OIKOS

Research article

A drought year favored drier-adapted origins over local origins in a reciprocal transplant experiment along a rainfall gradient

Johannes Metz[1] and Katja Tielbörger[2]

[1]Plant Ecology and Nature Conservation, Institute of Biology and Chemistry, University of Hildesheim, Hildesheim, Germany
[2]Plant Ecology Group, Institute of Evolution and Ecology, University of Tübingen, Tübingen, Germany

Correspondence: Johannes Metz (metzjo@uni-hildesheim.de)

Oikos
2023: e09806
doi: 10.1111/oik.09806
Subject Editor:
Gerlinde B. De Deyn
Editor-in-Chief:
Gerlinde B. De Deyn
Accepted 24 June 2023

When plant populations show local adaptation along climatic gradients, climate change may displace them from their current fitness optima. Unclear is whether foreign genotypes originating from sites that approximate future climatic conditions can attain higher fitness and support existing populations, because foreign genotypes may lack important adaptations to other local conditions besides climate. We conducted a fully reciprocal transplant experiment with the winter annual *Biscutella didyma* across four sites along a steep natural rainfall gradient in Israel. It experienced an exceptional drought event that approximated future climatic conditions. This unique opportunity allowed to test whether genotypes transplanted from drier sites outperform local genotypes under a drier climate. The four population origins showed consistent clines in germination fraction, phenology, and vegetative biomass that suggest local adaptation along the rainfall gradient. In terms of fitness (survival, seed number), however, local origins were outperformed by genotypes originating from the next-drier site along the gradient. Our results suggest that the experienced drought conditions favored origins from drier conditions over local origins despite local biotic interactions. Genotypes originating from drier sites may thus support existing populations and reduce their vulnerability to climate change. Moreover, we conceptualize under which conditions foreign genotypes may benefit local populations in general, which adds to clarify the importance of local adaptation to climatic and nonclimatic factors for populations under climate change.

Keywords: aridity gradient, assisted migration, biotic interactions, climate change adaptation, disrupted local adaptation, Mediterranean annual species

Introduction

Local adaptation is common among plant species (Leimu and Fischer 2008, Hereford 2009, Baughman et al. 2019, Lortie and Hierro 2022) and often found along natural climatic gradients (Davis and Shaw 2001, Midolo and Wellstein 2020, Johnson et al. 2021). This implies that local genotypes are better adapted to the local climate and therefore attain, on average, higher fitness than foreign genotypes originating from

NORDIC SOCIETY OIKOS

www.oikosjournal.org

© 2023 The Authors. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

other climatic conditions (the 'local versus foreign criterion'; Kawecki and Ebert 2004, Savolainen et al. 2013). However, ongoing climate change may displace locally adapted populations from their current climatic fitness optima and reduce plant fitness and population growth across large parts of a species' range (Davis and Shaw 2001, Anderson 2016, Anderson and Wadgymar 2020). Modelling studies have suggested accordingly that local adaptation may render species more vulnerable to climate change (Atkin and Travis 2010, Valladares et al. 2014, DeMarche et al. 2019).

The potential mismatch between current adaptation and future climate may in theory be compensated by immigration of genotypes that are pre-adapted to future climatic conditions, e.g. from warmer or drier sites. This assumption is implicit in many species distribution models (Valladares et al. 2014, Urban 2015, Warren et al. 2018). However, it has been cautioned that an isolated focus on climatic parameters may be biased as it ignores important nonclimatic factors of the local environment (Walther 2010, Bucharova 2017, Greiser et al. 2020). For example, sites differing in climate are also likely to differ in other factors such as soil properties (Zwikel et al. 2007, Greiser et al. 2020) and various biotic factors. The latter comprise e.g. interactions of plants with soil microbiota (Van der Putten et al. 2010, Pugnaire et al. 2019, Hamann et al. 2021), pollinators, and herbivores (Hamann et al. 2021), as well as competition and facilitation among plants (with often intensified competition in more benign sites; Bertness and Callaway 1994, He et al. 2013). Namely the biotic factors are likely to change further with climate change (Pugnaire et al. 2019, Hamann et al. 2021). Importantly, if these nonclimatic factors modulate local adaptation independently of climate, there might be no fitness advantage for immigrating genotypes that are pre-adapted to a future climate. Predictions based on climatic parameters alone would then overestimate the benefit of migration. It is therefore crucial to test whether genotypes originating from sites that approximate a future climate may indeed attain higher fitness than local genotypes under climate change conditions.

Here, we performed a test using a reciprocal transplant experiment across four sites along a steep natural aridity gradient in Israel, where mean annual rainfall is the key climatic factor determining plant community structure across sites (Golodets et al. 2013, Tielbörger et al. 2014). An asset of our experiment was that numerous earlier studies conducted along the same gradient provided a wealth of background information. For example, ecotypic differentiation along the gradient in drought-related traits has been demonstrated in many plant species under common garden conditions (Petrů et al. 2006, Kigel et al. 2011, Kurze et al. 2017, Metz et al. 2020, Penner et al. 2020), suggesting that local adaptation to rainfall conditions is common. However, sites along this gradient differ also in nonclimatic factors, including soil properties (Zwikel et al. 2007, Talmon et al. 2011) and biotic interactions. Namely, plants in wetter sites often experience intensified competition (Schiffers and Tielbörger 2006, Metz and Tielbörger 2016) and probably stronger herbivory (Metz et al. 2014). Competition and plant–soil interactions even overrode rainfall effects on plant performance in some studies along the gradient (Tomiolo et al. 2015, Rysavy et al. 2016). Lacking adaptation to these local nonclimatic factors might therefore compromise the fitness benefit of foreign genotypes independently of climate.

With climate change, the study region expects a further reduction in rainfall by approx. 10–40% (depending on climate scenario and sub-region) during the 21st century, including stronger and more frequent drought events (Hochman et al. 2018, 2020). An outlook on such conditions occurred during our study where an exceptional drought event reduced rainfall amounts substantially during the main growing season along the entire gradient (Israel Meteorological Service 2014a). The drought provided us with the unique opportunity to study potential climate change effects. In particular, it allowed testing whether climatic factors override nonclimatic factors in shaping local adaptation along the rainfall gradient. If this was the case, the drought event should shift the fitness optimum to a certain extent away from a site's local genotypes (Fig. 1) and toward genotypes from relatively drier origins (Davis and Shaw 2001, Anderson and Wadgymar 2020). This would be in line with species distribution models assuming that dispersal along climatic gradients can buffer climate change effects on populations (Valladares et al. 2014, Urban 2015, Warren et al. 2018).

Under exceptional conditions as in our case, the 'local versus foreign criterion' for plant fitness (Kawecki and Ebert 2004) may not reliably indicate whether populations had been locally adapted before, i.e. to former average climatic conditions. However, locally adapted populations should differ in functional traits that reflect adaptive strategies. Demonstrating clines in climate-related functional traits may then support the assumption that the studied populations

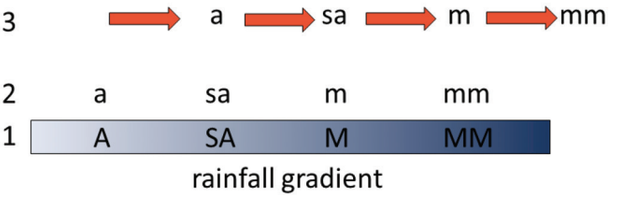


Figure 1. Hypothesized displacement of locally adapted populations under climate change in our experiment. 1) Four sites along a rainfall gradient (Arid, Semi-Arid, Mediterranean, Mesic-Mediterranean), where 2) the origin with the highest fitness is the corresponding local origin (in lower-case letters); however, 3) increasing drought with climate change shifts the fitness optima away from local origins toward drier origins along the gradient (here: the next-drier origins). Hypothesizing that specifically the next-drier origins outperform local origins is admittedly coarse and owed to our categorial design with four sites and origins. However, it is conservative and therefore robust because comparing primarily local with next-drier origins does not rule out that other, even-drier origins performed well in some cases. Identifying the optimal origin more precisely requires extensive transplant experiments with numerous origins and precisely quantifying the magnitude of drought, which is challenging for extreme events.

had been locally adapted to former climatic conditions and elucidate underlying mechanisms (Kawecki and Ebert 2004, Savolainen et al. 2013). Along aridity gradients, theory predicts for example that plants from drier sites express increased seed dormancy to hedge against more frequent unfavorable years (Cohen 1966, ten Brink et al. 2020), earlier flowering to ensure reproduction during shorter growing seasons (Cohen 1976, Kigel et al. 2011), and lower vegetative biomass due to slower growth under stress (Grime 1977, Reich 2014). For these traits, a number of previous studies have demonstrated corresponding clines in several species along our study gradient (Kigel et al. 2011, Kurze et al. 2017, Penner et al. 2020) including our study species (Petrů et al. 2006, Lampei et al. 2017, Metz et al. 2020). However, these studies have been done under controlled conditions that excluded important nonclimatic factors such as biotic interactions. It is therefore unclear whether the observed clines in functional traits persist under natural field conditions with complex biotic interactions.

