

1 **Whole plant community transplants across climates reveal structural community**
2 **stability due to large shifts in species assemblage**

3

4 **Article type: original research**

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17 **Running headline:** Community stability under climate change

18 **Keywords:** annual plant communities, climate change, Climatic Niche Groups,

19 community ecology, reciprocal transplants, determinants of plant community

20 diversity and assemblage, distribution range, community stability, field experiments

21

22

23 **Summary**

24

25 (1) Climate change will decrease precipitation and increase rainfall variability in
26 Eastern Mediterranean regions, with responses of plant communities largely
27 uncertain. Here, we tested short-term responses of dryland plant communities to
28 contrasting rainfall regimes using a novel experimental approach.

29 (2) We exposed three annual plant communities to sharp changes in climatic
30 conditions using whole community reciprocal transplants of soil and seed banks. We
31 tested for the role of climate *vs.* community origin on community response and
32 resistance. In parallel, we asked whether origin-specific climatic adaptations predict
33 compositional shifts across climates.

34 (3) For both community origins, the most dry-adapted species in each community
35 increased in dry climate and the wet-adapted species increased in wet climate. Dry
36 community origins showed large compositional shifts while maintaining stable plant
37 density, biomass and species richness across climates. Conversely, wet communities
38 showed smaller compositional shifts, but larger variation in biomass and richness.

39 (4) Asynchrony in species abundances in response to rainfall variability could
40 maintain structural community stability. This, in combination with seed dormancy,
41 has the ability to delay extinction in response to climate change. However, increasing
42 occurrence of extreme droughts may, in the long-term, lead to loss of wet-adapted
43 species.

44

45 **Introduction**

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

62 One of the predicted impacts of climate change is a re-assembly of plant
63 communities (Hobbs *et al.*, 2006; Williams & Jackson, 2007; Alexander *et al.*, 2016)
64 due to the differential ability of single species to either track their climatic niche or to
65 survive under changed conditions, by means of adaptation or plasticity (Fernandez-
66 Going *et al.*, 2013; Shi *et al.*, 2015). Such community reshuffling may be expressed in
67 a loss or gain of certain species, a shift in species relative abundance or both. In plant
68 communities already exposed to large inter-annual variations in climate, immediate
69 rearrangement of community assembly in response to climate extremes may be an
70 inherent property of plant communities, and may promote community stability in the
71 long-term. This effect is particularly pronounced when species numbers are large and
72 population sizes vary asynchronously (Doak *et al.*, 1998; Schindler *et al.*, 2015).
73 Indeed, ecological theory and models support the idea that high inter-annual variation
74 in species response to climate can lead to community-level stability (Anderson *et al.*,
75 1982; Tilman *et al.*, 1998; Thompson *et al.*, 2015; Abbott *et al.*, 2017). This may be
76 an important mechanism for maintaining dryland communities' stability in response to
77 large year-to-year variation in rainfall, and for slowing down ongoing selection

78 processes due to climate change (Bonebrake & Mastrandrea, 2010; Bilton *et al.*,
79 2016).

80 Although long-term climate manipulations are the gold standard in ecological
81 climate impact research and are fundamental for understanding long-term community
82 shifts (Brown *et al.*, 2001; Rinnan *et al.*, 2007; Blume-Werry *et al.*, 2016), they are
83 very costly to set up and maintain, often outliving funding cycles and scientific
84 research positions (Lindenmayer *et al.*, 2012). The monitoring of communities for
85 short-term responses may be a useful complement to long-term experiments, as
86 besides being less costly, it can be vitally important for parsing mechanistic
87 information about plant responses to large inter-annual variation, as well as extreme
88 events (De Dato *et al.*, 2006; Barbosa *et al.*, 2014; Blume-Werry *et al.*, 2016).
89 Reciprocal transplants represent a promising approach for indirectly studying plant
90 responses to climate change on a short temporal scale. These manipulative
91 experiments have been widely adopted in single species (e.g. Link *et al.*, 2003; Casper
92 & Castelli, 2007; Macel *et al.*, 2007; Alexander *et al.*, 2015; Tomiolo *et al.*, 2015) for
93 studying local adaptation and, more recently, for studying their responses to a climate
94 that matches conditions predicted by climate change scenarios (the so called "space-
95 for-time approach"). Reciprocal transplants have also been applied to entire
96 communities in studies of soil microbiomes (Waldrop & Firestone, 2006; Lazzaro *et al.*
97 *et al.*, 2011), leaf litter (Ayres *et al.*, 2009; Allison *et al.*, 2013), and occasionally to
98 whole plant communities in different habitats ranging from wetlands to alpine
99 grasslands (Maranon & Bartolome, 1993; Wetzal *et al.*, 2004; Wu *et al.*, 2012;
100 Alexander *et al.*, 2015). However, the potential for using whole community reciprocal
101 transplants to study plant community response to climate change has not been fully
102 exploited, particularly in dryland systems, which often provide ideal conditions.

