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RESEARCH ARTICLE

Aridity drives the loss of dung beetle taxonomic and functional diversity in three contrasting deserts

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Abstract

Aim: Aridity gradients are of great interest for understanding the responses of biodiversity to water availability and water stress. However, little is known about the responses of many animal groups, which are crucial for assessing the effects of climate change. Here, we study the effects of aridity on dung beetle communities, a group with well-known responses to large-scale environmental gradients.

Location: Sahara, Kalahari and Chihuahuan deserts.

Taxa: Dung beetles of the family Scarabaeidae.

Methods: We conducted standardized surveys along approximately 400 km aridity gradients in each of the three deserts, and measured species richness, abundance, evenness and three aspects of trait-based functional diversity (functional richness, functional evenness and functional dispersion). By using randomization tests and linear mixed models, we compared observed with expected values for functional diversity indices from null models that hierarchically incorporate additional assembly constraints.

Results: Overall, we found a decrease of both taxonomic richness and functional dispersion along the three aridity gradients. Also, aridity seems to have mild effects on functional richness and functional evenness. Besides these general trends, we identified differences between deserts in the responses of both taxonomic and functional diversity.

Main conclusions: Aridity shows greater importance than competition and other processes of limiting similarity or stochastic processes in community assembly. Also, the functional hypervolume of dung beetle desert communities decreases with aridity not only due to species loss, but also because of selection of a few distinct phenotypes under harsh environmental conditions. Last, we observed that the different regional pools respond to aridity in different ways. Therefore, understanding future responses of dung beetle communities to the progressive decreases in water availability driven by climate change requires determining how the characteristics of the species in the regional pool interact with aridity-driven assembly processes.

KEYWORDS
aridity, biotic interactions, community assembly, dung beetles, functional diversity, scarabaeidae, species richness

1 | INTRODUCTION

Understanding the determinants of the geographical distribution of biodiversity is one of the oldest and most persistent challenges in ecology (Hawkins, 2001; Pavoine & Bonsall, 2011; Pianka, 1966; Wiens & Donoghue, 2004). Among other things, species sort themselves along environmental gradients according to their requirements, interactions with other species, and dispersal ability (Götzenberger et al., 2012; Weiher et al., 2011; Willig et al., 2003). To address the origin of species diversity patterns, ecologists have studied variations in ecological communities along spatial gradients, such as altitude, latitude (Körner, 2007; le Bagousse-Pinguet et al., 2017; Sanders & Rahbek, 2012; Willig et al., 2003) or aridity (deCastro-Arrazola et al., 2018; Eldridge et al., 2020; Gross et al., 2013; le Bagousse-Pinguet et al., 2017; Song et al., 2019). The typically strong responses of community structure along such gradients permit compositional changes to be attributed to the filtering effects of particular environmental factors.

Aridity gradients are of great interest for understanding the responses of diversity to water availability, a key abiotic constraint for life (Hawkins et al., 2007; Polis, 1991; Rohde, 1992). Indeed, understanding how life responds to aridity is essential under the growing evidence of the global expansion of drylands due to climate change (Huang et al., 2016; Reynolds et al., 2007). However, for many taxonomic groups, there is a dearth of knowledge on how diversity responds to water stress, excepting perhaps, for reptiles, plants and bats (see e.g., Conenna et al., 2021; Cox & Cox, 2015; Maestre et al., 2021). Importantly, evidence points to responses being strongly context dependent, at least for some groups (Polis, 1991; Rohde, 1992; Willig et al., 2003).

Aridity acts as the main filter in drylands (Berdugo et al., 2019) and, as a result, the relative importance of aridity as an abiotic filter increases when moving from areas of high water-availability towards those of low-water-availability (see Berdugo et al., 2020). Furthermore, the relative importance of biotic interactions also changes along aridity gradients (Maestre, Callaway, et al., 2009; Maestre, Martínez, et al., 2009) where there is evidence of a change from competition-driven to facilitation-driven communities, even though facilitative interactions often collapse at the most extreme environments (Berdugo et al., 2019). Thus, it follows that understanding variation in diversity along aridity gradients requires an examination of community assembly processes.

Community assembly theory states that a series of rules filter the assembly of local communities from the regional species pool (Diamond, 1975; Weiher et al., 1998). Assembly rules are ecological processes determined by two main types of factors: abiotic conditions (i.e. temperature, precipitation) or biotic interactions (competition and processes of limiting similarity, facilitation) between species, which select for or against species from the regional pool (Götzenberger et al., 2012; Keddy, 1992). However, as these factors act together, it remains difficult to disentangle their relative roles from the observed patterns in local communities (de Bello et al., 2012; Götzenberger et al., 2012; Kraft et al., 2015). This is, certainly, the case for aridity gradients where responses to both the extreme abiotic environment and biotic interactions could promote either trait convergence (e.g., Conenna et al., 2021), even distribution of traits (see Maestre et al., 2021) or opposing patterns that neutralize each other, leading to practical and methodological limitations for separating factors driving different changes in traits (de Bello et al., 2012; Götzenberger et al., 2012). Disentangling effects may be assisted by new analytical approaches comprising novel frameworks, based on null models, which aim to incorporate hierarchical constraints to test if trait convergence/divergence is caused by abiotic, biotic, or stochastic processes (de Bello et al., 2012; López-Angulo et al., 2020). This approach provides a useful tool to study the relative importance of differences in assembly rules along any environmental gradient and, thus, assist in understanding the drivers of diversity patterns.

Dung beetles of the family Scarabaeidae are a well-known taxonomic group with responses to large-scale environmental gradients (e.g., Hortal et al., 2011; Hortal-Muñoz et al., 2000; Pessôa et al., 2021). However, the responses of dung beetle communities

to aridity have been seldom studied. Evidence shows that low water availability limits dung beetle diversity, especially species richness (Abdel-Dayem et al., 2016; Labidi et al., 2012; Tshikae et al., 2013a). There is also species replacement along aridity gradients (deCastro-Arrazola et al., 2018; Tshikae et al., 2013b). However, little is known about the effect of aridity on community assembly and functional diversity, which better explains ecosystem functioning (Hooper et al., 2005). Preliminary results from a study of temporal variations in community structure towards the Sahara show both a decrease in functional diversity with increasing aridity and a selection for specific traits which may be related to survival in low-water-availability environments (deCastro-Arrazola, 2018). Thus, it remains important to continue researching the consequences of water limitations on dung beetle communities with a focus on both identifying the different components of diversity as well as developing an understanding of the role of assembly rules in the sorting of these communities.

