

# Evaluating grazing response strategies in winter annuals: A multi-trait approach

Susanne Kurze<sup>1</sup>  | Mark C. Bilton<sup>2,3</sup>  | Leonor Álvarez-Cansino<sup>1</sup>  | Sara Bangerter<sup>4</sup> |  
Rüdiger Prasse<sup>4</sup> | Katja Tielbörger<sup>3</sup> | Bettina M. J. Engelbrecht<sup>1,5</sup> 

<sup>1</sup>Functional and Tropical Plant Ecology, Bayreuth Centre of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany

<sup>2</sup>Department of Agriculture and Natural Resources Sciences, Namibia University of Science and Technology (NUST), Windhoek, Namibia

<sup>3</sup>Plant Ecology Group, Institute of Evolution and Ecology, University of Tübingen, Tübingen, Germany

<sup>4</sup>Institute of Environmental Planning, Leibniz University Hannover, Hannover, Germany

<sup>5</sup>Smithsonian Tropical Research Institute, Balboa, Ancón, Panama

## Correspondence

Susanne Kurze  
Email: [Susanne.Kurze@uni-bayreuth.de](mailto:Susanne.Kurze@uni-bayreuth.de)

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## Abstract

1. Plants minimize fitness losses through grazing by three fundamental strategies: tolerance, avoidance and escape. Annual species have been traditionally assumed to escape grazing through their short life cycle and seed dormancy; however, their grazing response strategies remain almost unexplored. How traits and their coordination affect species' grazing responses, and whether the generalized grazing model, which posits convergent filtering by grazing and drought, is applicable to this ecologically and economically important species group thus remain unclear.
2. We used a trait-based approach to evaluate grazing response strategies of winter annuals from the Middle East. Across 23 species, we examined the coordination of 16 traits hypothesized to be relevant for grazing responses, and linked them to species' fecundity responses, as proxy for fitness responses, to simulated grazing in controlled conditions, to species' abundance responses to grazing in the field and to species' distribution along a large-scale rainfall gradient.
3. Winter annuals exhibited both grazing escape and to a lesser extent tolerance indicated by (a) independent coordination of escape and tolerance traits, and (b) maintenance of higher fecundity in species with more pronounced escape or tolerance traits under simulated grazing. In the natural habitat, species with a more pronounced escape but not tolerance strategy maintained higher abundance under grazing in dry habitats, indicating convergent favouring of escape by both grazing and drought. However, this finding at the local scale was not mirrored by a strategy shift along a large-scale rainfall gradient.
4. *Synthesis.* The convergent favouring of escape traits by grazing and drought in annuals is consistent with the generalized grazing model. This model, which has been developed for perennials based on the avoidance strategy, can thus be extended to annuals based on escape, a finding that should facilitate projecting consequences of global change in drylands dominated by annuals.

## KEYWORDS

annual species, ecological filtering, escape, plant–herbivore interaction, rainfall gradient, semi-arid rangelands, tolerance, trait coordination

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## 1 | INTRODUCTION

Grazing by ungulates influences plant performance, species' abundance and distribution, as well as community composition (Díaz et al., 2007; Milchunas et al., 1988). Species vary in their grazing responses, ranging from fitness losses to overcompensation (Agrawal, 2000). The traits and strategies, underlying these interspecific differences, and how they affect ecological filtering along environmental gradients have been mainly investigated in perennial species (e.g. Adler et al., 2004; Quiroga et al., 2010). However, in annual species, which exhibit a different life history and outlast unfavourable conditions as seeds (Levitt, 1980), grazing response strategies remain poorly understood despite the major ecological and economic relevance of annual grasses and forbs in semi-arid rangelands (Noy-Meir, 1973; Ruppert et al., 2015; Sternberg et al., 2015). Under global change, ecosystem services of annual-dominated systems are expected to deteriorate through intensification of land use and decreasing water availability (Maestre et al., 2016; Sala et al., 2000). Elucidating annuals' grazing response strategies and their ecological filtering is thus of increasing significance. It closes a conceptual gap of understanding strategies in species with different life histories (annuals vs. perennials), as well as provides crucial information for projecting and mitigating consequences of global change.

Grazing resistance in plants, that is, the ability to minimize fitness losses under grazing, can be mediated by three fundamental strategies, namely tolerance, avoidance and escape (Agrawal, 2000; Coley et al., 1985). Plant strategies (or syndromes) are characterized by suites of coordinated (i.e. correlated) traits (Reich et al., 2003), which together influence performance responses (i.e. growth, survival, reproduction, fitness) or abundance responses to different environmental conditions (Shipley et al., 2016). Different strategies form a continuum and are not mutually exclusive, but functional linkages or trade-offs in the underlying traits as well as coordinated selection pressures favour some trait combinations and preclude others (Levitt, 1980).

*Grazing tolerators* are characterized by a high ability to compensate tissue loss through regrowth. A high compensation ability can result from high photosynthetic rates of leaves with high nitrogen contents (low C:N ratio) and high specific leaf area but also from high biomass allocation to roots for carbon storage (Poorter et al., 2009; Strauss & Agrawal, 1999). *Grazing avoiders* reduce the accessibility of the plant tissue for herbivores. Morphological avoidance traits are a low stature, small leaf area and tough leaves with high leaf dry matter content (or low specific leaf area; Díaz et al., 2001, 2007; Hanley et al., 2007; Poorter et al., 2009). Chemical defences, such as high C:N ratios or secondary compounds, can also decrease herbivory (Herms & Mattson, 1992). *Escapers* exhibit a short life cycle, which increases the probability of reproduction before grazing or other adverse conditions, such as drought, occur (Kooyers, 2015). The strategy encompasses an early start of reproduction, small plant size and high biomass allocation to reproduction as well as traits that confer high growth and photosynthetic rates, such as nitrogen-rich leaves with a high specific leaf area and a high biomass allocation to leaves rather than to roots or carbon storage (Grime, 1977; Kooyers, 2015).

Seed dormancy, which spreads germination between years, buffers escapers against reproductive failure and acts as a bet-hedging mechanism (Philippi & Seger, 1989; Tielbörger et al., 2012).

Grazing tolerance or avoidance has been shown in perennials, with each strategy favoured under different environmental conditions (Adler et al., 2004; Díaz et al., 2001; Quiroga et al., 2010). Grazing-tolerant species have been hypothesized to dominate in resource-rich habitats, because this strategy requires high resource consumption but also allows for high growth and high competitive effect (Briske, 1996; Coley et al., 1985; Herms & Mattson, 1992). Conversely, in resource-poor habitats tissue replacement is costly, favouring species with grazing avoidance (Coley et al., 1985; Herms & Mattson, 1992). Grazing response strategies should therefore shift from tolerance to avoidance with decreasing resource availability. This shift should be especially pronounced along rainfall gradients, because several trait attributes concomitantly confer avoidance of grazing and desiccation (e.g. small stature and small, tough leaves; Milchunas et al., 1988). Ecological filtering under grazing and drought should thus be convergent (generalized grazing model; Milchunas et al., 1988). Accordingly, both communities under arid conditions and grazed communities should be highly resistant to increasing drought or grazing under global change, since their dominant species avoid both grazing and desiccation (Milchunas et al., 1988; Quiroga et al., 2010). The expected interspecific shift from grazing tolerance to avoidance with decreasing rainfall has been shown in several perennial-dominated communities (Adler et al., 2004; Díaz et al., 2007; Quiroga et al., 2010).

