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Clinal population divergence in an adaptive parental environmental effect that adjusts seed banking

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Summary

- Bet-hedging via between-year seed dormancy is a costly strategy for plants in unpredictable environments. Theoretically, fitness costs can be reduced through a parental environmental effect when the environment is partly predictable. We tested whether populations from environments that differ in predictability diverged in parental effects on seed dormancy.
- Common garden-produced seeds of the two annual plant species *Biscutella didyma* and *Bromus fasciculatus* collected along an aridity gradient were grown under 12 irrigation treatments. Offspring germination was evaluated and related to environmental correlations between generations and their fitness consequences at the four study sites.
- One species exhibited strong seed dormancy that increased with unpredictability in seasonal precipitation. The parental effect on seed dormancy also increased proportionally with the environmental correlation between precipitation in the parental season and seedling density in the following season; this correlation increased from mesic to arid environments. Because fitness was negatively related to density, this parental effect may be adaptive. However, the lack of dormancy in the second species indicates that bet-hedging is not the only strategy for annual plants in arid environments.
- Our results provide the first evidence for clinal variation in the relative strength of parental effects along environmental gradients.

Introduction

Parents can increase their fitness by influencing offspring phenotypes via adaptive parental effects (Mousseau & Fox, 1998). For example, parental environmental effects can use information about the parental environment to induce *particular* offspring phenotypes for maximizing the match with the offspring environment (Lacey, 1998; Uller & Helanterä, 2013). This requires that parental and offspring environments are correlated (Shea *et al.*, 2011; Burgess & Marshall, 2014; Ezard *et al.*, 2014; Leimar & McNamara, 2015). By contrast, plants also may evolve to produce *heterogeneous* offspring phenotypes when the environment is inherently unpredictable (Marshall & Uller, 2007). This is advantageous because it increases the probability that at least some offspring phenotypes will match the environmental conditions, even if some offspring may fail to reproduce (Kudo, 2001; Crean & Marshall, 2009; Simons, 2011). This strategy, known as diversifying bet-hedging (Slatkin, 1974; Philippi & Seger, 1989; Marshall & Uller, 2007; Simons, 2011), spreads the risk of suboptimal phenotypes among offspring and evolves in response to environmental uncertainty (Graham *et al.*, 2014).

The classic example for diversifying bet-hedging is between-year seed dormancy, which is the ability of a plant to produce seeds that differ in their germination probability (Cohen, 1966; Brown & Venable, 1988). This is especially important in arid environments, which are typically characterized by higher uncertainty in water availability (Noy-Meir, 1973; Siewert & Tielbörger, 2011; Golodets *et al.*, 2013). For instance, higher seed dormancy has been shown to increase dispersion of germination timing over three successive seasons in desert populations of *Hordeum spontaneum* (Volis *et al.*, 2002). This indicates the formation of a permanent seed bank (Fig. 1e), a common strategy among annual plants from arid ecosystems (Siewert & Tielbörger, 2011) that effectively reduces extinction risk in randomly varying environments (Kalisz & McPeek, 1993; Evans *et al.*, 2007). Similarly, seed dormancy has been associated with increased risk of dying before reproduction (Tielbörger *et al.*, 2012) and reduced variance in fitness across years (Venable, 2007; Gremer & Venable, 2014), which are key predictions from risk-spreading theory (Cohen, 1966). Thus, seed dormancy in annual dryland plants is a typical bet-hedging trait, reducing the chance of extinction in unpredictable environments. However, seed dormancy also infers a fitness cost, resulting from mortality of prematurely emerging seedlings and seeds remaining ungerminated in the seed bank (Fig. 1f1).

These fitness costs of between-year seed dormancy can be minimized through a parental environmental effect that reduces dormancy after dry seasons and increases dormancy after rainy

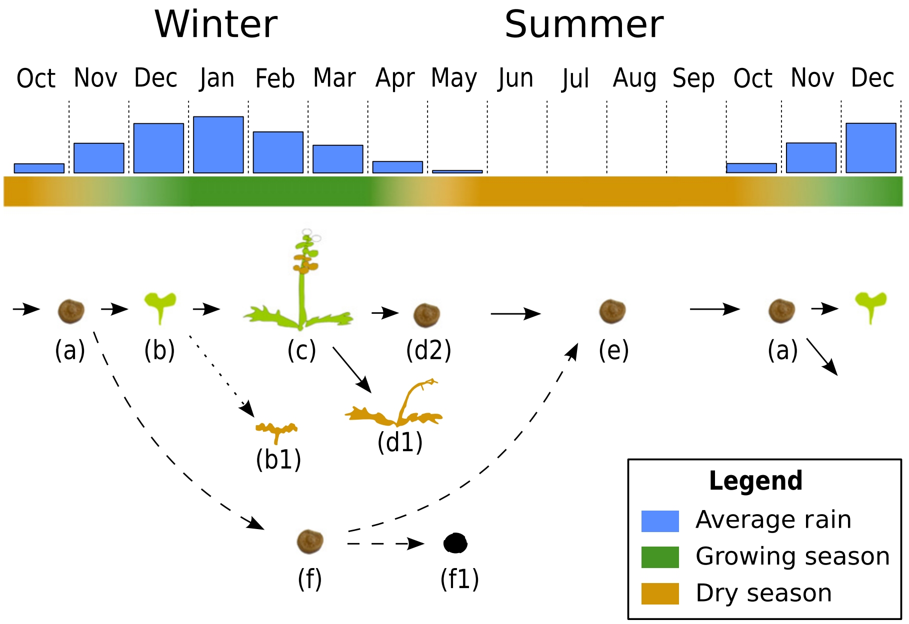

Fig. 1 Schematic life cycle of a Mediterranean winter annual, illustrated for *Biscutella didyma*. The seed bank contains the complete annual vegetation (a). A proportion of the seed bank germinates with onset of the rainy growing season (b), but some plants die before reproduction (b1). Production of seeds (c). All annuals die at the end of growing season (d1), but newly produced seeds (d2) enter the persistent seed bank (e) where the population persists over the dry season. Alternatively, seeds do not germinate (f) and remain in the soil seed bank (e) during the next growing season, bearing risk of death before germination (f1).

seasons (Nilsson *et al.*, 1994; Tielbörger & Valleriani, 2005). Rainy seasons are characterized by high seed production followed by increased seedling density in the following season (Metz *et al.*, 2015). This in turn reduces offspring fitness and, consequently, the inclusive fitness of parents. Therefore, by increasing the dormant fraction in seeds produced in rainy seasons, plants reduce the expected negative density effects on their offspring (Nilsson *et al.*, 1994; Fig. 1b1,d1) and increase contributions to the seed bank in times when offspring will have potentially lower success in reproducing. After dry years, when less competition is expected, fewer seeds are deposited into the seed bank, keeping the costs for bet-hedging low. This parental environmental effect has been observed in seeds of four annual Mediterranean plant species collected from the field (Tielbörger & Valleriani, 2005). It also has been confirmed through experimental manipulation of parental water availability under controlled and field conditions in several Mediterranean annuals (Arnold *et al.*, 1992; Philippi, 1993; Tielbörger & Petrů, 2010) and ruderal temperate species (Luzuriaga *et al.*, 2006; Eslami *et al.*, 2010). By adjusting the 'optimal germination fraction' to the expected amount of competition in the first growing season for offspring, the parental effect may reduce the fitness costs of bet-hedging.

An important aspect of this parental effect is that it depends on a correlation between *two different* environmental factors in the parental and the offspring generation (Tielbörger & Valleriani, 2005), namely the abiotic conditions (e.g. precipitation) in the parental environment and the biotic conditions (neighbour density) in the offspring environment. This is in contrast to the common assumption of temporal autocorrelation *within one* driving environmental factor (Galloway, 2005; Leimar & McNamara, 2015). This distinction may seem small, but it has important implications. Even though precipitation can vary unpredictably across years, it can still cause a correlated effect on neighbour density in the offspring environment (Metz *et al.*, 2015). Therefore, populations of annual plants that persist under these environmental conditions are expected to exhibit a parental environmental effect on between-year seed dormancy. Although bet-hedging and parental effects have mostly been studied independently, this framework allows us to study how they co-evolved.