We study how dung beetle diversity changes along aridity gradients in three different deserts (Sahara, Kalahari and Chihuahuan). The results are divided into the relative role of aridity and biotic interactions in the assembly of their communities along the gradients. The relative roles are elucidated using standardized transects and measurements of richness, abundance and several aspects of trait-based functional diversity. Specifically, we aim: (1) to determine how aridity affects taxonomic and functional diversity; and (2) to define the roles of aridity and biotic interactions in assembling dung beetle communities along the aridity gradients. We hypothesize that:

1. both taxonomic and functional diversity decrease with aridity. As increasing aridity will cause a loss in species richness, we expect dung beetle communities with less species and lower abundance of individuals in hyper-arid areas where some species will be overrepresented and, consequently, evenness will be low. In the case of functional diversity, we expect a decrease in functional volume when moving from semi-arid to hyper-arid areas. Also, with increasing aridity, we predict that species will be functionally more similar and cluster together.
2. the relative importance of each assembly process (i.e. aridity and biotic interactions) will change along the gradient although, towards hyper-arid areas, both will cause trait convergence. Greater aridity will cause stronger environmental filtering but lower availability of resources due to aridity will, at the same time, lead to greater competitive exclusion in hyper-arid areas.

2 | MATERIALS AND METHODS

2.1 | Study areas

We conducted surveys along three transects located in deserts from different biogeographical regions: Sahara (Palearctic), Kalahari (Afrotropical) and Chihuahuan (Nearctic) (Figure 1). All of these arid environments are defined by the existence of two strongly-marked seasons: a dry season with little or no rainfall, and a wet season that concentrates annual precipitation (Beck et al., 2018). However, there are slight climatic differences between the three deserts as regards their potential evapotranspiration, temperature and seasonality. While the dry season is strongly marked in the Sahara and Kalahari, it tends to be milder in the Chihuahuan Desert (Supplementary Appendix S1 Figure S1.1).

In each desert, we sampled a ca 400 km, linear transect following a gradient of increasing aridity (Figure 1). The Saharan transect was situated in Morocco near the border with Algeria, following a N-S gradient from a semiarid region at the Mediterranean coast (near Saïdia, 35° 5′ 59″ N, 2° 17′ 15″ W) towards the arid Sahara Desert (near Figuig, 32° 6′ 33″ N, 1° 13′ 47″ W). At these extremes of the gradient, annual rainfall was measured as 350 and 100 mm p.a. The Kalahari transect was situated in South Africa following an E-W gradient from an arid region in the east (near Douglas, 29° 06′ 02″ S, 23° 44′ 28″ E) to a very arid area in the west (near Brandvlei, 30° 29′ 04″ S, 20° 21′ 54″ E). At these extremes of the gradient, annual rainfall was measured as 350 and 130 mm p.a. The Chihuahuan transect was situated in Mexico along a W-E gradient extending from

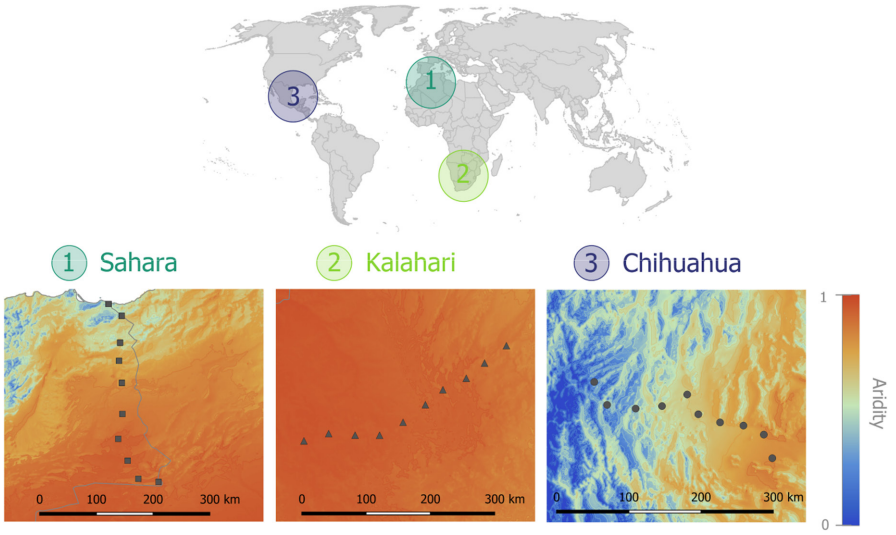

FIGURE 1 Location of the three desert transects on a global scale and of sample plots on a local scale. Maps include an aridity layer calculated as 1-(precipitation/evapotranspiration) from CHELSA layers (https://chelsa-climate.org/). All maps were drawn using a WGS 84 projection.

a semiarid region at the edge of the Sierra Madre Occidental (near Hidalgo del Parral, Chihuahua, 26° 38′ 60″ N, 105° 32′ 37″ W) to an arid extreme in the state of Coahuila (near San Pedro, 25° 39′ 49″ N, 102° 36′ 19″ W). At these extremes of the gradient, annual rainfall was measured as 430 mm and 170 mm p.a.

2.2 | Sampling design

Dung beetles were sampled during April 2014 in the Sahara, November 2014 in the Kalahari, and September 2015 in the Chihuahuan. All surveys were conducted after periods of significant rainfall (Supplementary Appendix S1). Each ca 400 km transect consisted of 10 field plots (Figure 1). On average, plots were distanced at 40.50 ± 7.84 S.D. km in the Sahara, 40.21 ± 2.76 km in the Kalahari and 34.79 ± 3.29 km in the Chihuahuan. Each plot consisted of two replicates, 1 km apart from each other and placed at least 100 m from the road margin. Each replicate consisted of five baited pitfall traps 20 m from one another in a straight line. The traps consisted of a 1 L plastic cup of 11.5 cm width and 14 cm depth covered by a 2 × 2 cm mesh over which we placed 300 g of fresh cattle dung as bait, following Lobo et al. (1988). Cattle dung is known to attract the majority of the dung beetle faunas of dry environments (e.g. deCastro-Arrazola et al., 2018; Tshikae et al., 2013c). Fresh cattle dung was harvested from a single organic farm for each transect and mixed to obtain a homogeneous consistency. To prevent insect degradation due to high temperatures, all traps were filled with 300 ml of a soapy preservative water solution with chloral hydrate (10 g/L). Traps were active for a standard period of 72 h (Labidi et al., 2012). After this period, species were transferred to 96 % ethanol and transported to the laboratory for identification to species level and measurement of traits. Plot composition was addressed by pooling all individuals from all traps in the plot. More details on the survey design can be obtained from deCastro-Arrazola et al. (2018).

