MISS JIMENA ELIZABETH CHAVES (Orcid ID : 0000-0002-1684-3243)

DR. MARIO GABRIEL GATICA (Orcid ID : 0000-0003-2883-2565)

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Title: Species and functional plant diversity enhance ecosystem functions in Central Monte desert

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Jimena E. Chaves[1,2], Julieta N. Aranibar[1,2], Gabriel Gatica[3]

[1]Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo, Mendoza, Argentina

[2]Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), CONICET, CCT-Mendoza, Mendoza, Argentina

[3]Departamento de Biología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, San Juan, Argentina

Correspondence
Jimena Chaves, now at Centro Austral de Investigaciones Científicas (CADIC), CONICET, Tierra del Fuego, Argentina.

E-mail: jimena.e.chaves@gmail.com

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ABSTRACT

Questions: Niche complementarity has been proposed as the underlying mechanism for optimizing resource use of plants in diverse ecosystems, usually associated with their functional traits and not with the species number *per se*. Our main questions were: i) does species diversity optimize the use of resources in arid ecosystems? ii) is there redundancy of species in the use of water and nutrients? and iii) what diversity component most affect ecosystem functions of water regulation and material cycling?

Location: Central Monte desert, Argentina.

Methods: We selected vegetation patches with different species (SD) and functional diversities (FD), where we measured indicators of water regulation and material cycling. At two soil depths, we measured soil nitrate, phosphate, organic matter, chloride, electrical conductivity, and pH. We also determined decomposition, plant water use efficiency (foliar δ^{13}C of C3 plants), and nitrogen use (δ^{15}N). These variables were used as response variables, while total plant cover, species richness, Shannon, Simpson, evenness, and Rao's functional diversity indexes were used as predictors.

Results: At the soil surface, response variables were better explained by models that included diversity (SD, FD or both) instead of evenness, total plant cover or null model. A diversity effect was not detected in deeper soil layers for most variables, except for electric conductivity, which had a positive effect of FD. Richness explained plant δ^{13}C but had no influence in plant δ^{15}N.

Conclusions: Diversity of plant community influences ecosystem processes, as it increases decomposition, soil organic matter, and nutrient availability at the surface, and decreases water losses to the subsoil and plant water use efficiency. Both SD and FD, explained one or more ecosystem processes of water regulation and material cycling, suggesting that individual species contribute to ecosystem functioning, with a low redundancy for arid areas.

Keywords

Plant diversity, functional diversity, ecosystem function, soil, biogeochemistry, isotopes, nitrogen, SOM, decomposition.

INTRODUCTION

Niche complementarity (i.e., temporal and spatial partitioning of resources use among organisms that coexist) is the most important mechanism accounting for the positive effect of biodiversity on ecosystem functioning (Cardinale et al., 2011; Loreau & Hector, 2001). The combined responses of species to environmental heterogeneity enhance ecosystem capacity to maintain functional stability in more diverse communities (Loreau & Hector, 2001). In drylands, plant diversity enhances aboveground productivity and soil functions at local (Flombaum & Sala, 2008), regional (Gaitán et al., 2014), and global scales (Maestre et al., 2012). Nevertheless, studies evaluating the impact of niche complementarity on ecophysiological, physical and microbiological mechanisms involved in resource use under natural conditions are scarce.

In plant communities, niche complementarity partitions resources use in time and space. Spatial partitioning in drylands is driven by differences in plant traits, such as roots distribution. Grass, shrub, and tree roots of the Monte desert and Patagonian steppe may differ in their vertical and horizontal distribution, exploiting different soil depths or spreading out of the canopy to absorb resources from bare areas(Guevara et al., 2010; Sala et al., 1989; Vega Riveros et al., 2020). This, in turn, minimizes nitrate leaching and water loss to deep soil layers, as shown in undisturbed and disturbed areas, where vegetation is partially removed (Aranibar et al., 2014; Meglioli et al., 2014). Temporal resource partitioning is driven by phenological-physiological plant traits (Golluscio et al., 2005). Water use efficiency and nitrogen source may vary temporally (i.e., with precipitation events), among species (*Prosopis flexuosa* and others), and with land use (Aranibar et al., 2014; Meglioli et al., 2014). In the Kalahari and Monte deserts, atmospheric N can be fixed by trees, grasses and forbs, depending on species, climate variability, and soil N pools (Aranibar et al., 2008, 2011). In the Chihuahuan desert, species diversity is also associated with different life form adaptations and photosynthetic pathways, using temporally variable water resources and promoting coexistence (Kemp, 1983; Shriver, 2017). Increases in species diversity would increase water retention and plant productivity, which would be evidenced by increases in soil organic matter, nutrients, and ions excluded during water absorption (i.e., chloride).

Ecosystem productivity increases in diverse communities, although individual plant performance may decrease by competition. *Prosopis flexuosa* trees growing in low productive, disturbed areas, surrounded by bare soils had an overall better performance (lower water use efficiency, higher stomatal conductance and nutrient contents, higher growth rates) than trees from more productive, relatively undisturbed ecosystems (Meglioli et al., 2016). Nitrogen losses relative to turnover, indicated by higher foliar δ^{15}N, are also higher in less productive areas, because of reduced competition and higher N availability (Meglioli et al., 2017). Thus, the responses of vegetation water and nitrogen use to biodiversity, indicated by stable isotopes, may differ with spatial scales. In the Monte desert, as in other drylands, ecosystems have a spatial configuration as a two-phase mosaic consisting of patches (vegetated zones of individual or segregated plants) immersed in a low or null vegetation cover matrix (Bisigato et al., 2009). Physiological and biogeochemical responses of plants and soils to biodiversity may then be relevant at the patch spatial scales, where neighboring species interact, rather than at larger, i.e., ecosystem, spatial scales.

