

The Role of Soil Gypsum Content and Aridity in Shaping Species Assembly in Australian Gypsophilous Ecosystems

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Abstract

Background and Aims

Gypsum systems are highly restrictive environments, occurring in arid and semi-arid regions, where strong physical and chemical constraints limit plant establishment. Nevertheless, they represent understudied biodiversity hotspots, particularly in southwestern Australia. In this context, we evaluated the extent to which aridity, soil conductivity and gypsum content, both independently and in interaction, determine the assembly of gypsophilous vegetation as well as their role as environmental filters.

Methods

We recorded species presence and cover in three salt lakes along an aridity gradient. To assess the effects of aridity, conductivity and gypsum content on community composition we used PERMANOVA analysis. Additionally, to evaluate the role of environmental filtering in species assembly, we analyzed taxonomic and phylogenetic diversity using mixed-effects models.

Results

Aridity emerged as the main driver of community composition and taxonomic diversity in these systems. In addition, the synergistic effect of three stress factors—high gypsum content, elevated conductivity and increasing aridity—shaped community assembly by promoting the coexistence of evolutionarily recent lineages. Assuming phylogenetic relatedness reflects deep functional strategies, this pattern supports the existence of strong hierarchical environmental filtering, with aridity acting as the primary filter followed by restrictive soil conditions such as salinity and gypsum content.

Conclusion

Increasing aridity in gypsum-rich soils significantly reduced phylogenetic diversity, indicating that evolutionarily close lineages possess specific adaptations to tolerate these restrictive conditions. In the light of the relatively recent origin of gypsum soils in southwestern Australia, our findings highlight the role of aridity-related preadaptations as a foundation for the evolution of gypsophytes.

INTRODUCTION

Gypsum soils are distributed over 100 million hectares worldwide (Eswaran and Zi-Tong 1991; Verheye and Boyadgiev 1997). These soils are found exclusively in arid or semi-arid regions (Boyadgiev and Verheye 1996; Casby-Horton et al. 2015; Eswaran and Zi-Tong 1991; Herrero et al. 2009), where low precipitation prevents the leaching of gypsum, thereby affecting plant performance and distribution (Escudero et al. 2015; Moore et al. 2014). Gypsum soils contain more than 40% calcium sulfate dihydrate

and possess a range of physical and chemical properties (Herrero and Porta 2000) that make plant establishment and growth challenging (Eswaran and Zi-Tong 1991). Among their chemical properties, low levels of nitrogen (N) and phosphorus (P), along with high levels of sulfur (S) and calcium (Ca), are known to cause nutritional imbalances that hinder plant performance (Casby-Horton et al. 2015; Cera et al. 2021; FAO 1990; Meyer et al. 1992; Ruiz et al. 2003). Additionally, hard surface crusts can physically impede germination and early growth (Escudero et al. 1999, 2000; Meyer, 1986). These limiting conditions, combined with the limited dispersal of many gypsum specialists (Peralta et al. 2023), make these habitats hotspots of biodiversity and endemism, sheltering a high number of threatened plant species (Escudero et al. 2015). Furthermore, predictions suggest these unique habitats will be significantly affected by increased aridity (IPCC, 2022), primarily due to their island-like structure (Luzuriaga et al. 2018).

Although gypsophytes (gypsum specialists) have been a hot topic for botanists for over two centuries, the earliest studies on community composition date back only to the mid-twentieth century (Braun-Blanquet and Bolòs 1957; Parsons, 1976). Subsequent studies addressing their ecology and evolution emerged later (see Meyer, 1986), linking gypsophily to gypsum soil content and particularly to aridity. Consequently, our understanding of gypsophilous vegetation and its ecological determinants is limited to specific regions of the world, such as the Iberian Peninsula (Luzuriaga et al. 2018, 2020; Martínez-Duro et al. 2010, 2012; Pueyo and Alados 2007; Mota et al. 2011; Pueyo et al. 2008) and North America (Huerta-Martínez et al. 2004; Meyer and García-Moya 1989; Meyer et al. 1992; Vargas-Colin et al. 2022). Despite these ecosystems being biodiversity hotspots and harboring high endemism (Escudero et al. 2015) and being critical for many local human populations (Palacio and Escudero 2014), most gypsum ecosystems worldwide have received little attention. One of the least studied gypsum soil-dominated regions is southwest Australia, despite its high number of endemic and highly threatened species (Hopper and Gioia 2004). Knowledge of species distribution and vegetation variability in gypsum ecosystems in Australia is very limited (Mokany et al. 2022; Symon, 2007).

Evidence suggests that phylogeny plays a critical role in the assembly of gypsophilous floras in the Iberian Peninsula (Palacio et al. 2022) and in Chihuahuan gypsum soils (Moore et al. 2014; Muller et al. 2017), involving pre-adaptations of certain clades along with very active in-situ microevolution, as well as nutritional convergence across distant gypsophilous lineages in both floras (Muller et al. 2024). As a consequence, phylogenetic relatedness among coexisting species is critical for the assembly of gypsophilous vegetation, both in semiarid Mediterranean (see Chaves et al. 2021; Luzuriaga et al. 2020, 2025, 2026) and in Chihuahuan gypsum ecosystems (Vargas-Colin et al. 2022). We aim to evaluate whether the known role of phylogeny in the assembly of gypsum vegetation remains crucial in Australian systems.