One possible first step towards identifying potentially adaptive traits and their environmental drivers is to compare populations from different environments (Mitchell-Olds & Schmitt, 2006). This may reveal a gradual change of phenotypes along environmental gradients, commonly referred to as clinal variation (Mayr, 1963; Endler, 1977; Mitchell-Olds & Schmitt, 2006; Hut *et al.*, 2013). However, clinal variation also can result from factors other than natural selection and is, therefore, insufficient as evidence for adaptive diversification (Mitchell-Olds & Schmitt, 2006; Monty *et al.*, 2009). Furthermore, the adaptive value of seed dormancy is virtually impossible to measure in the field because the fitness advantage manifests itself only after several generations (Cohen, 1966). However, parental effects have rarely been assessed in populations originating from systematically (e.g. gradually) changing environments (but see Monty *et al.*, 2009), and it is thus unknown whether clines in parental effects along environmental gradients exist that are consistent with theoretical predictions.

Here, we investigate whether populations of two annual plant species diverge in the relative strength of the parental effect on between-year seed dormancy according to theoretical predictions. We used four populations along a short and very steep aridity gradient from northern to southern Israel, where uncertainty of precipitation increases together with aridity, allowing for clear predictions in the evolution of bet-hedging (Tielbörger *et al.*, 2012). By using a multigeneration common garden approach, we ensured that differences between populations in the relative strength of the parental effects could be attributed to genetic differentiation. We also examined the predicted correlation between parental precipitation and seedling density, as well as the fitness effects of seedling density to identify the environmental context that favours the parental effect. Specifically, we tested the following predictions: parental effects cause lower offspring germination under higher water availability in the parental generation; arid populations exhibit stronger parental effects on seed dormancy than populations from mesic sites; and the underlying assumption that seedling densities are higher after rainy seasons and negatively affect offspring fitness.

Materials and Methods

Study sites

The populations are situated along a north–south transect in Israel, along a steep climate gradient from a mesic Mediterranean to an arid climate (Fig. 2; Supporting Information Fig. S1a,b), over four sites: Mesic Mediterranean (MM), Mediterranean (M), Semi-Arid (SA) and Arid (A). The sites are similar in terms of bedrock, exposure and mean annual temperature (Table 1; Petrů & Tielbörger, 2008). The growing season for annual plants lasts from winter to spring (Fig. 1) with its length decreasing sharply towards the arid site (months with rain > 20 mm in Table 1; Fig. S1b). In the same direction along this gradient, average seasonal precipitation decreases 8.7-fold (Table 1; Fig. S1a) and the coefficient of variation (CV) of seasonal rain increases 2.3-fold (Table 1). Precipitation records of > 50 seasons (1950–2005, Israel Meteorological Service, www.ims.gov.il) were used for all analyses of seasonal rain from weather stations at Eilon (6 km from MM; 55 seasons), Bet Jimal (8.5 km from M; 55 seasons), Lahav (4 km from SA; 53 seasons) and Sde Boker (1 km from A; 54 seasons).

Species

Two common winter-annual species *Biscutella didyma* L. (Brassicaceae) and *Bromus fasciculatus* C. Presl (Poaceae) were selected (nomenclature according to Feinbrun-Dothan (1986) for *B. fasciculatus* and Zohary (1966) for *B. didyma*). A typical life cycle for winter-annual plants in this region is shown in Fig. 1. Both species are predominantly selfing (Boaz *et al.*, 1990; Plitmann, 1993; Oja, 2002). Although *B. didyma* is common in all sites, *B. fasciculatus* is absent from MM. Both species showed considerable phenotypic variation along the gradient in earlier common garden experiments. *Biscutella didyma* plants decreased in size and showed more branching, higher reproductive allocation and earlier phenology towards the desert in the same populations (Petrů *et al.*, 2006; Petrů & Tielbörger, 2008; Hänel & Tielbörger, 2015). *Bromus fasciculatus* showed earlier phenology and higher reproductive allocation in arid sites in the same study region (Aronson *et al.*, 1992, 1993; Liancourt & Tielbörger, 2009), and broader leaves and hairier fascicles in our arid site (C. Lampei, pers. obs.). In a previous study on the same species in these same sites, germination fraction was negatively related to the species- and site-specific probability of dying before reproduction, which is consistent with bet-hedging theory (Tielbörger *et al.*, 2012). This study showed strong evidence for bet-hedging via seed dormancy in *B. didyma*; the results were more ambiguous in *B. fasciculatus* (Tielbörger *et al.*, 2012).

Experiment

Original seed material In late spring of 2005 (April/May), ripe seeds were collected from at least 60 plants per species within a 100 × 100 m area at all sites, with a minimum of 5 m between single donor plants (Fig. 2a). Over the summer, the seeds were subjected to natural after-ripening as described in Lampei & Tielbörger (2010).

From these seeds, 10 seed families (S1) per species and site, respectively, were established under common garden conditions in a glasshouse in Tübingen, Germany, during the winter of 2005/2006. For this and all later generations, 9 × 9 × 9 cm pots were used, containing a 1 : 1 mixture of sand and low-nutrient gardening soil. To each 40 l of substrate, 100 ml of Osmocote$^{®}$ (Scotts Australia, Bella Vista, NSW, Australia) slow-release fertilizer (15N–9P–5.9K) was added. Pollinators were excluded from the glasshouse and plants were wrapped in organza material at the onset of flowering to prevent cross-fertilization. S1 seeds had been kept in separate organza bags over the summer for each seed family at the Mediterranean field site, and these bags had been stored between two organza layers nailed to the dry ground to ensure natural but similar after-ripening for all seeds. Due to the naturally rainless summers, seeds stayed dry but were subjected to natural summer temperatures and air humidity.

Manipulation of the parental environment An automated irrigation gradient was constructed to manipulate water availability in the parental generation (S2) (Fig. 2a). We used a line-source irrigation system (Johnson *et al.*, 1982; Smith *et al.*, 2000), where plants receive less water per unit time with increasing distance from a sprinkler nozzle, resulting in three irrigation levels (Fig. 2b,c). In total, we had eight irrigation source lines. In order to realize 12 irrigation levels, two source lines were always assigned to one of four different irrigation durations of 1, 2, 5 or 10 min (Fig. 2a; Table 2). Therefore, each source line represented an incomplete block as it did not include all irrigation levels (Fig. 2b; Table 2). Irrigation was applied simultaneously to all 12 irrigation levels and scheduled to ensure that the majority of plants in irrigation level 10 (42.83 mm) just managed to reproduce. Summed across the duration of the experiment, the 12 irrigation levels reflected the range of average seasonal precipitation along the aridity gradient and soil moisture was similar to values typically observed in the field (Hänel, 2014).

In November 2006, one seedling per pot (S2) was reared under the irrigation gradient. Each of the 12 irrigation levels contained two plants from each seed family (i.e. one per replicate block), one of which had been randomly chosen for the parental effects test, resulting in 12 plants per seed family (one for each irrigation level), 120 plants per population, 360 plants of *B. fasciculatus* (three populations) and 480 plants of *B. didyma* (four populations). The ripe seeds were exposed to natural after-ripening as in the previous year.

