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# Diversity of plants and mammals as indicators of the effects of land management types in woodlands

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## Abstract

**Background:** The ecological indicators are useful tools to determine the effects of human disturbances on woodland biodiversity. Nevertheless, ecological indicators not always responded in the same way to disturbances, and the responses can differ among taxa. In arid and semiarid woodlands, the use of deadwood associated with cattle raising can affect biodiversity and Nature's contributions to people.

**Methods:** Our study aimed to assess changes in taxonomic and functional diversity of two assemblages, plants and mammals, in *Prosopis* woodlands under different land management types: grazed woodlands and a protected area. For plants, changes in structural diversity were also analyzed. *Prosopis* trees under different land management types were selected and their deadwood characteristics were registered. Through live traps and camera traps, we obtained data on the presence-absence of mammals per tree to estimate diversity indices. For plants, we measured the abundance of vegetation by species and by cover type through the Line-Intercept Method to estimate diversity. Finally, we built generalized linear models to assess the responses of diversity of each assemblage to covariables concerning deadwood and different land management types.

**Results:** We found that all diversity indices for plants were either negatively affected by the presence of deadwood on the ground, or favored by its extraction. For mammals, removal of deadwood increased taxonomic diversity, while functional diversity increased with deadwood on the trees. Both structural diversity of plants and functional diversity of mammals were greater in grazed woodlands.

**Conclusions:** The sustainable use of woodland resources is essential for the activities of rural communities. Our study results indicated that land management of grazed woodlands promoted the structural diversity of plant assemblages and the functional diversity of mammals. The presence of deadwood negatively affected plant diversity but it increased mammal functional diversity. It is advisable to maintain trees that preserve their wooden structure within the managed areas to promote the functional diversity of mammals, while trees with extraction from standing wood will favor the functional diversity of the plant assemblage. Understanding the effects of human disturbances can contribute to management for the conservation of woodlands diversity and Nature's contributions to people.

**Keywords:** Central Monte, Cattle raising, Deadwood extraction, Taxonomic diversity, Functional traits

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## Background

Land use change, such as land conversion for crops, livestock raising, and urban settlements, is the main factor affecting terrestrial ecosystems and the vital contributions made by living nature to humanity, referred to as Nature's contributions to people (NCP; Díaz et al. 2019). Nature's regulating contributions include functional and structural features of organisms and ecosystems that change environmental conditions experienced by people and regulate the generation of material and non-material contributions. Nature's material contributions to people are generally transformed and consumed when they are experienced, for example, plants or animals are converted into materials for ornamental or shelter purposes, food, or energy (Díaz et al. 2019).

In the framework of NCP, deadwood to use as firewood is the main woodland material used by rural communities. Also, deadwood is a major component in maintaining the function and biodiversity of forest ecosystems because it decreases soil erosion, stores and supplies nutrients and water to soil and plants, provides a regeneration substrate for some plants, and offers protection and food sites for organisms of several taxa (Harmon et al. 1986; Mac Nally et al. 2001; Stoklosa et al. 2016). Thus, the use of deadwood, associated with the land-use change produced by cattle raising, can affect some of NCP, such as maintenance of biodiversity and habitat creation.

In recent years, the development of ecological indicators based on functional traits has become a useful tool to determine the effects of human disturbances on biodiversity and their implications for the provision of NCP (Feld et al. 2009; Ehlers Smith et al. 2020). Even though traditionally ecologists have used species richness indicators as a measure of changes produced by people's use on ecosystems and communities (Leps et al. 2006), there is increasing evidence regarding the importance of functional traits of individual species and their interactions, even more than the number of species per se (Díaz and Cabido 2001; Villéger et al. 2008). This 'functional-type' approach focuses on the common attributes (Díaz and Cabido 2001), considering that communities' response to human disturbances mainly depends on the functional traits of species (Lavorel and Garnier 2002).

In general, it has been shown that the increase in land-use intensity decreases diversity, but the results can vary when taxonomic and functional diversity are analyzed, and depending on the context and the taxa being studied (Díaz et al. 2007; Carmona et al. 2012; Janeček et al. 2013; Hevia et al. 2016). Besides, in stressful habitats, plant and animal fitness is strongly affected by environmental filters which shape the traits of the species (Mouchet et al. 2010; Carmona et al. 2012). Thus, species taxonomically different tend to present similar traits,

resulting in a high functional redundancy (Chillo et al. 2017). Understanding the relationship between indicators of taxonomic and functional diversity allows for comprehending the effects of human use on community assembly and ecosystem functioning (Janeček et al. 2013).

In dry woodlands, trees are especially important because they ameliorate the microenvironment under their canopy, improving conditions for plant and animal life (Manning et al. 2006; López-Sánchez et al. 2016). In some cases, they can also cause substantial costs to local livelihoods and the environment when they are introduced species and become invasive, such as the case of species of *Prosopis* genus (e.g. Rejmánek and Richardson 2013; van Wilgen and Richardson 2014; Shackleton et al. 2015). However, in their natural distribution, *Prosopis* trees are key species from ecological and cultural points of view (e.g. Kingsolver et al. 1977; Mares et al. 1977; Moreno et al. 2018). *Prosopis flexuosa* is the main tree conforming open woodlands in the Monte ecoregion, and it plays a key role in providing important NCP to rural communities, such as forage for livestock and firewood (Alvarez and Villagra 2009).

In *P. flexuosa* woodlands, taxonomic and functional indices of vegetation and animal assemblages seem not to be strongly coupled (Chillo and Ojeda 2014) although a decrease in diversity under increasing grazing intensity has been observed (Chillo et al. 2017). In these woodlands, plant species richness is related to the abundance of adult trees (Campos et al. 2020), showing the importance of trees as fertility islands that contribute to the increase in total diversity (Rossi and Villagra 2003). *Prosopis flexuosa* is considered a nurse species because it facilitates the establishment of other plant species under its canopy (Rossi and Villagra 2003; Villagra and Alvarez 2019), increases habitat heterogeneity, and sustains high diversity of small mammals (Tabeni and Ojeda 2003; Corbalán and Ojeda 2004; Szymański et al. 2020).

Our study aimed to assess changes in biological diversity in *P. flexuosa* woodlands under different land management types: grazed woodlands and a protected area. Changes in taxonomic and functional diversity were evaluated on two assemblages, plants and mammals. For plants, changes in structural diversity were also analyzed. We evaluated the effects of variables related to components of deadwood (deadwood on the ground, in the tree and deadwood removed) and land management types in plant and mammal diversity. We expected lower diversity for both assemblages in grazed woodlands than in the protected area. In addition to this, when deadwood is removed, the availability of habitat and niche for animals can be reduced. Habitat loss drives functional trait loss (Ehlers Smith et al. 2020), hence we expected that deadwood extraction would decrease the availability of

resources and negatively impact mammal functional diversity. Also, we expected that the effects of the deadwood extraction process, such as trampling, would negatively impact plant diversity indices.