For the months when fieldwork was conducted, we obtained climatic data for each plot from CHELSA (https://chelsa-climate.org/). Aridity was calculated as 1−(precipitation/potential evapotranspiration), following Berdugo et al. (2020). Mean aridity across every transect was 0.77 ± 0.16 in the Sahara (ranging from 0.45 to 0.93), 0.91 ± 0.03 in the Kalahari (ranging from 0.84 to 0.95) and 0.55 ± 0.22 in the Chihuahuan (ranging from 0.11 to 0.79).

2.3 | Dung beetle trait measurements

Based on recent research (deCastro-Arrazola et al., 2020; deCastro-Arrazola et al., submitted), we measured a set of traits that may account for dung beetle responses to arid environments. These traits included several linear and area measurements of head, pronotum, elytra, wings and tibiae (Supplementary Table S1). We also included two behavioural qualitative traits comprising adult trophic preferences and dung relocation strategy for feeding purposes. These were obtained from the literature and expert knowledge (ALVD, CM, FSP and JH). All quantitative measurements were made using a Leica M165C Stereomicroscope and Leica Application Suite LAS V4.0. Not all quantitative traits could be measured for all of the sampled species due to the bad preservation of some specimens or their minute size, which impeded gathering precise measures with the available tools. Also, specimens of some very rare species (1-2 captured individuals) were used for obtaining molecular data or placed in reference collections instead of being used for trait measurements. Categorical trait values could be assigned with confidence to all species. In total, we measured 23 traits in 599 individuals (mean 5.8 ± 2.86 individuals per species for the Sahara, 3.5 ± 1.7 for the Kalahari and 4 ± 1.8 for the Chihuahuan Desert) leading to approximately 12,000 measurements. These measurements were complemented by further behavioural categorical traits gathered from the literature or our own observations in the field. Trait values for all species considered are provided in Supplementary Appendix S3.

2.4 | Calculating taxonomic and functional diversity indices

We measured the species and trait diversity at each field plot through a set of taxonomic and functional indices that focus on different aspects of community structure. Firstly, we assessed inventory completeness for each plot in each desert through sample coverage (Chao & Jost, 2012; Chao & Lee, 1992) as implemented in the 'iNEXT' R package (Hsieh et al., 2016). Species (i.e. taxonomic) diversity was measured through three criteria: (1) species richness (hereafter referred to as richness), i.e. the total number of species recorded in each sampling plot; (2) abundance, i.e. the total number of individuals collected in the plot; and (3) evenness, which was calculated through Pielou's index (Shannon H'/ln(S)) (Magurran, 2004).

We used three indices to characterize functional diversity, which are related to different attributes of the functional hypervolume defined by the traits of all species present in the community: (1) functional richness (FRic), (2) functional evenness (FEve) and (3) functional dispersion (FDis). Together, these three metrics provide an overall image of how communities respond to different assembly rules, including biotic interactions and habitat filtering caused by abiotic factors (Mason et al., 2013; Spasojevic & Suding, 2012). FRic measures the total functional hypervolume by using the minimum convex volume. This index aims to detect reductions of the hypervolume due to abiotic factors (Botta-Dukát & Czúcz, 2016; Cornwell et al., 2006). FEve measures the regularity of distancing between species in the hypervolume and, thus, may provide insights into the functional differences between species (Pla et al., 2012). FDis measures the distances of species to the centroid of the functional volume, thus describing the distribution of species inside the functional volume (Laliberte & Legendre, 2010; Mason et al., 2013). To calculate these indices, we first obtained a species-by-species trait distance matrix using Gower distance. This was calculated with the 'gowdis' function in the 'FD' package (Laliberté et al., 2014; Laliberte & Legendre, 2010; Figure 2). Different weights were given to the

