ECOLOGY

Drivers of woody dominance across global drylands

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Increases in the abundance of woody species have been reported to affect the provisioning of ecosystem services in drylands worldwide. However, it is virtually unknown how multiple biotic and abiotic drivers, such as climate, grazing, and fire, interact to determine woody dominance across global drylands. We conducted a standardized field survey in 304 plots across 25 countries to assess how climatic features, soil properties, grazing, and fire affect woody dominance in dryland rangelands. Precipitation, temperature, and grazing were key determinants of tree and shrub dominance. The effects of grazing were determined not solely by grazing pressure but also by the dominant livestock species. Interactions between soil, climate, and grazing and differences in responses to these factors between trees and shrubs were key to understanding changes in woody dominance. Our findings suggest that projected changes in climate and grazing pressure may increase woody dominance in drylands, altering their structure and functioning.

INTRODUCTION

Drylands are defined as areas with an aridity index (precipitation/potential evapotranspiration) below 0.65. They encompass a wide variety of biomes, including deserts, grasslands, steppes, shrublands, and savannas. Drylands are experiencing rapid changes in their structure and functioning due to human-induced global changes, which are affecting their capacity to deliver essential ecosystem services (*1*, *2*). One of the most noticeable changes being observed across global drylands is the increasing abundance of woody plants, especially in grass-dominated ecosystems (*3*–*7*). The ratio between the cover of woody and herbaceous species is a key feature of terrestrial ecosystems, and variations in this ratio have been related to both positive (e.g., increases in carbon sequestration) and negative (e.g., declines in forage quantity and quality) changes in the delivery of ecosystem services (*5*, *8*–*10*). Understanding the drivers of woody plant cover in drylands, which represent 41% of terrestrial surface and are expected to be among the ecosystems most affected by climate change (*11*, *12*), is thus critical for predicting and managing the impacts of global change on terrestrial ecosystems. Yet, most existing literature on woody dominance is based on humid (non-dryland) or subhumid savannas, and we still lack a global assessment of the main drivers of woody vegetation across other dryland biomes (*6*, *13*, *14*).

The drivers of the abundance of woody species are diverse (*14*–*17*) and include biotic interactions (*18*), spatial and temporal variation in the availability of resources due to climatic and soil factors (*19*–*21*), and disturbance regimes such as fire or grazing (*7*, *22*). Previous regional and subcontinental studies investigating coexistence between woody and herbaceous plants have mainly focused on the role of climate, soil heterogeneity, disturbances, and increasing atmospheric CO_2 (*15*, *19*, *23*–*25*). For example, increases in maximum tree cover and mean woody cover with increasing mean annual precipitation (MAP) have been described for African savannas (*4*, *13*). In addition, coarser soil textures are associated with higher shrub and tree cover because of increased infiltration and water availability in deeper soil layers (*17*, *19*, *21*). Other key aspects of the precipitation regime, such as seasonality, have been reported to be key drivers of savanna structure and dynamics (*26*–*30*). However, there are still considerable uncertainties about how ongoing global warming will affect woody dominance in drylands, as findings regarding the influence of temperature on the population dynamics and cover of woody species reveal contrasting outcomes (*4*, *24*, *31*, *32*).

Grazing and fire are key disturbances known to have large effects on dryland vegetation (*1*, *33*–*36*). However, there is a lack of consensus about how grazing and fire determine woody dominance patterns. Grazing has been reported to increase (*4*, *7*), decrease (*21*, *37*), or have no effect (*13*, *38*) on woody abundance in drylands, while fire has been reported to decrease (*4*, *39*) or not affect woody abundance at all (*40*, *41*). These contrasting results indicate that the actual effects of grazing and fire may depend on other interacting factors. Grazing effects on woody dominance may depend on

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stocking rate and herbivore species (*37*, *42*, *43*). Aridity can play an important role too, as increases in grazing pressure could potentially promote shifts from grasslands to shrub steppes to deserts under increasing aridification (*44*). Declines in water availability under increased aridity can also represent a bigger constraint to woody cover than the fire regime itself (*40*, *41*). Further, the connectivity among vegetation patches is usually lower at high aridity sites, reducing the probability of fire spread (*45*). We still lack a global synthesis of how grazing and fire may change woody cover and how they interact with other variables such as herbivore identity and aridity.

