Whole plant community transplants across climates reveal total community stability due to large shifts in species assemblage

Authors: Sara Tomiolo[a,b*], Mark C. Bilton[a], Katja Tielbörger[a]

Affiliation:

a- Department of Ecology and Evolution, Plant Ecology Group, University of Tübingen, Auf der Morgenstelle 5, 72076 Tübingen, Germany

b- Department of Bioscience, Aarhus University, Vejlsøvej 25, 8600 Silkeborg, Denmark

Contacts:

*Corresponding author: sara.tomiolo@gmail.com; **Orcid ID:** orcid.org/0000-0002-5071-5851

Mark C. Bilton: mark.bilton@uni-tuebingen.de

Katja Tielbörger: katja.tielboerger@uni-tuebingen.de

Running headline: Community stability under climate change

Keywords: annual plant communities, climate change, Climatic Niche Groups, community ecology, reciprocal transplants, determinants of plant community diversity and assemblage, distribution range, community stability, field experiments

Abstract

Climate change will decrease average precipitation and increase rainfall variability in Eastern Mediterranean regions. This may affect the performance of many plant species either directly or via altered biotic interactions in ways that are hard to predict. In such highly fluctuating climates, year-to-year community variation may override long-term selection processes, thus masking directional community responses to climate change.

Here we tested short-term responses of dryland plant communities to sharp changes in climatic conditions, by means of whole community reciprocal transplants of soil and seed banks. We exposed annual plant communities to two very different climates (Mediterranean and semi-arid) and measured changes in community composition, total biomass, plant density, and species diversity. In addition, we grouped species into dry-adapted and wet-adapted species in each community.

Our results revealed that climate played a large role in determining community assembly. For both community origins, we observed a relative increase of dry-adapted species when exposed to the drier climate, and a relative increase in wet-adapted species in the wetter climate. However, the compositional shifts were much larger in semi-arid origin communities. At the same time community density, biomass and species richness remained remarkably stable across climates, indicating that community stability was maintained between climates by predictable asynchronous shifts of species. Similar but smaller shifts were present in the Mediterranean origin communities, where exposure to the drier climate reduced biomass and species richness.

Our study suggests that large asynchronous variation in species abundances, matching high year-to-year rainfall variability, may provide a mechanism for

community homeostasis, and slow down selection processes in response to climate change. However, increased occurrence of extreme droughts exceeding the climatic fluctuations to which species are adapted may, in the long-term, lead to loss of wet-adapted species.

Introduction

Understanding how climate may alter overall available resources (Sardans et al. 2008, Garcia et al. 2014) and impact upon community structure (Tilman and Downing 1994, Gilman et al. 2010) is a major challenge in current ecological research (Maestre et al. 2012, Parmesan and Hanley 2015). In cold regions for example, warming is likely to improve growing conditions and thus increase plant community biomass by increasing nutrient mobilization and expanding the length of the growing season (Garcia et al. 2014). In contrast, decreased rainfall in drier regions will likely have negative impacts on primary productivity, community composition, and their corresponding ecosystem services (Sala and Lauenroth 1982, Peñuelas et al. 2007, Miranda et al. 2011). These effects may be particularly strong in those dryland ecosystems for which climate predictions indicate increasing incidents of droughts (Cubasch et al. 1996, Smiatek et al. 2011). Here, droughts and increasing temperatures will increase evapotranspiration, shorten the growing season and limit access to nutrients, thereby decreasing total community biomass (Peñuelas et al. 2007, Doblas−Miranda et al. 2015, Harrison et al. 2015). In extreme cases, this may lead to the collapse of entire ecological communities (Forey et al. 2010).

One of the predicted impacts of climate change is a re-assembly of plant communities (Hobbs et al. 2006, Williams and Jackson 2007, Alexander et al. 2016) due to the differential ability of single species to either track their climatic niche or to survive under changed conditions, by means of adaptation or plasticity (Fernandez-Going et al. 2013, Shi et al. 2015). Such community reshuffling may be expressed in a loss or gain of certain species, a shift in species relative abundance or both. In plant communities already exposed to large inter-annual variations in climate, immediate rearrangement of community assembly in response to climate extremes may be an

inherent property of plant communities, and may promote community stability in the long-term. This effect is particularly pronounced when species numbers are large and population sizes vary asynchronously (Doak et al. 1998, Schindler et al. 2015). Indeed, ecological theory and models support the idea that high inter-annual variation in species response to climate can lead to community-level stability (Anderson et al. 1982, Tilman et al. 1998, Thompson et al. 2015, Abbott et al. 2017). This may be an important mechanism for maintaining dryland communities' stability in response to large year-to-year variation in rainfall, and for slowing down ongoing selection processes due to climate change (Bonebrake and Mastrandrea 2010, Bilton et al. 2016).

Although long-term climate manipulations are the gold standard in ecological climate impact research and are fundamental to understanding long-term community shifts (Brown et al. 2001, Rinnan et al. 2007, Blume-Werry et al. 2016), they are very costly to set up and maintain, often outliving funding cycles and scientific research positions (Lindenmayer et al. 2012). The monitoring of communities for short-term responses may be a useful complement to long-term experiments, as besides being less costly, can be vitally important for parsing mechanistic information about plant responses to large inter-annual variation, as well as extreme events (De Dato et al. 2006, Barbosa et al. 2014, Blume-Werry et al. 2016). Reciprocal transplants represent a promising approach for indirectly studying plant responses to climate change on a short temporal scale. These manipulative experiments have been widely adopted in single species (e.g. Link et al. 2003, Casper and Castelli 2007, Macel et al. 2007, Alexander et al. 2015, Tomiolo et al. 2015) for studying local adaptation and, more recently, for studying their responses to a climate that matches conditions predicted by climate change scenarios (the so called "space-for-time approach"). Reciprocal

transplants have also been applied to entire communities in studies of soil microbiomes (Waldrop and Firestone 2006, Lazzaro et al. 2011), leaf litter (Ayres et al. 2009, Allison et al. 2013), and occasionally to whole plant communities in different habitats ranging from wetlands to alpine grasslands (Maranon and Bartolome 1993, Wetzel et al. 2004, Wu et al. 2012, Alexander et al. 2015). However, the potential for using whole community reciprocal transplants to study plant community response to climate change has not been fully exploited, particularly in dryland systems, which often provide ideal conditions.

