


RESEARCH ARTICLE

WILEY

Goat grazing reduces diversity and leads to functional, taxonomic, and phylogenetic homogenization in an arid shrubland

Cristian Salgado-Luarte^{1,2*}  | Víctor M. Escobedo^{1*} | Gisela C. Stotz^{1,3} |
Rodrigo S. Rios^{1,3} | Gina Arancio¹ | Ernesto Gianoli^{1,4}

¹Departamento de Biología, Universidad de La Serena, Casilla 554, La Serena 1722069, Región de Coquimbo, Chile

²Instituto de Ecología y Biodiversidad (IEB), Casilla 653, Santiago 7800003, Región Metropolitana, Chile

³Universidad de La Serena, Instituto Multidisciplinario de Investigación en Ciencia y Tecnología, La Serena 1722069, Región de Coquimbo, Chile

⁴Departamento de Botánica, Universidad de Concepción, Casilla 160-C, Concepción 4070386, Región del Biobío, Chile

Correspondence

Cristian Salgado-Luarte, Departamento de Biología, Universidad de La Serena, Casilla 554 La Serena, Chile.
Email: csalgado@userena.cl

Funding information

Fondo Nacional de Desarrollo Científico y Tecnológico, Grant/Award Number: 3120122; Rufford Foundation, Grant/Award Number: 10852; Facultad de Ciencias Agronómicas, Universidad de Chile

Abstract

Livestock production is an important activity in drylands. However, lack of adequate regulation of ranching activities can lead to the degradation of plant communities, which in turn can impact ecosystem functioning. In the arid ecosystems of north-central Chile, unregulated goat grazing is widespread. Because the vegetation has a relatively short evolutionary history of grazing, it is expected to be highly susceptible to this activity. In this study, we evaluated the effects of goat grazing on plant taxonomic, functional, and phylogenetic community structure by comparing 39-year-old grazing exclusion plots and unprotected plots in an arid shrubland in north-central Chile. By integrating analyses of the impact of goat grazing on functional and phylogenetic diversity and dispersion, we studied the mechanisms behind goat impact and the potential consequences. Loss of functional and/or phylogenetic diversity can result in important losses in ecosystem function. As a measure of functional diversity, we recorded plant growth form, life span, and life form. We also reconstructed a phylogeny of all plant species found at the study site and determined the phylogenetic structure of the plant community in ungrazed and grazed areas. We found that goat grazing affected diversity and community composition, leading to taxonomic, functional, and phylogenetic biotic homogenization and causing overall community impoverishment. Goats acted as a habitat filter, increasing functional convergence and promoting the establishment of exotics plants, which can lead to further losses of biodiversity, decreased ecosystem function and overall lower ecosystem stability. Our results indicate that sustainable management strategies are necessary to prevent the further degradation of these ecosystems.

KEYWORDS

goat, grazing, habitat filtering, homogenization, shrubland

1 | INTRODUCTION

Arid and semiarid ecosystems sustain wildlife and provide important ecosystem services (Asner, Elmore, Olander, Martin, & Harris, 2004;

Puigdefábregas, 1998). However, worldwide, arid, and semiarid ecosystems are being degraded by uncontrolled livestock grazing (Petz et al., 2014), which can have important consequences for biodiversity, ecosystem function, and ultimately, human well-being (Cardinale et al., 2012; Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2015; MEA, 2005; Petz et al., 2014). In order to design sustainable practices

*These authors contributed equally to this work.

and preserve ecosystem functioning, we need a better understanding of how livestock grazing can affect different aspects of community structure and function (Eldridge et al., 2015), which can be achieved by integrating taxonomic, functional, and phylogenetic diversity measures (Cadotte, 2013; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011; Gerhold et al., 2011).

The effects of heavy grazing by livestock on community structure in arid ecosystems depend on the evolutionary history of the plant-herbivore interaction (Cingolani, Noy-Meir, & Díaz, 2005; Milchunas & Lauenroth, 1993). Introducing nonindigenous grazers as farming animals, is a common activity practiced throughout arid lands in South America, but nonindigenous herbivores can differ in their feeding habits from native herbivores, and thus result in even greater negative impacts on the native plant community (Holmgren, 2002). Further, they tend to facilitate the establishment of exotic plants, especially of those that have long evolutionary histories with grazing (Eldridge, Delgado-Baquerizo, Travers, Val, & Oliver, 2017). Although plants in arid communities may be less susceptible to herbivores in general, because plant adaptations to drought (e.g. thorns, tough leaves, greater investment in roots over shoots) may increase their tolerance to grazing (Milchunas & Lauenroth, 1993; Milchunas, Sala, & Lauenroth, 1988), nonindigenous herbivores can promote exotic plant dominance and richness by disproportionately reducing the abundance of native species (Parker, Burkepile, & Hay, 2006). Thus, in spite of those plant adaptations, heavy grazing by nonindigenous herbivores can affect negatively plant communities (Carmona et al., 2012; Hoffman, Dean, & Allsopp, 2003; Navarro, Alados, & Cabezudo, 2006). For instance, removal of canopy biomass may weaken the role of shrubs as nurse plants in arid ecosystems, which is essential for the successful recruitment of a large number of species (Gutiérrez & Squeo, 2004; Tracol, Gutiérrez, & Squeo, 2011; van Zonneveld, Gutierrez, & Holmgren, 2012). Furthermore, in arid and semiarid ecosystems grazing by introduced herbivores may interact with aridity, leading to the establishment of alternative community states by altering and homogenizing communities exposed to heavy grazing (Augustine & McNaughton, 1998; Holmgren, 2002; Holmgren, López, Gutiérrez, & Squeo, 2006; Holmgren & Scheffer, 2001). Transitions from one state to the other may be discontinuous, that is, separated by critical thresholds and transitions across such boundaries are difficult to reverse (Holmgren, 2002; Holmgren & Scheffer, 2001).

By excluding species from the community, grazing can alter the functional and phylogenetic structure and diversity of the community (de Bello et al., 2013; Escobedo, Rios, Salgado-Luarte, Stotz, & Gianoli, 2017), which are important indicators of ecosystem function and services (Altesor, Oesterheld, Leoni, Lezama, & Rodríguez, 2005; Leoni, Altesor, & Paruelo, 2009; Piñeiro, Paruelo, Oesterheld, & Jobbágy, 2010). Grazing can act as a 'habitat filter' (de Bello et al., 2013; Laliberté, Norton, & Scott, 2013), where only species with particular traits or strategies are able to establish and persist in the community (Kraft et al., 2015). This would result not only in species loss but also in loss of functional diversity within sites and, if prevalent enough, in the functional homogenization among sites (Mouillot, Graham, Villéger, Mason, & Bellwood, 2013). Species loss can reduce phylogenetic diversity depending on whether the traits allowing species to persist under grazing are phylogenetically conserved or

not (Pausas & Verdú, 2010; Webb, Ackerly, McPeck, & Donoghue, 2002). Functional and phylogenetic approaches provide complementary information (Cadotte, 2013), and their integration improves our understanding of the assembly processes structuring the community (Gerhold, Cahill, Winter, Bartish, & Prinzing, 2015; Li, Ives, & Waller, 2017) and the consequences of biodiversity loss for ecosystem function (Flynn et al., 2011). Loss of functional and phylogenetic diversity can result in lower ecosystem stability, altered nutrient cycling and litter decomposition rates, and lower community resistance to invasions (Cadotte, Dinnage, & Tilman, 2012; Flynn et al., 2011; Gerhold et al., 2011).

In the arid shrubland from north-central Chile, livestock production is a common economic activity, mainly consisting of breeding of the nonindigenous goat *Capra hircus* (Bovidae; INE, 2015). Goat production is an unregulated activity, with a predominance of unmanaged semiferous systems characterized by low production and large numbers of goats (INE, 2015). Goat herds—around 150 individuals each—are typically confined to farms and periodically released to the adjacent slopes, which may result in a strong deterioration of this arid ecosystem (Quiroz, 2007). This region concentrates around 61% of the goats of Chile with about 600,000 heads (INE, 2015). Estimates indicate that goat density has exceeded the recommended carrying capacity for this area, resulting in the overgrazing of about 64% of regional lands (INE, 2015; Quiroz, 2007). Goat grazing constitutes a significant disturbance in the arid shrubland because goats remove large amounts of biomass. Although they show preference for tender shoots and seedlings of native shrubs, they use a range of plants for subsistence, including trees, shrubs, forbs, grasses, even bark, and dead plant material (Bahre, 1979; Contreras, Menesses, & Rojas, 2001). Goats were introduced by the Spaniards about 400 years ago (Fuentes & Muñoz, 1995; Holmgren, 2002) and are not functionally equivalent to the native ungulate *Lama guanicoe* (guanaco) (Fuentes & Muñoz, 1995; Holmgren, 2002), which is a low-impact grazer compared with goats. Goats generally uproot the plants and trample the soil, further reducing the already low recruitment of plant species in the study area (Gutiérrez, Holmgren, Manrique, & Squeo, 2007), whereas guanacos lack hooves (their feet have soft, leather-like pads on the bottom that prevent soil compaction), have cleft lips and continued-growth cutting dentition that allow them to select the plants parts they consume without uprooting plants and distribute their browsing among a variety of plants, thus minimizing their impact on the community (Erlach, 1984; Puig, Videla, & Cona, 1997). Studies in Chilean *matorral* have shown that goats ate shrubs five to 10 times faster than *L. guanicoe*, even if there was nothing else to eat, and the evidence available suggests a strong difference in the browsing/grazing preferences exhibited by goats when compared with guanacos (Fuentes, Poaini, & Molina, 1987; Gutiérrez et al., 2007; Gutiérrez & Squeo, 2004; Holmgren, 2002; Simonetti & Fuentes, 1983). However, the overall impact of goats on community structure and function is still poorly understood, yet key to the development of a more sustainable management plan. In this study, we compare communities inside and outside a 39-year-old goat enclosure using taxonomic, functional, and phylogenetic approaches to assess the effect of goat grazing on (a) community structure and diversity, (b) plant invasions, and (c) assembly processes. We expected goat grazing to be a major driver