For the present reciprocal transplant experiment across four sites, we therefore assessed by functional traits whether the four population origins were locally adapted to their former average climatic conditions along the rainfall gradient. Accordingly, we hypothesized that plants from drier origins express higher dormancy, earlier flowering and smaller vegetative biomass in the field sites. Assuming that local adaptation was present, we further tested whether the drought conditions in our experiment provided a climatic fitness advantage to relatively drier origins that overruled the adaptation of local origins to nonclimatic factors. As this climatic advantage may diminish again for origins from too arid sites, our main hypothesis was that namely the origins from adjacent, next-drier sites outperform the local origins (illustrated in Fig. 1).

Material and methods

Field sites

We chose four sites across approx. 240 km of a steep natural rainfall gradient from north to south Israel (Fig. 2). They share the same Mediterranean-type climate with mild, rainy winters and hot, rainless summers, yet receive 780 mm (mesic-Mediterranean, MM), 540 mm (Mediterranean, M), 300 mm (semi-arid, SA), and 90 mm (arid, A) mean annual precipitation, respectively. The average length of the rainy growth season declines from MM (October–May) to A (December–March). Inversely, rainfall variability among years increases from MM (25% coefficient of variation) to A (40% CV). Most other abiotic characteristics are similar among sites, including altitude (470–620 m a.s.l.), mean annual temperature (17.7–19.1°C), and bedrock (limestone), notwithstanding some site-specific differences in soil texture, soil organic carbon and $CaCO_3$ (Zwikel et al. 2007).

All sites are semi-natural shrublands typical for the region with annual plants dominating the open spaces between shrubs.

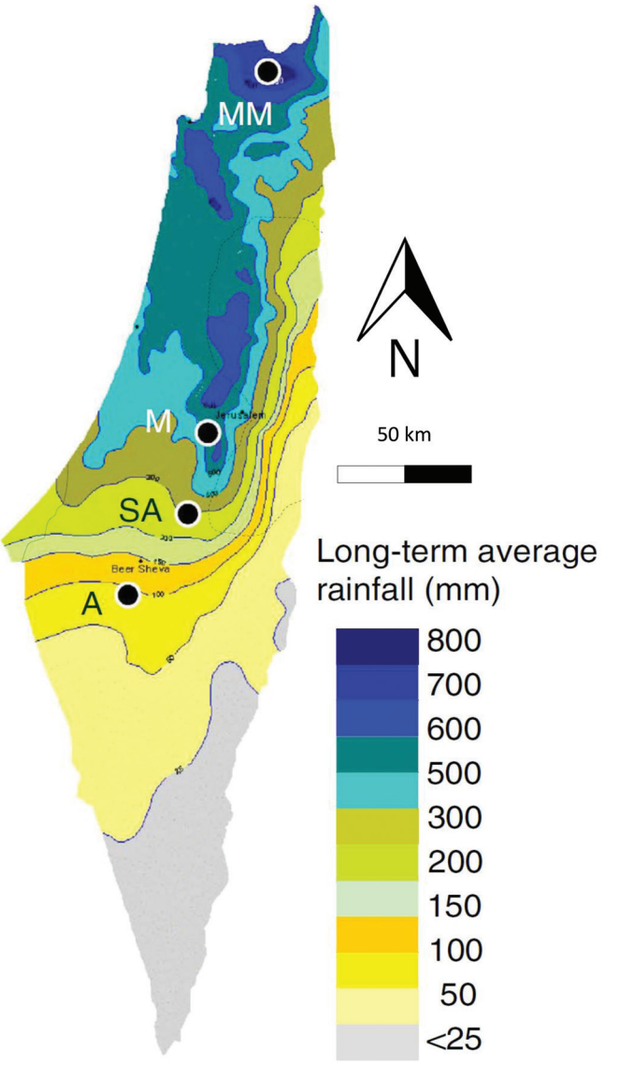


Figure 2. The four study sites are located along a steep natural precipitation gradient from north to south Israel (adapted from Tielbörger et al. 2014).

The rainfall gradient produces a steep productivity gradient where density and biomass of vegetation increase consistently with annual rainfall (Golodets et al. 2013, Tielbörger et al. 2014). Shrub cover increases from < 5% in A to ca 70% in MM and the herbaceous cover between shrubs increases from 0–15% in A to up to 100% in MM (details in the Supporting information). Alongside, competition intensifies toward wetter sites (Schiffers and Tielbörger 2006, Metz and Tielbörger 2016), although competition intensity may vary among years (Ariza and Tielbörger 2011, Metz and Tielbörger 2016).

Study species

Biscutella didyma (Brassicacea) is a medium-sized 15–30(60) cm winter annual of Mediterranean and Irano-Turanian

distribution that spans ca 100 to >1000 mm mean annual rainfall (Feinbrun-Dothan and Danin 1998). It is primarily selfing (Boaz et al. 1990) and produces fruits with a single, rather large (ca 0.7 mg) seed (Feinbrun-Dothan and Danin 1998, Metz et al. 2010). *Biscutella didyma* is one of few species occurring in all our four sites, while remaining a typical subordinate species that does not attain dominance in any of our sites. Greenhouse studies that excluded biotic interactions showed clinal variation among populations along the rainfall gradient in various climate-related traits such as seed dormancy, phenology, stomata density, vegetative growth and reproductive allocation (Petrů et al. 2006, Lampei et al. 2017, Metz et al. 2020).

Reciprocal transplant experiment

For obtaining seed material, seeds of 100 naturally occurring *B. didyma* individuals (genotypes) that grew at least 1.5 m (usually more) apart were collected in each field site within approx. 0.5 ha area in April 2012 and bagged separately per genotype for a parallel study (Metz et al. 2020). We then raised one generation with one offspring per genotype under standardized greenhouse conditions with regular watering in Tübingen, Germany, where cross-pollination was prevented among genotypes (details in Metz et al. 2020). In this way, we minimized potential parental effects from field conditions and amplified seed material. Additionally, this prevented confounding of germination fractions with seed viability because *B. didyma* produces virtually 100% viable seeds under regular watering (Lampei et al. 2017). Subsequently, we randomly chose 35 genotypes originating from site MM, M and SA, and 32 genotypes from A, where fewer genotypes had germinated from field collected seeds, resulting in 137 genotypes in total.

For the full-factorial reciprocal transplant, we planted these 137 genotypes in all four sites with one transplant per genotype per site (total n = 548), i.e. all four origins mm, m, sa, a (origins hereafter denoted by lower case letters) in all four sites MM, M, SA, A (sites hereafter denoted by upper case letters). Per transplant, 15 intact seeds of one genotype were sown in July 2013 within one small spot of 5 cm diameter (ca 20 cm^2) that was surrounded by a small plastic ring, covered thinly with local soil and subsequently covered with transparent fabric (organza) nailed to the ground (Fig. 3a). This timing mimicked the natural life-cycle where seeds produced in spring experience several months of hot, dry summer conditions for natural after-ripening and breaking transient summer dormancy. The ring and organza kept seeds in place until the rainy season commenced in autumn (Ariza and Tielbörger 2011). The organza cover was removed after the onset of the rainy season (in mid-December 2013 at all sites), while the rings remained throughout the experiment to help identifying target plants (Fig. 3B–C). Approximately two weeks after completed germination (10–12 January 2014), emerging seedlings were thinned to one random target individual per transplant (i.e. the one closest to the center of the ring). Natural surrounding vegetation was not altered throughout the experiment to ensure site-specific plant–plant interactions (Fig. 3).