Biodiversity, as the hypothesized control of ecosystem functions, has different components. Therefore, different diversity indices may be used to estimate biodiversity effects on ecosystem functions. Species richness and Simpson index would indicate niche complementary of all or dominant species, respectively (Grime 1998). Shannon index indicates the importance of rare and abundant species equally, based on their abundances (Morris et al., 2014). The mass ratio effect, indicated by species evenness index (E) may explain ecosystem functions when they are driven by changes in dominance and not by shifts in species richness (Grime, 1998). Furthermore, some studies show that functional diversity, based on plant functional traits and strategies, better control ecosystem responses than species diversity (Cadotte et al., 2011; Díaz & Cabido, 2001). The relative importance of species and/or functional diversity for ecosystem functions may depend on relationships between species richness and trait variations in communities. Higher plant functional variations occur when niche differentiation among coexisting species is relatively higher (Díaz & Cabido, 2001), and then functional diversity may override the effects of species diversity on ecosystem functioning (Cadotte et al., 2011). In contrast, under considerable functional redundancy (i.e. greater coexistence of similar plant traits), species richness increases at higher rate than functional diversity, and then species diversity may be more important for ecosystem processes (Cadotte et al., 2011; Díaz & Cabido, 2001). In any case, this complexity highlights the need to consider different species and functional diversity indices for a better understanding of diversity-functioning relationships in natural conditions.

We performed an observational study to evaluate relationships between plant species and functional diversity and ecosystem functions of material cycling, and water regulation of an arid region. We hypothesized that niche complementarity given by plant diversity increases ecosystem functions because it minimizes water and nutrients losses and maximizes their absorption. We also hypothesised a low redundancy of species, with rare species being important in ecosystem functions, particularly in the surface of the soils. Ecosystem functions were estimated with indicators of a) water regulation: soil chloride and salts concentration (indicating plant water uptake and loss to the subsoil), foliar $\delta^{13}C$ (plant water use efficiency); and b) material cycling: soil organic matter -SOM- (which indicates carbon accumulation), decomposition, phosphate and nitrate concentrations (nutrients production, losses and availability), pH (acidification by soil respiration), and foliar $\delta^{15}N$ values (N losses if high, N_2 fixation if close to 0 per mil). Soil variables were estimated at two depths, to capture the effects of surface inputs to soils, and resource retention in the soil below the maximum rooting density (1 m depth) (Aranibar et al., 2011). We expected species and functional diversity to positively affect i) soil chloride concentrations and salinity, ii) SOM and nitrate concentrations, iii) phosphate availability, iv) decomposition, v) plant $\delta^{13}C$ values; and negatively affect vi) soil pH, and vii) plant $\delta^{15}N$. Among all diversity indices, we expected richness, which weights all species equally, to explain much of the variability in surface soils, while functional diversity, or indices that emphasize dominant species (D), to explain variability at 1 m depth.

MATERIALS AND METHODS

Study area

The study was done in Telteca Natural and Cultural Reserve, located in NE Mendoza, Argentina (32° 20'S: 68° 00'W; 500-550 m a.s.l.). Topographically, the area is formed by a dune-interdune system with height differences of 8-20 m between interdune lowlands and dune crests. The soils are sandy (> 95%) and poorly developed entisols (Jobbágy et al., 2011). The sediments are mainly composed of very fine and fine sands (Gomez et al., 2014), with low organic matter and nutrients, which increase in vegetated patches (Aranibar et al., 2011; Guevara et al., 2010). The climate is arid with a mean annual temperature of 18.5 °C, and a mean maximum and minimum of 27°C and 9.3°C, respectively. Mean annual precipitation is around 150 mm, mainly concentrated as pulses in spring and summer (September-March) (Estrella et al., 1979).

Vegetation communities of the region (nomenclature: Flora Argentina- Anton & Zuloaga, 2018) are characterized as a combination of three layers: trees, shrubs and herbs. The tree layer can be composed of *Prosopis flexuosa*, in the form of open or closed small forests, commonly combined with *Atriplex lampa*, *Suaeda divaricata*, *Tricomaria usillo*, or *Larrea divaricate* (Villagra et al., 2004). A second tree layer may be present, represented by *Bulnesia retama* or *Geoffrea decorticans*. The shrub layer can be composed of *Capparis atamisquea*, *Lycium tenuispinosum*, *Senna aphylla,* and the species from the tree layer. The herbaceous layer can be formed by grasses like *Trichloris crinita*, *Setaria leucopila*, *Sporobolus rigens*, *Panicum urvilleanum* along with forbs as *Heliotropium mendocinum*, among others (Villagra et al., 2004). Local inhabitants extract vegetation resources, modifying its structure according to their needs, including vegetation cover, species composition, and biodiversity (Goirán et al., 2012; Meglioli et al., 2014; Villagra et al., 2009).

Experimental design and biodiversity estimates

We selected five sites, in different dune flanks with similar geomorphic features (sediments, topography), distanced between 0.79 and 3.39 km from each other, and 0.5 to 0.79 km from livestock settlements to exclude highly disturbed areas. Dunes topography, vegetation cover, and fine sediments facilitate transport and resources losses from dune flanks to the inter-dunes valleys (Aranibar et al., 2011; Jobbágy et al., 2011), therefore, we sampled dune flanks to capture the effect of vegetation community on nutrient retention and losses.

We selected 45 vegetation patches and 5 bare soil areas (9 patches and 1 bare soil per site). Total plant cover and individual species cover were estimated by intercept method using two perpendicular transects of 2 m on each patch. On each transect we recorded plant species interceptions every 4 cm, to calculate the percent cover of a given species. The number and cover of vascular plant species recorded were used to calculate the following species diversity (SD) indices: species richness (S, all species equally important), Shannon index (H, weights species according to their abundance), Simpson index (D, dominant species more important), and Evenness (E, indicates if abundances are equally distributed among species) (Appendix S1).