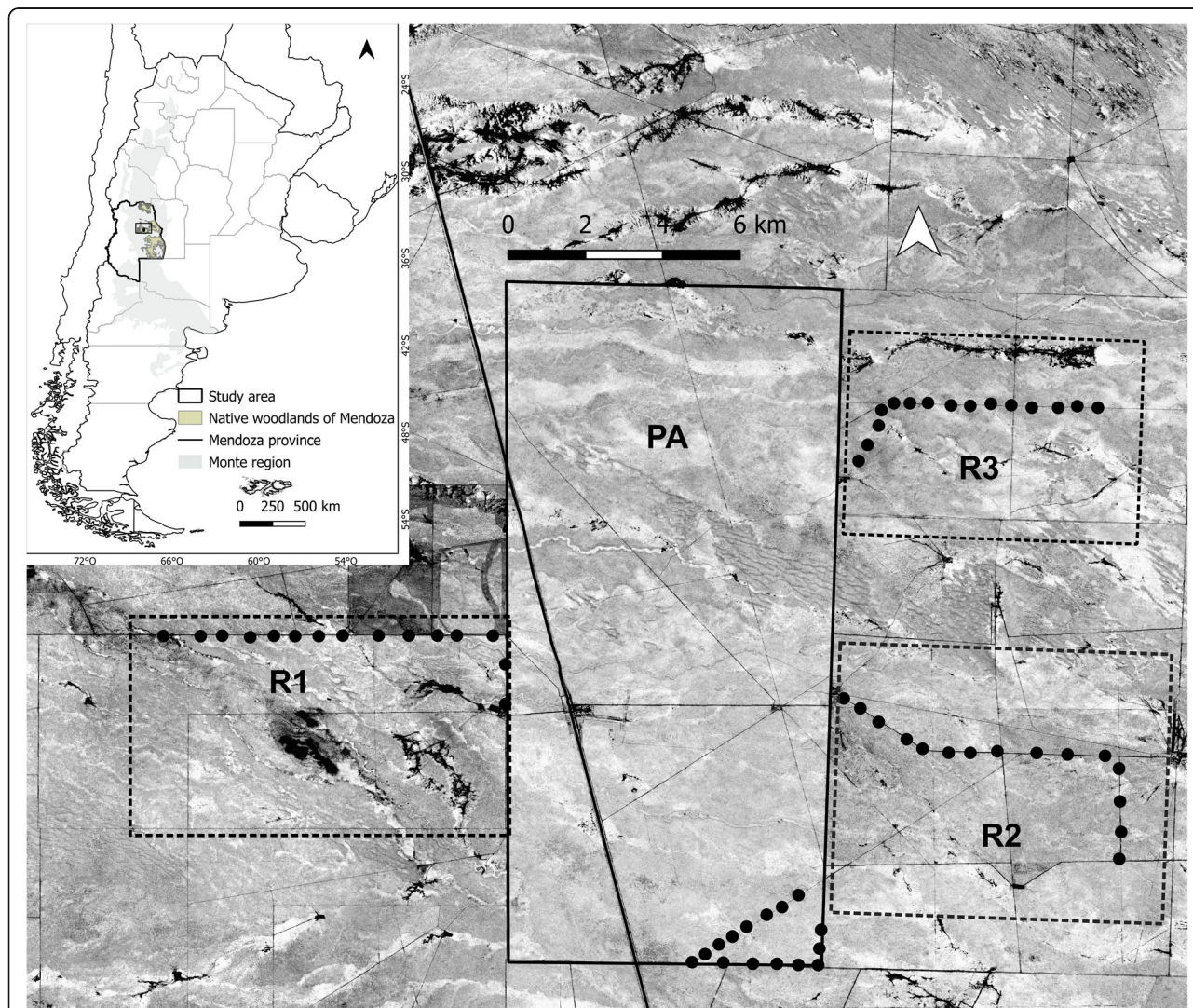
**Methods**

**Study area**

The study site is located in the Monte biogeographic region (24°35′–44°20′ S; 62°54′–69°05′ W), Argentina. We selected two dominant land management types to conduct the research: a protected area, the Biosphere Reserve Nacuñán (BRÑ hereafter) where *Prosopis* woodlands are destined for conservation, and private surrounding woodlands, where cattle grazing and deadwood extraction are the most common activities conducted by rural communities (Fig. 1).

The BRÑ was created in 1961 to protect the *Prosopis* woodland that had been cut down at the beginning of the nineteenth century to extract wood for the development of the irrigated oases, and devoted to livestock use (Abraham and Prieto 1999). In 1972 cattle were excluded, and the BRÑ was incorporated as a Man and Biosphere Reserve in 1986. The native vascular flora has been recovered after approximately 50-year of grazing exclusion (Tabeni and Ojeda 2005).

The climate is semiarid to arid with a wide annual and daily temperature range. Mean annual temperatures vary between 13 °C and 18 °C. The mean annual rainfall is 326 mm (Labraga and Villalba 2009). Vegetation is composed of three main communities: a) shrubland dominated by *Zygophyllaceae* species; b) edaphic steppe of halophytic shrubs (*Suaeda divaricata*, *Atriplex* spp.,



**Fig. 1** Location of the study site in the Monte region. Protected area surrounding private grazed woodlands (R1, R2 and R3) are showed. Each thick point corresponds to one sample station around a *Prosopis* tree



*Alleronfea vaginata*); and c) woodland where *P. flexuosa* is the dominant tree accompanied by shrubs and grasses (*Larrea divaricata*, *L. cuneifolia*, *Condalia microphylla*, *Pappophorum* spp., *Trichloris crinita* and *Digitaria californica*, among others) (Villagra et al. 2004).

Local assemblages of small and medium-sized mammals comprise more than 20 species, with different body sizes, activity periods, space use, and diets (e.g. Campos et al. 2001; Ojeda and Tabeni 2009). Four orders are represented: a) Didelphimorphia (*Thylamys pallidior*, *Didelphis albiventris*); b) Cingulata (*Chaetophractus villosus*, *C. vellerosus*, *Zaedyus pichiy*, *Chlamyphorus truncatus*); c) Carnivora (*Puma concolor*, *Herpailurus yagouaroundi*, *Leopardus colocolo*, *L. geoffroyi*, *Galictis cuja*, *Lyncodon patagonicus*, *Conepatus chinga*, *Lycalopex gymnocercus*); and d) Rodentia (*Dolichotis patagonum*, *Microcavia maenas*, *Galea leucoblephara*, *Ctenomys mendocinus*, *Eligmodontia typus*, *Graomys griseoflavus*, *Akodon dolores*, *Calomys musculus*). Two exotic species occur in the area, *Sus scrofa* and *Lepus europaeus*.