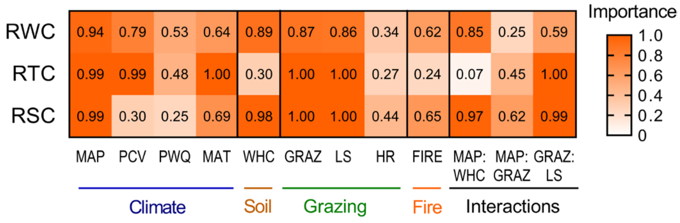
There is growing recognition of the need to simultaneously consider multiple drivers and their interactions to accurately predict and manage vegetation change (*4*, *29*, *34*). While climatic drivers can be better studied at large spatial scales, others, such as grazing, require detailed local-scale information to elucidate the mechanisms that determine vegetation responses. Previous studies carried out at local scales (*46*) have resulted in context-dependent hypotheses, whereas those at regional or subcontinental scales (*4*, *13*) lacked detail on the local disturbance regime. In addition, previous large-scale studies usually reported correlations instead of explicitly accounting for grazing pressure differences at the local scale. Overcoming these limitations requires a comprehensive and standardized assessment of the local effects of increasing grazing pressure and aridity on woody dominance across drylands worldwide.

Here, we report results from a standardized global field survey conducted in 92 sites located in 25 countries from six continents to assess the joint influence of climate, soil properties, grazing, and fire disturbance on woody dominance across global drylands (table S1 contains a detailed list of studied factors, rationale, and references). We also used this survey to test two hypotheses related to grazing not explored before for drylands at a global scale: (i) a lack of response to increasing grazing pressure on relative woody cover (RWC) as aridity increases, due to plant traits related to grazing and drought tolerance converging in arid systems (*47*, *48*); and (ii) the effect of increasing grazing pressure on RWC varies with the dominant livestock species because of different foraging behaviors (e.g., grazers versus browsers) and changes in herbivore selectivity (*36*, *37*, *43*, *49*).

RESULTS

Climate, soil properties, and grazing were the most important variables correlated with RWC across global drylands (Fig. 1). The best-fitting model for RWC included the interactions between MAP and soil water holding capacity (WHC) and between grazing pressure and dominant livestock species (Fig. 2A). RWC increased with increasing MAP, but only in sites with soil WHC values below 27% (table S4). Increasing grazing pressure in sites with cattle or horses increased RWC (Figs. 2A and 3A), which also increased with precipitation seasonality (Fig. 2A and table S4).

The importance of RWC predictors changed when tree and shrub cover were analyzed separately. Variables linked to grazing and climate were important in relation to relative tree cover (Fig. 1), with MAP and seasonality positively related to it (Fig. 2B and table S4). We also found a nonlinear pattern related to temperature, with relative tree cover increasing with temperature before reaching an optimum of 15°C and decreasing after (Fig. 4B and table S4). The best-fitting model included a significant interaction between grazing pressure and dominant livestock species (Fig. 2B). In sites with cattle or horses, we found increases in relative tree cover with increasing grazing pressure (Fig. 3B). However, relative tree cover declined as goat grazing pressure increased (a 66% lower cover across all grazed versus ungrazed plots). Relative shrub cover was mainly explained by grazing pressure × livestock species (Fig. 3C) and MAP × soil WHC (Fig. 1) interactions. In areas grazed by sheep and goats, relative shrub cover decreased by 27% and increased by 60%, respectively, at high grazing pressure plots compared to that in ungrazed ones. When precipitation was lower than 383 mm, relative shrub cover was higher at sites with higher soil WHC than at sites with lower soil WHC, while the opposite pattern was found when precipitation was higher than 383 mm (Fig. 4A and table S4). Sites that experienced fire in the last 20 years had on average 38% less relative shrub cover than sites without fire, but this effect was not statistically significant ($P = 0.06$). Inter-site variability was significant for relative woody, tree, and shrub cover (table S5).



	MAP	PCV	PWQ	MAT	WHC	GRAZ	LS	HR	FIRE	MAP: WHC	MAP: GRAZ	GRAZ: LS
RWC	0.94	0.79	0.53	0.64	0.89	0.87	0.86	0.34	0.62	0.85	0.25	0.59
RTC	0.99	0.99	0.48	1.00	0.30	1.00	1.00	0.27	0.24	0.07	0.45	1.00
RSC	0.99	0.30	0.25	0.69	0.98	1.00	1.00	0.44	0.65	0.97	0.62	0.99

Fig. 1. Importance of predictors of relative woody, tree, and shrub cover across global drylands. Importance is based on the sum of Akaike weights of all models where each predictor is present using a multimodel inference approach. PCV, precipitation seasonality; PWQ, % precipitation in warmest quarter; MAT, mean annual temperature; WHC, soil water holding capacity; GRAZ, grazing pressure; LS, dominant livestock species; HR, herbivore richness; and FIRE, fire occurrence during the 2001–2019 period. Geographical variables (latitude and longitude) are not shown because they were included in all possible models for relative woody cover (RWC: tree + shrub), relative tree cover (RTC), and relative shrub cover (RSC).