of plant community structure acting as a habitat filter, resulting in taxonomic, functional, and phylogenetic diversity loss, reduced vegetation complexity and homogenization.

2 | METHODS

2.1 | Study site

This research was conducted at Las Cardas Experimental Station (5,436 ha; Universidad de Chile) located in the Coquimbo Region, south of the Atacama Desert (Chile; 30°15'S - 71°17'W; Figure 1 a, b). This site has a mean annual temperature of 14.9°C and a mean annual precipitation of 90.24 mm (<http://www.ceazamet.cl/>). Las Cardas is an open shrubland (main woody species: *Gutierrezia resinosa*, *Flourensia thurifera*, *Acacia caven*, *Senna cumingii*) with a temporally active herbaceous stratum (winter and beginning of spring).

2.2 | Experiment and sampling design

In the study site, there is a ~18 ha-fenced area from which livestock has been excluded since 1972 (Cepeda-Pizarro, 1989; Figure 1 c,d). To assess the long-term impact of grazing on plant community structure, we sampled and compared vegetation exposed with and protected from goat grazing (Figure 1d). To this end, 16 paired plots,

each plot of 0.25 ha, were established along a fence that separates the goat exclusion area (18 ha) and the 'open' grazed area (Figure 1 c). Eight 50 × 50 m plots were located just inside (i.e., ungrazed plots) and the other eight plots just outside (i.e., grazed plots) the enclosure (Figure 1 b,c). This approach resulted in an unreplicated trial, but unfortunately, there are no other long-term enclosures available in the region. We argue that the differences observed between open and protected plots can be attributed to goat grazing because within this experimental station, all other activities are being monitored and controlled. In spite of its limitation, this approach can yield valuable ecological knowledge, especially for conservation purposes and has been successfully employed in other studies (e.g., El-Kablawy, 2017; Milchunas, Lauenroth, & Chapman, 1992; Todd & Hoffman, 2009). Pairs of ungrazed versus grazed plots were located at least 50 m apart from each other (eight experimental blocks). Blocks were laid out along the ≈2 km fenced perimeter. Within each plot, five parallel 50 m transects were established (at 10 m distance from each other), and in each transect, 10 quadrats of 1 m² were sampled, every 5 m, for a total of 50 quadrats per plot (Figure 1c). Within each quadrat, all individuals were recorded and identified to species; seven specimens were identified only to genus. For each taxon, we determined three categorical life history traits: growth form (GF), plant life span (LS), and life form (LF; see Figure 2), following standard references (Pérez-Harguindeguy et al., 2013) and regional floras (Marticorena, Squeo, Arancio, & Muñoz, 2001). We also recorded species origin

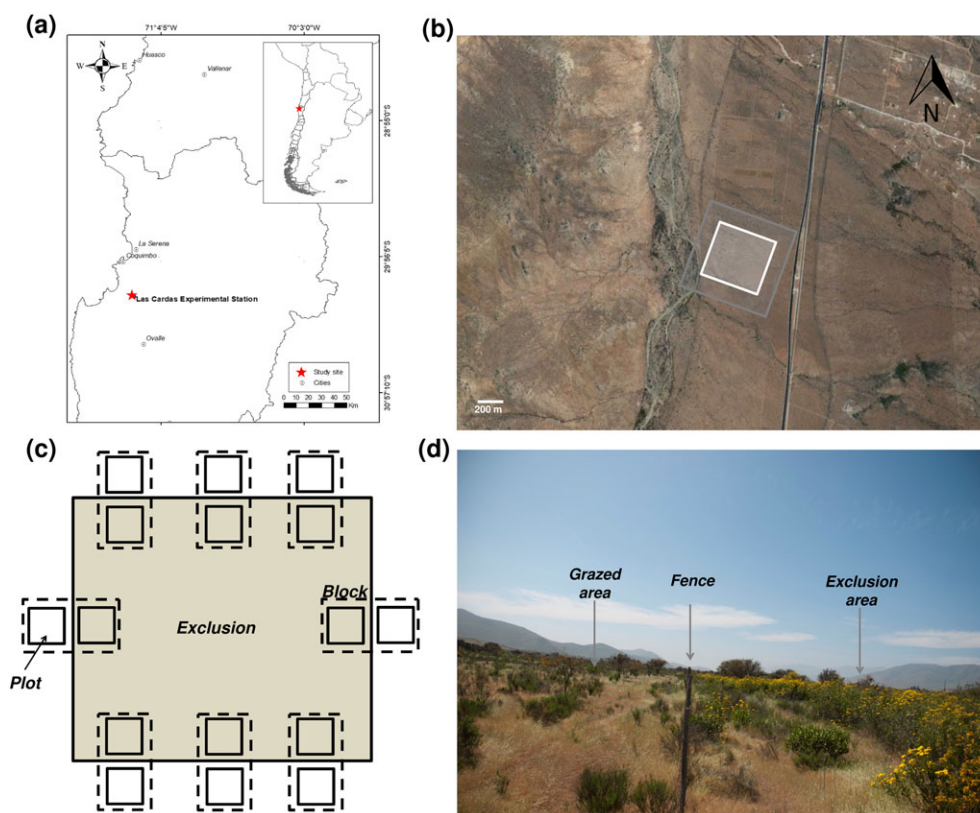


FIGURE 1 (a) Map showing the location of the study area in the arid region of north-central Chile. (b) Aerial image of the study area. The grazing exclusion area is delimited by the white perimeter and the gray perimeter enclose the whole study area. (c) Sampling design. The eight blocks (16 paired plots: eight grazed and eight ungrazed) located just inside and just outside the exclusion area. (d) Vegetation contrast between the exclusion (ungrazed) area and the open area subjected to grazing by goats (grazed) [Colour figure can be viewed at wileyonlinelibrary.com]