#### Sampling design and data collection

*Prosopis flexuosa* trees were selected inside the protected area and in three neighboring grazed fields (Fig. 1). All individuals presented a mean crown diameter of approximately 5 m. Fifteen trees at least 500 m apart were chosen at each area ( $N = 60$  trees). The trees were selected in accessible areas to reduce the risk of mortality of captured animals in live capture traps.

Data for the study were collected in the period of highest population abundance of the mammal species (Corbalán 2006), during March and April of 2017, and 2018. The total sample effort was 4800 trap-nights and 10,080 h of total camera operation.

#### Deadwood surveys

*Prosopis flexuosa* is a heliophilous tree with low tolerance to shade, whose branches die and remain on the

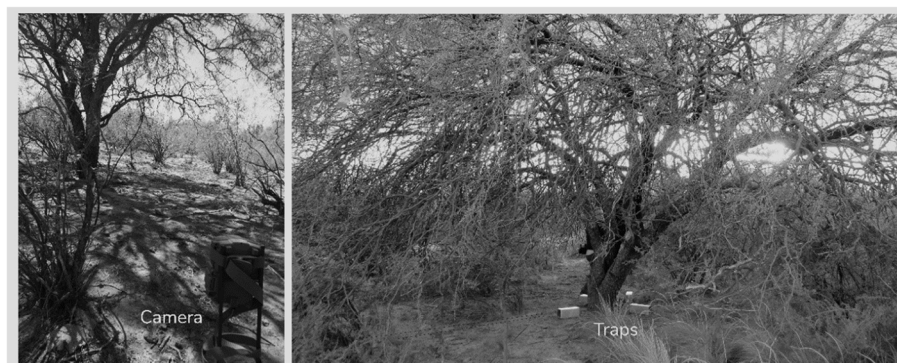
tree (Alvarez et al. 2011). Thus, we recorded variables related to deadwood for each tree. The amount of deadwood in the tree (DW in trees;  $\text{kg}\cdot\text{tree}^{-1}$ ) and deadwood removed from the tree (DW removed;  $\text{kg}\cdot\text{tree}^{-1}$ ) were estimated from the DAB (diameter at base height), according to the methodology described by Alvarez et al. (2011) for *Prosopis* forests of Northeast Mendoza. We visually estimated the amount of deadwood on the ground (DW on ground) as the percentage of area under the tree crown covered by deadwood.

#### Plant survey

Under each tree, we set four transects of 10 m oriented to the cardinal points. We measured the abundance of vegetation by species and by cover type (grasses, forbs, shrubs, subshrubs, and trees) through the Line-Intercept Method (Cummings and Smith 2000). We started from the trunk of the tree and marked every 0.30 m with a 3-m graduated pole placed vertically. Then, the abundance of each plant species and the proportion of cover type were estimated to obtain both an index of taxonomic diversity (TD) and an index of structural diversity (SD).

#### Mammal survey

In order to detect mammals of different body sizes, two sampling methods were used to obtain presence-absence data per tree. The capture method is the most suitable way to detect the presence of small rodents (Lettink and Armstrong 2003), due to their naturally low abundances and nocturnal habits in drylands. We arranged four transects under each tree following the cardinal points. In each transect, we placed five Sherman live traps at 2-m intervals, baited with rolled oats and vegetable oil (20 traps per tree) (Fig. 2). Traps remained open overnight for four consecutive days and they were checked in the morning. We identified captured animals by species, and then we released the animals at the place where they had been captured. Presence-absence data by species of



**Fig. 2** Experimental design showing sample station in *Prosopis flexuosa* trees, the location of trapping transects starting from trunk and the location of camera traps under tree canopy

small mammals at each tree were determined from a total of 4800 trap-nights. All procedures were performed according to guidelines of the Purdue Animal Care and Use Committee (PACUC) and the Animal Care and Use Committee of the American Society of Mammalogists (Sikes and Gannon 2011) and under certificate for wild-life manipulation (Res. Number 320–2016 and 408–2018).

To survey medium-sized and large mammals, we placed two camera traps (Moultrie, M-900i, Alabaster, AL, USA) under the cover of each of the 60 trees (Fig. 2). Cameras were mounted on a 0.50-m high backing and vegetation surrounding the detection zone was cleared to allow animals identification. The cameras took three consecutive pictures whenever animal movement was detected, with a 15-s delay between shoots, over an 84-h period (total camera operation = 10,080 h; 120 camera traps per 84 h per camera). Animal species were identified from photos based on fur color, tail and body length and other species-specific physical traits (Ojeda 1989; Braun et al. 2000; Giannoni et al. 2001; Tognelli et al. 2001). We recorded species' names, and we combined the data from the two cameras of each tree to generate presence-absence estimates.

#### Diversity indices

Considering that types of diversity do not always respond similarly to disturbances (Carmona et al. 2012; Hevia et al. 2016), we analyzed taxonomic and functional diversity indices for plants and mammals, and also a structural diversity index for plants.

**Taxonomic diversity** The Shannon-Weiner index ( $H'$ ) (Magurran 2004) was estimated for plants and Chao 2 index ( $S_{\text{Chao2}}$ ) (Chao 1984, 1987) was estimated for mammals, both of them as a proxy of taxonomic diversity (hereafter TD). For plants, abundance per species by tree was used to estimate Shannon-Weiner index (1) with BiodiversityR package (Kindt and Kindt 2015) in the R statistical environment (R Core Team 2018). For mammals, Chao 2 index (2) was selected because allows estimating the richness across assemblages with presence-absence data (Chao 1984, 1987). Chao 2 index was calculated with EstimateS software (Colwell and Elsensohn 2014).

$$H' = -\sum_{i=1}^S (p_i \times \log_2 p_i) \quad (1)$$

where  $S$  is the number of species, and  $p_i$  is the proportion of the total sample that belongs to the  $i$ -th species.

$$S_{\text{Chao2}} = S_{\text{obs}} + \frac{a^2}{2b} \quad (2)$$

where  $S_{\text{obs}}$  is the actual number of species in the sample,

$a$  is the number of species found in only one sample and  $b$  is the number of species found in only two samples.

**Structural diversity** Taking into account differences in the structure of vegetation of grazed fields and the BRÑ (Tabeni and Ojeda 2005; Campos et al. 2016; Miguel et al. 2018), we estimated an index of vegetation structure considering the plant cover types. The structural diversity was calculated analogously to taxonomic diversity, but considering life forms (grasses, forbs, shrubs, subshrubs, and trees) instead of species (hereafter SD). A structurally complex site is characterized by a greater diversity of cover types (Sukma et al. 2019).