Analogous to relative cover, MAP, grazing pressure, and livestock species were the most important variables correlated with absolute cover of woody species, trees, and shrubs (fig. S3). In addition, the importance of predictor variables shifted when analyzing tree and shrub cover separately. Specifically, interactions involving MAP with grazing pressure were important to explain tree cover (figs. S3 and S4). Contrary to relative cover, the MAP × soil WHC interaction had low importance values to explain the absolute covers of woody species. The best-fitting models accounted for a substantially smaller proportion of variation compared to models for relative cover (fig. S3).

DISCUSSION

MAP accounted for half of the explained variation in RWC across global drylands. The pattern of increased RWC with greater MAP was driven by tree cover, for which growth and survival is usually limited by water. This result is consistent with previous studies conducted in savannas (*4*, *13*, *17*, *32*). The seasonality of precipitation, which was positively associated with relative tree cover, was another climatic feature important to explain changes in RWC. Grasses may outcompete tree species for water in the upper soil layers (*17*), so a higher water availability and a higher frequency of large rainfall events may allow more water infiltration to deeper layers that may be used by deeper-rooted tree species (*26*, *28*, *50*–*52*). Higher mean annual temperature was correlated with an increase in relative shrub

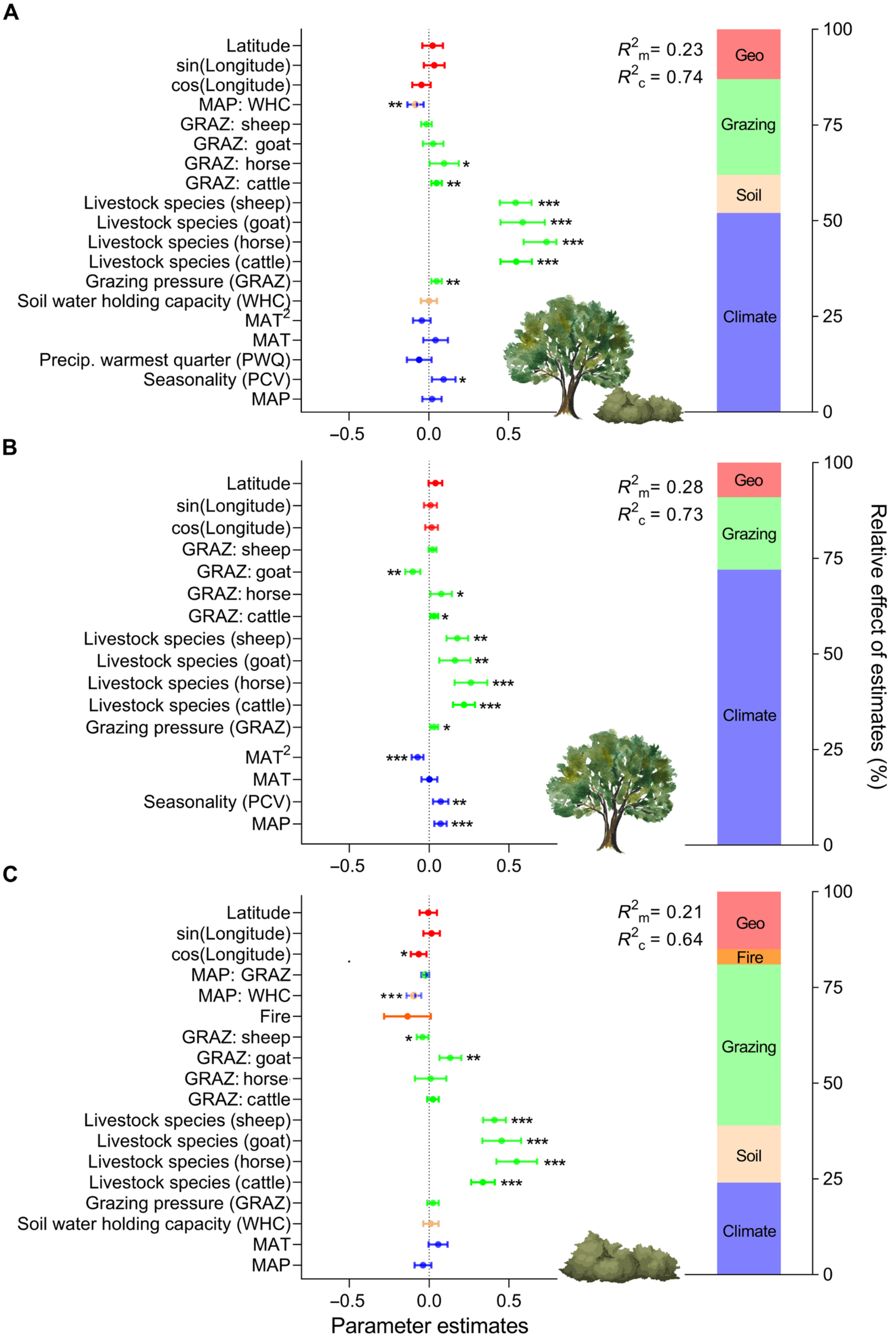


Fig. 2. Parameter estimates of the lowest AICc models (best-fitting models). The models predicted relative woody (tree + shrub) cover (**A**), relative tree cover (**B**), and relative shrub cover (**C**). Standardized regression coefficients and 95% confidence intervals are plotted for each explanatory variable. The right panels show relative effects of each group of variables estimated with a variation partitioning approach [semi-partial coefficient of determination (R^2)]. $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. Abbreviations as in Fig. 1.