Here, we address the following questions: 1) To what extent is the assembly of Australian gypsophilous vegetation shaped by aridity, soil gypsum content and soil conductivity? That is, do these factors act as major environmental filtering to plant species in Australian gypsum systems? 2) Do these environmental factors act independently, or do they interact, in ways that modify their individual effects? We expect that

under harsher conditions (i.e., high aridity and high gypsum content), species persisting in these environments must possess specific adaptations that enable them to tolerate such stressful conditions. If ecological strategies to cope with these stressful conditions are phylogenetically conserved, increasing environmental stress should result in communities composed of more closely related species (i.e., low phylogenetic diversity) and denote environmental filtering. Conversely, if the adaptive strategies to withstand stressful conditions have evolved independently across lineages, we would expect higher phylogenetic diversity.

METHODS

Study area

The study was conducted in three regions of SW Australia (see Fig. 1a) along a gradient of increasing aridity, spanning from southern to northern areas with De Martonne aridity indices ranging from 14.4 to 6.9. These regions were around Lake King (33° 0.1' 37.8" S, 118° 56' 3.8" E; elevation 302 m), Lake Moore (30° 2' 1.5" S, 117° 31' 50.0" E; elevation 311 m), and, the most arid one, Lake Austin (26° 54' 49.3" S, 118° 16' 0.2" E; elevation 431 m). They are topographically subdued landscapes with gypsum deposits occurring as lunettes and flats associated with major salt-lake systems, with low levels of disturbance and minimal or low land use (some sporadic cattle grazing in certain areas of Lake Austin). Sulfur soil content ranged from 11.4% to 18.7% and conductivity from 2340 to 5738 $\mu\text{S}/\text{cm}$. These three regions were composed of patches of woody vegetation (e.g., *Eucalyptus* spp., *Callitris canescens*, *Melaleuca halmaturorum*) embedded in a matrix of bare soil, where predominantly perennial herbaceous plants could be found (e.g., *Roepera compressa*, *Roepera tetraptera*). The percentage of bare soil ranged from 4.5% to 87%, and the percentage of vegetation cover ranged from 8.2% to 71.2% (Supplementary Table 1 in Online resource 1). The dominant vegetation consisted of *Eucalyptus striatocalyx* trees at Lake Austin, and Lake Moore on elevated lunettes with various communities dominated by *Tecticornia* spp. and *Frankenia* spp. on broad flats. At Lake King gypsum lunettes were lower in elevation and included *Callitris canescens*, *Casuarina obesa*, *Melaleuca halmaturorum*, and *Maireana oppositifolia*. Flats at Lake King were also dominated by *Tecticornia* spp. (see species list in Supplementary Table 2 in Online resource 1).

Experimental design

Six plots (30 x 30 m) on non-disturbed areas were established per region with a minimum distance of three kilometres between them, to capture the vegetation heterogeneity in each region. Among the 18 plots sampled across the three study regions, one exhibited outlier values for soil properties in the Lake King region. Notably, this plot deviated significantly from the typical characteristics of gypsiferous soil, which was the primary focus of our study. Consequently, we excluded this plot from our analyses (N = 17 plots) (Supplementary Table 1 in Online resource 1). Sampling was performed in September 2019 (i.e. spring season). The geographical coordinates, altitude, slope, orientation, land management type, and

degree of disturbance were recorded for each plot. Characterization of the plot in terms of percentage of bare soil, biological soil crust, rock and vegetation cover (Supplementary Table 1 in Online resource 1) was carried out using data collected from six sub-plots (3 x 3 m) located at the plot margins (Fig. 1b). The composition and structure of perennial plant species were evaluated using 30 m length transects, placed at 5, 15 and 25 m from the upper left corner of the plot. In cases where vegetation cover was low, a greater number of transects were established to better represent the vegetation structure. All species in contact with the transect were recorded, each patch dimension was obtained by measuring the two perpendicular diagonals and every species inside patches were also recorded (Fig. 1b). Based on these values, the percentage cover for each species at the plot level was estimated.

For the chemical composition of the soil, five samples (10 cm deep and 5 cm in diameter) were collected from the area outside the vegetation patches in each plot (N = 90), as this area was considered more representative of the underlying substrate. All soil samples were air-dried and subsequently sieved through a 2 mm mesh sieve for physical and chemical analysis. Total soil Sulfur (S) was analysed by ICP-OES. A subsample of each soil sample was finely ground, dissolved in HCl-HNO₃ (9:3) by microwave digestion and the filtered extract solution was used to measure total S using inductively coupled plasma-optical emission spectrometry (ICP-OES, Varian ICP 720-ES) at Estación Experimental del Zaidín (EEZ-CSIC) Analytical Services, Spain with a detection limit of 0.025 µg g⁻¹. Soil electrical conductivity was measured using a conductivity meter (Orio StarA215, Thermo Scientific, Waltham-MA, USA), with the samples diluted in distilled water at a ratio of 1:5 (w/v).