103 Dryland ecosystems are often dominated by annual plants that survive the dry
104 season as a permanent seed bank (Cohen, 1966). Therefore, the community (i.e. the
105 seed bank) can be conveniently transplanted as a whole during the dry season without
106 any damage to the plants. In addition, by transplanting seed banks with their
107 associated soil, it is possible to evaluate plant communities' responses to climate
108 while preserving soil abiotic and biotic interactions. To test the response of dryland
109 annual plant communities characterized by very different climates, we transplanted
110 home soil with seed bank among three sites situated along a steep aridity gradient in
111 the Eastern Mediterranean region, ranging from arid to Mediterranean climate. In this

112 region, rainfall is the main limiting factor for plant growth (Ziv *et al.*, 2014) and
113 differs up to eight-fold between the driest and wettest site (Holzapfel *et al.*, 2006). We
114 classified species based on their climatic requirements, adopting the Climatic Niche
115 Group approach (CNG; *sensu* Bilton *et al.* 2016) that has been successfully employed
116 for the species in our study region (Bilton *et al.*, 2016) and in other dryland
117 ecosystems (Liu *et al.*, 2018). By identifying those species responsive to drier or
118 wetter conditions, this approach provided us with testable predictions about directions
119 of shifts in community assembly across climates within the reciprocal transplants.
120 Finally, the study sites used for our reciprocal transplant also hosted a long-term
121 climate manipulation experiment (Tielbörger *et al.*, 2014). This allowed for a
122 qualitative comparison between long-term dynamics, resulting from consistently
123 imposed climate change, and the short-term responses observed in our transplant
124 experiment.

125 We predicted that the community emerging from the reciprocal soil transplants
126 would be greatly determined by community origin, with fewer individuals emerging
127 from drier origins than wetter origins. Secondly, we hypothesized that, regardless of
128 their origin, communities emerging at the drier transplant site (i.e. lower rainfall
129 availability) would experience a reduction in total biomass and plant density. We also
130 predicted that climate would select the emerging community from the species pool of
131 each origin in a predictable manner, with more wet adapted species emerging when
132 communities were exposed to wetter climates, and more dry-adapted species in drier
133 climates.

134

135 **Methods**

136 **Study area**

137 This study was conducted in Israel at three fenced sites (area approximately 100 m
138 x 400 m) with respectively Mediterranean (M), semi-arid (SA) and arid (A) climate.
139 The three study sites share the same calcareous bedrock, southern aspect, altitude and
140 mean annual temperatures, so that they differ chiefly in mean and variance of annual
141 rainfall, and vegetation. The M site is located southwest of Jerusalem (N 31° 42' E
142 35° 3') at 620 masl, on Terra Rossa soil. The climate is characterized by 550 mm
143 average annual rainfall with 20% inter-annual variation. The SA site (N 31° 23' E 34°
144 54') is located in the northern portion of the Negev Desert near the city of Beersheba,

145 at 590 masl, on Light Brown Rendzina. Average annual rainfall is 270 mm with
146 approximately 30% inter-annual variation. The A site is located in the central Negev
147 near Sde Boqer (N 30°52' E 34°46') at 470 masl, on desert Lithosol. Average annual
148 rainfall amounts to 90 mm with 43% inter-annual variation (Holzapfel *et al.*, 2006).
149 The plant communities at the three sites are semi-natural shrublands dominated by
150 *Sarcopoterium spinosum* (L.) Spach, and winter annuals (approx. 85% of all species)
151 that persist during summer in the form of dormant seed banks stored in the soil (Noy-
152 Meir, 1973; Alon & Steinberger, 1999). The species pool is overlapping among sites,
153 and annual plant cover amounts to 25% at the M site, 10% at the SA site, and < 1% at
154 the A site (Tielbörger *et al.*, 2014).

155 **Experimental set up**

156 During summer of 2010, we collected soil with seed bank from forty square plots
157 (20cm x 20cm, depth: 5cm) at the M and A sites and sixty plots at the SA site. Within
158 each site, plots were situated at least 20 cm apart from each other, and away from
159 rocks and shrubs. Following Tomiolo *et al.* (2015) soil collected from each site was
160 pooled to produce a baseline community. Previous studies showed that small-scale
161 heterogeneity in the soil seed bank may be very large, with some patches having
162 almost no seeds and others very many (Siewert & Tielbörger, 2010). Therefore, we
163 pooled the soil samples per site prior to the transplant, following the procedure
164 adopted in many previous studies using field soil (Maranon & Bartolome, 1993;
165 Macel *et al.*, 2007; Burns & Strauss, 2011; Lazzaro *et al.*, 2011).