Evaluating parental effects In November 2007, we evaluated the effects of parental irrigation levels on germination of S3 seeds under common garden conditions (Fig. 2a). First, average seed

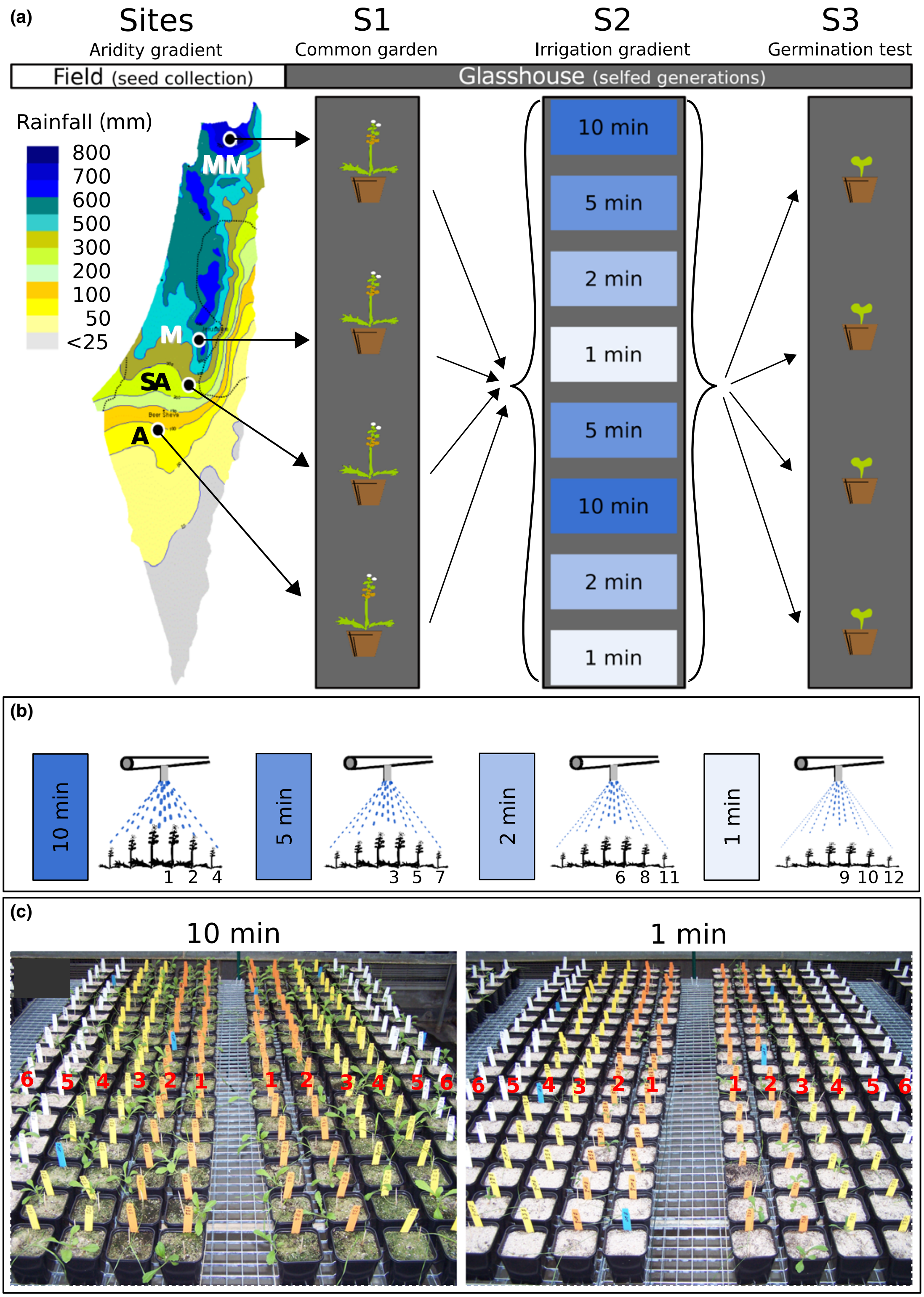

Fig. 2 (a) Schematic of experimental protocol, illustrated for *Biscutella didyma*. Seeds were collected from four population sites (Sites) along a natural rainfall gradient in Israel (map adapted from Sternberg *et al.* (2009)). We refer to the sites as Mesic Mediterranean (MM), Mediterranean (M), Semi-Arid (SA) and Arid (A). The S1 generation was raised and selfed under common glasshouse conditions in a complete randomized design to minimize field environmental effects. Their offspring (S2) were reared under an irrigation treatment in an incomplete block design with four pairs of treatment replicates, resulting in eight blocks. S3 germination was determined in a complete randomized design. (b) The 12-level irrigation gradient to generate controlled parental environmental effects. Each treatment included three irrigation levels, ordered from wet to dry, corresponding to irrigation levels in Table 2. (c) Photo of a wet and a dry treatment block. Label colour (orange, yellow, white) indicates pots of the same irrigation level. Red numbers indicate rows (compare with Eqn 1). Pots were re-randomized within row and position of row was changed within irrigation level before every irrigation.

Table 1 Coordinates, environmental conditions and characterizations of the plant communities at the four sites, modified from Petrů & Tielbörger (2008)

Population	Abbr.	Latitude	Longitude	Altitude (m asl)	Average seasonal rainfall (mm); CV	Months with rain > 20 mm	Soil type	Vegetation
Mesic Mediterranean	MM	33°00′N	35°14′E	500	789; 22	6	Hard chalk, Terra Rossa	Mediterranean maquis/garrigue, annuals, geophytes
Mediterranean	M	31°42′N	35°03′E	620	530; 31	5	Hard chalk, Terra Rossa	Dwarf shrubland, annuals, geophytes
Semi-Arid	SA	31°23′N	34°54′E	590	300; 38	4	Brown Rendzina	Dwarf shrubland, annuals, geophytes
Arid	A	30°52′N	34°46′E	470	90; 51	2	Desert Lithosol	Annuals, scattered shrubs, geophytes

The meteorological data were provided by the Israel Meteorological Service (http://www.ims.gov.il/IMSEng/CLIMATE); long-term data are given as the mean and coefficient of variation (CV) for 54–56 yr of records (1950–2005), depending on the site. asl, above sea level.

Table 2 Overview of the experimental set-up

Irrigation levels ordered (amount)	Irrigation duration (min)	Mean distance to source line (cm)	Single irrigation (ml)	Total irrigation (mm)	Viability testing pools
1	10	20	31.75	857.25	I
2		40	17.48	471.96	I
4		60	9.86	266.22	II
3	5	20	16.44	443.88	II
5		40	9.52	257.04	III
7		60	3.77	101.79	IV
6	2	20	6.35	171.45	III
8		40	3.70	99.90	IV
11		***60***	***1.47***	***39.69***	–
9	1	20	3.00	81.00	IV
10		40	1.59	42.83	–
12		***60***	***0.35***	***9.45***	–

Irrigation treatments correspond to treatments in Fig. 2, differing in duration of automated irrigation. Irrigation levels within treatment depend on the distance from the irrigation source line (see Fig. 2b). Single irrigation equals the volume of one irrigation event. Total irrigation is given as the sum of all irrigation events throughout the experiment as millimetre water column to facilitate comparison with natural precipitation. Irrigation levels with the same Roman numerals for 'viability testing pools' were combined in the seed viability experiment, with three levels not included. Irrigation levels that also were excluded from the parental effects experiment are highlighted in bold italics.

weight of the S3 seeds was obtained for each seed family at each irrigation level by weighing 10 randomly chosen seeds. Then, all seeds were germinated under identical watering conditions in a complete randomized design to obtain germination fractions. The germination fraction under moist conditions is a function of seed viability and physiological seed dormancy as defined by Vleeshouwers *et al.* (1995). Pots were marked in a way that their identity was hidden in order to minimize observer bias. In two pots per parent plant, we sowed 20 seeds. If only 20–40 seeds were available per parent, they were evenly divided between the two pots. When the parental line had < 20 seeds, only one pot was sown. This resulted in 80% of the pots having 20 seeds, 6% having 15–20 seeds and 14% having 10–15 seeds. The pots in this 14% group were evenly distributed across irrigation levels, because the two driest irrigation levels were excluded from the germination trial due to limited survival under drought stress. The germination experiment comprised a total of 1320 pots (839 *B. didyma* with 167 MM, 204 M, 231 SA, 237 A; 481 *B. fasciculatus* with 152 M, 154 SA, 175 A). Irrigation was applied manually every other day during the first 9 d to simulate a first significant rain storm, causing simultaneous germination across all pots. After a week without watering, irrigation was continued as described above. Most germination (94%) occurred within the first 12 d after the initial irrigation (recorded in four counting sessions). To avoid density effects on germination (Tielbörger & Prasse, 2009), all seedlings exceeding the fourth seedling (which were reared for evaluation at later developmental stages) were removed after counting. Recording ended after 22 d because < 1% of total seedlings germinated after Day 13.