The 137 transplants in each site were arranged in 4–13 patches of similar herbaceous vegetation outside of shrub canopies. The patches contained equal numbers of genotypes per origin in randomized order and accounted for spatial heterogeneity and availability of space within sites (Fig. 3B). However, 29 transplants in site MM were fully destroyed by wild boar at the start of the vegetation season (5, 6, 8, 10 from origins mm, m, sa, a, respectively), while the organza fabric of many other transplants in MM were slightly damaged, presumably by seed-eating birds.

Weather conditions

The weather during the transplant experiment was marked by two extremes. First, the start of the vegetation season in all four sites was dominated by extremely heavy rainfall mixed

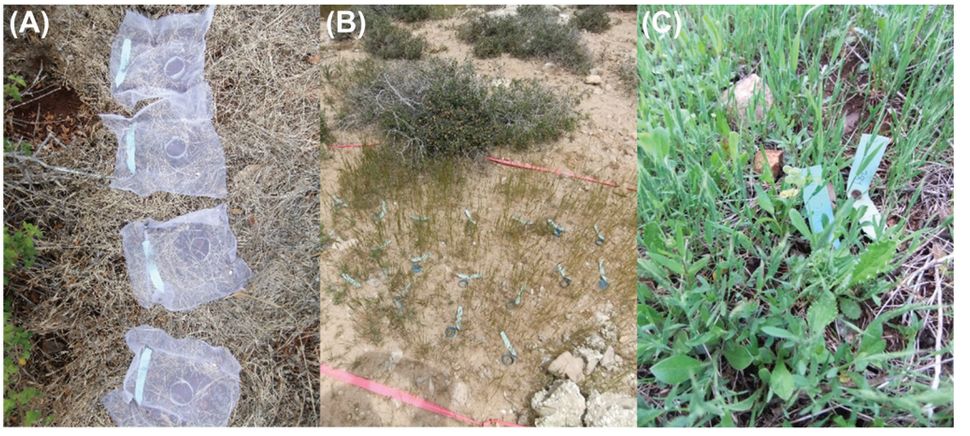


Figure 3. (A) Four out of 137 rings (5 cm diameter) in the mesic-Mediterranean site after set-up in July 2013. Each ring contained 15 seeds of a single genotype and was covered with organza fabric until the onset of winter rains. (B) A patch in the semi-arid site in April 2014 with typical surrounding vegetation. (C) A fruiting target individual of *Biscutella didyma* (center, left of the blue label) in the mesic-Mediterranean site at peak growth season in late March 2014; note the dense surrounding vegetation in this site in (A) and (C). Photo credit: J. Metz.

with snow in mid-December 2013 (Israel Meteorological Service 2014b, Supporting information). It triggered the main germination event nearly simultaneously in all sites, although some minor rainfall had occurred earlier in October and November in sites M and MM without triggering germination. Second and most importantly, an exceptional drought occurred in the main growing season from January to mid-March. It lasted for 2.5 months and was the most severe drought during that period since official records began in Israel more than 70 years ago (Israel Meteorological Service 2014a). In January and February, the sites A, SA, M, MM received only 7, 7, 22, 104 mm rainfall, respectively (Supporting information) which corresponded to approx. 6–20% of the average rainfall for that period per site (Israel Meteorological Service 2014a). Many target plants desiccated during that period. Late-season rainfall after the drought (March–April) was about average (Supporting information).

Measured plant traits

Plants were inspected weekly throughout the growth season. We measured three functional traits germination fraction, days to first flower and vegetative biomass to assess clinal ecotypic differentiation among origins as indication for local adaptation to former average climatic conditions. Fitness of the transplants was quantified by survival (from seedling stage to reproduction) and seed number.

Germination fraction was the proportion of seedlings that emerged from the 15 sown seeds per transplant. It can be interpreted as the inverse of between-year seed dormancy (Cohen 1966, Tielbörger et al. 2012, ten Brink et al. 2020) when ungerminated seeds are known to be viable (as was shown earlier for *B. didyma*; Eberhart and Tielbörger 2012, Lampei et al. 2017). Virtually all germination occurred within three weeks after the major rain event in mid-December and later inspections yielded no additional seedlings. Days to first flower was the number of days from the main germination wave to the first open flower of the remaining target plant after thinning, based on the weekly inspections. It indicated the phenological transition from the vegetative to the reproductive stage and quantified the speed of the life cycle (Cohen 1976, Kigel et al. 2011). Note that sample size was ca 50% lower for that trait because many plants died before flowering during the drought. Vegetative biomass quantified growth and included all aboveground parts except seeds. It was weighed after 24 h drying at 60°C after a target plant had died naturally either before or after reproduction. Approximately 10% of the target plants had missing values because they had vanished before sampling (e.g. eaten or blown away by wind).

Survival (from seedling stage to reproduction, hereafter survival for brevity) assessed whether the target seedling that remained after thinning had reached seed production or died before producing seeds (1/0, respectively). Hence, survival assessed the fitness component of whether genotypes were able to contribute any seeds (regardless of number) to the next generation after the drought year (Violle et al. 2007). Seed number was the total number of seeds produced per individual including dead plants with zero seeds. Seed size and hence seed quality differs little between the studied populations (Metz et al. 2020). Seed number therefore summarized well the life-time fitness from the seedling stage to death within the annual life-cycle.

Statistical analyses

All analyses were done in R ver. 4.0.3 (www.r-project.org).

We first tested for all five traits whether their expression differed among the four planting sites along the rainfall gradient and among the four origins by calculating mixed effect models separately per trait. These five models included the same categorical fixed effects site (MM, M, SA, A), origin (mm, m, sa, a), and their interaction; the crossed random effects patch and genotype accounted in all models for spatial heterogeneity among patches within a site and for the none-independence of transplants descending from the same genotype (one within each site), respectively. Other model specifications were adjusted for matching the data type of the trait in question and corresponding model assumptions. Namely, germination fraction (proportional data of germinated seeds out of 15 seeds per transplant) was analyzed with a generalized linear mixed model (glmm) with binomial error distribution and logit link function with function *glmer* in package 'lme4' (Bates et al. 2015). This model included an additional observation-level random effect (transplant) to correct for mild overdispersion (ratio 1.92) (Bolker et al. 2022). Days to first flower (continuous data, untransformed) and vegetative biomass (continuous data, log-transformed) were analyzed with linear mixed models with Gaussian error distribution in function *lmer* in package 'lme4' (Bates et al. 2015). Survival (binomial data 0/1) was analyzed with a glmm with binomial error distribution and logit link function (no overdispersion) with function *glmer* in package 'lme4' (Bates et al. 2015). Seed number (integer count data) was analyzed with a glmm with negative binomial error distribution and logarithmic link with function *glmm.nb* in package 'MASS' (Venables and Ripley 2002).

Importantly, a significant site × origin interaction in fitness (survival, seed number) can indicate local adaptation when the ranking of origins differs among sites in a way that the corresponding local origin in each site performs better than other origins (Kawecki and Ebert 2004) – or according to our main hypothesis, in each site the corresponding next-drier origin. However, testing for local adaption via site × origin has limited statistical power in full-factorial reciprocal transplants with more than two sites (Blanquart et al. 2013). This is because the main test statistic (usually F or χ^2) for the interaction term includes all site-origin combinations even though most of them are not relevant for the hypothesis; the main test statistic is therefore calculated against unnecessary high numerator degrees of freedom (df = 9 in our case, Table 1).

As our principal, statistically stronger test for local adaptation, we therefore calculated a second set of models for

Table 1. Results of mixed models testing the effect of four planting sites (MM mesic-Mediterranean, M Mediterranean, SA semi-arid, A arid) and their four corresponding population origins (in lower-case letters) on five plant parameters in a fully reciprocal transplant experiment with *Biscutella didyma*. [1]The origins m and sa were intermediate, yet marginally (p = 0.065) not significantly separated from a and mm, respectively. *p < 0.05, **p < 0.01, ***p < 0.001.