Annual precipitation and mean annual temperature from 1970 to 2000 were obtained from WorldClim using R (R Core Team 2023) with the packages *sp* (Pebesma and Bivand 2005) and *raster* (Hijmans and Van Etten 2012). These variables were used to calculate the De Martonne annual aridity Index (Croitoru et al. 2013; De Martonne, 1926; Paltineanu et al. 2007). De Martonne index was calculated as follows:

$$\text{De Martonne Index} = \frac{P}{T+10},$$

Where, P is mean annual precipitation (mm) and T is the mean annual temperature (°C) at 0.5-degree resolution. The larger values of De Martonne index indicate high humidity, while lower values indicate regions with great aridity. In our statistical models we used the inverse of Martonne index (Aridity, hereinafter), so that the increase in this index reflects an increase in aridity intensity.

Taxonomic and phylogenetic diversity indexes

Taxonomic and phylogenetic indices were calculated at the plot level (30 x 30 m). Species richness was the sum of every species occurring in each plot. For the taxonomic diversity of species, we employed the inverse Simpson index computed using the *vegan* package (Oksanen et al. 2017) in 4.3.0 R version (R Core Team 2023) and evenness, calculated by dividing Simpson's inverse index by species richness. The *V.PhyloMaker* R package (Jin and Qian 2019) was used to construct the phylogenetic tree of the 114 species registered in our study (Supplementary Table 2 in Online resource 1). This package attaches the

inputted species to a tree of 73 533 vascular plant species. The branch lengths of the resulting tree represent the evolutionary divergence between species or taxa. Four complementary phylogenetic indices were used: Phylogenetic Species Variability (PSV), Phylogenetic Species Evenness (PSE), Mean Pairwise Distance (MPD) and Mean Nearest Taxon Distance (MNTD). The PSV measures the phylogenetic relatedness among species in a community, with values close to zero indicating closely related species and values of one indicating more distantly related species (Helmus et al. 2007). The PSE incorporates the relative abundance of species and reaches the maximum value of one when species abundances are equal and unrelated to each other (Helmus et al. 2007). The MPD index quantifies the mean phylogenetic distance among all pairs of species in a community, thereby capturing its phylogenetic structure at deeper evolutionary levels. In contrast, the MNTD index measures the mean phylogenetic distance to each species' closest relative (Webb et al. 2002), reflecting the more recent phylogenetic structure associated with terminal nodes and recent evolutionary processes.

The MPD and MNTD were converted to their standardized effect sizes (MPD.SES and MNTD.SES) as follows:

$$\text{MPD.SES} = \frac{\text{MPD}_{\text{obs}} - \text{MPD}_{\text{null}}}{\text{sdMPD}_{\text{null}}},$$

where MPD_{obs} is the observed mean pairwise distance, MPD_{null} is the mean pairwise distance calculated from 999 random assemblages, and sdMPD_{null} is the standard deviation of these 999 randomly generated MPD values (Mazel et al. 2015). The MNTD was standardized in an analogous way.

To generate the 999 null model assemblages, the independent swap algorithm was used, with the same number of species as the observed community and with fixed occupancy rates (Gotelli and Entsminger 2001). MPD.SES and MNTD.SES indicate whether the observed phylogenetic diversity is higher or lower than expected by chance (Webb 2000). If their value is significantly greater than zero, it indicates that the phylogenetic divergence is higher than expected by chance, and if it is lower, it indicates the opposite. The diversity indices were calculated at the plot level using *Picante* package (Kembel et al. 2010) in R.

Statistical analyses

We included the following fixed variables in the statistical models: the inverse Martonne index (Aridity), soil sulfur percentage (S) as a proxy for soil gypsum content, soil electrical conductivity (C) as an indicator of salinity, and the total plant cover per plot (Cover) as a surrogate of primary productivity. We checked for correlations among all explanatory variables to avoid any increase in the variance. To assess differences in species composition among the 17 plots, we log transformed the species abundance data to reduce the influence of highly dominant species. We conducted a PERMANOVA analysis using Bray-Curtis distances and type III sum of squares with the *adonis2* function of the *vegan* package (Oksanen et al. 2017). Together with the above-mentioned fixed variables, we also included the interaction term between aridity, soil sulfur content, and conductivity. Non-parametric Multidimensional Scaling (NMDS) was used to graphically represent differences in species composition, using the *metaMDS*. The variables

aridity, soil gypsum content, conductivity and vegetation cover were graphically represented as explaining variables and the 10 species with the highest cover were graphically represented using the *envfit* function of the *vegan* package (Oksanen et al. 2017). Generalized linear mixed models (GLMMs) were used to model dependent variables (richness, inverse Simpson index, evenness, PSV, PSR, PSE, MPD.SES and MNTD.SES) using the described fixed variables and interactions. To prevent convergence issues in error distribution models that cannot handle negative values, we transformed MPD.SES and MNTD.SES into positive values by adding a small constant to each value in both variables. Region (Lake Austin, Lake Moore, or Lake King) was used as a random factor. The *glmmTMB* function from the *glmmTMB* package (Brooks et al. 2017) was used to perform GLMMs. Tests to assess over- and under-dispersion and normality were performed using the *simulateResiduals* function from the *DHARMa* package (Hartig 2017). The error distribution family and the link function that best suited the nature of our dependent variable and provided the best fit for each model were chosen (see Table 2). To generate the figures, we used model predictions calculated with the *ggpredict* function from the *ggeffects* package (Lüdtke 2018) and then plotted them using the *ggplot* function from the *ggplot2* package (Wickham 2016). R version 4.3.0 (R Core Team 2023) was used for all analyses.

