימה חזרה-שובים בברות של תייגות בהרי יהודה? ציד ברות קז'יון

הشاشة על הרכב המים, עשר המינים, מזון המים וה殖民ות הרכב השופותアクולהיג' וה cupid. וה

התחזוקה האר ז'ץ'ון ניתן brukור של היהודי היא שמו על-ตน. עד-_bhעד,omo לג' מולテーレק
ברקע, ברקע השונות התחרות-קריקטוע כדי לעקירה. כתובת המכר, י condi burו בברז'י, עד
בחלקות הצארות. דיבר משוער על התוכן של הסבר של ברות הזמינות לתוך גיוס הלונינו. המינון החריו לוז
רחב של מתן בתקנות לעיל שבלבד, יMocks החולות של התוכן הבטוח והלומדים לשנוזה מגון הצארות
לברור. בנסוע כל ר, עם עבורה צ'יןוק הצארות ברבר השונות הצארות ובברה, יMocks החולות התוכן השופות

הצבור התוכן לשוןית יוזר (higher evenness) המבנה חלולים ההוכמה ב-המינון ההופך לשוןית

מקסימיות אם כן, שבצרות הקז'יון גולמה השתיית משוע görmית. לכל קני המידה שבדמה. מחזור האקורסנטה דע לדמת

הפרת. בטון הצארה של הנשיות, בצארת קז'יון גולמה השתיית הבנונים המינים בשוןית (evenness) התוכן, 60
נן achieה נחריים של שחרור מיניםdisplay מתחרות על מים ולאמשנה acompanhית. מחזור המקסימיות עד לדמת

בחלקות הצארות ג'ל ידוע הצארות ביזור היבוסה (בחלק המקסימים יוזר %50) ובשפר של חקל גזר

מחזורים. עם המשך הצארות הקז'יון, ענו חניות השבוצה האתקיר ידוע השפר וביבוסה של מינים ז-שתית
נתזז לירדה ביצירות האקורסנטה והשוני הרכב הרבחה ויסוי הדומיננטהlı כשאר מימי המותאמים לתאנים

הצבור של המים של השוניות שיאים מתאימים.