**Functional traits and functional diversity** For plants, all traits selected were qualitative and related to dispersion, establishment and persistence, taking into account previous studies developed in the Monte region (Chillo et al. 2017) (Table 1). For mammals, we chose two quantitative and seven qualitative traits linked to resource use and niche dimensions (Table 1) (Sukma et al. 2019). Trait values for each species were provided by experts and obtained from literature (e.g. Campos and Ojeda 1997; Campos et al. 2001; Ojeda and Tabeni 2009; Villagra et al. 2011; Campos and Velez 2015).

Functional dispersion for both plants and mammals was calculated as an indicator of functional diversity (hereafter FD) with the species records for each sampled tree combined with trait information (Villéger et al. 2008; Pla et al. 2012; Mason and Mouillot 2013). Functional dispersion (3) is a multivariate index that is calculated as the mean distance of each species to the community centroid, weighted by its abundance (Sukma et al. 2019; Salgado-Luarte et al. 2019). This index is closely related to Rao's quadratic entropy but it can be used for statistical analysis of unweighted data (presence-absence records) (Laliberté and Legendre 2010). For mammals, species presence-absence data were used jointly with functional traits to compute FD. For plants, the abundance of species and functional traits were used to estimate FD. Functional diversity indices were calculated with the FD package (Laliberté et al. 2014) in the R statistical environment (Core Team 2018).

$$\text{FD}_{\text{is}} = \frac{\sum a_j z_j}{\sum a_j} \quad (3)$$

where  $a_j$  is the abundance of species  $j$  and  $z_j$  is the distance of species  $j$  to the weighted centroid. For presence-absence data, functional dispersion is the unweighted mean distance to the centroid (Laliberté and Legendre 2010).

**Table 1** Traits of plants and ground-dwelling mammal species

Taxa	Trait	Levels
Vegetation	Growth form	Grass
		Forb
		Subshrub
		Shrub
		Tree
	Life cycle	Annual
		Deciduous
		Perennial
	Leaf size	Small (< 2 cm)
		Medium (2–5 cm)
		Big (> 5 cm)
	Main root system	Taproot
		Lateral
Lateral spread	Single root	
	Several stems	
	Stolons/rhizomes	
Leaf texture	Tough	
	Intermediate	
	Membranous	
Leguminosae	Legume/non legume	
Storage organs	Yes/no	
Attractive fruits	Yes/no	
Mammals	Activity period	Nocturnal
		Diurnal
	Body mass	Natural log of mean mass in grams (continuous)
	Ecological role in <i>Prosopis</i> seeds dispersal	Seed predator
		Seed disperser
	Locomotion habit	Scansorial
		Cursorial
		Fossorial
		Semifossorial
	Nest type	Caves
		Burrows and hollow on ground
		Hollow on tree
	Origin	Native
Exotic and domestic		
Exotic and wild		
Main food type	Omnivore-folivore	
	Omnivore-insectivorous	
	Omnivore-granivore	
	Omnivore	
	Herbivore	
	Insectivore	
Carnivore		
Litter size	Continuous variable derived from the mean of reported values	

### Statistical analysis

We built generalized linear models (GLM) to assess the responses of diversity indices of each assemblage to covariates concerning deadwood (deadwood in the tree, deadwood removed and the amount of deadwood on the ground) and different land management types (protected area and grazed woodlands). All quantitative explanatory variables were standardized and centered to directly

compare the coefficients. We applied GLM with Normal distribution to model TD and SD, and GLM with Beta distribution to model FD, taking into account the AIC associated with different distributions for continuous variables. We built a set of candidate models with the possible combination of additive covariates. The models were ranked following the AIC and we eliminated from the set those models that did not converge. Because no

single model was clearly superior to some of the others in the set, we used estimates from multiple candidate models, hence calculating model-averaged estimates (Burnham et al. 2011). We selected a set of candidate models and ranked them starting from the best until Akaike's cumulative weight reached 0.95, and then we rejected the rest (Symonds and Moussalli 2011). The objective was to generate a 'confidence set' of models that are the most likely to be the best approximation model (Burnham and Anderson 2004). The direction and magnitude of the effect size of each covariate were based on model-averaged estimates (Burnham et al. 2011). The relative importance of each covariate under consideration was estimated by summing the Akaike weights for each model in which that covariate appeared (Symonds and Moussalli 2011). Covariates with summed model weights (SW) > 0.5 were considered the most statistically important (Barbieri and Berger 2004). The  $R^2$  coefficient was computed to evaluate the goodness of fit (Schielzeth and Nakagawa 2013), and graphical methods were employed to confirm that models adjusted to assumptions of normality in the residuals and homogeneity of variances.

Modeling was carried out using *betareg* (Zeileis et al. 2016) and *lme4* (Bates et al. 2018) packages, and model-averaging was performed with the *MuMIn* (Barton 2015) package, in R 3.4.2 language and environment (Core Team 2018).

## Results

Relationships between diversity indices and covariates related to deadwood and land management types were

statistically significant for both assemblages, but model fit varied from moderate to poor (in example:  $R^2$  for plants' SD index = 0.58;  $R^2$  for mammals' FDis = 0.14). In summary, land management of grazed woodlands was associated to higher plants structural diversity and mammal functional diversity. By contrast, deadwood had differential effects on the different types of diversity and on assemblages.