Dryland ecosystems are often dominated by annual plants that survive the dry season as a permanent seed bank (Cohen 1966). Therefore, the community (i.e. the seed bank) can be conveniently transplanted as a whole during the dry season without any harm to the plants. In addition, by transplanting seed banks with their associated soil, it is possible to evaluate plant communities' response to climate while preserving soil abiotic and biotic interactions. To test the response of dryland annual plant communities characterized by very different climates, we transplanted home soil with seed bank among three sites situated along a steep aridity gradient in the Eastern Mediterranean region, ranging from an arid to Mediterranean climate. In this region, rainfall is the main limiting factor to plant growth (Ziv et al. 2014) and differs up to 5-fold between the driest and wettest site(Holzapfel et al. 2006). The study sites used for our reciprocal transplant also hosted a long-term climate manipulation experiment (Tielbörger et al. 2014). This allowed for a comparison between long-term dynamics, resulting from consistently imposed climate change, and the short-term responses observed in our transplant experiment. Finally, we classified species based on their climatic requirements, adopting the Climatic Niche Group approach (CNG; *sensu* Bilton et al. 2016) that has been successfully employed for the species in our study

region (Bilton et al. 2016) and in other dryland ecosystems (Liu et al. 2018). By identifying those species responsive to drier or wetter conditions, the CNG approach provided us with testable predictions about shifts in community assembly across climates within the reciprocal transplants.

We predicted that the community emerging from the reciprocal soil transplants would be greatly determined by community origin, with less individuals emerging from drier origins than wetter origins. Secondly, we hypothesized that the climate (i.e. rainfall availability) at the transplant site would affect the emerging communities, resulting in less biomass and less individuals emerging from community origins exposed to drier climates. We also predicted that climate would select the emerging community from the species pool of each origin in a predictable manner, with more wet adapted species emerging in communities exposed to wetter climates, and more dry-adapted species in drier climates.

Methods

Study area

This study was conducted in Israel at three fenced sites (area approximately 100 m x 400 m) with respectively Mediterranean (M) semi-arid (SA), and arid (A) climate. The three study sites share the same calcareous bedrock, southern aspect, altitude and mean annual temperatures, so that they differ chiefly in mean and variance of annual rainfall, and vegetation. The M site is located southwest of Jerusalem (N 31° 42’ E 35° 3’) at 620 masl, on Terra Rossa soil. The climate is characterized by 550 mm average annual rainfall with 20% inter-annual variation. The SA site (N 31° 23’ E 34° 54’) is located in the northern portion of the Negev Desert near the city of Beersheba, at 590 masl, on Light Brown Rendzina. Average annual rainfall is 270 mm with

approximately 30% inter-annual variation. The A site is located in the central Negev near Sde Boqer (N 30º52' E 34º46') at 470 masl, on desert Lithosol. Average annual rainfall amounts to 90 mm with 43% inter-annual variation (Holzapfel et al. 2006). The plant communities at the three sites are semi-natural shrublands dominated by *Sarcopoterium spinosum* (L.) Spach, and winter annuals (approx. 85% of all species) that persist during summer in the form of dormant seed banks stored in the soil (Noy-Meir 1973, Alon and Steinberger 1999). The species pool is overlapping among sites, and annual plant cover amounts to 25% at the M site, 10% at the SA site, and < 1% at the A site (Tielbörger et al. 2014).

Experimental set up

During the summer of 2010, we collected soil with seed bank from forty square plots (20cm x 20cm, depth: 5cm) at the M and A sites and sixty plots at the SA site. Within each site, plots were situated at least 20 cm apart from each other and away from rocks and shrubs. Following Tomiolo et al. (2015) soil collected from each site was pooled to produce a baseline community as there is substantial small-scale heterogeneity in the seed bank (Siewert and Tielbörger 2010). The soil was stored in a net-house at the University of Rehovot, Israel, where it experienced summer temperatures necessary for breaking seed dormancy (Baskin et al. 1993). In September 2010, twenty of the previously excavated plots at each site were randomly selected and filled with home soil, while the remaining plots were filled with soil from the closest away-from-home site (i.e. M site received M and SA soil; SA site received M, SA and A soil; A site received SA and A soil, Supplementary Material Appendix 1 Fig. A1). Transplanted soil was separated from the surrounding soil by a layer of absorbent paper that provided initial isolation between soils, while not impeding water percolation. After transplanting, we placed patches of organza (a thin

transparent fabric) over the surface of each plot to avoid contamination from seed dispersal or seed predation (Petrů and Tielbörger 2008), and we removed them at the time of germination.

Because the transplants were carried out during the dormant season we could relocate the community of dormant seeds and soil biota with minimum damage. By transplanting communities with their maternal soil we could test direct effects of climate (e.g. decreasing rainfall) while preserving biotic interactions with neighbouring plants and soil biota, which are also affected by the novel climate (Emmett et al. 2004). At peak development (spring 2011), we recorded the identity and number of individuals of the emerging species in each plot. In order to minimize edge effects, we excluded plants growing in the outer 1 cm margin of each plot. After species identification, aboveground biomass was collected, oven-dried at 70°C for 48 hours and weighed.

Unfortunately, the season of recording was very dry and the arid site received only 30% of the average annual rainfall. Therefore, only a handful of seedlings of two desert species (*Stipa capensis*, *Erodium touchyanum*) emerged at the arid site. As a result, there was no home arid community to be compared to the transplants, and we had to restrict our subsequent analyses to the reciprocal transplants between the SA and M community origins.

Climatic Niche Groups (CNG)

Each species within the target communities was assigned to a Climatic Niche Group (Bilton et al. 2016) classified by their distribution range in relation to rainfall. A similar method has been employed for defining thermal niches of species in high elevation and tundra habitats (Gottfried et al. 2012, Elmendorf et al. 2015), and

ideologically similar for Ellenberg values, which determine species habitat requirements based on several abiotic parameters (Ellenberg 1974).

The rationale for the CNG grouping is that rainfall is the main driver of community composition in the region, therefore species sharing similar climate adaptations (approximated by the realized climatic rainfall niche) are likely to co-occur in the same community by virtue of habitat filtering (García-Camacho et al. 2017). Species realized climatic niche values were derived as in Bilton et al. (2016). For each single species the observed occurrences within Israel (distribution range) were overlaid with mean annual rainfall climate data, and the mean value was taken (obtained from BioGIS 2012, available at http://www.biogis.huji.ac.il/). Boundaries between climatic niche groups spanned similar ranges of average annual rainfall (approximately 130 mm) and resulted in four groups that ranked species with respect to their hypothesized response to climate. Climatic Niche Group 1 (CNG1) represented species associated with the lowest rainfall extremes of the gradient, conversely CNG4 gathered species distributed in areas with high rainfall. Species from all four CNGs were present in both communities (Supplementary Material, Appendix 2 Table A1), but varied in their proportional representation at each site, and could therefore be compared across sites and climates (Bilton et al. 2016).