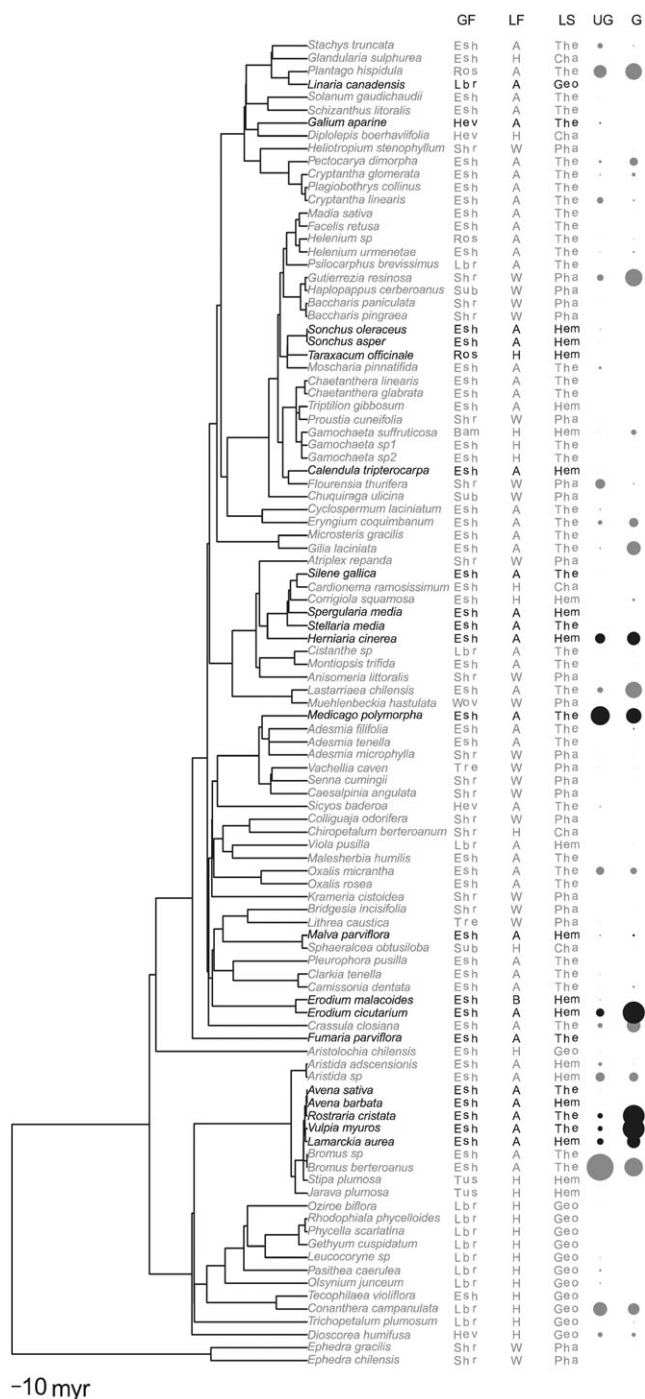


FIGURE 2 Phylogenetic tree showing all 103 studied species. Exotic and native species are shown in bold and grey, respectively. Life history traits are also shown. Growth form categories are: extensive-stem herb (Esh), herbaceous vine (Hev), leaf-bearing rhizomatous (Lbr), rosette plant (Ros), subshrub (Sub), shrub (Shr), tree (Tre), tussock (Tus). Lifeform categories are: chamaephyte (Cha), geophyte (Geo), hemicryptophyte (Hem), phanerophyte (Pha), therophyte (The). Plant lifespan categories are: annual herb (A), perennial herb (H), woody plant (W). Circles represent the relative abundance of the species in ungrazed and grazed communities. For details, see the supplementary Table S1

(OR) as 'native' or 'exotic' (Fuentes, Pauchard, Sánchez, Esquivel, & Marticorena, 2013). Here an exotic plant is defined as any species in a given area whose presence is due to intentional or accidental introduction as a result of human activity (Richardson et al., 2000).

2.3 | Phylogenetic tree construction

We assembled a phylogenetic tree with all 103 taxa sampled (20 exotic and 83 native species; Figure 2) using the *S.PhyloMaker* function implemented for R version 3.2.3 (R Core Team, 2016), in combination with the BLADJ algorithm (as in Phylocom; Qian & Jin, 2016), to assign branch lengths (all analyses were performed using the R software environment). Tree topology was based on an updated version of the megaphylogeny of seed plants of Zanne et al. (2014). Finally, the few polytomies in the tree were resolved randomly using the *multi2di* R-function from the *ape* package.

2.4 | Impacts of grazing on alpha and beta diversity

To test whether goat grazing has negative effects on plant community structure, we compared ungrazed and grazed communities in terms of alpha and beta diversity for taxonomic, functional, and phylogenetic approaches. For taxonomic alpha diversity, we estimated species richness (hereafter: richness) and species frequency (hereafter: abundance) per plot. Abundance was estimated as the sum of occurrences in the 50 quadrats of 1 m² in each plot (i.e., frequency: 0–50). For functional alpha diversity, we estimated the Functional Dispersion index (FDi; Laliberté & Legendre, 2010) per plot. FDi is based on principal coordinate analysis and is calculated as the mean distance of each species to the community centroid, weighted by its abundance. FDi values were obtained through the *dbFD* R-function from *FD* package. For phylogenetic alpha diversity, we estimated the abundance-weighted Mean pairwise Phylogenetic Distance index (MPD; Webb et al., 2002) per plot. MPD is the mean of all the phylogenetic distances among individuals in each plot and was obtained through the *ses.mpd* R-function from the *picante* package. We used Generalized Linear Mixed Models (GLMMs) with block as a random effect to assess the effects of grazing on alpha taxonomic, functional, and phylogenetic diversity.

For beta diversity, we estimated dissimilarity in taxonomic, functional, and phylogenetic composition between paired plots of ungrazed and grazed communities, as well as differences in the degree of homogenization within each community. To test for taxonomic, functional, and phylogenetic dissimilarity between ungrazed and grazed communities, we used a nonparametric Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson & Walsh, 2013) from the *vegan* package, using the *adonis* R-function with blocks as groups within which to constrain permutations (i.e., 'strata' argument). PERMANOVA was performed on a Bray–Curtis dissimilarity matrix for taxonomic data. For functional and phylogenetic data, we performed PERMANOVA on abundance-weighted intercommunity mean pairwise distance matrices, which were obtained through the *comdist* R-function from the *picante* package.

The degree of homogenization of ungrazed and grazed communities was estimated as the multivariate dispersion in species composition within each community, using the *betadisper* R-function (Anderson, Ellingsen, & McArdle, 2006). This approach evaluates the distances of each replicate (plot) within group (grazing condition) to the group's median as a measure of dispersion (Anderson et al.,

2006), where shorter distances to the centroid indicate greater degree of biotic homogenization. Then, to test for significant differences in degree of biotic homogenization, we performed a Permutation test of multivariate homogeneity of group dispersions on multivariate dispersion data, using the *permutest* R-function.

2.5 | Impact of grazing on the plant invasion process

First, we examined whether native and exotic species show preference for any grazing condition. Then, we estimated a correlation index (phi coefficient of association; $r_{g/\phi}$) using the *multipatt* R-function from the *Indicspecies* package, not considering combinations of assemblages (De Cáceres & Legendre, 2009). To test whether grazing drives the plant invasion process, we estimated the taxonomic, functional, and phylogenetic contribution of exotic species in ungrazed and grazed communities. For taxonomic contribution, we used the percentage of abundance (cAbundance) and richness (cRichness) of exotic species per plot. For functional contribution, we used the relative contribution of exotic species to FDis (cFDis) following Escobedo et al. (2017). For phylogenetic contribution, we used the contribution of exotic species to Phylogenetic Species Evenness (Helmus, Bland, Williams, & Ives, 2007) per plot. To estimate the phylogenetic contribution (cPSE), we modified the *psv.spp* R-function, incorporating species abundance information. To compare the cFDis and cPSE

between ungrazed and grazed communities, we performed GLMMs using the same procedure used for alpha diversity.

To evaluate whether exotic and native assemblages are functionally different, we performed Principal Components Analysis and PERMANOVA on a binary functional trait matrix. To test whether exotic and native assemblages belong to different clades, we tested whether OR showed phylogenetic signal (Mi et al., 2012).

2.6 | Underlying assembly processes

To elucidate the underlying community assembly processes involved in the effects of goat grazing on biodiversity change and ecosystem functioning, we estimated the standardized effect size ($_{SES}$) for FDis and MPD using 9,999 randomly generated null communities: $FDis_{SES} = (FDis [or MPD]_{observed} - FDis [or MPD]_{null}) / s.d.FDis [or MPD]_{null}^{-1}$. We randomized the community abundance matrices within species, therefore assuming that all species of the pool are able to colonize any plot within Las Cardas Experimental Station. SES-values >0 indicate functional divergence and phylogenetic overdispersion (through two-tailed *t* tests), whereas SES-values <0 indicate functional convergence and phylogenetic clustering. We used $FDis_{SES}$ and MPD_{SES} approaches to study the interplay between trait-based assembly process and macroevolutionary diversity. We tested for phylogenetic signal of GF, LS, and LF to determine whether these functional

