1 **Whole plant community transplants across climates reveal total community**

2 **stability due to large shifts in species assemblage**

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19

Abstract

21   Climate change will decrease average precipitation and increase rainfall

22   variability in Eastern Mediterranean regions. This may affect the performance of

23   many plant species either directly or via altered biotic interactions in ways that are

24   hard to predict. In such highly fluctuating climates, year-to-year community variation

25   may override long-term selection processes, thus masking directional community

26   responses to climate change.

27   Here we tested short-term responses of dryland plant communities to sharp

28   changes in climatic conditions, by means of whole community reciprocal transplants

29   of soil and seed banks. We exposed annual plant communities to two very different

30   climates (Mediterranean and semi-arid) and measured changes in community

31   composition, total biomass, plant density, and species diversity. In addition, we

32   grouped species into dry-adapted and wet-adapted species in each community.

33   Our results revealed that climate played a large role in determining community

34   assembly. For both community origins, we observed a relative increase of dry-adapted

35   species when exposed to the drier climate, and a relative increase in wet-adapted

36   species in the wetter climate. However, the compositional shifts were much larger in

37   semi-arid origin communities. At the same time community density, biomass and

38   species richness remained remarkably stable across climates, indicating that

39   community stability was maintained between climates by predictable asynchronous

40   shifts of species. Similar but smaller shifts were present in the Mediterranean origin

41   communities, where exposure to the drier climate reduced biomass and species

42   richness.

43   Our study suggests that large asynchronous variation in species abundances,

44   matching high year-to-year rainfall variability, may provide a mechanism for

45   community homeostasis, and slow down selection processes in response to climate

46   change. However, increased occurrence of extreme droughts exceeding the climatic

47   fluctuations to which species are adapted may, in the long-term, lead to loss of wet-

48   adapted species.

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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

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75   inherent property of plant communities, and may promote community stability in the

76   long-term. This effect is particularly pronounced when species numbers are large and

77   population sizes vary asynchronously (Doak et al. 1998, Schindler et al. 2015).

78   Indeed, ecological theory and models support the idea that high inter-annual variation

79   in species response to climate can lead to community-level stability (Anderson et al.

80   1982, Tilman et al. 1998, Thompson et al. 2015, Abbott et al. 2017). This may be an

81   important mechanism for maintaining dryland communities' stability in response to

82   large year-to-year variation in rainfall, and for slowing down ongoing selection

83   processes due to climate change (Bonebrake and Mastrandrea 2010, Bilton et al.

84   2016).

85   Although long-term climate manipulations are the gold standard in ecological

86   climate impact research and are fundamental to understanding long-term community

87   shifts (Brown et al. 2001, Rinnan et al. 2007, Blume-Werry et al. 2016), they are very

88   costly to set up and maintain, often outliving funding cycles and scientific research

89   positions (Lindenmayer et al. 2012). The monitoring of communities for short-term

90   responses may be a useful complement to long-term experiments, as besides being

91   less costly, can be vitally important for parsing mechanistic information about plant

92   responses to large inter-annual variation, as well as extreme events (De Dato et al.

93   2006, Barbosa et al. 2014, Blume-Werry et al. 2016). Reciprocal transplants represent

94   a promising approach for indirectly studying plant responses to climate change on a

95   short temporal scale. These manipulative experiments have been widely adopted in

96   single species (e.g. Link et al. 2003, Casper and Castelli 2007, Macel et al. 2007,

97   Alexander et al. 2015, Tomiolo et al. 2015) for studying local adaptation and, more

98   recently, for studying their responses to a climate that matches conditions predicted

99   by climate change scenarios (the so called "space-for-time approach"). Reciprocal

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100   transplants have also been applied to entire communities in studies of soil

101   microbiomes (Waldrop and Firestone 2006, Lazzaro et al. 2011), leaf litter (Ayres et

102   al. 2009, Allison et al. 2013), and occasionally to whole plant communities in

103   different habitats ranging from wetlands to alpine grasslands (Maranon and

104   Bartolome 1993, Wetzel et al. 2004, Wu et al. 2012, Alexander et al. 2015). However,

105   the potential for using whole community reciprocal transplants to study plant

106   community response to climate change has not been fully exploited, particularly in

107   dryland systems, which often provide ideal conditions.

