RESEARCH ARTICLE

Community-level responses to increasing dryness vary with plant growth form across an extensive aridity gradient

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Abstract

Aim: Perennial plant communities are crucial for regulating ecological processes and maintaining ecosystem functions. Variation in community structure is driven by both biotic and abiotic factors, reflecting adaptation strategies of plant communities to various environments. Although much is known about the response of individual perennial plants to drier climates, empirical evidence of the community-level responses to increasing dryness is limited.

Location: Eastern Australia; 1500 km gradient.

Taxon: Perennial plants.

Methods: We measured the abundance and size distribution (median, skewness and variance) of perennial plant communities from different growth forms (trees, shrubs and grasses), the spatial arrangement of trees in the overstorey and both biotic (competition) and abiotic (climate, soil properties) factors at 150 sites along an extensive aridity gradient from humid to arid areas. We used regression analyses and linear models to explore variation in community structure with increasing aridity and key driving factors for different perennial plant communities.

Results: Variation in community structure differed with growth form. As aridity increased, trees had wider canopies and were spatially aggregated, shrubs became miniaturised, but highly variable in size, and grasses comprised more larger individuals. Biotic and abiotic factors exerted different effects on different growth forms, with trees and shrubs consistently affected by competition and aridity, respectively, whereas grasses were weakly affected by aridity, summer rainfall and soil texture.

Main conclusions: Our study highlights the idiosyncratic adaptation strategies used by trees, shrubs and grasses in response to drying climates at the community level through their effect on the size distribution or spatial aggregation. The structure of different perennial growth forms was influenced by different effects from either biotic (competition) or abiotic (climate, soil) factors. Under forecasted drier climates, canopy expansion and greater aggregation of trees might enhance resource sinks and shelter for diverse biota, potentially shielding plant communities against predicted aridification.

KEYWORDS
climate change, plant community, resource competition, size distribution, skewness, soil texture, vegetation pattern

1 | INTRODUCTION

The majority of Earth's land surface is covered by perennial plants, which affect multiple ecological processes (e.g., species interactions and energy/mass flow) and support critical ecosystem services such as productivity, carbon sequestration and habitat provision (Berdugo et al., 2017; Díaz et al., 2016; Trumbore et al., 2015). The extent to which perennial plants regulate these crucial functions depends on different elements of community structure such as cover, size distribution and spatial arrangement (McElhinny et al., 2005), and both biotic and abiotic environmental factors (Berdugo, Soliveres, et al., 2019; Soliveres & Maestre, 2014). Climate and soils are known to determine plant cover and abundance by affecting the availability of essential resources (Sankaran et al., 2005; Tilman, 2020), whereas biotic factors can influence plant populations *via* species competition or grazing disturbance (Callaway, 2007; Travers & Berdugo, 2020). The extent and relative importance of biotic and abiotic effects are likely to change under hotter and drier climates, where environmental conditions could shift from light limited to water/nutrient limited. This could potentially alter resource availability and species interactions and induce major changes in plant community structure (Berdugo, Maestre, et al., 2019; Ludwig et al., 1999; Meron et al., 2004). Most studies of perennial plant communities, however, have focused within narrow climatic envelopes (e.g., temperature forests and drylands; Berdugo, Maestre, et al., 2019; Carrer et al., 2018), and empirical evidence of structural variation across large climatic gradients is lacking. As the structure of perennial communities is inextricably tied to ecosystem structure and function, a better understanding of its variation and driving mechanisms across extensive climatic gradients is essential to improve our understanding of predicted changes in ecosystem functions and services under climate change scenarios.