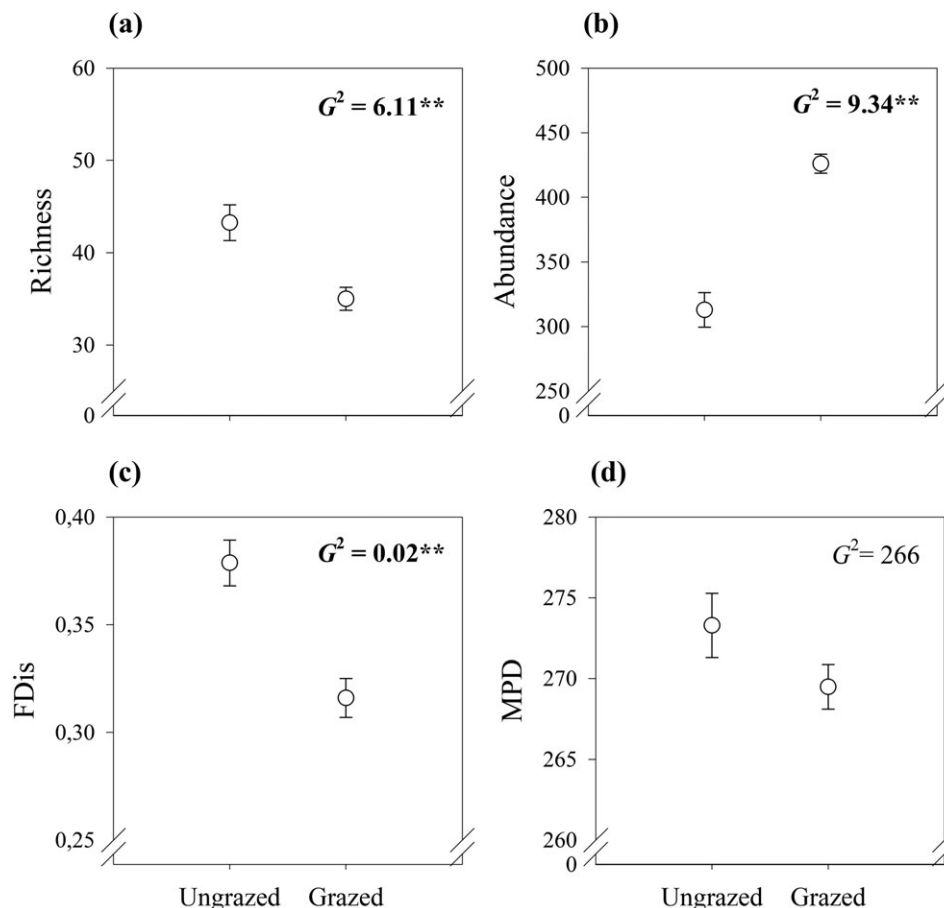


FIGURE 3 (a) Species richness, (b) abundance, (c) functional diversity, and (d) phylogenetic diversity for grazed and ungrazed communities (mean ± standard error). Decreased distance to the median indicates biotic homogenization.** $p < 0.01$

traits are phylogenetically dependent (Losos, 2008). We used Pagel's λ (Pagel, 1999) to estimate phylogenetic signal, using the *fitDiscrete* R-function from the *Geiger* package; to determine the significance of λ , we compared the maximum likelihood estimate of λ against the maximum likelihood of models when $\lambda = 0$ (from a tree without phylogenetic signal) using Likelihood Ratio Tests. λ values normally vary between 0 (traits are phylogenetically independent) and 1 (traits evolved according to a Brownian-motion model), but values greater than 1 indicate that phylogenetic signal is greater than expected from a Brownian-motion process (Losos, 2008).

3 | RESULTS

3.1 | Impacts of grazing on alpha and beta diversity

Although dominant species were found both in grazed and ungrazed plots, 31 species appeared solely in the enclosure, and 20 species were found only in the open area. We found that goat grazing decreased alpha diversity (Figure 3) and altered community composition (Figure 4), resulting in taxonomic, functional, and phylogenetic homogenization (Figure 6). Richness and functional diversity were lower, and abundance was higher in grazed communities compared with ungrazed communities (Figures 3a, 2c, 2b). Grazed and ungrazed communities did not differ in MPD (Figure 3d) but did differ in their taxonomic ($F_{[1, 14]} = 11.26$, $R^2 = 0.44$, $p < 0.01$, Figure 4) and phylogenetic composition ($F_{[1, 14]} = 1.08$, $R^2 = 0.10$, $p < 0.01$), whereas functional composition was only marginally different ($F_{[1, 14]} = 1.03$, $R^2 = 0.07$, $p < 0.06$). When evaluating particular

functional groups, we found that whereas the abundance and/or diversity of trees, shrubs, vines, and geophytes tended to decrease in grazed plots, the abundance and/or diversity of annuals, rosettes, and hemicryptophytes increased in grazed plots (Figure 5). Moreover, grazed communities showed lower taxonomic, functional, and phylogenetic multivariate dispersion than ungrazed communities, which indicate greater biotic homogenization (Figure 6).

3.2 | Impact of grazing on the plant invasion process

We found that goat grazing favoured plant invasion. The analysis of preference showed that 24 species (18 natives and six exotics) had a significant association with either grazed or ungrazed assemblages (Figure 4). In addition, 44.4% of native species and 66.6% of exotic species were associated with grazed communities.

The contribution of exotic species to abundance (Figure 7b), as well as to functional and phylogenetic diversity, was higher in grazed communities (Figure 7c,d). However, the contribution of exotics to richness did not differ between grazing conditions (Figure 7a).

We found significant functional distinctiveness between native and exotic assemblages ($F_{[1, 102]} = 6.69$, $R^2 = 0.06$, $p < 0.01$). Several categorical life history traits, such as rosette plant, tussock, dwarf shrub, shrub, tree, herbaceous vine, and woody vine for GF, perennial for LS, and phanerophyte, chamaephyte, and geophyte for LF were nonrepresented or underrepresented in the exotic flora (Figure 2, Figure 5). In addition, we found phylogenetic distinctiveness between native and exotic assemblages: a significant phylogenetic signal for OR ($\lambda = 0.72$, $p < 0.01$; Figure 2). From the phylogenetic standpoint, exotic taxa form several clusters along the phylogenetic

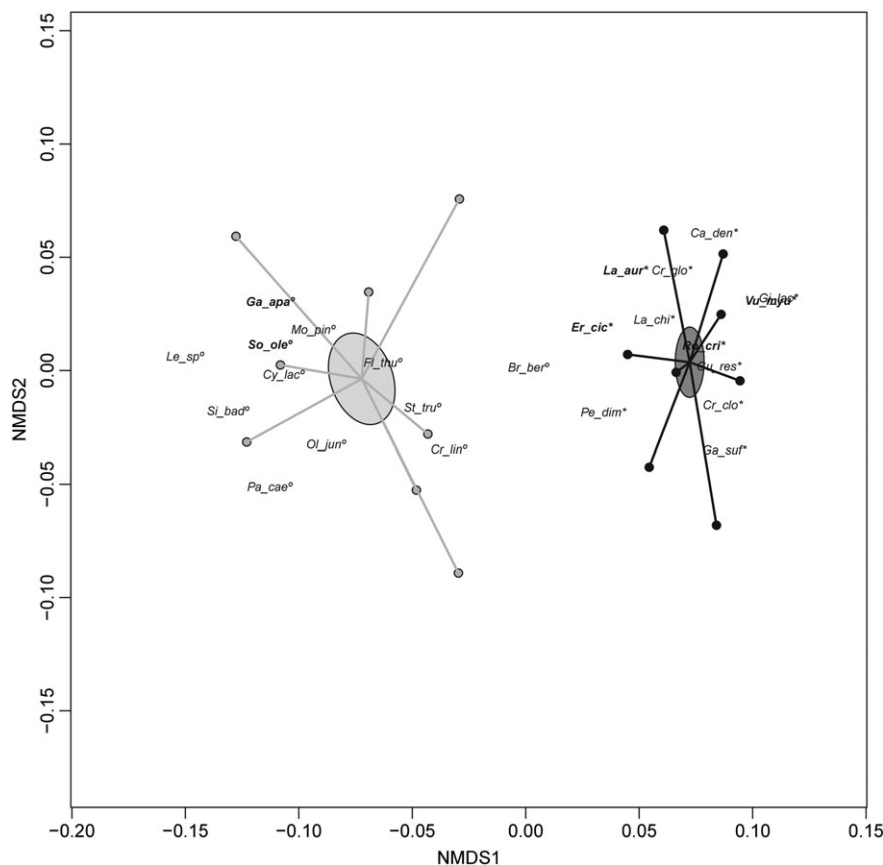


FIGURE 4 Differences in species composition between ungrazed (light grey) and grazed (dark grey) communities. Patterns are based on a nonmetric multidimensional scaling analysis. Exotic species are in bold. An asterisk indicates a significant correlation index (r_g/ϕ). Species codes are given in Supplementary Data Table S1

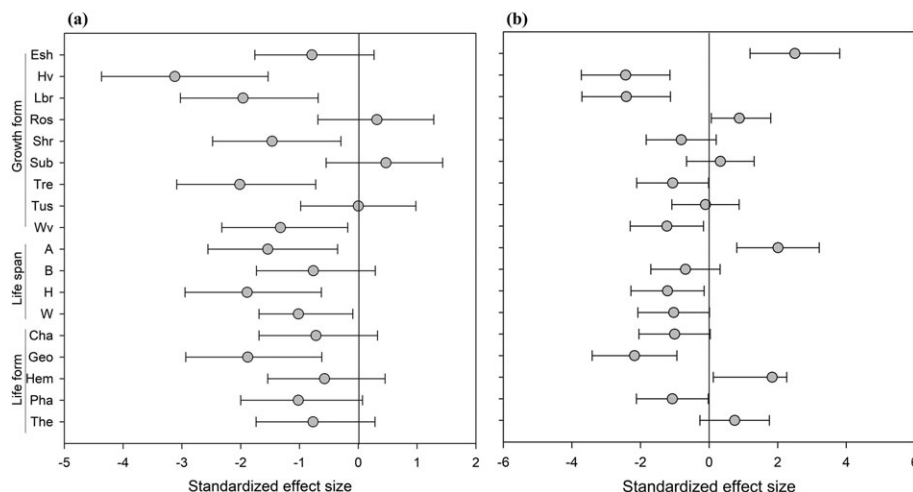


FIGURE 5 Change in species richness (a) and species abundance (b) for each functional group. Change was calculated as Cohen's d (standardized effect size), where negative values reflect lower values in grazed plots compared with ungrazed plots, whereas the opposite is true for positive values. Error bars: 95% confidence interval. Abbreviations of functional groups are given in the Figure 2 legend

tree (e.g., Asteraceae, Caryophyllaceae, Geraniaceae, and Poaceae) and contribute plant families, which are otherwise absent from the local native flora (i.e., Geraniaceae, Papaveraceae, and Rubiaceae).