We used effect traits that affect different processes related to water regulation and material cycling to estimate functional diversity (FD), including physiological, structural and phenological attributes. We calculated Rao's functional diversity index (FD_Q), because it allows the use of different type of traits, and the relative abundances of species (Botta-Dukát, 2005; Leps et al., 2006). Leps et al. (2006) method was followed to calculate first the trait dissimilarity and then a functional diversity index for each sampling unit (i.e., each of the 45 vegetated patches and 5 bare soils). Selected traits and range of values are shown in Table 1, and species attribute values in Appendix S2.

Soil and plant sampling

In each patch, at the end of the summer (March 2016) soil samples were taken from the surface and from one-meter depth. The surface sample was composed of a pool sample from four different points around the patch centre (0-10 cm depth), and the deep sample was extracted at 1 m depth with a soil core. The samples were dried at 60°C for 24 hours, sifted to discard litter larger than 2 mm, and homogenized with a mortar.

At the same sampling period, mature leaves from healthy plant species of each patch were sampled, removing approximately 10 leaves from different places of the plants to reduce variability given by microenvironmental conditions, and combining them into one sample per species. These were dried at 60 °C for 24h, and ground with a grinder for stable isotope determinations.

Soil analysis

We selected a common substrate for decomposition determinations, in order to highlight the importance of plant traits other than litter quality (Eviner & Chapin III, 2003; Hector et al., 2000). Cellulose substrates (filter papers of 7 cm diameter) were weighed, placed inside nylon net bags (1.8 mm openings) and buried in the middle of each vegetation patch at a soil depth of 5-10cm. Incubations started at the beginning of the growing season, in January 2016, before the seasonal precipitations started, and concluded at the end of the growing season, after 108 days of incubation. The filter papers were dried at 60°C to stop decomposition and then weighed, to calculate the percentage of mass lost during the incubation period.

Nitrate was determined in soil extracts with an extraction solution, composed of 2.5 g of $CuSO_4 \cdot H_2O$, 0.15 g of Ag_2SO_4, and 0.62 g of H_3BO_3 in 1000 ml of distilled water (10 g: 25 ml, soil: extraction solution). Mixtures were shaken for one hour, filtered and neutralized at pH 7 with NaOH (1%). Nitrate concentrations were determined with a spectrophotometer (HACH DR2800) using a cadmium reduction method (with reactive pillows NitraVer®5) (Hach Company, 2004).

Soil organic matter (SOM) was determined by mass lost by calcination at 430 °C.

Available phosphorus was determined with the Olsen method, in soils extracted with sodium bicarbonate solution ($NaHCO_3$, 0.5 M, pH 8.5) (5 g: 40 ml), shaken at a constant rate for 30 minutes and filtered. Phosphate concentrations in these extracts were determined with a spectrophotometer (880 nm) after reaction with ammonium molybdate (Okalebo et al., 1993).

Electric conductivity (EC) and pH were measured in soil extracts -soil and distilled water (25: 50 g)- after shaking for one hour, with a multiparametric Thermo equipment using specific electrodes. For chloride determinations, an ionic strength adjustor solution (ISA, ammonium solution 2 M, volumetric relation 1:100) was added, and chloride concentration was measured with an ion-specific electrode.

Plant stable isotopes

Plant $\delta^{15}N$ and $\delta^{13}C$ values were determined with a Thermo Scientific DELTA V Advantage mass spectrometer coupled to a Flash 2000 elemental analyser in LIECA (Stable Isotopes in Environmental Sciences Laboratory, Mendoza, Argentina), with an overall precision of 0.1 per mil. The results are expressed in the “delta” notation, in relation to the standards for N and C, which were atmospheric air and Vienna Pee Dee Belemnite (VPDB), respectively (Hoefs, 1997).

Data Analysis

We used generalized linear mixed models (GLMM) to analyse the influence of diversity and vegetation cover on SOM, nitrate, phosphate, EC, chloride, pH, decomposition, and stable isotopes. We considered vegetation cover and diversity indices as fixed effects, and “site” (5 dune flanks) as a random effect (random intercept model, Zuur et al. 2009) for soil variables. We fitted our models using Gaussian error distribution for nitrate, phosphate, EC, chloride and pH, and Beta error distribution for SOM and decomposition. Because there are strong correlations among different diversity indices (Appendix S3), we fit different models for each explanatory and response variable, and separately for surface and deep soils. We compared the models, including the null model, with Akaike Information Criterion (AIC). We considered the models with $\Delta AIC < 2$ to explain the variations of the target response variable, and the one with the lowest AIC to best fit the data (Burnham & Anderson, 2002). We used regression coefficients and their 95% confidence intervals for the best models to infer direction and magnitude of bivariate relationships between predictor and response variables.

Similarly to soil functions, we used linear mixed models and multi-model inference to test diversity-plant isotopes (^{13}C and ^{15}N) relationships. Plant foliar samples were collected from different plant species in each patch sampled. Because inter-specific differences may affect part of the variance in stable isotopes (Gatica et al., 2017), we included species identity and site as random factors, to estimate intercept and slope parameters for all and each species (intercept and slope model, Zuur et al., 2009). Gaussian and homoscedasticity assumptions were graphically tested using standardized residuals for all fitted models (Zuur et al., 2009).

All statistical analyses were performed in R 3.4.0 software (R Core Team, 2017) using "lme4" (Bates et al., 2015), "glmmTMB" (Brooks et al., 2017), and "MuMIn" (Barton, 2020) packages to fit mixed effect models. In order to visualize the effect of diversity, only the best predicting variable according to the models was plotted with each response variable (diversity-nutrient relation) using the "ggplot2" package (Wikham, 2016).

