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Grazing Modulates the Multiscale Spatial Structure of Dryland Vegetation

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ABSTRACT

Plants can facilitate their local environment and create a two-phase spatial structure of vegetation and bare soil in drylands, which largely influences ecosystem functioning. Although an increasing number of studies have examined how global change drivers like aridity influence vegetation spatial structure in drylands (e.g., the patch size distribution), it remains unclear how grazing impacts differ from those of climatic gradients, how these effects vary with herbivore feeding habits, and which plant-level traits—such as size and life form—mediate these spatial responses. Here, we coupled spatial vegetation pattern analyses of ecosystem images with field data analyses of the size distribution and dominant life forms of plants from 326 plots sampled across 25 countries and six continents to explore the effects of herbivores on the spatial structure of dryland vegetation. The effects of herbivores on vegetation spatial

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structure were opposite to the effects of aridity. Specifically, vegetation in grazed areas was clustered into larger patches, with fewer small patches, which skewed the patch-size distribution towards larger patches. These effects differed between browsing and grazing herbivores. Grazing effects were partially explained by the fact that grazing reduced average plant size, increased shrub density, and promoted facilitation among species of contrasting sizes. Similar effects were also confirmed by using model simulations that accounted for positive plant interactions. By linking remotely sensed images, a global field survey, and a mathematical model, our study uncovers the species-level mechanisms by which herbivores shape ecosystem-level spatial patterns and provides insights into the consequence of herbivory pressure on the resilience of drylands.

1 | Introduction

Dryland ecosystems exhibit characteristic two-phase spatial mosaics, where vegetation is clustered in patches separated by open areas (Klausmeier 1999; Kéfi et al. 2007). This spatial structure is driven by local feedbacks between the vegetation and its local environment (Rietkerk 2004; Callaway 2007), which increase soil fertility and moisture, limit evaporation (Aguiar and Sala 1999; Eldridge et al. 2024), and enhance vegetation growth (D'Odorico et al. 2007). This patch structure is key to limiting water runoff and erosion and concentrating nutrients and water lost from bare areas (Tongway and Ludwig 1994; Bautista et al. 2007). The spatial structure of the vegetation has also been associated with higher nutrient and carbon storage and cycling (Berdugo et al. 2017; Kéfi et al. 2024).

A large number of studies have observed how vegetation patches become more fragmented due to the loss of the largest patches, resulting in a less heavy-tailed patch-size distribution in drier areas (e.g., Eby et al. 2017; Kéfi et al. 2024). While substantial effort has been devoted to understanding climatic drivers of vegetation spatial structure across large areas, a global picture of the role of local grazing pressure (level of consumption of herbivores), a key land degradation and desertification driver (Asner et al. 2004), is lacking. Specifically, our understanding is limited regarding how grazing pressure and herbivore feeding habits—such as the balance between grazing and browsing—influence vegetation spatial structure, as well as the specific ecological pathways through which these effects occur.

Grazing has a multifaceted impact on the structure and functioning of drylands by affecting carbon and nutrient cycling, vegetation cover (Lin, Han, et al. 2010; Maestre, Le Bagousse-Pinguet, et al. 2022), and species diversity (Merdas et al. 2021). Herbivores, for example, generate nutrient hotspots via excretions that may improve seedling recruitment in the neighborhood of existing patches (Lin, Hong, et al. 2010; Allington and Valone 2014; Eldridge et al. 2016), although recent findings suggest no association between the presence of herbivores and nutrient hotspots associated with vegetation (Eldridge et al. 2024). The effects of grazing on ecosystem attributes interact synergistically or antagonistically with larger climatic gradients such as temperature and aridity (Gaitán et al. 2018; Maestre, Le Bagousse-Pinguet, et al. 2022). However, local studies have shown that the specific effects of grazing on plant spatial structure are highly variable. For instance, the presence of sheep and goats has been shown to be associated with both increases (Oñatibia and Aguiar 2018) and decreases (López et al. 2013; Oñatibia et al. 2018) in the distance between vegetation patches, and with greater (Lin, Han, et al. 2010) or lower (Kéfi et al. 2007; Oñatibia et al. 2018) frequency of small vegetation patches. Such apparent discrepancies likely stem from (i) the feeding habits of dominant herbivores (balance of browsing vs. grazing), (ii) the multiple processes through which herbivores might alter the spatial structure of vegetation, and (iii) the possible interactions with local climatic conditions (Oñatibia et al. 2020; Carboni et al. 2023).

We hypothesize that herbivores influence plant spatial patterns through different mechanisms: (i) by promoting woodier species, (ii) by changing the size distribution of communities, and (iii) by modulating small-scale interactions among plants. We detail each hypothesized pathway below. Herbivores might promote larger vegetation patches because they induce community turnover by preferentially consuming some palatable grass species (Berg et al. 1997; Adler et al. 2001) and promoting the recruitment of larger woody species (i.e., shrub encroachment; Van Auken 2000; Seifan and Kadmon 2006; Carboni et al. 2023). Yet, these effects likely depend on the feeding habits of herbivores because of differences in preferences for herbaceous compared with woody species (Staver et al. 2021; Travers and Berdugo 2020; Biancari et al. 2024). Furthermore, herbivores might modulate plant spatial patterns by shifting the balance between competition and facilitation among plants. In grazed areas, a higher frequency of positive associations between grasses and shrubs has been found, with unpalatable species protecting most palatable ones, a mechanism known as associative protection (Cipriotti and Aguiar 2005; Milchunas and Noy-Meir 2002; Baraza et al. 2006). This mechanism might ultimately lead to higher spatial aggregation of vegetation. Lastly, at the species trait level, plants tend to be smaller in grazed areas (Díaz et al. 2007), leading to a shift in community size distribution that likely leaves an imprint on the vegetation spatial patterns because patches would appear smaller.

There are therefore potential different pathways through which changes in community-dominant life form (e.g., grass *cf.* shrub) and size distributions of plant species drive ecosystem-level spatial patterns, but it remains unknown which pathways explain changes in plant spatial patterns and how grazing acts on these pathways. While the use of theoretical models could provide insights into the general mechanisms underlying grazing effects under different herbivory and climatic pressure (Schneider and Kéfi 2016; Irob et al. 2024), these models have yet to be compared with observations, as it is the case along aridity gradients (Eby et al. 2017; Kéfi et al. 2024).

In this study, we aim to: (i) determine how grazing pressure and feeding habits of herbivores shape plant spatial patterns in drylands and (ii) test our hypotheses regarding the species-level mechanisms underlying change in spatial patterns (e.g., change in size distributions, dominant life form, and species associations). For that, we combined field vegetation data from 326 dryland plots sampled across the globe, with remotely sensed ecosystem images at the location of those plots, and model simulations to permit a multiscale investigation of grazing effects on vegetation spatial structure in drylands (Figure 1). We first analyzed how grazing pressure and the identity of the dominant livestock species affected plant spatial patterns. Then, we identified the pathways underlying changes in plant spatial patterns using the field vegetation data. Lastly, we analyzed a model of dryland vegetation dynamics to test whether associative protection among plants could underlie observed changes in plant spatial patterns.