166 The soil was stored in a net-house at the University of Rehovot, Israel, where it
167 experienced summer temperatures necessary for breaking seed dormancy (Baskin *et al.*,
168 1993). In September 2010, twenty of the previously excavated plots at each site
169 were randomly selected and filled with home soil, while the remaining plots were
170 filled with soil from the closest away-from-home site (i.e. M site received M and SA
171 soil; SA site received M, SA and A soil; A site received SA and A soil,
172 Supplementary Material Appendix 1 Fig. A1). Transplanted soil was separated from
173 the surrounding soil by a layer of absorbent paper that provided initial isolation
174 between soils, while not impeding water percolation. After transplanting, we placed
175 patches of organza (a thin transparent fabric) over the surface of each plot to avoid
176 contamination from seed dispersal or seed predation (Petrů & Tielbörger, 2008), and
177 we removed them at the 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 This approach has proven powerful for predicting species-specific response to climate
199 change (Bilton *et al.*, 2016; Liu *et al.*, 2018). A similar method has been employed for
200 defining thermal niches of species in high elevation and tundra habitats (Gottfried *et*
201 *al.*, 2012; Elmendorf *et al.*, 2015), and it is conceptually similar to Ellenberg values,
202 which determine species habitat requirements based on several abiotic parameters
203 (Ellenberg, 1974).

204 The rationale for the CNG grouping is that rainfall is the main driver of
205 community composition in the region, therefore species sharing similar climate
206 adaptations (approximated by the realized climatic rainfall niche) are likely to co-
207 occur in the same community (García-Camacho *et al.*, 2017). Species realized
208 climatic niche values were derived as in Bilton *et al.* (2016). For each single species
209 the observed occurrences within Israel (distribution range) were overlaid with mean
210 annual rainfall climate data, and the mean value was taken (obtained from BioGIS,
211 2012, available at <http://www.biogis.huji.ac.il/>). Boundaries between climatic niche

212 groups spanned similar ranges of average annual rainfall (approximately 130 mm) and
213 resulted in four groups that ranked species with respect to their hypothesized response
214 to climate. Climatic Niche Group 1 (CNG1) represented species associated with the
215 lowest rainfall extremes of the gradient, conversely CNG4 gathered species
216 distributed in areas with high rainfall. Species from all four CNGs were present in
217 both communities (Supplementary Material, Appendix 2 Table A1), but varied in
218 their proportional representation at each site, and could therefore be compared across
219 sites and climates (Bilton *et al.*, 2016).

220

221 **Statistical analyses**

222 We first analyzed how total density (number of individuals per plot), total
223 biomass, species richness (number of species per plot) and diversity (Shannon-Wiener
224 Index) varied in response to climate, community origin and their interaction. In
225 addition, we analyzed how the number of individuals belonging to each climatic niche
226 group per plot (i.e. CNG density) varied in response to climate, community origin,
227 with respect to the four-level categorical explanatory variable CNG identity (i.e.
228 CNG1 – CNG4), including all two-way and three-way interactions. We applied
229 generalized linear models with negative binomial distribution to total individual, CNG
230 density and species richness using the MASS package (Venables *et al.*, 2002) within
231 the R software version 3.3.3 (R Development Core Team, 2014). Biomass and species
232 diversity were analyzed using linear models. To meet model requirements biomass
233 square root transformed. The significance of the models was assessed with a Type 3
234 ANOVA, using the “car” package (Fox & Weisberg, 2011).

235 Visual representation of the CNG density interactions was done using log-ratios
236 calculated from the overall mean abundance of each group in each climate or origin.
237 Showing relative change in overall abundances was also extremely helpful for
238 visualizing the significant interactions we found with our models.

239 For testing how species composition varied with community origin and climate
240 we used Redundancy Analysis (RDA, (Legendre *et al.*, 2011)) in the R package
241 ‘vegan’ (Oksanen *et al.*, 2015). The interaction term was included in a full model and
242 confirmed using a step-wise approach. The data were Hellinger transformed
243 (Legendre & Gallagher, 2001) and scaled within plots. Significance of the model was
244 tested using 999 permutations. To test if species composition could be explained by
245 rainfall distribution range we regressed the resulting RDA ‘species mean scores’

246 against the ‘climatic niche value’ of each species, both for individual species and for
247 the CNG classifications. Furthermore, we performed an RDA on the community-
248 weighted means (Garnier *et al.*, 2007) using the species ‘climatic niche value’ as a
249 pseudo-trait.

250

251 **Results**

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

258

259 **Total plant density, diversity, richness and biomass**

260 Number of species, species diversity, total plant density and total biomass (Fig. 1,
261 Table 1) were all significantly higher for M community origins rather than SA
262 origins. Additionally, M community origins attained significantly lower species
263 richness and diversity and biomass (Fig. 1) when exposed to the drier SA climate
264 compared to their home M climate. For the SA community origins, climate had no
265 significant effect on total plant density, biomass, species richness or diversity (Fig.1,
266 Table 1).