RESULTS

We recorded 114 gypsophilous species with Amaranthaceae being the dominant family (Supplementary Table 2 in Online resource 1). We recorded 40 species from 14 families at Lake Austin, 69 species from 18 families at Lake Moore, and 75 species from 28 families at Lake King, representing a gradient from more arid to less arid conditions. The three regions shared 16 species with dominant species across all three regions including *Atriplex hymenotheca*, *Kippistia suaedifolia*, *Maireana appressa* and *Tecticornia pterygosperma*. Lake Austin and Lake Moore shared dominance of *Eucalyptus striatocalyx* and several species of *Frankenia* spp., while Lake Moore and Lake King shared dominant species such as *Casuarina obesa* and several species of *Tecticornia* spp. Total cover was the highest in Lake Moore ($37.6\% \pm 9$ S.E.), intermediate in Lake King ($20.4\% \pm 3.3$ S.E.) and lowest in the northern region, i.e. Lake Austin ($14.3\% \pm 2$ S.E.), which has lower values of S content and higher aridity. Only seven of the 114 species recorded were strict gypsophytes: *Austrostipa geoffreyi*, *Goodenia collaris*, *Goodenia gypsicola*, *Kippistia suaedifolia*, *Lawrencia chrysoderma*, *L. helmsii* and *Minuria gardneri* (according to Symon, 2007 and to Lyons pers. comm.). The remaining species are gypsovags, i.e., species that tolerate gypsum soils but can also grow on other substrates. Many of these taxa have distributions that include the array of saline substrates adjacent to gypsum occurrences.

In Western Australian gypsum systems, aridity emerged as the most relevant factor explaining species richness and composition (Table 1, Table 2; Fig. 2, Fig. 3). Aridity significantly reduced species richness and accounted for nearly 20% of the variability in species composition. Although neither soil sulfur content nor conductivity explained the variation in species composition, we detected a positive effect of sulfur (S) on taxonomic evenness, as well as a positive effect of conductivity on both taxonomic diversity (inverse Simpson index) and evenness. Moreover, the negative and significant interaction between sulfur and conductivity ($S \times C$) on the inverse Simpson index indicates that, although taxonomic diversity was

low under low conductivity conditions ($< 4284 \mu\text{S}/\text{cm}$), increasing sulfur content led to higher values of this diversity metric (Table 2, Fig. 3b).

Table 1

Results of PERMANOVA models at plot level ($n = 17$ plots) for the the 3 regions (Lake Austin, Lake Moore and Lake King). Species covers were square root transformed. Aridity (inverse of Martonne index), total soil sulfur content, conductivity and the interaction term among them were used as fixed factors. Vegetation cover per plot (Cover) was used to statistically control for plant productivity differences among plots. Models were based on Bray-Curtis distances and Type III sums of squares. Degrees of freedom (Df), sums of squares (SS), the proportion of variance explained by each variable (R^2), the F-statistic (F), and the associated p-values are shown. Number of permutations = 9999.

Cover	Df	SS	R2	F	p
	1	0.3	0.05	1.03	0.9
Aridity (A)	1	1.1	0.19	3.67	0.001***
Sulfur (S)	1	0.28	0.05	0.93	0.54
Conductivity (C)	1	0.18	0.03	0.59	0.87
A * S	1	0.28	0.05	0.95	0.51
A * C	1	0.23	0.04	0.77	0.7
S * C	1	0.25	0.04	0.84	0.61
A * S * C	1	0.28	0.05	0.94	0.51
Residuals	8	2.41	0.41		
Total	16	5.92	1.0		

Regarding phylogenetic diversity (Table 2), our results showed that MPD.SES was not significantly associated with any of the explanatory variables included in the model, suggesting that in our study system there is no deep evolutionary structuring linked to abiotic conditions. In contrast, we detected significant effects of soil sulfur content, aridity and conductivity for the remaining phylogenetic diversity indices (PSV, PSR, PSE, and MNTD.SES). This indicates that the phylogenetic structure associated with these environmental factors reflects relatively recent evolutionary processes. Specifically, the main effect of sulfur content significantly increased both the PSV and PSE indices, that are usually correlated to taxonomic evenness. Furthermore, a significant interaction was detected between Aridity (A) and Sulfur content (S) for all phylogenetic diversity indices except the MPD.SES. Meaning that increasing aridity in soils with high sulfur content drastically reduced phylogenetic diversity, favouring species assemblages with evolutionarily close lineages (Fig. 3a,c,e,g).

Table 2

Results of the GLMM models (n = 17 plots) for the the 3 regions (Lake, Austin, Lake Moore and Lake King). Taxonomic and phylogenetic diversity indices were modelled using as fixed factors: aridity (inverse of Martonne index), total soil sulfur content, conductivity and the interaction term among them. Vegetation cover per plot (Cover) was used to statistically control for plant productivity differences among plots. Region was used as a random factor. MPD.SES and MNTD.SES were transformed to be positive values to allow modelling. Type III Sum of squares were used. The error distribution families with the link functions that best fitted data are indicated: logarithmic (Log), identity (Id), and Logit. A. Aridity (inverse Martonne), S: Sulfur content, C: Conductivity. Coefficient signs are indicated in parentheses. The p-values are represented as follows: *: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$; ***: $p < 0.001$.