2 | Methods

2.1 | Spatial Analyses

2.1.1 | Collecting Ecosystem Images on BIODESERT Sites

We used the BIODESERT dataset, which contains different soil (carbon, nitrogen, and phosphorus) and plant trait attributes of plants from 326 plots (surveyed in 98 sites from 25 countries across six continents; Maestre, Eldridge, et al. 2022). These sites cover a wide range of climatic conditions with aridity index (1-precipitationpotential evapo-transpiration) ranging from 0.46 to 0.99 (i.e., from dry sub-humid to hyper-arid drylands). Mean annual temperature across the surveyed sites ranged from −1.2°C to 29.2°C. At each site, different plots were defined based on a known history of different grazing pressures. These plots were selected along a local grazing gradient, either at different distances from the closest water point (ponds, impoundments, or drinking troughs) or in paddocks or allotments with different levels of grazing pressure (ungrazed, low, moderate, or high). The local grazing gradients were compared and validated with the number and mass of dung or pellets collected on the plots, information about livestock density whenever it was available, and measurements of the size of herbivore tracks across the plots. We refer to Maestre, Le Bagousse-Pinguet, et al. (2022) for further details on the validation of the local grazing gradients used. We recorded the dominant livestock species (cattle, sheep, horse, or goat) by recording the species that dominated the dung collected in the field. It is also noteworthy that wild herbivores were present in the plots even though these local grazing gradients were defined based on livestock pressure. All vegetation and trait data were collected at these 326 sites using standardized protocols (see Maestre, Eldridge, et al. 2022; Gross et al. 2024 for a complete description of the sampling procedure). That is, at each 45 × 45 m plot, four transects were sampled, each consisting of 25 quadrats of 1.5 m × 1.5 m. For each quadrat, the relative abundance of species in the plot was recorded. In addition, the maximum lateral spread was measured on perennial plants using two perpendicular width measurements as a proxy for plant size. For a complete description of how plant traits were measured please see Gross et al. (2024).

At each site, we collected three dryland images of size 50 m × 50 m using Google Earth (https://earth.google.com/) or VirtualEarth (http://www.bing.com/maps) with a

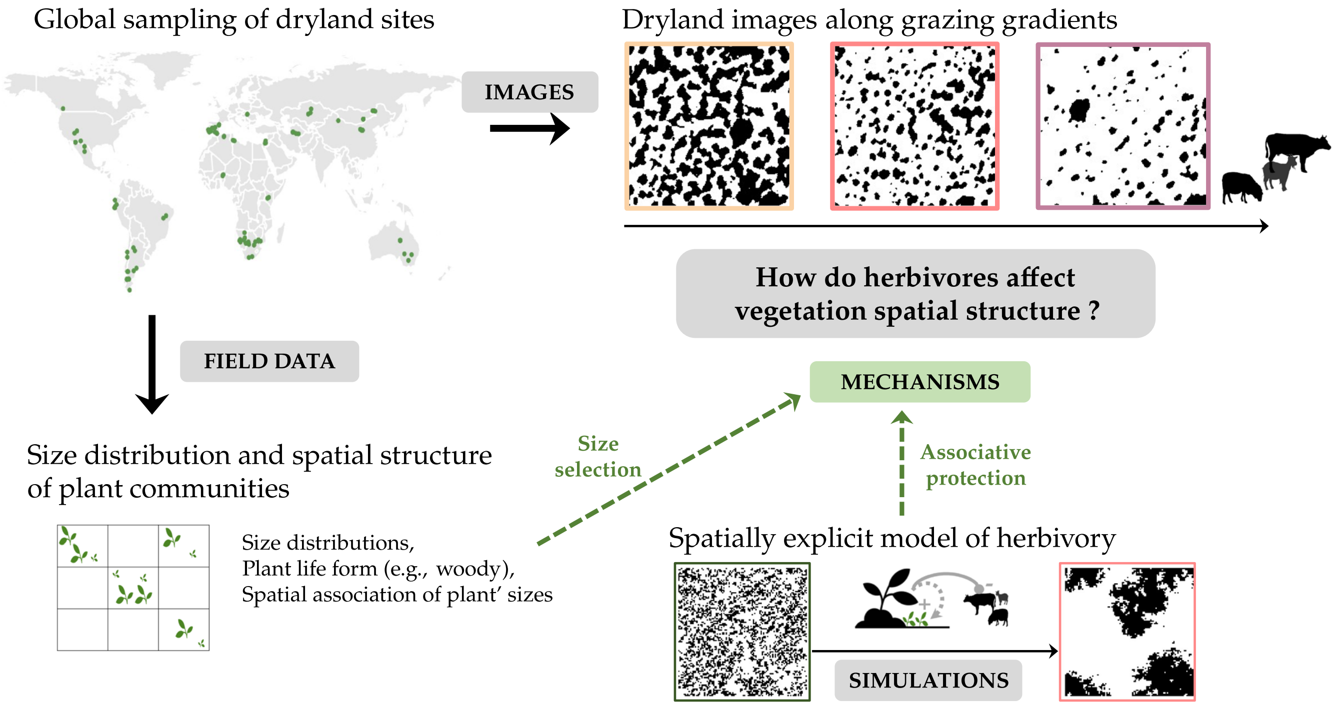

FIGURE 1 | Overview of the methodology. Representation of the questions and methodology to investigate how grazing pressure affects the spatial structure of vegetation in drylands. A total of, 326 plots were sampled across the globe (Maestre, Eldridge, et al. 2022), and three ecosystem images were collected on each plot. After characterizing how herbivory pressure shapes plant spatial patterns (right part), we used both spatially explicit simulations and field community data on plant size (spatial distribution of lateral spread and average community values) to propose hypotheses underlying herbivory mechanisms on the spatial structure of vegetation. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

spatial resolution allowing the identification of vegetation (i.e., < 0.3 m/pixel). By default, we used VirtualEarth. However, for each image we went through the Google Earth images and we replaced the VirtualEarth images when it improved the quality of the image or when there were visual artifacts (e.g., clouds, see Note S1). Each pixel of each image was classified as vegetation or bare soil using a K-mean clustering of individual pixels based on their colors. Vegetation patches are defined as areas of perennial vegetation that are connected by at least one side of a pixel. We then used the vegetation cover measured in the field on perennial species to verify the cover in these images and discarded images where there were large differences in vegetation cover between the field and the image (Note S1). This resulted in 504 images of sufficient quality that were in agreement with field measured vegetation cover. While it is true that there are marked seasonal patterns in the abundance of annual plants within drylands (as seen on productivity timeseries e.g., Buxton et al. 2022), we believe that this does not impact our methodology and results for two reasons. First, plant spatial patterns in drylands are largely determined by the presence of perennial plants that can live decades, and therefore do not change much over time (see for instance Deblauwe et al. 2012; Bestelmeyer et al. 2018). Secondly, images were transformed to binary images such that field cover (measured on perennial plants) was close to the image cover. In that sense we believe that we have controlled for the effect of seasonality, as all the methodology, from traits and local cover to the images, focuses on perennial plants.

2.1.2 | Quantitative Descriptors of the Vegetation Spatial Structure

Dryland spatial structure can be characterized by the patch-size distribution (hereafter PSD; Kéfi et al. 2007) or the connectivity of bare areas (Tongway and Ludwig 1994; Mayor et al. 2019), and been shown to be a good indicator of land degradation and ecological resilience in drylands. We therefore assessed how grazing impacted the spatial structure of vegetation by computing multiple spatial statistics related to the PSD and the connectivity of bare areas for each image (Table S1): mean patch-size (log-transformed), the fraction of the image covered by the largest patch (size biggest patch/total number of pixels), the exponent of the power-law or truncated power-law which best fitted the PSD, and the number of patches of the smallest size (the lowest size possible being 1: a pixel). We also measured the flow-length (log-transformed), which quantifies how water and nutrients can flow from bare soil areas to vegetation patches (Rodríguez et al. 2018), and is therefore a good proxy for the fragmentation of vegetation patches and soil erosion (Bautista et al. 2007). If an exponential law was the best fit for the PSD, we set the exponent value of the image to NA ($n = 131$). Lower exponent values are associated with a less heavy-tailed patch-size distribution. The different spatial statistics were computed using the functions *patchdistr_sews* and *flowlength_sews* from the **spatialwarnings** package (v3.0.3; Génin et al. 2018).