3.3 | Underlying assembly processes

We found that grazed and ungrazed communities differed in local assembly processes ($G^2_{[1, 7]} = 1.33, p < 0.01$, Figure 8). We found evidence of limiting similarity in ungrazed communities (functional divergence; $t_{[1, 7]} = 3.17, p < 0.05$) and of habitat filtering in the grazed communities (functional convergence; $t_{[1, 7]} = -3.81, p < 0.01$). Moreover, we found that closely related species tended to be more functionally similar, at least in terms of life history traits, as evidenced by the phylogenetic signal of all life history traits: growth form ($\lambda = 0.86, p < 0.01$), plant lifespan ($\lambda = 0.81, p < 0.01$), and life form ($\lambda = 0.78, p < 0.01$). Although there was phylogenetic signal for all traits, the assembly processes did not alter the phylogenetic structure of the community ($G^2_{[1, 7]} = 20.47, p = 0.21$; Figure 8).

4 | DISCUSSION

A comprehensive analysis of community structure, integrating taxonomic, functional, and phylogenetic approaches, can provide a better understanding of how goat grazing can shape plant communities and alter ecosystem function and services (Cadotte et al., 2012; Flynn et al., 2011). As predicted, this arid shrubland was found to be susceptible to grazing: Goats operated as a habitat filter, leading to a taxonomic, functional, and phylogenetic impoverishment of the community but tended to facilitate the establishment of exotic species. The loss of overall taxonomic, functional, and phylogenetic diversity can further result in lower ecosystem stability and fundamental changes in community assembly, structure, and function (Cadotte et al., 2012). This new degraded community may represent an alternative community state, which can be extremely difficult to reverse (Holmgren & Scheffer, 2001).

Arid systems are thought to be generally tolerant to grazing (Milchunas et al., 1988). Our results support the notion that heavy grazing can have a significant impact on these communities (Anderson & Hoffman, 2011; Haarmeyer, Schmiedel, Dengler, & Bösing, 2010). The strong impact of goat grazing on this arid ecosystem may be due to a relatively short evolutionary history of heavy grazing, especially from introduced grazers (Cingolani et al., 2005; Milchunas et al., 1988). The flora in the study region has evolved in habitats with transient exposure to low grazing pressure for at least 10,000 years (Fuentes & Simonetti, 1982; Simonetti & Fuentes, 1983). Although we have no direct evidence of past herbivory pressures, the historical reports and the limited fossil record suggest that they have been relatively low compared with recent and current goat densities (see Bahre, 1979; Fuentes & Simonetti, 1982; Gay, 1847; Simonetti & Fuentes, 1985). The main herbivore inhabiting the region, the camelid *L. guanicoe* (guanaco), was scarce by the time of Spanish colonization in the 16th century (Bahre, 1979). In contrast with introduced ungulates, this native herbivore is considered a 'low impact grazer' (see Introduction). Goats were introduced to north-central Chile ca. 400 years ago (Fuentes & Muñoz, 1995; Holmgren, 2002), reaching a high stock during the first half of the 19th century, when heavy grazing history started (Bahre, 1979). Thus, goats are not functionally equivalent to native herbivores (Simonetti & Fuentes, 1983) and are—in evolutionary terms—a novel disturbance to which many plant species are not adapted (Simonetti & Fuentes, 1983; Simonetti & Fuentes, 1985).

Goats were found to alter species composition and reduce overall species diversity (Figure 3, Figure 4). Olf and Ritchie (1998) suggested that grazing on arid lands increased extinction rates by extirpating subordinate or rare palatable species from the community (Milchunas et al., 1988; Osem, Perevolotsky, & Jaime, 2002). Accordingly, we found that although dominant species were found in grazed and ungrazed plots alike, 31 species appeared solely in ungrazed plots; 20 species were found only in grazed plots. An even greater abundance of dominant species in grazed plots may explain why abundance was higher in grazed compared with ungrazed plots (Figure 3). Yet by

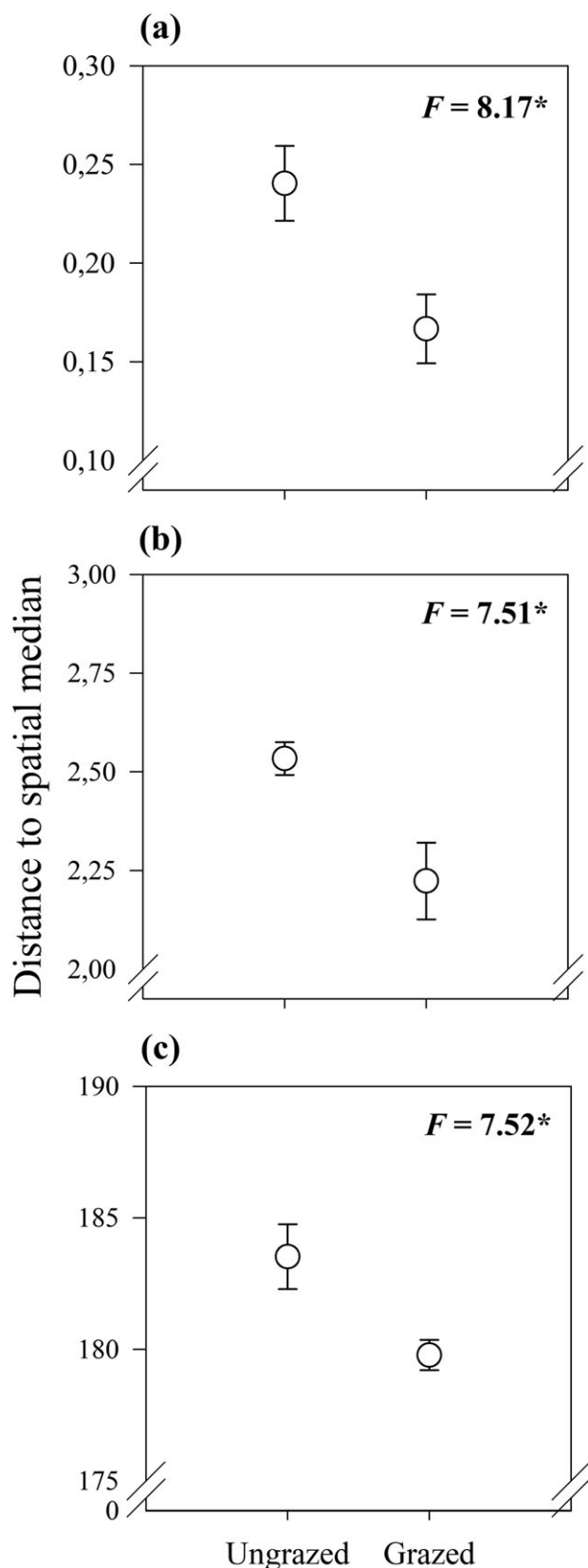


FIGURE 6 Taxonomic (a), functional (b), and phylogenetic (c), beta diversity (calculated as the average distance from the group's median) for grazed and ungrazed communities in an arid shrubland. Decreased distance to the median indicates biotic homogenization. Error bars: standard error. * $p < 0.05$

excluding rare species, grazing not only acted to reduce diversity within each sampled site but also led to the homogenization of previously distinct sites. Homogenization is an important form of biotic impoverishment, can lead to increased species extinction risk and may decrease the system's resilience to large-scale disturbances (Olden & Poff, 2003).