		Planting site (df = 3)			Origin (df = 3)			Site × origin (df = 9)		Genotype (random factor, df = 1)	
	Total n	χ^2	p-value	Posthoc contrasts	χ^2	p-value	Posthoc contrasts	χ^2	p-value	χ^2	p-value
Germination fraction	515	371.9	<0.0001***	A < MM < SA < M	171.9	<0.0001***	a,sa < m < mm	13.51	0.14	33.94	p < 0.0001***
Days to first flowering	260	116.7	< 0.0001***	SA < MM,A < M	66.33	< 0.0001***	a < sa < m < mm	27.86	0.0010**	7.95	0.0048**
Veget. Biomass	430	6.20	0.10		11.51	0.0093**	a <mm[1]	17.56	0.041*	8.07	0.0045***
Survival	456	41.92	< 0.0001***	A < M < SA < MM	22.49	0.0002***	mm < m,a,sa	13.10	0.16	0.0002	0.99
Seed number	455	47.92	< 0.0001***	A < M < SA < MM	10.17	0.017*	mm < a,sa,m	25.26	0.0027**	9.33	0.0023**

survival (binomial glmm with logit link using *glmer* in 'lme4' as above) and seed number (negative binomial glmm with logarithmic link using *glmm.nb* in 'MASS' as above). These models included the two categorial fixed effects site, relative origin (instead of origin), and their interaction, as well as the crossed random effects patch and genotype as above. Importantly, relative origin re-coded origins specifically for each site in three groups that directly reflected our main hypothesis (Fig. 1): 'local origin' (mm in MM, m in M, sa in SA), 'next-drier origin' (m in MM, sa in M, a in SA), and 'other origins' (the two remaining origins per site). Using this coding, the *main* effect of relative origin assessed the fitness difference between these three groups. The main effect of relative origin (against only df = 2, Table 2) could therefore test directly our main hypothesis regarding local adaptation, i.e. whether local origins or the corresponding next-drier origins performed best across sites. This approach was inspired by – although not identical with – Blanquart et al. (2013) who showed that testing local adaptation does not require fully reciprocal transplantation and suggested instead testing local genotypes against a sample of twice as many foreign genotypes. Note that the driest site A was excluded for these models because no 'next-drier origin' was available for that site. This was negligible as most values in this site were zeros as only 11 out of 137 transplants had reached reproduction.

To corroborate our grouping approach for relative origin, we ran supplementary tests whether drier origins outperformed local origins. These tests related the fitness differences among origins (relative seed number, relative survival) directly to the numerical differences in mean annual rainfall between the site of origin and the planting site (Supporting information).

Significance of fixed effects in all above models was assessed with Wald II X^2 tests in the package 'car' (Fox and Weisberg 2019). In case of significant main effects of site, origin or relative origin, posthoc tests identified contrasting levels within these factors using the package 'multcomp' (Hothorn et al. 2008) with p-values corrected for false discovery rate sensu Benjamini and Hochberg (1995). Significance of the random effect genotype was assessed by likelihood-ratio tests of the models with versus without genotype.

Results

Clinal variation in functional traits

We found significant origin effects for all three functional traits germination fraction, days to first flower and vegetative biomass, with a clear clinal ranking among origins indicative of clinal ecotypic differentiation along the rainfall gradient (Table 1, Fig. 4A–C). Namely, plants from drier origins had lower germination fraction (i.e. higher dormancy), flowered earlier, and produced less vegetative biomass compared to plants from wetter origins (Table 1, Fig. 4A–C). This clinal ranking among origins was consistent across all sites, merely its magnitude differed between sites for days to first flower

Table 2. Results of mixed models testing the fitness response of *Biscutella didyma* plants in three planting sites and depending on their relative origin along the rainfall gradient: local origins are plants originating from the same site, next-drier origins originated from the corresponding next-drier site, other origins originated from the two remaining sites. [1]The local relative origin was intermediate, yet marginally (p = 0.089) not significantly separated from other and next-drier origins. *p < 0.05, **p < 0.01, ***p < 0.001.

		Planting site (df = 2)			Relative origin (df = 2)			Site × relative origin (df = 4)	
	Total n	χ^2	p-value	Post hoc contrasts	χ^2	p-value	Post hoc contrasts	χ^2	p-value
Survival	357	17.00	0.00020***	M < SA,MM	14.36	0.00076***	other,local < next-drier	8.30	0.081
Seed number	356	34.07	< 0.0001***	M < SA < MM	14.09	0.00087***	Other < next-drier[1]	7.78	0.10

and vegetative biomass (significant site × origin interactions, Table 1).

Furthermore, planting sites had significant main effects on germination fraction and days to first flower but not on vegetative biomass (Table 1, Fig. 4A–C). Overall, germination fraction increased from the driest site A (0.1–0.55 depending on origin) to SA (0.4–0.85) and M (0.5–0.9), and fell again in MM (0.25–0.7) (Fig. 4A); this pattern was positively related to the rainfall amount that a given site received during the germination phase in November and December (p = 0.033, Supporting information). Days to first flower differed significantly among sites but with no apparent pattern along the rainfall gradient (Fig. 4B). Vegetative biomass was overall similar across sites (Fig. 4C).

Fitness and local adaptation

Averaged across all four origins, both fitness traits (survival, seed number) increased from the driest planting site A (approx. 10% survival and one seed per plant) to the wettest site MM (approx. 90% survival and six seeds per plant) (Fig. 4D,E). The statistical main effect of site indicated that this increase was significant and steady for three out of four sites (A, SA, MM). The remaining site M did not fully fit that increase because survival and seed number were only second lowest and similar (seed number) or only slightly higher (survival) to the driest site A (Table 1, Fig. 4D–E).

A significant main effect of origin for survival and seed number indicated that the wettest origin mm had overall

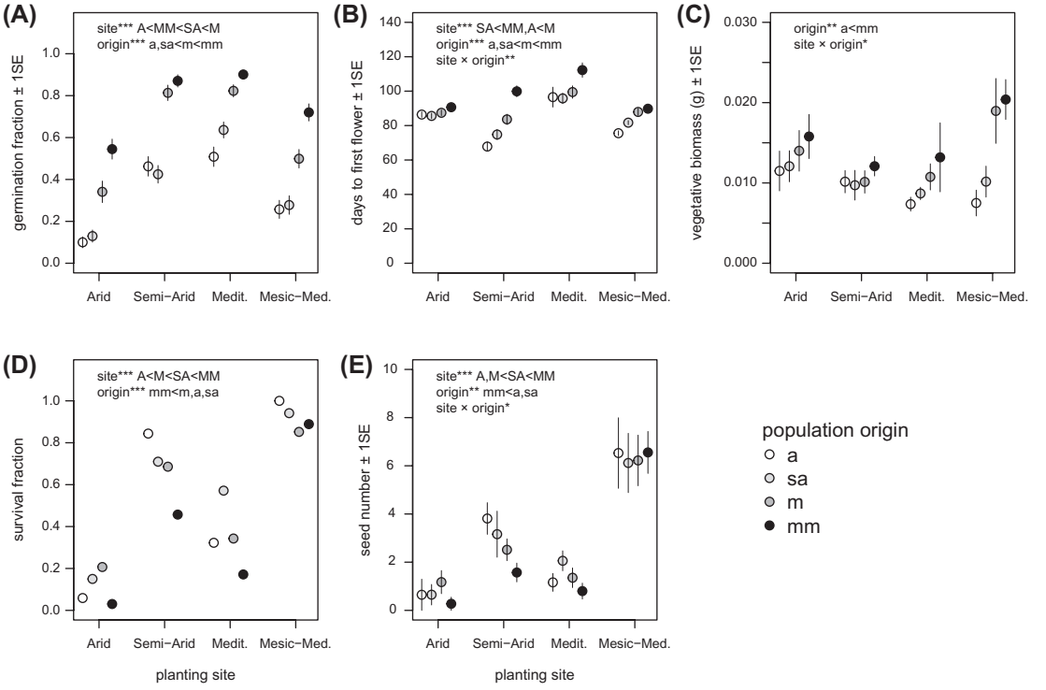


Figure 4. Trait and fitness expression of *Biscutella didyma* plants from four origins (mm mesic-Mediterranean, m Mediterranean, sa semi-arid, a arid) that were reciprocally transplanted along a rainfall gradient across the corresponding four sites. ***p < 0.001, **p < 0.01, *p < 0.05; see Table 1 for full statistical results.

lowest fitness in this experiment; the remaining three origins were overall not significantly different across sites (Table 1, Fig. 4D–E). However, the ranking of origins varied between sites, i.e. different origins had highest fitness in the four sites (Fig. 4D–E), which was underlined by a site × origin interaction for seed number (Table 1). Whether this ranking conformed with our hypothesis regarding local adaptation, however, was assessed by the more powerful models below to avoid false-negative conclusions.

