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Water storage dynamics across different types of vegetated patches in rocky highlands of central Argentina

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Abstract

Rivers originating in the granitic highlands of seasonally dry central Argentina provide water to 2 million people. These highlands comprise a complex landscape where a matrix of outcropping rock hosts vegetated patches that vary in response to long-term grazing and fire. We characterized water storage dynamics across 20 sites representing 6 vegetation-soil conditions with similar mid-upslope positions in the landscape. We measured temporal and spatial variability of water inputs (rain and fog) and water stored at the unsaturated and saturated zones. We found that rainfall was highly seasonal, but fog occurred year-round, likely representing an extra water source in areas with complex vegetation structure. Moreover, fog seems to regulate evapotranspiration/topsoil water dynamics. Water was stored in the saturated zone only during the rainy season. Piezometric response to rainfall was rapid but transient (dropping an average 15 cm/day), possibly buffering peak stormflows, reducing sediment yield, and delivering subsurface water downslope for potential storing throughout the year. Spatially, a reduction in soil depth (from 100 up to 9 cm) and vegetation structure (from woodlands to stonelands), with a degradation of topsoil conditions for infiltration were accompanied by a decline in water storage at the unsaturated (from 32% up to 14%) and saturated (from 46.3 up to 0 cm) zones. Taken together, our results support the infiltration trade-off hypothesis, which states that vegetation structure benefits fog interception, soil properties that enhance water infiltration, subsurface flow paths, and storage. Long-term disturbances have likely triggered a degradation of the hydrological function of seasonal highlands in central Argentina.

KEYWORDS

fog, infiltration trade-off hypothesis, land-cover change, saturated zone, soil depth, unsaturated zone, vegetation structure, water yield

1 | INTRODUCTION

Mountains play a fundamental role in water provisioning services to the inhabitants of the surrounding lowlands (Messerli, Viviroli, & Weingartner, 2004; Ponette-González et al., 2014; Viviroli, Dürr, Messerli, Meybeck, & Weingartner, 2007). Hence, understanding water storage dynamics in mountain environments is of paramount importance for human well-being. In this sense, water stored in the soil at the unsaturated and saturated zones depends not only on climatic variables but also on topography, soil, and vegetation features (Pan, Wang, Jia, Chen, & He, 2008; Qiu, Fu, Wang, & Chen, 2001; Tromp-van Meerveld & McDonnell, 2006). Thus, land-cover changes due to human-induced disturbances are a potential menace for water storage. However, despite the importance of water provisioning services and accelerated changes on mountain ecosystems, the consequences of anthropogenic changes in vegetation-soil conditions for ecohydrological processes had only recently been recognized (DeFries & Eshleman, 2004; Stonestrom, Scanlon, & Zhang, 2009).

Ecohydrological processes that determine water storage dynamics rely primarily on water input through precipitation, that is, rain, fog, and snow. Therefore, quantifying spatial and temporal distribution of precipitations is necessary for understanding site-specific water dynamics. A fraction of precipitation is intercepted by the canopy and immediately lost through evaporation, another is quickly lost as run-off. The remaining fraction, which infiltrates into the soil, can be either returned to the atmosphere through evapotranspiration or temporarily stored within different soil layers. Diverse factors determine this partitioning (Asbjornsen et al., 2011). It has been suggested that complex vegetation structure (i.e., with more biomass, height, and architectural complexity) favours water infiltration, percolation, storage, and slow release into streams in the dry season, the so called "infiltration trade-off hypothesis" (Bruijnzeel, 1989, 2004). The hypothesis postulates that the vegetation's positive effect over infiltration opportunities overcompensates its negative effect over losses by transpiration and interception. The rationale behind is that vegetation structural complexity decreases run-off, protects soil from aeolian and hydric erosion, and contributes to litter accumulation, thereby enhancing physical–chemical soil properties that promote infiltration and increases hydraulic conductivity (Bonell et al., 2010; Germer, Neill, Krusche, & Elsenbeer, 2010; Neary, Ice, & Jackson, 2009; Zhang, Yang, & Zepp, 2004). Moreover, the infiltration trade-off hypothesis postulates that negative effects of vegetation are particularly counterbalanced in foggy mountains by frequent fog events that lower the evaporative demand and offer an extra water input by fog drip and/or direct fog absorption through leaves (Bruijnzeel, 2002, 2004; Giambelluca, DeLay, Nullet, Scholl, & Gingerich, 2011). Supporting results for this hypothesis come from tropical ecosystems (Ghimire, Bruijnzeel, Lubczynski, & Bonell, 2014; Krishnaswamy et al., 2013; Roa-García, Brown, Schreier, & Lavkulich, 2011).

In seasonal ecosystems, soil water storage is key for maintaining various site-specific processes and, ultimately, baseflows during the dry season (Bruijnzeel, 2004). At site scale, water stored at the unsaturated zone is variable in time and space in mountains (Famiglietti, Rudnicki, & Rodell, 1998; Famiglietti, Ryu, Berg, Rodell, & Jackson, 2008; Gómez-Plaza, Alvarez-Rogel, Albaladejo, & Castillo, 2000; Gómez-Plaza, Martınez-Mena, Albaladejo, & Castillo, 2001; Penna, Brocca, Borga, & Dalla Fontana, 2013). Over time, soil humidity at the unsaturated zone tends to be lower and less stable in the dry than the humid season in different ecosystems (Gómez-Plaza et al., 2000; Zhao, Peth, Wang, Lin, & Horn, 2010). Across space, topography strongly influences soil humidity, which tends to be higher on lower topographic positions with large upslope contributing areas (Famiglietti et al., 1998; Gómez-Plaza et al., 2001; Qiu et al., 2001). Spatial variability of water content in the unsaturated zone can also be related to other topographic controls, as well as to edaphic and vegetation features such as soil texture, bulk density, organic matter, soil depth, vegetation biomass, and root channels (Jia, Shao, & Jia, 2013; Tromp-van Meerveld & McDonnell, 2006; Yen, Bond, Shenton, Spring, & Mac Nally, 2013; Zhang & Shao, 2013). Spatial controls on moisture at the unsaturated zone can change between seasons of the year (Famiglietti et al., 1998). Water that percolates to deeper soil layers and is stored at the saturated zone is fundamental for maintaining base flows (Jencso et al., 2009). Recharge of the saturated zone is influenced by hillslope topographical features and bedrock topography (Freer et al., 2002; Tromp-van Meerveld & McDonnell, 2006), besides the effects of soil and vegetation that influence percolation. Given the importance of topography for water recharge, when evaluating the effect of vegetation and soil changes on water storage dynamics at site scale, it is necessary to control for topographic variations.

Understanding the effect of anthropogenic changes in vegetation-soil properties on soil water storage dynamics in non-tropical mountains with strong rainfall seasonality is of paramount importance considering the amount of people who rely on dry season baseflows from these headwater catchments around the world. This is the case of seasonally dry highlands of central Argentina, where rivers provide water to over two million people. Here, rain inputs are constrained to the months of higher evaporative demand. Frequent fog events suggest that fog may constitute a relevant extra input of water. The vegetation-soil complex is distributed in patches within a rocky matrix. Moreover, grazing and fire disturbance shape vegetation structure and soil properties of those patches, contributing to set up a complex and contrasting landscape. These disturbances can even trigger strong erosion, transforming the vegetated patches into rocky areas with small spots of soil (Cingolani, Cabido, Renison, & Solís Neffa, 2003; Cingolani, Renison, Tecco, Gurvich, & Cabido, 2008; Cingolani et al., 2013, 2014; Renison, Hensen, Suarez, & Cingolani, 2006; Renison et al., 2010; Renison et al., 2015; Poca, Cingolani, Gurvich, Whitworth-Hulse, & Saur Palmieri, 2018). We have previously shown that as long-term grazing and fire simplified vegetation structure, soil depth, organic matter content, field capacity, and infiltration rate were reduced, whereas soil impedance and bulk density increased. This lead to lower soil water storage capacity, suggesting that water dynamics could be altered and storage could be reduced, negatively impacting on dry season baseflows (Poca et al., 2018). Furthermore, Cingolani et al. (2015) suggested that soil loss in valley bottoms may reduce streamflow in the dry season.

Therefore, in this study, we sought to characterize the effects of changes in vegetation-soil patches due to long-term grazing and fire disturbances on water storage dynamics in the highlands of central Argentina. Our specific objectives were to (a) determine temporal and spatial variability of precipitation inputs (rain and fog); (b) analyse temporal dynamics of water stored at the unsaturated and saturated zones and their relation with precipitation inputs; and (c) analyse spatial variability of water storage and determine to what extent it results from anthropogenic-induced changes in vegetation and soil properties due to the named disturbances. On the basis of the infiltration trade-off hypothesis, we expect to find higher water storage at sites with higher vegetation cover and structural complexity, as well as with soil properties that enhance infiltration opportunities.

2 | METHODS

2.1 | Study area

The present study was conducted in the highlands of the Córdoba mountains, in central Argentina. These mountains have a north–south orientation and the highest peak is the Champaquí mount at 2,789 m a.s.l. However, most of the area has an altitude that varies between 2,000 and 2,300 m a.s.l. and consists of a dissected plateau, the "Pampa de Achala," a remnant ancient crystalline peneplain. The landscape consists of hills and plains with gentle valleys. Typical soils are mollisols, derived from the weathering of granitic bedrock and aeolian deposits of fine texture (Cabido, Breimer, & Vega, 1987). Mean temperatures of the coldest and warmest month are of 5.1 °C and 11.5 °C, respectively, and there is no frost-free period (Colladon, 2004). Mean annual precipitation is 900 mm, concentrated in the warmer months, between October and April (Colladon, 2014), but the rainy season can be delayed as much as to November in extreme dry years. Potential evapotranspiration is estimated in 576 mm (Cingolani et al., 2015). Occasional winter snow events cover the soil for a few days a year. The driest months are June, July, and August.