Viability test of S3 seeds In order to test for potential differences in seed viability, an additional random set of seeds from the same S2 plants (i.e. the same seed batches as in the germination experiment) was germinated on filter paper in a complete randomized setup. Ungerminated seeds were tested for viability with the method described by Pake & Venable (1996), where imbibed ungerminated seeds are poked with a needle through the seed coat. As viable imbibed seeds exhibit strong turgor pressure, they offer resistance followed by leakage of exudates, which is not observed for dead seeds. For the viability test, equal numbers of seeds from each seed family from at least two parental irrigation levels were sorted to 'viability testing pools' (Table 2), as the number of available seeds was limited. However, no seeds were tested from the three lowest irrigation levels, as two had been excluded (Table 2) and in the third (42.83 mm), all seeds had been used in the main experiment (Table 2). In the next three irrigation levels of 81.00, 99.90 and 101.79 mm, there were so few available seeds that these three levels were pooled for the test (Table 2). Each viability testing pool consisted of 100 seeds, composed of 5 random seeds per seed family and irrigation level. The pool from the lowest irrigation levels consisted of 3 seeds per seed family and irrigation level plus 1 seed each from 10 randomly chosen parent plants from these irrigation levels.

Density monitoring and biomass estimates In order to test whether seedling density depends on the precipitation during the previous season, densities of the natural plant communities at all four sites were monitored over 10 consecutive years (2002–2011) at the beginning of each growing season (i.e. seedling stage of annuals). To this end, 50 permanent quadrats of 20 × 20 cm were laid out in 25 random pairs at all sites. One quadrat per pair was located under shrub canopies, and the other nearby in open patches to account for differences between microhabitats (Holzapfel *et al.*, 2006). Total density of emerged seedlings was counted in all quadrats and seasons *c.* 4 wk after the first major rain had triggered germination (see Metz *et al.* (2010) for details).

In order to assess whether higher community densities reduced individual fitness, we used final aboveground biomass as a proxy for fitness. This proxy was estimated nondestructively at the end of each season in permanent quadrats: vegetation cover was multiplied by mean plant height and calibrated with dry mass of similar vegetation harvested outside the study plots (Tielbörger *et al.*, 2014). The average 'fitness' per plant in a quadrat was then calculated by dividing biomass by seedling density ('biomass per seedling'). Using seedling instead of adult densities also accounts for density-dependent mortality. Note, however, that biomass estimates were not available for all sites in all seasons (MM: 8, M: 9, SA: 9, A: 5).

Data analysis

In order to test whether populations differed in seed viability (binary value) depending on parental irrigation, a generalized linear model (GLM) with binomial error (logit link) was fitted for each species separately. It included the main effects of population and irrigation, and their interaction effects. When the interaction was significant, predefined treatment contrasts were performed to identify 'viability testing pools' (Table 2) with significantly reduced viability.

In order to estimate the effect of parental irrigation on germination, we removed irrigation levels with reduced seed viability from the data (see the Results section) and fitted a generalized additive mixed model (GAMM) with binomial error (logit link) separately for each species (R package GAMM4; Wood & Scheipl, 2014). A GAMM was chosen because random effects were required, and initial analysis suggested a nonlinear germination response. Nonlinear response curves are the generally expected phenotypic response because a genotype may respond to one environment but not to another (Scheiner, 1993). Germination odd ratio (GOR) was analysed according to the following equation:

$$\begin{aligned}\mathrm{GOR}_{ijk} = \mu + O_i + f_j(S) + f_k(I) + f_{k(i)}(I(O)) + B_l \\ + B(R)_{l(m)} + G_n + P(G)_{o(n)} + \varepsilon_{lmno(ijk)}.\end{aligned} \qquad \text{Eqn 1}$$

The fixed effects included the overall intercept μ, the effect of origin i (O_i), and separate smoothing functions for seed weight ($f_j(S)$), the effect of parental irrigation ($f_k(I)$) and the deviation from this main effect for each origin ($f_{k(i)}(I(O))$). The latter is comparable to an interaction effect in a common linear model. The random effects included the effect of block l (B_l), the effect of row m in block l ($B(R)_{l(m)}$) (see Fig. 2), the effect of seed family n (G_n) and the effect of parent plant o within seed family n ($P(G)_{n(o)}$). The random effects reflect the experimental setup in the irrigation gradient (S2-generation); all other generations were completely randomized (Fig. 2). The term $\varepsilon_{lmno(ijk)}$ is the residual associated with an individual offspring plant. The smoothing functions were based on thin-plate regression splines (Wood, 2003). In short, they evaluate local optima that are added and smoothed, instead of finding the best global linear fit. An initial model with separate smoothing functions for seed weight in each population showed that they were not different among populations for both species. The significance of smoothing functions was inferred from Bayesian credible intervals according to Wood (2013) and the significance of factor levels by a Wald *Z*-test on the Bayesian covariance matrix.

Because parental effects are often linked with environmental autocorrelations, we tested for between-season autocorrelations in precipitation with the function acf from the R package STATS (R Development Core Team, 2016). The autocorrelation function is the correlation among points in a time-series at defined time lags under the assumption of second-order stationarity, that is, same mean and variance (see Venables & Ripley (2002) for details).

We further tested whether precipitation in the parental season is a predictor for subsequent community densities in the offspring season, based on the seedling counts in the four natural habitats. We fitted a generalized linear mixed model (GLMM) with Poisson error distribution (log link) to seedling density D_{ij} in each population with the following model equation:

$$D_{ij} = \mu + \mathrm{PPS}_i + \mathrm{POS}_j + \mathrm{PPS} \times \mathrm{POS}_{ij} + \mathrm{MH}_k + \varepsilon_{k(ij)}, \qquad \text{Eqn 2}$$

(μ, overall intercept; PPS_i, precipitation in the parental season I; POS_j, precipitation in the offspring season j; their interaction ($\mathrm{PPS} \times \mathrm{POS}_{ij}$) as fixed effects; MH_k, random effect of microhabitat k (shrub, open)). At sites MM, M and SA, an observation-level random effect was added to account for overdispersion (Browne *et al.*, 2005). At site A, overdispersion was not observed. Significance was inferred via a likelihood ratio test comparing the full model with a model missing the factor of interest. These marginal effects are equivalent to hypotheses tests (Zuur *et al.*, 2009).

Finally, we tested whether higher plant densities in the natural habitats indeed reduced individual plant fitness. We fitted a linear model to the seasonal average of 'biomass per seedling' with the seasonal average of seedling density, site and microhabitat as explanatory variables. A log transformation was applied to improve normality of residuals. To account for heteroscedasticity, variances were estimated separately for each site. In addition, to understand the within-season density effect across quadrats, a linear mixed-effects model was fitted to 'biomass per seedling' with site, seedling density, seasonal precipitation and their interactions as fixed effects. Seasonal precipitation was scaled to the population average and standard deviation to retain only within-site variability. Square-root transformation was applied to improve normality of residuals. The model contained the nested random effects of quadrat within plot within site and season. To account for heteroscedasticity, the variances were modelled with a power function of seedling density and seasonal rainfall using the varComb and the varPower functions of the R-package NLME (Pinheiro *et al.*, 2016). All statistical tests were performed with R 3.3.0 (R Development Core Team, 2016). All data used for the analysis and figures is published at the KNB Data Repository (doi: 10.5063/F10Z716V).

Results

Irrigation differences had strong effects on parental fecundity

The differential irrigation had strong effects on the parental phenotype. Fecundity increased 10- to 20-fold in *B. didyma* and 5- to 7-fold in *B. fasciculatus* from 42.83 mm to the highest irrigation level, indicating that water availability was a key limiting factor in this experiment.

Seed viability was reduced by parental drought

High viability was observed for *B. didyma* seeds from the SA and A populations (Fig. 3). However, a significant population × irrigation interaction indicated that other populations had reduced seed viability in some testing pools ($F = 5.06$, $P = 0.007$). Planned contrasts showed that only seeds from the driest parental treatments in population M and MM exhibited decreased viability, with *c.* 10% dead seeds ($Z = -1.87$, $P = 0.061$) and 19% dead seeds ($Z = -3.13$, $P = 0.002$), respectively (Fig. 3). Except for this effect of extreme drought on plants from mesic environments, there were no further effects of parental irrigation on seed viability. In *B. fasciculatus,* viability of S3 seeds was high, and differences among seed pools were not significant (Fig. 3; population × irrigation: $F = 1.61$, $P = 0.23$). To isolate parental effects from seed viability differences, all irrigation levels that contributed to viability testing pools with significantly or marginally significantly reduced viability (levels 7, 8, 9) were excluded in the respective populations (MM, M) from further analysis.