In addition, because grazing might impact the fine-scale geometry of vegetation patches, we computed the circularity of patches as the fraction between the area covered by the core pixels within a patch to the total patch area, as well as the Moran index that measures the level of spatial autocorrelation of the vegetation. A high positive autocorrelation and circularity mean that vegetation pixels are more spatially aggregated into patches, and that such patches are more circular, respectively. By contrast, lower values of these spatial indicators indicate more scattered vegetation. We give in Figure S1 an example of the patch-size distribution on three observed dryland vegetation landscapes.

Since spatial statistics can be partially correlated, we performed a principal component analysis (PCA) on all spatial statistics used to distinguish the main spatial structural components (Figure S2). The first axis explained 57.7% of the variance and distinguished vegetation images with relatively high average patch size and spatial autocorrelation (high values of the first principal component; PC1).

In addition, almost all these descriptors were closely correlated with vegetation cover (Figure S3a). To disentangle the direct effect of grazing on the spatial organization of the vegetation from its effect through the vegetation cover (Figure S4), we corrected each spatial statistic S by the vegetation cover using a simple linear regression and performing all the following analysis on the residuals of this regression. Each spatial statistic corrected by the cover is hereafter noted $\overline{S}$. The resulting statistics have a nearly null correlation with the vegetation cover as illustrated in Figure S3b.

2.1.3 | Grazing Effects on the Spatial Structure

We aimed to quantify the linear effects of grazing pressure, along with other environmental drivers, on the spatial organization of the vegetation. To assess the direct effects of grazing, we used linear mixed-effect models. For any spatial statistic $\overline{S}$, we define $\overline{S}_{lp}$ by its value at image l in plot p in site s, and consider the following model:

$$
\begin{aligned}
\overline{S}_{lps} = {} & \beta_0 + \beta_1 \mathrm{AI}_{ps} + \beta_{2\cdot\mathrm{Grazing}_{ps}} + \beta_3 \mathrm{MAT}_{ps} + \beta_4 \mathrm{Sand}_{ps} \\
& + \beta_5 \mathrm{OrgC}_{ps} + \beta_{6\cdot\mathrm{Habitat}_{ps}} + \beta_{7\cdot\mathrm{Dominant\ sp.}_{ps}} \\
& + \beta_{8.\mathrm{Grazing}_{ps}} \times \mathrm{AI}_{ps} + \gamma.\,\mathrm{Geo}_{ps} + \phi_s + \epsilon_{lps} \\
& \phi_s \sim \mathcal{N}\left(0, \omega^2\right), \quad \epsilon_{pls} \sim \mathcal{N}\left(0, \sigma^2\right)
\end{aligned}
\tag{1}
$$

where AI_{ps} is the level of aridity (measured as 1-precipitation/potential evapo-transpiration), MAT_{ps} is the mean annual temperature, OrgC_{ps} is the soil organic carbon in the neighborhood of vegetation patch, Sand_{ps} is the soil sand content and $\mathrm{Habitat}_p$ is the type of habitat (forest, shrubland or grassland), which have all previously been shown to influence plant spatial patterns (Berdugo et al. 2019). Geo_{ps} is a vector of quantitative geographical covariables (latitude, longitude cos- and sine-transformed respectively, elevation and slope of the area) used to control for potential effect of geography, and we used a random site effect ϕ_s. The grazing pressure $\mathrm{Grazing}_{ps}$ is an ordered factor (ungrazed, low, medium, and high grazing), with ungrazed areas being the reference grazing modality ($\beta_{2\{\mathrm{ungrazed}\}} = 0$). We included an interaction term $\beta_{8.\mathrm{Grazing}_{ps}} \times \mathrm{AI}_{ps}$ to investigate synergy or antagonism of aridity and grazing on the spatial structure. We also ran the models in Equation (1) with the spatial statistics not corrected by vegetation cover to understand the combined effect of grazing on vegetation cover and spatial structure. All the predictors used in this model were only weakly correlated (Figure S5). We centered and reduced the quantitative variables, and used the **lme4** package (v1.1-27; Bates 2010) to fit the models. The model residuals were normally distributed and we verified the model's assumptions using the *mcp.fnc* function (**LMERConvenienceFunctions**-R package). We tested for model multicollinearity using variance inflation factors, but multicolinearity was not observed (VIF were below 3).

To quantify the effects of grazing on the different spatial statistics, we used the partial residuals of the models (Equation 1) against grazing pressure and evaluated the significance of each grazing modality (low, medium, high) relatively to ungrazed plots using bootstrap (1000 replicates). Since aridity and mean annual temperature represent two independent climatic gradients in our dataset ($\rho_{\text{pearson}} = 0.19$), and that grazing effects may differ depending on the dominant herbivore species, we repeated the analysis using partial residuals from the models with respect to aridity, mean annual temperature, and herbivore identity. This approach allowed us to disentangle the distinct effects of climatic gradients versus grazing pressure, and to capture species-specific herbivore impacts.

2.2 | Mechanisms Underlying Grazing Effects

2.2.1 | Community Composition and Plant Size

Using vegetation and plant size data sampled in the field, we investigated mechanisms underlying grazing effects on the spatial structure. Specifically, we aimed to determine whether shifts in vegetation spatial structure in grazed areas were driven by changes in the dominant plant life form (woody vs. non-woody), average plant size, and the relative roles of competition and facilitation among plant species—all of which are known to influence spatial patterning in vegetation (Figure 1). To assess these plant community attributes, we examined the percentage of woody species across all quadrats and the community mean plant size (cLS; Equation 2) to characterize the dominant plant life form and the average size of species in the communities, respectively.

$$\text{cLS}_p = \sum_k A_{kp} \text{LS}_{kp} \tag{2}$$

where A_{kp} is the relative abundance of species k in the plot p and LS_{kp}, its lateral spread (cm^2). Higher cLS_p means that large plant species are more dominant.

2.2.2 | Spatial Distribution of Plant Size

We quantified the level of spatial aggregation or dispersion of plant sizes as a functional proxy of the balance between facilitation and competition between species of different sizes (Gross et al. 2013). For this metric, we were only interested in the spatial distribution of plant size and not their numeric value. Because plant size can change along aridity and grazing gradients, we standardized plant size values of each species within a plot p, by subtracting the mean of all measured species' sizes in plot p and dividing by the range of species' size values in plot p. Then, we computed the cLS for each of the 100 quadrats q of each plot ($\text{cLS}_{q,\text{obs}}$, $q = 1, \ldots, 100$) using Equation (2) with the relative abundances of species within each quadrat q, A_{kqp}. This gave a distribution of 100 $\text{cLS}_{q,\text{obs}}$ values from which we extracted its standard-deviation as a measure of the dispersion of the spatial dispersion of cLS. A high dispersion occurs for quadrats differing in plant size distributions, while a low dispersion for quadrats with similar ones, which respectively denotes, for a the same set of individuals, that plants are clustering in space by size class vs. are forming clusters of plants with contrasting sizes.