Taxonomic indices					
	Richness	Inv Simpson	Evenness		
Family	<i>Poisson</i>	<i>Gamma</i>	<i>Beta</i>		
Link	<i>Id</i>	<i>Log</i>	<i>Logit</i>		
Cover	(-) 0.3	(-) 7.6**	(-) 4.5*		
Aridity (A)	(-) 27.0***	(-) 1.1	(+) 1.6		
Sulfur (S)	(+) 0.2	(+) 2.4	(+) 7.0**		
Conductivity (C)	(+) 0.003	(+) 12.2***	(+) 8.2**		
A * S	(-) 1.1	(-) 3.2	(-) 0.2		
A * C	(-) 0.05	(+) 0.3	(-) 0.03		
S * C	(-) 0.2	(-) 3.9*	(-) 1.4		
A * S * C	(-) 0.3	(+) 3.9*	(+) 6.1*		
Phylogenetic indices					
	PSV	PSR	PSE	MPD.SES	MNTD.SES
Family	<i>Beta</i>	<i>Gamma</i>	<i>Beta</i>	<i>Gamma</i>	<i>Gaussian</i>
Link	<i>Logit</i>	<i>Identity</i>	<i>Logit</i>	<i>Log</i>	<i>Log</i>
Cover	(-) 6.9**	(-) 7.6**	(-) 38.8***	(-) 0.1	(-) 1.1
Aridity (A)	(-) 0.1	(-) 200.8***	(-) 0.9	(-) 0.001	(-) 0.6
Sulfur (S)	(+) 8.7**	(+) 1.8	(+) 13.4***	(+) 0.1	(-) 0.8
Conductivity (C)	(+) 0.01	(+) 0.2	(+) 9.3**	(+) 0.02	(-) 1.2
A * S	(-) 8.7**	(-) 9.2**	(-) 66.3***	(-) 1.8	(-) 5.2*
A * C	(-) 0.9	(+) 0.8	(-) 6.3*	(-) 0.7	(-) 14.1***
S * C	(-) 3.2	(-) 0.9	(-) 2.3	(-) 2.6	(-) 6.0*

Taxonomic indices					
	Richness	Inv Simpson	Evenness		
A * S * C	(+) 0.7	(-) 0.006	(-) 5.2*	(+) 0.2	(-) 3.3

Remarkably, in saline soils (conductivity > 4284 $\mu\text{S}/\text{cm}$) increasing aridity and soil sulfur content resulted in reduced PSE and MNTD.SES values, thus the joint effect of high conductivity with high aridity and sulfur content, synergistically reduced phylogenetic distance among coexisting species.

DISCUSSION

Aridity is the primary driver of taxonomic diversity in Australian gypsophilous vegetation. Increased aridity resulted in lower species richness and significant shifts in species composition, consistent with findings from other drylands worldwide (Lloret et al. 2004; Miranda et al. 2009; Mulhouse et al. 2016). These results also align with evidence in the well-studied gypsum outcrops of the Iberian Peninsula (Luzuriaga et al. 2020; Peralta et al 2019) and the Chihuahuan Desert in Mexico (Meyer and García-Moya 1989, Meyer et al. 1992; Vargas-Colin et al. 2022). Furthermore, some studies demonstrated that species with higher affinity for gypsum soils (i.e. strict gypsophytes) were favoured towards the most arid conditions, denoting that adaptation to gypsum was inherently linked to adaptation to drought (Luzuriaga et al. 2020; Saiz et al. 2014).

In addition, although salinity—measured as soil electrical conductivity—can be mitigated by the gypsum content in the soil (Ilyas et al., 1997; Kim et al., 2018), as reflected in the effect on the inverse of Simpson (Table 2, Fig. 3b), Australian gypsum ecosystems are among the most saline gypsum environments in the world (see Supplementary Table 1 in Online resource 1). High electrical conductivity is known to impose significant physiological stress on plants from the earliest stages of their life cycle, reducing both germination and subsequent growth (Arif et al. 2020). Our results indicate that the combined influence of three stressors, i.e, high gypsum content, elevated conductivity, and increasing aridity, acts synergistically to shape species assemblages in these communities. Specifically, their joint effect appears to promote the coexistence of closely related taxa, favouring lineages that have diverged more recently in evolutionary terms, as reflected by the MNTD.SES index.

Assuming that phylogenetic relatedness is a reliable estimator of functional strategies of species, beyond easily measurable characteristics (Cadotte et al. 2017; de Bello et al. 2017; Kraft et al. 2015; Webb et al. 2002), we may expect that the phylogenetic convergence associated with more stressful conditions would be the expression of intense environmental filtering, that results in the selection of species with phenotypes adapted to cope with such restrictive conditions. In contrast, Carvajal et al. (2023) reported that under hyperarid environmental conditions, such as those of the Atacama Desert, community assembly was driven primarily by stochastic processes. The absence of detectable environmental filtering in their study may be attributable to the extreme aridity of the system (De Martonne index: 3.2 to 0.5), in comparison with the more moderate but still arid Western Australian sites

examined here (De Martonne index: 14.4 to 6.9) and the reduced number of species. These highly restrictive conditions in the Atacama likely exclude most species a priori, resulting in a flora already pre-filtered for tolerance to extreme aridity. Taken together, our findings suggest that aridity and soil stressful conditions function as hierarchical environmental filters: first, through a stringent aridity filter, and subsequently through harsh edaphic constraints, namely, high conductivity and gypsum content (see also Luzuriaga et al. 2015).