Annuals, in contrast to perennials, are traditionally assumed not to withstand unfavourable environmental conditions, such as grazing or drought, in the vegetative and reproductive stage, but endure them as dormant seeds forming a seed bank (Grime, 1977; Levitt, 1980). They are thus commonly considered to exhibit an escape strategy (Kooyers, 2015; Levitt, 1980). However, pooling annuals in a single homogeneous functional strategy might be too simple. The high diversity and abundance of annual species in an enormous range of environmental conditions (e.g. Guo et al., 2002; Tielbörger et al., 2014) suggest that they exhibit a wide variation of trait attributes (see Li & Shipley, 2017). Additionally, annuals are an important source of forage (Noy-Meir, 1973; Sternberg et al., 2015), indicating that they are exposed to grazing by livestock in their vegetative and reproductive phase, and do not (only) escape, but also tolerate it.

Winter annuals in Mediterranean and subtropical desert climates grow and reproduce in the rainy, mild season (winter) and survive the dry and hot season (summer) as seeds, that is, they restrict growth and reproduction to the favourable period and evade (=escape) the unfavourable dry season. Additionally, they buffer unpredictable catastrophic events by between-year seed dormancy (Tielbörger et al., 2012). Due to this specific life history, rainfall patterns should act as strong ecological filter, favouring annual species with a more pronounced escape strategy (faster life cycle and associated traits, including between-year seed dormancy) in areas with a longer dry season and less predictable rainfall (arid areas). Intraspecific studies on annuals indeed show an increasing expression of escape traits towards arid conditions (Aronson

et al., 1993; Kurze et al., 2017; Tielbörger et al., 2012). However, across species, it has not yet been evaluated whether ecological filtering favours species with a more pronounced escape strategy towards arid areas. How drought and grazing interact and modulate interspecific changes of grazing response strategies (and underlying traits) along moisture gradients in annuals, and whether the generalized grazing model is applicable to this species group thus remain unclear.

We suggest that there may be two possible scenarios. In the first scenario, a short life cycle associated with drought escape also minimizes the probability of tissue loss through grazing before reproduction. In this scenario, grazing and drought act as convergent ecological filters in annuals, similar to perennials (see above), but favour the escape instead of the avoidance strategy towards arid conditions. In the following, we refer to this as the convergence scenario. It might be most likely under grazing regimes where early reproduction allows to successfully escape grazers.

In the second scenario, a pronounced drought escape strategy is traded-off with grazing avoidance or tolerance. Species with a pronounced drought escape strategy should be vulnerable to grazing in the vegetative or reproductive phase (i.e. if escape is not successful), since several escape traits, including high growth rate, low biomass allocation to roots and low carbon storage, are incompatible with grazing avoidance or tolerance. In this scenario, grazing and drought thus do not act as convergent ecological filters in winter annuals under arid conditions, but the long dry season and unpredictability favour escape, while grazing favours avoidance under low resource availability, as in perennials (see above). However, unlike in perennials, grazing avoidance does not concurrently lead to increased drought avoidance in annuals. Instead, the slow-growth traits associated with grazing avoidance should increase the probability to be negatively affected by drought before reproduction under unpredictable, arid conditions (see Carvajal et al., 2019 for shrubs), and thus decrease drought resistance in annuals. In the following, we refer to this as the trade-off scenario. This scenario is consistent with the few relevant data from annual-dominated communities, which indicate lower (rather than higher) grazing resistance of annual plant communities in arid areas (Osem et al., 2002; M. C. Bilton, P. Liancourt, S. Bangerter, R. Prasse, & K. Tielbörger, unpubl. data). It might be most likely when high grazing intensity precludes successful escape of grazers.

In both scenarios, annuals with a grazing tolerance strategy should be favoured in moister conditions, since this strategy should confer annuals a high competitive effect in more dense vegetation (Liancourt & Tielbörger, 2009).

The two scenarios have different implications for the vulnerability of annual-dominated communities to global change. In the convergence scenario, annuals favoured under drought or grazing should be pre-adapted to an increasing intensity of both factors, as perennials (see above). In the trade-off scenario, annuals are either adapted to drought (escapers) or grazing (avoiders or tolerators), but not both. Species should thus be more vulnerable to the respective other factor.

Here, we examine grazing response strategies in winter annuals from the Middle East. This region is ideal for our study, since winter

annuals comprise the majority of plant species, the long grazing history by domesticated ungulates spans more than 10,000 years, and the area exhibits pronounced large-scale rainfall gradients for assessing species' ecological filtering (Noy-Meir & Seligman, 1979; Tielbörger et al., 2014). We used a trait-based approach to identify the grazing response strategies. Across 23 annuals, a comprehensive set of 16 traits hypothesized to be associated with the three grazing response strategies (escape, avoidance and tolerance) was measured under common, controlled conditions. We tested the following hypotheses:

1. Traits relevant for grazing responses are coordinated along three major axes in annual species, reflecting the three grazing response strategies: escape, tolerance and avoidance.

Species' positions along the trait axes, that is, the strength of their trait-based escape, tolerance and avoidance strategy, explain interspecific differences in fitness responses and abundance responses to grazing, and are related to their distribution across rainfall gradients. Specifically:

2. Under simulated grazing, species with more pronounced trait-based grazing tolerance show lower fitness losses.
3. In the field, either (a) species with more pronounced escape (convergence scenario) or (b) species with more pronounced avoidance (trade-off scenario) show lower abundance declines in response to grazing in drier habitats. In both scenarios, species with more pronounced tolerance exhibit lower abundance declines in moister habitats.
4. Along large-scale rainfall gradients, a strategy shift occurs: either grazing escape (convergence scenario) or grazing avoidance (trade-off scenario) is more pronounced in species associated with arid conditions, whereas grazing tolerance is more pronounced in species associated with moist conditions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

The Levant region in the Middle East comprises steep large-scale rainfall gradients, which allow us to test for species' ecological filtering. They range from north to south (across approx. 350 km) and from west to east (approx. 50 km) with higher and more predictable mean annual rainfall (MAR) in mesic-Mediterranean areas in the north (up to 800 mm/year  $\pm$  18%, mean  $\pm$  CV) and less, very unpredictable rainfall in the desert in the south (20 mm/year  $\pm$  55%) or towards the Dead Sea. The length of the rainfall season, which corresponds to the main growing season, as well as primary productivity and competition intensity decrease towards the arid end of the rainfall gradients (Liancourt & Tielbörger, 2009). The region is characterized by shrubs (desert to semi-arid) to small trees (Mediterranean), with winter annual species dominating the inter-shrub matrix.

A grazing enclosure experiment (see details below) was conducted in a semi-arid region in Jordan (MAR 200–400 mm/year) in Wadi Shuayb (32°01'10.34"N, 35°43'36.69"E).