108   Dryland ecosystems are often dominated by annual plants that survive the dry

109   season as a permanent seed bank (Cohen 1966). Therefore, the community (i.e. the

110   seed bank) can be conveniently transplanted as a whole during the dry season without

111   any harm to the plants. In addition, by transplanting seed banks with their associated

112   soil, it is possible to evaluate plant communities' response to climate while preserving

113   soil abiotic and biotic interactions. To test the response of dryland annual plant

114   communities characterized by very different climates, we transplanted home soil with

115   seed bank among three sites situated along a steep aridity gradient in the Eastern

116   Mediterranean region, ranging from an arid to Mediterranean climate. In this region,

117   rainfall is the main limiting factor to plant growth (Ziv et al. 2014) and differs up to 5-

118   fold between the driest and wettest site(Holzapfel et al. 2006). The study sites used

119   for our reciprocal transplant also hosted a long-term climate manipulation experiment

120   (Tielbörger et al. 2014). This allowed for a comparison between long-term dynamics,

121   resulting from consistently imposed climate change, and the short-term responses

122   observed in our transplant experiment. Finally, we classified species based on their

123   climatic requirements, adopting the Climatic Niche Group approach (CNG; *sensu*

124   Bilton et al. 2016) that has been successfully employed for the species in our study

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125   region (Bilton et al. 2016) and in other dryland ecosystems (Liu et al. 2018). By

126   identifying those species responsive to drier or wetter conditions, the CNG approach

127   provided us with testable predictions about shifts in community assembly across

128   climates within the reciprocal transplants.

129   We predicted that the community emerging from the reciprocal soil transplants

130   would be greatly determined by community origin, with less individuals emerging

131   from drier origins than wetter origins. Secondly, we hypothesized that the climate (i.e.

132   rainfall availability) at the transplant site would affect the emerging communities,

133   resulting in less biomass and less individuals emerging from community origins

134   exposed to drier climates. We also predicted that climate would select the emerging

135   community from the species pool of each origin in a predictable manner, with more

136   wet adapted species emerging in communities exposed to wetter climates, and more

137   dry-adapted species in drier climates.

138

139   **Methods**

140   **Study area**

141   This study was conducted in Israel at three fenced sites (area approximately 100 m

142   x 400 m) with respectively Mediterranean (M) semi-arid (SA), and arid (A) climate.

143   The three study sites share the same calcareous bedrock, southern aspect, altitude and

144   mean annual temperatures, so that they differ chiefly in mean and variance of annual

145   rainfall, and vegetation. The M site is located southwest of Jerusalem (N 31° 42' E

146   35° 3') at 620 masl, on Terra Rossa soil. The climate is characterized by 550 mm

147   average annual rainfall with 20% inter-annual variation. The SA site (N 31° 23' E 34°

148   54') is located in the northern portion of the Negev Desert near the city of Beersheba,

149   at 590 masl, on Light Brown Rendzina. Average annual rainfall is 270 mm with

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150   approximately 30% inter-annual variation. The A site is located in the central Negev

151   near Sde Boqer (N 30º52' E 34º46') at 470 masl, on desert Lithosol. Average annual

152   rainfall amounts to 90 mm with 43% inter-annual variation (Holzapfel et al. 2006).

153   The plant communities at the three sites are semi-natural shrublands dominated by

154   *Sarcopoterium spinosum* (L.) Spach, and winter annuals (approx. 85% of all species)

155   that persist during summer in the form of dormant seed banks stored in the soil (Noy-

156   Meir 1973, Alon and Steinberger 1999). The species pool is overlapping among sites,

157   and annual plant cover amounts to 25% at the M site, 10% at the SA site, and < 1% at

158   the A site (Tielbörger et al. 2014).

159   **Experimental set up**

160   During the summer of 2010, we collected soil with seed bank from forty square

161   plots (20cm x 20cm, depth: 5cm) at the M and A sites and sixty plots at the SA site.

162   Within each site, plots were situated at least 20 cm apart from each other and away

163   from rocks and shrubs. Following Tomiolo et al. (2015) soil collected from each site

164   was pooled to produce a baseline community as there is substantial small-scale

165   heterogeneity in the seed bank (Siewert and Tielbörger 2010). The soil was stored in a

166   net-house at the University of Rehovot, Israel, where it experienced summer

167   temperatures necessary for breaking seed dormancy (Baskin et al. 1993). In

168   September 2010, twenty of the previously excavated plots at each site were randomly

169   selected and filled with home soil, while the remaining plots were filled with soil

170   from the closest away-from-home site (i.e. M site received M and SA soil; SA site

171   received M, SA and A soil; A site received SA and A soil, Supplementary Material

172   Appendix 1 Fig. A1). Transplanted soil was separated from the surrounding soil by a

173   layer of absorbent paper that provided initial isolation between soils, while not

174   impeding water percolation. After transplanting, we placed patches of organza (a thin

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175   transparent fabric) over the surface of each plot to avoid contamination from seed

176   dispersal or seed predation (Petrů and Tielbörger 2008), and we removed them at the

177   time of germination.