Grazing favored more resistant functional groups and excluded less tolerant ones. Rosette life forms were particularly associated with grazed communities, a pattern that is consistent with previous evidence of grazing favoring small, prostrate, and rosette plants, over tall-growing plants (Klimešová, Latzel, de Bello, & van Groenendae, 2008). Geophytes, instead, were strongly suppressed by grazing. Although geophytes are thought to be tolerant to grazing (Cingolani et al., 2005; Todd & Hoffman, 2009), they can be susceptible to soil compaction, due to trampling by goats. Further, ephemeral species appear to be less affected by grazing than long-lived plants. Thus, grazed communities had a higher abundance of annual and herbaceous plants and a lower abundance and richness of woody species compared with ungrazed communities (Figure 5). Woody species are fundamental in this ecosystem because they generally support vines (which consequently declined in grazed areas, Figure 5) and—more importantly—play a key role as nurse plants, facilitating the establishment and persistence of other plants (Gutiérrez & Squeo, 2004; Tracol et al., 2011; van Zonneveld et al., 2012). The number of recruiting species under shrubs may be 100% greater than in open patches of the arid scrubland and seedling abundance may be 300% higher under shrubs than in open patches (van Zonneveld et al., 2012). Further, nurse shrubs are not only important for the establishment of annual and herbaceous species but also for the recruitment of woody species. Goat grazing reduced shrub cover in our study site, thus reducing the favorable sites for recruitment of new individuals. Such reductions in total nurse cover resulted in lower diversity and created open sites for colonization by exotic species, presumably more tolerant to drought and/or herbivory. In sum, the exclusion of particular functional groups can have major consequences for the shrubland community.

The change in functional and phylogenetic community patterns due to grazing indicates that goats acted as a filter, leading to the impoverishment and homogenization of these communities. Goat grazing led to a loss of functional diversity (loss of less tolerant functional groups, as seen above) and resulted in functional convergence, where coexisting species tended to be more functionally similar than expected by chance (Kraft et al., 2015). In contrast, within the enclosure species tended to be functionally divergent (Figure 8). Competition is one of the major processes driving the functional divergence among coexisting species (Mayfield & Levine, 2010) and hence likely to be important in exclusion areas. However, in open areas, grazing may reduce competition due to biomass removal, further limiting functional divergence. In contrast, we found no evidence of phylogenetic diversity loss (Figure 3) or phylogenetic clustering (Figure 8), but we did find a change in phylogenetic composition due to grazing. Not only did the most representative families differ between grazed and ungrazed plots but also less abundant families, such as Aristolochiaceae, Papaveraceae, and Solanaceae, were lost from the grazed community and replaced by Krameriaceae and Spindaceae. Functional diversity loss and the change in phylogenetic

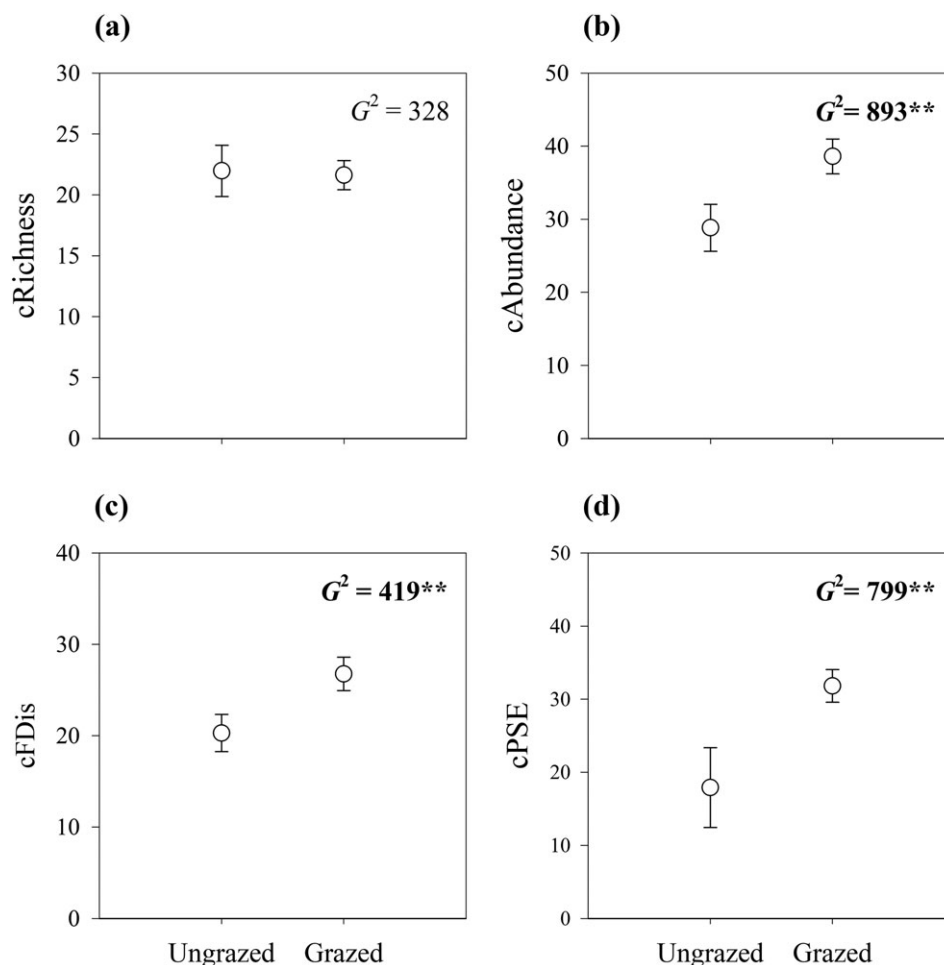


FIGURE 7 Relative contribution of exotic plants to richness (a), abundance (b), functional diversity (c), and phylogenetic diversity (d), in ungrazed and grazed communities (mean \pm standard error)

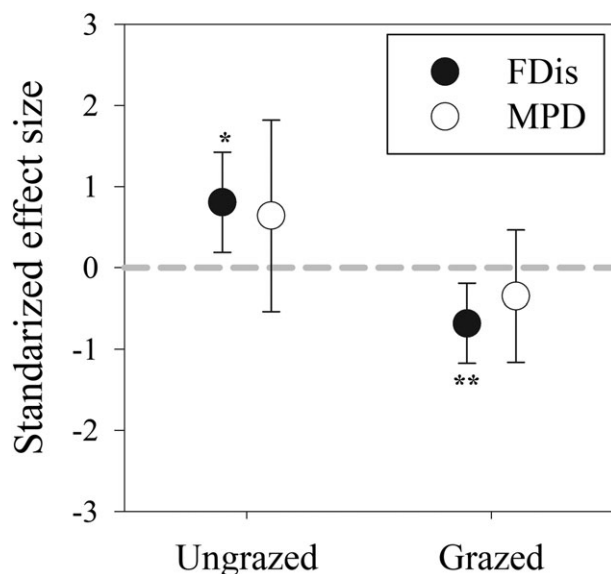


FIGURE 8 Differences in functional and phylogenetic divergence between ungrazed and grazed communities in an arid shrubland. Functional and phylogenetic patterns were estimated from standardized effect size values of Functional Dispersion index and Mean pairwise Phylogenetic Distance index, respectively. Error bars: standard error. * $p < 0.05$, ** $p < 0.01$

composition can result in lower ecosystem stability, changes in ecosystem functions, such as litter decomposition and nutrient cycling and in decreased resistance to invasions (Cadotte et al., 2012; Gerhold et al., 2011).

Disturbance caused by grazing can promote the establishment of exotic plants by increasing the availability of niche spaces for exotic species but also by decreasing competition through trampling and defoliation (Milchunas et al., 1992). Consistent with the idea that evolutionary history is a good predictor of grazing impact, most exotic plants found in this study are native to the Mediterranean region, where the plant community has a long evolutionary history of grazing and overgrazing (Fuentes et al., 2013). We found that, although exotic species contributed equally to species richness in grazed and ungrazed communities, they had a higher contribution to abundance and functional and phylogenetic diversity in grazed communities. In this shrubland, traits such as annual lifespan, extensive-stemmed growth, and hemicryptophyte life form are overrepresented in exotic species. Consequently, exotic plants showed low functional diversity, such functional redundancy of exotic species may partly account for the loss in functional diversity and the functional homogenization in grazed communities. Additionally, exotic species can further limit the establishment and performance of native species and lead to greater changes in ecosystem function (Vilà et al., 2011).

5 | CONCLUSIONS

We found that heavy, long-term grazing by goats has led to the transformation of a highly diverse community into a taxonomically, functionally, and phylogenetically impoverished community. Although there is evidence that restricted levels of grazing may be useful for ecosystem restoration purposes (Tälle et al., 2016), it is clear that the current level of unregulated goat grazing is unsustainable in this system. It is necessary to implement management strategies to establish more sustainable practices, which could include the regulation of stocking rates, rotational grazing, and establishing livestock-free areas, among others. For instance, because recruitment and establishment are key limiting stages in this arid ecosystem, protecting communities from grazing during opportunity windows (i.e., wet years) could help community recovery (Holmgren & Scheffer, 2001). Lastly, allowing herds to move across larger scales can help prevent overgrazing (van de Koppel et al., 2002). The current situation in north-central Chile is that goat herds are confined to relatively small territories, which result in the overexploitation and degradation of the system, as evidenced in this study.