RESULTS

Diversity

We recorded a total of 22 plant species in the 50 sampling units analysed, with a number of species per sampling unit ranging from zero (in bare soils) to eight (in vegetated patches), and with a mean value of 4.12 (SD ± 2.545). This suggests that our design represents an appropriate range of values of explanatory variables to test diversity and complementary effects on soil functions. Species composition and abundance also varied among vegetation patches, and a given species was present in up to 60% of patches (Appendix S4). This result reflects a considerable species turnover among patches and reduces the importance of sampling effects that can mask biodiversity effects (i.e. ecosystem functions driven by highly productive and dominant species). As many of our explanatory variables were correlated (Appendix S3), the separated use of each in the models is justified.

Factors explaining ecosystem functions

At the soil surface and for all soil variables, models with $\Delta AIC < 2$ included either species or functional diversity indices. Decomposition and SOM were also explained by plant cover (ΔAIC 0.16 and 1.5, respectively) although the best model (lowest AIC) included richness (S) and functional diversity (FD), respectively (Table 2). The effect of explanatory variables on response variables were positive in all cases, except pH. For pH, the best model included functional diversity, with a negative effect, but the null model had a ΔAIC of 1.5. Decomposition and phosphate were better explained by species richness, nitrate and SOM by FD, chloride and EC by H. For all response variables, the best model (lowest AIC) presented confidence intervals of the regression coefficient different from 0, indicating a significant effect of the explanatory variable on the response variable.

At 1 m depth, the null model had the lowest AIC for SOM, phosphate and pH. Nitrate, EC and chloride were best explained by FD (lowest AIC) while other models also presented $\Delta AIC < 2$, such as E for nitrate, H for EC, and null for chloride. However, even though the best models included a diversity estimate for these response variables, confidence intervals of the regression coefficients for nitrate and chloride included 0, indicating non/significant effects of the explanatory on the response variables. In the deeper soil layer analysed, only EC shows a positive and significant effect of functional diversity, with confidence intervals that did not include 0 (Table 3).

Richness is the best model explaining variations in C3 plant $\delta^{13}C$ (Table 4), with a negative effect for most plant species analysed (Figure 2), except for *Tricycla spinosa*. In contrast, the evenness (E) model was the best model for plant $\delta^{15}N$, but the confident intervals of the regression coefficient include 0 and the null model had a ΔAIC of 1.28, thus no effect was detected. Stable isotope data is presented in supplemental material (Appendix S5).

DISCUSSION

Either species (D, S, or H) or functional diversity, but not evenness, affected all biological processes analysed, including decomposition, nutrient production and availability, water retention, and water use efficiency. Our results thus indicate that niche complementary is the main mechanism involved in the regulation of multiple soil and plant functions in our study area. Diversity and niche complementary effects were evident in the soil surface for all processes, while only for water regulation (EC) at 1-m depth. These effects were observed with small changes in species numbers, from one up to eight species per patch, highlighting the importance of every species in the ecosystem. Our findings support theoretical (Loreau, 1998; Naeem et al., 2002) and empirical studies (Naeem et al., 1995; Schmid et al., 2002) that relate diversity with a variety of ecosystem processes, such as respiration, productivity, mineralization, decomposition, and accumulation of phosphorus and potassium.

Decomposition was best explained by species richness, and secondly by plant cover, which agrees with grassland studies that used litter as substrate (Hector et al., 2000), and differs from studies where functional diversity was the main control of decomposition (Scherer-Lorenzen, 2008). Vegetation influences decomposition through their effects on soil temperature, humidity, microbial community, and chemical factors, which are particularly associated with different species (i.e., legumes and grasses with associated bacteria). Microclimatic effects mediated by a more complex architecture in diverse patches may also favour decomposition (Scherer-Lorenzen, 2008). These effects may positively interact with a more diverse litter quality, which depends on species-specific traits (N fixers, high cellulose or lignin plants), increasing decomposer community diversity and biomass (Eisenhauer et al., 2010; Hector et al., 2000). Our results suggest that the ecosystem function of nutrient cycling, mediated by microbial community, improves with plant species richness rather than with the estimated functional diversity, supporting the singular hypothesis of biodiversity, which assumes that each species has a unique role on ecosystems (Naeem et al., 2002).

Soil organic matter accumulation and availability of limiting nutrients (nitrate and phosphate) were also affected by biodiversity, particularly in the soil surface. FD best explained increasing SOM and nitrate, while species richness best explained available phosphorus. The amount of SOM reflects the balance between inputs (debris, root exudates and microbial products), and outputs (respiration, charring, volatilization, and leaching of organic compounds) (Cotrufo et al., 2013; Klemmedson, 1989). Thus, microorganism, root, and litter diversity and activity can increase soil organic carbon stocks, increasing the accumulation of stable carbon pools (Lange et al., 2015). The negative effect of FD on pH is consistent with increasing root or microbial soil respiration in more diverse patches, which acidifies the soil (from pH 7.95 in bare soils to 6.53 in some patches). Acidification and the exudation of compounds that compete with P for adsorption surfaces would enhance phosphorus solubility and availability on surface soils of diverse patches (Eviner & Chapin III, 2003).