178   Because the transplants were carried out during the dormant season we could

179   relocate the community of dormant seeds and soil biota with minimum damage. By

180   transplanting communities with their maternal soil we could test direct effects of

181   climate (e.g. decreasing rainfall) while preserving biotic interactions with

182   neighbouring plants and soil biota, which are also affected by the novel climate

183   (Emmett et al. 2004). At peak development (spring 2011), we recorded the identity

184   and number of individuals of the emerging species in each plot. In order to minimize

185   edge effects, we excluded plants growing in the outer 1 cm margin of each plot. After

186   species identification, aboveground biomass was collected, oven-dried at 70°C for 48

187   hours and weighed.

188   Unfortunately, the season of recording was very dry and the arid site received

189   only 30% of the average annual rainfall. Therefore, only a handful of seedlings of two

190   desert species (*Stipa capensis*, *Erodium touchyanum*) emerged at the arid site. As a

191   result, there was no home arid community to be compared to the transplants, and we

192   had to restrict our subsequent analyses to the reciprocal transplants between the SA

193   and M community origins.

194

195   **Climatic Niche Groups (CNG)**

196   Each species within the target communities was assigned to a Climatic Niche

197   Group (Bilton et al. 2016) classified by their distribution range in relation to rainfall.

198   A similar method has been employed for defining thermal niches of species in high

199   elevation and tundra habitats (Gottfried et al. 2012, Elmendorf et al. 2015), and

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200   ideologically similar for Ellenberg values, which determine species habitat

201   requirements based on several abiotic parameters (Ellenberg 1974).

202   The rationale for the CNG grouping is that rainfall is the main driver of

203   community composition in the region, therefore species sharing similar climate

204   adaptations (approximated by the realized climatic rainfall niche) are likely to co-

205   occur in the same community by virtue of habitat filtering (García-Camacho et al.

206   2017). Species realized climatic niche values were derived as in Bilton et al. (2016).

207   For each single species the observed occurrences within Israel (distribution range)

208   were overlaid with mean annual rainfall climate data, and the mean value was taken

209   (obtained from BioGIS 2012, available at http://www.biogis.huji.ac.il/). Boundaries

210   between climatic niche groups spanned similar ranges of average annual rainfall

211   (approximately 130 mm) and resulted in four groups that ranked species with respect

212   to their hypothesized response to climate. Climatic Niche Group 1 (CNG1)

213   represented species associated with the lowest rainfall extremes of the gradient,

214   conversely CNG4 gathered species distributed in areas with high rainfall. Species

215   from all four CNGs were present in both communities (Supplementary Material,

216   Appendix 2 Table A1), but varied in their proportional representation at each site, and

217   could therefore be compared across sites and climates (Bilton et al. 2016).

218

219   **Statistical analyses**

220   We first analyzed how total density (number of individuals per plot), biomass,

221   species richness (number of species per plot), evenness (Simpson's evenness) and

222   diversity (Shannon-Wiener Index) varied in response to climate, community origin

223   and their interaction. In addition, we analyzed how the number of individuals

224   belonging to each climatic niche group per plot (i.e. CNG density) varied in response

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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**

249   Overall, 97 species were recorded, among which 12.3% were grasses, 23.7%

250   legumes and 64% belonged to other families (Supplementary Material, Appendix 2

251   Table A1). In total, 68 species emerged from the semi-arid soil seed bank, 81 from the

252   Mediterranean origin, and 53 species were shared between the two origins. Fourteen

253   of these appeared in all four combinations of community origin and climate.