The landscape consists of a mosaic of patches with variable vegetation structure within a matrix of granitic outcrops, including *Polylepis australis* Bitter woodlands, shrublands, tussock grasslands, grazing lawns, fernlands, and stonelands (Cingolani et al., 2003, 2008, 2013, 2014; Renison et al., 2006; Poca et al., 2018). All these vegetation types are, at least in part, the result of long-term disturbance by grazing and fire (Cingolani et al., 2003, 2008, 2013, 2014). Even though this area is characterized by relatively shallow soils (~1 m) and soil depth is naturally variable due to topography and micro roughness of the bedrock, disturbances act in synergy with these natural variations to reduce soil depth or even completely eliminate the soil profile, forming stonelands, which are clearly distinct from granitic outcrops (Cingolani et al., 2008, 2013; Poca et al., 2018). Grazing and fire also reduce soil organic matter content, field capacity, and infiltration rate, and increase soil impedance and bulk density (Poca et al., 2018). Additionally, these disturbances reduce the size and increase the mortality of *P. australis*, the main tree of the area, reducing altogether woodland cover (Cingolani et al., 2008; Giorgis, Cingolani, Teich, Renison, & Hensen, 2010; Renison et al., 2010; Teich, Cingolani, Renison, Hensen, & Giorgis, 2005), promoting their replacement by shrublands, tall tussock, and lawn patches, as well as stonelands. Lastly, in places with very strong disturbance pressure, woodland cover is restricted to small patches in deep ravines where trees are protected from fire and grazing, and stonelands with lawn patches dominate the landscape, together with patches of degraded tussock grasslands with isolated trees (Cingolani et al., 2003, 2008, 2013; Renison et al., 2006). In places that have been exposed to strong disturbance in the past but in which grazing and fire practices have been recently excluded, woodlands are slowly recovering (Giorgis et al., 2010; Teich et al., 2005). Therefore, at present, under livestock exclusion is easy to find a gradient from woodlands to shrublands dominated by *P. australis* or other woody species, closed tussock grasslands and fernlands. In 1997, part of this area was declared a national park (Quebrada del Condorito National Park). In some zones of the national park, grazing was excluded to prevent further erosion and allow the vegetation-soil complex to recover (APN, 2007).

In this study, we selected a 35-ha area, in a landscape dominated by hills at 2,000 m a.s.l. with a central point at 31°37′S, 64°45′W (Figure 1). We established 20 sites, 10 × 10 m each, taking into account the variability in vegetation structure. Sites were established in *P. australis* woodlands, shrublands, tussock grasslands, grazing lawns, fernlands, and stonelands. We focused on zones within the park without livestock and fire for at least 20 years and outside the park in two paddocks with current grazing practices. Within every site or very close (less than 10 m away), at least one *P. australis* individual was present. To control topography, the 20 sites were selected on moderate slopes, with south, southeast, and southwest aspect and relatively high topographic positions in the landscape (mid-upslope). In a previous study, we showed that for these sites, topographic features were not related with vegetation and soil properties (Poca et al., 2018). Therefore, we assumed that differences in soil and vegetation across our 20 sites were mostly caused by disturbance.

2.2 | Vegetation and soil

We characterized soil and vegetation at the 20 sites using a set of representative variables based in Poca et al. (2018). As vegetation variables, we considered a vegetation structure index calculated from the cover (%) and the modal height (cm) of each of all plant growth forms (trees, shrubs, thin and thick tussocks, graminoids, forbs, ferns, cacti, lichens, and mosses). This index varied from 1.14 to 204.01; the lowest values corresponded to stonelands with low plant cover and height, whereas the highest values were attained by woodlands with a more complex vegetation structure, where trees attained a maximum of 85% cover and 450-cm height. We also considered site leaf area index (LAI, LAI 2000 Li-Cor that varied from 0.27 to 3.06), and root density until 15-cm depth (from 0.001 and 0.03 g/cm^3). To characterize superficial soil properties (0–15 cm) we used: soil impedance (0.6 to 3.72 kg/cm^2), bulk density (from 0.28 to 1.55 g/cm^3), organic matter content (from 5.4 to 13.3 %), sand (from 67.6 to 82%), silt (from 12.6 to 23.6%), and field capacity (15.7 to 39.1%). We also used infiltration rate (from 7.06 to 1042.3 cm/h) and soil depth (measured randomly from 7 to 10 times per site, varied in average from 9.6 to 100 cm). All soil-related measurements in stonelands were performed on the remaining soil spots of those sites. For further details about the variables and how they were estimated, see Poca et al. (2018).

2.3 | Precipitations (rain and fog)

We measured rainfall (or vertical precipitation) using rain gauges, and fog (or horizontal precipitation) using passive fog gauges. Fog gauges were distributed at six sites in each of the vegetation structure types to evaluate spatial variation. Rain gauges were placed at the same sites as fog gauges. At sites dominated by trees, rain gauges were placed in small open areas nearby, no further than 3 m from a vertex of the site. Daily rainfall data (mm) was measured using an automatic meteorological station Watchdog 2000®. The station was placed at 5 km from the mid-equidistant point of all sites, and it registered accumulated rain for every half an hour with a precision of 0.1 mm.

Fog gauges had a metallic structure holding a 0.50 × 1-m screen with a double propylene mesh (raschel type at 60%), placed 50-cm above ground (slightly modified from the "standard fog gauges" described by Schemenauer & Cereceda, 1994, see Figure 1d). The propylene mesh thread was 1-mm wide, entangled in a triangular pattern. The weave achieved was of 0.7 cm. Fog collectors had a gable roof of

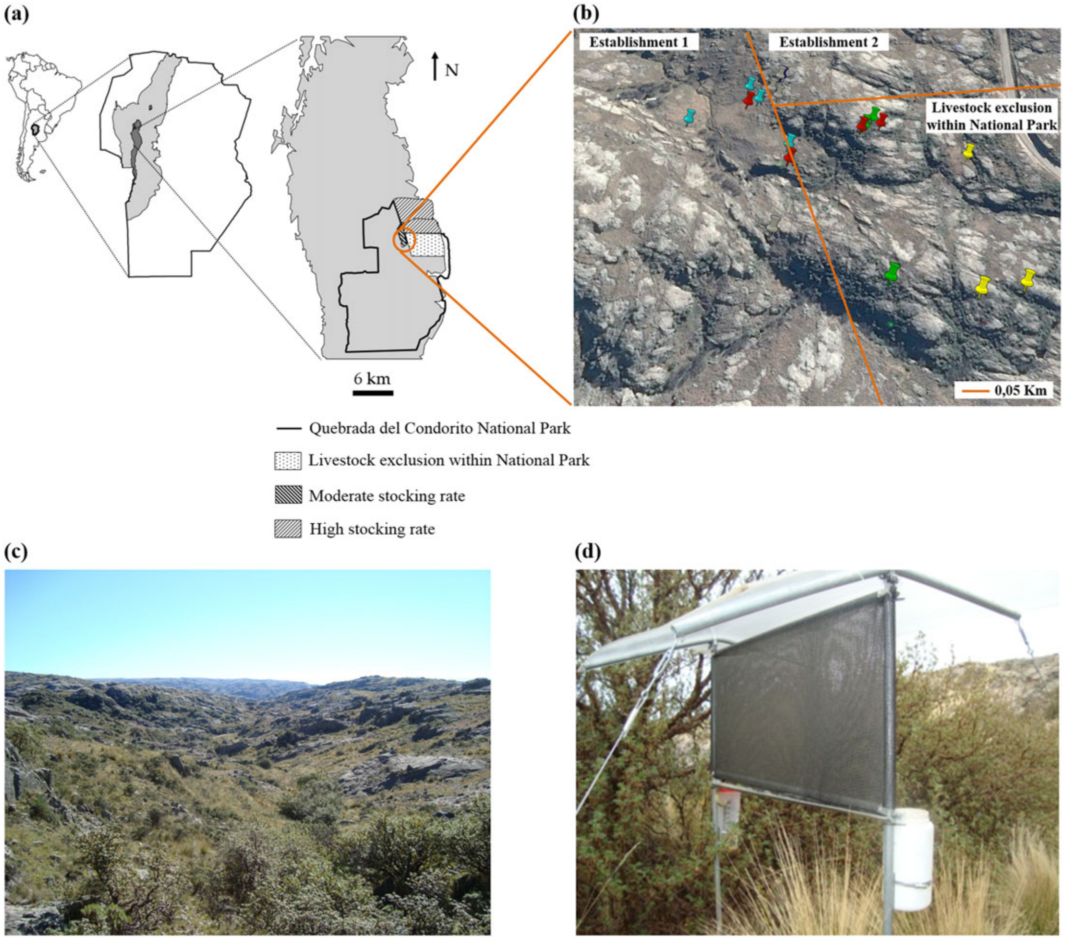

FIGURE 1 (a) Geographical position of the study area in Córdoba mountains, central Argentina; (b) Location of the 20 sites in Google Earth® in a 35-ha area, lines in orange divide paddocks with different management, pins with different colours show physiognomic types in which sites where visually classified: green for woodland; blue for shrubland; red for tussock grassland; light blue for lawn; yellow for fernland; grey for stoneland; (c) Landscape photograph of the study area; and (d) a passive fog gauge installed at the study site

alveolar polycarbonate (6-mm width) that covered 98 × 160-cm round to prevent the entrance of rain water. The screen with the mesh had a channel that collected fog water intercepted by the mesh and conducted it to a closed collecting recipient to prevent evaporation. Next to the fog collecting recipient, the structure also had a recipient located beside the screen and not connected to the channel that collected fog, for controlling the possible entrance of rain water with a smaller angle than 90° into the mesh. All six fog gauges were installed perpendicular to the slope of the sites with predominantly south orientation and were exposed to the prevailing winds of the region (north–south, Cabido et al., 1987). Fog gauges were installed within the vegetation patches. As a result, fog gauges were in some cases immersed or underneath the vegetation canopy. Mean height values of the main plant growth form in each of the sites with different physiognomy where gauges installed were 350, 200, 70, 15, 10, and 10 cm for the woodland, shrubland, tussock grassland, fernland, lawn, and stoneland, respectively.