## Plants

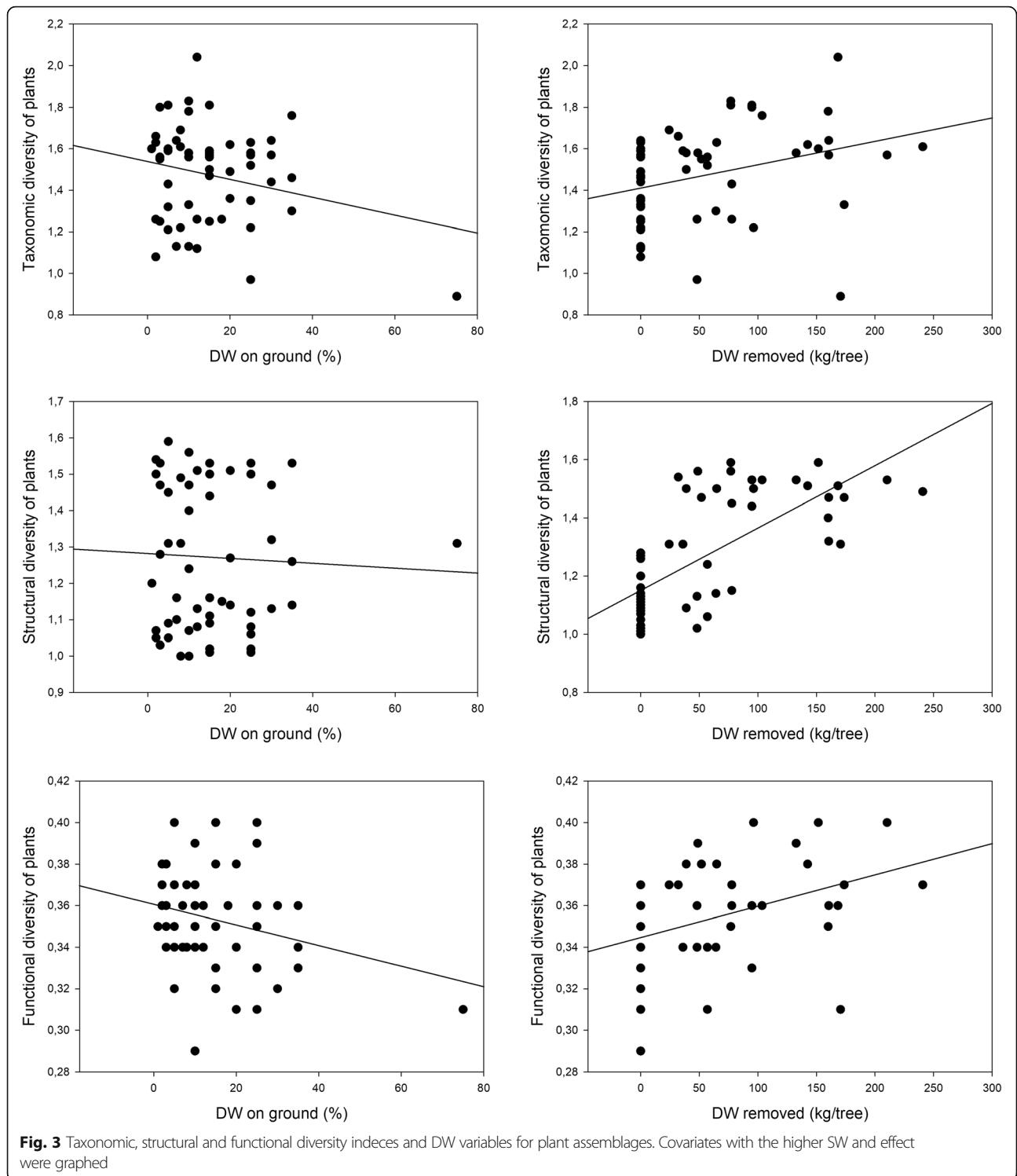
From fifteen candidate models built to analyze the taxonomic diversity of plants, we selected only nine models according to a 95% confidence set of models ( $R^2$  ranging from 0.06 to 0.20) (Table 2). Deadwood on ground and deadwood removed appeared in all models, and they presented the higher relative importance. Moreover, they were the covariates with the greatest effect on the taxonomic diversity of plants. Deadwood on ground decreased the plant's taxonomic diversity, while deadwood removed increased it (Fig. 3).

Fifteen models were built for the structural diversity of plants, but only six models were selected within a 95% confidence set of models ( $R^2$  ranging from 0.49 to 0.58) (Table 3). The covariates with the highest relative importance were deadwood removed, deadwood on ground and land management type, but only deadwood removed appeared in all models (Table 3). Besides, deadwood removed was the covariate with the greatest effect on the structural diversity of plants (between two and four times greater than other variables related to deadwood), presenting a positive relationship with the response variable (Fig. 3). The land management type is the following

**Table 2** Summary of the model selection procedure for taxonomic diversity index of plants

	int	$x_1$	$x_2$	$x_3$	$x_4$	df	log(L)	AIC	$\Delta i$	$w_i$	$R^2$
	1.48		-0.08	0.09		4	9.75	-10.71	0.00	0.47	0.20
	1.47		-0.08	0.10	0.06	5	10.11	-9.03	1.68	0.20	0.21
	1.48	0.01	-0.08	0.09		5	9.82	-8.44	2.26	0.15	0.20
	1.47	0.01	-0.08	0.10	0.06	6	10.13	-6.55	4.16	0.06	0.21
	1.48			0.07		3	6.04	-5.61	5.10	0.04	0.09
	1.48		-0.06			3	5.39	-4.33	6.38	0.02	0.06
	1.47			0.08	0.05	4	6.28	-3.78	6.93	0.01	0.09
	1.48	0.00		0.07		4	6.04	-3.30	7.41	0.01	0.09
	1.50		-0.06		-0.05	4	5.72	-2.65	8.06	0.01	0.08
SW	1.00	0.23	<b>1.00</b>	<b>0.96</b>	0.28						
$\beta$	1.48	0.01	<b>-0.08</b>	<b>0.09</b>	0.06						
SE	0.03	0.03	0.03	0.03	0.08						

Model averaging was carried out with a 95% confidence subset of models. For each model of the subset, we reported parameter estimates, total number of estimable parameters ( $k$ ), the log-likelihood log(L), AIC criterion,  $\Delta i = AIC_i - \min AIC$ , Akaike weight ( $w_i$ ), and adjusted  $R^2$ . Models are ordered in terms of  $\Delta i$  for AIC. At the bottom of the table, we reported model-averaged estimates  $\beta$  with their standard errors (SE) and their sum of weights (SW), for the four variables (quantitative variables:  $x_1$  - DW in tree,  $x_2$  - DW on ground,  $x_3$  - DW removed; categorical variable:  $x_4$  - land management type (protected area/grazed woodlands-intercept-))



covariate in importance, and it can be observed that the structural diversity is lower in the protected area (Table 3). Also, deadwood on ground negative affected SD.

We built fifteen candidate models to analyze the functional diversity of plants, but we only selected four models taking into account a 95% confidence set of

models ( $R^2$  ranging from 0.31 to 0.35) (Table 4). The covariates related to deadwood presented the highest relative importance, but only deadwood on ground and deadwood removed appeared in all models, being their relative importance equal to 1 (Table 4). Also, deadwood on ground and deadwood removed were the covariates



**Table 3** Summary of the model selection procedure for structural diversity index of plants

	int	x <sub>1</sub>	x <sub>2</sub>	x <sub>3</sub>	x <sub>4</sub>	k	log(L)	AIC	Δi	w <sub>i</sub>	R <sup>2</sup>
	1.30		-0.04	0.13	-0.09	5	33.92	-56.65	0.00	0.39	0.57
	1.30	0.02	-0.05	0.13	-0.11	6	34.54	-55.37	1.28	0.21	0.58
	1.27		-0.05	0.15		4	31.97	-55.15	1.50	0.18	0.54
	1.30			0.12	-0.10	4	31.10	-53.42	3.22	0.08	0.52
	1.27	0.01	-0.05	0.15		5	32.14	-53.09	3.56	0.07	0.54
	1.27			0.14		3	29.17	-51.87	4.78	0.04	0.49
SW	1.00	0.30	<b>0.86</b>	<b>1.00</b>	<b>0.71</b>						
β	1.29	0.02	<b>-0.05</b>	<b>0.13</b>	<b>-0.10</b>						
SE	0.03	0.02	0.02	0.03	0.05						

Model averaging was carried out with a 95% confidence subset of models. For each model of the subset, we reported parameter estimates, total number of estimable parameters (k), the log-likelihood log(L), AIC criterion, Δi = AIC<sub>i</sub> - minAIC, Akaike weight (w<sub>i</sub>), and adjusted R<sup>2</sup>. Models are ordered in terms of Δi for AIC. At the bottom of the table, we reported model-averaged estimates β with their standard errors (SE) and their sum of weights (SW), for the four variables (quantitative variables: x<sub>1</sub> - DW in tree, x<sub>2</sub> - DW on ground, x<sub>3</sub> - DW removed; categorical variable: x<sub>4</sub> - land management type (protected area/grazed woodlands-intercept))

with the greatest effect on the functional diversity of plants. Deadwood on ground negatively affected functional diversity, while deadwood removed did positively (Fig. 3).