Perennial plant communities are likely to exhibit a distinct structure along climatic gradients, reflecting different adaptation strategies to environmental conditions (Caylor et al., 2006; Tilman, 2020). For example, compared with mesic ecosystems, plant communities from hot, dry environments (i.e., drylands) comprise typically smaller (e.g., short stems, constrained canopies) plants that exhibit a patchy (heterogeneous) spatial distribution. These recurring vegetation patterns result from resources redistribution among unvegetated and vegetated patches (Noy-Meir, 1973; Tongway & Ludwig, 1990), such as *Acacia* spp. groves in arid Australia (Ludwig et al., 2005), *Brousse tigree* patterned woodlands in Africa (Valentin et al., 2001), and grass rings in the western United States (Ravi et al., 2008), Africa and the Middle East (Danin & Orshan, 1995). The impacts of biotic and abiotic factors also change with climate regimes. Compared with mesic environments, sandy soils in drier environments often support denser plants than finer soils (Inverse Texture Hypothesis; Noy-Meir, 1973), and species competition generally shifts from aboveground (light and space) to belowground (water and nutrients), resulting in a less regular plant distribution (Moustakas et al., 2008). Furthermore, the relatively importance of biotic and abiotic factors is likely to vary with climate regimes (Soliveres & Maestre, 2014). In more mesic environments, biotic interactions such as species competition are more likely to determine plant dynamics (Stress Trade-off Hypothesis; Louthan et al., 2015), whereas studies centred on global drylands reveal that resource availability and grazing are key drivers of plant communities as aridity increases (Berdugo, Maestre, et al., 2019; Oñatibia et al., 2020). Although much is known about the response of perennial plants to declining rainfall at individual (e.g., plant functional traits; Givnish et al., 2014) and landscape (e.g., vegetation patterns; Meron et al., 2004) scales, less is known about how they respond to increasing dryness at the community level. Furthermore, these community-level responses and their driving mechanisms are likely to be complicated by changes in plant growth form (e.g., trees, shrubs, grasses; Díaz et al., 2016), but there are few empirical studies spanning over extensive climatic gradients.

Different plant growth forms are likely to vary in their response to increasing dryness due to differences in plant traits (e.g., morphology), resource utilization (e.g., rooting depth, shade tolerance), strategies to cope with stress and their ability to regulate ecological processes (Šímová et al., 2018; Westoby, 1979). For example, woody plants with deep tap roots are more likely to tolerant drought by shedding leaves or extending their roots (Schenk & Jackson, 2002; Sharma, 1976), whereas shallow-rooted grasses avoid drought by promoting seed yield for reproduction (Noy-Meir, 1973). At the landscape scale, trees and shrubs forming larger vegetation patches have a greater ability to capture runoff, ameliorate evaporation and retain soil moisture than grasses (Belsky et al., 1989; Eldridge & Wong, 2005). However, these individual-level responses do not directly scale up to the community-level due to inter-specific variations and plant interactions (Caylor et al., 2006; Tilman, 2020). It remains unknown, therefore, how tree, shrub and grass communities respond to intense dryness and the relative importance of biotic and abiotic factors on regulating their community structure across the climatic gradient.

To address these issues, we analysed the variation in community structure of different perennial growth forms (trees, shrubs and grasses), and the impact of both biotic and abiotic drivers at 150 sites along an extensive aridity gradient, ranging from humid forests to arid shrublands, across 1500 km of eastern Australia. We used climatic (aridity, summer rainfall) and soil (texture) attributes as our abiotic drivers as they affect the supply of water and nutrients for plant growth (Noy-Meir, 1973). We used competition as the biotic driver to represent species interactions within and among the plant community (Weiner, 1990). Regression analyses and linear models were used to address three predictions. First, we expected that variation in community structure of woody plants would differ from that of grasses, as grasses have different reproduction strategies, rooting depths and resource acquisition abilities to woody plants (Noy-Meir, 1973; Westoby, 1979). Second, we hypothesised that community structure would become less variable as aridity increases due to the effect of environmental filtering, which results in a convergence of plant traits and selects for species that can adapt to abiotic stresses (de Bello et al., 2013). Third, consistent with the Stress Trade-off Hypothesis (Louthan et al., 2015), we expected that abiotic factors

that regulate resource availability such as aridity, summer rainfall and soil properties, rather than biotic factors (competition) would be the major factors associated with plant community structure in harsher (e.g., drier, nutrient-poor) environments (Berdugo, Maestre, et al., 2019).