One species shows a strong parental effect on offspring germination

In *B. didyma,* germination decreased with increasing parental irrigation (Table 3; Fig. S2). There was a marginally significant positive association of seed weight with the probability of germination (Table 3; Fig. S2). In *B. fasciculatus,* however, germination was unaffected by parental irrigation but was positively correlated with seed weight, especially in the lower range of seed weight (Table 3; Fig. S1).

Clinal variation in the strength of the parental effect on seed dormancy in one species

There was a consistent increase in the intensity of the parental effect towards arid environments along the natural rainfall gradient in *B. didyma.* Germination in this species was generally affected by origin ($\chi^2 = 22.7$, df = 3, $P < 0.001$). Namely, the populations SA and A showed lower germination than MM (Table 3). However, this resulted mainly from a parental irrigation × origin interaction due to a progressively negative and nonlinear effect of parental irrigation on germination probability in more arid populations. This is illustrated by the plotted reaction norms (Figs 4, S3) and the effective degrees of freedom (edf) parameter (Table 3), which steadily increases from 1 with progressing nonlinearity. The changing shape of the reaction norm curve indicates that the sensitivity of parental plants to irrigation differences changed among populations, with arid populations being insensitive to differential irrigation at high levels. This coincides with the changing width of the distribution of seasonal rain that becomes more and more narrow towards site A (Fig. S1a).

In *B. fasciculatus,* however, germination probability was generally very high with no overall difference between populations ($\chi2 = 4.3$, df = 2, $P = 0.12$). Increasing parental irrigation had no overall effect and induced only a small, marginally significant increase in germination in the most mesic population, M (Fig. 4; Table 3).

Parental precipitation predicts community seedling densities

Precipitation was not correlated among seasons in any of the sites up to a lag of 10 (Fig. 5a). Instead, seedling densities of the natural plant communities showed a positive correlation with total precipitation in the preceding *parental* season ('PPS', Table 4) at all sites

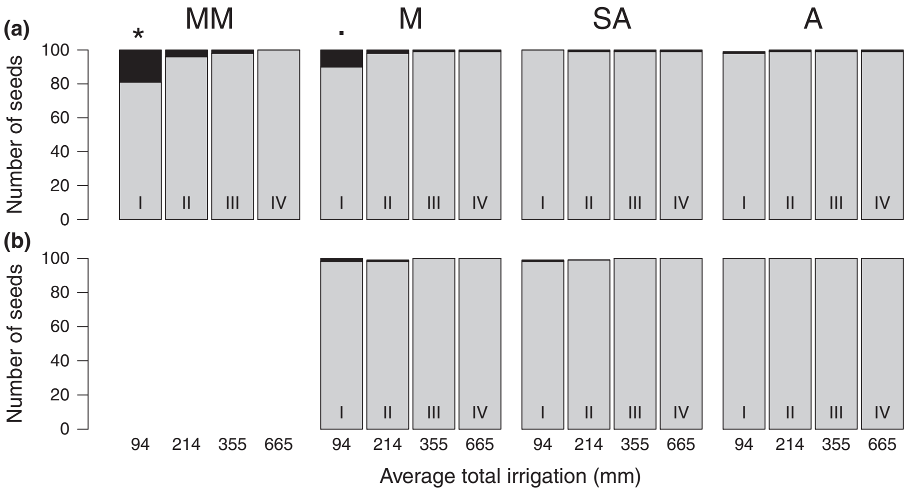

Fig. 3 Seed viability displayed as the number of nonviable seeds (black) in a pool of 100 seeds for (a) *Biscutella didyma* and (b) *Bromus fasciculatus*, separately for each population (MM, Mesic Mediterranean; M, Mediterranean; SA, Semi-Arid; A, Arid). Pools were constructed with seeds from three (I) or two (II, III, IV) irrigation levels. Roman numerals indicate seed pool number (Table 2). All irrigation levels belonging to a pool contributed equal numbers of seeds to this pool. The average parental irrigation is the mean of total irrigation across the irrigation levels that contributed to a seed pool. Seed pools with significantly reduced seed viability compared to pool IV are indicated (●, $P < 0.1$; *, $P < 0.05$).

Table 3 Estimated parameters and variance terms from the generalized additive mixed effects model (GAMM) on germination probability as a function of seed size, parental irrigation and site of origin for both species

Fixed effects

Species	Term	Effect	Estimate	*Z*	edf	χ^2	*P*-value
Biscutella didyma	**Factor origin**	**MM (Intercept)**	0.76	**4.31**			**< 0.001**
		M	0.74	−0.29			0.772
		SA	0.53	**−2.94**			**0.003**
		A	0.44	**−3.94**			**< 0.001**
	Smooth	***Seed weight***	See Fig. S2		1.00	***3.45***	***0.063***
	Smooth	**Irrigation**	See Fig. S2		1.00	**11.69**	**< 0.001**
	Smooth	Irrigation MM	See Figs 4, S3		0.00	0.00	0.338
	Smooth	Irrigation M	See Figs 4, S3		0.00	0.00	0.906
	Smooth	**Irrigation SA**	See Figs 4, S3		**2.08**	**5.47**	**0.036**
	Smooth	**Irrigation A**	See Figs 4, S3		**3.50**	**24.60**	**< 0.001**
Bromus fasciculatus	Factor origin	**M (Intercept)**	0.94	**18.75**			**< 0.001**
		SA	0.94	0.66			0.507
		A	0.92	−1.35			0.177
	Smooth	**Seed weight**	See Fig. S2		**2.06**	**11.04**	**0.005**
	Smooth	Irrigation	See Fig. S2		1.00	0.06	0.807
	Smooth	***Irrigation M***	See Fig. 4		***1.86***	***4.14***	***0.062***
	Smooth	Irrigation SA	See Fig. 4		0.00	0.00	0.391
	Smooth	Irrigation A	See Fig. 4		0.00	0.00	0.421

Random effects

Species	Effect	Variance
Biscutella didyma	Plant in seed family	1.09
	Seed family	0.43
	Row in block	0.05
	Block	0.02
Bromus fasciculatus	Plant in seed family	1.01
	Seed family	3.0×10^{-9}
	Row in block	3.3×10^{-6}
	Block	2.1×10^{-6}

Sites are abbreviated as: MM, Mesic Mediterranean; M, Mediterranean; SA, Semi-Arid; A, Arid. Effective degrees of freedom (edf) from cross-validation estimates the degree of nonlinearity of the smoothing estimate; edf is 0 when the curve is linear and increases proportionally to the increase in nonlinearity. Factor test statistics are treatment contrasts with the most mesic population representing the model intercept. The irrigation × origin interaction was tested by estimating the significance of deviations in each origin from the irrigation main effect. Significant terms are highlighted in bold and marginally significant terms in bold italics.

(Fig. 5b). This correlation became stronger along the gradient (site × PPS: $\chi^2 = 18.6$, df = 3, $P < 0.001$), with precipitation of the previous season being a better predictor for community density in more arid sites (Table 4). In the MM and the M site, total precipitation during the *offspring* season ('POS'), as experienced by the seeds, did not affect seedling density. This changed in sites SA and A, where POS showed a positive correlation with seedling densities (Table 4; site × POS: $\chi^2 = 44.3$, df = 3, $P < 0.001$). There was no PPS × POS interaction for any of the sites.

Seedling density negatively affects plant fitness

Across seasons, the average biomass produced per individual of the community (a fitness proxy) was negatively correlated with average seedling density at the MM, M and SA sites (Fig. 5c; Table 5), that is, the more seedlings germinated in a season, the less biomass a single individual could obtain. In addition, the significant seedling density × microhabitat interaction indicated that this density-dependent effect was stronger under shrubs (Table 5), particularly in MM (Fig. 5c). At site A, however, densities were not correlated with individual biomass across seasons (Fig. 5c). This was probably influenced by lower sample size (i.e. biomass from only five seasons) and a single extremely rainy season that dominated the pattern in this site (2006/2007 with 150 mm, > 90% quantile of the records). This deviation of site A from the overall pattern, however, did not result in a significant seedling density × site interaction (Table 5).