ACKNOWLEDGMENTS

We thank CEZA (Centro de Estudios de Zonas Áridas) and Facultad de Ciencias Agronómicas, Universidad de Chile for granting permits to work in Las Cardas experimental station. We are particularly grateful to Claudia Torres, farm manager of Las Cardas experimental station. We also thank Mónica Cisternas for her valuable help with data sorting. We acknowledge the financial support of The Rufford Small Grant Foundation 10852 and FONDECYT postdoctoral fellowship 3120122 to CSL.

ORCID

Cristian Salgado-Luarte  <http://orcid.org/0000-0003-0845-2928>

REFERENCES

- Altesor, A., Oesterheld, M., Leoni, E., Lezama, F., & Rodríguez, C. (2005). Effect of grazing on community structure and productivity of a Uruguayan grassland. *Plant Ecology*, 179, 83–91. <https://doi.org/10.1007/s11258-004-5800-5>
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9, 683–693. <https://doi.org/10.1111/j.1461-0248.2006.00926.x>
- Anderson, M. J., & Walsh, D. C. I. (2013). PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecological Monographs*, 83, 557–574. <https://doi.org/10.1890/12-2010.1>
- Anderson, P. M. L., & Hoffman, M. T. (2011). Grazing response in the vegetation communities of the Kamiesberg, South Africa: Adopting a plant functional type approach. *Journal of Arid Environment*, 75, 255–264. <https://doi.org/10.1016/j.jaridenv.2010.10.012>
- Asner, G. P., Elmore, A. J., Olander, L. P., Martin, R. E., & Harris, A. T. (2004). Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, 29, 261–299. <https://doi.org/10.1146/annurev.energy.29.062403.102142>
- Augustine, D. J., & McNaughton, S. J. (1998). Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, 62, 1165–1183. <https://doi.org/10.2307/3801981>
- Bahre, C. J. (1979). *Destruction of the natural vegetation of north-central Chile* (p. 132). Berkeley, CA: University of California Press.
- Cadotte, M. W. (2013). Experimental evidence that evolutionarily diverse assemblages result in higher productivity. *Proceedings of the National Academy of Sciences*, 110, 8996–9000. <https://doi.org/10.1073/pnas.1301685110>
- Cadotte, M. W., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93, S223–S233. <https://doi.org/10.1890/11-0426.1>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 489, 326. <https://doi.org/10.1038/nature11373>
- Carmona, C. P., Azcárate, F. M., de Bello, F., Ollero, H. S., Lepš, J., & Peco, B. (2012). Taxonomical and functional diversity turnover in Mediterranean grasslands: Interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology*, 49, 1084–1093. <https://doi.org/10.1111/j.1365-2664.2012.02193.x>
- Cepeda-Pizarro, J. G. (1989). Actividad temporal de tenebriónidos epígeos (Coleoptera) y su relación con la vegetación arbustiva en un ecosistema árido de Chile. *Revista Chilena de Historia Natural*, 62, 115–125. <https://doi.org/10.4067/S0716-078X2005000400005>
- Cingolani, A. M., Noy-Meir, I., & Díaz, S. (2005). Grazing effects on rangeland diversity: A synthesis of contemporary models. *Ecological Applications*, 15, 757–773. <https://doi.org/10.1890/03-5272>
- Contreras, O., Menesses, R., & Rojas, O. (2001). Razas caprinas para zonas áridas y semiáridas de Chile. *Tierra Adentro*, 41, 41–43.
- Core Team, R. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- De Bello, F., De Vandewalle, M., Reitalu, T., Lep, J., Prentice, H. C., Lavorel, S., & Sykes, M. T. (2013). Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology*, 101, 1237–1244. <https://doi.org/10.1111/1365-2745.12139>
- De Cáceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, 90, 3566–3574. <https://doi.org/10.1890/08-1823.1>
- Eldridge, D. J., Delgado-Baquerizo, M., Travers, S. K., Val, J., & Oliver, I. (2017). Do grazing intensity and herbivore type affect soil health? Insights from a semi-arid productivity gradient. *Journal of Applied Ecology*, 54, 976–985. <https://doi.org/10.1111/1365-2664.12834>
- Eldridge, D. J., Poore, A. G. B., Ruiz-Colmenero, M., Letnic, M., & Soliveres, S. (2015). Ecosystem structure, function and composition in rangelands are negatively affected by livestock grazing. *Ecological Applications*, 26, 1273–1283. <https://doi.org/10.1890/15-1234>
- El-Kablawy, A. (2017). Impact of fencing and irrigation on species composition and diversity of desert plant communities in the United Arab Emirates. *Land Degradation & Development*, 28, 1354–1362. <https://doi.org/10.1002/ldr.2599>
- Erlach, A. (1984). *Guanaco* (Mamíferos). Buenos Aires, Argentina: Centro Editor de América Latina (eds.), 274–283 pp.
- Escobedo, V. M., Rios, R. S., Salgado-Luarte, C., Stotz, G. C., & Gianoli, E. (2017). Disturbance by an endemic rodent in an arid shrubland is a habitat filter: Effects on plant invasion and taxonomical, functional and phylogenetic community structure. *Annals of Botany*, 119, 659–670. <https://doi.org/10.1093/aob/mcw258>
- Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity—Ecosystem-function relationships. *Ecology*, 92, 1573–1581. <https://doi.org/10.1890/10-1245.1>
- Fuentes, E. R., & Muñoz, M. R. (1995). The human role in changing landscapes in central Chile: Implications for intercontinental comparisons. In M. T. K. Arroyo, P. H. Zedler, & M. D. Fox (Eds.), *Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia* (pp. 401–417). New York: Springer. https://doi.org/10.1007/978-1-4612-2490-7_17