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255   **Diversity, richness and biomass**

256   Total biomass, plant density, number of species and species diversity (Fig. 1b, 2a,

257   b, Table 1) were all significantly higher for communities of M origin rather than SA

258   origin. Additionally, for the M community origins, plant biomass, species richness,

259   diversity (Fig.1a, b, d) and total density (Fig 2.a, b) were significantly lower when

260   communities were exposed to the drier SA climates compared to their home climate,

261   whereas evenness remained the same across climates (Fig. 1c). For the SA

262   community origins, climate had no significant effect on any of the whole community

263   parameters total density (Fig. 2a, b, Table 2), biomass, species richness or diversity

264   (Fig.1, Table 1). Higher evenness was found in SA community origins exposed to M

265   climate compared to M community origins exposed to SA climate (Fig. 1c, Table 1).

266

267   **Relative abundance of CNG across sites and community origins**

268   Relative density of individuals changed considerably across community

269   origins and CNG groups (Table 2). In particular, the relative abundance of CNGs

270   shifted significantly across climates and community origins as indicated by the

271   significant two-way interactions (Table 2, Fig. 2a-d, Supplementary Material

272   Appendix 2 Table A2). In SA community origins, the mean abundance of individuals

273   belonging to dry CNGs (CNG 1and 2) was halved in M climate compared to SA

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274 climate; on the other hand individuals belonging to CNG 4, the wettest adapted group,

275 were 6.5 times more abundant in M climate (Fig. 2a, c). In M communities, the shift

276 in CNG relative abundances was less strong but the relative hierarchical response of

277 the CNGs was in the same order (densities of CNG1 and 2 higher in SA climate;

278 CNG3 and 4 higher in M climate). The largest shift was seen in CNG4 that counted

279 twice as many individuals in home *vs.* away from home climate (Fig. 2b, d). The

280 different magnitude in CNG shifts across community origins and climates was

281 confirmed by a significant 3-way interaction (CNG x community origin x climate,

282 Table 2, Fig. 2e, f).

283 The RDA indicated four distinct communities emerging from the respective

284 treatments, with a significant effect of community origin and climate on species

285 assembly, as well as a significant interaction between these terms (Fig. 3a, b). Using

286 simple correlations we assessed which plots/species scores changed and had most

287 impact on each axis. We obtained three main RDA axes describing the species

288 composition. For plot mean scores: RDA1 (9.2% explained) was highly correlated to

289 overall differences between community origins, whereas the constrained RDA2

290 (3.3%; explained) and RDA3 (1.7%; explained) distinguished the climate x

291 community origin interaction term. For species mean scores, RDA1 was positively

292 correlated to species Climatic Niche values, and the correlation was positive but less

293 strong for RDA2 and RDA3 (Fig. 3c). Results were further validated by an RDA on

294 the community weighted mean traits using species Climatic Niche values as a trait,

295 and showed significant community origin and climate effects ($p<0.05$). In

296 combination, these results suggest that rainfall niche strongly explained variation in

297 species composition across treatments.

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Discussion

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300   Our results revealed that climate played a large role in determining the species

301   assemblages in our whole community transplant experiment, and that such changes

302   were predictably related to possible species-specific climatic adaptations. One of our

303   most notable findings was that large shifts in species composition occurred when

304   transplants were exposed to vastly different climates, whereas total community

305   parameters such as biomass, density, and diversity remained remarkably stable.

306   Perhaps unsurprisingly, and as predicted from previous observations across the

307   rainfall gradient (Tielbörger et al. 2014), communities establishing from the

308   Mediterranean (M) origin soil had higher individual density and total biomass than

309   semi-arid (SA) origins. This is also similar to other dryland systems, where rainfall

310   acts as a limiting resource (Guo and Brown 1997, Cleland et al. 2013). Consistently,

311   all four CNGs had higher densities of individuals establishing from the M origin

312   compared to SA origin. However, the wetter species groups (CNG 3 & 4) were

313   proportionally more represented in M community origins, and the drier species groups

314   (CNG 1 & 2) were more abundant in SA community origins. This, consistently with

315   the findings of Bilton et al. (2016), suggests that CNGs are representative of species

316   rainfall requirements and possibly climatic adaptations at the different sites. All

317   communities rapidly matched the concomitant climate with shifts in community

318   composition across climates that were strikingly well explained by hierarchical

319   switches in relative CNG abundances. Plants establishing from both community

320   origins showed a relative increase of species assumed to be most dry adapted when

321   exposed to the drier (SA) climate. Accordingly, wet adapted species were more

322   abundant in both communities when exposed to the wetter (M) climate. Therefore,

323   CNGs revealed species responses to short-term climate effects in a predictable way,

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324   suggesting potential short-term selection mechanisms that act on the communities in

325   response to yearly or extreme differences in rainfall.