A similar pattern appeared when density effects on individual biomass were compared *within* seasons: individual biomass was generally lower in high-density quadrats (Fig. 5d; Table 6). However, the significant POS × site interaction indicates that this trend differed among sites, depending on rain in the offspring season (Table 6). The interaction was driven by a strong difference between wet and dry seasons at our most arid site A, where water availability in the extremely rainy season 2006/2007 was so high that no negative density effect was observed, indicating that precipitation is indeed a major limiting factor in this system. For all other seasons, however, site A did show a negative density

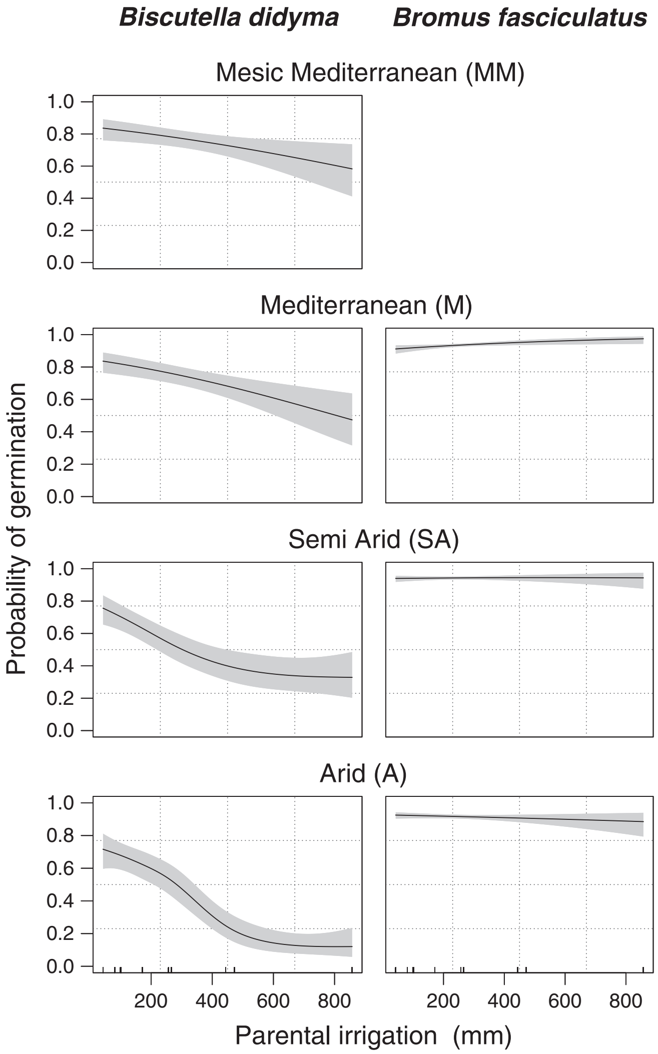

Fig. 4 Parental irrigation × origin interaction displayed as separate germination probability estimates for each population in both species based on GAMM. The shaded area displays the point-wise 95% credible interval. Smoothing functions differed increasingly from a flat line in *Biscutella didyma* (MM, $\chi^2 = 3.2$, $P = 0.074$; M, $\chi^2 = 9.5$, $P = 0.002$; SA, $\chi^2 = 20.3$, $P < 0.001$; A, $\chi^2 = 59.6$, $P < 0.001$). In *Bromus fasciculatus*, only the smoothing function for the Mediterranean population differed from zero (M, $\chi^2 = 5.5$, $P = 0.02$; SA, $\chi^2 = 0.01$, $P = 0.87$; A, $\chi^2 = 1.0$, $P = 0.31$). The frequency of observations for the covariate parental irrigation is indicated as a rug-plot.

dependence of individual biomass, despite low densities (Fig. 5d).

Environmental variables predict population differentiation in the parental effect and bet-hedging

The continuous reaction norms displayed in Fig. 4 illustrate the population-specific parental effect on germination (slope) and the potential of a population to express bet-hedging via seed banking (lowest germination fraction). The clinal variation in both traits could be predicted by environmental variables that, in theory, favour their evolution. Namely, the slope shifted proportionally to the correlation between parental rainfall and seedling density (Fig. 6a) and the lowest germination fraction shifted proportionally to the coefficient of variation of seasonal rainfall (Fig. 6b).

Discussion

In one of two species, our study demonstrated a directional cline in the relative strength of parental environmental effects on the bet-hedging trait, between-year seed dormancy. Namely, parental effects on seed dormancy were observed for all the studied populations of this species, but these effects increased consistently and markedly with increasing aridity. Moreover, at all four sites along the aridity gradient, seedling density depended on precipitation in the previous season, and higher densities had a negative effect on approximated fitness. These results indicate that competition among offspring after a wet season could be the main factor driving parental effects on seed dormancy. However, the absence of both seed dormancy and the parental effect in the second study species demonstrate the existence of alternative survival strategies in the annual plants of arid ecosystems.

Parental effects on offspring germination in one species

Parental effects on seed dormancy were detected in only one of our two species, thus providing only partial support for what we suggested is a general phenomenon. However, the parental effects in *B. didyma* were very strong and highly consistent with theory, which makes us confident that the observed pattern was not random. First of all, germination of *Biscutella didyma* steadily decreased with higher parental irrigation in all populations. In other words, seeds germinated less readily when the parent was reared under more favourable conditions and showed higher fecundity. This pattern is predicted by theory on seed dormancy as a parental effect, which may evolve in response to increased offspring densities in the subsequent season (Tielbörger & Valleriani, 2005). When reduced fitness is expected from intense competition after wet seasons, the offspring gain an advantage if more seeds enter a persistent seed bank. Notably, our findings resulted from a direct parental effect on seed dormancy and not from reduced seed viability (Finch-Savage & Leubner-Metzger, 2006). Also, the parental effect could not have resulted from competition in the parental generation (Vitalis *et al.*, 2004) because these plants were reared individually in separate pots. Although similar parental effects have been previously observed in this species in seeds collected from field sites subjected to rainfall manipulations (Tielbörger & Petrů, 2010) and in other plant species (Arnold *et al.*, 1992; Philippi, 1993; Luzuriaga *et al.*, 2006; Eslami *et al.*, 2010), we verified it here in a controlled multi-generation experiment. Using a fine-grained gradient of parental irrigation, we showed that seed dormancy indeed changes as a function of parental water availability.

The second species, *Bromus fasciculatus*, showed very high germination overall with negligible differences between populations and parental irrigation levels. These results correspond to earlier observations of low dormancy in *B. fasciculatus* seeds produced in glasshouse (Lampei & Tielbörger, 2010). In another study, however, dormancy differed remarkably between seeds collected from