Statistical analyses

We first analyzed how total density (number of individuals per plot), biomass, species richness (number of species per plot), evenness (Simpson's evenness) and diversity (Shannon-Wiener Index) varied in response to climate, community origin and their interaction. In addition, we analyzed how the number of individuals belonging to each climatic niche group per plot (i.e. CNG density) varied in response

225 to climate, community origin, with respect to the four-level categorical explanatory
226 variable CNG identity (i.e. CNG1 – CNG4), including all two-way and three-way
227 interactions. We applied generalized linear models with negative binomial
228 distribution to total individual, CNG density and species richness using the MASS
229 package (Venables et al. 2002) within the R software version 2.14 (R Development
230 Core Team 2014). Biomass, species diversity and evenness were analyzed using
231 linear models. To meet model requirements, evenness was log transformed and
232 biomass square root transformed. The significance of the models was assessed with a
233 Type 3 ANOVA, using the "car" package (Fox and Weisberg 2011). Post-hoc tests
234 were conducted using Tukey HSD test. Visual representation of the CNG density
235 interactions was done using log-ratios (log(SA density + 1) - log(M density +1)).
236 For testing how species composition varied with community origin and climate
237 we used Redundancy Analysis (RDA, (Legendre et al. 2011)) in the R package
238 'vegan' (Oksanen et al. 2015). The interaction term was included in a full model and
239 confirmed using a step-wise approach. The data were Hellinger transformed
240 (Legendre and Gallagher 2001) and scaled within plots. Significance of the model
241 was tested using 999 permutations. To test if species composition could be explained
242 by rainfall distribution range we regressed the resulting RDA 'species mean scores'
243 against the 'climatic niche value' of each species, both for individual species and for
244 the CNG classifications. Furthermore, we performed an RDA on the community-
245 weighted means (Garnier et al. 2007) using the species 'climatic niche value' as a
246 pseudo-trait.
247
248 **Results**

Overall, 97 species were recorded, among which 12.3% were grasses, 23.7% legumes and 64% belonged to other families (Supplementary Material, Appendix 2 Table A1). In total, 68 species emerged from the semi-arid soil seed bank, 81 from the Mediterranean origin, and 53 species were shared between the two origins. Fourteen of these appeared in all four combinations of community origin and climate.

Diversity, richness and biomass

Total biomass, plant density, number of species and species diversity (Fig. 1b, 2a, b, Table 1) were all significantly higher for communities of M origin rather than SA origin. Additionally, for the M community origins, plant biomass, species richness, diversity (Fig.1a, b, d) and total density (Fig 2.a, b) were significantly lower when communities were exposed to the drier SA climates compared to their home climate, whereas evenness remained the same across climates (Fig. 1c). For the SA community origins, climate had no significant effect on any of the whole community parameters total density (Fig. 2a, b, Table 2), biomass, species richness or diversity (Fig.1, Table 1). Higher evenness was found in SA community origins exposed to M climate compared to M community origins exposed to SA climate (Fig. 1c, Table 1).

Relative abundance of CNG across sites and community origins

Relative density of individuals changed considerably across community origins and CNG groups (Table 2). In particular, the relative abundance of CNGs shifted significantly across climates and community origins as indicated by the significant two-way interactions (Table 2, Fig. 2a-d, Supplementary Material Appendix 2 Table A2). In SA community origins, the mean abundance of individuals belonging to dry CNGs (CNG 1and 2) was halved in M climate compared to SA

climate; on the other hand individuals belonging to CNG 4, the wettest adapted group, were 6.5 times more abundant in M climate (Fig. 2a, c). In M communities, the shift in CNG relative abundances was less strong but the relative hierarchical response of the CNGs was in the same order (densities of CNG1 and 2 higher in SA climate; CNG3 and 4 higher in M climate). The largest shift was seen in CNG4 that counted twice as many individuals in home *vs.* away from home climate (Fig. 2b, d). The different magnitude in CNG shifts across community origins and climates was confirmed by a significant 3-way interaction (CNG x community origin x climate, Table 2, Fig. 2e, f).

The RDA indicated four distinct communities emerging from the respective treatments, with a significant effect of community origin and climate on species assembly, as well as a significant interaction between these terms (Fig. 3a, b). Using simple correlations we assessed which plots/species scores changed and had most impact on each axis. We obtained three main RDA axes describing the species composition. For plot mean scores: RDA1 (9.2% explained) was highly correlated to overall differences between community origins, whereas the constrained RDA2 (3.3%; explained) and RDA3 (1.7%; explained) distinguished the climate x community origin interaction term. For species mean scores, RDA1 was positively correlated to species Climatic Niche values, and the correlation was positive but less strong for RDA2 and RDA3 (Fig. 3c). Results were further validated by an RDA on the community weighted mean traits using species Climatic Niche values as a trait, and showed significant community origin and climate effects ($p<0.05$). In combination, these results suggest that rainfall niche strongly explained variation in species composition across treatments.

Discussion

Our results revealed that climate played a large role in determining the species assemblages in our whole community transplant experiment, and that such changes were predictably related to possible species-specific climatic adaptations. One of our most notable findings was that large shifts in species composition occurred when transplants were exposed to vastly different climates, whereas total community parameters such as biomass, density, and diversity remained remarkably stable.

Perhaps unsurprisingly, and as predicted from previous observations across the rainfall gradient (Tielbörger et al. 2014), communities establishing from the Mediterranean (M) origin soil had higher individual density and total biomass than semi-arid (SA) origins. This is also similar to other dryland systems, where rainfall acts as a limiting resource (Guo and Brown 1997, Cleland et al. 2013). Consistently, all four CNGs had higher densities of individuals establishing from the M origin compared to SA origin. However, the wetter species groups (CNG 3 & 4) were proportionally more represented in M community origins, and the drier species groups (CNG 1 & 2) were more abundant in SA community origins. This, consistently with the findings of Bilton et al. (2016), suggests that CNGs are representative of species rainfall requirements and possibly climatic adaptations at the different sites. All communities rapidly matched the concomitant climate with shifts in community composition across climates that were strikingly well explained by hierarchical switches in relative CNG abundances. Plants establishing from both community origins showed a relative increase of species assumed to be most dry adapted when exposed to the drier (SA) climate. Accordingly, wet adapted species were more abundant in both communities when exposed to the wetter (M) climate. Therefore, CNGs revealed species responses to short-term climate effects in a predictable way,

suggesting potential short-term selection mechanisms that act on the communities in response to yearly or extreme differences in rainfall.