The hydrological year extended from August 28, 2012, to September 6, 2013. On August 28, all rain and fog gauges were installed and containers for both types of collectors were filled with at least 1-cm layer of vegetal oil to prevent evaporation (Scholl, Eugster, & Burkard, 2011). Rain and fog were measured every 15 days from September 11, 2012, to September 6, 2013, and a new layer of vegetal oil was added after every measurement. Given the absence of rain during winter (mainly June and July), during this period, gauges were visited monthly. There was a total of 23 observation dates for precipitation input.

2.4 | Water storage at the unsaturated zone

Every 15 days during the hydrologic year, we estimated the water storage of the unsaturated zone through the volumetric water content (%) of the first 7.6 cm of soil at each of the 20 sites using time domain reflectometry (TDR; Moisture Probe Meter®). At each site and for each measuring date, we conducted 15 random measurements and averaged them to obtain one value per site per date. Due to logistical issues, we were not able to collect data for all sites on October 30, 2012, and therefore, we discarded this observation date. In total, we obtained 22 observation dates of water storage at the unsaturated zone along the hydrologic year.

2.5 | Water storage at the saturated zone

Every 15 days, we measured water stored at the saturated zone at each of the 20 sites using piezometers. These consisted of 10-cm diameter PVC tubes with a length equivalent to the average soil depth of each site, installed where this depth was found. At the distal part of the piezometer, we drilled six lateral slots that allowed free water to enter into the tube. The superior (opposite) part of the tube that was in contact with the surface air was covered to prevent rain falling directly into the tube. Piezometers were visited every 15 days to measure saturated water thickness (cm) from the base to the top, which resulted in a total of 22 measurements along the year. Given that we detected saturated water during the rainy season only (see results), we performed a total of 12 extra measurements during that season. For this, we visited all piezometers after five rain events until they ran out of free water or a new rainfall event occurred. This expanded our data set to 34 measurements.

2.6 | Statistical analyses

2.6.1 | Spatial variations and temporal dynamics of precipitations (rain and fog)

The volume of rain (ml) captured by rain gauges was transformed to water surface (mm) by considering the diameter of the recipient. However, the volume of fog captured by fog gauges was not transformed because the relationship between the area of the mesh and vegetation surface is not straightforward. It is difficult to determine how many meshes are equivalent to the vegetation per unit area in the terrain able to capture fog (Bruijnzeel, 2002; DeLay & Giambelluca, 2010). Consequently, the passive fog gauges offer useful information for approximate estimation of potential fog interception and examination of temporal and spatial variability, without rigorously focusing on the absolute values.

To meet our first objective, temporal and spatial variability of rain and fog was analysed using a two-way analysis of variance (period and site). Given that the raw data did not meet the assumptions of normality and homogeneity of variance, we added one to all values and log transformed the data. Given temporal variability was significant for both types of precipitation (see results), we analysed if they co-varied through time. This was achieved by calculating, both for rain and for fog, one value per period as the average of all gauges and then correlating both sets of values through Pearson (n = 23 periods). Likewise, we analysed if both variables were correlated to the control recipient of the fog gauges, also by averaging sites per period.

Given that fog exhibited spatial as well as temporal variation (see results), we examined the association of this variation with vegetation features. We calculated the total annual fog captured by each fog gauge and performed Pearson correlations (n = 6) between these values and vegetation-related variables at the sites where gauges were installed.

2.6.2 | Temporal dynamics of water storage at the unsaturated and saturated zones

To meet our second objective, we performed a temporal analysis considering each date as a case (n = 22), so for each date, we calculated the across-site average of (a) volumetric water content at the unsaturated zone (%) and (b) water thickness at the saturated zone (cm). Additionally, we calculated (c) the proportion of sites with presence of water at the saturated zone for each date (%). We correlated the three across-site descriptive variables (volumetric water content at the unsaturated zone, water thickness at the saturated zone, and the proportion of sites with presence of water at the saturated zone for each date) among them, as well as with the temporal variability of rain and fog (averages for each observation date or period of the variables; n = 22), through Pearson correlations. To account for the cumulative effect of precipitations, we performed correlations considering different temporal frames of precipitations (15 days, 30 days, etc.).

For descriptive purposes only, we further calculated the across-site annual (i.e., averaging all dates, n = 22) and seasonal averages of the same three variables of water stored at the unsaturated and saturated zones. The dry season spanned from May 1 to September 30 (n = 10), whereas the wet season was from October 1 to April 30 (n = 12). The criterion for this separation between wet and dry months was based on historical data of precipitation for the study area by Colladon (2014). We also calculated the coefficient of variability for each season.

2.6.3 | Spatial variations of water storage at the unsaturated and saturated zones

For the spatial analysis, we considered each site as a case (n = 20). We calculated (a) annual, (b) wet season, and (c) dry season per site averages of the volumetric water content at the unsaturated zone (%). Also, we calculated the (d) annual per site average of water thickness at the saturated zone (cm) and (e) the proportion of dates each site presented water at the saturated zone (%) throughout the year. We did not consider seasonal averages for water storage at the saturated zone-related variables because none of the piezometers showed water during the dry period (see results). Instead, we calculated a relative index of these two variables using only the observation dates in which at least one piezometer contained water, considering as well the extra measurements to the bi-weekly ones; hereafter named as (f) water thickness at the saturated zone index (cm) and (g) water prevalence at the saturated zone index (%). Indexes do not represent, in absolute terms, site's real averages of water thickness or proportion of dates they presented water. However, they are good relative indicators of the water content at the saturated zone of the sites during the rainy season. We performed pair-wise Pearson correlations across space between the seven mentioned water storage variables to check their degree of relation and better approach the following objective.

To meet our third objective, we run forward regression models for each of all seven unsaturated and saturated water-related variables as dependent variables. As independent variables, we used the following 11 vegetation and soil features: vegetation structure index, leaf area index, root density, soil impedance, bulk density, organic matter content, sand and silt content, and field capacity, as well as infiltration rate and soil depth. With these analyses, we intended to identify if changes in soil and vegetation due to disturbances were traduced into changes on water stored at the unsaturated and saturated zones.

For all statistical analysis, we used InfoStat version 2013 (Di Rienzo, Casanoves, Balzarini, González, & Tablada, 2013). Significance was set at $p < .05$.

3 | RESULTS

3.1 | Spatial variation and temporal dynamics of precipitations (rain and fog)

Rain did not differ among the six rain gauges ($F = 0.82$, $p = .53$), giving a total accumulated average of 661 ± 52 mm of rain (min = 590 mm, max = 727 mm). As expected, rain varied temporally ($F = 101.4$, $p < .001$; Figure 3a), with more than 90% of total rainfall concentrated between September and March. December was the rainiest month with a total of 138 mm on average for the six rain gauges. The longest period without rain was from May 24 to August 1, 2013. We also registered a shorter rainless period between August 19 and September 6, 2013 (Figure 2a).

Captured fog (ml) varied temporally ($F = 10.3$, $p < .001$; Figure 2b) and spatially ($F = 10.4$, $p < .001$; Figure 3a). The highest amount of fog captured was registered between November 27 and December 11, whereas the periods that none of the six fog gauges registered fog were short and during different times of the year (Figure 2b). The amount of fog captured varied significantly among fog gauges. The fog gauge in the shrubland presented the lowest value (a total of 2,140 ml/year) compared with the one in the stoneland (a total of 18,365 ml/year). Fog captured by the gauge disposed in the shrubland presented low values almost year-round (Figure 3b). When fog was registered, this was always higher in the stoneland, and when fog was not captured by the gauge in the stoneland, it was not captured in the shrubland. It is worth noting that the fog gauge in the woodland had similar values to the one in the shrubland (Figure 3a). Moreover, we found a negative association between captured fog and vegetation

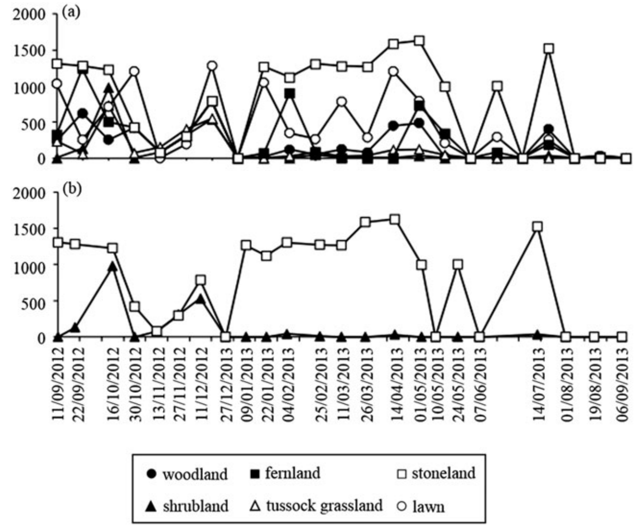

FIGURE 3 Fog (ml) intercepted along the year by the fog gauges installed in (a) all six sites with different physiognomy and (b) shrubland and stoneland. In all cases, symbols indicate fog gauges installed in sites of different physiognomy