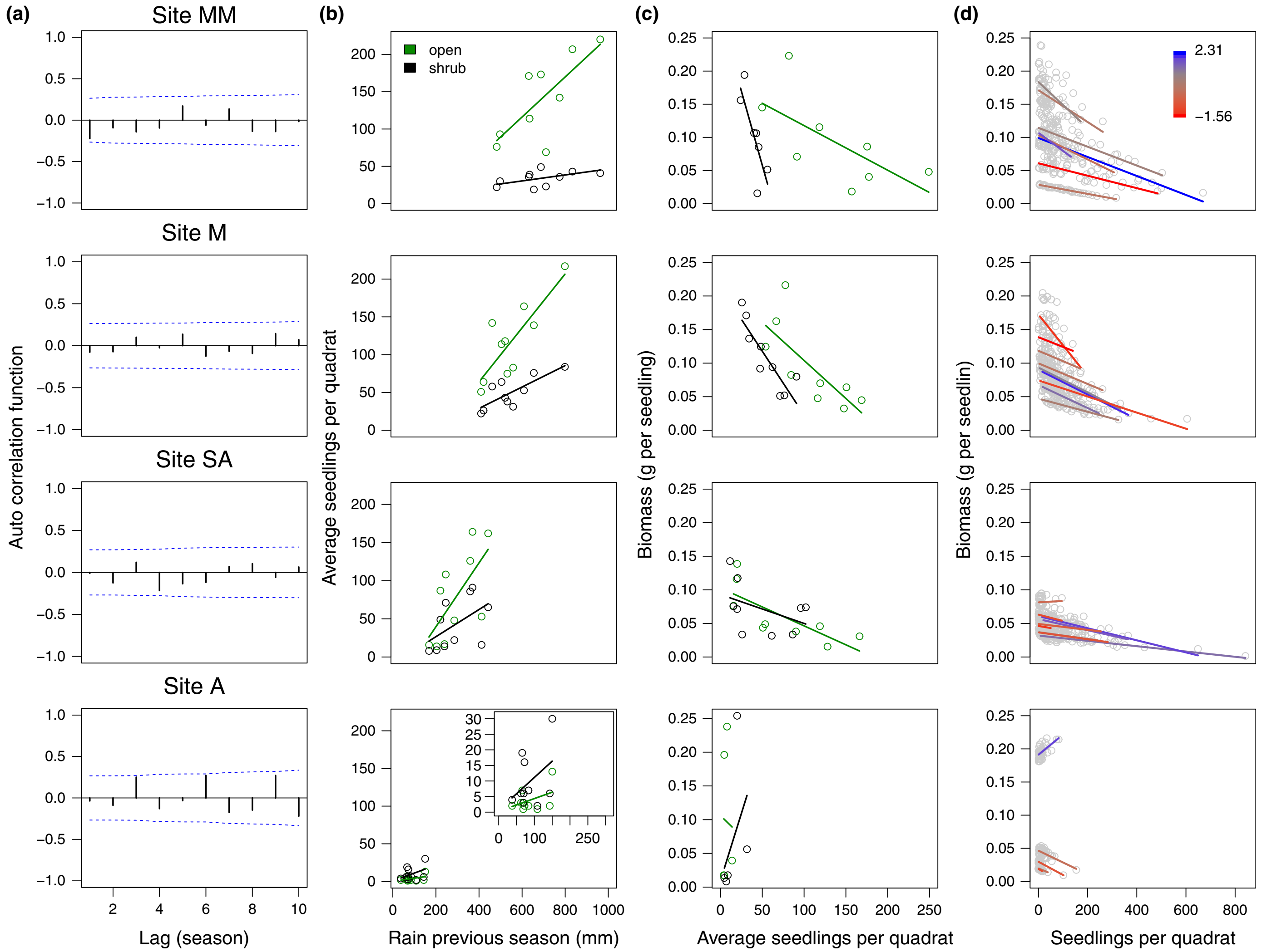

Fig. 5 (a) Seasonal rain autocorrelation function across 53–55 seasons for each site. Vertical bars indicate the strength and sign of a correlation among seasons for a given time lag. The blue dotted lines indicate the moving average 95% confidence interval. (b) Average seedling density (across permanent quadrats of 400 cm^2) as a function of average rain in the preceding season for microhabitats under shrub canopy (black) and in the open (green) at each site. (c) Average biomass reached per seedling at the end of the season as a function of average seedling density. (d) Average biomass per seedling as a function of seedling density and resource availability (rainfall in a season). Line colours display the amount of rain in a season (high rain, blue; low rain, red) centred to the population average and scaled by the population standard deviation. Site abbreviations: MM, Mesic Mediterranean; M, Mediterranean; SA, Semi-Arid; A, Arid.

the field and those raised in glasshouses (Tielbörger *et al.*, 2012), indicating that environmental variables other than parental water availability may affect seed dormancy in this species. For instance, ambient temperature during seed maturation also can affect germination (Penfield & Springthorpe, 2012; Burghardt *et al.*, 2015). Although the findings for *B. fasciculatus* contradict our initial hypothesis, the high congruence of the observed parental effect with theoretical predictions in one species suggests that parental effects on dormancy do occur in Mediterranean winter annuals, but that there are also alternative strategies to face environmental uncertainty. This is consistent with observations from the Sonoran Desert that annual dryland species can strongly differ in seed dormancy and variation in fitness (e.g. differ in bet-hedging) (Venable, 2007). A potential alternative strategy to bet-hedging is ‘predictive germination’, in which all of the environmental information directly available to a seed is used to time germination events (Cohen, 1967; Gremer *et al.*, 2016). After all, germination under field conditions depends on many environmental factors (Saatkamp *et al.*, 2014) and is not directly comparable to germination under controlled conditions. Furthermore, in our system, grasses are usually better competitors (Segre *et al.*, 2014) and possess higher and more constant survival rates across years (Metz *et al.*, 2010), which suggests that another alternative strategy could be to rely on adult survival in years when resource availability is low.

Clinal population differentiation in parental effects on seed dormancy

In *B. didyma*, seed dormancy increased with the aridity at the site of origin, corroborating earlier studies on clinal variation in seed dormancy along aridity gradients (Hacker, 1984; Hacker &

Table 4 Parameter and variance estimates from GLMMs with Poisson error distribution (log link) testing effect of total precipitation (prec.) of the parental season (PPS) and offspring season (POS) on annual plant seedling density over 10 seasons (2002–2011)

Fixed effects

Site	Effect	Estimate	χ^2	*P*-value
Mesic Mediterranean	**PPS**	**0.23**	**9.66**	**0.002**
	POS	−0.11	1.76	0.184
	Interaction PPS × POS	0.07	0.40	0.526
Mediterranean	**PPS**	**0.28**	**16.22**	**< 0.001**
	POS	0.17	2.82	0.093
	Interaction PPS × POS	−0.14	2.95	0.086
Semi-Arid	**PPS**	**0.37**	**11.74**	**< 0.001**
	POS	**0.63**	**19.98**	**< 0.001**
	Interaction PPS × POS	−0.21	2.44	0.118
Arid	**PPS**	**0.62**	**42.43**	**< 0.001**
	POS	**0.34**	**12.08**	**< 0.001**
	Interaction PPS × POS	−0.06	0.08	0.779

Random effects

Site	Effect	Variance
Mesic Mediterranean	Microhabitat	0.47
	Individual-level random effect	0.06
Mediterranean	Microhabitat	0.42
	Individual-level random effect	0.05
Semi-Arid	Microhabitat	0.08
	Individual-level random effect	0.14
Arid	Microhabitat	0.24

Random effects included two microhabitats (open or under shrub canopy) per site and an individual-level effect to correct for overdispersion when indicated. In the model including all sites, PPS × site and POS × site interactions were significant ($\chi^2 = 18.6$, df = 3, $P < 0.001$; $\chi^2 = 44.3$, df = 3, $P < 0.001$). Significant terms are highlighted in bold.

Table 5 ANOVA table of marginal effects of average seedling density, site and microhabitat (shrub, open) on the average biomass produced per seedling across seasons

Effect	*F*-value	df	*P*-value
Seedling density	**6.20**	**1**	**0.017**
Site	**3.15**	**3**	**0.034**
Microhabitat	1.27	1	0.266
Seedling density × site	0.74	3	0.531
Seedling density × microhabitat	**4.48**	**1**	**0.040**
Site × microhabitat	0.66	3	0.578
Seedling density × microhabitat × site	1.90	3	0.142

Variance function

Site	Variance coefficient (*C*)
Mesic Mediterranean	1.00
Mediterranean	0.97
Semi-Arid	1.32
Arid	2.89

The variance was estimated for each site independently using the varIdent function of the R package NLME (Pinheiro *et al.*, 2016). Significant terms are highlighted in bold.

Table 6 Type III sum of squares table for the effect of seedling density and site-standardized offspring season precipitation (POS) on biomass at the end of the season based on restricted maximum-likelihood estimates

Fixed effects

Effect	χ^2	df	*P*-value
Seedling density	**30.20**	**1**	**< 0.001**
Site	**17.06**	**3**	**< 0.001**
Seasonal rain (POS)	0.31	1	0.579
Seedling density × site	3.91	3	0.423
Seedling density × POS	7.59	1	0.573
Site × seasonal rain	**13.70**	**3**	**0.003**
Seedling density × POS × site	0.92	3	0.819

Random effects

Effect	Variance
Year	0.04
Site (in year)	0.04
Plot (in site in year)	0.03
Quadrat (in plot in site in year)	0.02

Variance function

Variance covariate	Variance coefficient (*C*)
Seedling density	−0.44
POS	−0.09

The variance was modelled with power functions for seedling density and POS of the form $f(v) = |v|^{(2 \times C)}$ (v, variance; C, variance function coefficient). Significant terms are highlighted in bold.