It is important to remark that gypsum soils in Australia are geologically young having formed during the Quaternary period (approximately 50,000 to 16,000 years ago) (Magee, 1991; Warren, 1982), in contrast to other gypsum areas of the world, such as the Chihuahuan Desert, where gypsum soils appeared in Permian or Jurassic periods (approximately 300 to 200 million years ago) (Webber and Kottowski 1959). In this context, the filtering effect of soil gypsum on species assembly constitutes one of the most noteworthy findings of this study. Since gypsum soils are geologically young phylogenetic clades have had limited time to evolve specific adaptations to cope with the restrictive conditions imposed by these soils. This temporal constraint may explain why environmental filtering is expressed primarily as phylogenetic convergence among closely related species at proximal nodes of the phylogenetic tree (as reflected by the MNTD.SES index), rather than across deeper evolutionary branches (MPD.SES index). These results suggest that closely related species had pre-adaptations, that allowed plants to cope with soil chemical stressful conditions, such as Ca to Mg imbalance and S accumulation (Cera et al. 2021), which may have a physiological role in nutritional and osmotic adjustments or serve as a defence mechanism against herbivory (Cera et al. 2023). These pre-adaptations may also be critical to deal with physical restrictive conditions of gypsum systems such as the physical soil crust that hinders seed germination and seedling early development (Escudero et al. 1999, 2000; Meyer, 1986; Ortiz et al. 2023; Peralta et al. 2019). Evidence has shown that in ancient gypsum ecosystems, gypsophytes evolved from ancestral gypsovag clades (Moore and Jansen 2007; Moore et al. 2014; Palacio et al. 2022), most likely from species preadapted to cope with stressful environments characterized by resource-scarce conditions and dryness. In this context, we may expect that, even within the relatively short geological time since gypsum soil formation in these evaporitic basins, we can already detect the initial stages of species specialization to the conditions posed by gypsum in the soil. This has resulted in the relatively low number of strict gypsophytes occurring in southwestern Australia, with only seven gypsophytes out of the 114 species registered occurring in gypsum-dominated soils (Symon, 2007 and to Lyons pers. comm.).

To sum up, the combined effects of climate and soil conductivity and gypsum content determined species assembly of gypsophilous vegetation in Western Australia. Our results align with other studies that demonstrate the crucial filtering effect of aridity in drylands (Luzuriaga et al. 2020; Peralta et al. 2019; Vargas-Colin et al. 2022) together with the effect of gypsum soil content on species assemblages (Luzuriaga et al. 2015). The impact of increasing aridity on soils with high gypsum content results in reduced phylogenetic diversity. This is particularly important in the context of global climate change, which predicts greater aridification of these valuable ecosystems (IPCC, 2022). Remarkably, this study evidenced that certain clades seem to have developed specific adaptations to cope with extremely

restrictive conditions (high gypsum content and high aridity). These results together with the evolutionarily short time spans since the origin of SW Australian gypsum soils suggest the importance of species' preadaptations to arid conditions as a starting point for the evolution of strict gypsophytes.

Declarations

Competing Interest.

The authors have non-financial interests to disclose.

Data Availability

The datasets generated and analysed during this study are available on request.

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Author contribution:

SP, AE, ALL: conceived the main ideas. AE, AC, ML, RC, LP, JJJ, DMF, LO, ALL: collected data. ML and MLan: identified the species. OBV, AC and ALL: performed the statistical analysis and led the writing of the manuscripts. All co-authors contributed to the main text.