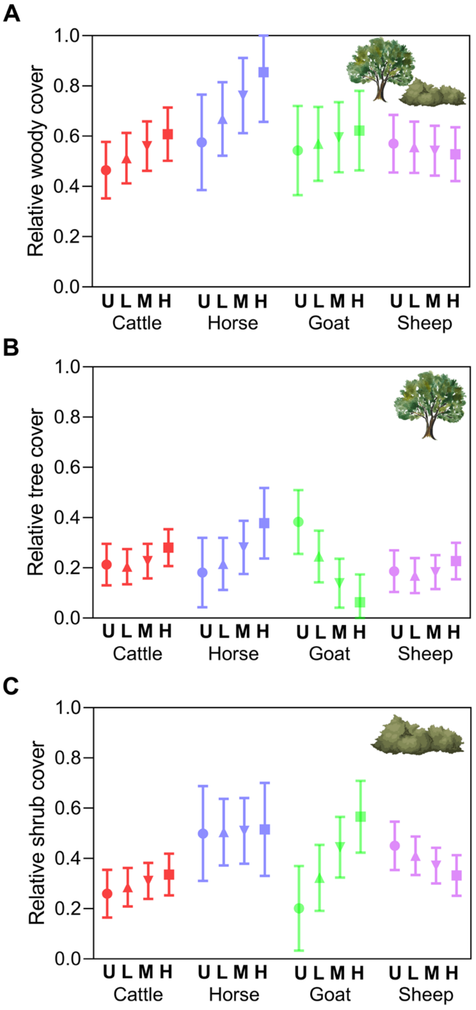


Fig. 3. Effects of livestock species and grazing pressure on woody vegetation cover across global drylands. Relative cover of woody species (**A**), trees (**B**), and shrubs (**C**). U, ungrazed; L, low grazing pressure; M, medium grazing pressure; and H, high grazing pressure. Estimated marginal means and 95% confidence intervals are shown.

cover, suggesting that the increase in evaporative demand could disadvantage grasses more than shrubs, as grasses rely more on available water in the upper layers, reducing to a greater extent their rain-use efficiency (*53*). In contrast to shrubs, relative tree cover showed a bimodal response to temperature. It increased with temperature before reaching a threshold of 15°C, possibly due to the positive effects of temperature on tree species' vital rates [higher seedling establishment and lower frost-induced mortality; (*4*, *54*)]. However, the relative tree cover decreased beyond this temperature threshold, as higher temperatures could have a negative effect on tree species due to increases in water stress and associated mortality (*31*). Climatic projections indicate widespread increases in temperature and atmospheric aridity across drylands worldwide (*11*). Thus, our findings suggest that ongoing global warming could lead to an increase in shrub cover. In addition, while our results suggest a potential decrease in tree dominance across global drylands due to higher temperatures in warmer sites combined with lower precipitation, the intensification of intra-annual precipitation variability and the rising levels of CO_2 could counterbalance the predicted decreases in tree cover at warmer dry biomes (*25*, *28*, *55*). We acknowledge that temporal inferences based on the space-for-time approach used must be done with caution. Nevertheless, this approach remains valid in the investigation of uncertain and time-sensitive ecological patterns and processes (*56*), and its reliability in evaluating temporal changes in drylands has been substantiated (*57*).