Our principal, more powerful test for local adaptation used models assessing the main effect of relative origin. This main effect was significant for both fitness traits survival and seed number (Table 2, Fig. 5). It indicated that next-drier origins had on average highest fitness (survival and seed number) across planting sites, followed by local origins, while other origins attained lowest fitness (Table 2, Fig. 5). This ranking among relative origins was largely consistent across sites as the site × relative origin interactions were (marginally) not significant for survival ($p = 0.08$) and seed number ($p = 0.1$) (Table 2, Fig. 5).

Our supplementary analyses confirmed the above pattern (Supporting information). Relative seed number showed a significant unimodal shape ($p = 0.019$) that peaked where genotypes originated from sites with ca 250 mm lower mean annual rainfall than the planting site (Supporting information). This number matched well the average rainfall difference to next-drier sites (230 mm). Relative survival increased linearly toward drier origins ($p = 0.019$) while the unimodal tendency was not significant ($p = 0.15$); i.e. the survival advantage for drier origins over local origins continued beyond the next-drier origin (Supporting information).

The random effect genotype was significant for all three functional traits germination fraction, days to first flower and vegetative biomass as well as for seed number (Table 1), indicating that significant genotypic variation was present within the origins and contributed to the variation in functional and fitness traits.

Discussion

We found that genotypes transplanted from populations of next-drier sites (i.e. next-drier origins) attained higher fitness than local genotypes in an exceptional drought year. This key result suggests that the drought year favored drier origins over local origins. Moreover, the four population origins expressed clinal variation in drought-related functional traits that persisted across all planting sites; i.e. plants from drier origins had higher dormancy, flowered earlier, and produced less vegetative biomass. These clines suggest that the populations possessed adaptations to different rainfall niches along the gradient that likely reflect local adaptation to former average rainfall conditions (Kawecki and Ebert 2004, Savolainen et al. 2013). Below, we will first discuss the clines in functional traits as the basis of our main hypothesis, and we then discuss our key result in the context of fitness under changing climate.

Clinal variation in functional traits

The observed lower germination fractions in plants from drier origins aligned with bet-hedging theory predicting greater

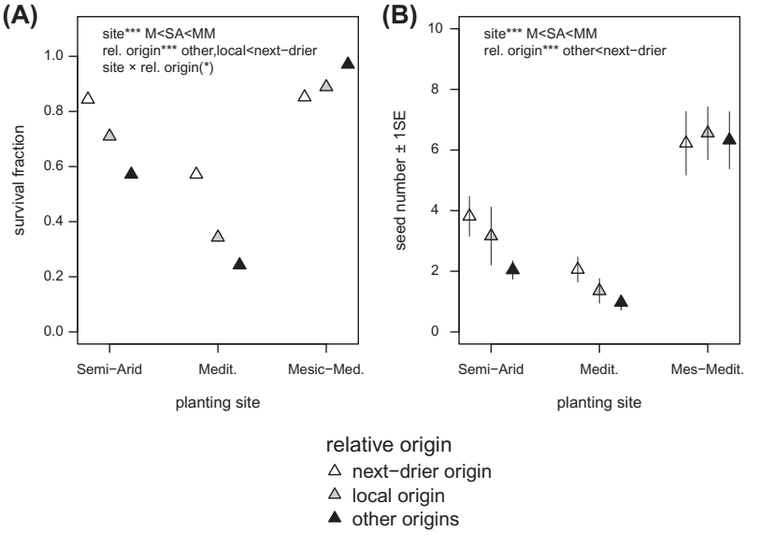


Figure 5. The fitness (survival, seed number) of *Biscutella didyma* plants across three planting sites depending on their relative origin along the rainfall gradient: local origins are plants originating from the same site, next-drier origins originated from the corresponding next-drier site, other origins originated from the two remaining sites. Note, that these three groups contained different origins in each site, and that the arid site A was excluded because no 'next-drier origin' was available. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, (*)$p < 0.1$; see Table 2 for full statistical results.

portions of dormant seeds in drier sites to buffer against more frequent unfavorable years (Cohen 1966, Tielbörger et al. 2012, ten Brink et al. 2020). In fact, our study year with 90% mortality in the driest site but only 10% mortality in the wettest site illustrates this greater risk from extreme years in drier sites. Furthermore, our germination results under field conditions confirmed earlier studies showing lower germination fractions of drier origins in *Biscutella didyma* under greenhouse conditions (Lampei et al. 2017, Metz et al. 2020) and in the field (Petrů and Tielbörger 2008). The same cline has been found in other species worldwide (reviewed by Cochrane et al. 2015) although not in all investigated species (Tielbörger et al. 2012, Metz et al. 2018).

Germination fractions varied also plastically across sites. The germination fractions increased for all origins by roughly 40% from the arid to the Mediterranean site. This increase correlated with the rainfall amount that a given site received during the germination phase (Supporting information) and confirmed greenhouse studies where improved water availability likewise increased germination fractions (Lampei and Tielbörger 2010, Lampei et al. 2017). Our findings, obtained under natural field conditions, support Cohen's (1967) theory about 'predictive germination', i.e. that germination fractions are adjusted plastically to the quality of the early season.

We also observed earlier flowering in plants from drier origins. This is expected in annual plants from drier sites for ensuring reproduction during shorter growing seasons before the onset of drought spells (Cohen 1976, Kigel et al. 2011). Earlier flowering is very well documented under controlled conditions with virtually no exception in annual species along rainfall gradients worldwide (Del Pozo et al. 2002, Kigel et al. 2011, Kurze et al. 2017, Penner et al. 2020), including our study species (Petrů et al. 2006, Metz et al. 2020). Our results confirm that drier origins maintain earlier flowering also when transplanted to natural field conditions (Etterson 2004, Galliart et al. 2020). The importance of earlier flowering for drought adaption was corroborated by selection analyses showing that earlier flowering confers higher fitness under drier conditions (Hall and Willis 2006) including our species (Metz et al. 2020). Moreover, annual species rapidly evolved earlier flowering under intensified drought (Nguyen et al. 2016, Hamann et al. 2018, Lambrecht et al. 2020), which was also shown for our study populations as an adaptative response to changing climate (Metz et al. 2020). Earlier flowering thus presents a well-supported adaptation to drier climates in annuals.

Plants from drier origins attained also less vegetative biomass. This clinal trend was in line with our theoretical expectation that adaptation to more stressful, arid sites comprises reduced vegetative growth (Grime 1977, Reich 2014). It confirmed similar clines in growth parameters observed for our study species in the greenhouse (Petrů et al. 2006, Metz et al. 2020). Selection analyses under controlled conditions confirmed for our species that reduced investment in vegetative biomass is adaptive under drier conditions (Metz et al. 2020). Surprisingly, vegetative biomass was not significantly different among sites along the gradient despite greatly differing rainfall. As our experiment maintained natural surrounding vegetation, this finding was most likely because the greater density and biomass of herbaceous neighbors in wetter sites (Tielbörger et al. 2014) imposed intensified competition (Schiffers and Tielbörger 2006, Liancourt and Tielbörger 2009), underlining that biotic interactions play an important role in our study system.