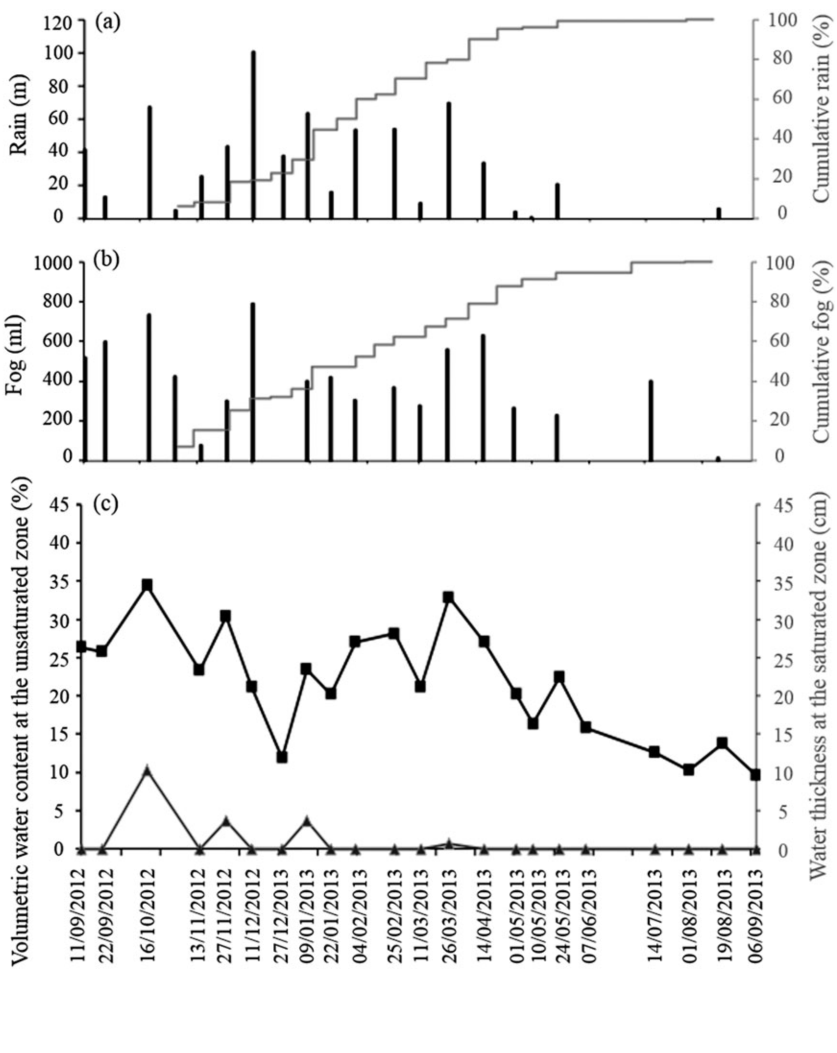

FIGURE 2 Across-site average temporal dynamics of (a) rain (mm), (b) fog (ml), (c) volumetric water content at the unsaturated zone (%, in black squares), and water thickness at the saturated zone (cm, in grey triangles). $n = 6$ for rain and fog, and $n = 20$ for water stored at the saturated and unsaturated zones

structure index; sites with more structured vegetation captured less fog along the year than the ones in less structured vegetation (r = −.90, p < .01, n = 6). We corroborated that topographical variables of the sites were not associated to fog interception (data not shown).

Both types of precipitations were positively and significantly correlated through time (r = .64, p < .001, n = 23). However, fog was intercepted even during the dry season, when no rainfall was registered (Figure 2a and 2b). The rain control recipient in fog gauges registered a total of 75 mm throughout the hydrological year in average for the six sites. It did not correlate with the average per date fog (r = .39, p = .07, n = 23), though it did correlate with rain (r = .73, p < .001, n = 23).

3.2 | Temporal dynamics of water storage at the unsaturated and saturated zones

Volumetric water content at the unsaturated zone, as a proxy of water storage, varied in averages across sites between 10% (on September 6) and 34% (on October 16). Year-round average was 22%, whereas for the dry and wet season, averages were 17% and 25%, respectively (Figure 2c). Furthermore, it was more variable in the dry (CV = 35.2) than in the wet season (CV = 24.8).

Across sites, water storage at the unsaturated zone followed the trend of precipitations 15 days prior the measurement of soil water content (r = .65, p < .001 for rain and r = .70, p < .001 for fog, n = 22). When considering the accumulated precipitation of the previous 30 days, correlation coefficients and the level of significance diminished (r = .48, p < .05 for rain and r = .61, p < .01 for fog, n = 22). With longer periods, these parameters were progressively weaker (data not shown). The last rainfall event bigger than 1 mm registered by the weather station was of 4.8 mm on May 18; since then, volumetric water content showed an abrupt drop. A decline can even be perceived since the end of March, moment in which rain events were less frequent and abundant (see Figure 2).

Water thickness at the saturated zone average across sites varied between 0 cm at various dates and 10.3 cm at October 16. Accordingly, the proportion of sites with presence of water at the saturated zone varied between 0% and 30%. Year-round averages for water thickness and proportion of sites with presence of water were 0.8 cm and 3%, respectively. Water storage at the saturated zone occurred only during the wet season, with an average for this period of 1.5 cm in a 6% of the sites. However, saturated water thickness was still extremely variable for this period (CV = 202), as well as the proportion of sites that exhibited water in the piezometers (CV = 175).

Temporal variation of water thickness at the saturated zone followed rain trend (Figure 2). Since March 26, no water was found in any piezometer, even though it rained until May 18 according to the meteorological station. In line with these results, across site averages of water thickness correlated positively, though marginally significantly, with rain 15 days prior to the measurement date (r = .41, p = .06). This correlation was not significant with fog 15 days prior to the observation date (r = .37; p = .09), neither when considering a longer period (30 days) of both types of precipitation (r = .18, p = .42 for rain; r = .27, p = .22 for fog). The proportion of sites with water at the saturated zone was significantly correlated to rain when considering 15 days prior the observation date precipitation, (r = .44, p < .05) but was not related to fog (r = .35, p = .11). These correlations were not significant when considering both types of precipitation 30 days before the observation dates (r = .20, p = .38 for rain and r = .19, p = .40 for fog). By considering longer periods, the degree of association with precipitations decreased even more for both saturated water-related variables (data not shown).

As volumetric water content at the unsaturated zone increased, so did water thickness at the saturated zone (r = .50, p < .05, n = 22), and the proportion of sites that exhibited water in their piezometers (r = .54, p < .01, n = 22) during the hydrological year. Both variables related to water storage at the saturated zone were tightly correlated among themselves (r = .97, p < .001, n = 22).

Following five rain events, we observed that in general, as the rain event was smaller and as days passed by, both the average water thickness and the proportion of sites with water at the saturated zone diminished following the same trend (Figure 4). As rainfall events were larger, the proportion of sites that exhibited water in piezometers on the first day after the rain event was higher (80% after a rain event of almost 80 mm and 60% after a rain event of 29.2 mm, compared with 5% after a rain event of 8 mm). The same trend stands for how long water lasted in the piezometers. The event of 32 mm seems to be the exception because it showed zero piezometric response. However, it is worth noting that during the month before that particular rain event, there were unusually only 30 mm of accumulated rain. Actually, another very similar event of 29.2 mm did show piezometric

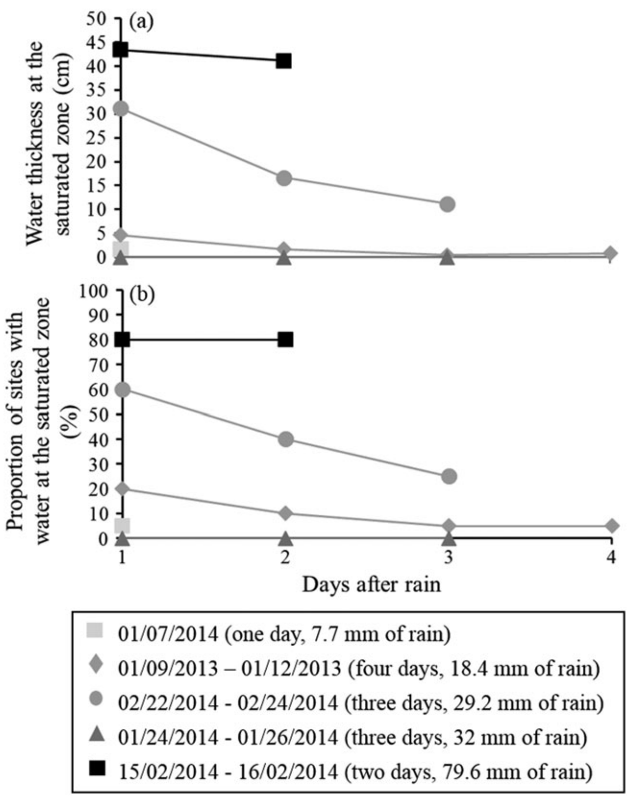

FIGURE 4 Water storage dynamics at the saturated zone after five rain events of different magnitudes: (a) water thickness at the saturated zone (average for the 20 sites) and (b) proportion of sites with water stored at the saturate zone. Different symbols indicate the different rain events, and colours represent their magnitude in crescent order from light grey to black

response in 60% of the sites on the day after the rain event (Figure 4). For all piezometers that showed response to these rain events, water thickness at the saturated zone drop was, in average, of 15 cm/day.

3.3 | Spatial variations of water storage at the unsaturated and saturated zones

Annual average of the volumetric water content at the unsaturated zone varied between sites from 14% in a stoneland to 32% in a fernland, whereas for the wet period was 16% in a lawn and 36% in a tussock grassland and for the dry period 9% in a stoneland and 28% in a tussock grassland. Water thickness at the saturated zone and the proportion of dates each site presented water at the saturated zone varied from 0 cm and 0% in several sites with different physiognomies to 5.2 cm and 18% in a fernland, respectively. The indexes of water stored at the saturated zone, that is, average water stored during days where at least one piezometer presented saturated water, varied from 0 cm and 0% in several sites with different physiognomies to 46.3 cm and 79% in a fernland for the thickness and the proportion of dates with water at the saturated zone, respectively.

Indexes for water at the saturated zone had better distributions than annual-basis ones, and both ways of calculating variables were tightly correlated (r = .58, p < .01, n = 20 for water thickness; r = .75, p < .001, n = 20 for the prevalence of/or proportion of dates with water); also, regression models were very similar (data not shown). Thus, from here forward, we present results for the index-basis ones only for the following analyses. Both indexes of water stored at the saturated zone were strongly associated (r = .88, p < .001, n = 20). Annual average of volumetric water content at the unsaturated zone was positively correlated with water thickness (r = .57, p < .01, n = 20) and the proportion of dates that sites presented water at the saturated zone (r = .61, p < .01, n = 20).