326   Our most intriguing finding was that climate not only selected for predictable

327   species groups, but that the community origins differed greatly in the magnitude of

328   the community shifts. The SA origin, with the more variable rainfall regime – both

329   between and within years (Tielbörger et al. 2014) – also experienced the greater shifts

330   in community composition. This result matches other studies showing that

331   communities from drier climates often have higher inter-annual turnover of species

332   composition (Guo and Brown 1997, Cleland et al. 2013). Fascinatingly, the

333   magnitude of the compositional shifts between transplanted community origins was

334   inversely related to changes in total community parameters across climates. Namely,

335   in SA community origins total density, biomass and species richness remained

336   constant. Conversely, for the M origin transplants, which had smaller compositional

337   shifts, total density, biomass and richness decreased when exposed to the drier SA

338   climate. Large inter-annual variation in species abundances often leads to higher

339   community stability across time (Bai et al. 2004, Grime et al. 2008). Similar patterns

340   have been previously explained in plant community studies, albeit in a different

341   context, by the portfolio effect (Doak et al. 1998, Schindler et al. 2015). The portfolio

342   effect predicts that greater numbers of species in a community lead both

343   mathematically and ecologically to a greater chance of asynchronous relationships

344   forming year-to-year. Here we show, consistent with a previous study (Cleland et al.

345   2013), that in the community with the lower species richness (SA origin), greater

346   asynchrony and greater species turnover led to greater stability across climates. This

347   asynchrony is not random, but directly linked to species-specific climatic adaptations.

348   Thus, asynchronous shifts in relative abundance of species according to their climate

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349   adaptations may allow for fast responses to year-to-year climatic variation in dryland

350   annual communities (Abbott 2017).

351   In the short-term, high species turnover may assure community stability, by

352   maintaining stable biomass and density, but in the long-term, such processes may also

353   lead to greater resistance and stability of dry (SA) communities to rainfall fluctuations

354   by favoring species adapted to more arid conditions. The high turnover is possible

355   without immediate loss of species because in dryland environments subject to large

356   year-to-year climatic variability, plants often display bet-hedging strategies such as

357   long-lived seed banks and seed dormancy that can buffer against inter-annual

358   fluctuations (Petrů and Tielbörger 2008, Tielbörger et al. 2012). Delayed germination

359   of dormant seeds during unfavorable years decreases the risk of extinction over time

360   and also promotes coexistence of species with different climatic requirements via

361   storage effects (Chesson and Grubb 1990, Pake and Venable 1995). Interestingly, the

362   findings from this short-term community transplant study are consistent with those of

363   a parallel long-term experiment conducted at the M and SA sites (Tielbörger et al.

364   2014), where community composition was monitored for 10 years in permanent plots

365   receiving respectively ambient rainfall, experimental drought (-30% rainfall) or

366   increased rainfall (+30% rainfall). Plant communities exposed to the long-term

367   climate manipulation treatments showed no detectable long-term effect on total

368   density, species richness and community biomass (Tielbörger et al. 2014). This

369   unexpected community resistance may be attributable to the large variability in

370   rainfall to which plant species in both community origins are pre-adapted (Tielbörger

371   et al. 2014, Tomiolo et al. 2015). Also at the two time-scales, selection of species in

372   relation to their CNG was observed (Bilton et al. 2016). However, while in the current

373   study we found stronger short-term selection for SA origin communities, long-term

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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

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399   predicted by climate change scenarios for the next 50-80 years (Smiatek et al. 2011,

400   Tomiolo et al. 2015). These results suggest that, as long as inter-annual climatic

401   fluctuations keep within the limits of climatic variability commonly experienced by

402   these communities, and rainy years that replenish the seed bank periodically occur,

403   wet adapted species will persist within the communities. However, with increasing

404   drought and unpredictability, communities are likely to experience species loss that

405   will affect primarily species with high rainfall requirements (Tielbörger et al. 2014,

406   Bilton et al. 2016). The similar results from the long-term experiment with our

407   reciprocal transplant indicate that the latter may be a powerful complement to long-

408   term field experiments. However, it should be noted that annual communities are

409   particularly suited for this approach and the same may not hold for long-lived

410   communities. Moreover, the fast response observed in our communities is uncommon

411   compared to temperate systems, where a lag between shifts in climatic conditions and

412   subsequent changes in community structure is often observed (Adler and Levine

413   2007, Jones et al. 2016). This suggests a higher resistance and resilience of dryland

414   ecosystems to extreme events compared to temperate ecosystems (Ruppert et al.