267

268 **Species composition**

269 The RDA indicated four distinct communities emerging from the respective
270 treatments, with a significant effect of community origin and climate on species
271 assembly, as well as a significant interaction between these terms (Fig. 2a, b). Using
272 simple correlations we assessed which plots/species scores changed and had most
273 impact on each axis. We obtained three main RDA axes describing the species
274 composition. For plot mean scores, RDA1 (9.2% explained) was correlated to overall
275 differences between community origins, whereas the constrained RDA2 (3.3%;
276 explained) and RDA3 (1.7%; explained) distinguished the climate x community
277 origin interaction term. For species mean scores, RDA1 was positively correlated to
278 species Climatic Niche values, and the correlation was positive but less strong for

279 RDA2 and RDA3 (Fig. 2c). Results were further validated by an RDA on the
280 community weighted mean traits using species Climatic Niche values as a trait, and
281 showed significant community origin and climate effects ($p < 0.05$). In combination,
282 these results suggest that rainfall niche partially explained variation in species
283 composition across treatments.

284

285 **CNG density across sites and community origins**

286 Overall, densities of individuals in each CNG group significantly differed
287 (CNG identity effect: Fig. 3a, b, Table 2), and all group densities were higher in M
288 origin than SA origin (Origin and Origin x CNG effect; Fig. 3c; Table 2). The
289 representation of CNGs in the communities also changed significantly across
290 climates, dry groups were more abundant in SA climate and wet groups were more
291 abundant in M climate (Climate x CNG effect: Fig. 3c, Table 2, Supplementary
292 Material Appendix 2 Table A2). The magnitude in CNG shifts across climates was
293 different among community origins as indicated by a significant 3-way interaction
294 (CNG identity x community origin x climate, Table 2, Fig. 3e, f). In SA community
295 origins, the mean abundance of individuals belonging to dry CNGs (CNG 1 and 2)
296 was halved in the wet (M) compared to the dry (SA) climate; on the other hand
297 individuals belonging to CNG 4, the wettest adapted group, were 6.5 times more
298 abundant in SA communities origins emerging in the wet climate (Fig. 3a, e). In M
299 community origins, the shift in CNG densities across climates was less strong
300 compared to SA origins, but the hierarchical response of the CNGs was in the same
301 order (i.e. densities of dry CNGs were higher in the dry climate and densities of wet
302 CNGs were higher in the wet climate). The largest shift in density was seen in the
303 wettest CNG that counted twice as many individuals in wet vs. dry climate (Fig. 3b,
304 f).

305

306 **Discussion**

307 Our results revealed that climate played a large role in determining the species
308 assemblages in our whole community transplant experiment, and that such changes
309 were predicted by species-specific climatic adaptations. One of our most notable
310 findings was that the communities showed different qualitative and quantitative
311 responses to climate change depending on their origin. Mediterranean community

312 origins from a wetter and more predictable climate, responded with changes in species
313 richness, diversity and total biomass, but showed small shifts in community
314 composition. Conversely, semi-arid community origins, from a drier and more
315 unpredictable climate, showed little variation in species richness, diversity and
316 biomass, and large shifts in species and CNG composition.

317 Perhaps unsurprisingly, and as predicted from previous observations across the
318 rainfall gradient (Tielbörger *et al.*, 2014), communities establishing from the
319 Mediterranean (M) origins had higher individual density and total biomass than semi-
320 arid (SA) origins. This is also consistent with other dryland systems (Guo & Brown,
321 1997; Cleland *et al.*, 2013). The higher plant density in Mediterranean community
322 origins corresponded with higher densities of individuals for all CNG groups,
323 Interestingly, the species composition and CNG abundances in the experimental
324 communities rapidly matched the concomitant climate. Namely, plants establishing
325 from both community origins showed a relative increase of dry adapted species (CNG
326 1 and 2) when exposed to the drier (SA) climate. Similarly, wet adapted species
327 (CNG 3 and 4) were more abundant in both communities when exposed to the wetter
328 (M) climate. This response was particularly large for semi-arid community origins
329 where the reshuffling in community composition was strikingly well explained by
330 hierarchical switches in CNG abundances. Therefore, CNGs revealed species
331 responses to short-term climate effects in a predictable way, suggesting potential
332 short-term selection mechanisms (e.g. environmental filtering) that act on the
333 communities in response to yearly differences in rainfall. This result is consistent with
334 the findings of Bilton *et al.* (2016), and suggests that CNGs are representative of
335 species rainfall requirements and possibly climatic adaptations at the different sites.