## 2.2 | Study species and plant material

The study focussed on 23 winter annual species, including 15 forbs (four legumes) and eight grasses (Table S1). Species were selected based on (a) coverage of different distribution ranges along the large-scale rainfall gradients based on BioGIS (2018), (b) a large taxonomic range (i.e. seven plant families), (c) high abundance in the region and (d) seed availability. The species belonged to 20 genera, and all had the C3 photosynthesis pathway. Seeds for the experiments were collected in the mid-range of the rainfall gradient in two sites in Israel, approximately 40 km apart (Lahav MAR 300 mm/year and Matta MAR 540 mm/year, for details see Tielbörger et al., 2014). They were collected from a minimum of 50 maternal sibships per species within an area of 1.0–1.5 km<sup>2</sup> in April 2012.

Seeds were grown under common, favourable conditions in a greenhouse during winter 2013–2014 to obtain a F1 generation with minimized maternal effects. The F1 seeds were over-summered for two months to break summer dormancy (compare Tielbörger et al., 2012). For the trait measurements (except seed dormancy) and the grazing simulation experiment, we grew plants from the F1 seeds under common favourable conditions (i.e. high water and nutrients, without biotic interactions, see details below) in the greenhouse. This approach enabled us to comparatively assess trait differences and fecundity responses (as proxy for fitness responses) across species, and to minimize bias introduced by intraspecific variation due to maternal effects, phenotypic plasticity or ecotypic differentiation. Our comparative measurements of species' traits under favourable conditions should be relevant for the field, since species' trait rankings commonly hold under different environments (stable species hierarchy hypothesis; Kazakou et al., 2014).

## 2.3 | Plant cultivation in the greenhouse

Plants were germinated and grown in a greenhouse in cylindrical pots (1 L volume, 36 cm depth, Deepot Cells, Stuewe & Sons) with a 1:1 mixture of nutrient-poor sand and compost supplemented with 5 g of amorphous silicon (Aerosil 300, Evonik Industries AG). Temperature in the greenhouse was set to 20–23°C in winter and 20–26°C in spring, and daytime photosynthetic active radiation ranged between 150 and 800 μmol photons/(s m<sup>2</sup>). Day length was adjusted to the natural variation in Israel for unbiased phenology. Pots were randomly distributed in the greenhouse and rearranged every second week.

All individuals received ample water and nutrient supply to avoid any resource limitation. They were wrapped in light transparent fabric (organza) when they started to produce seeds to prevent seed

loss. Plants were grown until the end of their life cycle after seed ripening when leaves senesced (30–36 weeks after sowing).

## 2.4 | Trait measurements

Sixteen morphological, anatomical, physiological, and life-history traits that are hypothesized to be associated with the three grazing response strategies (i.e. escape, tolerance and avoidance, see Table 1) were measured on unclipped plants or on seeds under favourable conditions (see above). We measured 5–16 replicates per species and trait and followed standardized protocols for trait measurements where available (for details, see Table 1 and Method S1). Different sets of plants were measured for leaf traits, whole plant traits, seed dormancy and growth rate (for details, see Table 1). Compensation ability was calculated based on total biomass of clipped and control plants (see below and Method S1).

## 2.5 | Grazing simulation experiment in the greenhouse

To assess and compare species' fecundity responses (as proxy for fitness responses) to grazing and their ability to compensate tissue loss, we conducted a grazing simulation experiment under controlled conditions (see above). In this experiment, plants were either clipped or served as controls. Each treatment comprised 10–16 individuals per species. We clipped plants once 15 weeks after sowing, which corresponds to peak grazing season in the field. Singular grazing events (rather than chronic grazing) are the typical grazing regime in our study system. At clipping, several species had started flowering, but none had ripe fruits or started senescence (i.e. escaped the simulated grazing). All species were thus potentially able to re-grow, but differed in their current investment in reproduction.

We clipped with scissors and removed about 75% of the above-ground biomass in all species based on visual estimation and previous species-specific assessments of above-ground biomass. Within each species, all individuals were clipped to the same size to ensure that they had similar resources for regrowth. Clipping encompassed mainly distal leaves and stems but also the removal of any already existing reproductive biomass (only in *Filago palaestina* some reproductive biomass remained). Our approach ensured a similar loss of relative biomass in all species independent of size or growth form, and thus allowed us to compare fecundity responses and compensation abilities across species without risking plant death. It did not aim to mimic selective grazing by ungulates in the field.

We harvested plants in random order when most species started to show senescence. Both clipped and unclipped individuals had enough time to go through their life cycle (i.e. within species, the number of individuals that produced ripe seeds did not differ between clipped and unclipped plants). Fecundity responses were assessed based on the weight of all seeds per individual (total seed

**TABLE 1** Traits hypothesized to influence grazing responses considered in this study, their expected association with the three grazing response strategies, escape, tolerance and avoidance, their abbreviation, unit, and the number of measured individuals (replicates) in each species (N). + or – indicate whether a high or low trait value is expected to be associated with higher grazing resistance in the respective strategy. The column 'Method' gives a brief overview of the definition of the traits, the measurement or the reference. Detailed information is provided in Method S1. Superscript letters at the trait name indicate plant sets for the trait measurements

Trait	Abbreviation	Unit	Escape	Tolerance	Avoidance	N	Method
Seed dormancy <sup>a</sup>	Dormancy	–	+			13–15 <sup>1</sup>	Proportion of ungerminated seeds in germination trials (Tielbörger et al., 2012)
Flowering time <sup>b</sup>	Flowering	day	–			8–11	Visual checking for first reproductive organs
Leaves at flowering <sup>b</sup>	Leaves flower	count	–			8–11	Count of leaf number at onset of flowering
Leaf area <sup>c</sup>	LA	cm <sup>2</sup>			–	8–15	Area of individual leaf, Pérez-Harguindeguy et al. (2013)
Specific leaf area <sup>c</sup>	SLA	mm <sup>2</sup> /mg	+	+	–	8–15	Pérez-Harguindeguy et al. (2013)
Leaf dry matter content <sup>c</sup>	LDMC	mg/g	–	–	+	9–15	Pérez-Harguindeguy et al. (2013)
Leaf toughness <sup>c</sup>	Toughness	N/mm			+	7–15	Measured as force to punch, Pérez-Harguindeguy et al. (2013)
Photosynthetic rate <sup>d</sup>	A <sub>max</sub>	μmol/(m <sup>2</sup> s)	+	+		9–14	Pérez-Harguindeguy et al. (2013)
C:N ratio <sup>d</sup>	C:N	%/%	–	–	+	5–9	Pérez-Harguindeguy et al. (2013)
Height at seed set <sup>c</sup>	Height	cm	–		–	12–16	Distance between soil surface and highest point of the plant
Total biomass <sup>c</sup>	Tot. biomass	g	–			12–16	Above- and belowground biomass at the end of the life cycle
Leaf mass fraction <sup>c</sup>	Leaf MF	g/g	+		–	12–16	Leaf biomass per total plant biomass
Root mass fraction <sup>c</sup>	Root MF	g/g	–	+		12–16	Root biomass per total plant biomass
Reproductive mass fraction <sup>c</sup>	Rep. MF	g/g	+			10–16	Total seed weight per total plant biomass
Absolute growth rate <sup>e</sup>	AGR	g/day	+	+	–	6–9	Rate of total biomass increase in vegetative phase
Compensation ability <sup>f</sup>		unitless	–	+	–	1 <sup>2</sup>	Difference between total biomass of clipped and control plants

<sup>1</sup>13–15 Petri dishes each with 14–18 seeds for each species (*Plantago cretica* with 32 seeds).