Nitrate availability, which is regulated by many biological and physical processes (i.e., nitrogen fixation and release from roots, nitrification, nitrate leaching to the subsoil, plant absorption) was positively affected by diversity (FD and H) in the soil surface. Legume litter with low C:N ratio induces microorganism activity, may slow down N immobilization, favour mineralization rates, and increase soil nitrate concentrations (Eviner & Chapin III, 2003; Scherer-Lorenzen et al., 2003). Most of our richer patches had one or two legume (i.e., *Prosopis flexuosa*, *Prosopidastrum globosum*) or grass species (i.e., *Aristida mendocina*, *Sporobolus rigens*), with $\delta^{15}N$ values that indicated N fixation (Appendix S5). Most plants, however, indicated soil N uptake, enriched in ^{15}N, as found in previous studies (Aranibar et al., 2014). Increasing functional diversity may increase the chances to have N fixing organisms in the community, and increase N availability. In addition, differentiation in the form of N absorbed, indicated by the high variability of $\delta^{15}N$ values within patches and species (McKane et al., 2002), may optimize N use and reduce N losses, supporting the niche complementarity hypothesis, as shown in grasslands (Kahmen et al., 2006).

Maximization of soil water absorption in a patch is indicated by soil chloride and salt concentrations, because plant roots absorb water while exclude ions, which accumulate in zones of high water uptake and low water drainage (Phillips, 1994). Water absorption was affected by species diversity in the surface (H), and functional diversity at depth. Different spatial roots distribution in grasses and shrubs optimized water use in the Monte desert and Patagonian steppe, using water from upper and deeper soil layers, respectively (Cavagnaro & Passera, 1991; Sala et al., 1989). Phenological differences may cause temporal differentiation in water uptake (Reynolds et al., 2004), given by perennials such as *Larrea*, deciduous such as *Morrenia*, and species that produce leaves and fruits after every rain pulse, such as *Lycium* *tenuispinosum* (personal observations). All life forms, such as annuals, forbs, shrubs, trees, and climbers, exploit surface soils, while only deep rooted trees and shrubs exploit deep soil layers. Then, deep soils are less sensitive to species numbers and more sensitive to functional traits. Previous studies showed that well developed, relatively undisturbed vegetation reduces water losses to the aquifer (Meglioli et al., 2014). Our observations indicate the species diversity, particularly Shannon index, which weighs all species according to their abundance, further optimizes water use in the surface, supporting the singularity hypothesis.

Plant water use efficiency (ratio of carbon fixed to water lost, indicated by foliar $\delta^{13}C$), was negatively influenced by richness (S), contrary to our hypothesis (i.e., higher water use efficiency given by competition in more diverse patches). This strikingly indicates that diversity either increases soil water availability or decreases atmospheric demand. Hydraulic lift by deep rooted species may redistribute water from deep, denuded areas to surface soils, increasing water availability to plants (Guevara et al., 2010; Jobbágy et al., 2011), as observed in other ecosystems (Cardon et al., 2013). Shading in more complex patches may decrease atmospheric demand, and increase stomatal conductance to CO_2 in understory plants. This positive biodiversity effect on water availability could provide a positive feedback for other ecosystem processes, such as photosynthesis, litter production, nutrient, and organic matter accumulation.

Our results highlight the importance of plant community diversity on the ecosystem functions of material cycling, and water regulation: small changes on species numbers account for significant effects on most analysed variables. Moreover, the same species were present or dominated highly diverse, as well as less diverse patches, indicating that diversity and species assemblages, instead of a particular species identity, increased ecosystem functioning. Species diversity (richness and Shannon) explained more variables than functional diversity, indicating unknown, exclusive traits of each species. Particularly in the soil surface, species diversity was positively related to decomposition, phosphate, plant water uptake and negatively related to plant water use efficiency. Among species diversity components, the simplest index that weights all species similarly, richness, explained two response variables (phosphate and decomposition). Shannon, an index that weights species according to their abundance, explained water related variables (chloride and EC). Our findings support the singular hypothesis of biodiversity, i.e., each species contributes to water regulation and material cycling, with a low redundancy for arid areas. Plant diversity promotes soil processes that have a direct relation with nutrient cycling, and water regulation, pointing to diversity as the cause and effect of the ecological processes analysed, and the existence of complex feedbacks among biodiversity and ecosystem functions.

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Author contributions

JEC and JNA participated in fieldwork, sample processing, data analysis and writing. GG participated in the design of the study, data analysis and writing.

Data availability statement

The data used in this research is available in Supplementary Information (Appendix S6 and S7).

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SUPPORTING INFORMATION

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

Appendix S1. Formulas of diversity indexes.

Appendix S2. Functional trait values for the analysed species.

Appendix S3. Correlation between explanatory variables

Appendix S4. Frequency and relative abundance of each species.

Appendix S5. Mean natural abundance of carbon and nitrogen stable isotopes for each species.

Appendix S6. Data of plant patches, diversity indices and response variables.

Appendix S7. Isotope data for each species.

TABLES and FIGURES

Table 1 Functional traits and categorical values used to calculate Rao's functional diversity index, according to Leps et al. (2006). Each trait is associated to different processes (Perez-Harguindeguy et al., 2013) of the two ecosystem functions evaluated (WR-water regulation, MC-material cycling)

Plant trait	**Process affected**	**Ecosystem Function**	**Value**
Life history	Temporal differentiation in water and nutrient absorption, and litterfall.	WR	Deciduous Perennial
Legumes	N fixation, nutrient availability and decomposition	MC	No Yes
Main root system	Spatial differentiation in water absorption	WR	Lateral Taproot
Photosynthetic pathway	Water and nitrogen demand, litter quality and decomposition	WR, MC	C3 C4
Growth form	Spatial differentiation in light absorption and evapotranspiration, litter quality and decomposition, shading and evapotranspiration of neighbouring plants	WR, MC	Grass Subshrub Shrub Tree Climber
Leaf size	Evapotranspiration, litter quality	WR, MC	Small Medium Large Leafless
Lateral spread	Spatial differentiation in water and nutrient absorption and carbon contributions to SOM	WR, MC	Tussock Single shoot Stolons/rhizome Several stems
Leaf texture	Litter quality, decomposition	MC	Soft Intermediate Tough