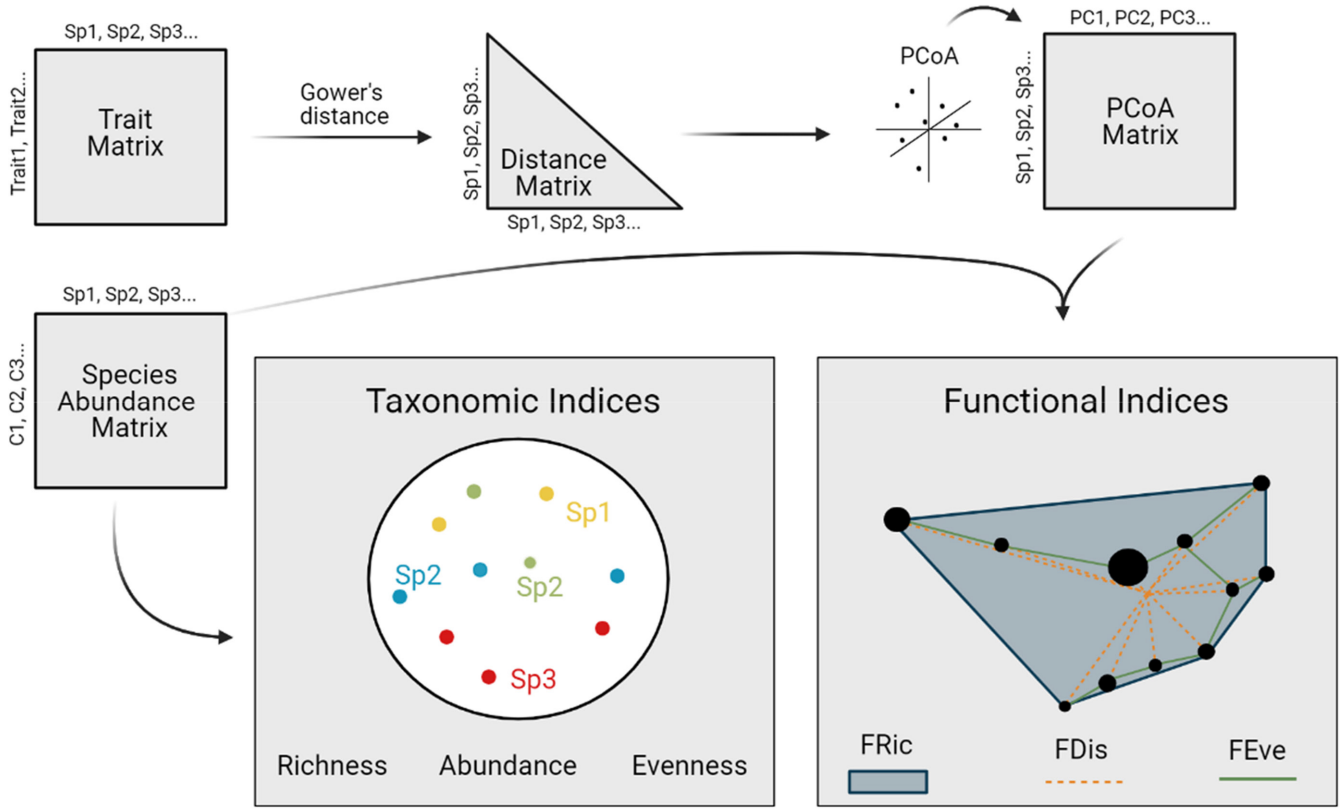

FIGURE 2 Analytical framework used to measure the taxonomic and functional indices. Taxonomic indices (richness, abundance and evenness) were calculated from the species abundance matrix, which contains abundance data for every species in every community. Functional indices were computed by constructing a distance matrix based on the trait matrix, using a principal coordinates analyses to transform pairwise species distances into a multi-dimensional space. Based on the PCoA matrix and the species abundance matrix, we calculated Functional Richness (FRic), Functional Dispersion (FDis) and Functional Evenness (FEve).

traits during the construction of this matrix in order to avoid over-representing body structures (see Supplementary Figure S1). Then, we computed all three indices per sampling plot using the 'dbFD' function in the 'FD' package (Laliberté et al., 2014).

2.5 | Statistical analyses

To assess the effect of aridity on taxonomic and functional indices, we performed linear models (LMs) with desert as a covariate. In each model we included one of the indices as a response variable. Thus, we fitted a total of six models and used aridity as predictor. In the models for the functional indices, we also included richness as a factor to account for the possible effects of differences in the number of species on functional diversity metrics (Table 1). To account for homoscedasticity and normality of the residuals in the model, richness and abundance were log-transformed and FRic and FDis were square-root transformed. For every index, we selected "beyond optimal" for model construction, which included all the fixed effects to fit the model. By including subsets of the predictors, the Akaike information criterion corrected for small sample sizes (hereafter referenced as AICc) was calculated for all possible models that varied in their fixed effects. Akaike weight (Wi) was also calculated for each model to determine the probability that any given model was the best to explain that particular variable. A 95% confidence set of models was constructed by summing the Wi values of models, starting with the highest ranked and progressing sequentially downward, until a cumulative Wi value of 0.95 was reached (Symonds & Symonds & Moussalli, 2011). We performed post-hoc pairwise Tukey tests to study the differences between the three deserts in those competing models where this variable was included. Finally, we assessed marginal and conditional R^2 for the selected models by using the function 'r.squaredGLMM' in the 'MuMIN' package. We used diagnostic plots

TABLE 1 Structure of the linear models performed to study the relationship between aridity and different taxonomic and functional indices

Model	Response variable	Explanatory variables
Richness	log (Richness)	Aridity + Desert
Abundance	log (Abundance)	Aridity + Desert
Evenness	Evenness	Aridity + Desert
Fric	sqrt (FRic)	Aridity + Richness + Desert
FDis	sqrt (FDis)	Aridity + Richness + Desert
FEve	FEve	Aridity + Richness + Desert

of the residuals to study the assumptions of normality, homoscedasticity and linearity in our LMs (see Supplementary Appendix S5). All of these analyses were conducted in the R environment.

2.6 | Null model analyses

We used null models to identify the assembly rules that may be operating along the three aridity gradients (Gotelli, 2000; Götzenberger et al., 2012, 2016; Perronne et al., 2017). In particular, the models were used to create virtual communities under different constraining assembly rules by randomizing the identity of the species present in each plot from among those present in the species pool (all species in each desert). This method ensured that observed and simulated communities had identical taxonomic richness and abundance distributions. For each desert, the randomization of the species pool was performed by considering hierarchical assembly constraints (de Bello et al., 2012; López-Angulo et al., 2020). Thus, we used: (1) random null models in which all plots are equally accessible for any species (classical randomization test); (2) an environmental null model for which the accessibility of a plot depends on the response of each species to aridity; and (3) a co-occurrence null model in which species occurrences depend on the presence of other species in the assembly. These models included the effects of abiotic conditions as well as biotic interactions, thus helping to separate the role of stochastic processes in community assembly (Supplementary Figure S2).

For every null model we first fitted the probability of occurrence of each species according to the described constraints, as follows:

1. *Random null model*. All species had the same probability of occurrence in any desert plot.
2. *Environmental null model*. To estimate the probability of occurrence of every species as a function of aridity, we used presence/absence data and fitted generalized linear models (GLMs) with a binomial error distribution. We assessed the best predictive model for every species by computing the AICc for all models, with and without aridity as a predictor. Then, we used the function 'stepAIC' in the 'MASS' package to perform a stepwise model selection. Furthermore, we used the function 'predict.glm' in the 'stats' package (R Core Team, 2021) to estimate the probability of occurrence of each species in every plot of the transect. Finally, we tested for uniformity of the residuals in every model by using the Kolmogorov-Smirnov test as implemented in the 'DHARMa' package (Hartig & Lohse, 2020).
3. *Co-occurrence null model*. Probabilities of species occurrence in a plot were estimated using Beals smoothing (Beals, 1984; De Cáceres & Legendre, 2008; López-Angulo et al., 2020). The 'Beals' function in the 'vegan' package (Oksanen et al., 2010) estimated the probability of occurrence of each species accounting for the known occurrences of the rest of the species.