<sup>2</sup>Compensation ability was based on clipped and control plants, 10–16 individuals each.

weight, TSW = seed number × individual seed mass), and compensation ability based on total biomass per individual (see Method S1).

We calculated fecundity response as the standardized difference between total seed weight of clipped and control plants in each species:

$$\text{Fecundity response} = \text{mean}(\log(\text{TSW}_{\text{clipped}} + 1)) - \text{mean}(\log(\text{TSW}_{\text{control}} + 1)).$$

This response parameter is equivalent to the widely used response ratio (Hedges et al., 1999;  $RR = \log(a/b) = \log(a) - \log(b)$ ), except we natural log-transformed TSW before calculating the mean for each treatment (clipped vs. control), since data were not normally distributed. One was added before log transformation due to zero values. As in response ratios, negative or positive values refer to a negative or positive species' fecundity response to clipping, respectively.

Fecundity responses based on the total seed weight that the individuals produced during their lifetime considered both the number of possible offspring (i.e. seed number) and the probability of plant

survival that is related to seed mass (Metz et al., 2010). We consider this a solid proxy for fitness responses.

## 2.6 | Grazing enclosure experiment in the field

The response of annuals to grazing in the field (Jordan) was assessed by comparing species' abundances in fenced plots to exclude sheep and goats with paired adjacent intensively grazed plots (plot size 1,200 m<sup>2</sup> each). Plot pairs (grazed and ungrazed) were installed on a south-facing and a north-facing slope (4 pairs on each slope) in each of four sites located within 10 km (2 slopes × 4 plot pairs × 4 sites = 32 plot pairs; 64 plots, Figure S1). Each plot contained six randomly chosen permanent quadrats (20 × 20 cm), in which the abundance of each species (i.e. number of individuals) was determined at the peak of the vegetation development in each spring (for further details, see M. C. Bilton, P. Liancourt, S. Bangerter, R. Prasse, & K. Tielbörger, unpubl. data). The experiment ran from November 2005 until spring 2009. We

analysed the abundance responses to grazing in the 20 species that overlapped with the greenhouse experiment (see Table S1) for the years 2007–2009, when seed input already originated from manipulated (ungrazed vs. grazed) parental generations.

Opposite slopes differ in their environmental conditions with a more arid microclimate, lower soil moisture and lower standing biomass on south-facing slopes compared with more humid conditions on north-facing slopes, and corresponding differences in species composition (Kutiel, 1992; Kutiel & Lavee, 1999; M. C. Bilton, P. Liancourt, S. Bangerter, R. Prasse, & K. Tielbörger, unpubl. data). These exposure differences are independent of inter- and intra-annual rainfall variability and site characteristics, and thus represent consistent soil moisture differences. We thus consider south-facing slopes as dry habitats and north-facing slopes as moist habitats in the grazing enclosure experiment and quantified species' responses to grazing separately for each slope.

For each species, we calculated standardized abundance differences for each plot pair (grazed vs. ungrazed) in each year (response ratio; Hedges et al., 1999), and then averaged them across each slope:

$$\text{Abundance response} = \text{mean}(\log((\text{abundance}_{\text{grazed}} + 1)/(\text{abundance}_{\text{ungrazed}} + 1))).$$

Averaging species' abundance responses in each slope across sites and years focussed the analyses on the moisture difference between drier and moister slopes. Including site as additional factor turned out impossible because the low abundances of several species caused zero-inflation and heteroscedasticity. The low species' abundances also prevented us from analysing species' abundances across sites independently of the grazing effects.

## 2.7 | Species distribution across the large-scale rainfall gradient

Species' distribution along the large-scale rainfall gradients in the Levant region was characterized based on their occurrences (presence/absence data) in independent biological records in Israel (BioGIS, 2018). The BioGIS database provides the mean annual rainfall niche of each species (at 100 m resolution), which is modelled as the average of local mean annual rainfall across all occurrence sites of a respective species.

## 2.8 | Statistical analyses

The main aims of the statistical analyses were (a) to determine the main axes of variation of grazing-relevant traits in annuals, and (b) to evaluate whether species' positions along these axes are related to their grazing responses in different environments (controlled conditions or field), and to their distribution along the rainfall gradient.

We initially tested species differences in each of the 16 traits (natural log-transformed to improve normality and homoscedasticity, except seed dormancy and reproductive mass fraction) with *F*

tests on linear models. Pairwise trait correlations were assessed with Spearman rank correlation coefficients based on species' average trait values.

The coordination of the 16 traits was assessed with a principal component analysis. We identified those principal component axes (PCA axes), which reflected trait coordination consistent with the hypothesized grazing response strategies. Species' positions (i.e. scores) on these PCA axes were used to characterize how strongly a species exhibited the respective trait-based strategy. To ensure that larger values consistently correlate with (hypothesized) higher grazing resistance, species' scores were multiplied with  $-1$ , if necessary (in the following referred to as inverse axis).

The effect of simulated grazing on fecundity was tested with *F* tests on a linear model including total seed weight (natural log-transformed after adding 1) as response variable, and species, treatment (clipped vs. control) and interaction term as explanatory variables. The significance of fecundity differences between clipped and control plants within each species was assessed with separate *t* tests, and the significance level adjusted according to Holm–Bonferroni sequential correction (Gaetano, 2013).

We tested whether species differ in their abundance responses to grazing in each slope (dry vs. moist slope) with separate linear mixed models (package `lme4`, Bates et al., 2014). These linear mixed models included species as fixed explanatory variable, and site and year as random factors (see details in Method S2).

We assessed whether species' fecundity responses to simulated grazing or their abundance responses to grazing in the field were determined by their scores along the PCA axes (i.e. the strength of their trait-based strategy) with *F* tests on separate linear models. Each linear model contained species' scores on one PCA axis as explanatory variable and either their fecundity responses or their abundance responses in one of the slopes as response variable. To improve normality, abundance responses in each slope were natural log-transformed (after adding the lowest value to attain positive values) in the linear models with species' scores along PCA axis 1 as explanatory variable. We similarly tested whether species' mean annual rainfall niches are related to their scores along the PCA axes or their fecundity responses with *F* tests on separate linear models. Each linear model contained species' scores on one PCA axis or species' fecundity responses as explanatory variable. We also considered species' minimum and maximum rainfall niche (BioGIS, 2018), but results did not change qualitatively (Figure S4). In all linear models, described above, heterogeneous species' distribution along PCA axis 3 could not be resolved by transformation.