336 Our most intriguing finding was that climate filtered for predictable species
337 groups, but the magnitude of the structural community shifts was largely different
338 among community origins. In addition, the magnitude of the compositional shifts
339 between transplanted community origins was inversely related to changes in total
340 community parameters across climates. Mediterranean origin transplants, had smaller
341 compositional shifts, but larger shifts in biomass and richness. Conversely, semi-arid
342 community origins, with higher between- and within-year rainfall variability
343 (Tielbörger *et al.*, 2014), experienced the greatest shifts in community composition,
344 while showing only marginal response in community parameters. Consistent with our
345 results, large interannual compositional shifts were observed also in other

346 communities from drier and highly variable climates (Guo & Brown, 1997; Cleland *et*
347 *al.*, 2013). Interestingly, we did not record an increase in total biomass or total density
348 in semi-arid community origins when exposed to wetter climates. This is possibly the
349 result of an increase in wet CNGs in the communities, which have a core distribution
350 in wetter regions where there are larger plant densities, productivity, and a higher
351 intensity of competition (Schiffers & Tielbörger, 2006; Liancourt & Tielbörger,
352 2009). Wet CNGs may possess a better competitive ability and might have curbed the
353 growth and density of dry CNGs, thus leading to little changes in total biomass and
354 total density.

355 Large inter-annual variation in species abundances in the short-term may lead to
356 higher community stability in the long-term (Bai *et al.*, 2004; Grime *et al.*, 2008).
357 Similar patterns have been previously explained in plant community studies, albeit in
358 a different context, by the portfolio effect (Doak *et al.*, 1998; Schindler *et al.*, 2015).
359 The portfolio effect predicts that greater numbers of species in a community lead both
360 mathematically and ecologically to a greater chance of asynchronous relationships
361 forming year-to-year. Here we show, consistent with previous studies (Cleland *et al.*,
362 2013; Hallett *et al.*, 2014), that in the community originating in a more unpredictable
363 climate (in our case the semi-arid community origin), greater asynchrony and greater
364 species turnover led to greater stability across climates. Plant species in more variable
365 climates have been found to exhibit a larger phenotypic plasticity (Sultan, 1987; Pratt
366 & Mooney, 2013; Lazaro-Nogal *et al.*, 2015; Spence *et al.*, 2016), which results in
367 fitness homeostasis (Richards *et al.*, 2006; Nicotra *et al.*, 2010). This could be an
368 explanation for the higher resistance of species in SA communities but also reveals an
369 interesting analogy with the community level, where ‘homeostasis’ may be associated
370 with a larger compositional change. Overall, we suggest that asynchronous shifts in
371 abundance of species according to their climate adaptations may allow for fast
372 responses to year-to-year climatic variation in dryland annual communities (Abbott *et*
373 *al.*, 2017).

374 In the short-term, high species turnover may assure community stability in
375 biomass and density, but in the long-term, such processes may also lead to greater
376 resistance and stability of dry communities to rainfall fluctuations by favoring species
377 adapted to arid conditions. This high turnover is possible without immediate loss of
378 species because in dryland environments, plants often display bet-hedging strategies
379 such as long-lived seed banks and seed dormancy that can buffer against inter-annual

380 fluctuations (Petrů & Tielbörger, 2008; Tielbörger *et al.*, 2012). Delayed germination
381 of dormant seeds during unfavorable years decreases the risk of extinction over time
382 and also promotes coexistence of species with different climatic requirements via
383 storage effects (Chesson & Grubb, 1990; Pake & Venable, 1995). Interestingly, the
384 findings from this short-term community transplant study are consistent with those of
385 a parallel long-term experiment conducted at the same study sites (Tielbörger *et al.*,
386 2014), where community composition was monitored for 10 years in permanent plots
387 receiving respectively ambient rainfall, experimental drought (-30% rainfall) or
388 increased rainfall (+30% rainfall). Plant communities exposed to the long-term
389 climate manipulation treatments showed no detectable long-term effect on total
390 density, species richness and community biomass (Tielbörger *et al.*, 2014). However,
391 at both time-scales, shifts in species abundance in relation to their CNG was observed
392 (Bilton *et al.*, 2016). While in our short-term study we found these effects to be more
393 pronounced for semi-arid community origins, the long-term study found stronger
394 patterns in Mediterranean communities (Bilton *et al.*, 2016). This suggests that high
395 inter-annual community fluctuations may contribute to stability in community
396 composition in the long run, whereas low species turnover across years may result in
397 long-term loss of wet-adapted species.

398 Our overall findings allow some careful conclusions about the potential
399 response of these communities to climate change. It should be noted that the variation
400 in rainfall experienced by the community origins in our study approximated the
401 extremes of climatic variability at each site, but exceeded the decrease in rainfall
402 predicted by climate change scenarios for the next 50-80 years (Smiatek *et al.*, 2011;
403 Tomiolo *et al.*, 2015). These results suggest that, as long as inter-annual climatic
404 fluctuations keep within the limits of climatic variability commonly experienced by
405 these communities, and rainy years that replenish the seed bank periodically occur,
406 wet adapted species will persist within the communities. However, with increasing
407 drought and unpredictability, communities are likely to experience species loss that
408 will affect primarily species with high rainfall requirements (Tielbörger *et al.*, 2014;
409 Bilton *et al.*, 2016). The similarity of results between the long-term experiment and
410 our reciprocal transplant indicate that the latter may be a powerful complement to
411 long-term field experiments. However, annual communities are particularly suited for
412 our experimental approach and the same may not hold for long-lived communities.
413 For example, in temperate systems a lag between shifts in climatic conditions and

414 subsequent changes in community structure is often observed (Adler & Levine, 2007;
415 Jones *et al.*, 2016). The unexpected community resistance and resilience of dryland
416 ecosystems to extreme events compared with temperate ecosystems (Ruppert *et al.*,
417 2015), may be attributable to the large variability in rainfall to which plant species are
418 pre-adapted via bet hedging strategies (Tielbörger *et al.*, 2012; Gremer & Venable,
419 2014) or enhanced phenotypic plasticity (Petrů *et al.*, 2006). Such differences among
420 rainfall variability and plant life history should be taken into account when drawing
421 comparisons among habitats.