We compared this dispersion with ones obtained after shuffling individuals across quadrats $\text{cLS}_{q,\text{null}}$ (see Figure S6a,b for illustration):

$$\text{DevLS}_\text{p} = sd\left(\text{cLS}_{q,\text{obs}}\right) - sd\left(\text{cLS}_{q,\text{null}}\right) \tag{3}$$

We shuffled individuals across all quadrats q (199 randomizations) while keeping species richness in each quadrat constant to only disturb species identify and not quadrat diversity, thereby allowing to remove the effect of biotic processes on the spatial distribution of plant sizes. This was done using the *permatfull* function from the **vegan** R-package (v2.5–7; Oksanen et al. 2007). Comparing the observed plant size dispersion with the mean of the 199 ones obtained from the null distributions thus indicates whether species with contrasting sizes are more spatially aggregated or dispersed than expected by chance (Figure S6c for illustration). Specifically, when plant size dispersion is lower in observation as compared to in the null distributions ($sd\left(\text{cLS}_{q,\text{obs}}\right) < sd\left(\text{cLS}_{q,\text{null}}\right)$), species of contrasted sizes are more aggregated compared to what is expected by chance, potentially due to facilitating mechanisms, while competitive mechanisms among plant of different sizes would lead to lower dispersion in observation compared to the null distributions because plant with similar size would aggregate in space.

2.2.3 | Path Analysis

Using these three species-attributes variables, we tested the possible mechanisms underlying grazing effects on the spatial structure by performing a path analysis (Shipley 2016). In this analysis, drivers (aridity, mean annual temperature, and grazing) modulate community composition (% of woody cover), and the size structure of plant communities (cLS, the mean plant size cLS, and DevLS, the spatial distribution of plant size), which in turn shape plant spatial patterns (PC1 axis of the PCA on spatial statistics). We refer to Note S2 for rationale behind tested relationships. Grazing was considered a continuous variable to obtain a global estimate along grazing pressure gradient (Lefcheck 2016), and we controlled for geographical covariates and the site-level random effects similarly as in Equation (1). Since the percentage of woody species and the community average plant size (log-transformed for normality assumption) were correlated ($\rho_{\text{pearson}} = 0.53$), we used partial least squares when these two predictors were together in the same model to avoid multicollinearity. All standardized path coefficients were estimated using bootstrap (1000 replicates), and we also computed direct, indirect and total effects between drivers and the different components of this path analysis.

2.3 | Exploring Mechanism of Grazing Effects Using a Spatial Model

Path analysis only partially explains grazing effects on the spatial structure (see Section 3). Consequently, we used an individual-based spatial model of dryland vegetation dynamics to explore whether associative protection, an indirect facilitation mechanism among plants against herbivory, resulted in similar effects as the effects of grazing on spatial patterns (Schneider and Kéfi 2016). An extensive description of the model is provided in Note S3. In brief, the model simulates the life history of perennial, facilitative plants (represented as a vegetated cell), all sharing identical strategies: seed dispersal and colonization of fertile cells, juvenile recruitment, and adult mortality. Each plant enhances its local environment by increasing the probability of transition of neighboring degraded cells (from erosion or salinization) to fertile cells (fertile island effect; Eldridge et al. 2024). These fertile cells then become available for colonization by other plants, reinforcing spatial expansion through facilitation.

Plant mortality arises from two mechanisms. The model assumes a mortality due to aridity, which applies similarly to all plants, no matter their neighborhood (spatially homogeneous stress). In addition, mortality is also a result of herbivory (plant consumption), which is implicitly modeled as a higher mortality on isolated plants than on plants that are part of a vegetation patch (spatially heterogeneous stress). This creates a spatially heterogeneous stress, stronger on isolated plants, thereby mimicking the positive effect of associative protection among plants in patches on their survival to herbivory pressure (Baraza et al. 2006). Using this model, we simulated images with three different vegetation covers and three scenarios for plant mortality: a scenario with mortality due to aridity, a scenario with mortality due to herbivory, and an intermediate scenario. This allowed investigating the effect of herbivory compared to aridity-driven mortality while controlling for changes in vegetation cover (as for the observed images). Last, to understand the consequence of this spatially heterogeneous mortality on dryland resilience, we investigated the risk of abrupt desertification (change to a desert state deprived of vegetation) in the different scenarios of plant mortality (as we detail in Note S3). Simulations were performed using the **chouca** R-package (Génin et al. 2024) (v0.0.99), and we computed for each simulation the above-mentioned spatial statistics for each simulation.

3 | Results

3.1 | Grazing Effects on Spatial Structure

Plants were aggregated into larger patches in the presence of herbivores, as indicated by the increase in both the spatial autocorrelation of the vegetation, the mean patch size, and the loss of the smallest vegetation patches (Figure 2a, middle panel). As a result, patch-size distributions were on average more heavy-tailed in grazed than in ungrazed areas (i.e., the power-law exponent of the PSD increases; Figure S7). Since plants are aggregated into larger vegetation patches, water and nutrients can flow more easily between vegetation patches, as exemplified by the increase in connectivity of bare areas and the decrease in the number of smallest vegetation patches (Figure 2a, middle panel).

Importantly, we did not find differences of effects between grazing pressures, suggesting that the presence of herbivores is associated with changes in vegetation spatial structure, but that differences between grazing pressures are only driven by vegetation cover without additional changes in the spatial organization of the vegetation (Figure 2, Figure S8). By contrast, when not controlling for changes in vegetation cover, only spatial autocorrelation was significantly higher in areas where grazing pressure is high, while all other spatial statistics (e.g., mean patch-size, exponent of the PSD) were lower (Figure S9a, middle panel).

The effects of herbivores on the spatial structure of vegetation were remarkably similar to those of mean annual temperature but opposite to those of aridity (Figure 2a, left and right panels, Figure S10). It is noteworthy that despite grazing being a local gradient, it has similar effect sizes as aridity and mean annual temperature, suggesting its strong impact on the spatial structure of dryland plant communities.

Aridity effects were nevertheless modulated by local grazing pressure. With increasing grazing pressure, aridity effects on the patch-size distribution and the connectivity of bare soil areas weakened, suggesting that high grazing levels can offset aridity effects on spatial structure (Figure S11a,d). Yet, this was not the case for all spatial statistics. We found that aridity can act in synergy with grazing, for example, by reinforcing the loss of small vegetation patches (Figure S11c).

Beyond grazing pressure, we also observed that grazing effects on the spatial structure of vegetation differed depending on the dominant livestock species. For example, in sites dominated by goats and sheep, vegetation was characterized by higher spatial autocorrelation and connectivity of bare areas, and a more heavy-tailed PSD than sites dominated by horses and cattle (Figure 3, pink and orange compared to blue points). While there were no differences between goats and sheep, we observed differences between cattle and horses, as areas dominated by horses tended to exhibit smaller vegetation patches, connectivity of bare areas, and less heavy-tailed PSD than those dominated by cattle (Figure 3 blue points).