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted a field survey along an extensive aridity gradient (1500 km) in eastern Australia, from the east coast to the dry interior. Average annual rainfall ranged from 184 to 1299 mm, with summer dominance in the north-east, uniform in the centre and predominantly winter dominance in the south-west (Bureau of Meteorology, 2019). Average annual temperature varied from 13°C to 21°C and soil texture ranged from loams in humid areas to clayey sands in arid areas. Aridity (United Nations Environment Programme, 1992) was obtained from Consortium for Spatial Information (CGIAR-CSI) for the 1950–2000 period (Zomer et al., 2008) (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/) and was determined as:

$$\text{Aridity} = 1 - (\text{precipitation/potential evapotranspiration}).$$

We surveyed 150 sites at regular intervals of aridity (e.g., 0.007 aridity difference among sites, on average) along the aridity gradient, which covers humid, dry subhumid, semiarid and arid areas. To avoid potential confounding effects of overgrazing, fire history, additional water resource or past land management practices (e.g., clearing or timber removal) on plant communities, we restricted our sampling to conservation areas or reserves (e.g., national parks, nature reserves and state forests), remote from rivers or wetlands, that had been unburned in the last 50 years, and where grazing levels were relatively low, and kangaroos were the major herbivores. Sites were sampled where communities contained both woody species (e.g., trees, shrubs) and perennial grasses, and species composition across the gradient was highly variable, with tree species dominated by *Eucalyptus*, *Callitris* and *Acacia* species in the overstorey. Midstorey (shrub) species were dominated by *Leptospermum*, *Dodonaea* and *Eremophila* species, and grasses by *Lomandra*, *Aristida*, *Austrostipa* and *Enteropogon* species.

2.2 | Field survey

At each site, we measured the community structure of trees, shrubs and perennial grasses along a 100 m long transect, with transect width adjusted from 10 to 40 m, in order to capture at least 20 trees, 20 shrubs and 50 perennial grasses at each site. The differences in plots size across the aridity gradient did not affect, either inflate or reduce, species richness (Figure S1.1). To ensure that the sampling regime captured the plant structure, we focused on surveying mature woody plants (i.e., tree height > 4 m, shrub height > 0.4 m) and grasses that form a tussock. For each woody plant (tree, shrub), we measured aboveground architecture such as plant height (m) and canopy diameter (m) as its size. We also recorded the spatial position (*x*- and *y*-coordinates in relation to the transect) for each tree as a measure of overstorey plant distribution and measured the diameter at breast height (DBH, cm) for each tree to calculate an index of competition. We measured basal diameter (cm) as the size of perennial grass tussocks, randomly starting along the transect in a band 1 m wide and measuring each grass that we encountered. We measured the basal area of perennial grasses at the soil surface and did not account for the width of overhanging foliage in order to avoid potential effects of herbivory. At each site, plant density and species richness of trees, shrubs and perennial grasses were measured as indicators of the abundance of each plant growth form.

We measured soil texture (i.e., soil sand content) as the predictor of plant community structure under two replicates of each plant growth form that represented the dominant tree, shrub and grass patches at that site. Within a circular (64-cm diameter), we assessed soil sand content using a categorical scale whereby higher values represented greater sand content (1 = silty to heavy clay; 2 = sandy clay loam to sandy clay; 3 = sandy to silty loam; 4 = sand to clayey sand; Tongway, 1995). Grazing intensity at each site was assessed by counting the dung of different herbivores within the quadrats and converting counts to dry mass of dung per herbivore type per hectare (kg/ha) using algorithms relating dung counts to dung mass (Eldridge et al., 2017).

2.3 | Statistical analysis

To obtain the community structure of different plant growth forms at each site, we calculated the median, the skewness (degree of asymmetry) of the size distribution and the coefficient of variation (CV%) for canopy diameter and height of woody plants and basal diameter of grass tussocks. We then fitted linear regressions between measures of community structure and aridity to explore whether the community structure of each plant growth form significantly changes with increasing aridity. Skewness is calculated as below.

$$\text{Skewness} = \frac{\mu_3}{\mu_2^{\frac{3}{2}}},$$

where μ_2 and μ_3 are the second and third central moments, respectively.

To quantify the spatial arrangement of trees, we calculated the distance of each tree from the nearest neighbour based on its spatial position and we calculated CV% of the nearest distance to evaluate the variability in tree spacing at the site level. We measured resource competition (e.g., compete for light, space, water and nutrients) from neighbours for each tree using Hegyi Competition Index (Hegyi, 1974). We used Clark-Evans Index (i.e., aggregation index) as our measure of spatial distribution pattern (range 0–2.15), with values

<1 indicating an aggregated distribution, equal to 1 suggesting a random distribution (Clark & Evans, 1954). Rather than establishing a radius around the target tree and only considering those closest, we considered all trees within the transect as neighbours when calculating these indices.

$$\text{Hegyi} = \sum_{i}^{n} \left(\frac{D_j}{D_i} \times \frac{1}{d_{ij}} \right),$$

where D_j is the DBH (cm) of neighbouring trees, D_j is the DBH (cm) of the target tree, d_{ij} is the distance (m) between neighbouring trees and the target tree.

$$\text{Clark - Evans} = \frac{1}{n} \sum_{i}^{n} r_i 2\sqrt{\rho}.$$

r_i is the distance from one tree to the next neighbour and ρ is the density of trees per square metre.