All significant regression models for annual volumetric water content at the unsaturated zone, water thickness at the saturated zone index, and water prevalence index at the saturated zone retained only one independent variable and are shown in Table 1. The same was the case for wet and dry season volumetric water content at the unsaturated zone, and models are shown in Table 2. Water storage at the unsaturated zone increased at sites with deeper soils (Table 1a, Figure 5). It was also higher in sites with higher LAI, vegetation structure index, organic matter content, and field capacity, as well as lower soil impedance and bulk density (Table 1a). Sites with higher infiltration rate showed a trend of having higher superficial soil moisture as well (R^2 = .15; p = .09, n = 20). When considering wet and dry season superficial soil water separately, the models were practically the same as for the annual average (Table 2).

Water thickness at the saturated zone index was higher in sites with deeper soils (Figure 5). This was also the case in sites with higher LAI, organic matter content, and field capacity, as well as when soil impedance and bulk density were lower (Table 1b). A higher infiltration rate marginally increased water thickness index (R^2 = .18; p = .06, n = 20). Water prevalence at the saturated zone index was higher in sites with higher field capacity (Figure 6). Sites that presented more days with water at the saturated zone also had deeper soils and higher organic matter content, as well as lower soil

TABLE 1 All significant regression models for each of the three dependent variables[a]

	R^2	p value
(a) Annual volumetric water content at the unsaturated zone		
15.2 + 0.1 (soil depth)	.65	<.001
27.6–4.0 (soil impedance)	.49	<.001
16.2 + 3.6 (LAI)	.41	<.01
10.3 + 0.5 (field capacity)	.38	<.01
29.2–7.9 (soil bulk density)	.37	<.01
19.3 + 0.03 (vegetation structure index)	.28	<.05
12.4 + 0.9 (organic matter)	.24	<.05
(b) Water thickness at the saturated zone index		
−3.8 + 0.3 (soil depth)	.53	<.001
−20.3 + 1.3 (field capacity)	.39	<.01
−19.8 + 3.4 (organic matter)	.36	<.01
33.9–21.9 (soil bulk density)	.33	<.01
27.0–9.5 (soil impedance)	.32	<.01
1.8 + 7.4 (LAI)	.20	<.05
(c) Water prevalence at the saturated zone index		
−22.9 + 2.1 (field capacity)	.38	<.01
7.0 + 0.4 (soil depth)	.37	<.01
50.3–14.1 (soil impedance)	.28	<.05
59.5–31.5 (soil bulk density)	.27	<.05
−9.7 + 4.0 (organic matter)	.20	<.05

Note. LAI = leaf area index.

[a]In all cases, we used 11 independent variables related to vegetation and soil features with a forward procedure. For each model, n = 20 sites, and the equation R^2 and p value are shown.

TABLE 2 All significant regression models for (a) wet and (b) dry season volumetric water content at the unsaturated zone[a]

	R^2	p value
(a) Volumetric water content at the unsaturated zone wet season		
19.3 + 0.1 (soil depth)	.55	<.001
31.0–3.9 (soil impedance)	.47	<.001
19.9 + 3.5 (LAI)	.39	<.01
22.7 + 0.03 (vegetation structure index)	.32	<.01
15.2 + 0.4 (field capacity)	.30	<.01
31.6–6.7 (soil bulk density)	.27	<.05
16.9 + 0.8 (organic matter)	.24	<.05
(b) Volumetric water content at the unsaturated zone dry season		
10.3 + 0.1 (soil depth)	.55	<.001
23.5–4.2 (soil impedance)	.48	<.001
26.3–9.4 (soil bulk density)	.47	<.001
4.5 + 0.5 (field capacity)	.46	<.01
11.7 + 3.7 (LAI)	.40	<.01
7.1 + 1.06 (organic matter)	.27	<.05
15.2 + 0.03 (vegetation structure index)	.22	<.05

Note. LAI = leaf area index.

[a]In all cases, we used 11 independent variables related to vegetation and soil features with a forward procedure. For each model, n = 20 sites, and the equation R^2 and p value are shown.

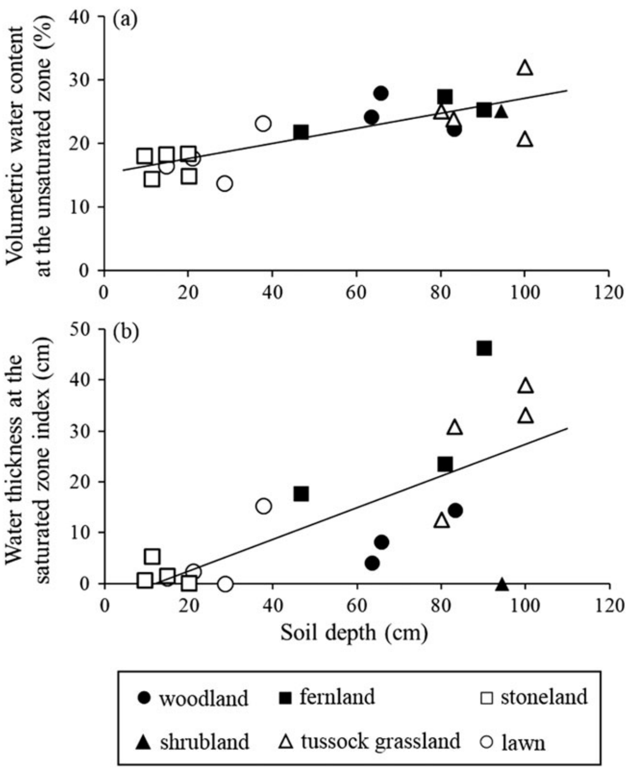

FIGURE 5 (a) Annual average volumetric water content at the unsaturated zone (%) and (b) water thickness at the saturated zone index (cm), as a function of soil depth for the 20 sites. Symbols indicate the physiognomy of the sites. The corresponding models are reported in Table 1a and 1b, respectively

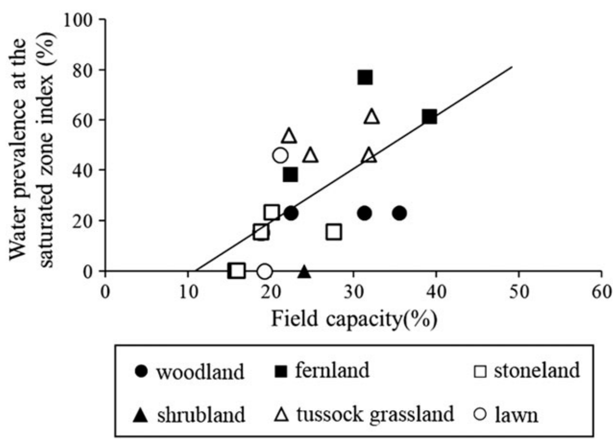

FIGURE 6 Water prevalence at the saturated zone index as a function of field capacity. Symbols indicate the physiognomy of the 20 sites. The corresponding model is reported in Table 1c

impedance and bulk density (Table 1c). Sites with higher LAI presented a tendency of showing more proportion of days with water at the saturated zone (R^2 = .16; p = .08, n = 20).

4 | DISCUSSION

4.1 | Water inputs

Through the use of passive fog gauges, we were able to quantify fog presence throughout the year for the first time for the highlands of central Argentina. Fog and rain were correlated, suggesting that either rain and fog co-occurred or precipitation input was mixed, occurring in form of drizzle (Frumau et al., 2011; Schemenauer & Cereceda, 1992). Fog input is spread-out through the year and not constrained to the wet season only, in comparison with rainfall. Most important, fog is the only water source available during the dry season, when water stress reaches its maximum. A total of approximately 2,000 ml of fog was intercepted, in average between the six fog gauges, during the dry season, which corresponds to 27% of year-round fog. This interception occurred during 26% of the observation periods, when no or little rainfall was registered.

The amount of intercepted fog by gauges differed among sites, in spite of the identical design and similar topographical features of the sites. The fog gauge in the stoneland, followed by the one in the lawn and the fernland, intercepted the highest amount of fog, whereas the shrubland and woodland gauges intercepted the least fog. Moreover, vegetation structure was negatively correlated to total fog intercepted by the gauges. Our interpretation of these results is that fog gauges are intercepting what the immediate surrounding vegetation is not. In stonelands/lawns, vegetation is absent or very short, then fog is being captured by the gauge given there is no vegetation surrounding it; but in shrublands/woodlands, fog would be colliding first into the surrounding vegetation before colliding with the mesh of the gauge. We infer then that fog captured by the gauges is an inverse indicator of the fog captured by the surrounding vegetation. Fog, because it moves horizontally, needs a vertical impact surface such as vegetation for being intercepted (Frumau et al., 2011; Schemenauer & Cereceda, 1992). Different studies show that as vegetation structure is more complex, in terms of height, architecture, and foliar area, the more it promotes fog drip into the soil (Ingwersen 1985; Ewing et al., 2009; del-Val et al., 2006; Ponette-González, Weathers, & Curran, 2010). It has even been suggested that a simplification of vegetation structure and a reduction of vegetation cover may reduce fog interception decreasing net precipitation (Gomez-Peralta, Oberbauer, McClain, & Philippi, 2008; Ponette-González et al., 2010). Thus, changes in vegetation structure associated to grazing and fire disturbances described for our study area (Poca et al., 2018) could be promoting a lesser interception of fog with consequences for the water balance.