3.2 | Mechanisms of Herbivory Effects

Consistent with our hypotheses, all three pathways (% of woody species, average plant size, and spatial aggregation of the species with contrasted sizes) were associated with a higher level of aggregation of the vegetation and explained 38% of the variance of the PC1-axis (Figure 4a). We found that the presence of herbivores was directly associated with a slight decrease in average plant size. This effect was nevertheless offset by the increase in the percentage of woody species, which are relatively large plant species that are more frequently observed in high grazing areas than those ungrazed (Figure S13a; Biancari et al. 2024). As a comparison, in most dry areas, aridity was also associated with smaller average

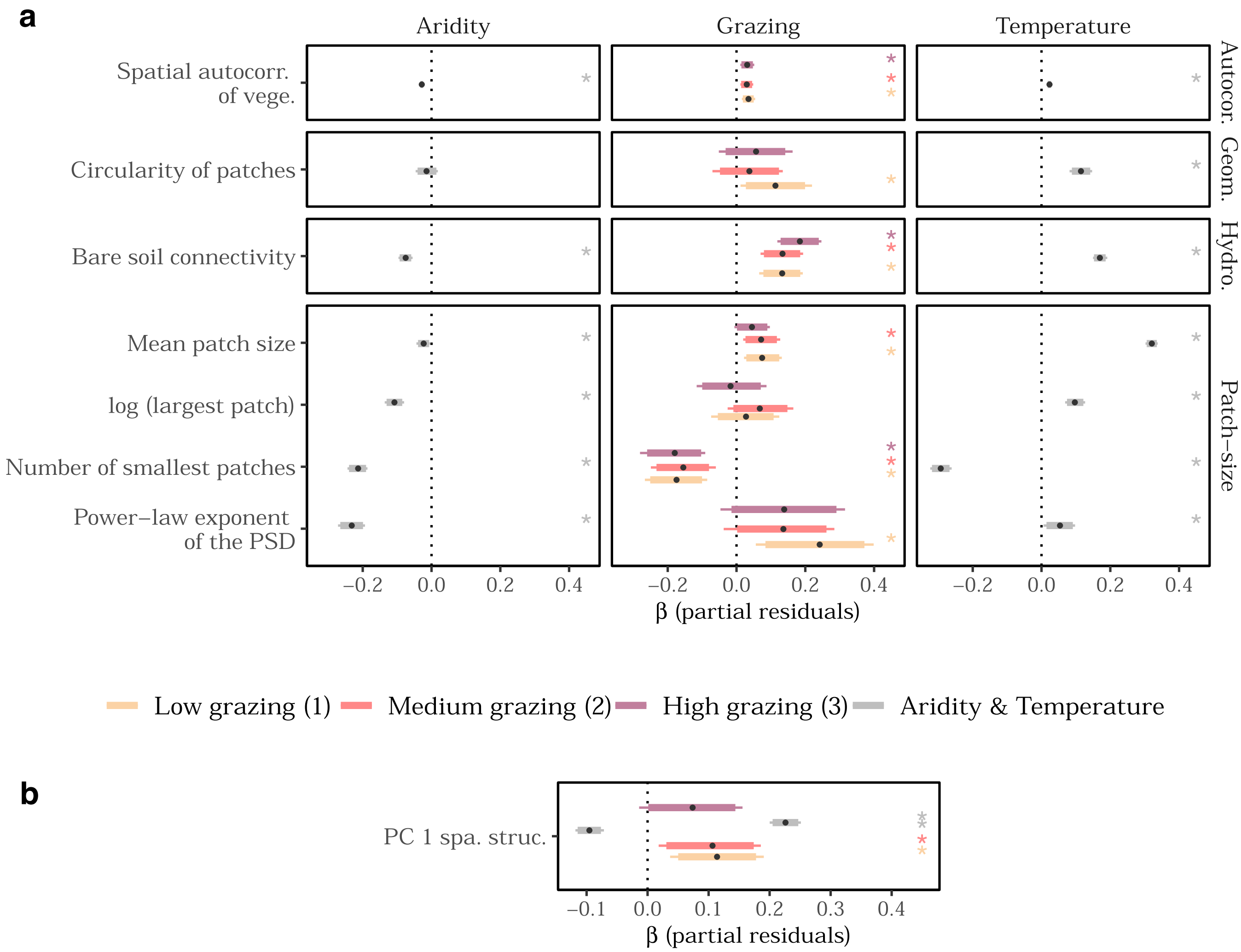

FIGURE 2 | Contrasted effects of grazing and temperature compared to aridity on the spatial structure of the vegetation. (a) Predicted changes in spatial statistics (related to spatial autocorrelation, patch-geometry, hydrological processes and the patch-size distribution) using partial residuals from the model (Equation 1) of each spatial statistic along grazing pressure, aridity, and mean annual temperature gradients. (b) Same as (a) but using the first principal component of a principal component analysis (PCA) performed on all spatial statistics. The first principal component distinguishes between aridity (associated with lower mean patch-size and more heavy-tailed patch-size distribution [PSD]), and both grazing and mean annual temperature effects (associated with larger mean patch-size and less heavy-tailed PSD; see Figure S2 for the PCA). All grazing effects are relative to the ungrazed plot reference. The confidence intervals were estimated by bootstrap (1000). The bars correspond to the 90% confidence intervals and lines extend to the 95% ones. The symbols on the right indicate results that are significantly different from ungrazed plots (for grazing) or from zero (for temperature and aridity) ($*p<0.05$). We refer to Figure S9 for the same analysis but without controlling each spatial statistics for its correlation with vegetation cover.

plant sizes (cLS), both directly and through the decrease in the fraction of woody species, but its effect was about six times the one observed for grazing (total effects = −0.06 for grazing and −0.36 for aridity; Figure 4b). In addition, we observed that aridity was consistently associated with higher spatial aggregation of species with contrasted sizes (smaller DevLS), while grazing had only a weak positive indirect effect on such spatial aggregation (Figure 4b). It is noteworthy that while mean annual temperature and grazing had similar effects on vegetation spatial structure (Figure 2), their effects were mediated by different mechanisms, as warmer drylands were associated with larger and more woody plant species and lower spatial aggregation of species with contrasting sizes.

While these pathways provide a plausible explanation for the contrasted temperature and aridity effects, they only partially explained how grazing affects plant spatial patterns. In fact, the presence of herbivores was associated with a near null effect on the PC1, which suggests that other mechanisms further add up to the three pathways explored (Figure 4) to explain the contrasted aridity and grazing effects on plant spatial structure found (Figure 2).

3.3 | Model Simulations of Herbivory Effects

By increasing the relative importance of spatially heterogeneous mortality (i.e., assumed to mimic herbivory), we observed similar effects as those from increased grazing pressure in the data (Figure 5b): patch-size distribution became more heavy-tailed due to the loss of smaller patches (Figure S15), while mean patch size and the area occupied by the largest patch increased

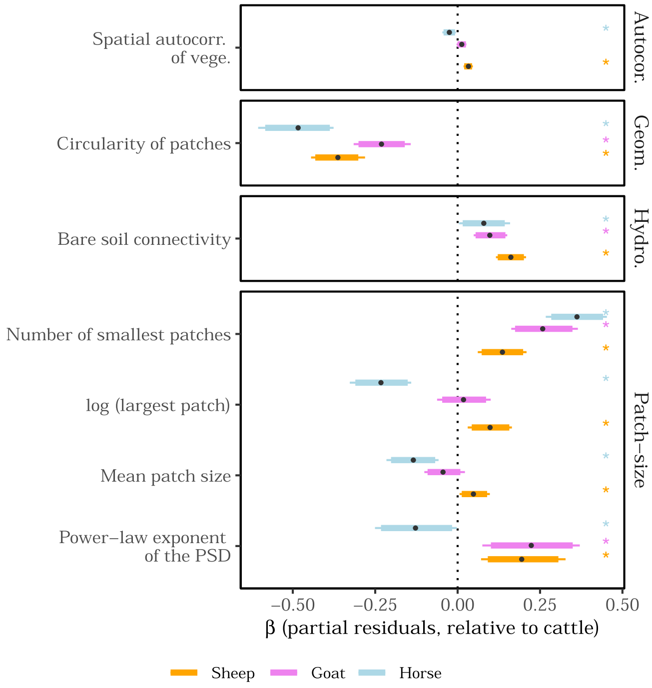

FIGURE 3 | Effect of the dominant livestock species on the spatial structure of the vegetation. Predicted changes in spatial statistics (related to spatial autocorrelation, patch-geometry, hydrological processes and the patch-size distribution) using partial residuals from the model (Equation 1) of each spatial statistic along the different types of herbivores. The confidence intervals were estimated by bootstrap (1000). The bars correspond to the 90% confidence intervals and lines extend to the 95% ones. The symbols on the right indicate results that are significantly different from the cattle (*$p < 0.05$).