We constructed separate linear models for trees, shrubs and grasses with attributes of community structure (i.e., median, skewness, CV%, density, nearest distance, Clark-Evans index) as response variables. As predictors, we included climatic variables (i.e., aridity, summer rainfall), soil properties (i.e., soil sand content) and competition within the growth form (i.e., species richness of tree, shrub, grass) for all the models. In addition, we included an index of competition (Hegyi Competition Index) in the model for trees to test the impact of neighbouring competition on tree community structure except for tree density and nearest distance between trees, and we included tree canopy cover in models for shrubs and grasses to test competition from the overstorey. We also fitted an additional model for the community structure of grasses by including grazing intensity as a predictor to take account of the impact of native herbivores grazing on grasses. Summer rainfall was estimated by the percentage of rainfall in the warmest quarter of the year (summer in the Southern Hemisphere, December to February) based on data derived from WorldClim 1.4 database averaged across 1970–2000 with 30-s resolution (https://www.worldclim.org/). To fit the linear model (see Appendix S2 for a detail model fitting procedure), we (1) checked for collinearity among all the predictors using the variance inflation factors test (Table S2.1); (2) checked the normality of response variables and predictors, log transformed those that were highly positively skewed (Table S2.2), then standardised all the predictors and response variables using z-score standardization to enable comparison among coefficients; (3) fitted the linear model (Table S2.3) and compared it with the model that includes quadratic terms for aridity based on AIC (Table S2.4) and (4) finally, after comparison, used the linear model without the quadratic term to explore the relationship among environmental drivers and community structure. A summary of the linear model fitting (e.g., R^2, p value) is presented in Table S2.5.

Nearest distance was calculated using 'raster' packages (Hijmans et al., 2015). Skewness was calculated from the 'moments' package (Komsta & Novomestky, 2015). Figures were created using 'ggplot2' packages (Wickham, 2016) and linear regressions fitted in R 3.4.1 (R Core Team, 2018).

3 | RESULTS

3.1 | Variation in community structure with increasing aridity

The community structure of trees, shrubs and grasses changed markedly with increasing aridity (Figure 1; Figures S3.2 and S3.3). Average tree height was shorter, but canopies wider, with increasing aridity, with more short and wide individuals and lower variability in size (i.e., height and canopy). Shrubs tended to become miniaturised (i.e., decline in both height and canopy) with increasing aridity, with increasing frequency of small individuals that were more variable in size. Grass communities comprised a
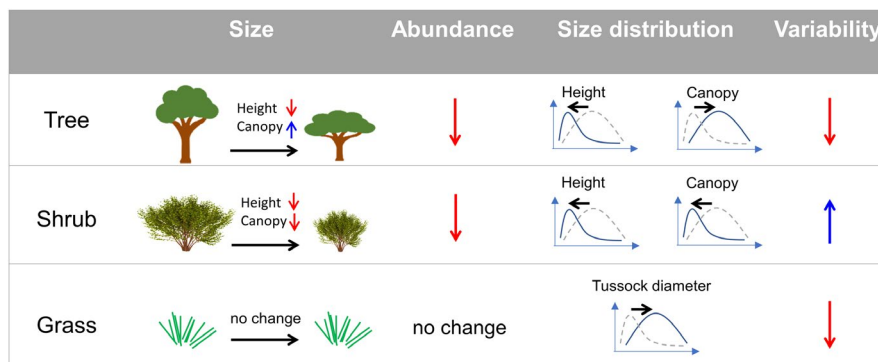

FIGURE 1 Summary of changes in size (height and canopy of woody plants and tussock diameter of grasses; median values), abundance (density and richness), size distribution (skewness) and variability (CV%) of size for trees, shrubs and grasses along aridity gradient (Figures S3.2 and S3.3; Table S5.6). Blue arrows, red arrows and 'no changes' represent significant increases, decreases and no significant changes with increasing aridity, respectively. Black horizontal arrows represent the direction of change in relation to increasing aridity. Grey dash lines and blue solid lines represent size distributions in humid areas and arid areas, respectively

greater number of larger individuals with lower variability in size but exhibited no changes in abundance nor grass size with increasing aridity.