Our most intriguing finding was that climate not only selected for predictable species groups, but that the community origins differed greatly in the magnitude of the community shifts. The SA origin, with the more variable rainfall regime – both between and within years (Tielbörger et al. 2014) – also experienced the greater shifts in community composition. This result matches other studies showing that communities from drier climates often have higher inter-annual turnover of species composition (Guo and Brown 1997, Cleland et al. 2013). Fascinatingly, the magnitude of the compositional shifts between transplanted community origins was inversely related to changes in total community parameters across climates. Namely, in SA community origins total density, biomass and species richness remained constant. Conversely, for the M origin transplants, which had smaller compositional shifts, total density, biomass and richness decreased when exposed to the drier SA climate. Large inter-annual variation in species abundances often leads to higher community stability across time (Bai et al. 2004, Grime et al. 2008). Similar patterns have been previously explained in plant community studies, albeit in a different context, by the portfolio effect (Doak et al. 1998, Schindler et al. 2015). The portfolio effect predicts that greater numbers of species in a community lead both mathematically and ecologically to a greater chance of asynchronous relationships forming year-to-year. Here we show, consistent with a previous study (Cleland et al. 2013), that in the community with the lower species richness (SA origin), greater asynchrony and greater species turnover led to greater stability across climates. This asynchrony is not random, but directly linked to species-specific climatic adaptations. Thus, asynchronous shifts in relative abundance of species according to their climate

adaptations may allow for fast responses to year-to-year climatic variation in dryland annual communities (Abbott 2017).

In the short-term, high species turnover may assure community stability, by maintaining stable biomass and density, but in the long-term, such processes may also lead to greater resistance and stability of dry (SA) communities to rainfall fluctuations by favoring species adapted to more arid conditions. The high turnover is possible without immediate loss of species because in dryland environments subject to large year-to-year climatic variability, plants often display bet-hedging strategies such as long-lived seed banks and seed dormancy that can buffer against inter-annual fluctuations (Petrů and Tielbörger 2008, Tielbörger et al. 2012). Delayed germination of dormant seeds during unfavorable years decreases the risk of extinction over time and also promotes coexistence of species with different climatic requirements via storage effects (Chesson and Grubb 1990, Pake and Venable 1995). Interestingly, the findings from this short-term community transplant study are consistent with those of a parallel long-term experiment conducted at the M and SA sites (Tielbörger et al. 2014), where community composition was monitored for 10 years in permanent plots receiving respectively ambient rainfall, experimental drought (-30% rainfall) or increased rainfall (+30% rainfall). Plant communities exposed to the long-term climate manipulation treatments showed no detectable long-term effect on total density, species richness and community biomass (Tielbörger et al. 2014). This unexpected community resistance may be attributable to the large variability in rainfall to which plant species in both community origins are pre-adapted (Tielbörger et al. 2014, Tomiolo et al. 2015). Also at the two time-scales, selection of species in relation to their CNG was observed (Bilton et al. 2016). However, while in the current study we found stronger short-term selection for SA origin communities, long-term

374 selection patterns were found to be weaker in SA and stronger for M communities
375 (Bilton et al. 2016), suggesting that high inter-annual fluctuations result in stable
376 composition in the long run, whereas low species turnover across years results in long
377 term loss of wet-adapted species.

378 Finally, the observation of the community-level responses among climates
379 prompts an interesting parallel with well-known concepts of population ecology. High
380 environmental variability may select for a high degree of phenotypic plasticity (Sultan
381 1987, Pratt and Mooney 2013, Lazaro-Nogal et al. 2015, Spence et al. 2016). Thus,
382 when exposed to novel climates, individuals will display a large plasticity in adaptive
383 traits (Reed et al. 2011, Liancourt et al. 2015, Mathiasen and Premoli 2016). A better
384 match between the new trait value and the novel climate (Valladares et al. 2014)
385 confers an adaptive advantage and may result in stable fitness across home and away
386 environments, i.e. fitness homeostasis (Richards et al. 2006, Nicotra et al. 2010) and
387 may eventually assure the persistence of a species in changing climates. We propose
388 an analogy to that concept on a community level, where relative species abundances
389 (rather than trait values) shift across years (and sites) in order to better match the
390 current climate. Here, we show that the SA community origin, which is historically
391 exposed to larger year-to-year climatic variability (Holzapfel et al. 2006, Tielbörger et
392 al. 2014), experienced a greater compositional fluctuation (or "compositional
393 plasticity"), and this led to greater "community homeostasis" (i.e. maintenance of
394 stable density and biomass) across climates.

395 Our overall findings allow some careful conclusions about the potential
396 response of these communities to climate change. It should be noted that the variation
397 in rainfall experienced by the community origins in our study approximated the
398 extremes of climatic variability at each site, but exceeded the decrease in rainfall

predicted by climate change scenarios for the next 50-80 years (Smiatek et al. 2011, Tomiolo et al. 2015). These results suggest that, as long as inter-annual climatic fluctuations keep within the limits of climatic variability commonly experienced by these communities, and rainy years that replenish the seed bank periodically occur, wet adapted species will persist within the communities. However, with increasing drought and unpredictability, communities are likely to experience species loss that will affect primarily species with high rainfall requirements (Tielbörger et al. 2014, Bilton et al. 2016). The similar results from the long-term experiment with our reciprocal transplant indicate that the latter may be a powerful complement to long-term field experiments. However, it should be noted that annual communities are particularly suited for this approach and the same may not hold for long-lived communities. Moreover, the fast response observed in our communities is uncommon compared to temperate systems, where a lag between shifts in climatic conditions and subsequent changes in community structure is often observed (Adler and Levine 2007, Jones et al. 2016). This suggests a higher resistance and resilience of dryland ecosystems to extreme events compared to temperate ecosystems (Ruppert et al. 2015).

Declarations: KT and ST developed the experimental design. ST set up the experiments and collected the data. MB and ST performed statistical analyses. ST wrote the first draft of the manuscript and all authors contributed substantially to revisions. We declare that we do not have conflicts of interest.

Acknowledgements: Jaime Kigel and Marcelo Sternberg provided logistic support. The Hebrew University of Jerusalem (Rehovot) kindly provided material for

fieldwork. We thank Jake Alexander for providing comments on a previous version of the manuscript. This study is part of the GLOWA Jordan River Project and was funded by the German Ministry of Education and Research (BMBF). Further support for MB and ST was obtained by the German Research Foundation (TI338_12-1; TI338_11-1; and TI338_11-2; TI 338/15-1).

References

Abbott, R. E. et al. 2017. Portfolio effects, climate change, and the persistence of small populations: analyses on the rare plant *Saussurea weberi*. — Ecology 98: 1071-1081.

Adler, P. B. and Levine, J. M. 2007. Contrasting relationships between precipitation and species richness in space and time. — Oikos 116: 221-232.

Alexander, J. M. et al. 2015. Novel competitors shape species' responses to climate change. — Nature 525: 515-518.

Alexander, J. M. et al. 2016. When climate reshuffles competitors: a call for experimental macroecology. — Trends in Ecology and Evolution 31: 831-841.

Allison, S. D. et al. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. — Ecology 94: 714-725.

Alon, A. and Steinberger, Y. 1999. Response of the soil microbial biomass and nematode population to a wetting event in nitrogen-amended Negev desert plots. — Biol. Fertility Soils 30: 147-152.

Anderson, R. et al. 1982. Variability in the abundance of animal and plant species. — Nature 296: 245-248.

454 Ayres, E. et al. 2009. Home-field advantage accelerates leaf litter decomposition in
455 forests. — Soil Biol. Biochem. 41: 606-610.