(Figure 5a,b). This model analysis suggests that if the presence of herbivores is associated with associative protection between plant species (as assumed in the model), this could result in larger vegetation patches and a more heavy-tailed PSD, consistent with what is observed in the data. In addition, the model predicts that such spatially heterogeneous mortality can impact dryland resilience by promoting more abrupt desertification to a desert state deprived of vegetation (Figure S16, panel b vs. c). This abrupt desertification is also associated with more frequent bistability (i.e., the coexistence of a vegetated and desert state for similar conditions; Figure S16, panel d vs. e), suggesting that drylands are more sensitive to disturbances and can hardly be restored once desertified.

4 | Discussion

In this study, we integrated field data on plant cover and size, remote sensing imagery from drylands, and model simulations to investigate the multiscale impacts of grazing on vegetation spatial structure and the underlying ecological mechanisms. We found that increases in grazing pressure in our study were associated with larger vegetation patches and the loss of smaller patches, which tended to make the patch-size distribution more heavy-tailed. These grazing effects changed depending on the dominant livestock species and could be partially explained by the decrease in average plant size and the increase of both size-based spatial aggregation and woody species with increasing grazing level. The use of model simulations suggested that associative protection could be a process that accounted for the observed changes in vegetation spatial structure.

4.1 | Higher Spatial Aggregation Is Found in Grazed Areas

Beyond decreasing vegetation cover, the presence of herbivores was associated with fewer small-size patches, and surprisingly, larger vegetation patches on average. Together, this makes the patch-size distributions more heavy-tailed in highly grazed areas compared to ungrazed plots. This contrasts with previous studies across local gradients in drylands, which found negative (Oñatibia et al. 2018) or no association (Oñatibia and Aguiar 2018) between mean patch size and the presence of grazers, and an increase in the frequency of small vegetation patches (Lin, Han, et al. 2010). Such discrepancies may be explained by the fact that these previous studies did not control for changes in vegetation cover along grazing gradients, so that changes in mean patch size merely reflected a change in vegetation cover. In our study, however, even without controlling the spatial statistics for changes in vegetation cover (see Methods), we also observe higher spatial autocorrelation and a lower number of smallest patches for all grazing levels. This suggests that, beyond methodology, the presence of herbivores changes plant spatial patterns in a rather singular way that is similar to the effect of temperature on plant spatial patterns. By contrast, and consistently with previous studies on aridity (Moreno-de Las Heras et al. 2011; Kéfi et al. 2024), we observe opposite associations between aridity and the spatial structure of the vegetation compared to grazing: drier areas have smaller average patch sizes and less heavy-tailed patch-size distributions.

4.2 | Mechanisms Behind Grazing Effects

Grazing and aridity act in synergy by decreasing mean plant size, consistent with previous studies along local or regional aridity gradients (Adler et al. 2004; Díaz et al. 2007; Gross et al. 2013) or studies of grazing and aridity (Oñatibia et al. 2020). In communities where plants are smaller, such as in cold, dry, and grazed dryland sites, species with contrasted sizes are more spatially associated within quadrats. This is consistent with previous studies showing that plant traits determine plant–plant interactions in drylands (Soliveres et al. 2014, 2015). The increase in the spatial dispersion of plant sizes therefore suggests a switch from more competitive interactions to facilitation among species of contrasted sizes in drier and more grazed areas in agreement with the stress-gradient hypothesis (Bertness and Callaway 1994). As opposed to competitive interactions that can limit spatial aggregation of tall species, thereby promoting more patchy distributions of species (e.g., Gilad et al. 2007) and more regular spatial patterns (Wojcikiewicz et al. 2024), this relative increase in the spatial aggregation of species with different sizes might indicate that small beneficiary plants are more often protected by large facilitating species (Navarro-Cano et al. 2021), thereby generating larger vegetation patches.

Grazed and warm areas display smaller and more woody species (Van Auken 2000), which contrasts with fewer woody species found in more arid places. This effect is consistent

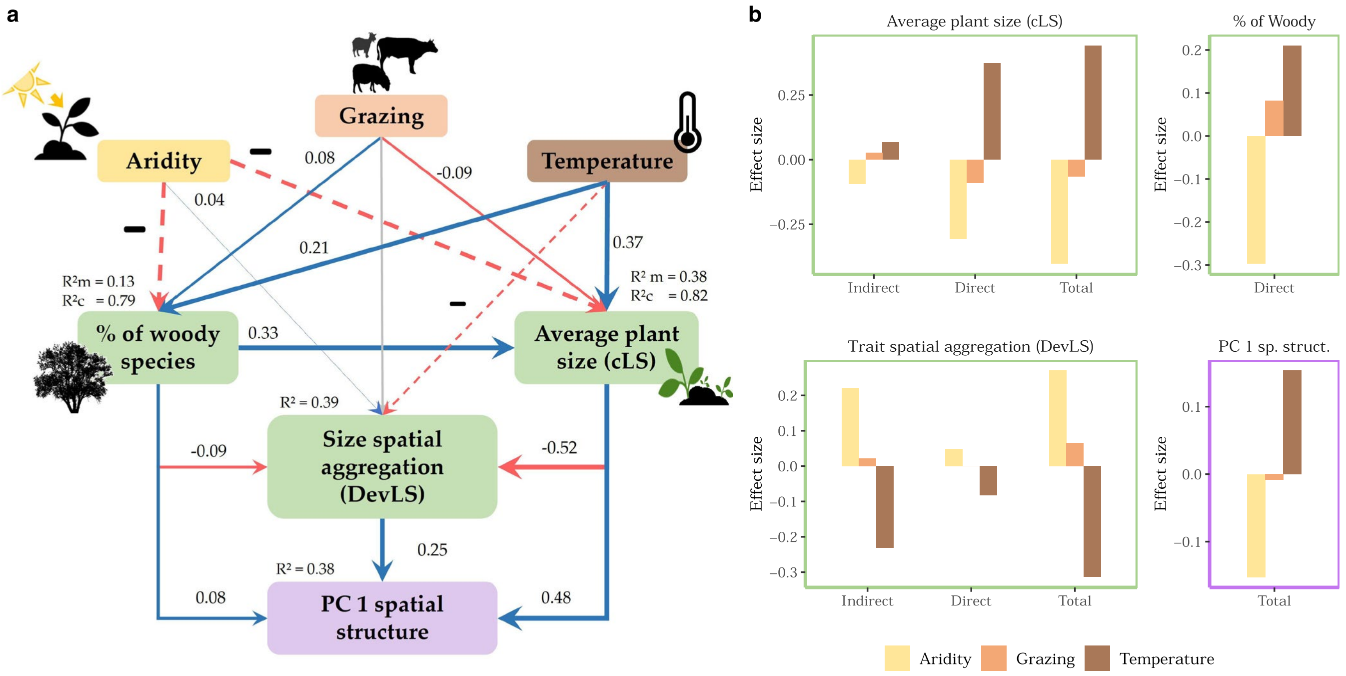

FIGURE 4 | Community size and composition identify unique pathways of grazing, aridity, and mean annual temperature effects on the spatial structure of the vegetation. (a) Structural equation model decomposing the effects of grazing, aridity and mean annual temperature through the changes in community composition (% of woody species in quadrats), and functional structure of the community (cLS: CWM lateral spread and DevLS: the spatial organization of plant size in quadrats as inferred by the deviation from null expectation of the dispersion of cLS across quadrats). Red (*resp.* blue) lines correspond to negative (*resp.* positive) direct effects, while full (*resp.* dashed) lines correspond to linear (*resp.* quadratic) effects. We refer to Table S2 for all coefficients, in particular for non-linear effects for which we only indicate the effect sign here. Non-significant paths are shown in grey. The R^2 of the models are shown in the top of each SEM box. Note that the link between MAT and woody is only slightly significantly different from 0 ($p = 0.066$; Table S2). (b) Direct, indirect and total (direct + indirect) effects aridity (yellow), grazing (orange), and mean annual temperature (dark yellow) on the community structure and plant spatial patterns.