Our study shows the importance of grazing in determining global patterns of woody dominance and reveals that its effects are more complex than the general models previously proposed [e.g., increases in grazing pressure leading to woody encroachment; (*24*, *58*)]. We found that the effects of grazing pressure were largely dependent not only on the livestock species as hypothesized but also on the vegetation type considered (i.e., trees or shrubs). The contrasting patterns in woody dominance observed depending on livestock species and feeding strategies (browsers or grazers) support the idea of a complementary effect among mammalian herbivores (*36*). Animal species differ in dietary preferences and foraging behaviors (*49*, *59*), which can directly affect the vital rates of certain plant species (e.g., via defoliation or trampling) or indirectly, by modifying interactions among life forms (*16*, *60*). In sites where cattle and horses are present, increases in grazing pressure were linked to higher

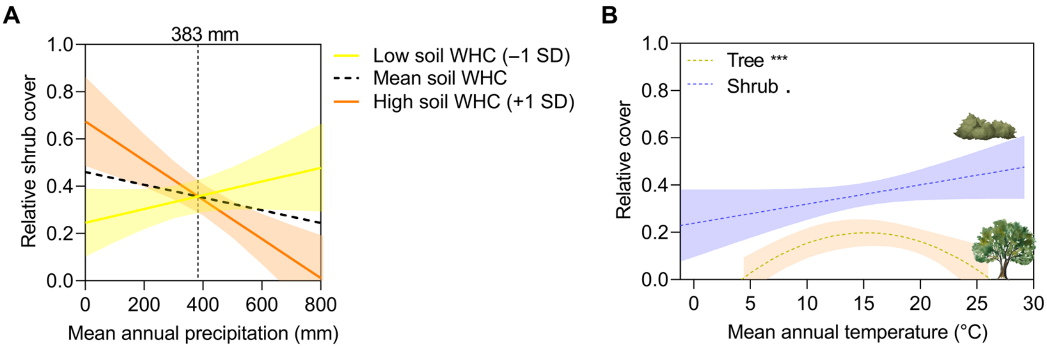


Fig. 4. Changes of relative shrub and tree cover with environmental variables across global drylands. Predicted responses of relative shrub cover in relation to MAP for three levels of soil WHC (**A**) and relative tree and shrub cover in relation to mean annual temperature (**B**). Panel (A) indicates the threshold of texture effect at MAP of 383 mm. "." indicates $P < 0.1$; $^{***}P < 0.001$. Estimated marginal means and 95% confidence intervals are shown.

RWC. This outcome was expected, as cattle and horses prefer to consume grasses over woody plants (*49*). However, this pattern was not observed in sites grazed and browsed by goats and sheep, as these animals can consume both woody and herbaceous species. At sites with goats, relative tree cover declined with increasing herbivore pressure, possibly due to a historic effect from browsing on tree saplings, leading to a reduction in relative tree cover and an increase in relative shrub cover (*61*). Goats are typically mixed feeders but, in a browser-grazer gradient, can be considered the most prominent "browser" among the four livestock species considered in this study (*62*). At sites with sheep, relative shrub cover declined with increasing grazing pressure, while relative woody and tree cover remained unaffected. This outcome may seem unexpected, as sheep are considered to be more selective grazers (*62*). However, grass species replacement from palatable to less-preferred species can buffer reductions in grass cover (*63*, *64*). In addition, some shrub species may be defoliated by sheep during dry years or when they consume flowers during the growing season. Yet, it is important to notice that the number of sites with goats or horses is lower than the number of sites with sheep or cattle in our dataset (table S2). This implies that the strength of our inferences for horses or goats may be lower than for sheep or cattle. We did not find evidence for the hypothesized interaction effect between precipitation and grazing pressure for RWC. However, this interaction was important to explain changes in tree cover, where the positive slopes along the precipitation gradient were gentler as grazing pressure increased, and grazing exclusion increased tree cover only at more mesic sites. This pattern of absolute cover may be a result of tree species traits related to grazing and drought tolerance converging in arid ecosystems as stated in our first hypothesis (*47*, *48*). Another complementary ecological mechanism is that lower grazing pressures only benefit tree establishment and growth when there is sufficient water content in deeper soil layers, something that occurs at sites with higher precipitation (*17*, *21*).