We simulated 999 null assemblages for every plot, every type of null model and every desert. Finally, to assess the differences between the observed and the simulated values we used standardized effect size (SES) for every model in every plot as in Gotelli and McCabe (2002). To test the effect of aridity and the null model on the SES for every index, we used linear mixed models (LMMs) and included the plot identity as a random effect. In every model, we included the SES of every index as a response variable. Thus, we fitted a total of three models with aridity, null model, and their interaction as response variables (see Table 2) and desert identity was as a covariate. Then, we compared all of the possible models, accounting for all of the predictor combinations, following the same procedure described previously for LMs fitted for taxonomic and functional indices. All LMMs were fitted using the 'lme' function in the 'nlme' package (Pinheiro et al., 2021). We considered that the fitted null model coefficients were significant when their 95%-confidence intervals did not overlap with zero.

TABLE 2 Structure of the linear mixed models fitted to study the drivers of the standardized effect size (SES) for the three functional diversity indices

Response variable	Fixed factors	Random effect
SES (FRic)	Aridity * Null model + Desert	Plot
SES (FDis)	Aridity * Null model + Desert	Plot
SES (FEve)	Aridity * Null model + Desert	Plot

3 | RESULTS

We captured 15,567 individuals in all three deserts (11,086 individuals of 54 species in the Sahara, 3,310 individuals of 57 species in the Kalahari and 1,191 individuals of 12 species in the Chihuahuan). The average sample coverage was 97.31%, albeit with minimum values of 70.37% and 84.92% in the plots located at the hyper-arid extreme of the gradient in the Kalahari. Strikingly, out of the taxonomic indices only richness showed a significant decrease with aridity (Table 3; Figure 3a) whereas the effect of aridity on evenness and abundance was only included in some of the competing models, suggesting that aridity causes a slight decrease of these taxonomic indices (Table 3). Results for functional indices show a mild negative effect of increasing aridity on FDis (Figure 3b), as well as FRic, with a slight positive effect on FEve (Table 3). In the case of FRic, four models accounted for more than 95% of cumulative Akaike weight, but only two included aridity as a predictor (Table 3). For FEve, only two of the four competing models showed a positive effect of aridity (Table 3). For FDis, two of the four competing models included the negative effect of aridity, including the model with the lowest AIC (which accounted for almost 50% of cumulative Akaike weight). Further, desert identity also had an effect on most of the taxonomic and functional indices. Regarding taxonomic diversity, species richness was significantly higher in the Kalahari and the Sahara compared to the Chihuahuan ($p < 0.001$), while abundance was higher in the Sahara compared to the Chihuahuan ($p = 0.005$). In the case of functional diversity, FRic

TABLE 3 Model selection for the linear models analysing the effect of aridity on taxonomic and functional indices. Desert was added as covariate in every model, while richness and its interaction with aridity was added as covariate in the models for functional indices. The set of consecutive models until cumulative value of 0.95 was reached are marked in bold

Response variable	Aridity	Richness	Desert	*df*	Int	AICc	ΔAICc	Wi	R^2
log(Richness)	**−1.71**		+	**5**	**2.35**	**48.20**	**0.00**	**0.96**	**0.67**
			+	4	1.41	54.38	6.17	0.04	0.57
				2	2.27	75.75	27.55	0.00	0.00
	0.96			3	1.56	76.22	28.01	0.00	0.062
log(Abundance)			+	**4**	**4.42**	**107.78**	**0.00**	**0.72**	**0.32**
	−1.33		+	**5**	**5.15**	**109.87**	**2.09**	**0.25**	**0.33**
				2	5.31	114.83	7.05	0.02	0.00
	0.39			3	5.02	117.22	9.44	0.01	0.00
Evenness			+	**4**	**0.75**	**−30.15**	**0.00**	**0.42**	**0.17**
				2	**0.77**	**−29.62**	**0.53**	**0.32**	**0.00**
	−0.15		+	**5**	**0.83**	**−28.21**	**1.94**	**0.16**	**0.19**
	0.05			**3**	**0.74**	**−27.29**	**2.86**	**0.10**	**0.00**
sqrt(FRic)		**0.003**	+	**5**	**0.14**	**−92.79**	**0.00**	**0.46**	**0.72**
	−0.07	**0.002**	+	**6**	**0.18**	**−91.49**	**1.29**	**0.24**	**0.73**
	−0.10		+	**5**	**0.21**	**−90.77**	**2.02**	**0.17**	**0.70**
			+	**4**	**0.15**	**−90.35**	**2.44**	**0.13**	**0.67**
	−0.21			3	0.22	−71.60	21.18	0.00	0.34
	−0.20	−0.001		4	0.23	−69.39	23.39	0.00	0.34
				2	0.064	−61.58	31.21	0.00	0.00
		−0.002		3	0.10	−61.42	31.37	0.00	0.07
FEve				**2**	**0.57**	**−26.23**	**0.00**	**0.46**	**0.00**
	0.13			**3**	**0.47**	**−24.97**	**1.26**	**0.24**	**0.04**
		−0.0002		**3**	**0.57**	**−23.74**	**2.49**	**0.13**	**0.00**
	0.15	**−0.001**		**4**	**0.47**	**−22.45**	**3.78**	**0.07**	**0.04**
			+	**4**	**0.54**	**−22.13**	**4.11**	**0.06**	**0.034**
		−0.003	+	5	0.55	−19.82	6.41	0.02	0.05
	0.11		+	5	0.48	−19.56	6.67	0.02	0.04
	0.07	−0.003	+	6	0.51	−16.78	9.45	0.00	0.05
sqrt(FDis)	**−0.22**		+	**5**	**0.36**	**−53.83**	**0**	**0.56**	**0.38**
			+	**4**	**0.24**	**−51.94**	**1.89**	**0.22**	**0.28**
	−0.24	**−0.001**	+	**6**	**0.38**	**−51.05**	**2.78**	**0.14**	**0.37**
		0.0001	+	**5**	**0.24**	**−49.04**	**4.79**	**0.05**	**0.28**
				2	0.29	−46.38	7.45	0.01	0.00
		0.003		3	0.25	−46.18	7.65	0.01	0.07
	0.05			3	0.25	−44.21	9.62	0.00	0.01
	0.01	0.003		4	0.24	−43.52	10.31	0.00	0.07

Note: *df*, degrees of freedom; Int, intercept; Wi, akaike weight of the model; R^2m, marginal R^2; R^2c, conditional R^2; +, categorical variable included in the model.

was significantly higher in the Chihuahuan compared to the Sahara and the Kalahari ($p = 0.001$ and $p = 0.0242$, respectively), while the Kalahari showed significantly greater FDis. All of these results remained qualitatively similar when using extrapolated richness data to account for potential unevenness in biodiversity coverage caused by the limited sample coverage observed in the most arid localities of the Kalahari Desert (Supplementary Appendix S2).