422

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

427

428 **Acknowledgements:** Jaime Kigel and Marcelo Sternberg provided logistic support.
429 The Hebrew University of Jerusalem (Rehovot) kindly provided material for
430 fieldwork. We thank Jake Alexander for providing comments on a previous version of
431 the manuscript. This study is part of the GLOWA Jordan River Project and was
432 funded by the German Ministry of Education and Research (BMBF). Further support
433 for MB and ST was obtained by the German Research Foundation (TI338_12-1;
434 TI338_11-1; and TI338_11-2; TI 338/15-1).

435

436 **Data Accessibility:** upon publication data will be made accessible on Dryad

437

438

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440

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719 **Figures and tables**

720

721 **Table 1: Type III ANOVA table results for the models applied to individual density, species**
722 **richness, species diversity, and total biomass. Lines correspond to response variables and**
723 **columns to explanatory variables of each model. In each column the first value represent Chi-**
724 **square test values and the second the p-value. Probability values for significant terms are**
725 **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
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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728 **Table 2: Type III ANOVA table of results for Generalized Linear Models determining the effect**
729 **of community origin, climate and Climatic Niche Group (CNG) on plant community densities**
730 **establishing from seed bank.**

Effect	DF	LR Chi-sq.	P-value
		236.9	
Origin	1	3	<0.001
Climate	1	2.35	0.12540
		343.2	
CNG	3	1	<0.001
Origin x Climate	1	0.07	0.78714
Origin x CNG	3	83.55	<0.001
Climate x CNG	3	50.09	<0.001
Origin x Climate x CNG	3	16.85	<0.001

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753 **Figure Captions:**

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

758

759 **Figure 2: Graphical representation of Redundancy Analysis (RDA) showing species**
760 **composition in community origins (M, SA) exposed to two different climates (M, SA). The**
761 **ellipses represent the 95% confidence intervals for the groupings/categories. Fig. 2 a, b**
762 **represents the plot centroids of each community origin-climate combination. Lines are vectors**
763 **from the centre of a category to each site score (points). RDA-axis 1: correlated to distance**
764 **between origins, RDA-axis 3: the effect of climate on SA community origins, and RDA-axis 2 the**
765 **effect of climate on M community origins. In red: SA community origins - SA climate; yellow:**
766 **SA origins - M climate; blue: M origins- M climate; green: M origins -SA climate. Fig. 2c**
767 **represents the species centroids for each Climatic Niche Group (CNG). Lines are vectors**
768 **connecting the centre of each group with species scores. In red: CNG1, yellow: CNG2, green:**
769 **CNG3, blue: CNG4.**

770

771 **Figure 3: Impact of community origin, climate and Climatic Niche Group (CNG) on plant**
772 **densities establishing from seed banks in home vs. away-from-home climate. Each Climatic Niche**
773 **Group (CNG) aggregates species with similar climatic adaptation, ranging from dry climates**
774 **(CNG 1) to wetter climates (CNG 4). Fig. 3 a, b: Total mean individuals' densities across climates**
775 **and origins are broken down according to CNG abundances. Fig. 3 c-f: Shifts in the abundance**
776 **of CNG densities across community origins (3c), climates (3d) and the combination of the two (3**
777 **e, f). Shifts in densities of CNG groups are expressed as log ratios, thus visualizing changes in**
778 **plant density on a relative scale. Positive values indicate higher CNG abundances in SA**
779 **community origins or climate, whereas negative values indicate higher CNG abundances in M**
780 **community origins or climate.**