with a positive effect of temperature on shrub encroachment, but contrasts with the negative association between aridity and the percentage of shrub species in the field. In areas where grasses and shrubs coexist, as in the Patagonian or Mediterranean steppes, there is a two-phase structure with patches of grasses and shrubs diluted on a low-cover matrix devoid of perennial plants (Maestre and Cortina 2004; Cipriotti and Aguiar 2005). Previous studies have emphasized that the presence of herbivores tends to strengthen the association between grasses and shrubs in patches by preferentially feeding on palatable grasses in open areas (Cipriotti and Aguiar 2005; Gaitán et al. 2018; but see Seifan and Kadmon 2006). The preference of some herbivore species for herbaceous species likely releases competition between shrub and herbaceous species, allowing shrubs to grow. In addition, while not all sites present this two-phase structure, this form of community turnover is also observed in other dryland types (Eldridge et al. 2013). By studying grazing in arid steppes and semi-desert, Carboni et al. (2023) found that the presence of herbivores is associated with a drastic decrease in grass but an increase in the cover and size of shrub species.

We observed differences in the effects of dominant livestock species on vegetation spatial patterns. Some of these differences may reflect known feeding habits—ranging from mixed feeding with a tendency toward browsing (as in sheep and goats; Staver et al. 2021) to predominantly grazing behavior (as in cattle and horses). However, while no significant differences emerged between sheep and goats, the contrasting effects observed between horses and cattle point to a more nuanced picture beyond the classic grazer–browser dichotomy (Robbins et al. 1995). For example, horses influenced spatial vegetation patterns differently than cattle, as their presence was linked to smaller mean patch sizes and greater patch fragmentation compared to cattle. These differences may stem from the behavioral plasticity of herbivores, whose feeding strategies can shift depending on vegetation quality or life form (Espunyes et al. 2019). Because our analysis derived average global effects for each herbivore species, such context-dependent behaviors were not fully captured. Further research is therefore needed to understand how specific herbivore species shape vegetation spatial structure under varying ecological conditions.

Taken together, these mechanisms nevertheless only partially explain the specificity of grazing effects on spatial structure, as compared to aridity, as grazing had a negligible indirect effect on plant spatial patterns through community plant size and woody composition. By contrast, mean annual temperature has similar effects on spatial structure compared to grazing, but mediated by the presence of larger and more woody species. There are nevertheless other mechanisms that could explain grazing effects on the spatial patterns of vegetation. For example, as the presence of shrubs and herbivores are both associated with higher soil fertility (Allington and Valone 2014; Eldridge et al. 2011; Maestre, Eldridge, et al. 2022), there might be a higher probability of seedling recruitment in the neighborhood

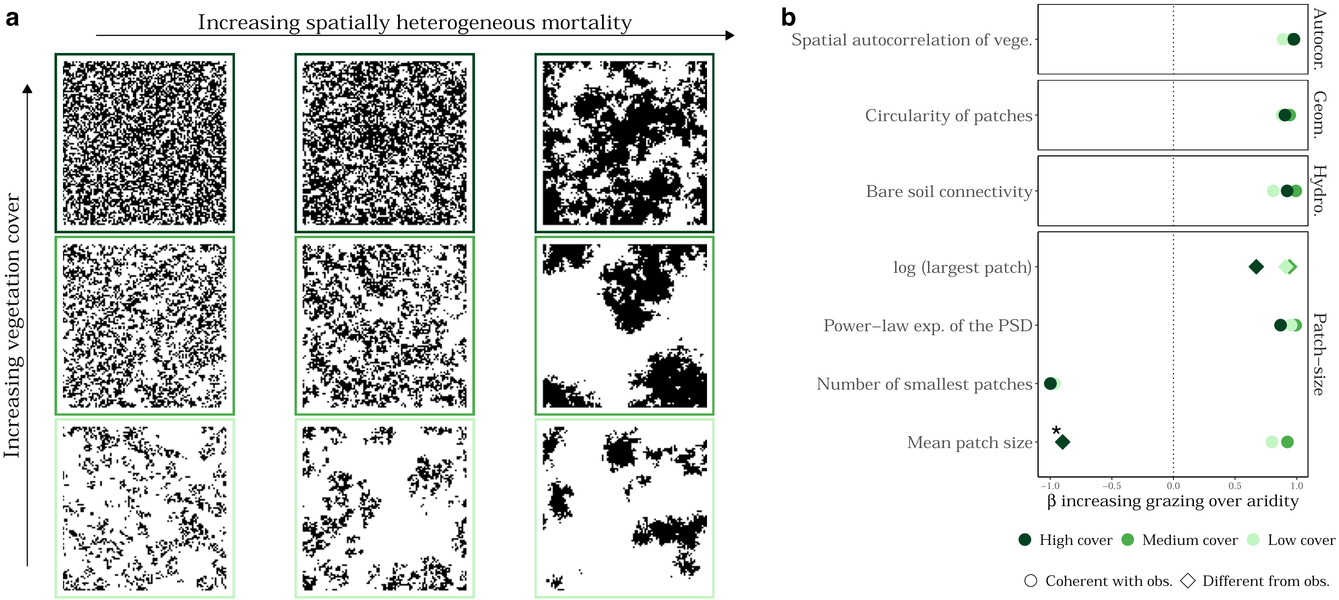

FIGURE 5 | Simulations with spatially explicit mortality reveal similar effects compared to grazing effects on observed spatial structure. (a) We simulated images with three different vegetation covers (top row: 0.55, middle row: 0.35 and bottom row: 0.17) and three scenarios for plant mortality: from no effect of herbivores (i.e., only spatially homogeneous stress; left column) to a large effect (mainly spatially heterogeneous stress; right column). An image for each parameter set, at its asymptotic state, is shown. (b) For each image, we computed the different spatial metrics, and we indicate the effect size (slope of a linear model) of each spatial statistic against the spatially heterogeneous mortality parameter. The color distinguishes the three vegetation covers at which this effect size was computed, and the shape indicates whether our simulation results are coherent with observations (circle) or not (diamond). *For simulations with high vegetation cover, percolation can occur in a typical output simulated image with spatially homogeneous mortality (see top left image), meaning that there is a large patch occupying most of the image. This is, however, not observed for simulations with spatially heterogeneous pressure. Consequently, mean patch size decreases with higher importance of spatially heterogeneous mortality (negative effect size) due to the desegregation of this large percolating patch.

of vegetation patches, which may further reinforce the increase in the average patch size in grazed areas. This can also be the consequence of compensatory growth in the presence of herbivores (McNaughton 1983; Oñatibia and Aguiar 2016), especially at low grazing pressure, where grazing is associated with slightly higher vegetation cover compared to ungrazed plots (Figure S4).