**Mammals**

Fifteen candidate models were built to analyze the mammal taxonomic diversity, but only six were selected (R<sup>2</sup> ranging from 0.44 to 0.50) (Table 5). The covariate deadwood removed appeared in all models, being its relative importance equal to 1. Furthermore, this covariable presented the greatest effect on the taxonomic diversity of mammals (three times greater than the variable that follow in importance), being this effect negative (Fig. 4). Deadwood on ground also presented an importance greater than 0.5, showing a negative effect on TD.

Of the fifteen models built to analyze the functional diversity of mammals, thirteen of them corresponded to a 95% confidence set of models (R<sup>2</sup> ranging from 0.01 to 0.14) (Table 6). In the averaged-model, deadwood in tree and land management type were the covariates with higher SW, but deadwood on ground was also important

(Table 6). Functional diversity of mammals was mainly affected by land management type (magnitude of land management type was twice that deadwood in tree and deadwood on ground), being lower in protected area (Table 6). Deadwood in the tree was positively related to functional diversity, while deadwood on ground negatively affected it (Fig. 4).

**Discussion**

Human-induced changes are usually assumed to cause the loss of species and thus a decrease of the diversity of functional traits, but the responses of different diversity indices could follow different patterns (Carmona et al. 2012; Hevia et al. 2016). Our results showed that woodland management produces changes in biodiversity, but the effects differed among the assemblages and the approaches of biodiversity studied. In summary, land management type of grazed woodlands was associated to higher plants structural diversity and mammal functional diversity. By contrast, deadwood had differential effects on the different types of diversity and on assemblages. Presence of deadwood on ground negatively affected

**Table 4** Summary of the model selection procedure for functional diversity index of plants

	int	x <sub>1</sub>	x <sub>2</sub>	x <sub>3</sub>	x <sub>4</sub>	k	log(L)	AIC	Δi	w <sub>i</sub>	R <sup>2</sup>
	-0.61	0.02	-0.04	0.05		5	141.68	-272.17	0.00	0.47	0.35
	-0.61		-0.04	0.05		4	140.01	-271.23	0.94	0.29	0.31
	-0.61	0.02	-0.04	0.05	0.00	6	141.69	-269.67	2.50	0.13	0.35
	-0.60		-0.04	0.06	0.01	5	140.06	-268.92	3.25	0.09	0.31
SW	1.00	0.61	<b>1.00</b>	<b>1.00</b>	0.23						
β	-0.61	0.02	<b>-0.04</b>	<b>0.05</b>	0.00						
SE	0.01	0.01	0.01	0.01	0.03						

Model averaging was carried out with a 95% confidence subset of models. For each model of the subset, we reported parameter estimates, total number of estimable parameters (k), the log-likelihood log(L), AIC criterion, Δi = AIC<sub>i</sub> - minAIC, Akaike weight (w<sub>i</sub>), and adjusted R<sup>2</sup>. Models are ordered in terms of Δi for AIC. At the bottom of the table, we reported model-averaged estimates β with their standard errors (SE) and their sum of weights (SW), for the four variables (quantitative variables: x<sub>1</sub> - DW in tree, x<sub>2</sub> - DW on ground, x<sub>3</sub> - DW Removed; categorical variable: x<sub>4</sub> - land management type (protected area/grazed woodlands-intercept))

**Table 5** Summary of the model selection procedure for taxonomic diversity index of mammals

	int	$x_1$	$x_2$	$x_3$	$x_4$	$k$	$\log(\mathcal{L})$	AIC	$\Delta i$	$w_i$	$R^2$
	15.98	0.39	-0.58	-1.60		5	-113.07	237.35	0.00	0.30	0.50
	15.98		-0.51	-1.60		4	-114.29	236.36	0.01	0.29	0.48
	15.98			-1.72		3	-116.15	238.76	1.42	0.15	0.44
	16.17		-0.51	-1.54	-0.25	5	-114.21	239.62	2.28	0.09	0.48
	15.98	0.29		-1.74		4	-115.50	239.79	2.45	0.09	0.45
	15.99	0.39	-0.58	-1.59	-0.02	6	-113.07	239.86	2.51	0.08	0.50
SW	1.00	0.47	<b>0.77</b>	<b>1.00</b>	0.18						
$\beta$	15.99	0.37	<b>-0.54</b>	<b>-1.62</b>	-0.14						
SE	0.35	0.27	0.27	0.29	0.71						

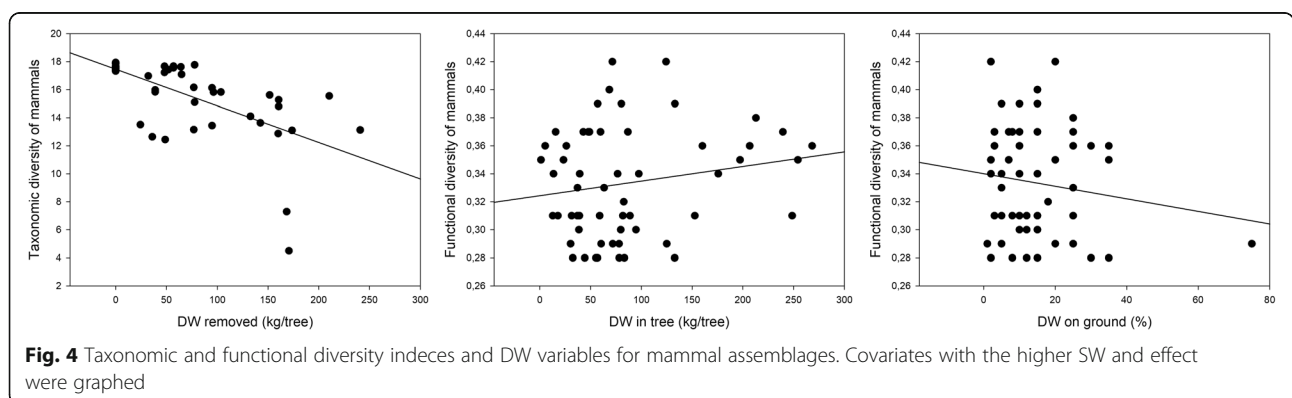
Model averaging was carried out with a 95% confidence subset of models. For each model of the subset, we reported parameter estimates, total number of estimable parameters ( $k$ ), the log-likelihood  $\log(\mathcal{L})$ , AIC criterion,  $\Delta i = AIC_i - \min AIC$ , Akaike weight ( $w_i$ ), and adjusted  $R^2$ . Models are ordered in terms of  $\Delta i$  for AIC. At the bottom of the table, we reported model-averaged estimates  $\beta$  with their standard errors (SE) and their sum of weights (SW), for the four variables (quantitative variables:  $x_1$  - DW in tree,  $x_2$  - DW on ground,  $x_3$  - DW Removed; categorical variable:  $x_4$  - land management type (protected area/grazed woodlands-intercept))