Finally, our null models show differences between the SESs of the functional indices although we only found effects of aridity on SES (FRic) and SES (FEve) (Table 4). In the case of SES (Fric), the six models accounting for 0.95 Wi included the null model. The effect of aridity was present in four models, including the best two, which account for *circa* 0.8 cumulative Wi. In these cases, all null models were significantly lower than zero when aridity was low. However,

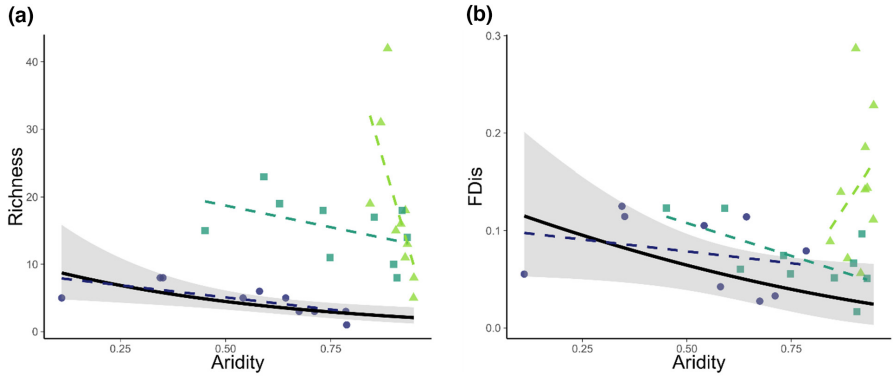

FIGURE 3 Relationships between (a) aridity and species richness, (b) aridity and FDis. The results reflect the negative correlation between both indices and aridity, according to the best models (see Table 3). Grey areas represent the confidence intervals at 95% and symbols the observed values for every desert (blue dots: Chihuahua, light green triangles: Kalahari, and dark green squares: Sahara). The specific trends in each desert are represented by dashed lines.

as an indication of trait convergence, only the random model was significantly different from zero at high values of aridity (Figure 4a). In the case of SES (FEve), there was a clear effect of aridity, the null model and the interaction between aridity and the null model. In this case, only the random null model was significantly different from zero when aridity was high, indicating trait convergence (Figure 4b). For SES (FDis), none of the effects of aridity or null model was clear based on the set of selected models, but the best model showed an effect according to the type of null model. Even though we did not find any differences between observed and simulated values, the random null model seemed to show lower values than other models (Figure 4c). Furthermore, desert identity may be playing a significant role on dung beetle functional responses to aridity, but our results remain inconclusive as this effect only appears in half of the competing models for every index. In every case, conditional R^2 accounted for most of the variance, indicating that most of the variance in our data is attributable to plot identity.

4 | DISCUSSION

Our results show that desert dung beetle communities are subject to strong filtering processes associated with limited water availability. Although both species richness and functional dispersion decrease as aridity increases, changes in abundance and species evenness are not that dependent from this gradient, probably as a result of large increases in population size of particular species. Null model analyses show that trait convergence is the main assembly rule operating in the three desert dung beetle communities. Although such filtering is mostly evident for species richness and functional dispersion, aridity also exerts a weak, but, perceptible effect on functional richness and evenness. However, in this case, the most arid environments tend to host dung beetle communities with more even trait distributions.

Dung beetles follow the well-known decrease in taxonomic and functional diversity along aridity gradients (deCastro-Arrazola et al., 2018; Eldridge et al., 2020; Gross et al., 2013; le Bagousse-Pinguet et al., 2017; Song et al., 2019). This steep reduction contrasts with the limited importance of water availability for large-scale dung beetle species richness gradients in both the Palearctic (Hortal et al., 2011) and the Neotropics (Pessôa et al., 2021). Such apparent disagreement shows the importance of the water–energy balance for diversity of this group of insects (Tshikae et al., 2013b). As a limiting factor, water availability becomes more important than energy only in drylands where aridity imposes a series of physiological and ecological constraints for life (Hawkins et al., 2007; see also Berdugo et al., 2020). Importantly, functional richness and dispersion also show a decline, indicating that loss of species as aridity increases is subject to directional filtering. This results in a sharp reduction in the total size of the functional hypervolume occupied by the communities due to the strong selection of the few trait combinations that are adequate to survive in hyper-arid areas (le Bagousse-Pinguet et al., 2017).

Community assembly could be driven by three main processes at the scale of our study: (1) environmental filtering along the strong aridity gradients of the three deserts; (2) biotic interactions; and (3) stochastic processes (Götzenberger et al., 2012). In our null model analysis, the random model shows stronger trait convergence than the other two suggesting that dung beetle community assembly along aridity gradients is mainly driven by environmental conditions (see López-Angulo et al., 2020). This finding provides support for the idea that limitations in water availability underlie trait convergence in communities inhabiting arid environments (Conenna et al., 2021; Stomeo et al., 2013). Indeed, dung beetles show higher levels of endemism with increasing aridity in the Iberian Peninsula, associated with adaptations for use of the drier, smaller dung pellets typical of mammals from arid environments (Verdú & Galante, 2002, 2004; see also Tshikae et al., 2013b with regards to the southwest Kalahari).