In addition, studies testing the outcome of plant–plant interactions across grazing gradients have found increasing facilitation among plant species, as nurse plants can provide physical refuges to the most palatable species (Baraza et al. 2006; Graff et al. 2007; Graff and Aguiar 2011). When accounting for herbivore selective feeding strategy and associative protection of palatable species in a model, this generates a spatially heterogeneous plant mortality that mimics the observed effects of grazing on the spatial structure. Compared to previous theoretical studies of grazing effects on plant spatial patterns that did not confront model outputs with empirical observations for validation (Schneider and Kéfi 2016; Szangolies et al. 2023; but see Irob et al. 2023), the similar effects observed between simulations and observations suggest that we can use these models to identify possible pathways of degradation in grazed areas. Taken together, our approach combining field data, ecosystem images, and simulations provides a comprehensive understanding of the effects of grazing on plant spatial patterns. Furthermore, it enhances previous studies that locally examine changes in vegetation spatial structure along local abiotic or biotic gradients in three ways. Firstly, the global sampling across different ecosystem types allows the effect of grazing pressure to be contrasted with the type of herbivore, highlighting the specific effects of the different herbivore species on plant spatial patterns. Secondly, the field data showed that grazing and climate affected the spatial structure of vegetation through changes in average plant size, life forms, and both direct and indirect facilitation among plants. Finally, the validation of a model of grazing effects in drylands against observations paves the way for future studies aiming at understanding how the interplay between different species attributes (size, woodiness, interactions…) scales up to generate plant spatial patterns, and to generate a more mechanistic understanding of grazing impacts on dryland ecosystems.

4.3 | Grazing-Induced Fragmentation and Resilience

We found that grazing was associated with higher connectivity of bare soil areas. While bare areas are more connected, which can lead to increased erosion, runoff, and flows of sediments between vegetation patches (Mayor et al. 2008; López et al. 2013), vegetation patches are large and can therefore capture more nutrients, seeds, and dust, further reinforcing their fertile island effect (Ludwig and Tongway 1995; Ludwig et al. 2000). These mechanisms might ultimately increase the size of vegetation patches and can be further reinforced by community turnover in plant communities. For example, in our dataset, surveyed shrublands and forests are characterized by more woody species and higher bare soil connectivity than grasslands (Figure S14). Such increasing bare soil connectivity is not without consequences for the stability of drylands. When accounted for in models, Mayor et al. (2019) found that an increase in bare soil connectivity can foster a positive feedback between bare soil connectivity and the availability of water and nutrients, which promotes more abrupt and faster desertification of drylands through greater nutrient leaching and erosion.

Associative protection against herbivory also generates a positive feedback between vegetation patch size and herbivory pressure, which promotes larger vegetation patches. When accounted for in the model, it predicts that such positive feedback can promote more abrupt desertification and larger bistability (Figure S16; Schneider and Kéfi 2016). This bistability implies that once a dryland area would be desertified (deprived of vegetation in the model), decreasing herbivory pressure would not necessarily lead to the restoration of the vegetation cover. Overgrazing combined with the rapid increase in aridity in some areas (Huang et al. 2016) might thereby promote the desertification of large areas (Burrell et al. 2020). More than just an additive effect, we found that interactions between aridity and grazing, with aridity reinforcing the loss of smaller patches in grazed areas but not in ungrazed ones. Such interactions between drivers also likely act on individual plant resilience. For example, lower levels of plant regrowth have been demonstrated in more arid compared to mesic areas, but only when plants were grazed (Louthan et al. 2013). Similarly, sheep grazing was found to have more severe impacts on plant communities in drier than in more mesic sites because grazing effects were partly balanced by the increase in shrub size and cover in the more mesic sites (Carboni et al. 2023).

4.4 | Perspective

Current assessments of resilience in dryland ecosystems often rely on coarse, community-scale approaches, such as analyzing spatial vegetation patterns from images (Pichon, Donnet, et al. 2024) or using remotely sensed productivity indices to quantify stability over time (García-Palacios et al. 2018). However, our study suggests that a shift toward incorporating individual-level attributes such as plant traits can provide more precise insights into the mechanisms, thereby contributing to the understanding of the pathways by which species-level patterns scale up to ecosystem-level vegetation spatial structure. This shift is important for enhancing our understanding of dryland resilience and ultimately pinpointing the most resilient communities. For example, functional diversity of plant strategies (Irob et al. 2023) and leaf traits (Song et al. 2024) has been associated with higher resilience or resistance in theory and experiments, respectively. Plant traits have also been identified as a key driver of plant–plant interaction outcomes in drylands (Soliveres et al. 2014). In addition, this diversity of plant strategies is key to maintaining high diversity of species despite dry conditions or high competition among plants (e.g., see Bera et al. 2021; Pichon, Gounand, et al. 2024).

Continuing in this direction by expanding to different traits will likely capture how the different drivers (e.g., grazing and aridity) affect plant functional structure (Frenette Dussault et al. 2013; Gross et al. 2013; Blumenthal et al. 2020), and how such species-level attributes scale up to ecosystem-level properties such as spatial structure and resilience. For example, in the context of grazing, we would expect that species with different defense mechanisms against herbivory (e.g., production of phenols or thorns, or low palatability with higher leaf dry mass content) might be more spatially aggregated within a patch when grazing pressure is high, consistent with Graff and Aguiar (2011), since associative protection is likely a mechanism that drives the observed changes in plant spatial patterns. By establishing clear linkages between species-level attributes and ecosystem-level properties, our study provides an improved understanding of the different pathways through which grazing and climate influence the structure, the dynamics, and the resilience of drylands. Our approach and findings not only improve our understanding of the different feedbacks between herbivores and the vegetation within dryland ecosystems, but also open new avenues for integrating diverse sources of information to assess the risk of desertification across drylands worldwide.

Author Contributions

Benoît Pichon: conceptualization, formal analysis, investigation, methodology, software, visualization, writing – original draft. **Sonia Kéfi:** conceptualization, methodology, supervision, validation, visualization, writing – review and editing. **Isabelle Gounand:** conceptualization, methodology, supervision, validation, visualization, writing – review and editing. **Nicolas Gross:** conceptualization, data curation, writing – review and editing. **Yoann Le Bagousse-Pinguet:** conceptualization, data curation, writing – review and editing. **Josquin Guerber:** data curation, writing – review and editing. **David Eldridge:** data curation, writing – review and editing. **Enrique Valencia:** data curation, writing – review and editing. **César Plaza:** data curation, writing – review and editing. **Jaime Martínez-Valderrama:** data curation, writing – review and editing. **Hugo Saiz:** data curation, writing – review and editing. **Victoria Ochoa:** data curation, writing – review and editing. **Beatriz Gozalo:** data curation, writing – review and editing. **Emilio Guirado:** data curation, writing – review and editing. **Miguel García-Gómez:** data curation, writing – review and editing. **Juan J. Gaitán:** data curation, writing – review and editing. **Sergio Asensio:** data curation, writing – review and editing. **Betty Josefina Mendoza:** data curation, writing – review and editing. **Sophie Donnet:** conceptualization, methodology, supervision, validation, visualization, writing – review and editing. **Fernando T. Maestre:** data curation, project administration, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Zenodo at http://doi.org/10.5281/zenodo.15762242 and Github at https://github.com/bpichon0/Grazing_patch_vegetation/tree/grazing_submission. The BIODESERT survey data were obtained from FigShare at https://doi.org/10.6084/m9.figshare.14923065.v1. Climate data were obtained from WorldClim at https://www.worldclim.org/.

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Supporting Information

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