The above independent lines of evidence from theory, similar observations, and selection analyses suggest that the observed clines in germination, phenology and vegetative growth provided plants from drier origins with better adaptation to arid conditions. It is plausible that these clines reflect local adaptation to former average rainfall conditions along the gradient (Kawecki and Ebert 2004, Savolainen et al. 2013). A strength of our study is that it was conducted under realistic field conditions including natural biotic interactions. Our results show that genotypes from different origins express different phenotypes under field conditions where they are likely to contribute to differential fitness among origins.

Fitness under changing climate

Despite the indication for local adaptation to former average rainfall conditions along the gradient, plants from local origins did not attain the highest fitness (survival, seed number) in our drought year. Instead, highest fitness was attained by the 'next-drier origins', i.e. by genotypes that were transplanted from the adjacent next-drier site along the gradient. Thus, the drought year apparently displaced local genotypes from their climate optima and favored drier-adapted origins over local origins. As climate change will intensify drought conditions in our study region (Hochman et al. 2018, 2020), this key finding suggests that genotypes originating from drier sites may support local populations and reduce their vulnerability to climate change.

Our results suggest that adaptation to drier conditions was sufficient for plants from foreign, next-drier origins to gain a fitness advantage over local origins. At first glance, this finding contradicts the frequent cautioning that climate change predictions are biased when they focus solely on climatic factors and exclude nonclimatic factors, e.g. soil and biotic interactions (Walther 2010, Van der Putten et al. 2010, Tomiolo et al. 2015, Rysavy et al. 2016, Bucharova 2017, Pugnaire et al. 2019, Greiser et al. 2020). This contradiction can be resolved by conceptualizing the different effects on fitness. Namely, the fitness ranking among origins is not determined by the overall effects of climate and nonclimatic factors per se (i.e. their statistical main effects), as these will affect all origins alike. Our results therefore do not refute that nonclimatic factors are important. Instead, the fitness ranking among origins results from origin-*specific* effects of climate and nonclimatic factors, i.e. the interactions of origin × climate and origin × nonclimatic factors. A fitness-advantage for origins adapted to drier conditions is thus overturned only when these origins suffer a disadvantage of larger magnitude from nonclimatic factors, i.e. when origin × nonclimatic factors is larger than origin × climate. Unfortunately,

the present study did not manipulate nonclimatic factors, i.e. we cannot disentangle and quantify these interaction terms directly. We can merely infer from our results that origin × climate outweighed origin × nonclimatic factors. However, earlier experiments in our system support our interpretation. These experiments manipulated competition by neighbors (Liancourt and Tielbörger 2009, Ariza and Tielbörger 2011, Tomiolo et al. 2015, Rysavy et al. 2016) and soil conditions (Tomiolo et al. 2015). They detected strong (statistical main) effects of neighbor competition and soil on fitness. Importantly though, the origin × neighbor and origin × soil interactions were never significant, i.e. origins responded largely similar to neighbors and soil. These earlier experiments support that origin-specific (local) adaptation to nonclimatic factors (i.e. origin × nonclimatic factors) is rather weak in our system (although not necessarily absent; Liancourt and Tielbörger 2009). Nonclimatic factors may thus rarely overturn a fitness ranking of origins that is caused by climate. This situation may also hold for other systems because two global meta-analyses indicated that local adaptation to biotic interactions was rather weak and context-dependent, especially outside the tropics (Briscoe Runquist et al. 2020, Hargreaves et al. 2020).

Moreover, the exceptional magnitude of the drought in our experiment probably magnified the importance of drought adaptation. The origin × climate interaction was therefore more likely to govern the fitness-ranking among origins. Conversely, the importance of nonclimatic factors (i.e. origin × nonclimatic factors) was perhaps diminished because of weaker plant competition during drought years (Bertness and Callaway 1994, He et al. 2013, Metz and Tielbörger 2016). It is also important to consider that biotic interactions during one drought year may not fully reflect those that develop under long-term climate change, as the species composition of biotic communities changes more slowly (Tielbörger et al. 2014, Pugnaire et al. 2019). The biotic interactions in our experiment may therefore still tend toward former conditions. Interestingly, this suggests that when local origins benefited to some extent from better (local) adaptation to former biotic interactions in our experiment, this benefit will further diminish with changing species composition in the future. The observed fitness-advantage of next-drier origins during our short-term drought event appears thus as a conservative result that is rather underestimating than overestimating their fitness-advantage in the future.

We have argued that the balance between a 'climatic advantage' and a 'nonclimatic disadvantage' (i.e. between origin × climate and origin × nonclimatic factors) will determine whether foreign origins from 'future' climatic conditions may outperform local origins under climate change. The equivocal results of earlier studies underline that the outcome of this balance is case-specific. On one side are several cases where local origins were not outperformed by foreign origins despite altered climate. This was observed for example in two transplant experiments along latitudinal gradients with arctic tundra perennials under warming (McGraw et al. 2015, Bjorkman et al. 2017), in a comparison of central and south European ecotypes of four perennial grasses under simulated warming and drought (Beierkuhnlein et al. 2011), and in a study across four common gardens in Germany comparing ecotypes of six perennials during a natural heatwave (Bucharova et al. 2016). On the other side is a growing number of cases where local origins were outperformed – as in our study. Along elevational gradients for example, climate warming favored origins from relatively lower elevations in the Rocky Mountains herb *Boechera stricta* along most of the species' altitudinal range (Anderson and Wadgymar 2020) and similarly in *Mimulus guttatus* (Kooyers et al. 2019, Peterson et al. 2020). Along latitudinal gradients, warmer origins outperformed local origins in the forest tree *Populus tremuloides* across five sites in Canada in *Arabidopis thaliana* accessions planted in five common gardens across Europe (Wilczek et al. 2014), and in northern range-edge populations of the North American annual *Clarkia pulchella* (Bontrager and Angert 2019). While further research is needed for specifying common conditions under which foreign origins from 'future' climates attain higher fitness than local origins, our study adds hitherto rare evidence across multiple sites along aridity gradients (Gellie et al. 2016).

Overall, our field experiment along a natural aridity gradient showed that migration from drier to wetter sites may benefit populations under drought and reduce their climate change vulnerability – despite other nonclimatic factors. This main result validates an important implicit assumption in many species distribution models (Valladares et al. 2014, Urban 2015, Warren et al. 2018). However, short average seed dispersal distances (Siewert and Tielbörger 2010) and restricted outcrossing (Boaz et al. 1990) of annual species in our study region may substantially hamper the extent of migration and hence its beneficial role under climate change. Conservation measures that promote habitat connectivity and dispersal along climatic gradients may therefore be a means to support vulnerable species in an era of climate change (Heller and Zavaleta 2009).

Acknowledgements – We are highly grateful for ambitious help during field work by K. Pöge, N. Shtirberg, Y. Kriger and I. Granat, and for logistic support by I. Giladi, J. Grünzweig, J. Kigel, M. Seifan and M. Sternberg. L. Henneberg was of invaluable help for raising the preceding maternal generation in the greenhouse.
Funding – The study was founded by the DFG SPP 1529 (Adaptomics) of the German Research Foundation to KT (TI338/11-1 and TI338/11-2).

Author contributions

Johannes Metz: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Katja Tielbörger**: Conceptualization (supporting); Funding acquisition (lead); Supervision (lead); Writing – review and editing (supporting).

Data availability statement

The data supporting our results are publicly available at https://data.goettingen-research-online.de via https://doi.org/10.25625/ZLLZ3M (Metz and Tielbörger 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Anderson, J. T. 2016. Plant fitness in a rapidly changing world. – New Phytol. 210: 81–87.

Anderson, J. T. and Wadgymar, S. M. 2020. Climate change disrupts local adaptation and favours upslope migration. – Ecol. Lett. 23: 181–192.

Ariza, C. and Tielbörger, K. 2011. An evolutionary approach to studying the relative importance of plant–plant interactions along environmental gradients: evolutionary approach to interactions in gradients. – Funct. Ecol. 25: 932–942.

Atkins, K. E. and Travis, J. M. J. 2010. Local adaptation and the evolution of species' ranges under climate change. – J. Theor. Biol. 266: 449–457.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Baughman, O. W., Agneray, A. C., Forister, M. L., Kilkenny, F. F., Espeland, E. K., Fiegener, R., Horning, M. E., Johnson, R. C., Kaye, T. N., Ott, J., St. Clair, J. B. and Leger, E. A. 2019. Strong patterns of intraspecific variation and local adaptation in Great Basin plants revealed through a review of 75 years of experiments. – Ecol. Evol. 9: 6259–6275.

Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E. and Kreyling, J. 2011. Ecotypes of European grass species respond differently to warming and extreme drought: grass ecotypes and drought. – J. Ecol. 99: 703–713.

Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. – J. R. Stat. Soc. Ser. B Methodol. 57: 289–300.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.

Bjorkman, A. D., Vellend, M., Frei, E. R. and Henry, G. H. R. 2017. Climate adaptation is not enough: warming does not facilitate success of southern tundra plant populations in the high Arctic. – Global Change Biol. 23: 1540–1551.

Blanquart, F., Kaltz, O., Nuismer, S. L. and Gandon, S. 2013. A practical guide to measuring local adaptation. – Ecol. Lett. 16: 1195–1205.

Boaz, M., Plitmann, U. and Heyn, C. C. 1990. The ecographic distribution of breeding systems in the Cruciferae (Brassicaceae) of Israel. – Isr. J. Bot. 39: 31–42.

Bolker, B. and others 2022. GLMM FAQ. Online document. – https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html.

Bontrager, M. and Angert, A. L. 2019. Gene flow improves fitness at a range edge under climate change. – Evol. Lett. 3: 55–68.

Briscoe Runquist, R. D., Gorton, A. J., Yoder, J. B., Deacon, N. J., Grossman, J. J., Kothari, S., Lyons, M. P., Sheth, S. N., Tiffin, P. and Moeller, D. A. 2020. Context dependence of local adaptation to abiotic and biotic environments: a quantitative and qualitative synthesis. – Am. Nat. 195: 412–431.

Bucharova, A. 2017. Assisted migration within species range ignores biotic interactions and lacks evidence: missing evidence for assisted migration. – Restor. Ecol. 25: 14–18.

Bucharova, A., Durka, W., Hermann, J., Hölzel, N., Michalski, S., Kollmann, J. and Bossdorf, O. 2016. Plants adapted to warmer climate do not outperform regional plants during a natural heat wave. – Ecol. Evol. 6: 4160–4165.

Cochrane, A., Yates, C. J., Hoyle, G. L. and Nicotra, A. B. 2015. Will among-population variation in seed traits improve the chance of species persistence under climate change? – Global Ecol. Biogeogr. 24: 12–24.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. – J. Theor. Biol. 12: 119–129.

Cohen, D. 1967. Optimizing reproduction in a randomly varying environment when a correlation may exist between the conditions at the time a choice has to be made and the subsequent outcome. – J. Theor. Biol. 16: 1–14.

Cohen, D. 1976. The optimal timing of reproduction. – Am. Nat. 110: 801–807.

Davis, M. B. and Shaw, R. G. 2001. Range shifts and adaptive responses to quaternary climate change. – Science 292: 673–679.

Del Pozo, A., Ovalle, C., Aronson, J. and Avendaño, J. 2002. Ecotypic differentiation in *Medicago polymorpha* L. along an environmental gradient in central Chile. I. Phenology, biomass production and reproductive patterns. – Plant Ecol. 159: 119–130.

DeMarche, M. L., Doak, D. F. and Morris, W. F. 2019. Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. – Global Change Biol. 25: 775–793.

Eberhart, A. and Tielbörger, K. 2012. Maternal fecundity does not affect offspring germination – an empirical test of the sibling competition hypothesis. – J. Arid Environ. 76: 23–29.

Etterson, J. R. 2004. Evolutionary potential of *Chameacrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. – Evolution 58: 1446.

Feinbrun-Dothan, N. and Danin, A. 1998. Analytical Flora of Eretz-Israel. – CANA Publishing House.

Fox, J. and Weisberg, S. 2019. An {R} companion to applied regression. – Sage.

Galliart, M., Sabates, S., Tetreault, H., DeLaCruz, A., Bryant, J., Alsdurf, J., Knapp, M., Bello, N. M., Baer, S. G., Maricle, B. R., Gibson, D. J., Poland, J., St Amand, P., Unruh, N., Parrish, O. and Johnson, L. 2020. Adaptive genetic potential and plasticity of trait variation in the foundation prairie grass *Andropogon gerardii* across the US Great Plains' climate gradient: implications for climate change and restoration. – Evol. Appl. 13: 2333–2356.

Gellie, N. J. C., Breed, M. F., Thurgate, N., Kennedy, S. A. and Lowe, A. J. 2016. Local maladaptation in a foundation tree species: implications for restoration. – Biol. Conserv. 203: 226–232.

Golodets, C., Sternberg, M., Kigel, J., Boeken, B., Henkin, Z., Seligman, N. G. and Ungar, E. D. 2013. From desert to Mediterranean rangelands: will increasing drought and inter-annual rainfall variability affect herbaceous annual primary productivity? – Clim. Change 119: 785–798.