415   2015).

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655 **Figures and tables**

656
657 **Table 1: Type III ANOVA table results for the models applied to individual density, species**

658 **richness, species diversity, evenness and total biomass. Lines correspond to response variables**

659 **and columns to explanatory variables of each model. In each column the first value represent**

660 **Chi-square test values and the second the p-value. Probability values for significant terms are**

661 **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**

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664 **Table 2: Type III ANOVA table of results for Generalized Linear Models determining the effect**

665 **of community origin, climate and Climatic Niche Group (CNG) on plant community densities**

666 **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**

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683   **Figure Captions:**

684 **Figure 1: Mean ±1SE A) species richness (i.e. number of species per plot), B) total biomass, C)**

685 **evenness, D) diversity, of annual plant communities established from two community origins**

686 **('M' Mediterranean; 'SA' Semi-Arid) grown in two sites (i.e. climates: 'M' Mediterranean; 'SA'**

687 **Semi-Arid).**

688

689   **Figure 2: Impact of community origin, climate and Climatic Niche Group (CNG) on plant**

690 **densities establishing from seed banks in home *vs*. away-from-home climate. Each Climatic Niche**

691 **Group (CNG) aggregates species with similar climatic adaptation, ranging from dry climates**

692 **(CNG 1) to wetter climates (CNG 4). Fig. 2 a, b: Total mean individuals density across climates is**

693 **broken down according to CNG relative abundance. Fig. 2 c-f: Differences in relative densities of**

694 **CNG groups are expressed as log ratios, where positive values indicate higher CNG relative**

695 **abundances in SA community origins or sites, whereas negative values indicate higher CNG**

696 **relative abundances in M community origins and climate. Community composition shifts are**

697 **represented across community origins (2c), climates (2d) and the combination of the two (2 e,f).**

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700   **Figure 3: Redundancy Analysis (RDA) of species compositional change in community origins**

701 **emerging in home *vs.* away-from-home climates. Indicated are the 95% confidence intervals for**

702 **the groupings/categories (ellipses). Fig. 3 a, b represents the plot centroids of each community**

703 **origin-climate combination. Lines are vectors from the centre of a category to each site score**

704 **(points). RDA-axis 1: correlated to distance between origins, RDA-axis 3: the effect of climate on**

705 **SA community origins, and RDA-axis 2 the effect of climate on M community origins. In red: SA**

706 **community origins - SA climate; yellow: SA origins - M climate; blue: M origins- M climate;**

707 **green: M origins -SA climate. Fig. 3c represents the species centroids for each species group.**

708 **Lines are vectors connecting the centre of each group with species scores. In red: CNG1, yellow:**