Ratcliff, 1989; Volis *et al.*, 2002; Kronholm *et al.*, 2012; Tielbörger *et al.*, 2012; Wagmann *et al.*, 2012). More intriguingly, this was the result of an origin × parental irrigation interaction, suggesting that the relative strength of the parental effect increased in a clinal fashion. To the best of our knowledge, this is the first evidence of clinal population divergence in a *parental environmental effect.* Natural variation in a parental effect on germination has also been observed in *Arabidopsis thaliana* (Penfield & Springthorpe, 2012), but the patterns of differentiation and selective factors were not investigated in that study. Clinal variation also has been observed previously in the *within-generation plasticity* of germination to ambient temperatures along a temperature gradient (Simons, 2014), but this requires predictability only at the developmental and not at the generational timescale (Leimar & McNamara, 2015; Tufto, 2015). We furthermore observed that the continuous reaction norms of the parental effect became increasingly nonlinear in more arid environments. One reason for nonlinear reaction norms are constraints by physiological limits (Chevin *et al.*, 2010), which is an unlikely explanation in our experiment as *B. didyma* seeds were never 0 or 100% dormant. More likely, the steepest slope of the reaction norm in each population coincided with the range of environmental parameter values commonly encountered in nature, as was observed for abdominal pigmentation that regulates thermal balance in *Drosophila melanogaster* (David *et al.*, 1990). Similarly, there was a close match between irrigation levels that caused the greatest changes in offspring phenotype (i.e. steepest slope) and the seasonal rain values commonly encountered in the field sites.

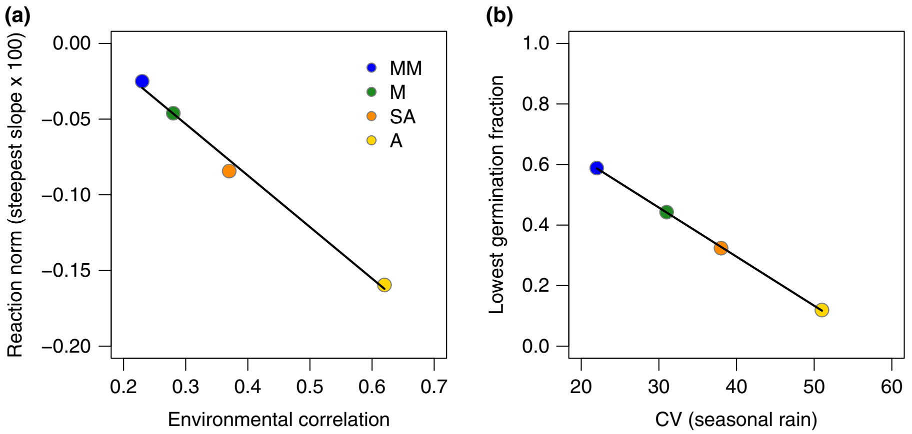

Fig. 6 Clinal population differentiation in *Biscutella didyma* predicted by among-site variation in environmental variables. (a) The environmental correlation (PPS in Table 4) was regressed against the steepest slope of the reaction norm curve (see Fig. 4) for each population ($b = -0.34$, $t = -16.1$, $P = 0.004$, $R^2 = 0.98$). This indicates that the strength of environmental correlations between generations can predict the strength of the parental effect that evolved in a population. (b) The coefficient of variation of seasonal rain (see Table 1) was regressed against the lowest germination fraction (see Fig. 4) of each population ($b = -0.016$, $t = -94.28$, $P < 0.001$, $R^2 = 0.99$). This indicates that the unpredictability of resources can predict the ability of a population to use bet-hedging via seed banking. Point colour indicates the site of origin: MM, Mesic Mediterranean; M, Mediterranean; SA, Semi-Arid; A, Arid.

This is an additional indication that clinal divergence in the parental effect on seed dormancy may have emerged from natural selection at the sites. In contrast to alternative causes of population divergence, natural selection increases the match between the average population phenotype and its environment.

Parental precipitation is correlated with offspring seedling density, which negatively effects plant fitness

We did not observe autocorrelations in seasonal precipitation at any of our study sites and therefore parental rainfall did not provide any reliable cues for offspring rainfall conditions. Instead, a potential explanation for the existence of as well as the cline in parental effects stems from the observation that parental precipitation was positively correlated with seedling densities in the following season at all sites. This correlation became markedly stronger towards arid sites, providing a more reliable prediction of offspring competition intensity in drier environments. This is interesting because high predictive ability of the parental cue (e.g. parental rainfall) is one of the factors favouring adaptation via parental effects (Leimar & McNamara, 2015). The other important factor is a good match between new offspring phenotype and offspring environment (Burgess & Marshall, 2014). Indeed, at three sites, plants had higher approximated fitness in low-density seasons than in high-density seasons, indicating that the probability of successful reproduction was reduced in the latter. The only exception was at site A, but this was most likely due to limited data and not to the absence of competition. This is supported by our observation that at all four sites, negative density effects were observed across permanent quadrats during most seasons. These results from community data confirm earlier observations for both study species. Namely, neighbour removal in the field had a positive effect on seed and biomass production (Schiffers & Tielbörger, 2006; Liancourt & Tielbörger, 2009). This means that the observed environmental correlation among generations indeed partly predicted the expected fitness in the offspring season. Correspondingly, we found that the strength of this correlation accurately predicted the strength of the parental effect in a population. In turn, the ability of a population to exhibit bet-hedging via seed banking was predicted by site differences in the predictability of seasonal rain. Taken together, our results corroborate model predictions that higher competition among seedlings after years with high resource availability selects for parental effects on bet-hedging behaviour (Tielbörger & Valleriani, 2005) and that environmental unpredictability selects for stronger bet-hedging via seed banking. Parental effects were mostly expected to evolve in response to correlations between parental and offspring environment in the *same* environmental factor (i.e. autocorrelations; but see Burgess & Marshall, 2014). In our case, however, the correlation between *abiotic* conditions in the parental environment and *biotic* conditions in the offspring habitat are likely to have promoted the parental effect on seed dormancy (Tielbörger & Valleriani, 2005).

Limitations of our study

We chose a detailed study on the parental effect along a steep gradient using few populations. Future studies on clines in parental effects should include more populations, species and, ideally, independent environmental gradients. This would help disentangle selection-neutral and non-neutral variation among populations along geographical trajectories, where distance and environmental changes covary (Mitchell-Olds & Schmitt, 2006; Lotterhos & Whitlock, 2015). Also, as a correlative study, our experiment does not fulfil the requirements of formal tests of local adaptation, although our findings are consistent with evolutionary model predictions and therefore are likely to represent an adaptive strategy. Further, our experimental set-up did not allow for testing seed viability in each individual case and, therefore, the dormant fraction may include dead seeds. However, because we removed treatments with reduced viability, we are confident that our results are not biased by seed viability differences among treatments or populations. Finally, the parental effect was detected in only one of our two species, thus providing only partial support for what we suggested was a general phenomenon.

Conclusions

In this study, we provide the first evidence for clinal variation in a parental effect. Our results for one of the species indicate that clinal variation in the effect of parental water availability on seed dormancy may demonstrate a bet-hedging strategy along a steep aridity gradient in Israel, which can be explained by theoretical models on the evolution of seed dormancy. Our results further confirm the assumption that parental precipitation can predict competition intensity in offspring. However, the lack of parental effect in the second species also indicates that alternative strategies exist to cope with environmental uncertainty, independent of parental water availability. In the future, studies should include more populations and species, additional aridity gradients, and assess within-population variations of the reaction norms.

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Author contributions

C.L. and K.T. conceived and designed the study; C.L. conducted the experiment; J.M. generated density and biomass data; C.L. did the statistical analysis and artwork; and C.L., J.M. and K.T. wrote the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Distribution of precipitation across years and months.

Fig. S2 Smoothing functions of the main effects seed weight and parental irrigation.

Fig. S3 Smoothing functions displaying the population specific deviation from the main effect parental irrigation.