We calculated pairwise correlations of individual traits with species' fecundity responses to simulated grazing, abundance responses to grazing in each slope and mean annual rainfall niche using Spearman rank correlation coefficients. The importance of single traits for species' abundance responses to grazing in each slope was additionally assessed with a random forest algorithm (see Method S3). This algorithm accounts for nonlinear relations or interactions among traits (Breiman, 2001). Variables with an importance value greater than the largest negative value (corresponding to the

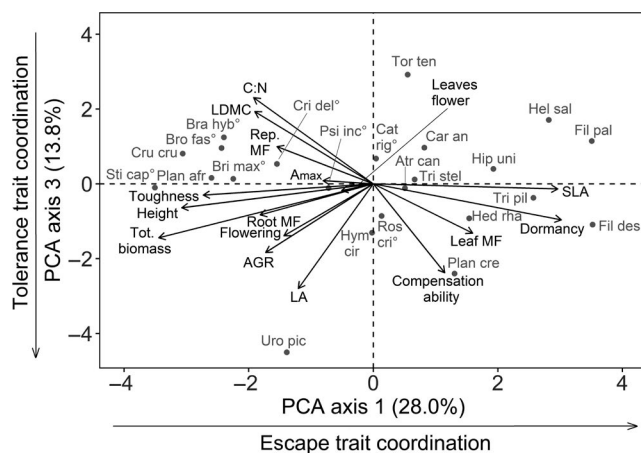
maximum random noise in the dataset) were considered important (alike significant, see Holmes et al., 2015).

All analyses were conducted with R 3.3.3 (R Core Team, 2017).

### 3 | RESULTS

All species re-grew and reproduced after simulated grazing. All 16 traits hypothesized to be associated with the grazing response strategies (Table 1) varied across the 23 species (all  $p < 0.001$ , 2- to 150-fold variation of trait values, Table S2). Pairwise correlations between single traits were predominantly weak (Table S3).

Trait coordination associated with PCA axis 1 (explaining 28% of variation, in the following referred to as axis 1) and PCA axis 3 (14%, axis 3) corresponded to two of the hypothesized grazing response strategies, namely the escape (axis 1) and tolerance strategy (axis 3), and formed independent axes (Figure 1; Table 2). Species with a positive score on axis 1 were characterized by high seed dormancy, early flowering, small height, low total biomass, low root mass fraction, high leaf mass fraction, high specific leaf area and low toughness (Figure 1; Table 2). These traits are consistent with the hypothesized escape strategy (Table 1). Unexpectedly, axis 1 was also associated with low (rather than high) growth rate and to a lesser extent with high (rather than low) compensation ability (Figure 1; Table 2). Species with a negative score on axis 3 exhibited high compensation ability, high root mass fraction, high growth rate, late flowering and large, nitrogen-rich leaves (low C:N ratio) with low leaf dry matter content (Figure 1; Table 2). These traits refer to the hypothesized grazing tolerance strategy (Table 1). None of the PCA axes reflected the expected grazing avoidance strategy. Instead, the avoidance traits (small, tough leaves with high leaf dry matter content, small height) were differently associated with several PCA axes (Figure 1;



**FIGURE 1** Coordination of 16 traits hypothesized to influence grazing responses (see Table 1) in 23 winter annual species (° indicates grasses). PCA axes 1 and 3 of a principal component analysis are shown, which summarized trait coordination corresponding to the hypothesized grazing escape and tolerance strategy (see Table 2 for trait loadings on PCA axes 1–4). See Tables 1 and S1 for trait and species abbreviations, respectively

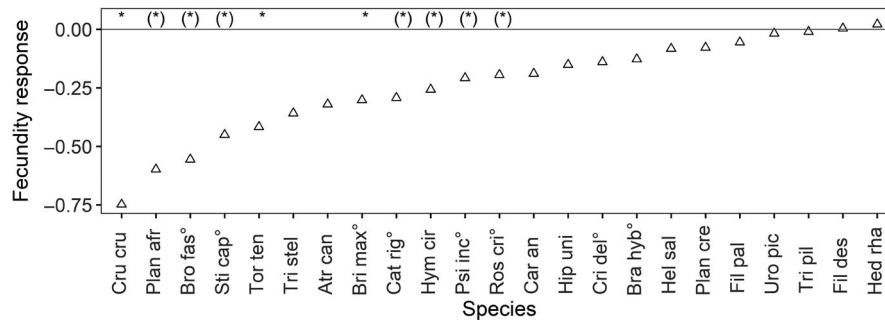
Table 2). PCA axis 2 (explaining 20% of variation) and PCA axis 4 (11%) did not reflect any hypothesized grazing response strategy (Table 2).

Simulated grazing decreased fecundity (i.e. the total weight of produced seeds per individual) in all species (no overcompensation occurred). On average, fecundity was reduced by 30% in clipped compared to control plants (Figure 2, linear model statistics: treatment  $F_{1,615} = 66.74$ ,  $p \leq 0.001$ ). The fecundity responses significantly differed across species (Figure 2, linear model statistics: species  $F_{22,615} = 93.45$ ,  $p \leq 0.001$ , interaction  $F_{22,615} = 2.03$ ,  $p = 0.003$ ,  $R^2 = 0.76$ ). Species' fecundity responses were positively related to their scores along the escape axis (axis 1) and to a lesser extent ( $p = 0.08$ ) to their scores along the tolerance axis (inverse axis 3, Figure 3; Table 3). Thus, species with pronounced escape or tolerance traits maintained higher fecundity under simulated grazing. Correlations of single traits with species' fecundity responses were overall weak ( $R < 0.6$ ), except for positive relations with compensation ability and specific leaf area (Table S3).

Grazing in the field decreased the abundance of most of the species in both dry and moist slopes with an average reduction of species abundance by 30% in grazed compared to ungrazed plots. Abundance responses varied significantly across species (Figure S2).

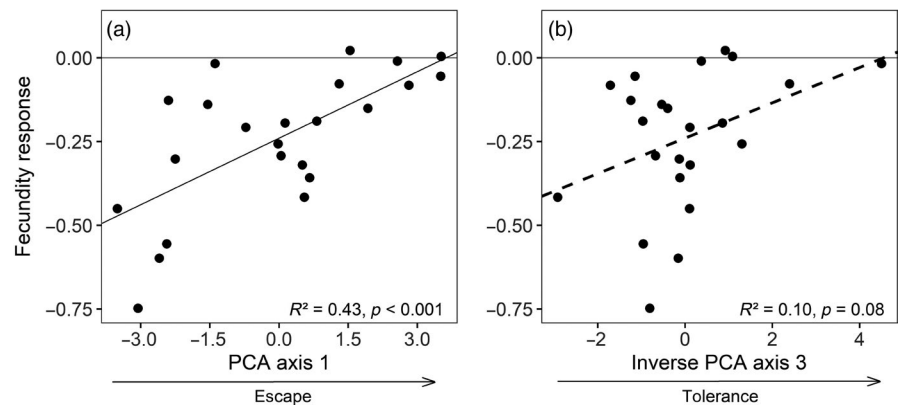
**TABLE 2** Loadings of the 16 traits hypothesized to influence grazing responses (see Table 1) on the first four axes of the principal component analysis with 23 annual species (see Figure 1). Traits were ordered according to their |loading| on PCA axis 1. Traits hypothesized to be associated with an escape strategy exhibit high loadings on PCA axis 1, whereas traits hypothesized to be associated with a tolerance strategy exhibit low (negative) loadings on PCA axis 3. Characteristic traits for both strategies (see Table 1) are highlighted in bold. PCA axes 2 and 4 did not reflect any hypothesized grazing response strategy