- Fuentes, E. R., Poaini, A., & Molina, J. D. (1987). Shrub defoliation in the Chilean matorral: What is its significance? *Revista Chilena de Historia Natural*, 60, 276–283.
- Fuentes, E. R., & Simonetti, J. A. (1982). Plant patterning in the Chilean matorral: Are the roles of native and exotic mammals different? In C. E. Conrad, & W. C. Ochel (Eds.), *Dynamics and management of Mediterranean type ecosystems* (p. 637). Berkeley, CA: USDA: General Technical Report. PSW-58.
- Fuentes, N., Pauchard, A., Sánchez, P., Esquivel, J., & Marticorena, A. (2013). A new comprehensive database of alien plant species in Chile based on herbarium records. *Biological Invasions*, 15, 847–858. <https://doi.org/10.1007/s10530-012-0334-6>
- Gay, C. (1847). *Historia física y política de Chile*, Zoología (p. 496). Paris: Chile: en el Museo de historia natural de Santiago, En casa del autor.
- Gerhold, P., Cahill, J. F., Winter, M., Bartish, I. V., & Prinzing, A. (2015). Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Functional Ecology*, 29, 600–614. <https://doi.org/10.1111/1365-2435.12425>
- Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminée, J. H., ... Prinzing, A. (2011). Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *The American Naturalist*, 177, 668–680. <https://doi.org/10.1086/659059>
- Gutiérrez, J. R., Holmgren, M., Manrique, R., & Squeo, F. A. (2007). Reduced herbivore pressure under rainy ENSO conditions could facilitate dryland reforestation. *Journal of Arid Environments*, 68, 322–330. <https://doi.org/10.1016/j.jaridenv.2006.05.011>
- Gutiérrez, J. R., & Squeo, F. A. (2004). Importancia de los arbustos en los ecosistemas semiáridos de Chile. *Ecosistemas*, 13, 36–45. 10045/8801
- Haarmeyer, D. H., Schmiedel, U., Dengler, J., & Bösing, B. M. (2010). How does grazing intensity affect different vegetation types in arid Succulent Karoo, South Africa? Implications for conservation management. *Biological Conservation*, 143, 588–596. <https://doi.org/10.1016/j.biocon.2009.11.008>
- Helmus, M. R., Bland, T. J., Williams, C. K., & Ives, A. R. (2007). Phylogenetic measures of biodiversity. *The American Naturalist*, 169, E68–E83. <https://doi.org/10.1086/511334>
- Hoffman, M. T., Dean, W. R. J., and Allsopp, N. (2003) Landuse effects on plant and insect diversity in Namaqualand, Paper read at Proceedings of the VIth International Rangelands Congress, 26th July - 1st August 2003, at Durban, South Africa Landscape change and ecological processes in relation to land-use in Namaqualand, South Africa, 1939 to 2005.
- Holmgren, M. (2002). Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. *Biological Invasions*, 4, 25–33. <https://doi.org/10.1023/A:1020535628776>
- Holmgren, M., López, B. C., Gutiérrez, J. R., & Squeo, F. A. (2006). Herbivory and plant growthrate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. *Global Change Biology*, 12, 2263–2271. <https://doi.org/10.1111/j.1365-2486.2006.01261.x>
- Holmgren, M., & Scheffer, M. (2001). El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems*, 4, 151–159. <https://doi.org/10.1007/s100210000065>
- INE (2015). *Encuesta de ganadería caprina Instituto nacional de estadística, Chile*. Santiago, Chile: Subdepartamento de Estadísticas Agropecuarias.
- Klímešová, J., Latzel, V., de Bello, F., & van Groenendae, J. M. (2008). Plant functional traits in studies of vegetation changes in response to grazing and mowing: Towards a use of more specific traits. *Preslia*, 80, 245–253.
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, 29, 592–599. <https://doi.org/10.1111/1365-2435.12345>
- Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305. <https://doi.org/10.1890/08-2244.1>
- Laliberté, E., Norton, D. A., & Scott, D. (2013). Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. *Journal of Vegetation Science*, 24, 834–842. <https://doi.org/10.1111/jvs.12044>
- Leoni, E., Altesor, A., & Paruelo, J. M. (2009). Explaining patterns of primary production from individual level traits. *Journal of Vegetation Science*, 20, 612–619. <https://doi.org/10.1111/j.1654-1103.2009.01080.x>
- Li, D., Ives, A. R., & Waller, D. M. (2017). Can functional traits account for phylogenetic signal in community composition? *New Phytologist*, 214, 607–618. <https://doi.org/10.1111/nph.14397>
- Losos, J. B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecology Letters*, 11, 995–1003. <https://doi.org/10.1111/j.1461-0248.2008.01229.x>
- Marticorena, C., Squeo, F. A., Arancio, G., & Muñoz, M. (2001). Catálogo de la Flora Vascular de la IV Región de Coquimbo. In F. A. Squeo, G. Arancio, & J. R. Gutiérrez (Eds.), *Libro Rojo de la Flora Nativa y de los Sitios Prioritarios para su Conservación: Región de Coquimbo* (pp. 105–142). La Serena, Chile: Ediciones Universidad de La Serena.
- Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, 13, 1085–1093. <https://doi.org/10.1111/j.1461-0248.2010.01509.x>
- MEA (2005). *Millennium ecosystem assessment synthesis report* (p. 160). Washington, DC: Island Press.
- Mi, X. C., Swenson, N. G., Valencia, R., Kress, W. J., Erickson, D. L., Perez, A. J., ... Ma, K. P. (2012). The contribution of rare species to community phylogenetic diversity across a Global Network of Forest Plots. *American Naturalist*, 180, E17–E30. <https://doi.org/10.1086/665999>
- Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs*, 63, 327–366. <https://doi.org/10.2307/2937150>
- Milchunas, D. G., Lauenroth, W. K., & Chapman, P. L. (1992). Plant competition, abiotic, and long-term and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. *Oecologia*, 92, 520–531. <https://doi.org/10.1007/BF00317844>
- Milchunas, D. G., Sala, O. E., & Lauenroth, W. K. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, 132, 87–106. <https://doi.org/10.1086/284839>
- Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28, 167–177. <https://doi.org/10.1016/j.tree.2012.10.004>
- Navarro, T., Alados, C. L., & Cabezudo, B. (2006). Changes in plant functional types in response to goat and sheep grazing in two semi-arid shrublands of SE Spain. *Journal of Arid Environment*, 64, 298–322. <https://doi.org/10.1016/j.jaridenv.2005.05.005>
- Olden, J. D., & Poff, N. L. (2003). Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist*, 162, 442–460. <https://doi.org/10.1086/378212>
- Olf, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution*, 13, 261–265. [https://doi.org/10.1016/S0169-5347\(98\)01364-0](https://doi.org/10.1016/S0169-5347(98)01364-0)
- Osem, Y., Perevolotsky, A., & Jaime, K. (2002). Grazing effect on diversity of annual plant communities in a semi-arid rangeland: Interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology*, 90, 936–946. <https://doi.org/10.1046/j.1365-2745.2002.00730.x>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>

- Parker, J. D., Burkepile, D. E., & Hay, M. E. (2006). Opposing effects of native and exotic herbivores on plant invasions. *Science*, 311, 1459–1461. <https://doi.org/10.1126/science.1128946>
- Pausas, J. G., & Verdú, M. (2010). The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *Bioscience*, 60, 614–625. <https://doi.org/10.1525/bio.2010.60.8.7>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. <https://doi.org/10.1071/BT12225>
- Petz, K., Alkemade, R., Bakkenes, M., Schulp, C. J. E., van der Velde, M., & Leemans, R. (2014). Mapping and modelling trade-offs and synergies between grazing intensity and ecosystem services in rangelands using global-scale datasets and models. *Global Environmental Change*, 29, 223–234. <https://doi.org/10.1016/j.gloenvcha.2014.08.007>
- Piñeiro, G., Paruelo, J. M., Oesterheld, M., & Jobbágy, E. G. (2010). Pathways of grazing effects on soil organic carbon and nitrogen. *Rangeland Ecology & Management*, 63, 109–119. <https://doi.org/10.2111/08-255.1>
- Puig, S., Videla, F., & Cona, M. (1997). Diet and abundance of the guanaco (*Lama guanicoe*) in four habitats of northern Patagonia, Argentina. *Journal of Arid Environment*, 36, 343–357. <https://doi.org/10.1006/jare.1996.0186>
- Puigdefábregas, J. (1998). Ecological impacts of global change on drylands and their implications for desertification. *Land Degradation & Development*, 9, 393–406. [https://doi.org/10.1002/\(SICI\)1099-145X\(199809/10\)9:5<393::AID-LDR301>3.0.CO;2-F](https://doi.org/10.1002/(SICI)1099-145X(199809/10)9:5<393::AID-LDR301>3.0.CO;2-F)
- Qian, H., & Jin, Y. (2016). An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *Journal of Plant Ecology*, 9, 233–239. <https://doi.org/10.1093/jpe/rtv047>
- Quiroz, C. (2007). Diseño, implementación y seguimiento integral de desarrollo del secano, IV Región de Coquimbo. *Etapa 1* (p. 35). La Serena, Chile: INIA.
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, D. F., & West, C. J. (2000). Naturalization and invasion of alien plants—concepts and definitions. *Diversity and Distributions*, 6, 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Simonetti, J. A., & Fuentes, E. R. (1983). Shrub preferences of native and introduced Chilean Matorral herbivores. *Acta Oecologica*, 4, 269–272.
- Simonetti, J. A., & Fuentes, E. R. (1985). Guanacos versus cabras y conejos como moduladores del matorral de Chile central. In C. Venegas, & C. Cunazza (Eds.), *Acta IV convención internacional sobre camelidos sudamericanos* (pp. 76–87). Punta Arenas: Universidad de Magallanes.
- Tälle, M., Deák, B., Poschlod, P., Valkó, O., Westerberg, L., & Milberg, P. (2016). Grazing vs. mowing: A meta-analysis of biodiversity benefits for grassland management. *Agriculture, Ecosystems & Environment*, 222, 200–212. doi.org/10.1016/j.agee.2016.02.000
- Todd, S. W., & Hoffman, M. T. (2009). A fence line in time demonstrates grazing-induced vegetation shifts and dynamics in the semiarid Succulent Karoo. *Ecological Applications*, 19, 1897–1908. <https://doi.org/10.1890/08-0602.1>
- Tracol, Y., Gutiérrez, J. R., & Squeo, F. A. (2011). Plant area index and microclimate under shrub species from a Chilean semiarid community. *Journal of Arid Environment*, 75, 1–6. <https://doi.org/10.1016/j.jaridenv.2010.08.002>
- van de Koppel, J., Rietkerk, M., van Langevelde, F., Kumar, L., Klausmeier, C. A., Fryxell, J. M., ... Prins, H. H. T. (2002). Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *American Naturalist*, 159, 209–218. <https://doi.org/10.2307/3078978>
- van Zonneveld, M. J., Gutierrez, J. R., & Holmgren, M. (2012). Shrub facilitation increases plant diversity along an arid scrubland-temperate rain forest boundary in South America. *Journal of Vegetation Science*, 23, 541–551. <https://doi.org/10.1111/j.1654-1103.2011.01379.x>
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., ... Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, 14, 702–708. <https://doi.org/10.1111/j.1461-0248.2011.01628.x>
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Zanne, A. E., Tank, D. C., Cornwell, W. K., Eastman, J. M., Smith, S. A., FitzJohn, R. G., ... Beaulieu, J. M. (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89–92. <https://doi.org/10.1038/nature14371>

SUPPORTING INFORMATION

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

How to cite this article: Salgado-Luarte C, Escobedo VM, Stotz GC, Rios RS, Arancio G, Gianoli E. Goat grazing reduces diversity and leads to functional, taxonomic, and phylogenetic homogenization in an arid shrubland. *Land Degrad Dev*. 2019;30:178–189. <https://doi.org/10.1002/ldr.3208>