Biotic interactions have been hypothesized as important for maintaining relatively high levels of plant species and functional diversity in drylands (Berdugo et al., 2019; Maestre et al., 2021; Maestre, Callaway, et al., 2009). However, we did not find differences between species co-occurrence and environmental models, which points to a lack of relevance for the process of limiting similarity in the assembly of the three desert dung beetle communities. Furthermore, our results show that the reduction of the trait hypervolume towards the most arid areas is not

TABLE 4 Model selection for the analyses of the drivers of the standardized effect size for the three functional diversity indices studied. The set of consecutive models until cumulative value of 0.95 was reached are marked in bold

Response variable	Aridity	Null model	Desert	Aridity: Null model	*df*	Int	AICc	ΔAICc	Wi	R^2m	R^2c
SES (Fric)	**0.64**	+		+	**8**	**−0.78**	**100.46**	**0.00**	**0.40**	**0.20**	**0.69**
	0.91	+			**6**	**−0.98**	**100.55**	**0.09**	**0.39**	**0.18**	**0.67**
		+			**5**	**−0.31**	**104.40**	**3.94**	**0.06**	**0.05**	**0.67**
	0.81	+	+		**8**	**−0.98**	**104.67**	**4.21**	**0.05**	**0.18**	**0.71**
		+	+		**7**	**−0.56**	**104.71**	**4.25**	**0.05**	**0.14**	**0.70**
	0.54	+	+	+	**10**	**−0.79**	**104.78**	**4.32**	**0.05**	**0.1**	**0.72**
	0.91				4	−1.07	108.86	8.39	0.01	0.13	0.60
	0.81		+		6	−1.07	112.79	12.33	0.00	0.13	0.64
					3	−0.39	112.79	12.33	0.00	0.00	0.60
			+		5	−0.64	112.93	12.46	0.00	0.09	0.64
SES (FEve)	**−0.21**	+		+	**8**	**0.07**	**108.57**	**0.00**	**0.92**	**0.04**	**0.96**
	−0.13	+	+	+	**10**	**0.04**	**113.67**	**5.10**	**0.07**	**0.04**	**0.96**
		+			5	−0.09	118.47	9.90	0.01	0.02	0.95
	−0.55	+			6	0.32	120.39	11.81	0.00	0.03	0.95
		+	+		7	0.05	122.92	14.34	0.00	0.03	0.95
	−0.46	+	+		8	0.29	125.28	16.71	0.00	0.03	0.95
					3	−0.21	143.73	35.16	0.00	0.00	0.92
	−0.55				4	0.20	145.57	36.99	0.00	0.01	0.92
			+		5	−0.07	148.01	39.44	0.00	0.01	0.92
	−0.46		+		6	0.17	150.28	41.70	0.00	0.0	0.93
SES (FDis)		+			**5**	**0.1**	**98.47**	**0.00**	**0.30**	**0.00**	**0.95**
		+	+		**7**	**−0.12**	**99.25**	**0.78**	**0.20**	**0.12**	**0.95**
	0.34	+			**6**	**−0.16**	**100.60**	**2.13**	**0.10**	**0.01**	**0.95**
	−1.00	+	+		**8**	**0.41**	**100.83**	**2.36**	**0.09**	**0.14**	**0.95**
	0.27	+		+	**8**	**−0.1**	**100.96**	**2.49**	**0.09**	**0.01**	**0.95**
	−1.07	+	+	+	**10**	**0.46**	**101.39**	**2.92**	**0.07**	**0.14**	**0.96**
					3	**0.05**	**101.89**	**3.42**	**0.05**	**0.00**	**0.94**
			+		**5**	**−0.16**	**102.50**	**4.03**	**0.04**	**0.11**	**0.95**
	0.34				4	−0.2	103.94	5.46	0.02	0.01	0.95
	−1.00		+		6	0.36	103.98	5.51	0.02	0.13	0.95

Note: *df*, degrees of freedom; Int, intercept; Wi, Akaike weight of the model; R^2m, marginal R^2; R^2c, conditional R^2; +, categorical variable included in the model.

accompanied by either a reduction of the functional distances between species or a species clustering within the hypervolume as would have occurred if trait filtering processes were also acting within the hypervolume. Following Götzenberger et al. (2012), these results point to stochastic processes playing a relevant role in the location of species in the functional hypervolume occupied by dung beetles in these three desert systems. This indicates that a reduction of the functional space is not linked to the selection of any particular subset of trait values in apparent contrast to evidence that aridity selects for functional and life history strategies that allow survival in low-water-availability environments (Eldridge et al., 2020; Song et al., 2019). Rather, we believe that dung beetles may not show the increase in functional complementarity hypothesized by Maestre et al. (2021) for plants because of the absence or limited extent of facilitation or other positive interactions in dung beetles. Despite this belief, rather than a simple clustering of a few highly similar species, the strong filtering to an even selection of species in the trait space indicates that there may be several ways in which dung beetles adapt to aridity, perhaps by selecting for several kinds of successful phenotypes and/or life history strategies (see Grime, 2006). This process over increasing aridity may be behind the relevance in desert dung beetle assemblages of widely neglected interactions such as brood parasitism (González-Megías & Sánchez-Piñero, 2003) and the promotion of generalist trophic preferences that allow use of more types of dung or even saprophagy as found by deCastro-Arrazola et al. (2018) and Tshikae et al. (2013c).

As opposed to species identity, functional approaches in ecology focus on how species perform (Dísaz & Cabido, 2001),