Table 2 Generalized linear mixed model results for the analysed variables in the surface soil samples with each of the fixed factors. Suitable models ΔAIC<2 are highlighted in bold. EC: electric conductivity. SOM: soil organic matter. S: species richness. Indices: FD_Q: Rao's functional diversity; E: evenness; D: Simpson; H: Shannon

Response	Predictor	Estimate (CI)	Low CI	High CI	ΔAIC	R^2 marginal	R^2 conditional
Decomposition	**S**	0.171	0.084	0.259	**0**	0.236	0.236
	Cover	0.0151	0.0071	0.0232	**0.16**	0.206	0.206
	D	0.298	0.116	0.480	3.62	0.176	0.176
	H	0.582	0.173	0.991	5.98	0.136	0.136
	FD_Q	1.280	0.129	2.43	8.74	0.0869	0.0869
	E	0.726	-0.110	1.56	10.48	0.0457	0.0457
	Null				11.3	0.052	0.052
NO_3^-	**FD_Q**	2.38	1.56	3.20	**0.0**	0.41	0.41
	H	0.886	0.587	1.19	**1.2**	0.42	0.42
	Cover	0.0181	0.0126	0.0236	4.8	0.47	0.47
	S	0.182	0.113	0.252	8.6	0.36	0.36
	D	0.358	0.218	0.499	8.0	0.35	0.35
	Null				22.9	0	0
	E	0.493	-0.264	1.25	23.3	0.03	0.03
SOM	**FD_Q**	1.46	0.774	2.14	**0**	0.3	0.3
	H	0.502	0.269	0.736	**0.3**	0.27	0.27
	Cover	0.0112	0.0045	0.018	**1.5**	0.33	0.33
	S	0.0982	0.0463	0.150	3.8	0.21	0.21
	D	0.178	0.0788	0.277	5.3	0.18	0.18
	Null				14.1	0	0
	E	0.202	-0.251	0.655	15.4	0.01	0.01
PO_4^{3-}	**S**	3.084	0.936	5.24	**0**	0.14	0.2
	FD_Q	19.9	-8.83	47.7	**0.4**	0.04	0.1
	H	9.99	-0.224	20.0	**0.7**	0.07	0.14
	Cover	0.305	0.124	0.486	2.4	0.19	0.25

Response	Predictor	Estimate (CI)	Low CI	High CI	ΔAIC	R^2 marginal	R^2 conditional
	E	7.87	-14.1	29.0	2.4	0.01	0.07
	D	4.29	-0.295	8.70	2.6	0.07	0.14
	Null				7.5	0	0.05
Cl^-	**H**	0.483	0.120	0.852	**0.0**	0.12	0.18
	D	0.232	0.0741	0.395	**0.4**	0.14	0.19
	FD_Q	0.784	-0.257	1.83	2.2	0.04	0.1
	S	0.111	0.0302	0.192	2.6	0.13	0.19
	Null				2.9	0	0.06
	E	-0.164	-0.928	0.618	4.8	0	0.06
	Cover	0.00773	0.0006	0.015	10.0	0.08	0.14
EC	**H**	0.703	0.466	0.943	**0**	0.41	0.44
	S	0.161	0.109	0.212	**0.9**	0.44	0.48
	FD_Q	1.66	0.953	2.37	5.7	0.31	0.34
	D	0.291	0.180	0.402	5.9	0.36	0.37
	Cover	0.0135	0.009	0.018	7.9	0.41	0.44
	Null				21.2	0	0
	E	0.265	-0.346	0.877	23.0	0.01	0.01
pH	**FD_Q**	-0.476	-0.899	-0.052	**0**	0.1	0.1
	Null				**1.5**	0	0
	H	-0.174	-0.330	-0.018	2.1	0.09	0.09
	E	-0.277	-0.586	0.032	2.3	0.06	0.06
	D	-0.086	-0.154	-0.018	2.5	0.12	0.12
	S	-0.033	-0.068	0.002	6.3	0.07	0.07
	Cover	-0.003	-0.006	0.000	10.9	0.08	0.08

Table 3 General and linear mixed model results for the analysed variables in the surface soil samples with each of the fixed factors. Suitable models ΔAIC<2 are highlighted in bold. EC: electric conductivity. SOM: soil organic matter. S: species richness. Indices: FD_Q: Rao's functional diversity; E: evenness; D: Simpson; H: Shannon

Response	Predictor	Estimate	Low CI	High CI	ΔAIC	R^2 marginal	R^2 conditional
NO_3^-	$\mathbf{FD_Q}$	5.76	-2.10	13.6	**0**	0.04	0.04
	E	-4.34	-10.0	1.33	**0.5**	0.05	0.05
	H	1.01	-1.93	3.95	3.6	0.01	0.01
	Null				4.7	0	0
	D	0.31	-1.03	1.65	5.4	0	0
	S	0.406	-0.248	1.06	5.6	0.03	0.03
	Cover	0.017	-0.045	0.079	11.5	0.01	0.01
SOM	**Null**				**0**	0	0.22
	E	-0.21	-0.540	0.118	**0.5**	0.03	0.25
	D	-0.0247	-0.101	0.052	**1.6**	0.01	0.22
	Cover	0.00104	-0.0028	0.0049	**1.7**	0.01	0.22
	S	0.00751	-0.030	0.045	**1.8**	0	0.22
	H	-0.0328	-0.199	0.134	**1.8**	0	0.21
	FD_Q	-0.00828	-0.466	0.449	2	0	0.21
PO_4^{3-}	**Null**				**0**	0	0
	FD_Q	-0.13	-0.780	0.530	2.2	0	0
	E	-0.11	-0.569	0.349	2.8	0	0
	H	-0.00015	-0.238	0.238	4.4	0	0
	D	-0.004	-0.112	0.104	5.9	0	0
	S	0.009	-0.044	0.063	7.3	0	0
	Cover	-0.0012	-0.0061	0.0038	11.9	0	0
Cl^-	$\mathbf{FD_Q}$	0.903	-0.042	1.87	**0**	0.06	0.28
	Null				**1.8**	0	0.24
	H	0.259	-0.099	0.613	3.4	0.03	0.28
	E	0.0283	-0.693	0.781	4.0	0	0.23
	D	0.0838	-0.080	0.248	5.9	0.02	0.25