456 Bai, Y. et al. 2004. Ecosystem stability and compensatory effects in the Inner
457 Mongolia grassland. — Nature 431: 181.

458 Barbosa, E. R. M. et al. 2014. Short-term effect of nutrient availability and rainfall
459 distribution on biomass production and leaf nutrient content of savanna tree
460 species. — Plos One 9:

461 Baskin, C. C. et al. 1993. Annual seed dormancy cycles in two desert winter annuals.
462 — J. Ecol. 81: 551-556.

463 Bilton, M. C. et al. 2016. Climatic niche groups: A novel application of a common
464 assumption predicting plant community response to climate change. —
465 Perspect. Plant Ecol. Evol. Syst. 19: 61-69.

466 BioGIS 2012. Israel Biodiversity Information System [http://www.biogis.huji.ac.il/
467]. p available at http://www.biogis.huji.ac.il/.

468 Blume-Werry, G. et al. 2016. Short-term climate change manipulation effects do not
469 scale up to long-term legacies: effects of an absent snow cover on boreal forest
470 plants. — J. Ecol. 104: 1638-1648.

471 Bonebrake, T. C. and Mastrandrea, M. D. 2010. Tolerance adaptation and
472 precipitation changes complicate latitudinal patterns of climate change

473 impacts. — Proceedings of the National Academy of Sciences of the United
474 States of America 107: 12581-12586.

475 Brown, J. H. et al. 2001. Regulation of diversity: maintenance of species richness in
476 changing environments. — Oecologia 126: 321-332.

477 Casper, B. B. and Castelli, J. P. 2007. Evaluating plant-soil feedback together with
478 competition in a serpentine grassland. — Ecol. Lett. 10: 394-400.

479 Chesson, P. L. and Grubb, P. 1990. Geometry, heterogeneity and competition in
480 variable environments. — Philosophical Transactions of the Royal Society of
481 London B: Biological Sciences 330: 165-173.

482 Cleland, E. E. et al. 2013. Sensitivity of grassland plant community composition to
483 spatial vs. temporal variation in precipitation. — Ecology 94: 1687-1696.

484 Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. — J.
485 Theor. Biol. 12: 119-129.

486 Cubasch, U. et al. 1996. Estimates of climate change in Southern Europe derived from
487 dynamical climate model output. — Clim. Res. 7: 129-149.

488 De Dato, G. D. et al. 2006. Effects of warmer and drier climate conditions on plant
489 composition and biomass production in a Mediterranean shrubland
490 community. — Forest@ 3: 511-526.

Doak, D. F. et al. 1998. The statistical inevitability of stability-diversity relationships in community ecology. — Am. Nat. 151: 264-276.

Doblas−Miranda, E. et al. 2015. Reassessing global change research priorities in mediterranean terrestrial ecosystems: how far have we come and where do we go from here? — Global Ecol. Biogeogr. 24: 25-43.

Ellenberg, H. 1974. Indicator values of vascular plants in central Europe. — Scripta Geobotanica 9: 97.

Elmendorf, S. C. et al. 2015. Experiment, monitoring, and gradient methods used to infer climate change effects on plant communities yield consistent patterns. — Proc. Natl. Acad. Sci. U.S.A. 112: 448-452.

Emmett, B. A. et al. 2004. The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. — Ecosystems 7: 625-637.

Fernandez-Going, B. M. et al. 2013. Climate interacts with soil to produce beta diversity in Californian plant communities. — Ecology 94: 2007-2018.

Forey, E. et al. 2010. Does disturbance drive the collapse of biotic interactions at the severe end of a diversity-biomass gradient? — Plant Ecol. 206: 287-295.

Fox, J. and Weisberg, S. 2011. An R Companion to Applied Regression. — Sage Publications.

Garcia, R. A. et al. 2014. Multiple Dimensions of Climate Change and Their Implications for Biodiversity. — Science 344:

García-Camacho, R. et al. 2017. Phylogenetic structure of annual plant communities along an aridity gradient. Interacting effects of habitat filtering and shifting plant–plant interactions. — Isr. J. Plant Sci. 1-13.

Garnier, E. et al. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. — Ann. Bot. 99: 967-985.

Gilman, S. E. et al. 2010. A framework for community interactions under climate change. — Trends Ecol. Evol. 25: 325-331.

Gottfried, M. et al. 2012. Continent-wide response of mountain vegetation to climate change. — Nature Clim. Change 2: 111-115.

Grime, J. P. et al. 2008. Long-term resistance to simulated climate change in an infertile grassland. — Proceedings of the National Academy of Sciences of the United States of America 105: 10028-10032.

Guo, Q. and Brown, J. H. 1997. Interactions between winter and summer annuals in the Chihuahuan Desert. — Oecologia 111: 123-128.

Harrison, S. P. et al. 2015. Climate-driven diversity loss in a grassland community. — Proceedings of the National Academy of Sciences of the United States of America 112: 8672-8677.

Hobbs, R. J. et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. — Global Ecol. Biogeogr. 15: 1-7.

Holzapfel, C. et al. 2006. Annual plant-shrub interactions along an aridity gradient. — Basic Appl. Ecol. 7: 268-279.

Jones, S. K. et al. 2016. Altered rainfall patterns increase forb abundance and richness in native tallgrass prairie. — Scientific Reports 6: 20120.

Lazaro-Nogal, A. et al. 2015. Environmental heterogeneity leads to higher plasticity in dry-edge populations of a semi-arid Chilean shrub: insights into climate change responses. — J. Ecol. 103: 338-350.

Lazzaro, A. et al. 2011. Field-scale transplantation experiment to investigate structures of soil bacterial communities at pioneering sites. — Appl. Environ. Microbiol. 77: 8241-8248.

Legendre, P. and Gallagher, E. D. 2001. Ecologically meaningful transformations for ordination of species data. — Oecologia 129: 271-280.

Legendre, P. et al. 2011. Testing the significance of canonical axes in redundancy analysis. — Methods Ecol. Evol. 2: 269-277.

Liancourt, P. et al. 2015. Leaf-trait plasticity and species vulnerability to climate change in a Mongolian steppe. — Global Change Biol. 21: 3489-3498.

Lindenmayer, D. B. et al. 2012. Value of long−term ecological studies. — Austral Ecol. 37: 745-757.

Link, S. O. et al. 2003. A reciprocal transplant experiment within a climatic gradient in a semiarid shrub-steppe ecosystem: effects on bunchgrass growth and reproduction, soil carbon, and soil nitrogen. — Global Change Biol. 9: 1097-1105.

Liu, D. et al. 2018. Species selection under long−term experimental warming and drought explained by climatic distributions. — New Phytol. 217: 1494-1506.

Macel, M. et al. 2007. Climate vs. soil factors in local adaptation of two common plant species. — Ecology 88: 424-433.