The inverse texture hypothesis (*65*) postulates that finer soils with higher water-holding capacity promote productivity in areas with high precipitation, and coarser soils with lower water retention positively affect productivity in areas with low precipitation. This hypothesis has been demonstrated previously for grasslands and shrublands in North America (*20*, *66*). Our results (Fig. 4) suggest that the inverse texture hypothesis also holds for the global scale. Our estimated point of no texture effect on the precipitation–shrub cover relationship was very similar to previous estimations [370 mm in (*66*) cf. 383 mm in our study], highlighting the robustness of this phenomenon. However, we detected this MAP × soil WHC interaction only on shrubs and not on trees. As this interaction was not important to explain absolute shrub cover (fig. S3), the observed MAP × soil WHC interaction would be an outcome of changes in grass cover (*20*, *66*). Overall, our results indicate that the interaction between MAP and soil WHC should be considered a key element of shrub:grass coexistence models for global drylands.

Fire is considered a crucial variable in understanding woody cover dominance worldwide (*29*, *33*). While the effect of fire was included in the best fitting model for relative shrub cover, there was substantial variability in the response to fire among our study sites. This can be explained by the low statistical power available to test the fire effect because of the low occurrence of fire in our sample sites. The low importance of fire observed here may be an intrinsic feature of drylands, as some studies suggest that fire is more important in mesic than in xeric ecosystems (*13*, *40*), as drylands tend to accumulate less fuel and have a lower patch connectivity than mesic areas (*45*). The lack of fire effects at our study sites may be also explained by the low fire frequency observed, providing enough time for trees to grow to adult fire-resistant size classes (*22*, *67*, *68*).

While we have identified several factors significantly associated with woody dominance in global drylands, a considerable amount of inter-site variability remains unexplained by our models. Nonetheless, our results offer valuable insights into potential areas for future research efforts to better understand the variability in woody cover among sites. First, differences in taxonomic composition and traits among sites may imply varied and diverse response groups to the studied drivers (*69*). Second, inter-site variability could be related to differences in the evolutionary history and human use across biomes (*70*). Future studies could address whether the importance of these drivers depends on biogeographical regions or classifications related to human land-use history. For example, the importance of the drivers may be different for communities that evolved with large herbivores or may depend on the time because livestock were introduced in different continents. Third, while the patterns and relationships between variables described in this study are global, different context-dependent mechanisms may come into play at the local scale. For instance, the responses of woody cover to drivers might be constrained if alternative stable states exist or may be influenced by the network of ecological interactions, among other possible mechanisms (*16*, *27*, *71*). In addition, different physiognomies probably involve different rangeland practices even with the same livestock species. Therefore, we emphasize the importance of continued ecological studies on coexistence at multiple spatial scales.

Our results highlight the importance of both climate and grazing as joint determinants of woody species dominance across global drylands. Notably, the significance and direction of these influencing factors were contingent on the woody functional group under examination. The impacts of grazing were not solely dictated by the intensity of grazing pressure but were also influenced by the dominant livestock species. Our findings also underscore the pivotal role of grazing management decisions in shaping woody dominance in drylands. For instance, implementing a strategy that involves mixed grazing and browsing herds with diverse feeding behaviors, coupled with judicious herbivore pressures, could serve as a viable approach to mitigate woody encroachment, which our results suggest may increase under ongoing global warming. However, this must be corroborated by future studies specifically evaluating the effects of mixed herds on woody vegetation dominance. Last, our findings highlight the imperative need to consider the interactions among climate, soil properties, and grazing dynamics to gain a comprehensive understanding of how woody vegetation and the associated ecosystem functions and services respond to ongoing global change in drylands.

MATERIALS AND METHODS

Study sites

We used data gathered in 304 plots from 92 experimental sites, located in 25 countries of six continents (fig. S1), which are a subset of the data used in (*1*). Site selection aimed to capture a large range of environmental heterogeneity (both abiotic and biotic) of global dryland rangelands (fig. S2 and table S2). The survey included a wide variety of vegetation (e.g., grasslands, steppes, open shrublands, and savannas), climatic conditions, and soil types (see table S1 for the ranges of each climate, soil, and grazing explanatory variables used in our analyses). Additional details on study site selection and environmental characteristics can be found in (*1*, *72*).

