



Vegetation Cover Dynamics in Saline High-Altitude Wetlands of the Andes for Environmental Factors

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Abstract

The vegetation of high Andean wetlands in hyperarid environments is typically azonal; however, differentiated responses between permanent and temporary vegetation cover have been observed, driven by environmental factors. These responses create dynamic boundaries in vegetation cover, complicating the monitoring, assessment, and management of wetlands. Using the Tilopozo wetland as the study area, we aimed to identify permanent vegetation cover and evaluate its stability over time and determine changes in temporary vegetation cover and the environmental factors that influence them. The surface covered with vegetation was analyzed using six time-series from 1985 to 2019 based on the normalized difference vegetation index. The stability of permanent vegetation cover was assessed using the Kappa coefficient, while temporary vegetation cover was correlated with environmental factors (precipitation, evapotranspiration, and water table levels). Vegetation maps were used to determine the dominant species for both types of cover. The results revealed that permanent vegetation exhibited high temporal stability, with Kappa coefficients ranging from “very good” to “excellent,” dominated by *Schoenoplectus americanus* and *Baccharis juncea*, two strict hygrophilous species. Conversely, temporary vegetation cover was significantly influenced by precipitation and evapotranspiration and composed of transitional hygrophilous species such as *Distichlis spicata* and *Tessaria absinthioides*. These findings present an approach to delineate stable boundaries and estimate the maximum potential extent of wetlands (dynamic boundaries), and assessing their spatiotemporal variability and the environmental drivers of these changes. This information is crucial for the effective management and conservation of wetland ecosystems in these environments.

Keywords Permanent vegetation cover · Temporary vegetation cover · Strict hygrophilous · Transitional hygrophilous · Precipitation · Evapotranspiration

Introduction

Wetlands are biodiversity-rich ecosystems that play a crucial role in sustaining diverse biological communities and providing ecosystem services (Minckley et al. 2013). However, they are highly vulnerable to natural factors, such as climate variability (including precipitation, evapotranspiration,

and hydrology), and anthropogenic activities, such as agriculture, livestock farming, water resource extraction, and pollution. The effects of climate change amplify these vulnerabilities, particularly for wetlands in semi-arid, arid, and hyper-arid environments (De la Fuente et al. 2021; Zhu et al. 2023), such as arid regions of the Americas, Africa, and Australia, where wetlands are experiencing ongoing stress, resulting in reduced area and functional degradation (Zhu et al. 2023). Therefore, effective management and protection of wetlands are essential (Reis et al. 2017). However, wetlands are often overlooked in conservation efforts. To achieve effective management, it is crucial to understand the ecological dynamics of wetlands, particularly the behavior of the vegetation they support.

Historically, in hyperarid contexts, wetland vegetation has been classified as azonal, implying that such vegetation is unaffected by the climatic conditions of its

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surrounding environment. However, studies have shown that the responses of azonal vegetation to the environment can be influenced by climatic factors, such as precipitation and evapotranspiration (Sieben 2019). For example, strictly hygrophilous species, a type of azonal species that are dependent on fully flooded areas or soil with high water saturation, thrive in environments with groundwater outcrops, surface flows, or lakes, creating a permanent cover in wetlands (Sieben 2019). In contrast, transitional hygrophilous species, known for their ability to obtain water through capillary rise from the water table or precipitation events, are typically found along the edges of wetlands, forming a temporary vegetation cover (Ruthsatz 1995; Fariña et al. 2018; Sieben 2019).