Maestre, F. T. et al. 2012. Plant species richness and ecosystem multifunctionality in global drylands. — Science 335: 214-218.

Maranon, T. and Bartolome, J. W. 1993. Reciprocal transplants of herbaceous communities between *Quercus agrifolia* woodland and adjacent grassland. — J. Ecol. 81: 673-682.

Mathiasen, P. and Premoli, A. C. 2016. Living on the edge: adaptive and plastic responses of the tree *Nothofagus pumilio* to a long-term transplant experiment predict rear-edge upward expansion. — Oecologia 181: 607-619.

Miranda, J. D. et al. 2011. Climatic change and rainfall patterns: effects on semi-arid plant communities of the Iberian Southeast. — J. Arid Environ. 75: 1302-1309.

Nicotra, A. B. et al. 2010. Plant phenotypic plasticity in a changing climate. — Trends Plant Sci. 15: 684-692.

Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. — Annu. Rev. Ecol. Syst. 4: 25–51.

Oksanen, J. et al. 2015. vegan: Community ecology package.

Pake, C. E. and Venable, D. L. 1995. Is coexistence of Sonoran desert annuals mediated by temporal variablilty in reproductive success? — Ecology 76: 246-261.

Parmesan, C. and Hanley, M. E. 2015. Plants and climate change: complexities and surprises. — Ann. Bot. 116: 849-864.

Peñuelas, J. et al. 2007. Response of plant species richness and primary productivity in shrublands along a north–south gradient in Europe to seven years of

experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. — Global Change Biol. 13: 2563-2581.

Petrů, M. and Tielbörger, K. 2008. Germination strategies of annual plants under changing climatic conditions: teasing apart local and regional effects. — Oecologia 155: 717-728.

Pratt, J. D. and Mooney, K. A. 2013. Clinal adaptation and adaptive plasticity in *Artemisia californica*: implications for the response of a foundation species to predicted climate change. — Global Change Biol. 19: 2454-2466.

R Development Core Team 2014. R: A language and environment for statistical computing. . — In: Computing, R. F. f. S. (ed).

Reed, T. E. et al. 2011. Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. — Conserv. Biol. 25: 56-63.

Richards, C. L. et al. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. — Ecol. Lett. 9: 981-993.

Rinnan, R. et al. 2007. Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. — Global Change Biol. 13: 28-39.

Ruppert, J. C. et al. 2015. Quantifying drylands' drought resistance and recovery: the importance of drought intensity, dominant life history and grazing regime. — Global Change Biol. 21: 1258-1270.

Sala, O. E. and Lauenroth, W. K. 1982. Small rainfall events: an ecological role in semiarid regions. — Oecologia 53: 301-304.

Sardans, J. et al. 2008. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. — Global Change Biol. 14: 2304-2316.

Schindler, D. E. et al. 2015. The portfolio concept in ecology and evolution. — Front. Ecol. Environ. 13: 257-263.

Shi, Z. et al. 2015. Evidence for long-term shift in plant community composition under decadal experimental warming. — J. Ecol. 103: 1131-1140.

Siewert, W. and Tielbörger, K. 2010. Dispersal-dormancy relationships in annual plants: putting model predictions to the test. — Am. Nat. 176: 490-500.

Smiatek, G. et al. 2011. High-resolution climate change simulations for the Jordan River area. — J. Geophys. Res.-Atmos. 116:

Spence, L. A. et al. 2016. Short-term manipulation of precipitation in Mongolian steppe shows vegetation influenced more by timing than amount of rainfall. — J. Veg. Sci. 27: 249-258.

618 Sultan, S. E. 1987. Evolutionary Implications of Phenotypic Plasticity in Plants. — In:
619 Hecht, M. K. et al. (eds), Evolutionary Biology: Volume 21. Springer US, pp.
620 127-178.

621 Thompson, P. L. et al. 2015. Warming induces synchrony and destabilizes
622 experimental pond zooplankton metacommunities. — Oikos 124: 1171-1180.

623 Tielbörger, K. et al. 2012. Bet-hedging germination in annual plants: a sound
624 empirical test of the theoretical foundations. — Oikos 121: 1860-1868.

625 Tielbörger, K. et al. 2014. Middle-Eastern plant communities tolerate 9 years of
626 drought in a multi-site climate manipulation experiment. — Nature
627 Communications 5:

628 Tilman, D. and Downing, J. A. 1994. Biodiversity and stability in grasslands. —
629 Nature 367: 363-365.

630 Tilman, D. et al. 1998. Diversity-stability relationships: statistical inevitability or
631 ecological consequence? — The American Naturalist 151: 277-282.

632 Tomiolo, S. et al. 2015. Separating the role of biotic interactions and climate in
633 determining adaptive response of plants to climate change. — Ecology 96:
634 1298-1308.

Valladares, F. et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. — Ecol. Lett. 17: 1351-1364.

Venables, W. N. et al. 2002. Modern Applied Statistics with S. . — Springer.

Waldrop, M. P. and Firestone, M. K. 2006. Response of microbial community composition and function to soil climate change. — Microb. Ecol. 52: 716-724.

Wetzel, P. R. et al. 2004. Use a reciprocal transplant study to measure the rate of plant community change in a tidal marsh along a salinity gradient. — Wetlands 24: 879-890.

Williams, J. W. and Jackson, S. T. 2007. Novel climates, no-analog communities, and ecological surprises. — Front. Ecol. Environ. 5: 475-482.

Wu, Z. T. et al. 2012. Biogeochemical and ecological feedbacks in grassland responses to warming. — Nat. Clim. Chang. 2: 458-461.

Ziv, B. et al. 2014. Trends in rainfall regime over Israel, 1975–2010, and their relationship to large-scale variability. — Regional Environmental Change 14: 1751-1764.

Figures and tables

Table 1: Type III ANOVA table results for the models applied to individual density, species richness, species diversity, evenness and total biomass. Lines correspond to response variables and columns to explanatory variables of each model. In each column the first value represent Chi-square test values and the second the p-value. Probability values for significant terms are reported in bold.

	Origin	**Climate**	**Origin x Climate**
Density	312.86; **<0.001**	0.12; 0.72	0.59; 0.44
Species richness	281.29; **<0.001**	12.99; **<0.001**	0.085; 0.77
Evenness	11.96; **<0.001**	7.18; **0.009**	0.028; 0.86
Species diversity	130.41; **<0.001**	10.40; **0.001**	1.36; 0.24
Total biomass	103.86; **0.001**	2.34; 0.13	4.66; **0.03**

Table 2: Type III ANOVA table of results for Generalized Linear Models determining the effect of community origin, climate and Climatic Niche Group (CNG) on plant community densities establishing from seed banks. N=320.