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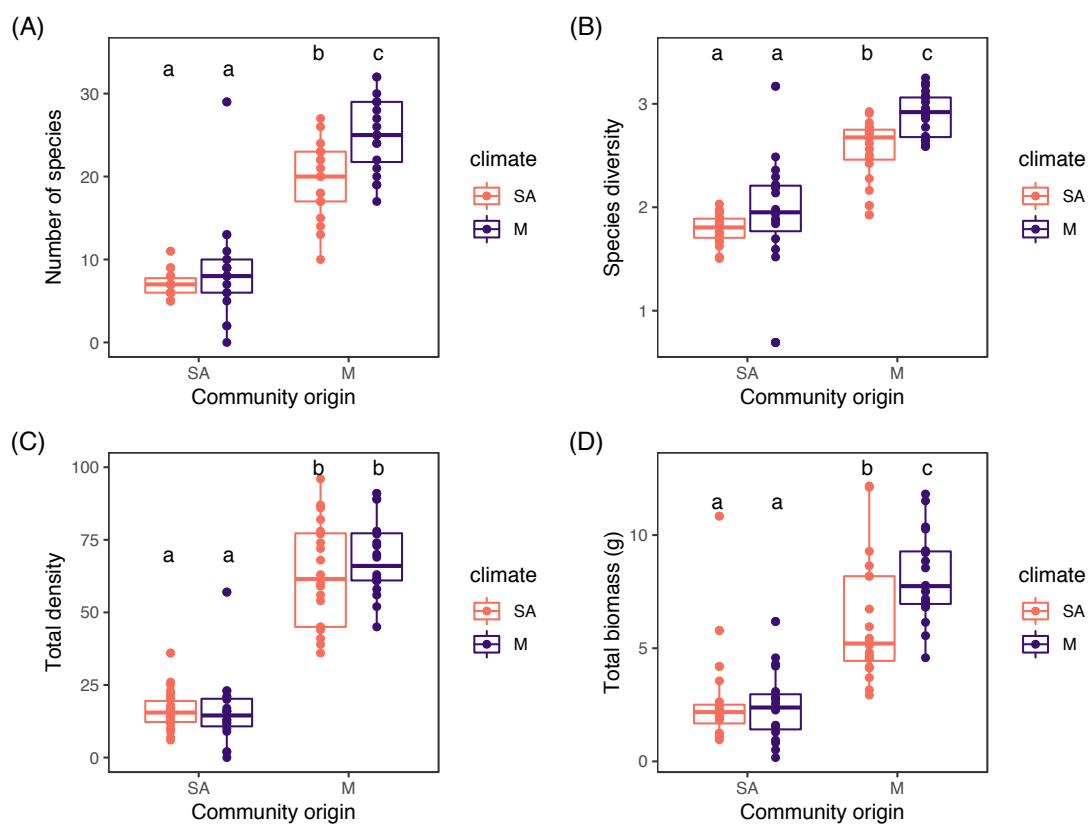
783 **Figure A1: Dots on the map represent the three experimental sites. On the right hand, the**
784 **the scheme of the community transplants at each sites. Communities (soil and relative seed bank)**
785 **were transplanted between the home and the closest away-from-home site.**

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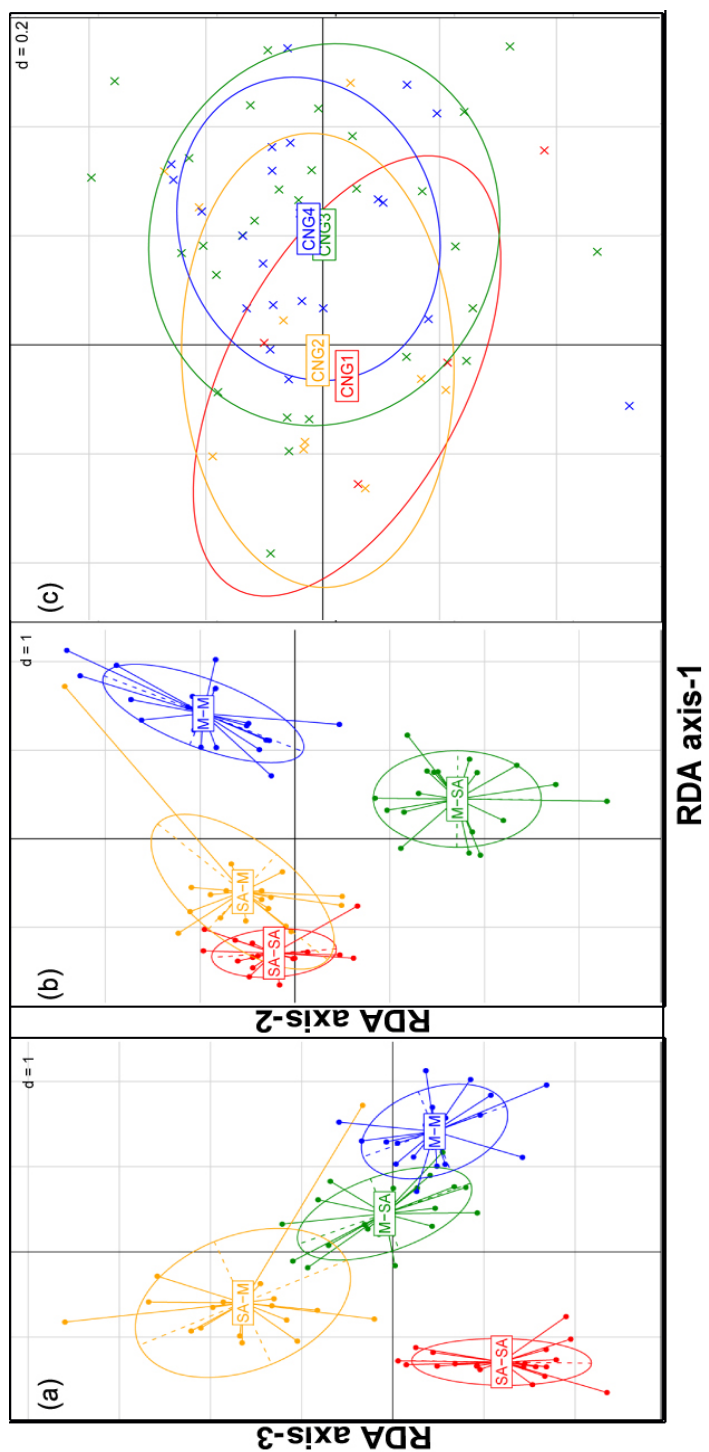