Although passive fog gauges do not realistically represent the natural canopy structure (DeLay & Giambelluca, 2010), we can carefully speculate on the magnitude of the annual contribution of fog in different physiognomies by making simple assumptions on the relation of fog gauges and vegetation. If we suppose that a tree in the terrain is equivalent to a fog gauge with a mesh of similar height and width and that there is less than a small tree every 100 m^2 in stonelands (personal observation), fog input would be less than 1 mm per year. On the contrary, if we suppose there is a tree of 4-m height and 4 m of canopy maximum width every 5 m^2 of terrain (Enrico, Funes, & Cabido, 2004, Giorgis et al., unpublished data; woodlands of our study were somewhat shorter in average, but individual trees were up to 4.5-m height; we are making an estimation considering more developed woodlands as those reported by Enrico et al., 2004), each tree would be equivalent to 32 (4 × 8) fog gauges. Thus, in woodland borders (i.e., using the capture values of isolated fog gauges) would intercept 118 mm of fog per year. Lastly, within woodlands, 28 mm/year of fog would be intercepted (using the capture values of fog gauges within woodlands). In other words, and regardless the absolute values, fog interception estimations vary considerably depending on how isolated trees and woodland patches are distributed on the landscape and on the border/surface ratio. Thus, disturbances at our study sites have the potential of reducing fog water inputs through the reduction of woodlands cover.

4.2 | Water storage dynamics through the year

Temporal patterns of water storage at the unsaturated and saturated zones varied considerably throughout the year associated to precipitation. In the case of the unsaturated zone, the temporal pattern of volumetric water content through the year was strongly associated to both types of precipitation. However, the association was tighter with fog compared with rain of 15 and 30 days prior to the field measurement of soil moisture, suggesting fog relevance on regulating topsoil water dynamics. The hydrological significance of fog occurrence throughout the year might be by reducing, or even suppressing in certain occasions, direct soil evaporation or even plant transpiration. Transpiration suppression due to cloud immersion has already been shown for tropical environments (Alvarado-Barrientos, Holwerda, Asbjornsen, Dawson, & Bruijnzeel, 2014; Oliveira, Eller, Bittencourt, & Mulligan, 2014). For our subtropical seasonally dry ecosystem, this may have even bigger implications given the atmospheric demand is higher and through longer periods.

A strong relation between rain and superficial water content has been reported mainly for arid systems (Pan et al., 2008); strong seasonality would be triggering the association of these variables on our sub humid system. When considering wet and dry seasons separately, water stored at the unsaturated zone on the dry season was more variable than on the wet one. This is coincident with studies in other seasonal ecosystems (Gómez-Plaza et al., 2000; Zhao et al., 2010). The mentioned studies suggest that fluctuations on the dry season are produced by losses through plant transpiration that exceed inputs of precipitation during this period. However, as we have discussed before, we expect relatively low evapotranspiration during in this time of the year compared with spring–summer (wet season). Moreover, some of the dominant species of the area lose a great quantity of leaves due to frequent frosts during the dry season, whereas others diminish their activity (Cingolani et al., 2008; Giorgis et al., 2010). Then the variation on water storage at the unsaturated zone in the dry season may be driven by fog pulses during this time of the year, rather than by vegetation consumption.

Water storage at the saturated zone was markedly seasonal, given none of the piezometers contained water during the dry period. By following specific rain events until it rained again, we were able to verify how rapid piezometric response to rain events is, how sensitive it is to rainfall magnitude, and how transient water storage at the saturated zone is in our mid-upslope study sites in the highlands of central Argentina (see Figure 4). When piezometers showed a response to rain events, this was always on the immediate following day. The proportion of sites with water at piezometers and the thickness of water stored there declined as days progressed because it rained no matter how copious rainfall was, lasting for only few days after each rain event. However, as the rain event was bigger, saturated water thickness and the proportion of sites with saturated water were higher and sustained for more days. Our results are coincident with results from the Italian Alps for similar precipitation ranges (Penna et al., 2013). They also agree with results from Krishnaswamy et al. (2013), who reported strong seasonality and rapid piezometric response after rain events for seasonal tropical mountains of India.

The transient nature of water at the saturated zone in our study sites in this headwater catchment suggests that vegetated patches at this topographic position may be able to buffer peak stormflows, rather than sustain baseflows. Our study sites were located at mid-up slope positions in the landscape. Discharge of piezometers at our sites few days after it rained indicates downslope subsurface water transport, rather than vegetation uptake given the magnitude of discharge rates. Saturated water thickness drops of piezometers following rain events analysed in Figure 4 was on average of 15 cm/day, ranging from 0.5 to 65 cm/day between piezometers for the first 48 hr after the rainfall events and considering only those piezometers that experienced recharge. These patterns are confirming a substantial water yield buffering by the studied patches because the magnitude of most of the observed saturated water thickness drops cannot be explained by local evapotranspiration but by lateral discharge. A reasonable maximum saturated water thickness drop caused by evapotranspiration would be in the order of 2.5 cm/day, assuming a high-end evapotranspiration rate of 5 mm/day and a low-end specific yield of 0.2 mm/mm. Discharge rates exceeded this hypothetical threshold in 87% of the studied situations. Then mid-upslope vegetated patches would be effective in capturing and delivering subsurface water to downslope positions with delay regarding run-off but fast enough to avoid evapotranspiration loses. This subsurface water probably contributes to valley bottom water storage and slow release into streams during the dry season. These results support the findings from Cingolani et al. (2015) in our study area, where they showed that dry season water discharge was higher in catchments with rugged landscapes and high proportion of deep valleys, with presumably deep soils. Longitudinal studies on hydrological connectivity at hillslope scale and streamflow generation are needed for further understanding on the whole-catchment water transport patterns (Jencso et al., 2009). Controls of patch storage and release are evaluated through the spatial analysis of saturated water of different vegetated patches across the landscape.

4.3 | Water storage variations across different vegetated patches

Water storage at the unsaturated and saturated zones were determined by the spatial variation of practically the same vegetation and soil features. In general terms, and in decrescent order of importance, water stored in the soil profile increased as soils were deeper, vegetation structure more complex (higher vegetation structure index and LAI), and as it prevailed topsoil properties that enhanced infiltration opportunities (higher organic matter content and field capacity and lower soil bulk density and impedance). Contrastingly to other studies within a wide range of ecosystems (tropical: Roa-García et al., 2011; humid–subtropical: Famiglietti et al., 1998; and semiarid: Qiu, Fu, Wang, & Chen, 2003, Jia et al., 2013), we found that controls of water stored at the unsaturated zone across space did not change between seasons for our study area. Furthermore, sites with higher water stored at the unsaturated zone also exhibited higher water stored at the saturated zone, suggesting a high hydraulic conductivity (however, note the different ways of measuring both variables).

Spatial variation of soil depth was key for controlling water storage at both the unsaturated and saturated zones. On the one hand, the influence of soil depth on superficial soil moisture can be explained by the increased soil moisture stability that is expected as the soil profile is deeper (Jia et al., 2013). On the other hand, it is not surprising that saturated water thickness was strongly determined by soil depth, considering it determines the maximum quantity of water that can be stored in optimal infiltration conditions. Vegetation structure, LAI, and topsoil properties that enhance infiltration opportunities were the other features that also determined water storage. It has been indicated that as vegetation structure is more complex, the better it buffers the impact of rain on the soil, avoiding the damage it may cause on topsoil structure (Neary et al., 2009; Potts, Scott, Bayram, & Carbonara, 2010) and reducing soil moisture fluctuations due to an amelioration of microclimatic conditions (Asbjornsen, Ashton, Vogt, & Palacios, 2004; Breashears, Rich, Barnes, & Campbell, 1997). Higher vegetation biomass is also expected to release a great quantity of litter that imply high organic matter inputs to the soil, promoting soil biota activity. Thereby, soil impedance and bulk density would be low and soil structure favoured, deriving in well-drained soils with great holding capacity (Bonell et al., 2010; Germer et al., 2010; Neary et al., 2009), promoting root proliferation and soil aeration, altogether increasing water infiltration opportunities (Throop, Archer, Monger, & Waltman, 2012).

Several works have shown that livestock browsing and trampling and fire occurrences lead to a simplification of canopy structure and a diminution of vegetation cover, contributing less organic matter into the soil, destroying topsoil structure, and augmenting soil bulk density and impedance (Altesor et al., 2006; Boone Kauffman, Thorpe, & Brookshire, 2004; Yong-Zhong, Yu-Lin, Jian-Yuan, & Wen-Zhi, 2005). Furthermore, these disturbances trigger soil erosion and consequent loss of profile depth (Pimentel & Kounang, 1998; Renison et al., 2010). Direct link between grazing and fire and vegetation and soil changes has been evidenced for the highlands of central Argentina as described before (Cingolani et al., 2003, 2008, 2013, 2014; Teich et al., 2005; Renison et al., 2006, 2010, 2015; Giorgis et al., 2010). Most important, woodland cover is reduced and replaced by different vegetated patches with a simplified structure such as grazing lawns and stonelands, exposing soil to erosive processes (Cingolani et al., 2014). Cingolani et al. (2013) have detected a loss of 0.6 cm/year of soil in grazed sites after a fire, compared with 0.4-cm loss if grazing is excluded. We previously showed in Poca et al. (2018) that soils in our sites have higher soil bulk density and became shallower as vegetation structure was simplified, with drastic decreases as from 100 to 10 cm of soil profile in woodlands compared with the remaining soil of stonelands. On the same work, we also showed how a simplification in vegetation structure also encompass a loss of edaphic properties that promote infiltration rate. Here, we show that a reduction in soil depth and simplification of vegetation structure, as well as a degradation of topsoil properties that enhance infiltration rate, also evidence a diminution in water storage, from 32% up to 14% for the unsaturated zone and as much as from 46.6 to 0 cm for the saturated zone.