As environments became drier, trees tended to be more sparsely distributed, with the average distance between neighbours increasing, and competition declining, particularly where aridity exceeded 0.5, the boundary between semiarid to arid areas (Figure 2a,c). In addition, trees tended to be more spatially aggregated (Figure 2d; Figure S4.4), with the distance between neighbours becoming more variable as aridity increased (Figure 2b).

3.2 | Drivers of community structure for different plant growth forms

We found that the dominant drivers of community structure varied among trees, shrubs and grasses (Figure 3). Competition was consistently associated with the community structure of trees (Figure 3a), with positive effects on size distribution (skewness, CV%) but negative effects on tree size (median value of height and canopy) and spatial distribution of trees (Clark-Evans index).

Aridity was the major driver of the community structure of shrubs (Figure 3b), whose size distribution became more skewed and variable, and whose size (median value of height and canopy) declined with increasing aridity. In addition, aridity was mainly negatively related to the community structure of trees, and to a lesser extent, grasses. Other abiotic factors such as the amount of summer rainfall and soil sand content had contrasting effects on different plant growth forms, with increasing values of summer rainfall reducing tree canopy size, but increasing the frequency of small grasses (skewness) and the variability in grass size. Higher soil sand content was positively associated with increasing grass size (median) and variability in grass size, but negatively associated with tree height (median) and the variability in tree size (i.e., height and canopy) (Figure 3a,c).

4 | DISCUSSION

Our study provides strong empirical evidence that variation in community structure with increasing dryness differs with plant growth forms (trees, shrubs, perennial grasses). As aridity increased, trees canopies were wider and showed spatial aggregation, shrubs became more miniature but were highly variable in size, and grasses comprised more larger individuals. Furthermore, our results highlight the fact that the relatively importance of biotic and abiotic drivers on community structure also varies with plant growth form, with trees and shrubs driven predominantly by resource competition and aridity, respectively, whereas grasses were weakly affected by aridity, summer rainfall and soil texture. Overall, our results demonstrate markedly different adaptation strategies of perennial plant communities to increasing dryness affected by different effects from either biotic (species competition) or abiotic (resource availability; climate and soil) factors. Our study provides insights into mechanisms driving the structure of different perennial communities in response to increasing aridity and how ecosystem functions might vary under future climate change scenarios.

4.1 | Plant growth form defines the response of community structure to increasing dryness

As water becomes more limiting, perennial plant communities vary in their responses, either becoming smaller to minimise their water stress or aggregating into patches, to maximise their capacity to access water captured by runon-runoff processes at the landscape scale (Givnish et al., 2014; Yair, 1983). Despite being affected by available resources, trees can modify water availability by altering their community structure (Caylor et al., 2006), with increasing aridity associated with a greater abundance of shorter, but wider, individuals. Selection for shorter height is a response to the risk of hydraulic failure and cavitation (Givnish et al., 2014), and canopy expansion is an effective mechanism to enhance rainfall harvesting *via* interception