Greiser, C., Hylander, K., Meineri, E., Luoto, M. and Ehrlén, J. 2020. Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. – Ecography 43: 637–647.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. – Am. Nat. 111: 1169–1194.
Hall, M. C. and Willis, J. H. 2006. Divergent selection on flowering time contributes to local adaptation in *Mimulus guttatus* populations. – Evolution 60: 2466–2477.
Hamann, E., Denney, D., Day, S., Lombardi, E., Jameel, M. I., MacTavish, R. and Anderson, J. T. 2018. Two decades of evolutionary changes in *Brassica rapa* in response to fluctuations in precipitation and severe drought. – Evolution 72: 2682–2696.
Hamann, E., Weis, A. E. and Franks, S. J. 2021. Review: plant eco-evolutionary responses to climate change: emerging directions. – Plant Sci. 304: 110737.
Hargreaves, A. L., Germain, R. M., Bontrager, M., Persi, J. and Angert, A. L. 2020. Local adaptation to biotic interactions: a meta-analysis across latitudes. – Am. Nat. 195: 395–411.
He, Q., Bertness, M. D. and Altieri, A. H. 2013. Global shifts towards positive species interactions with increasing environmental stress. – Ecol. Lett. 16: 695–706.
Heller, N. E. and Zavaleta, E. S. 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. – Biol. Conserv. 142: 14–32.
Hereford, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. – Am. Nat. 173: 579–588.
Hochman, A., Mercogliano, P., Alpert, P., Saaroni, H. and Bucchignani, E. 2018. High-resolution projection of climate change and extremity over Israel using COSMO-CLM. – Int. J. Climatol. 38: 5095–5106.
Hochman, A., Kunin, P., Alpert, P., Harpaz, T., Saaroni, H. and Rostkier-Edelstein, D. 2020. Weather regimes and analogues downscaling of seasonal precipitation for the 21st century: a case study over Israel. – Int. J. Climatol. 40: 2062–2077.
Hothorn, T., Bretz, F. and Westfall, P. 2008. Simultaneous inference in general parametric models. – Biom. J. 50: 346–363.
Israel Meteorological Service 2014a. Dry winter 2013/14. Online document. – https://ims.gov.il.
Israel Meteorological Service 2014b. Significant weather event December 2013. Online document. – https://ims.gov.il.
Johnson, L. C., Galliart, M. B., Alsdurf, J. D., Maricle, B. R., Baer, S. G., Bello, N. M., Gibson, D. J. and Smith, A. B. 2021. Reciprocal transplant gardens as gold standard to detect local adaptation in grassland species: new opportunities moving into the 21st century. – J. Ecol. 110: 1054–1071.
Kawecki, T. J. and Ebert, D. 2004. Conceptual issues in local adaptation. – Ecol. Lett. 7: 1225–1241.
Kigel, J., Konsens, I., Rosen, N., Rotem, G., Kon, A.and Fragman-Sapir, O. 2011. Relationships between flowering time and rainfall gradients across mediterranean-desert transects. – Isr. J. Ecol. Evol. 57: 91–109.
Kooyers, N. J., Colicchio, J. M., Greenlee, A. B., Patterson, E., Handloser, N. T. and Blackman, B. K. 2019. Lagging adaptation to climate supersedes local adaptation to herbivory in an annual monkeyflower. – Am. Nat. 194: 541–557.
Kurze, S., Bareither, N. and Metz, J. 2017. Phenology, roots and reproductive allocation, but not the LHS scheme, shape ecotypes along an aridity gradient. – Perspect. Plant Ecol. Evol. Syst. 29: 20–29.
Lambrecht, S. C., Gujral, A. K., Renshaw, L. J. and Rosengreen, L. T. 2020. Evolutionary and plastic changes in a native annual plant after a historic drought. – Ecol. Evol. 10: 4570–4582.
Lampei, C. and Tielbörger, K. 2010. Evolvability of between-year seed dormancy in populations along an aridity gradient. – Biol. J. Linn. Soc. 100: 924–934.
Lampei, C., Metz, J. and Tielbörger, K. 2017. Clinal population divergence in an adaptive parental environmental effect that adjusts seed banking. – New Phytol. 214: 1230–1244.
Leimu, R. and Fischer, M. 2008. A meta-analysis of local adaptation in plants. – PLoS One 3: e4010.
Liancourt, P. and Tielbörger, K. 2009. Competition and a short growing season lead to ecotypic differentiation at the two extremes of the ecological range. – Funct. Ecol. 23: 397–404.
Lortie, C. J. and Hierro, J. L. 2022. A synthesis of local adaptation to climate through reciprocal common gardens. – J. Ecol. 110: 1015–1021.
McGraw, J. B., Turner, J. B., Souther, S., Bennington, C. C., Vavrek, M. C., Shaver, G. R. and Fetcher, N. 2015. Northward displacement of optimal climate conditions for ecotypes of *Eriophorum vaginatum* L. across a latitudinal gradient in Alaska. – Global Change Biol. 21: 3827–3835.
Metz, J. and Tielbörger, K. 2016. Spatial and temporal aridity gradients provide poor proxies for plant–plant interactions under climate change: a large-scale experiment. – Funct. Ecol. 30: 20–29.
Metz, J. and Tielbörger, K. 2023. Data from: A drought year favored drier-adapted origins over local origins in a reciprocal transplant experiment along a rainfall gradient. – Göttingen Research Online repository, https://doi.org/10.25625/ZLLZ3M.
Metz, J., Liancourt, P., Kigel, J., Harel, D., Sternberg, M. and Tielbörger, K. 2010. Plant survival in relation to seed size along environmental gradients: a long-term study from semi-arid and Mediterranean annual plant communities. – J. Ecol. 98: 697–704.
Metz, J., Ribbers, K., Tielbörger, K. and Müller, C. 2014. Long- and medium-term effects of aridity on the chemical defence of a widespread Brassicaceae in the Mediterranean. – Environ. Exp. Botany 105: 39–45.
Metz, J., Freundt, H. and Jeltsch, F. 2018. Stable germination behavior but partly changing seed–seed interactions along a steep rainfall gradient. – Basic Appl. Ecol. 28: 5–16.
Metz, J., Lampei, C., Bäumler, L., Bocherens, H., Dittberner, H., Henneberg, L., Meaux, J. and Tielbörger, K. 2020. Rapid adaptive evolution to drought in a subset of plant traits in a large-scale climate change experiment. – Ecol. Lett. 23: 1643–1653.
Midolo, G. and Wellstein, C. 2020. Plant performance and survival across transplant experiments depend upon temperature and precipitation change along elevation. – J. Ecol. 108: 2107–2120.
Nguyen, M. A., Ortega, A. E., Nguyen, K. Q., Kimball, S., Goulden, M. L. and Funk, J. L. 2016. Evolutionary responses of invasive grass species to variation in precipitation and soil nitrogen. – J. Ecol. 104: 979–986.
Penner, S., Dror, B., Aviezer, I., Bar-Lev, Y., Salman-Minkov, A., Mandakova, T., Šmarda, P., Mayrose, I. and Sapir, Y. 2020. Phenology and polyploidy in annual *Brachypodium* species (Poaceae) along the aridity gradient in Israel. – J. Syst. Evol. 58: 189–199.
Peterson, M. L., Angert, A. L. and Kay, K. M. 2020. Experimental migration upward in elevation is associated with strong selection on life history traits. – Ecol. Evol. 10: 612–625.
Petrů, M. and Tielbörger, K. 2008. Germination behaviour of annual plants under changing climatic conditions: separating local and regional environmental effects. – Oecologia 155: 717–728.
Petrů, M., Tielbörger, K., Belkin, R., Sternberg, M. and Jeltsch, F. 2006. Life history variation in an annual plant under two

opposing environmental constraints along an aridity gradient. – Ecography 29: 66–74.
Pugnaire, F. I., Morillo, J. A., Peñuelas, J., Reich, P. B., Bardgett, R. D., Gaxiola, A., Wardle, D. A. and van der Putten, W. H. 2019. Climate change effects on plant–soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. – Sci. Adv. 5: eaaz1834.
Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. – J. Ecol. 102: 275–301.
Rysavy, A., Seifan, M., Sternberg, M. and Tielbörger, K. 2016. Neighbour effects on shrub seedling establishment override climate change impacts in a Mediterranean community. – J. Veg. Sci. 27: 227–237.
Savolainen, O., Lascoux, M.and Merilä, J. 2013. Ecological genomics of local adaptation. – Nat. Rev. Genet. 14: 807–820.
Schiffers, K. and Tielbörger, K. 2006. Ontogenetic shifts in interactions among annual plants. – J. Ecol. 94: 336–341.
Siewert, W. and Tielbörger, K. 2010. Dispersal–dormancy relationships in annual plants: putting model predictions to the test. – Am. Nat. 176: 490–500.
Talmon, Y., Sternberg, M. and Grünzweig, J. M. 2011. Impact of rainfall manipulations and biotic controls on soil respiration in Mediterranean and desert ecosystems along an aridity gradient: shrubland soil respiration and climate change. – Global Change Biol. 17: 1108–1118.
ten Brink, H., Gremer, J. R. and Kokko, H. 2020. Optimal germination timing in unpredictable environments: the importance of dormancy for both among- and within-season variation. – Ecol. Lett. 23: 620–630.
Tielbörger, K., Petrů, M. and Lampei, C. 2012. Bet-hedging germination in annual plants: a sound empirical test of the theoretical foundations. – Oikos 121: 1860–1868.
Tielbörger, K., Bilton, M. C., Metz, J., Kigel, J., Holzapfel, C., Lebrija-Trejos, E., Konsens, I., Parag, H. A. and Sternberg, M. 2014. Middle-Eastern plant communities tolerate 9 years of drought in a multi-site climate manipulation experiment. – Nat. Commun. 5: 5102.
Tomiolo, S., van der Putten, W. H. and Tielbörger, K. 2015. Separating the role of biotic interactions and climate in determining adaptive response of plants to climate change. – Ecology 96: 1298–1308.
Urban, M. C. 2015. Accelerating extinction risk from climate change. – Science 348: 571–573.
Valladares, F., Matesanz, S., Guilhaumon, F., Araújo, M. B., Balaguer, L., Benito-Garzón, M., Cornwell, W., Gianoli, E., Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H. and Zavala, M. A. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. – Ecol. Lett. 17: 1351–1364.
Van der Putten, W. H., Macel, M. and Visser, M. E. 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. – Phil. Trans. R. Soc. B 365: 2025–2034.
Venables, W. N. and Ripley, B. D. 2002. Modern Applied Statistics with S. – Springer.
Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. 2007. Let the concept of trait be functional! – Oikos 116: 882–892.
Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. – Phil. Trans. R. Soc. B 365: 2019–2024.
Warren, R., Price, J., Graham, E., Forstenhaeusler, N. and VanDerWal, J. 2018. The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. – Science 360: 791–795.
Wilczek, A. M., Cooper, M. D., Korves, T. M. and Schmitt, J. 2014. Lagging adaptation to warming climate in *Arabidopsis thaliana*. – Proc. Natl Acad. Sci. USA 111: 7906–7913.
Zwikel, S., Lavee, H. and Sarah, P. 2007. Temporal evolution of salts in Mediterranean soils transect under different climatic conditions. – CATENA 70: 282–295.