A reduction in soil depth, simplification of vegetation cover, and degradation of topsoil properties of vegetated patches of the highlands of central Argentina have impacted negatively on their hydrological functions. As others have noticed, there would be a lower fog interception and a reduction of total water inputs (Gomez-Peralta et al., 2008; Ponette-González et al., 2010), a decrease in water infiltration (Neary et al., 2009), and a consequent increase of run-off loses (Ziegler et al., 2004), altogether impacting negatively in water storage (Bruijnzeel et al. 1989, 2004). Then as the degradation of vegetated patches increases due to disturbances in highlands of central Argentina, more water would be lost during the rainy season directly into the streams by run-off and less water would be stored in the soil. At mid-upslope positions, as our study sites, this implies more water losses into downslope positions or even directly into streams, contributing to peak stormflows and sediment yield. Even though we cannot extrapolate our results to other topographic positions, we hypothesize that the pattern could be similar at downslope positions, with the difference that there water would be stored for longer periods, likely until the dry season, as suggested by Cingolani et al. (2015) for valley bottoms. Then at downslope positions the impact of disturbances could possibly be traduced on a reduction of dry season baseflows. Altogether, we show supporting evidence for the infiltration trade-off hypothesis (Bruijnzeel et al. 1989, 2004; Roa-García et al., 2011; Krishnaswamy et al., 2013; Ghimire et al., 2014), suggesting that higher vegetation biomass effects enhancing water infiltration opportunities and subsurface flow paths prevail over those favouring water loses through evapotranspiration. To our best knowledge, we provide the first evidence supporting this hypothesis from non-tropical ecosystems.

5 | CONCLUSIONS

Our study introduces key temporal and spatial lessons about the hydrology of the highlands of central Argentina. Temporally, (a) fog is a relevant water input throughout the year, possibly impacting on evapotranspiration/topsoil water dynamics and (b) mid-upslope vegetated patches store water at the saturated zone for a few days following rainfall events, buffering peak stormflows, reducing sediment yield, and delivering subsurface water downslope for potential storing throughout the year. Spatially, the alteration of vegetated patches of disturbances through a reduction in soil depth, a simplification of vegetation structure, as well as the degradation of topsoil properties for infiltration rate encompass a reduction of (a) fog water input and (b) water storage at the unsaturated and saturated zones. The implications of these changes on water storage dynamics at stand scale due to disturbances of grazing and fire are most possibly traduced to the water budget of the watershed.

Given the heterogeneity of the landscape, the relevance of surface and subsurface connectivity between vegetated patches along hillslopes should be essential for ecohydrological and biogeochemical processes in highlands of central Argentina. Despite their reduced depth, highland soils are important but vulnerable buffers. Vegetation and soil management including grazing and fire regulation should focus on this buffering capacity, because it is the key hydrological function behind one of the most relevant ecosystem service of these environments, which is the continuous supply of fresh water to the lowland inhabitants.

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REFERENCES

Altesor, A., Pi eiro, G., Lezama, F., Jackson, R. B., Sarasola, M., & Paruelo, J. M. (2006). Ecosystem changes associated with grazing in subhumid South American grasslands. *Journal of Vegetation Science*, *17*(3), 323–332.

Alvarado-Barrientos, M. S., Holwerda, F., Asbjornsen, H., Dawson, T. E., & Bruijnzeel, L. A. (2014). Suppression of transpiration due to cloud immersion in a seasonally dry Mexican weeping pine plantation. *Agricultural and Forest Meteorology*, *186*, 12–25.

APN (Administración de Parques Nacionales) (2007). *Plan de Manejo del Parque Nacional Quebrada del Condorito*. Ciudad Autónoma de Buenos Aires: Reserva Hídrica Provincial de Achala. Editorial APN.

Asbjornsen, H., Ashton, M. S., Vogt, D. J., & Palacios, S. (2004). Effects of habitat fragmentation on the buffering capacity of edge environments in a seasonally dry tropical oak forest ecosystem in Oaxaca, Mexico. *Agriculture, Ecosystems & Environment*, *103*(3), 481–495.

Asbjornsen, H., Goldsmith, G. R., Alvarado-Barrientos, M. S., Rebel, K., Van Osch, F. P., Rietkerk, M., … Dawson, T. (2011). Ecohydrological advances and applications in plant–water relations research: A review. *Journal of Plant Ecology*, *4*(1–2), 3–22.

Bonell, M., Purandara, B. K., Venkatesh, B., Krishnaswamy, J., Acharya, H. A. K., Singh, U. V., … Chappell, N. (2010). The impact of forest use and reforestation on soil hydraulic conductivity in the Western Ghats of India: Implications for surface and sub-surface hydrology. *Journal of Hydrology*, *391*(1), 47–62.

Boone Kauffman, J., Thorpe, A. S., & Brookshire, E. J. (2004). Livestock exclusion and belowground ecosystem responses in riparian meadows of eastern Oregon. *Ecological Applications*, *14*(6), 1671–1679.

Breashears, D. D., Rich, P. M., Barnes, F. J., & Campbell, K. (1997). Overstory-imposed heterogeneity in solar radiation and soil moisture in a semiarid woodland. *Ecological Applications*, *7*, 1201–1215.

Bruijnzeel, L. A. (1989). (De)Forestation and dry season flow in the tropics: a closer look. *Journal of Tropical Forest Science*, *1*(3), 229–243.

Bruijnzeel, L. A. (2002). Hydrology of tropical montane cloud forests: A reassessment. Hydrology and Water Management in the Humid Tropics, Panama, Proceedings of the Second International Colloquium. 22–26 March 1999 In J. S. Gladwell (Ed.), *IHP-V Technical Document in Hydrology* No. 52 (pp. 353–383). Paris: UNESCO.

Bruijnzeel, L. A. (2004). Hydrological functions of tropical forests: Not seeing the soil for the trees? *Agriculture, Ecosystems & Environment*, *104*(1), 185–228.

Cabido, M., Breimer, R., & Vega, G. (1987). Plant communities and associated soil types in a high plateau of the Córdoba mountains, central Argentina. *Mountain Research and Development*, *7*, 25–42.

Cingolani, A. M., Cabido, M. R., Renison, D., & Solís Neffa, V. (2003). Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. *Journal of Vegetation Science*, *14*(2), 223–232.

Cingolani, A. M., Poca, M., Giorgis, M. A., Vaieretti, M. V., Gurvich, D. E., Whitworth-Hulse, J. I., & Renison, D. (2015). Water provisioning services in a seasonally dry subtropical mountain: Identifying priority landscapes for conservation. *Journal of Hydrology*, *525*, 178–187.

Cingolani, A. M., Renison, D., Tecco, P. A., Gurvich, D. E., & Cabido, M. (2008). Predicting cover types in a mountain range with long evolutionary grazing history: A GIS approach. *Journal of Biogeography*, *35*(3), 538–551.

Cingolani, A. M., Vaieretti, M. V., Giorgis, M. A., La Torre, N., Whitworth-Hulse, J. I., & Renison, D. (2013). Can livestock and fires convert the sub-tropical mountain rangelands of central Argentina into a rocky desert? *The Rangeland Journal*, *35*(3), 285–297.

Cingolani, A. M., Vaieretti, M. V., Giorgis, M. A., Poca, M., Tecco, P. A., & Gurvich, D. E. (2014). Can livestock grazing maintain landscape diversity and stability in an ecosystem that evolved with wild herbivores? *Perspectives in Plant Ecology, Evolution and Systematics*, *16*(4), 143–153.

Colladon, L. (2004). Temperaturas medias mensuales. In *Cuenca del río San Antonio, Sistema del Río Suquía, Provincia de Córdoba*. Córdoba, Argentina: Instituto Nacional del Agua y del Ambiente (INA) y Centro de Investigaciones de la Región Semiárida (CIRSA).

Colladon, L. (2014). *Anuario pluviométrico 1992–2012. Cuenca del Río San Antonio, Sistema del Río Suquía, Provincia de Córdoba*. Córdoba, Argentina: Instituto Nacional del Agua y del Ambiente (INA) y Centro de Investigaciones de la Región Semiárida (CIRSA).

DeFries, R., & Eshleman, K. N. (2004). Land-use change and hydrologic processes: A major focus for the future. *Hydrological Processes*, *18*(11), 2183–2186.

DeLay, J. K., & Giambelluca, T. (2010). History of fog and cloud water interception research in Hawaii. In L. A. Bruijnzeel, F. N. Scatena, & L. S. Hamilton (Eds.), *Tropical montane cloud forests: Science for conservation and management* (pp. 332–341). Cambridge, UK: Cambridge University Press.

del-Val, E., Armesto, J. J., Barbosa, O., Christie, D. A., Gutiérrez, A. G., Jones, C. G., … Weathers, K. C. (2006). Rain forest islands in the Chilean semiarid region: Fog-dependency, ecosystem persistence and tree regeneration. *Ecosystems*, *9*(4), 598–608.

Di Rienzo, J. A., Casanoves, F., Balzarini, M. G., González, L., and Tablada, M. (2013). InfoStat versión 2013. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. http://www.infostat.com.ar.

Enrico, L., Funes, G., & Cabido, M. (2004). Regeneration of *Polylepis australis* Bitt. in the mountains of central Argentina. *Forest Ecology and Management*, *190*(2–3), 301–309.

Ewing, H. A., Weathers, K. C., Templer, P. H., Dawson, T. E., Firestone, M. K., Elliott, A. M., & Boukili, V. K. (2009). Fog water and ecosystem function: Heterogeneity in a California redwood forest. *Ecosystems*, *12*(3), 417–433.

Famiglietti, J. S., Rudnicki, J. W., & Rodell, M. (1998). Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas. *Journal of Hydrology*, *210*(1), 259–281.

Famiglietti, J. S., Ryu, D., Berg, A. A., Rodell, M., & Jackson, T. J. (2008). Field observations of soil moisture variability across scales. *Water Resources Research*, *44*(1), 1–16.

Freer, J., McDonnell, J. J., Beven, K. J., Peters, N. E., Burns, D. A., Hooper, R. P., … Kendall, C. (2002). The role of bedrock topography on subsurface storm flow. *Water Resources Research*, *38*(12), 5–1.

Frumau, K. F., Burkard, R., Schmid, S., Bruijnzeel, L. A., Tobón, C., & Calvo-Alvarado, J. C. (2011). A comparison of the performance of three types of passive fog gauges under conditions of wind-driven fog and precipitation. *Hydrological Processes*, *25*(3), 374–383.

Germer, S., Neill, C., Krusche, A. V., & Elsenbeer, H. (2010). Influence of land-use change on near-surface hydrological processes: Undisturbed forest to pasture. *Journal of Hydrology*, *380*(3), 473–480.