Response	Predictor	Estimate	Low CI	High CI	ΔAIC	R^2 marginal	R^2 conditional
	S	0.0305	-0.053	0.111	7.8	0.01	0.25
	Cover	0.0015	-0.0060	0.0094	13.0	0	0.23
EC	**FD_Q**	0.835	0.135	1.55	**0**	0.1	0.19
	H	0.307	0.045	0.562	2.0	0.10	0.22
	Null				3.1	0	0.09
	E	-0.114	-0.648	0.468	5.6	0	0.10
	D	0.099	-0.023	0.219	6.2	0.05	0.15
	S	0.052	-0.010	0.110	7.4	0.05	0.18
	Cover	0.00374	-0.0019	0.0096	13.3	0.03	0.11
pH	**Null**				**0**	0	0
	FD_Q	-0.295	-0.668	0.077	**1.1**	0.05	0.05
	H	-0.108	-0.245	0.029	3.1	0.05	0.05
	E	-0.0961	-0.371	0.179	3.6	0.01	0.01
	D	-0.0363	-0.0991	0.0266	5.8	0.03	0.03
	S	-0.0113	-0.0428	0.0201	7.9	0.01	0.01
	Cover	-0.0025	-0.0054	0.0003	10.3	0.06	0.06

Table 4 Linear mixed model results for plant stable isotopes as a function of different diversity indexes. Suitable models ΔAIC<2 are highlighted in bold. EC: electric conductivity. SOM: soil organic matter. S: species richness. Indices: FD_Q: Rao's functional diversity; E: evenness; D: Simpson; H: Shannon.

Response	Predictor	Estimate	Low CI	High CI	ΔAIC	R^2 marginal	R^2 conditional
$\delta^{13}C$	**S**	-0.22	-0.42	-0.08	**0**	0.016	0.85
	H	-0.89	-1.48	-0.32	5.86	0.02	0.80
	E	0.04	-1.36	3.30	6.27	0.006	0.85
	D	-0.004	-0.53	-0.06	8.61	0.013	0.85
	Null				8.77	0.84	0.84
	FD_Q	-0.02	-4.03	-0.34	9.47	0.013	0.85
	Cover	-0.01	-31.13	10.79	13.83	0.002	0.84
$\delta^{15}N$	**E**	0.739	-2.24	4.91	**0**	0.006	0.41
	Null				**1.28**	0.32	0.32
	S	-0.008	-0.45	0.18	4.56	0.06	0.35
	Cover	-0.514	-66.59	38.80	5.41	0.003	0.34
	D	-0.007	-0.80	0.25	6.11	0.001	0.33
	H	-0.011	-2.00	0.89	6.59	0.006	0.34
	FD_Q	0.012	-3.40	4.85	7.07	0.001	0.32