Effect	DF	LR Chi-sq.	P-value
Origin	1	236.93	**<0.00001**
Climate	1	2.35	0.12540
CNG	3	343.21	**<0.00001**
Origin x Climate	1	0.07	0.78714
Origin x CNG	3	83.55	**<0.00001**
Climate x CNG	3	50.09	**<0.00001**
Origin x Climate x CNG	3	16.85	**0.00076**

Figure Captions:

Figure 1: Mean ±1SE A) species richness (i.e. number of species per plot), B) total biomass, C) evenness, D) diversity, of annual plant communities established from two community origins ('M' Mediterranean; 'SA' Semi-Arid) grown in two sites (i.e. climates: 'M' Mediterranean; 'SA' Semi-Arid).

Figure 2: Impact of community origin, climate and Climatic Niche Group (CNG) on plant densities establishing from seed banks in home *vs*. away-from-home climate. Each Climatic Niche Group (CNG) aggregates species with similar climatic adaptation, ranging from dry climates (CNG 1) to wetter climates (CNG 4). Fig. 2 a, b: Total mean individuals density across climates is broken down according to CNG relative abundance. Fig. 2 c-f: Differences in relative densities of CNG groups are expressed as log ratios, where positive values indicate higher CNG relative abundances in SA community origins or sites, whereas negative values indicate higher CNG relative abundances in M community origins and climate. Community composition shifts are represented across community origins (2c), climates (2d) and the combination of the two (2 e,f).

Figure 3: Redundancy Analysis (RDA) of species compositional change in community origins emerging in home *vs.* away-from-home climates. Indicated are the 95% confidence intervals for the groupings/categories (ellipses). Fig. 3 a, b represents the plot centroids of each community origin-climate combination. Lines are vectors from the centre of a category to each site score (points). RDA-axis 1: correlated to distance between origins, RDA-axis 3: the effect of climate on SA community origins, and RDA-axis 2 the effect of climate on M community origins. In red: SA community origins - SA climate; yellow: SA origins - M climate; blue: M origins- M climate; green: M origins -SA climate. Fig. 3c represents the species centroids for each species group. Lines are vectors connecting the centre of each group with species scores. In red: CNG1, yellow: CNG2, green: CNG3, blue: CNG4.

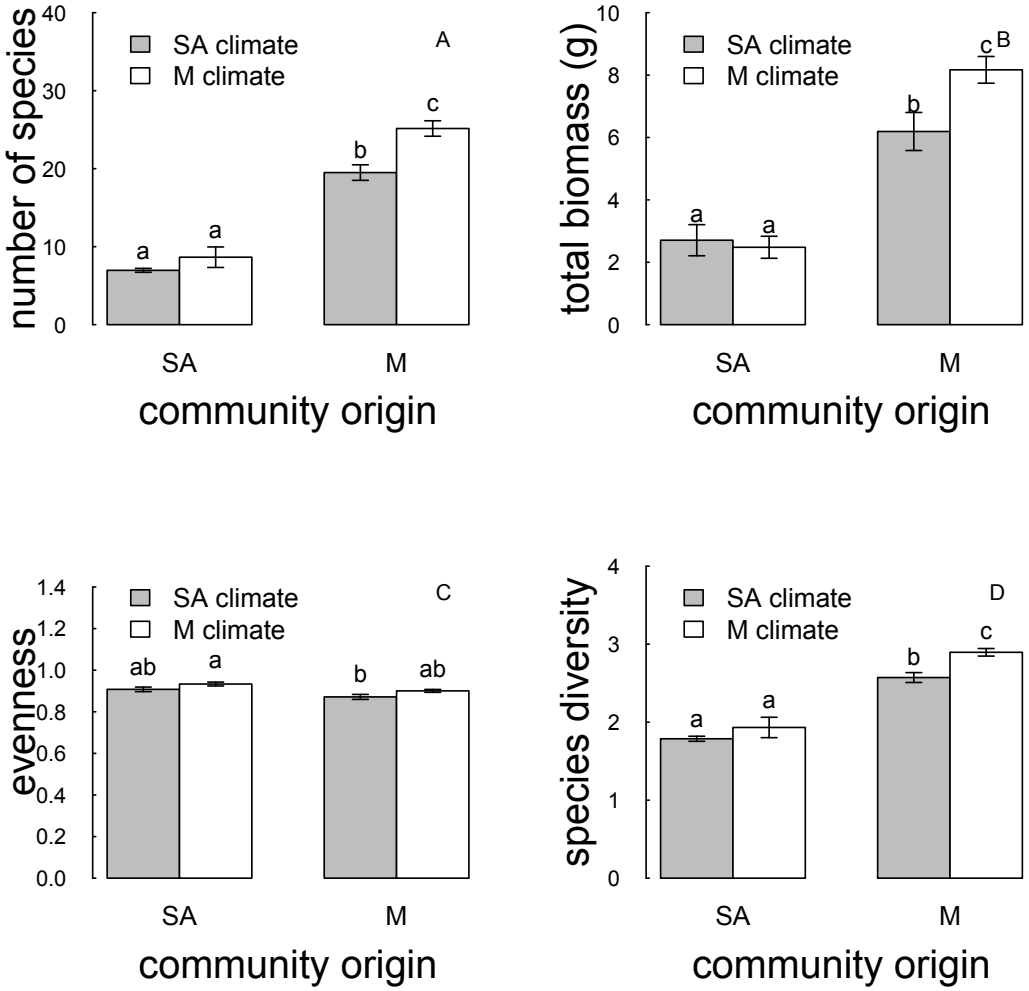
number of species
SA climate
M climate
A
a
a
b
c
SA
M
community origin
total biomass (g)
SA climate
M climate
B
a
a
b
c
SA
M
community origin
evenness
SA climate
M climate
C
ab
a
b
ab
SA
M
community origin
species diversity
SA climate
M climate
D
a
a
b
c
SA
M
community origin