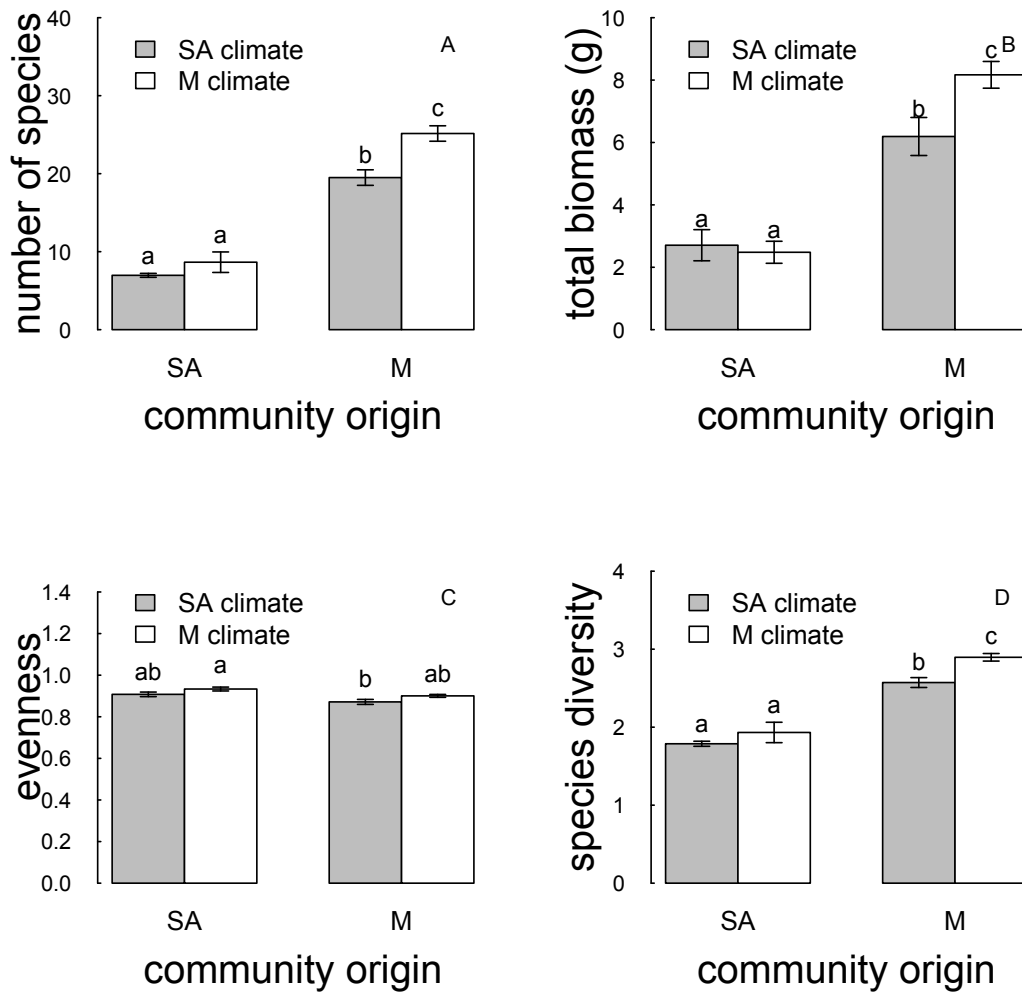709 **CNG2, green: CNG3, blue: CNG4.**
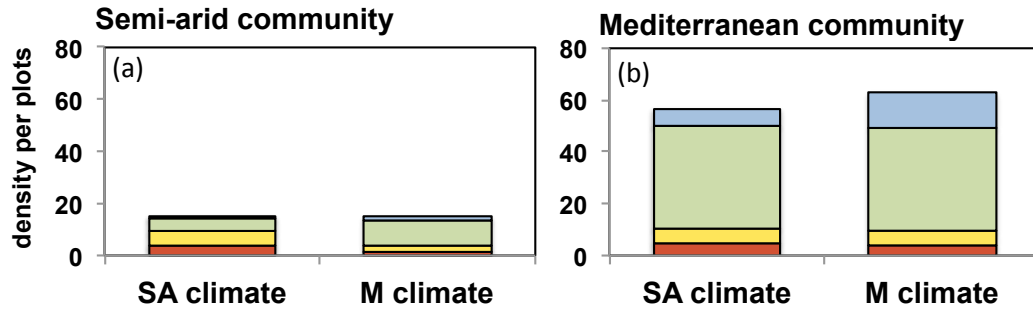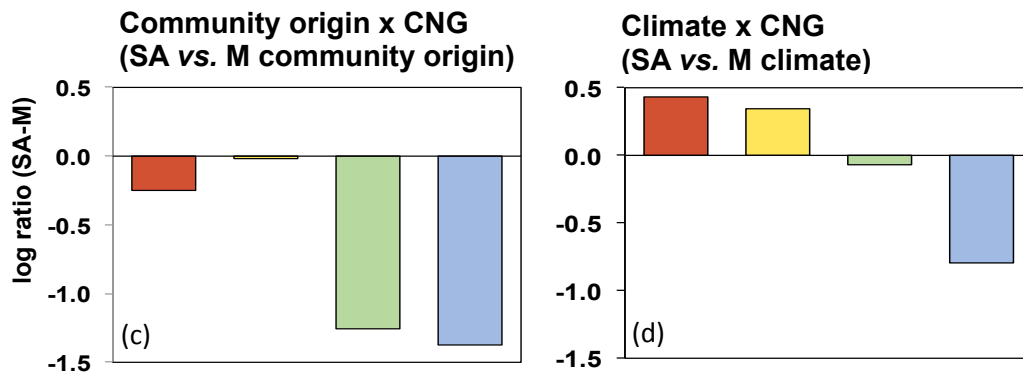
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717 **Figure 1**
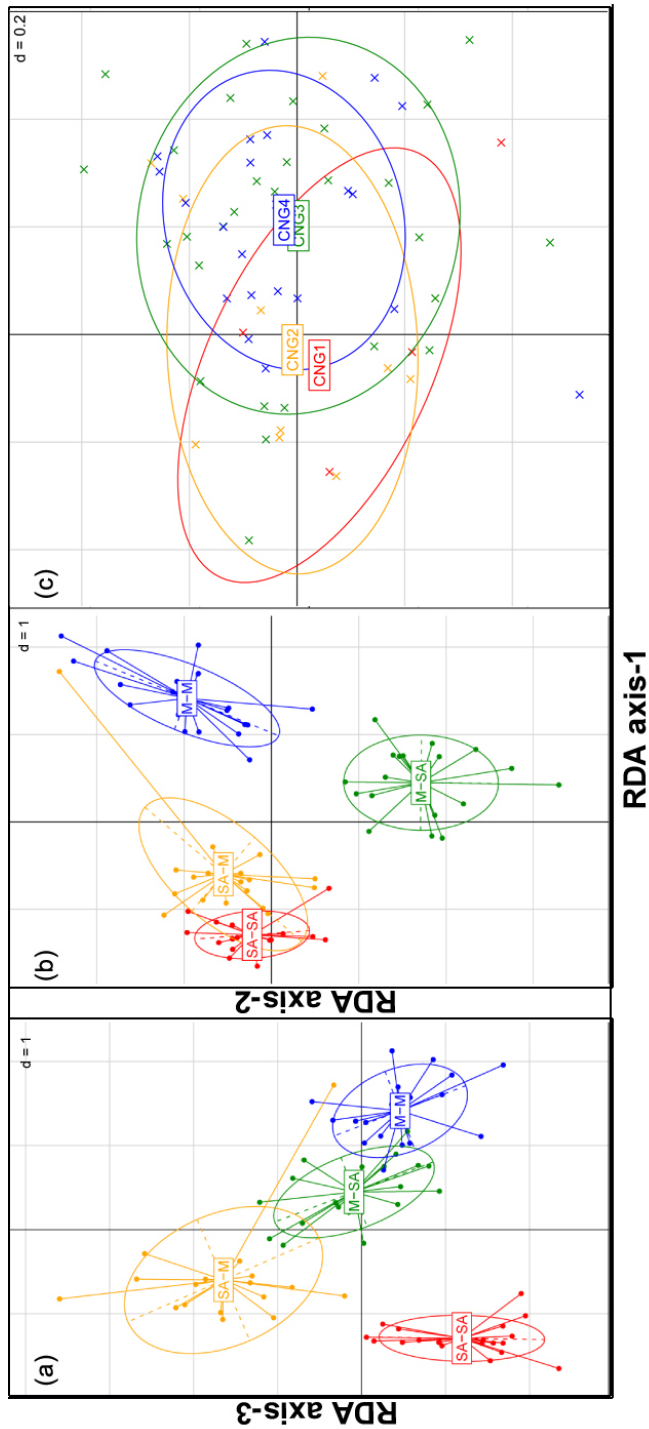718