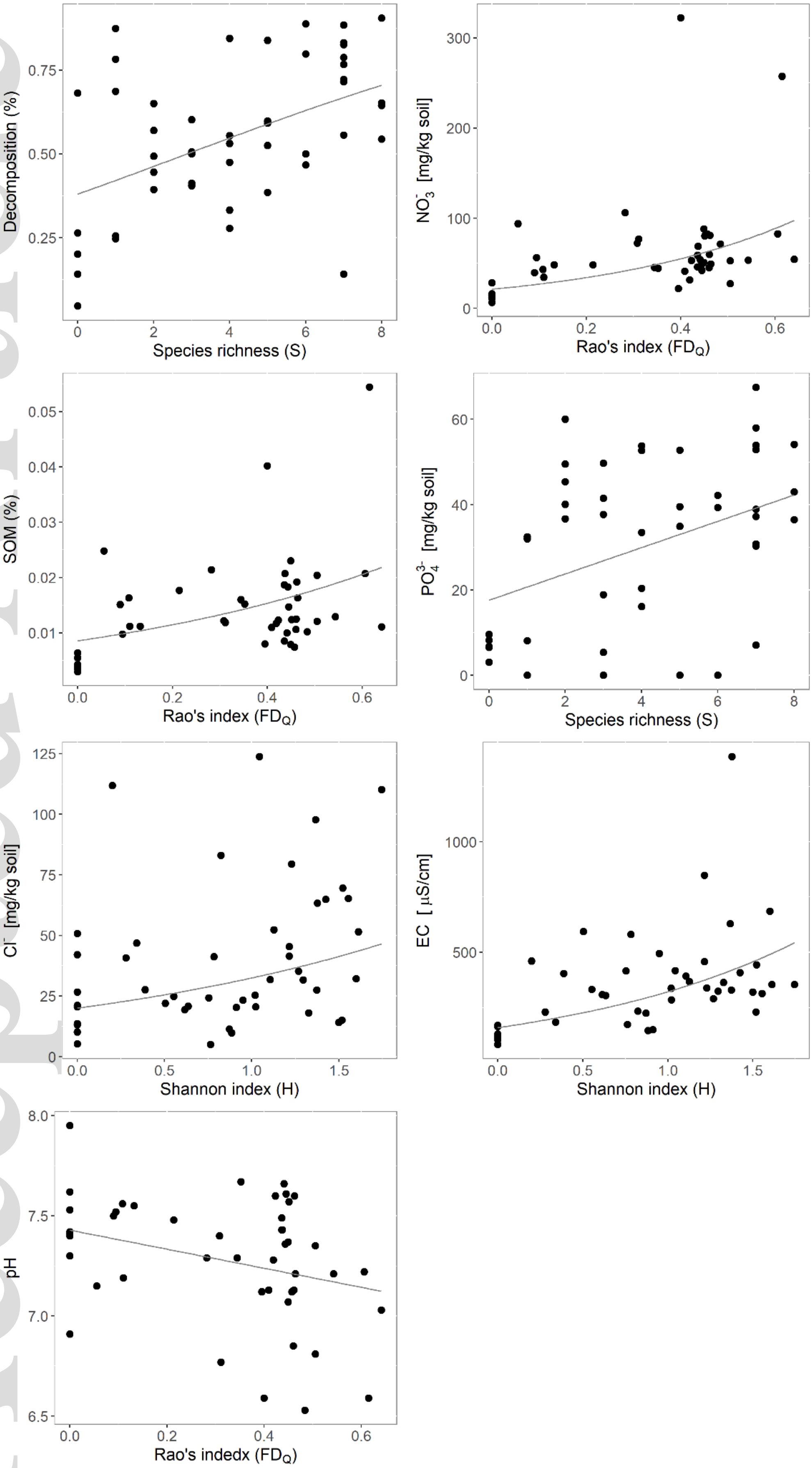
Decomposition (%)
0.25
0.50
0.75
0
2
4
6
8
Species richness (S)
NO$_3^-$ [mg/kg soil]
0
100
200
300
0.0
0.2
0.4
0.6
Rao's index (FD$_Q$)
SOM (%)
0.01
0.02
0.03
0.04
0.05
0.0
0.2
0.4
0.6
Rao's index (FD$_Q$)
PO$_4^{3-}$ [mg/kg soil]
0
20
40
60
0
2
4
6
8
Species richness (S)
Cl$^-$ [mg/kg soil]
0
25
50
75
100
125
0.0
0.5
1.0
1.5
Shannon index (H)
EC [µS/cm]
500
1000
0.0
0.5
1.0
1.5
Shannon index (H)
pH
6.5
7.0
7.5
8.0
0.0
0.2
0.4
0.6
Rao's indedx (FD$_Q$)

Figure 1 Bivariate relationships between best predictor, determined by their lower AIC on multiples GLMM models, and each response variable (decomposition, nitrate, soil organic matter -SOM-, phosphate, chloride, electric conductivity -EC- and pH) for surface soils (0-10 cm). Lines were drawn with parameters obtained with the models.

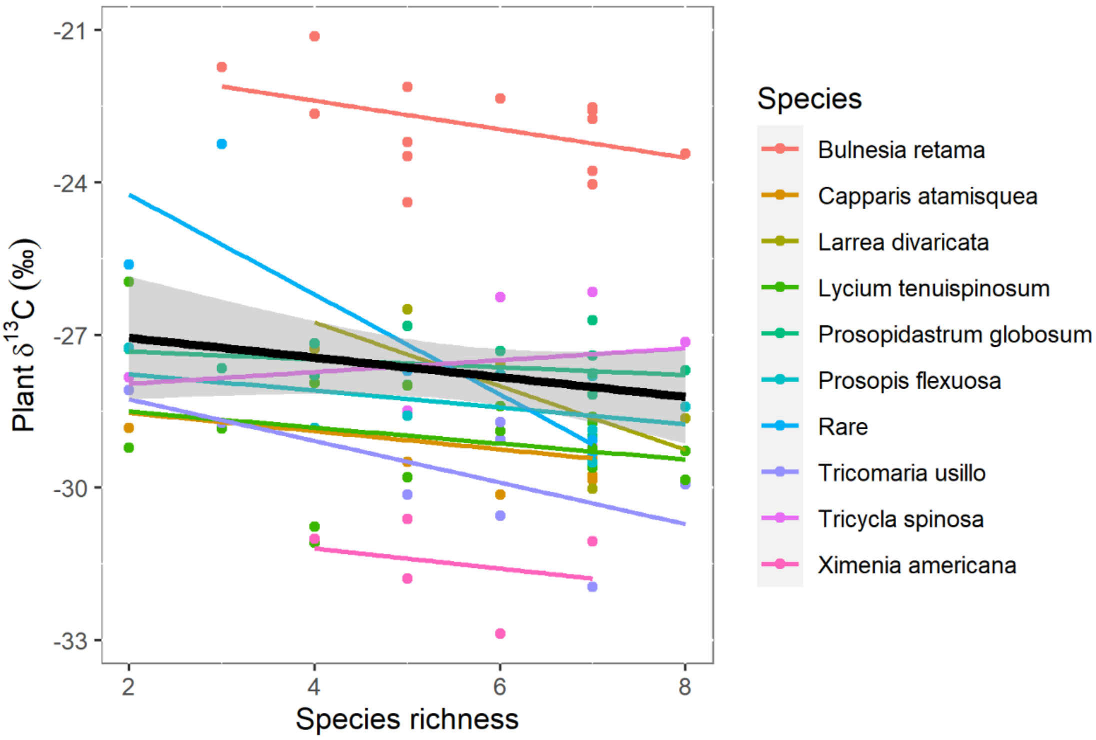

Figure 2 Foliar C3 plant $\delta^{13}C$ values as a function of species richness (S) for all species (black line) and for different species or group of species (colour lines). Rare: rare C3 species < 5 samples.