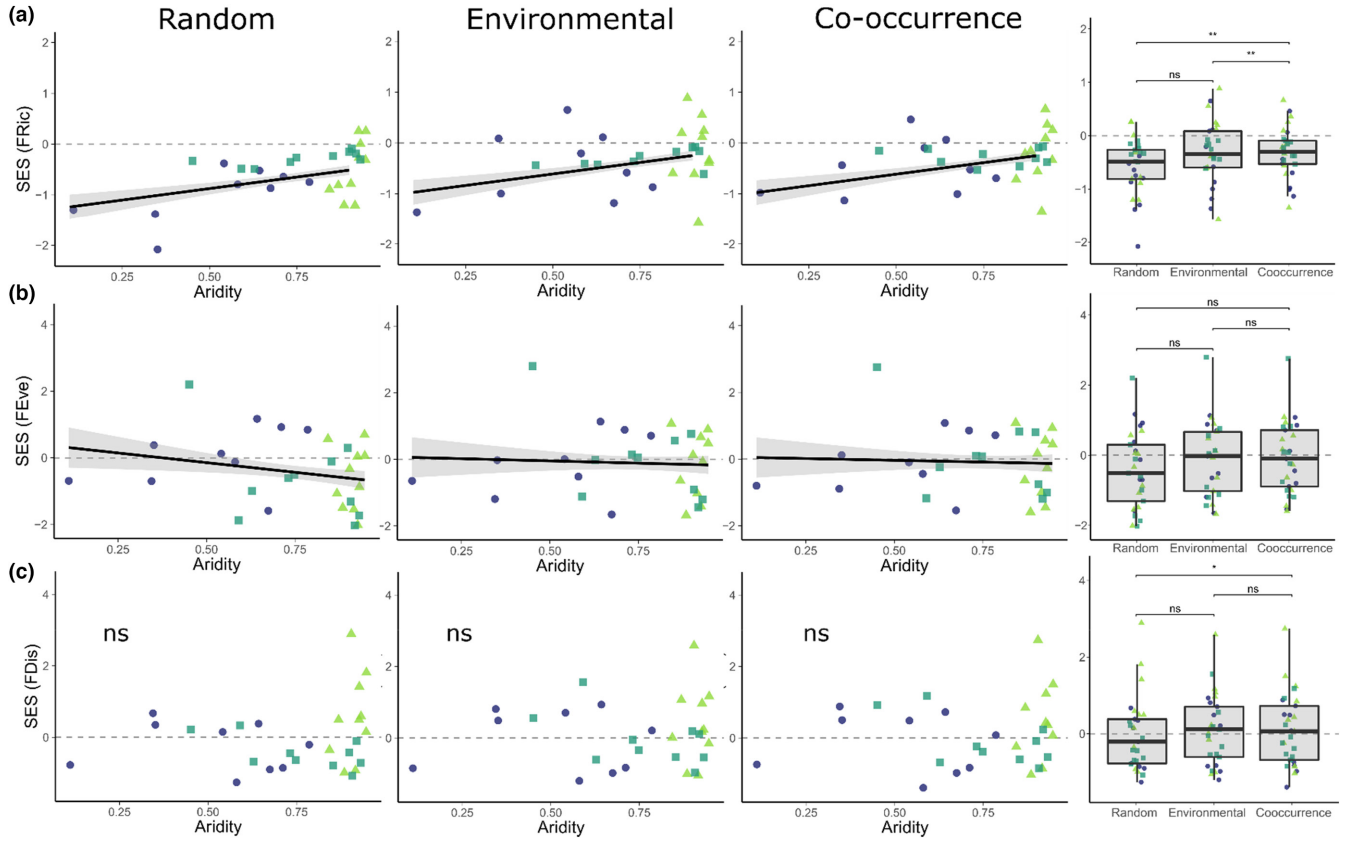

FIGURE 4 Main effects obtained in the best model for (a) SES (FRic), (b) SES (FEve) and (c) SES (FDis). Plots on the left represent the correlation between the SES of every index and aridity for every null model; grey areas represent the confidence intervals at 95%. On the right, boxplots are presented for every null model. Asterisks indicate significant differences ($p < 0.05$) according to post-hoc Tukey tests (**$p < 0.01$; *$p < 0.05$; and ns, not significant). Symbols represent the observed values for each desert (blue dots: Chihuahua, light green triangles: Kalahari, and dark green squares: Sahara).

leading to an expectation of more generalizable conclusions (Petchey & Gaston, 2006). However, our models show that desert identity has an effect in many cases. Hence, besides general physiological and functional constraints to inhabiting dry areas, there are important regional variations in the responses of dung beetle communities to aridity. Indeed, global drylands show great differences in their origins and biogeographical history (Maestre et al., 2021). Thus, evolutionary differences between their faunas and the different patterns of historical changes in climate through time result in different responses to low water availability (Hortal et al., 2008; Tello & Stevens, 2010). The low dung beetle species richness in the Chihuahuan desert results in greater variability in the functional richness of its local communities in contrast to the relatively high similarity of functional richness of the Kalahari communities despite their larger variations in species richness.

Three characteristics of our study may limit its generality. On the one hand, the selection and weighting of the functional traits relies on our own decisions. Although for other taxonomic groups (i.e. plants), there is stronger evidence for which traits should be measured (Pérez-Harguindeguy et al., 2013), such consensus and evidence is still limited for dung beetle ecology. Nevertheless, the studied traits are actually related to dung beetle functional performance (deCastro-Arrazola et al., 2020) and are among those identified as related to temperature and water responses by a recent review (deCastro-Arrazola, 2018). Furthermore, as mentioned above, the three deserts differ in terms of total numbers of species in the regional pool. Although the effect of regional pool size is explicitly considered by our analyses, the large differences between the three deserts may have prevented us from identifying some responses of functional diversity to aridity (Martins et al., 2012). This potential problem may have been further increased by differences between ranges of aridity in the three deserts. Hence, transects with greater similarity in ranges of aridity might have allowed us to identify clearer patterns. Also, although our data come from standardized surveys, the lower sample coverage in the hyper-arid extreme of the Kalahari Desert may have resulted in a steeper decay of richness with aridity. That said, given the consistency in such decay along the three deserts, we believe that the effect of such eventual undersampling on our results are minimal.

4.1 | Concluding remarks

To summarize, abiotic filtering is seemingly the main process sorting dung beetle communities in drylands. However, the reduced importance of processes of limiting similarity could play a role in the selection of species and traits towards the edges of aridity gradients. While

both taxonomic and functional diversity decrease along aridity gradients, decreases in the occupation of trait space are less pronounced. This probably owes to selection for different set of trait values, life history strategies and trophic preferences rather than convergence towards a unique kind of phenotype in the most arid areas. Although future scenarios of dryland expansion are likely to result in an impoverishment of dung beetle communities, the ecosystem functions they perform may take longer to collapse. However, as climate change drives progressive decreases in water availability and modifies the factors filtering the regional species pool, increasing stress may result in negative biotic interactions becoming stronger and more important. This would enhance the effect of abiotic conditions as the main filter in the assembly of dryland dung beetle communities.

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CONFLICT OF INTEREST

The authors do not have conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and R code supporting this study are available in the supplementary materials (Supplementary Appendix S3 and Supplementary Appendix S4, respectively).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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