The stability of vegetated areas is an important indicator of ecological health, as sudden changes can lead to spontaneous alterations and subsequent degradation (Zhang et al. 2013). In wetlands, delineating the areas of permanent and temporary vegetation cover to elucidate the natural dynamics is crucial for effective management and conservation (Reis et al. 2017; Lowman et al. 2018; De la Fuente et al. 2021). However, accurately defining areas of permanent and temporary vegetation cover in ecosystems with high natural surface variability, such as wetlands, remains a significant challenge (Jolly et al. 2008; Campbell 2010; Reis et al. 2017). Advances in satellite imagery have provided powerful tools for monitoring vegetation dynamics. Furthermore, these tools aid in delineating areas with permanent and temporary vegetation. For example, by studying the chrono-sequences of wetlands, Singh (1989) and Lu et al. (2005) successfully identified areas with changing vegetation cover. In arid zone wetlands of the Zambezi River Basin in Southern Africa, Lowman et al. (2018) identified areas of permanent and temporary vegetation and examined the climatic factors influencing these changes to inform their management using the MODIS instrument. Al-Maliki et al. (2022) in the Al Hammar wetland (Iraq) and Wen et al. (2023) in Macquarie (Australia) used Landsat images to distinguish permanent and temporary coverage zones, enabling wetland classification. This classification led to improved monitoring and management efforts and helped identify the environmental factors driving changes.

Despite these advancements, satellite analyses often lack the accuracy required to delineate permanent and temporary vegetation zones at finer scales. For more precise delineation, satellite analyses must be supplemented by detailed vegetation mapping and identifying the factors that drive vegetation changes (Lowman et al. 2018). This is crucial in the dynamic environments of arid wetlands, where high evapotranspiration and highly variable precipitation can significantly affect vegetation (Al-Maliki et al. 2022).

The Salar de Atacama, Chile, is one of the most arid regions on Earth and is home to numerous wetlands that rely on surface water, groundwater, and/or precipitation. Among these, the Tilopozo wetland system, located on the southern edge of the salt flat, is one of the largest. This system depends on groundwater discharge from the Monturaqui-Negrillar-Tilopozo (MNT) aquifer and precipitation. The aquifer has been subjected to industrial water extraction for metallic and non-metallic mining since 1986, with its effects on the water table taking approximately 10 years to become apparent near the wetland (Anderson et al. 2002). Additionally, Tilopozo wetlands are utilized by local communities for livestock grazing and ceremonial burnings (Soto et al. 2019).

Understanding the relationship between permanent and temporary vegetation cover and environmental factors in the Tilopozo wetland system is crucial for effective management and conservation. Therefore, this study aimed to (1) identify the permanent vegetation cover and evaluate its stability over time and (2) determine changes in temporary vegetation cover and the environmental factors that influence them across different time sequences.

Methods

Study Area and Ecological Characterization

The study area was the Tilopozo saline wetland system, located at the southern end of Salar de Atacama, Antofagasta Region, Chile (23°46'42" S; 68°14'39" W; 2,315 m.a.s.l.). The studied wetland system comprises three permanent water outcrops and their surrounding azonal vegetation, with an average slope of 4.96% (Fig. 1; Soto et al. 2019). From an ecohydrological perspective, two of its outcrops are classified as hydrowetlands, characterized by the presence of free-standing water, whereas the third demonstrates some hygrowetland characteristics but with water confined to the soil. Wetland feeding depends on the groundwater flow that drains from the MNT aquifer, categorizing it as a phreatogenic discharge wetland system (Brinson 1993; Zedler et al. 2008; Keddy 2010).

Based on data from 1975 to 2019 recorded at the Peine meteorological station of the General Directorate of Water (DGA, located 20 km north of Tilopozo (23°41'03" S, 68°03'29" W; 2,460 m.a.s.l.), the average monthly precipitation was 1.67 ± 2.31 mm, with an annual accumulation average of 20.00 mm. The monthly average evapotranspiration was $137.53 \text{ mm} \pm 39.48 \text{ mm}$, with an annual average of 1,650.53 mm.