diversity for plants while deadwood removed increased them. For mammals, deadwood on ground clearly decreased the both types of diversity analyzed, while the removal of deadwood decreased TD and presence of deadwood in tree increased FD. We found that taxonomic and functional diversity for both, plant and mammal assemblages did not vary consistently with the land management type. This could be showing differential responses of the diversity indices for both assemblages (Carmona et al. 2012; Chillo and Ojeda 2014), and it highlights the importance of considering functional and taxonomic diversity in evaluating the responses of woodland ecosystems to disturbances (Carmona et al. 2012).

For the plant assembly, taxonomic and functional diversity indices did not significantly change under different land management types. In stressful ecosystems, environmental filters are among the main factors structuring plant communities (Chillo et al. 2017). Particularly in drylands, the fitness of the individuals is strongly affected by the availability of water, which could make the relative importance of the disturbance less evident (Carmona et al. 2012). Also, in drylands that had co-evolved with large herbivores, selection pressures are

convergent and plant adaptations that enhance living in drylands also promote tolerance or avoidance of grazing (Sala 1988). Carmona et al. (2012) have reported a convergence in traits under the combined effect of grazing and drought conditions. Other factors also could be driving the diversity of vegetation. In *P. flexuosa* woodlands of the hyper-arid portion of the Monte Desert, Campos et al. (2020) reported that the vegetation richness is enhanced by the abundance of adult trees and the effect of facilitation provided by them seems to be very important in ecosystems under high abiotic stress. *Prosopis* trees increase local soil fertility through the accumulation of carbon and nitrogen, and modify the decomposition rate by increasing infiltration rate and protecting against high temperatures and radiation (Rossi and Villagra 2003). However, we observed that grazing and deadwood management promoted an increment in the structural diversity of plants, as previous studies have proposed (Tabeni and Ojeda 2005; Campos et al. 2016; Miguel et al. 2018).

Functional similarities are also expected for the assembly of animals living in stressful environments (Mouchet et al. 2010). We found that the taxonomic diversity of



**Table 6** Summary of the model selection procedure for functional diversity index of mammals

	int	$x_1$	$x_2$	$x_3$	$x_4$	$k$	$\log(\mathcal{L})$	AIC	$\Delta i$	$w_i$	$R^2$
	-0.66	0.05	-0.04		-0.11	5	107.05	-202.90	0.00	0.19	0.14
	-0.67	0.04			-0.10	4	105.46	-202.13	0.76	0.13	0.09
	-0.67				-0.08	3	103.99	-201.51	1.39	0.09	0.04
	-0.69	0.03				3	103.80	-201.13	1.77	0.08	0.03
	-0.67		-0.03		-0.08	4	104.89	-200.99	1.91	0.07	0.07
	-0.69	0.04	-0.03			4	104.85	-200.91	1.99	0.07	0.07
	-0.69		-0.03			3	103.52	-200.57	2.33	0.06	0.03
	-0.66	0.05	-0.04	0.01	-0.10	6	107.09	-200.46	2.44	0.06	0.14
	-0.69	0.04	-0.04	0.03		5	105.71	-200.22	2.68	0.05	0.10
	-0.69			0.02		3	103.26	-200.06	2.84	0.05	0.01
	-0.69		-0.03	0.03		4	104.30	-199.83	3.07	0.04	0.05
	-0.66	0.04		0.00	-0.10	5	105.46	-199.73	3.17	0.04	0.09
	-0.69	0.03		0.02		4	104.19	-199.59	3.31	0.04	0.05
SW	1.00	<b>0.67</b>	<b>0.56</b>	0.28	<b>0.60</b>						
$\beta$	-0.67	<b>0.04</b>	<b>-0.04</b>	0.02	<b>-0.10</b>						
SE	0.03	0.02	0.02	0.03	0.05						

Model averaging was carried out with a 95% confidence subset of models. For each model of the subset, we reported parameter estimates, total number of estimable parameters ( $k$ ), the log-likelihood  $\log(\mathcal{L})$ , AIC criterion,  $\Delta i = AIC_i - \min AIC$ , Akaike weight ( $w_i$ ), and adjusted  $R^2$ . Models are ordered in terms of  $\Delta i$  for AIC. At the bottom of the table, we reported model-averaged estimates  $\beta$  with their standard errors (SE) and their sum of weights (SW), for the four variables (quantitative variables:  $x_1$  - DW in tree,  $x_2$  - DW on ground,  $x_3$  - DW Removed; categorical variable:  $x_4$  - land management type (protected area/grazed woodlands-intercept-))

mammals did not change by land management type, but functional diversity increased in grazed woodlands. This may be showing that the management of grazed woodlands is leading to a decrease of functional redundancy for mammals. In the protected area, the exclusion of grazing and extractive activities for almost 50 years has driven the recovery of vegetation, but in turn causing homogenization in the habitat structure (Rossi 2004; Campos et al. 2016). Although more productive areas promote positive responses in functional diversity (Sukma et al. 2019), the homogenization of habitat structures leads to a decrease in niche availability, and consequently it diminishes the representation of traits capable of occupying that functional space. Usually, homogenized habitats do not contain a wide spectrum of functional traits (Carmona et al. 2012; Ehlers Smith et al. 2020). What is more, the homogenization involves the biotic impoverishment, decreasing the resilience of the system against disturbances (Salgado-Luarte et al. 2019). In the protected area, we observed that the homogenization of the habitat did not modify the taxonomic diversity of mammals but it influenced the functional diversity of mammals, presenting smaller values. By contrast, grazed woodlands did not present changes in taxonomic diversity in comparison to the protected area, but functional diversity was higher in grazed woodlands. When species with novel functional traits replace functionally redundant species within a community,