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	4.49	3.17	2.20	1.73
Explained variance [%]	28.0	19.8	13.8	10.8
Tot. biomass	<b>-0.41</b>	0.00	-0.24	0.01
Height	<b>-0.37</b>	-0.22	-0.11	0.11
Dormancy	<b>0.36</b>	0.00	-0.16	0.23
SLA	<b>0.35</b>	-0.13	-0.02	-0.07
Toughness	-0.32	0.23	-0.05	0.09
LDMC	-0.23	0.07	<b>0.33</b>	0.38
C:N	-0.23	-0.14	<b>0.39</b>	-0.37
Root MF	<b>-0.22</b>	0.15	-0.14	-0.49
Growth rate	-0.21	-0.30	<b>-0.31</b>	-0.03
Leaf MF	<b>0.19</b>	0.30	-0.22	-0.23
Rep. MF	-0.18	-0.28	0.17	0.28
Flowering	<b>-0.17</b>	0.46	-0.24	0.06
LA	-0.14	-0.26	-0.47	-0.04
Compensation ability	0.14	-0.13	<b>-0.40</b>	0.28
$A_{max}$	-0.10	0.37	0.01	0.43
Leaves flower	-0.06	0.37	-0.03	-0.08



**FIGURE 2** Fecundity responses to simulated grazing (clipping) of 23 winter annual species. Asterisks indicate significant differences between clipped and control plants within a species based on single *t* tests; \*remained significant after Holm–Bonferroni correction. Species' fecundity responses did not differ between grasses and forbs (Kruskal–Wallis test:  $\chi^2 = 1.4$ ,  $p = 0.25$ ; °indicates grasses). Species were ordered according to their fecundity response, see Table S1 for species abbreviations

**FIGURE 3** Relation between fecundity responses to simulated grazing and species' positions along the (a) escape axis (PCA axis 1) and (b) tolerance axis (inverse PCA axis 3). Significance ( $p$  value) and  $R^2$  values are given, see Table 3 for full statistical analyses



Species' abundance responses in dry slopes were positively related to their scores along the escape axis (axis 1), that is, species with pronounced escape traits exhibited lower abundance decreases in response to grazing (Figure 4; Table 3). In moist slopes, abundance responses were independent from species' scores along the escape (axis 1) or tolerance (inverse axis 3) axis (Figure 4; Table 3).

Different single traits were important (based on random forest) for the abundance responses to grazing in each slope (Figure S3). In dry slopes, reproductive mass fraction, height, total biomass, leaf dry matter content, toughness and specific leaf area were assessed as important (Figure S3). Several of these traits were consistent with the escape strategy identified along axis 1. In moist slopes, only C:N ratio emerged as important (Figure S3). Correlations between abundance responses and single traits were not significant, except of a weak one with toughness (Table S3).

Neither species' scores along the escape axis (axis 1), tolerance axis (inverse axis 3), nor any of the 16 single traits were related to species' mean annual rainfall niche (Figure 5; Table 3; Table S3; Figure S4). Consistently, species' fecundity responses to simulated grazing were independent from their mean annual rainfall niche (Figure 5; Table 3; Figure S4).

Species' scores along PCA axis 2 and PCA axis 4, which did not reflect the hypothesized grazing response strategies (see above), were unrelated with species' fecundity responses, abundance responses or mean annual rainfall niche (Table 3). Thus, there is no

indication that they represent previously unrecognized ecologically relevant strategies.

## 4 | DISCUSSION

Winter annuals exhibited two grazing response strategies, escape and to a lesser extent tolerance, reflected in lower fecundity declines of species with pronounced escape or tolerance traits under simulated grazing. In the field, only the escape but not the tolerance strategy was related with species' abundance responses. Lower abundance declines in species with pronounced escape traits in dry slopes indicate convergent small-scale favouring of escape traits by grazing and drought. However, grazing response strategies did not shift along large-scale rainfall gradients.

The identified escape strategy was overall consistent with the traits generally hypothesized to characterize annual species, including high seed dormancy, early flowering, small size (biomass and height), low root allocation and high specific leaf area (see Grime, 1977; Levitt, 1980). However, independently of the escape strategy, several annuals exhibited a trait coordination characteristic for the tolerance strategy known from perennials (see Strauss & Agrawal, 1999), that is, these annuals showed high compensation ability, high root allocation, high growth rate, low C:N ratio and low leaf dry matter content. As expected, some of these traits are



**TABLE 3** Results of linear models separately testing the effect of species' positions along the trait axes (escape: PCA axis 1; tolerance: inverse PCA axis 3) on their fecundity responses to simulated grazing, their abundance responses to grazing in the field in dry and in moist slopes (south- and north-facing slopes, respectively) or on their mean annual rainfall niche (i.e. species' distribution along the rainfall gradient); and testing the relation between species' fecundity response and mean annual rainfall niche. In the linear models with species' scores along PCA axis 1 as explanatory variable, abundance responses in both slopes were natural log-transformed. 23 annual species were considered in the grazing simulation experiment ( $F_{1,21}$ ) and 20 of these species were included in the grazing enclosure experiment ( $F_{1,18}$ ). Responses significantly related to one of the trait axes are highlighted in bold. Species' positions along PCA axes 2 and 4 were not related to fecundity responses, abundance responses or mean annual rainfall niche (all  $p > 0.18$ )

Trait	F	P	R <sup>2</sup>
PCA axis 1 (escape axis)			
<b>Fecundity response</b>	17.84	<0.001	0.43
<b>Abundance response dry slopes<sup>a</sup></b>	5.94	0.025	0.21
Abundance response moist slopes	0.00	0.998	-0.06
Mean annual rainfall niche	0.57	0.459	-0.02
Inverse PCA axis 3 (tolerance axis)			
<b>Fecundity response</b>	3.52	0.075	0.10
Abundance response dry slopes	0.70	0.413	-0.02
Abundance response moist slopes	1.75	0.202	0.04
Mean annual rainfall niche	0.19	0.664	-0.04
Fecundity response			
Mean annual rainfall niche	0.49	0.491	-0.02

<sup>a</sup>Relation remained marginally significant ( $F_{1,17} = 3.50$ ,  $p = 0.079$ ,  $R^2 = 0.12$ ) without species *Stipa capensis* (see Figure 4) with most negative abundance response.

consistent with both grazing tolerance and escape, but the high compensation ability combined with high root allocation and the lack of further characteristic escape traits (e.g. seed dormancy, early flowering, small size, see also Table 1) underline that this trait coordination reflects grazing tolerance. Interestingly, none of the trait coordination along any PCA axes were consistent with the expected avoidance strategy despite substantial interspecific differences in avoidance traits (e.g. low height, high leaf dry matter content and toughness). However, we did not consider chemical defence traits, which might contribute to an avoidance strategy in annuals (Herms & Mattson, 1992). Nevertheless, the two identified strategies of grazing tolerance and escape challenge the classical view that annuals form a single, homogeneous group of species escaping stress or disturbance (Grime, 1977; Kooyers, 2015).