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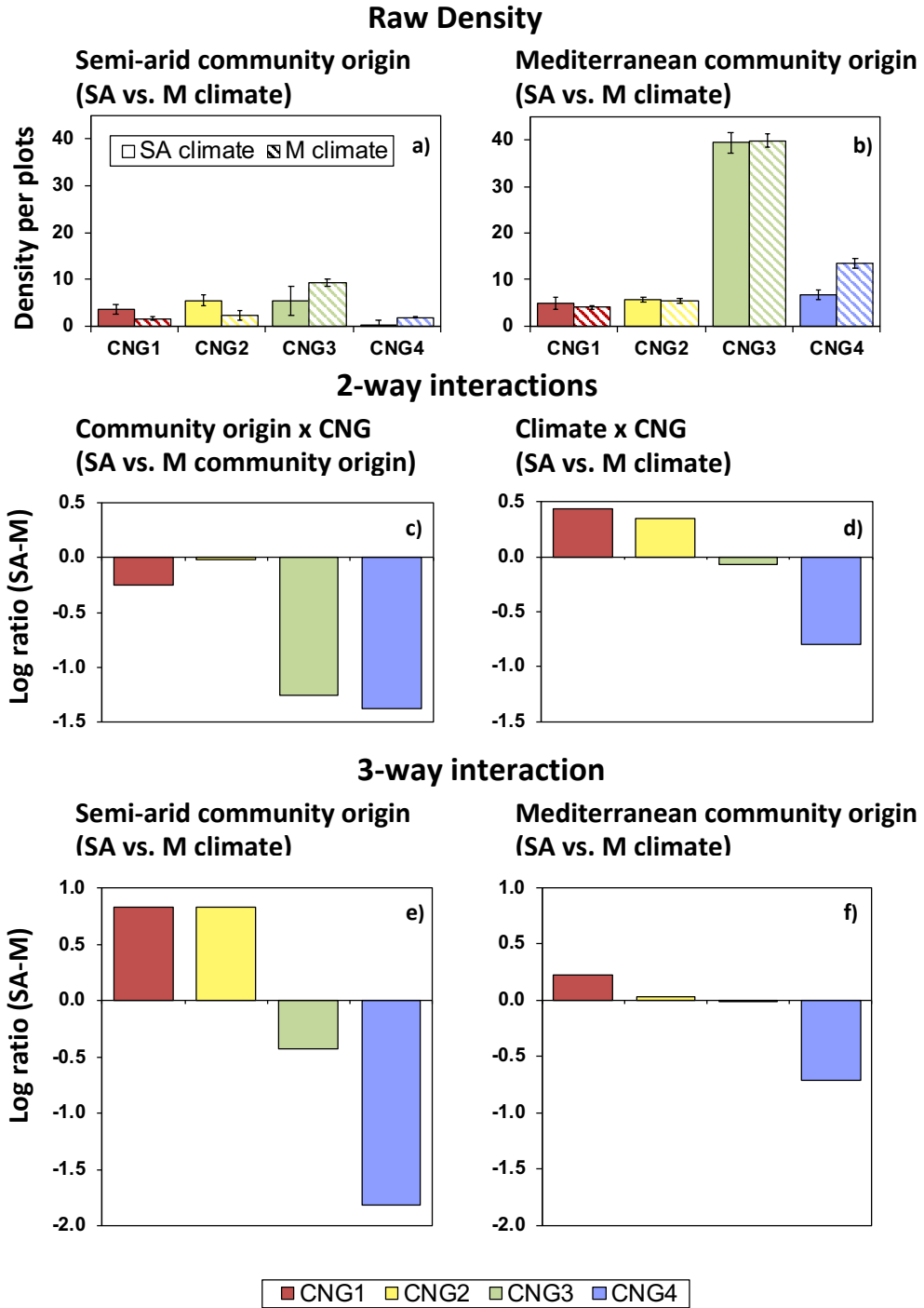
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Figure 1

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794 **Figure 2**
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798 Figure 3