Regarding water extraction near the Tilopozo wetland system, the MNT aquifer has been subject to industrial

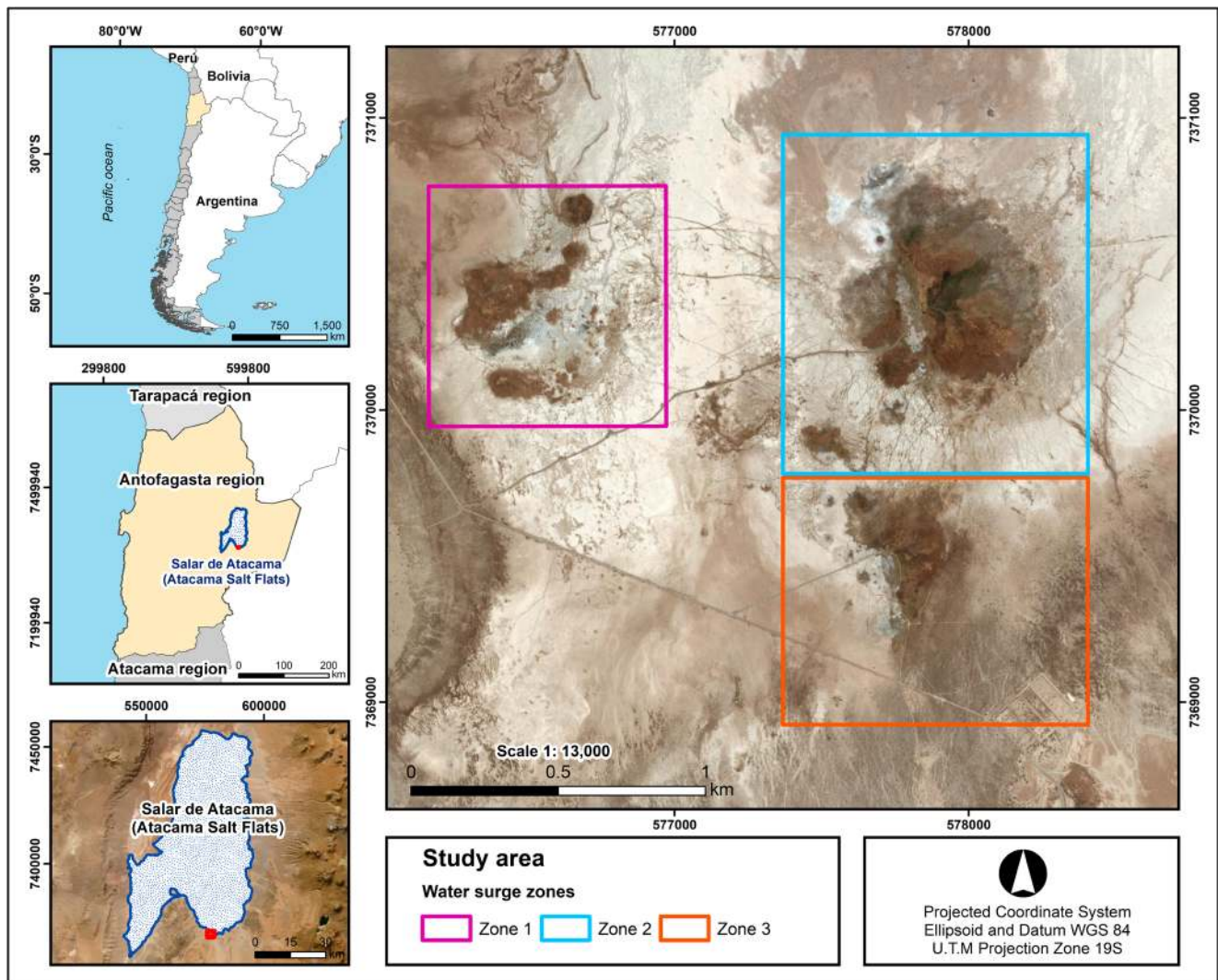


Fig. 1 Zones of groundwater outcrops constituting the Tilopozo wetland system and its surrounding azonal vegetation