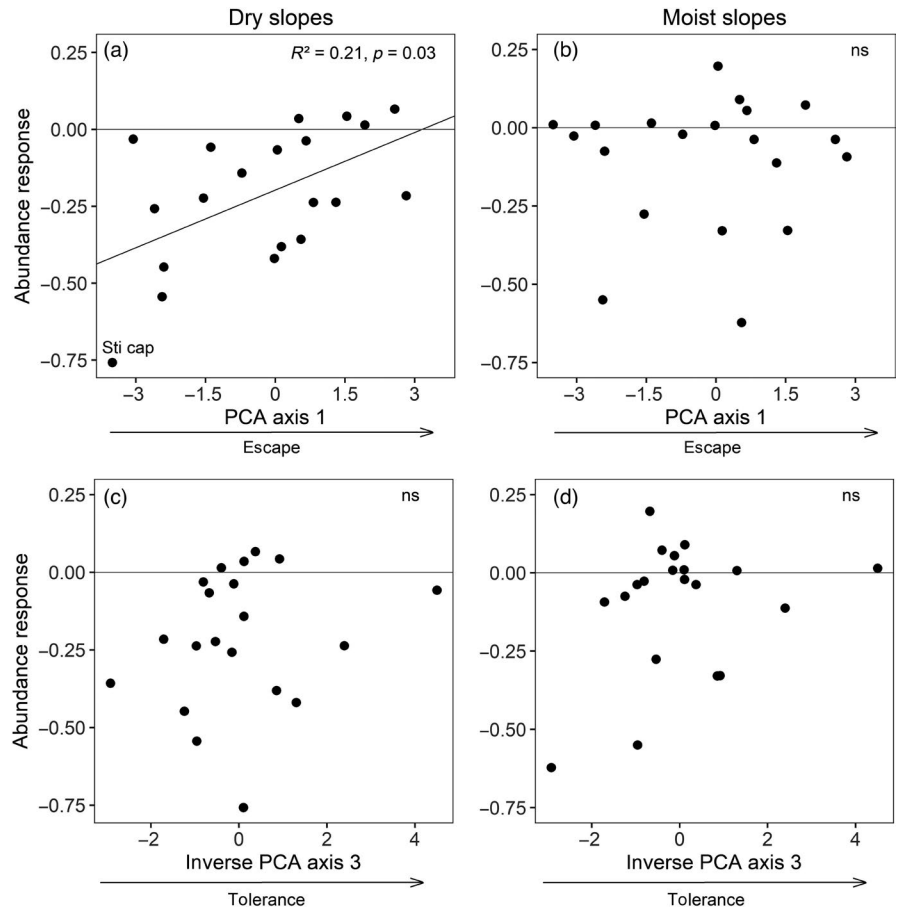
Grazing escape and tolerance emerged as independent axes of trait coordination and did not form the expected trade-off, that is, they were not associated with the opposite sides of one axis. This implies that both strategies are not mutually exclusive (see Levitt, 1980). Instead, species ranged along a continuum from less

to more pronounced escape and/or tolerance traits and can exhibit trait combinations pertaining to both strategies. Interestingly, both the tolerance and (to a lesser extent) the escape strategy encompassed high compensation ability, that is, even species with pronounced escape traits, re-grew and reproduced after simulated grazing in the greenhouse. The unexpectedly high compensation ability of escapers despite their low root allocation (indicative of low resource storage) may be due to their low growth rates, which decrease the resources necessary to compensate tissue losses compared to fast-growing species (Hilbert et al., 1981). The association between escape traits and high compensation ability undermined our assumption of the hypothesized trade-off scenario, that is, that species with a grazing escape strategy exhibit low compensation ability and thus experience high fitness losses when exposed to grazing.

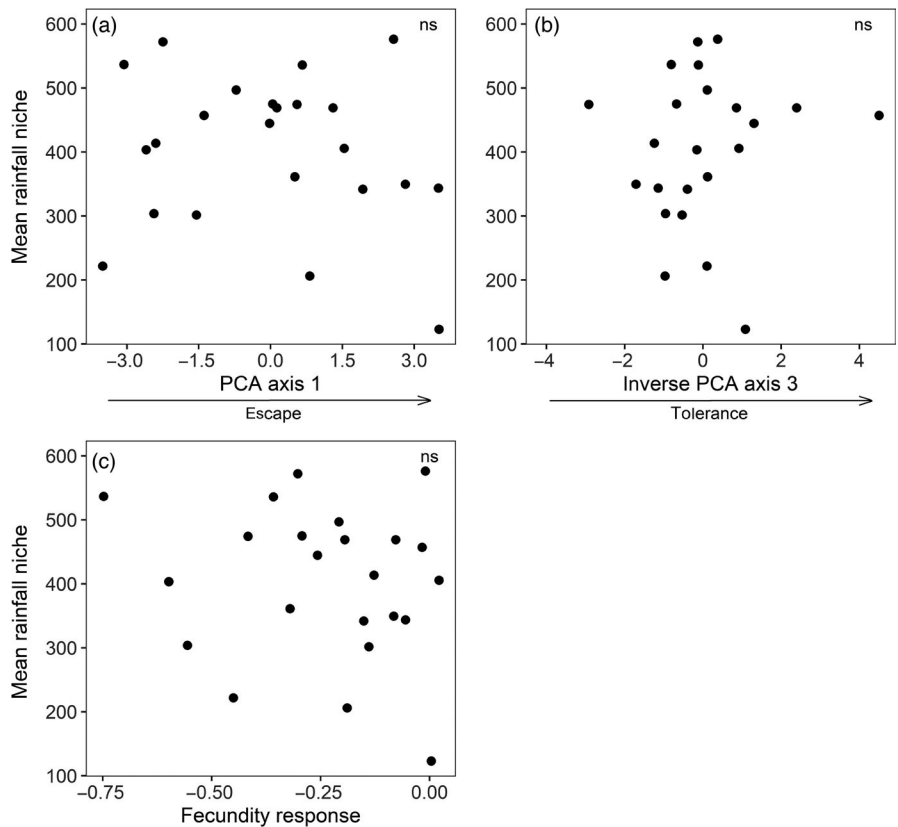
Both pronounced escape and (although less strongly) tolerance traits minimized negative fitness responses to tissue loss through grazing, as shown by the positive relationship between species' positions along both trait axes and their fecundity responses to simulated grazing. Surprisingly, escape traits emerged as the dominant fitness-relevant strategy even when escape per se was experimentally precluded (i.e. tissue was removed before successful reproduction). High compensation ability, which was associated with both strategies (see above), and also positively correlated with fecundity responses as a single trait, likely mediated this relation. The relationship between species' trait combinations along the escape and tolerance axis and their fecundity responses indicate that both trait coordination can influence fitness responses in annuals. Explicitly establishing this link is a prerequisite of trait-based ecology, since the direction and strength of interspecific trait-fitness response relations can vary across life-history strategies or biomes (Shiple et al., 2016). From an evolutionary point of view, it is clear that traits influence fitness differences of individuals within populations, but trait-based studies hardly addressed consequences of interspecific trait variation for differences in fitness responses across species (Shiple et al., 2016). Here, we closed this gap for trait combinations hypothesized to be mechanistically relevant for species' grazing responses in annuals. Working with annuals facilitated establishing this link, because it enabled us to assess fitness responses based on direct measurements of lifetime seed number and seed mass, a parameter hard to assess or even elusive in perennial species.