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Figures

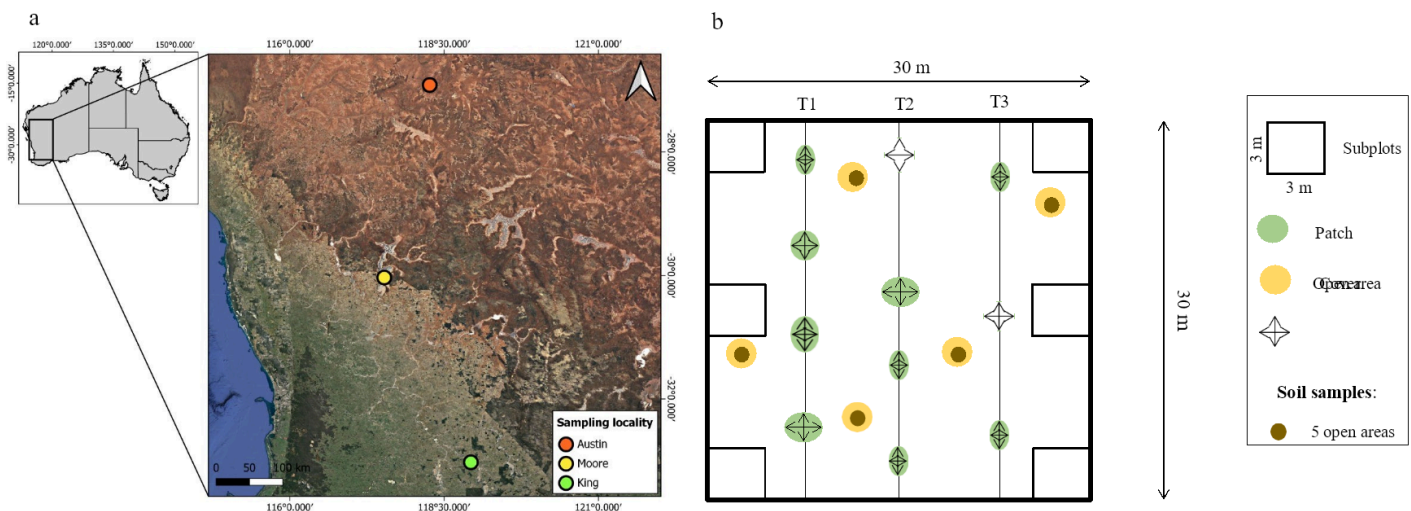


Figure 1

Study area and sampling design. a) Map showing the study sites in three disjunct regions: the lower Midwest (Lake Austin) and the inland SW of Western Australia (Lake Moore and Lake King). b) Six sampling plots measuring 30 × 30 m were established in each study area. Each plot contained transects (T) positioned at 5, 15, and 25 m, each extending 30 m in length and encompassing both vegetated and open microsites. Vegetation patch cover intersecting the transects was estimated by recording two perpendicular measurements for each patch (see cross in schematic). In addition, six 3 × 3 m subplots were placed along the margins of each plot to quantify the percentage cover of bare soil, biological soil crust, rock, and vegetation, as reported in Supplementary Table 1 in Online resource 1.

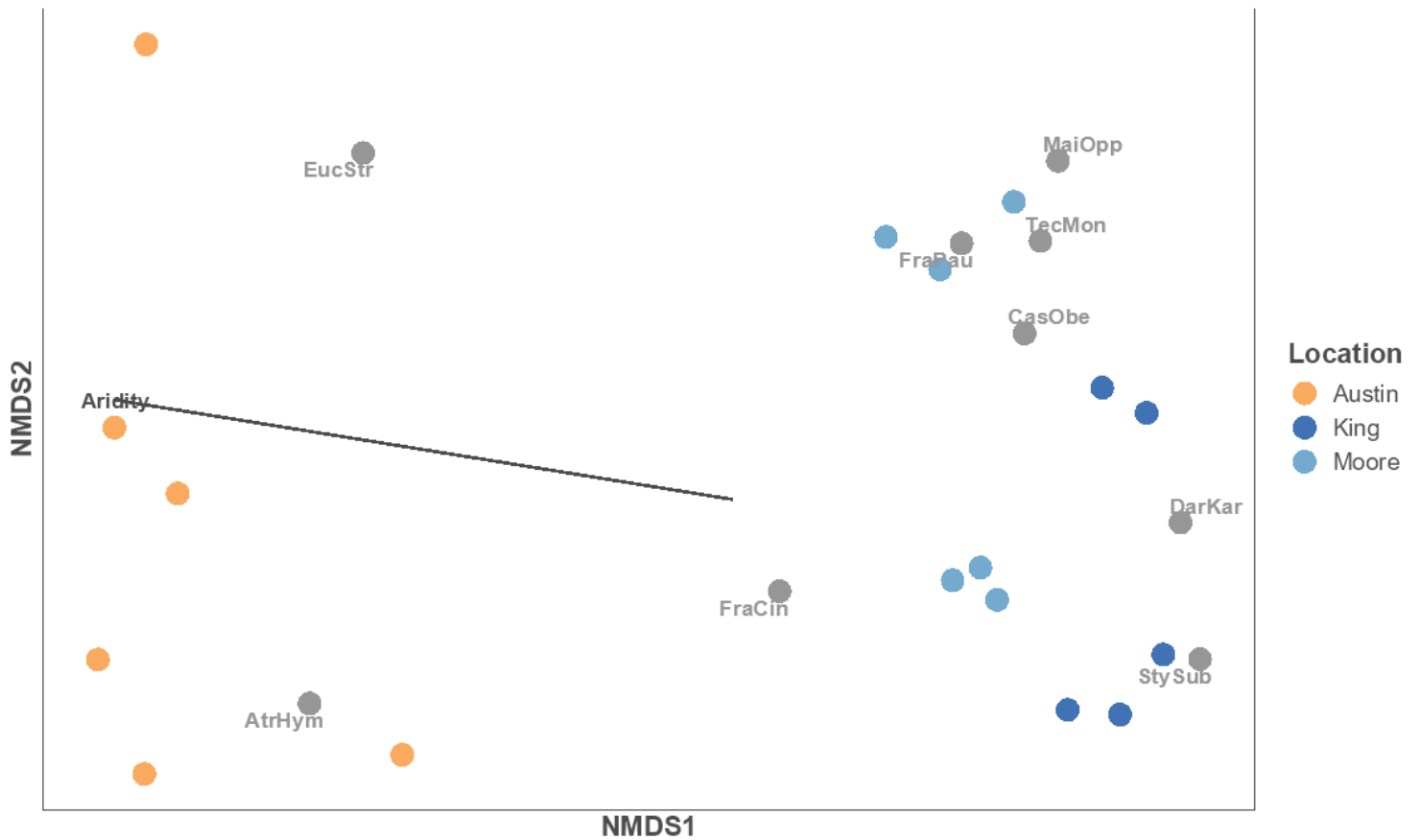


Figure 2

Non-Parametric Multidimensional Scaling (NMDS) was used to represent differences in species composition related to the main explaining variable: inverse of Martonne index (Aridity index). Plots from each location are represented in orange (Lake Austin), blue (Lake King) and light blue (Lake Moore). The length of the vector is related to the intensity of the effect of the variable. The 10 species with the highest cover in the three study localities are represented in grey. Abbreviations are indicated in Supplementary Table 2 in Online resource 1.