FIGURE 2 Variation in (a) nearest distance between tree neighbours, (b) coefficient of variation (CV%) of the nearest distance, (c) Hegyi Competition Index and (d) Clark-Evans Index along the aridity gradient (Tables S5.6 and S5.7). Blue lines were fitted using quadratic polynomial regressions (a,c) and linear regressions (b,d). Red horizontal line indicates the boundary where plants were more regularly distributed (Clark-Evans Index > 1) or more aggregated (Clark-Evans Index < 1) and * indicates significant changes
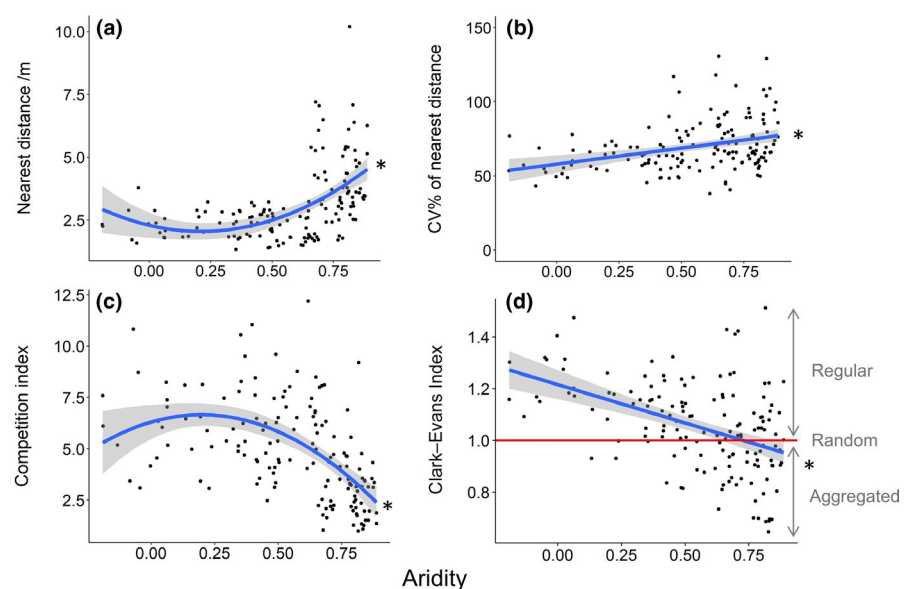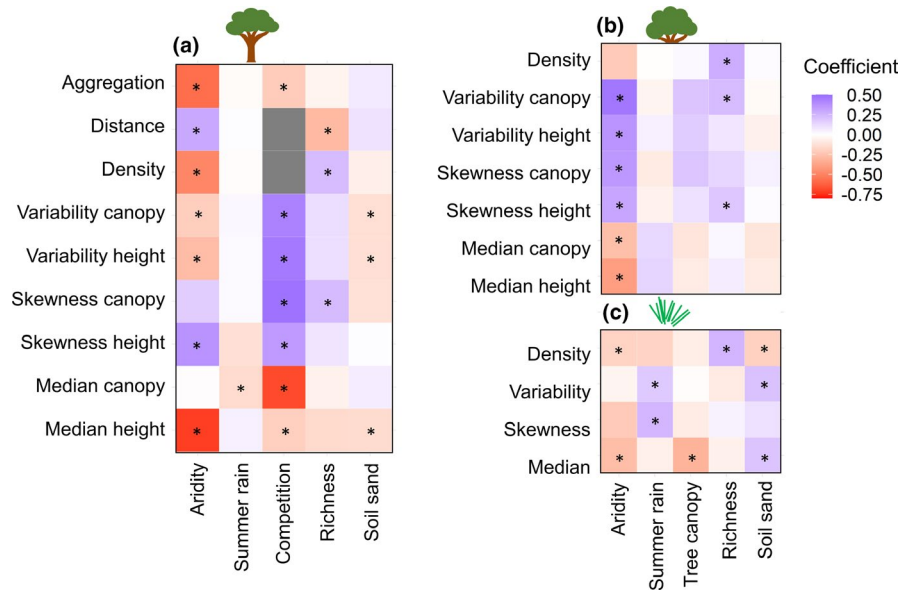
FIGURE 3 Heatmap of the coefficients of the linear models among community structure attributes and driving factors for (a) trees, (b) shrubs and (c) grasses (Tables S5.8–S5.11). A summary of the model fitting is presented in Table S2.5. *Significant coefficient (*p* < 0.05) and grey colour indicates that the predictor does not include in the linear model for the particular response variable. Variability: coefficient of variation (CV%); Distance: nearest distance to neighbours; Aggregation: Clark-Evans index; Summer rain: summer rainfall; Competition: Hegyi Competition Index; Richness: species richness of tree, shrub and grass respectively; Soil sand: soil sand content in tree, shrub and grass patch, respectively