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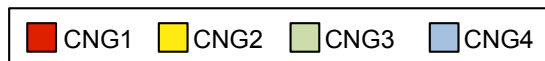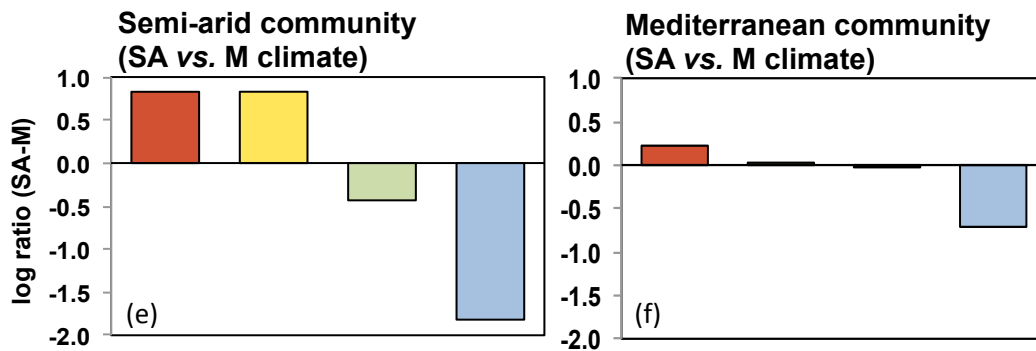
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723   **Figure 2**

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747 **Figure 3**

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