Field data and grazing pressure gradients

Fieldwork was conducted between January 2016 and September 2019. At each study site, we implemented a hierarchical experimental design featuring a varying number of 45 m–by–45 m plots based on grazing pressure levels (*1*, *72*). They were situated along a gradient of grazing pressure, encompassing high ($n = 91$), medium ($n = 90$), and low ($n = 80$) pressure levels, with some sites additionally incorporating a fourth level (ungrazed, $n = 43$). To establish the grazing gradients, we strategically positioned these plots at varying distances from artificial watering points, which were installed to provide a continuous water source for livestock (*73*). To ensure robust analyses and minimize potential confounding variables, these plots were placed in areas representative of the local vegetation and soil types. Proximity to the watering points served as a proxy for the intensity of grazing pressure, with closer distances indicating greater pressure. This methodology is widely acknowledged and applied for assessing the ecological repercussions of grazing pressure in drylands worldwide (*73*, *74*). We assumed that the domestic herbivores analyzed in this study did not differ substantially in their dependence on water. The chosen watering points were located at a minimum distance of 1 km from other watering points or landscape features, such as fences, which might influence the movement of mammalian herbivores. In 84 of the 92 sites, this methodology was consistently used. In the remaining eight sites, local variations in grazing pressure gradients were ascertained by observing different paddocks featuring varying grazing intensities [see (*1*) for details]. It is important to emphasize that while these grazing pressure gradients primarily resulted from domestic livestock, wild herbivores were present in the surveyed plots. In addition to assessing grazing pressure, we documented the dominant livestock species, identified as the domesticated species with the highest proportion of collected dung mass. We also quantified the richness of mammalian herbivores, which included both domesticated and wild species present at each plot (*1*). Local grazing gradients at each site were confirmed and validated using dung counts, livestock tracks, and livestock density data when available [see (*1*) for details].

At each plot, we located four transects separated 10 m each. Along each transect, we placed 25 contiguous quadrats (size of 1.5 m by 1.5 m). In each quadrat (100 per plot), we visually assessed the ground cover for each perennial species [see (*1*) for details]. This dataset was used to estimate the relative cover of woody species in each plot (i.e., trees and shrubs). We refer to the sum of these groups divided by total plant cover as RWC, which was used as our proxy of woody dominance. These cover values of woody functional groups are relative to the cover of all plants, following Eq. 1

$$\text{Relative woody cover (RWC)} = \frac{\text{Tree + shrub cover}}{\text{Total plant cover (all species)}} \quad (1)$$

We analyzed data of RWC, relative tree cover, and relative shrub cover. These three variables are the most appropriate variables to study woody dominance and coexistence between life forms because they consider both woody and herbaceous plant cover in relation to each other, instead of the more traditionally used absolute woody cover (*7*). An important feature of RWC is that it is inverse to relative herbaceous plant cover (including both perennial and annual species; see Eq. 1). As such, RWC helps explain changes in grass cover in terms of coexistence (*7*, *13*) and can thus contribute to understanding the drivers of forage production (*10*, *75*), which is the primary land use across global drylands (*1*). Our survey provides field data of both woody and herbaceous species that would, otherwise, be difficult to obtain using remotely sensed information (*76*). In addition, even within the woody life forms, identifying trees from shrubs using remote sensing products at the global scale is still challenging (*77*).

Climate and soil data

We obtained standardized climatic data from WorldClim 2.0, a high-resolution (30 arc sec or ~1 km at the equator) database based on comprehensive climate observations and topographical data for the 1970–2000 period (*78*). We used four climate variables, which have been previously shown to relate to differences in woody cover (table S1): MAP [it is inversely correlated with aridity in our dataset; correlation coefficient (r) = −0.89, $P < 0.0001$], mean annual temperature, precipitation at warmest quarter (% of annual precipitation during the three warmer months of the year), and precipitation seasonality (coefficient of variation of intra-annual precipitation).