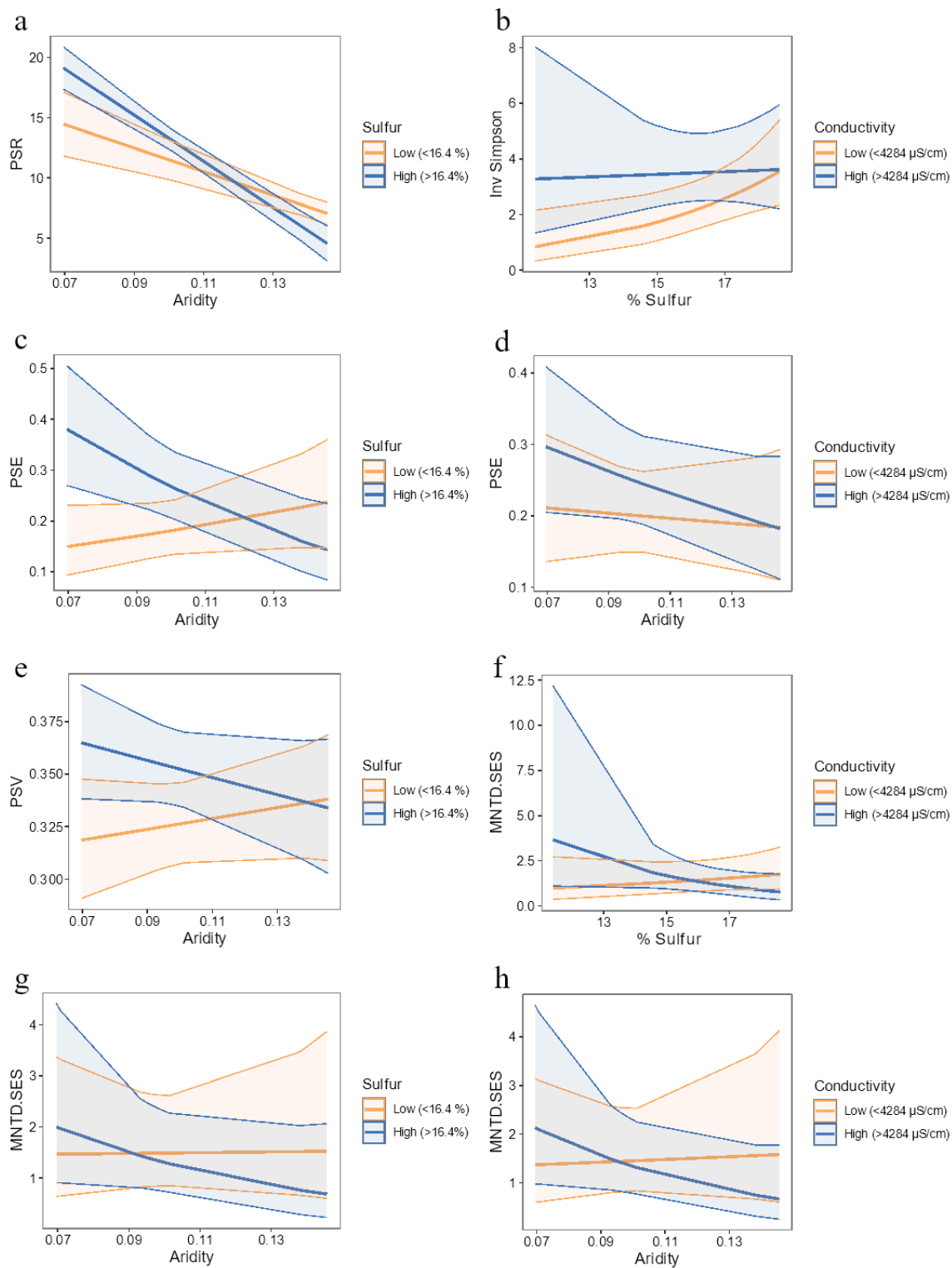


Figure 3

Graphs of mixed model fits and 95 % confidence intervals representing the relationships between: a) Phylogenetic Species Richness (PSR), and the interaction between aridity and sulfur; b) Inverse of Simpson and the interaction between sulfur and conductivity; c) Phylogenetic Species Evenness (PSE) and the interaction between aridity and sulfur; d) Phylogenetic Species Evenness (PSE) and the interaction between aridity and conductivity; e) Phylogenetic Species Variability (PSV) and the interaction between

aridity and sulfur; f) Mean Nearest Taxon Distance (MNTD.SES) and the interaction between sulfur and conductivity; g) Mean Nearest Taxon Distance (MNTD.SES) and the interaction between aridity and sulfur; h) Mean Nearest Taxon Distance (MNTD.SES) and the interaction between aridity and conductivity . Sulfur and conductivity values correspond to the mean of the values below the median (Low) and the mean of the values from the median upwards (High) within the range of values of our 17 plots

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