and stem flow (Slatyer, 1961), ensuring plant survival and seed production under drying conditions (Pressland, 1976). Furthermore, we found that the spatial arrangement of trees became more aggregated with increasing aridity. Trees are often regularly distributed in mesic environments as a result of intense aboveground competition for light and aboveground niches to establish (e.g., self-thinning; Moustakas et al., 2008), but shift to an aggregated distribution under drying conditions due to positive feedbacks between vegetation and runon-runoff processes (HilleRisLambers et al., 2001; Tongway & Ludwig, 1990). For example, vegetation patches characterised by high rates of soil infiltration often act as resource sinks for runoff water generated from sparsely vegetated upslope open areas (Wilcox et al., 2003; Yair, 1983). Additional resources and facilitative effects from vegetation communities (e.g., ameliorated microclimate; Belsky et al., 1989) promote clumped tree growth within the vegetated patch but increase the distance among patches due to intensified belowground competitive resource scavenging by tree roots (Barbier et al., 2008). These short-range facilitative and long-range competitive effects result in a highly spatially organised landscape characterised by mosaics of resource-rich tree patches and resource-poor interspaces (e.g., mulga groves and intergroves; Tongway et al., 2001).

As aridity increases, large aggregations of interconnected shrubs tend to contract, with individuals declining in size to reduce hydraulic demand (Westoby, 1979). Compared to trees and grasses, shrubs have a more physiologically efficient growth form (Slatyer, 1973), which can result in low water demand and reduced wilting through physiological and morphological adaptations (De Micco & Aronne, 2012; Noy-Meir, 1973). For example, *Dodonaea viscosa* can adapt to droughts by reducing dawn xylem water potential (Hodgkinson,

1992), and chenopod shrubs (*Atriplex* spp., *Maireana* spp.) can increase their water-use efficiency by having varied leaf morphology (e.g., more angled leaves with high turgidity; Mooney et al., 1977) and by their ability to shed up to 90% of their leaves without perishing (Sharma, 1976). Furthermore, reductions in aboveground biomass also enable shrubs to allocate more biomass to belowground structure in order to strengthen resource acquisition (Balanced-Growth Hypothesis; Schenk & Jackson, 2002). Conversely, only the size distribution of grass communities changed, with an increased frequency of large grasses as dryness intensified, consistent with a continental study showing that trait-climate relationships of herbaceous species are often weak and highly variable (Šímová et al., 2018). More rainfall and reduced herbivory in mesic areas promote the germination and growth of denser and smaller grasses (Travers & Berdugo, 2020), but they may often fail to persist under drying conditions (Ludwig et al., 1999). As dryness intensifies, grass communities tend to be dominated by a greater number of larger individuals that are functionally important for capturing resources, infiltrating water, and sustaining plant survival in water scarce environments (Ludwig et al., 2005).

4.2 | Biotic and abiotic drivers of community structure differ with plant growth form

The community structure of trees was consistently affected by resource competition from neighbours across the gradient, with intense neighbouring competition associated with greater spatial aggregation and size variability of trees. As competition for water intensifies, tree communities comprise both larger individuals with a strong water

scavenging capacity and smaller individuals with a lower water demand (De Micco & Aronne, 2012; Noy-Meir, 1973), resulting in the large variability in size that we recorded. Furthermore, competition for water is likely to be asymmetric, with larger plants having a greater competitive advantage over smaller plants, resulting in a patchwork of different competition levels within a community (Weiner, 1990). The zone of lower resource competition around large trees might provide shelter for smaller plants (competition-induced shelter; Nakagawa et al., 2015), or protégé species could benefit from greater surface moisture and seedling growth through mechanisms such as hydraulic lift, heat buffering and the perch effect (Caldwell & Richards, 1989; Soliveres et al., 2012). These two processes could lead to clustered individuals around large or nurse trees, resulting in a more aggregated distribution within communities dominated by trees. However, in our study, the community structure of shrubs and grasses was generally unaffected by competition among growth forms (i.e., tree canopy cover). Although dominant overstorey species are expected to suppress other subordinate species *via* resource competition (Mou et al., 2005), niche separation in light and water usage ensures the coexistence of different plant growth forms across climatic gradients (Schenk & Jackson, 2002; Silvertown, 2004). In addition, some shrubs in our study, such as *Rhagodia*, *Einadia*, and *Chenopodium* spp. benefited from growing beneath trees (protégé species) due to facilitation by overstorey canopies (e.g., fertile soils, ameliorated climate; Belsky et al., 1989) and enhanced seed dispersal by birds and herbivores (Soliveres et al., 2012). These facilitatory effects would likely complicate the competitive effect of trees across the gradient.