At each plot, we collected topsoil samples from bare ground areas devoid of perennial vegetation. We randomly placed five 50 cm–by–50 cm quadrats in these areas and collected a composite sample from each quadrat, consisting of five 145-cm^3 soil cores (depth of 0 to 7.5 cm) that were bulked and homogenized in the field. After sieving the samples using a 2-mm mesh, samples were air dried for 1 month and shipped to Rey Juan Carlos University in Móstoles (Spain) for analysis. We measured soil WHC, a variable driven by soil texture (it is inversely correlated with sand content; $r = -0.85$, $P < 0.0001$) that is a good proxy of soil hydrological function (*19*, *66*) and that has been found to be related to changes in woody cover (table S1). We weighed 10 g of dry soil per sample and added it to a funnel with moist filter paper. We added 10 ml of deionized water to each sample and covered the funnels with PARAFILM to prevent evaporation. The samples were allowed to drain into a test tube for 24 hours before we weighed them to calculate their WHC (%).

Fire data

We obtained fire data from MODIS MCD64A1 burned-area product (https://lpdaac.usgs.gov/products/mcd64a1v006/), which provides monthly images of burned areas at a 500 m–by–500 m spatial resolution. We used images from November 2000 to September 2019 (the date of the last field survey). The start date was determined by data availability but encompassed the period during which fire may have affected the current vegetation on some of the experimental sites. We estimated the fire frequency for each plot with Google Earth Engine (*79*). Only 25 plots from 10 sites (of the 92 experimental sites) experienced fire events during November 2000 to September 2019 (table S3). Each plot with fire experienced only one fire event during the 2000–2019 period, so it is probable that rangelands with higher fire frequency have been underrepresented in this survey. Thus, we used a binary variable to indicate whether a fire event had occurred or not in a given plot (0 = no fire and 1 = fire occurred). Although the 500 m–by–500 m spatial resolution of the fire data may include fire events outside the exact plot location, this information may still be valuable in characterizing the local fire disturbance regime, which is important because plant community responses may depend on the site's eco-evolutionary history of fire (*67*).

Statistical analyses

We used a combination of generalized linear mixed models [GLMMs; (*80*)] and multimodel inference (*81*) to analyze the relations among the explanatory variables with RWC (trees and shrubs) and the relative cover of trees and shrubs separately. Our statistical models included fixed effects for climate (precipitation, temperature, precipitation at warmest quarter, and precipitation seasonality), soil (WHC), grazing (grazing pressure, dominant livestock species, and mammalian herbivore richness), fire (fire occurrence in the 2000–2019 period), and latitude and longitude (to account for the spatial structure of the data). Longitude values were transformed with sine and cosine functions to address circularity. We also included three interactions: precipitation × WHC, precipitation × grazing, and grazing × livestock species. Random effects included random intercepts for sites. We also included quadratic terms for grazing pressure, MAP, and mean annual temperature to detect potential nonlinear patterns. The terms and interactions included in our models were based on our objectives and hypotheses (see table S1 for details). We checked the absence of variance inflation issues related to multicollinearity in our global model by estimating the variance inflation factor for each variable (*82*, *83*). To facilitate comparison with previous studies (*4*, *13*, *32*), we also repeated our analyses using absolute cover values.

The GLMM model used was fitted using the "lme" function of the nlme package (*84*). First, a dredging approach was used on the global model to adjust every possible model and order all models according to Corrected Akaike Information Criterion (AICc) with the "dredge" function of the MuMIn package (*85*). We then estimated the importance of each variable as the sum of Akaike weights of all the models in which each variable was present. Akaike weight values are based on AICc differences between consecutive models, ordered from the best-fitting to the worst-fitting model. We centered and standardized all explanatory variables before analysis as they have different scales and variances (*86*). After the multimodel inference approach, we identified the best-fitting models for each response variable based on AICc to describe the relations between response and predictors. Variation partitioning analysis was carried out using the function and package "partR2" (*87*) to estimate the response variability that each predictor set (climate, soil, grazing, and fire) explained. To test for spatial dependence, we performed spatial autocorrelation tests on the residuals of each model estimating Moran's I statistic with the function "moran.test" from the spdep package in R (*88*, *89*). Multiple tests were performed for each model, modifying the nearest neighbors' parameter from 10 to 50, to analyze spatial autocorrelation at different spatial scales. The alternative hypothesis of the Moran's I test was positive spatial autocorrelation (i.e., nearby values tend to be more similar than expected by chance). As we had high P values in the tests for each response variable (>0.9 in all cases), we assumed that there was no strong evidence of spatial dependence or spatial autocorrelation in the models after including latitude and longitude as fixed effects. A similar approach was already used in a previous study from the same global survey (*1*). All statistical analyses were conducted using R version 4.2.3 (*90*).

Supplementary Materials

This PDF file includes:
Figs. S1 to S4
Tables S1 to S5
References

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