Ghimire, C. P., Bruijnzeel, L. A., Lubczynski, M. W., & Bonell, M. (2014). Negative trade-off between changes in vegetation water use and infiltration recovery after reforesting degraded pasture land in the Nepalese Lesser Himalaya. *Hydrology and Earth System Sciences*, *18*(12), 4933–4949.

Giambelluca, T. W., DeLay, J. K., Nullet, M. A., Scholl, M. A., & Gingerich, S. B. (2011). Canopy water balance of windward and leeward Hawaiian cloud forests on Haleakalā, Maui, Hawai'i. *Hydrological Processes*, *25*(3), 438–447.

Giorgis, M. A., Cingolani, A. M., Teich, I., Renison, D., & Hensen, I. (2010). Do *Polylepis australis* trees tolerate herbivory? Seasonal patterns of shoot growth and its consumption by livestock. *Plant Ecology*, *207*(2), 307–319.

Gomez-Peralta, D., Oberbauer, S. F., McClain, M. E., & Philippi, T. E. (2008). Rainfall and cloud-water interception in tropical montane forests in the eastern Andes of Central Peru. *Forest Ecology and Management*, *255*(3), 1315–1325.

Gómez-Plaza, A., Alvarez-Rogel, J., Albaladejo, J., & Castillo, V. M. (2000). Spatial patterns and temporal stability of soil moisture across a range of scales in a semi-arid environment. *Hydrological Processes*, *14*(7), 1261–1277.

Gómez-Plaza, A., Martınez-Mena, M., Albaladejo, J., & Castillo, V. M. (2001). Factors regulating spatial distribution of soil water content in small semiarid catchments. *Journal of Hydrology*, *253*(1), 211–226.

Ingwersen, J. B. (1985). Fog drip, water yield, and timber harvesting in the Bull Run municipal watershed, Oregon. *JAWRA Journal of the American Water Resources Association*, *21*(3), 469–473.

Jencso, K. G., McGlynn, B. L., Gooseff, M. N., Wondzell, S. M., Bencala, K. E., & Marshall, L. A. (2009). Hydrologic connectivity between landscapes and streams: Transferring reach-and plot-scale understanding to the catchment scale. *Water Resources Research*, *45*, W04428. https://doi.org/10.1029/2008WR007225

Jia, Y. H., Shao, M. A., & Jia, X. X. (2013). Spatial pattern of soil moisture and its temporal stability within profiles on a loessial slope in northwestern China. *Journal of Hydrology*, *495*, 150–161.

Krishnaswamy, J., Bonell, M., Venkatesh, B., Purandara, B. K., Rakesh, K. N., Lele, S., … Badiger, S. (2013). The groundwater recharge response and hydrologic services of tropical humid forest ecosystems to use and reforestation: Support for the "infiltration-evapotranspiration trade-off hypothesis". *Journal of Hydrology*, *498*, 191–209.

Messerli, B., Viviroli, D., & Weingartner, R. (2004). Mountains of the world: Vulnerable water towers for the 21st century. *Ambio*, *13*, 29–34.

Neary, D. G., Ice, G. G., & Jackson, C. R. (2009). Linkages between forest soils and water quality and quantity. *Forest Ecology and Management*, *258*(10), 2269–2281.

Oliveira, R. S., Eller, C. B., Bittencourt, P. R., & Mulligan, M. (2014). The hydroclimatic and ecophysiological basis of cloud forest distributions under current and projected climates. *Annals of Botany*, *113*(6), 909–920.

Pan, Y. X., Wang, X. P., Jia, R. L., Chen, Y. W., & He, M. Z. (2008). Spatial variability of surface soil moisture content in a re-vegetated desert area in Shapotou, Northern China. *Journal of Arid Environments*, *72*(9), 1675–1683.

Penna, D., Brocca, L., Borga, M., & Dalla Fontana, G. (2013). Soil moisture temporal stability at different depths on two alpine hillslopes during wet and dry periods. *Journal of Hydrology*, *477*, 55–71.

Pimentel, D., & Kounang, N. (1998). Ecology of soil erosion in ecosystems. *Ecosystems*, *1*(5), 416–426.

Poca, M., Cingolani, A. M., Gurvich, D. E., Whitworth-Hulse, J. I., & Saur Palmieri, V. (2018). La degradación de los bosques de altura del centro de Argentina reduce su capacidad de almacenamiento de agua. *Ecología Austral*, *28*. https://doi.org/10.25260/EA.18.28.1.1.497

Ponette-González, A. G., Marín-Spiotta, E., Brauman, K. A., Farley, K. A., Weathers, K. C., & Young, K. R. (2014). Hydrologic connectivity in the high-elevation tropics: Heterogeneous responses to land change. *Bioscience*, *64*(2), 92–104.

Ponette-González, A. G., Weathers, K. C., & Curran, L. M. (2010). Water inputs across a tropical montane landscape in Veracruz, Mexico: Synergistic effects of land cover, rain and fog seasonality, and interannual precipitation variability. *Global Change Biology*, *16*(3), 946–963.

Potts, D. L., Scott, R. L., Bayram, S., & Carbonara, J. (2010). Woody plants modulate the temporal dynamics of soil moisture in a semi-arid mesquite savanna. *Ecohydrology*, *3*(1), 20–27.

Qiu, Y., Fu, B., Wang, J., & Chen, L. (2001). Soil moisture variation in relation to topography and land use in a hillslope catchment of the Loess Plateau, China. *Journal of Hydrology*, *240*(3), 243–263.

Qiu, Y., Fu, B., Wang, J., & Chen, L. (2003). Spatiotemporal prediction of soil moisture content using multiple-linear regression in a small catchment of the Loess Plateau, China. *Catena*, *54*(1), 173–195.

Renison, D., Chartier, M. P., Menghi, M., Marcora, P., Torres, R. C., Giorgis, M., … Cingolani, A. M. (2015). Spatial variation in tree demography associated to domestic herbivores and topography: Insights from a seeding and planting experiment. *Forest Ecology and Management*, *335*, 139–146.

Renison, D., Hensen, I., Suarez, R., & Cingolani, A. M. (2006). Cover and growth habit of Polylepis woodlands and shrublands in the mountains of central Argentina: Human or environmental influence? *Journal of Biogeography*, *33*(5), 876–887.

Renison, D., Hensen, I., Suarez, R., Cingolani, A. M., Marcora, P., & Giorgis, M. A. (2010). Soil conservation in Polylepis mountain forests of Central Argentina: Is livestock reducing our natural capital? *Austral Ecology*, *35*(4), 435–443.

Roa-García, M. C., Brown, S., Schreier, H., & Lavkulich, L. M. (2011). The role of land use and soils in regulating water flow in small headwater catchments of the Andes. *Water Resources Research*, *47*(5), 1–12.

Schemenauer, R. S., & Cereceda, P. (1992). Fog collection's role in water planning for developing countries. *United Nations Journal Natural Resources Forum 1994*, *18*(2), 91–100.

Schemenauer, R. S., & Cereceda, P. (1994). A proposed standard fog collector for use in high-elevation regions. *Journal of Applied Meteorology*, *33*(11), 1313–1322.

Scholl, M., Eugster, W., & Burkard, R. (2011). Understanding the role of fog in forest hydrology: Stable isotopes as tools for determining input and partitioning of cloud water in montane forests. *Hydrological Processes*, *25*(3), 353–366.

Stonestrom, D. A., Scanlon, B. R., & Zhang, L. (2009). Introduction to special section on impacts of land use change on water resources. *Water Resources Research*, *45*(7), 1–3.

Teich, I., Cingolani, A. M., Renison, D., Hensen, I., & Giorgis, M. A. (2005). Do domestic herbivores retard *Polylepis australis* Bitt. woodland recovery in the mountains of Córdoba, Argentina? *Forest Ecology and Management*, *219*(2), 229–241.

Throop, H. L., Archer, S. R., Monger, H. C., & Waltman, S. (2012). When bulk density methods matter: Implications for estimating soil organic carbon pools in rocky soils. *Journal of Arid Environments*, *77*, 66–71.

Tromp-van Meerveld, H. J., & McDonnell, J. J. (2006). On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale. *Advances in Water Resources*, *29*(2), 293–310.

Viviroli, D., Dürr, H. H., Messerli, B., Meybeck, M., & Weingartner, R. (2007). Mountains of the world, water towers for humanity: Typology, mapping, and global significance. *Water Resources Research*, *43*(7).

Yen, J. D., Bond, N. R., Shenton, W., Spring, D. A., & Mac Nally, R. (2013). Identifying effective water-management strategies in variable climates using population dynamics models. *Journal of Applied Ecology*, *50*(3), 691–701.

Yong-Zhong, S., Yu-Lin, L., Jian-Yuan, C., & Wen-Zhi, Z. (2005). Influences of continuous grazing and livestock exclusion on soil properties in a degraded sandy grassland, Inner Mongolia, northern China. *Catena*, *59*(3), 267–278.

Zhang, B., Yang, Y. S., & Zepp, H. (2004). Effect of vegetation restoration on soil and water erosion and nutrient losses of a severely eroded clayey Plinthudult in southeastern China. *Catena*, *57*(1), 77–90.

Zhang, P., & Shao, M. A. (2013). Temporal stability of surface soil moisture in a desert area of northwestern China. *Journal of Hydrology*, *505*, 91–101.

Zhao, Y., Peth, S., Wang, X. Y., Lin, H., & Horn, R. (2010). Controls of surface soil moisture spatial patterns and their temporal stability in a semi-arid steppe. *Hydrological Processes*, *24*(18), 2507–2519.

Ziegler, A. D., Giambelluca, T. W., Tran, L. T., Vana, T. T., Nullet, M. A., Fox, J., … Evett, S. (2004). Hydrological consequences of landscape fragmentation in mountainous northern Vietnam: Evidence of accelerated overland flow generation. *Journal of Hydrology*, *287*(1), 124–146.

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