functional diversity can increase without a change in species diversity under land-use change (Mayfield et al. 2010). In grazed woodlands, the heterogeneous spaces characterized by vegetation patches in a matrix of bare soil allow for the presence of mammals species needing open spaces to develop (Tabeni and Ojeda 2005). Previous studies have reported the presence of species such as *Dolichotis patagonum* or *Eligmodontia typus* only in grazed woodlands (Tabeni and Ojeda 2005), were traits such as locomotion habit allows them to avoid predation in open spaces (Taraborelli et al. 2003). At local scale, trees with a well-conserved structure of deadwood and grasses under their canopy produce a cascade effect in these grazed woodlands because they promote a web of plant and animal interactions which are especially beneficial for species needing more complex habitats (Szymański et al. 2020). Species associated with closed and homogeneous habitats, such as *G. griseoflavus* and *A. dolores*, can be found both in the protected area and in grazed woodlands (Tabeni and Ojeda 2005; Campos et al. 2016; Miguel et al. 2018). Thus, spatial heterogeneity of resource availability in grazed woodlands increases the functional trait dissimilarity, and the functional diversity of mammals. Opposite results have been reported for drylands in North-Central Chile, showing a homogenization of vegetation community under grazing pressure by goats (Salgado-Luarte et al. 2019). This stresses the fact that livestock grazing is a

complex disturbance, and highlights the importance of considering several factors that determine its effects, such as grazer identity and stocking rates, among many others (Chillo et al. 2017).

Our results disagree with those reported in other studies (Chillo et al. 2017; Salgado-Luarte et al. 2019), where increasing grazing intensity was linked to a decrease in taxonomic diversity and functional diversity of all plant and animal assemblages. Probably, the main difference is because our findings relate to moderate livestock loads in grazed woodlands and do not consider a grazing gradient, as did Chillo et al. (2017). In the study area, the carrying capacity for livestock production depends on precipitation but the recommended sustainable stocking rate is between 15 and 26 ha-AU<sup>-1</sup> (hectares per animal unit, one animal unit (AU) is defined as a 450-kg beef cow) (Guevara et al. 2009). For mammal assemblages, human disturbances, such as logging, fire, agriculture expansion and livestock grazing, have been reported to present negative effects on functional diversity in arid and semi-arid biomes, but herbivory is the disturbance that least affects the mammal functional diversity, probably because levels of grazing reported did not generate changes in resources and the initial state properties of ecosystems (Chillo and Ojeda 2012). Furthermore, the evolutionary history of the plant-herbivore interaction is one of the main factors that determines the effect of grazing on the plant community in arid ecosystems (Cingolani et al. 2005). Thus, maintaining appropriate levels of grazing could promote the heterogeneity of habitats which positively influences the structure, composition and functional diversity of mammal assemblages. Taking into account the results of the present study, management strategies of livestock production in grazed woodlands are compatible with the conservation of functional diversity of the analyzed assemblages. It has been reported for other arid lands that intermediate levels of grazing are desirable for the preservation of a threatened plant species (Martorell and Peters 2005).

Contrary to what we expected, the results showed that deadwood removal positively affected both taxonomic and functional diversity of plants, and the presence of deadwood on the ground negatively affected plant functional diversity. *Prosopis flexuosa* conserves the internal dry branches, occupying the space under the tree canopy. Thus, the presence of deadwood in the trees may be reducing the available space with good moisture and nutrient conditions for the regeneration and establishment of plants, affecting diversity indices. This fact becomes more relevant in arid environments, such as *Prosopis* woodlands, where trees act as nurse species, permitting the development of a network of interactions under their canopy (Rossi and Villagra 2003). Regarding the damage to plants resulting from the extraction

process, a possible explanation is that the trampling effect is not significant because the extraction level is low. The evidence for the effects of deadwood removal in forests around the world is not conclusive, and studies show negative, nil, or even positive effects on ecosystem functioning. In arid lands, the information is scarce, but there is evidence that deadwood extraction does not have significant effects on the cover, richness and composition of understory plants (Vázquez et al. 2011).

Deadwood seems to have a main role in the conservation of mammal diversity. In other forest ecosystems, such as boreal forests, deadwood represents an important forest component that furnishes habitats for invertebrates, in turn providing feeding sites for vertebrate species (Sullivan et al. 2017). In *P. flexuosa* woodlands, there is evidence that deadwood availability is positively associated with the presence of small rodents (Szymański et al. 2020). Our findings indicated that at local scale, deadwood in the tree is relevant for the conservation of mammal diversity. Deadwood in the tree is used by scansorial species, such as *G. griseoflavus*, a small rodent predator of *P. flexuosa* seeds (Giannoni et al. 2013). The arched branching pattern, with branches reaching the ground, defines the structure used by *M. maenas* in locating their colonies (Tognelli et al. 1995); this species is a seed disperser of *P. flexuosa* (Campos et al. 2017). Deadwood in the tree could be used as a resting site by climbing carnivores, such as *Leopardus geoffroyi*. Besides, deadwood provides feeding and nesting sites to small rodents, which in turn constitutes a source of food resources for carnivores. Thus, the vertical structure of deadwood on trees favors the presence of mammal species with different functional traits. By contrast, we found that the presence of deadwood on the ground decreased mammal diversity at tree scale. This may indicate an indirect effect because deadwood on ground decreased all plant diversity indices, which negatively affects species that do not use the vertical space, but prefer the complex habitat formed by plants.

The role of deadwood needs to be assessed in different forest ecosystems because management of this forest component should be included in management programs (Lassauce et al. 2011; Vázquez et al. 2011). This study is the first considering the role of deadwood in relation to the functional diversity of plant and mammal assemblages of drylands. Although the results are not conclusive, they are relevant because they fill an important knowledge gap in arid ecosystems. Also, taking into account the low variability explained by some of our models, future studies should consider other drivers of diversity, such as productivity, soil heterogeneity, woodland structure, multiple human disturbances and even climate change in order to achieve a better comprehension of biodiversity dimensions (Campos et al. 2020).



## Conclusions

Livestock loads of the studied sites promote the structural diversity of plant assemblages and the functional diversity of mammals. Regarding deadwood, opposite results were found in terms of diversity conservation of mammals and plants. At tree scale, it is advisable to maintain trees that preserve their wooden structure within the managed areas to promote the functional diversity of mammals, while trees with extraction from standing wood will favor the functional diversity of the plant assemblage.

## Abbreviations

NCP: Nature's contributions to people; BRÑ: Biosphere Reserve Nacuñán; DAB: Diameter at base height; DW: Deadwood; TD: Taxonomic diversity; SD: Structural diversity; FDis: Functional dispersion; FD: Functional diversity; GLM: Generalized linear models; AIC: Akaike Information Criterion; SE: Standard errors; SW: Sum of weights

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## Authors' contributions

All authors conceived the study, collected the data, performed statistical analysis and helped to draft manuscript. All authors read and approved the final manuscript.

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## Availability of data and materials

The datasets used during the present study are available from the corresponding author on reasonable request.

## Declarations

### Competing interests

The authors declare that they have no competing interests.

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