Aridity, which determines water supply and soil moisture availability, was the major abiotic factor influencing the community structure of shrubs, consistent with the Stress Trade-off Hypothesis (Louthan et al., 2015). However, contrary to our hypothesis of a simplification of plant structure due to environmental filtering, we detected a greater variability of shrub community structure with increasing aridity, potentially explained by changes in shrub assemblages along the gradient (Le Bagousse-Pinguet et al., 2017). As water becomes harder to access under conditions of increasing dryness, mesic shrub species are generally replaced by both drought-avoidant and drought-resistant analogues that comprise both large-sized plants such as *Eremophila* and *Dodonaea* spp., and smaller-sized plants such as *Atriplex* and *Maireana* spp., increasing size variability in drier environments (Eldridge, 1988). Apart from dryness, moisture availability is also regulated by patterns of water supply (summer rainfall) and soil texture (Fernandez-Illescas et al., 2001; Noy-Meir, 1973), which exert contrasting effects on different plant growth forms. For example, areas receiving predominantly greater summer rainfall are subjected to higher evaporation, recharging water moisture at mainly shallow depths (Schenk & Jackson, 2002). This promotes the germination and dominance of smaller grasses and thus increases the variability in grass size, but not the canopy expansion of trees that rely on water from the deeper soil layers (Noy-Meir, 1973). Despite the rapid drainage and low water retention of sandy soils (Fernandez-Illescas et al., 2001), we found that a greater sand content was associated with a sparser grass community but larger-sized grasses. This might be an adaptive strategy of grasses under harsh environmental conditions where plant density declines in response to limited water,

such that a large basal size can enhance their ability to rapidly absorb moisture from sandy soils before it evaporates (Fernandez-Illescas et al., 2001). Compared with trees and shrubs, grass community structure was weakly affected by different drivers such as aridity, summer rainfall and soil sand rather than showing a consistent response to any of these drivers, including grazing intensity which only had a negative effect on grass density (Table S5.11). This is potentially due to the fact that low levels of grazing by native macropods (kangaroos) have an almost negligible impact on grass communities (Travers & Berdugo, 2020), compared to domestic grazing, which has persistent and pervasive effects on ecosystems under increasing aridity (Oñatibia et al., 2020). In addition, the lack of consistent response in grasses could relate to differences in species composition along the aridity gradient, with both large- and small-sized taxa dominating in both mesic (e.g., *Lomandra*, *Dianella*, *Aristida* spp.) and xeric regions (e.g., *Triodia*, *Austrostipa*, *Enteropogon* spp.) and hence a highly varied community structure across the gradient.

5 | CONCLUSIONS

Our study provides novel evidence that trees, shrubs and grasses exhibit distinctive strategies to adapt to drying conditions at the community level across a large aridity gradient. Rather than simply becoming sparser with increasing dryness, woody communities (trees, shrubs) either shrink or aggregate to reduce their water demand and optimise resource harvesting, whereas grass communities comprised a greater number of larger individuals in order to maximize water capture. These idiosyncratic responses suggest that environmental filtering may not explain changes in plant traits along environmental gradients across all plant growth forms, and species with functionally contrasting strategies can still co-occur (de Bello et al., 2013). It also highlights the importance of considering specific mechanisms for particular growth forms in models aimed at predicting the response of community dynamics to changing climate. Furthermore, our study demonstrates the fact that the mechanisms driving community structure differ among plant growth forms, with trees, shrubs and grasses affected by different effects from biotic (resource competition) and abiotic (climate, soil) factors. Compared to shrubs and grasses, the community structure of trees is influenced mainly by resource competition from neighbours, suggesting that abiotic stress may not be the major constraint on all plant communities in harsher environments, as suggested by the Stress Trade-off Hypothesis (Louthan et al., 2015). Under predicted drier climates, expansion in tree canopies and aggregated spacing can be viewed as mechanisms that will shield tree communities against drier climates (Vincenot et al., 2016). Thus, larger tree patches would function as resource sinks (Belsky et al., 1989), maintaining ecosystem functions, improving ecosystem resilience, and providing refugia for diverse biota in the face of forecasted aridification (Huang et al., 2016).

DATA AVAILABILITY STATEMENT

Data used in the study are available via the Figshare repository (https://doi.org/10.6084/m9.figshare.14101349.v2).

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SUPPORTING INFORMATION

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