Figure 1

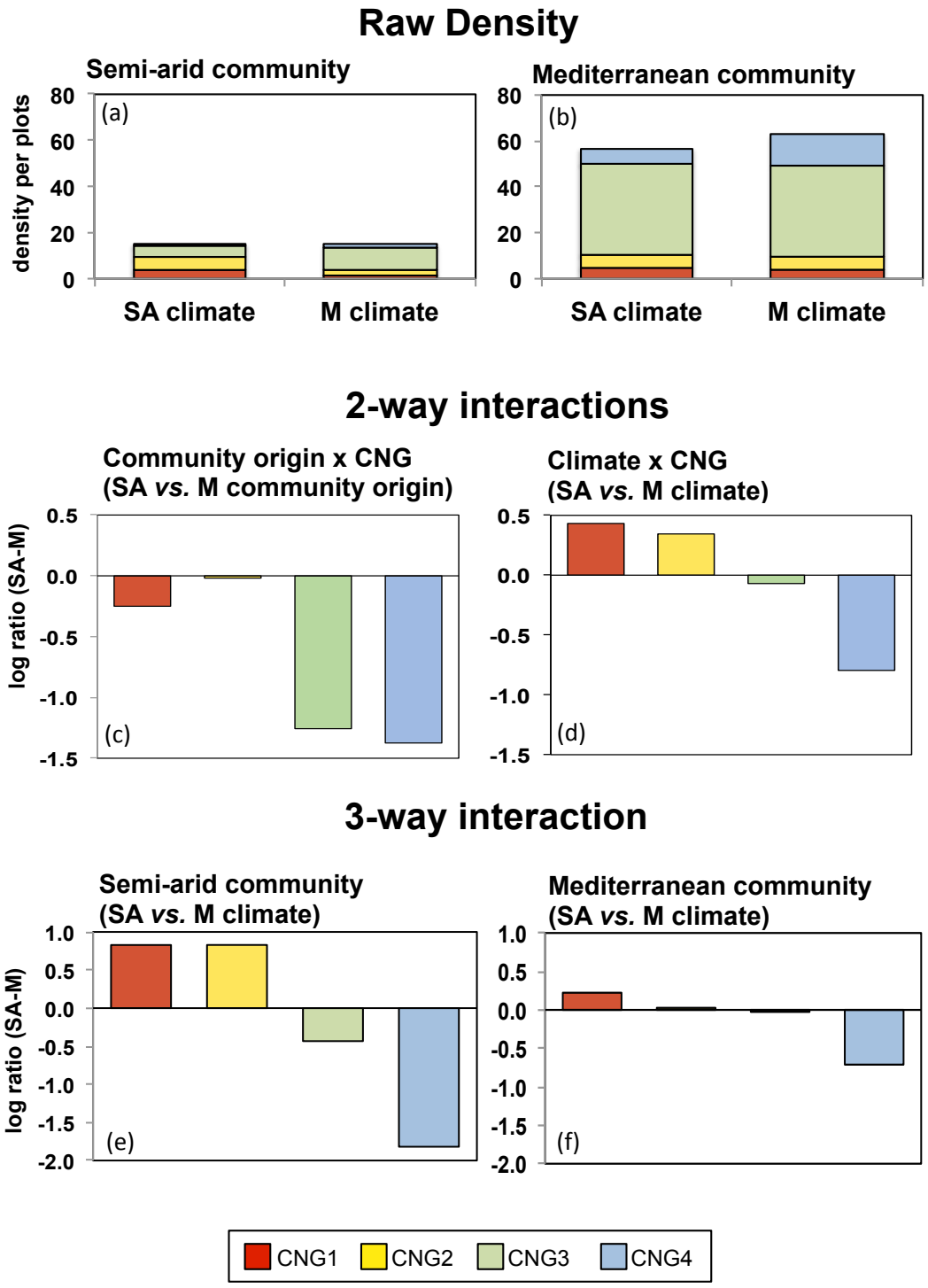
Raw Density
Semi-arid community
Mediterranean community
density per plots
80
60
40
20
0
(a)
(b)
SA climate
M climate
2-way interactions
Community origin x CNG
(SA vs. M community origin)
Climate x CNG
(SA vs. M climate)
log ratio (SA-M)
0.5
0.0
-0.5
-1.0
-1.5
(c)
(d)
3-way interaction
Semi-arid community
(SA vs. M climate)
Mediterranean community
(SA vs. M climate)
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
(e)
(f)
CNG1
CNG2
CNG3
CNG4

Figure 2

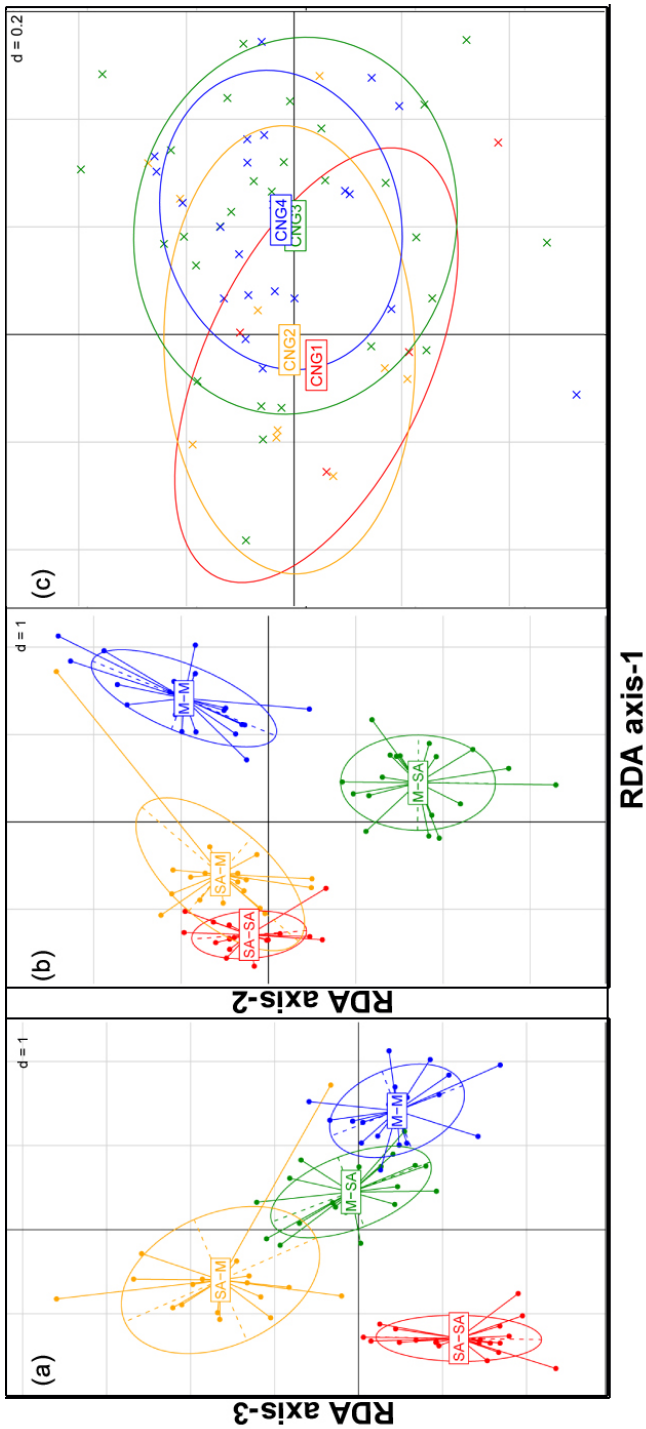
(a)
d = 1
SA−M
M−SA
M−M
SA−SA
RDA axis-3
(b)
d = 1
M−M
SA−M
SA−SA
M−SA
RDA axis-2
(c)
d = 0.2
CNG4
CNG3
CNG2
CNG1
RDA axis-1

Figure 3