In the field, species' positions along the escape axis but not along the tolerance axis were related with their abundance responses to grazing. This finding indicates that traits can influence differences in species' abundance despite the multitude of factors and processes that influence species' regeneration and abundance in the field (e.g. microsite heterogeneity, biotic interactions, Boeken, 2018) and that may weaken trait-abundance relations. In dry slopes, species with pronounced escape traits exhibited lower abundance declines in response to grazing. This finding is consistent with the hypothesized convergence scenario that similar trait attributes enable both grazing and drought escape in annuals. Indeed, the grazing escape traits identified in our study (in combination with high reproductive

**FIGURE 4** Relation between species' abundance responses to grazing in an enclosure experiment in the field, and their positions along the escape axis (PCA axis 1) or tolerance axis (inverse PCA axis 3) (a, c) in dry (south-facing) slopes, and (b, d) moist (north-facing) slopes. Significance ( $p$  value or ns, not significant) and  $R^2$  values are given, see Table 3 for full statistical analyses. In (a) and (b), abundance responses were natural log-transformed for analyses, but not in the figure. In (a), the relation remained marginally significant without the extreme species, *Stipa capensis* (Sti cap; see Table 3)



**FIGURE 5** Relation between species' mean annual rainfall niche (i.e. species' distribution along the large-scale rainfall gradient) and their positions along the (a) escape axis (PCA axis 1), (b) tolerance axis (inverse PCA axis 3) or (c) their fecundity responses to (simulated) grazing. See Table 3 for full statistical analyses (ns, not significant) and Figure S4 for species' entire distribution ranges along the rainfall gradient



allocation) have previously been shown to confer drought escape (e.g. Aronson et al., 1992, 1993; Kurze et al., 2017; Tielbörger et al., 2012). We had presumed that the convergence scenario, that is, the convergent filtering of escape traits by grazing and drought, might be most likely to emerge under grazing regimes where an escape strategy is viable, that is, infrequent or late grazing. In contrast, we identified grazing escape as a successful strategy even in sites that are intensively grazed at the peak of the growing season (i.e. precluding successful escape). This discrepancy likely again relied on the unexpected high compensation ability of escapers (see above), enabling them to minimize fitness losses under intense grazing. This result from the field is also consistent with our finding in the greenhouse that escapers successfully withstand tissue loss. Additionally, pronounced seed dormancy of escapers should reduce negative impacts of grazing on species' abundance. The observed favouring of escape traits by grazing and drought in winter annuals corresponds to the generalized grazing model, which states convergent filtering by grazing and drought in perennials with respect to avoidance (Milchunas et al., 1988). Our results thus indicate that the generalized grazing model can be extended to annuals, but with respect to escape, which has pervasive implications for projecting consequences of global change in drylands.

The convergent favouring of escape traits by grazing and drought that emerged at the local scale was expected to be mirrored by a strategy shift along the large-scale rainfall gradients, that is, grazing escapers should be associated with arid conditions, corresponding to the large-scale strategy shift expected by the generalized grazing model and observed in perennials (Adler et al., 2004; Díaz et al., 2007; Milchunas et al., 1988). However, the hypothesized filtering of strategies by grazing and drought was not reflected in species' large-scale distribution. Also, single grazing response traits were not related to species' distribution along the rainfall gradients. Instead, species with the whole range of weak to pronounced grazing escape and tolerance strategies occurred along the entire gradient, implying that alternative trait combinations are similarly successful under a wide range of rainfall conditions. This may be explained by the high temporal and spatial variability of grazing and rainfall in our study system (Sternberg et al., 2015; Tielbörger et al., 2014). Indeed, high inter-annual rainfall variability has been shown to facilitate the coexistence of species or strategies within plant communities, since each has an advantage (or disadvantage) in some years (Chesson et al., 2004). This effect might be increased by inter-annual variability of grazing. Filtering of strategies may also not have emerged along the large-scale rainfall gradients, since species' occurrences in our study system are strongly determined by small-scale hydrological differences, which are not captured by rainfall data (e.g. Kutiel, 1992), for example, locally favourable conditions in riverbeds can enable drought-sensitive species to occur in arid areas. The restriction to presence/absence data at the large scale may have additionally obscured changes in species abundance. However, ecological filtering of traits has been documented along large-scale rainfall gradients based on occurrences in this and other ecosystems (Griffin-Nolan et al., 2019; Kurze, Engelbrecht, et al., 2021; Thuiller

et al., 2004). Any potentially overseen large-scale shift of grazing response strategies in annuals should thus be weak.

Our study explicitly focussed on interspecific trait coordination and their relevance for species' differential fitness and abundance responses, and ecological filtering. If and to what extent trait expression of individuals in the natural habitat may weaken or strengthen such interspecific relations remains an important aspect for further studies (Yang et al., 2021). However, intraspecific variation is unlikely to override the observed (or missing) interspecific relations, since it is usually lower than interspecific variation (Kazakou et al., 2014; Siefert et al., 2015). This especially applies to steep environmental gradients and species-rich communities (Siefert et al., 2015), as we investigated here, and it has also been shown in our study species (L. Álvarez-Cansino, unpubl. data).

The co-occurrence of annuals with a wide range of grazing escape and tolerance traits along the large-scale rainfall gradient and their overall high grazing resistance are likely due to the long grazing history combined with the high temporal and spatial variability of rainfall and grazing in the Middle East (Noy-Meir & Seligman, 1979; Tielbörger et al., 2014). Under climate change, more intense drought events and a decreasing frequency of wet years (Smiatek et al., 2011) may nevertheless favour species with pronounced grazing escape traits that convergently confer high resistance to drought. Increasing abundance of escapers may lead to a decrease in forage quantity for livestock, since they produce less biomass and exhibit a shorter life cycle than tolerators. Interacting effects of intensified drought and grazing under global change will thus likely affect community composition and decrease economically important ecosystem services in areas dominated by winter annuals.

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## AUTHORS' CONTRIBUTIONS

B.M.J.E., L.Á.-C., M.C.B., K.T. and S.K. conceived the ideas and designed the study; S.K. coordinated and conducted the plant traits measurements and the grazing simulation experiment, M.C.B. conducted the seed dormancy assessments, and R.P., K.T. and S.B. conducted the grazing enclosure experiments; S.K. analysed the

data and wrote the manuscript with contributions by B.M.J.E. All co-authors revised and commented subsequent drafts of the manuscripts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.vhhmgqnt3> (Kurze et al., 2021).

## ORCID

Susanne Kurze  <https://orcid.org/0000-0002-6120-7457>

Mark C. Bilton  <https://orcid.org/0000-0001-5287-7734>

Leonor Álvarez-Cansino  <https://orcid.org/0000-0002-8346-303X>

Bettina M. J. Engelbrecht  <https://orcid.org/0000-0001-8314-0778>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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