withdrawals for metallic mining since 1993, with the nearest extraction well located approximately 30 km upstream (in a straight line) from the wetland system. Extraction rates have varied over time, from approximately 1,600 to 250 to L s^{-1} at present. In addition, since 1986, non-metallic mining operations have extracted brine from the Salar, outside the MNT aquifer, with the closest well located about 15 km downstream from Tilopozo. Brine extraction rates have also varied, ranging from approximately 50 to 2,000 L s^{-1} at present (Anderson et al. 2002; Marazuela et al. 2020). In response to extraction activities, a groundwater monitoring network associated with the MNT Aquifer Early Warning Plan was established in 2000. This network measures groundwater levels monthly through observation wells located around the Tilopozo wetland system. These wells include well TPZ-2, located at the center of the wetland (Soto et al. 2019).

The dominant azonal vegetation consists of strictly hygrophilous species, such as *Baccharis juncea* (Lehm.), *Juncus balticus* (Willd.), and *Schoenoplectus americanus* (Pers.), and transitional hygrophilous species, such as *Distichlis spicata* (L. Greene), *Lycium humile* (Phil.), and *Tessaria absinthioides* (Hook. & Arn.) (Soto et al. 2019).

Environmental Factors

Climatic Conditions

Monthly accumulated precipitation and temperature data (average, minimum, and maximum) from 1975 to 2019 were obtained from the Peine meteorological station of DGA. Both Tilopozo and Peine are situated in a transition zone between the Intermediate Desert and the Altiplano, known as the pre-Altiplano (Risacher et al. 1999). Using the

average, minimum, and maximum temperature data, along with the solar radiation data, the average monthly evapotranspiration was calculated using the equation proposed by Samani (2000).

The precipitation and evapotranspiration data were organized and analyzed to characterize the annual and monthly patterns within the historical series from 1975 to 2019 (Gómez and Medina 2012). Additionally, six subseries were established to evaluate changes over time. The reference subseries included the period before industrial water extraction from the MNT aquifer (pre-extraction), the transition period, and the period with evidence of reductions in the water table in the vicinity of Tilopozo wetland (aftereffects; Table 1).

In the historical series of total annual precipitation from 1975 to 2019, a cumulative deviation curve was developed. This curve enabled the plotting of trends for both wet and dry years, along with their intensities and relative magnitudes. It was standardized to identify the dry or wet years with respect to the historical annual average (20.00 mm for the study area). Mild events were defined as those with precipitation ranging between 0.00 and 19.00 mm, while extreme events were defined as those with precipitation greater than 20.00 mm (McKee et al. 1993). Subsequently, the trends of the historical series of total annual precipitation (1975–2019) and the cumulative deviation curve were analyzed using the Mann–Kendall test ($\alpha=0.01$; Bezerra and Luna 2020).

Water Table Conditions

Water table data for the Tilopozo wetland system were obtained from the water monitoring network of the MNT aquifer Early Warning Plan (Soto et al. 2019). Depth

Table 1 Temporal subseries considered in the study based on potential anthropogenic changes in the environment

Subseries	Name	Description
1985–1989 [#] 1989–1992	Pre-extraction	Period prior to the potential onset of decreases in the water table level in the Tilopozo wetland system.
1997–2000 2001–2004	Transition	Transition period, with the eventual onset of decreases in the water table levels in the Tilopozo wetland system.
2011–2015* 2016–2019	Aftereffects	Period of reductions in the water table level in the Tilopozo wetland system.

[#] Because of the low availability of satellite images for certain months between 1985 and 1986, the information was complemented by extending the subseries to 1989

* Because there were no satellite images in 2012, the subseries was extended to 2011

measurements from the TPZ-2A observation well (monthly scale) in the Tilopozo wetland system (23°46'57" S, 68°14'26" W; 2,308 m.a.s.l.) were analyzed from 2000–2019. These data were complemented with data from the nearby monitoring well TP-2 (23°46'12" S, 68°13'40" W; 2,311 m.a.s.l.; monthly data for 1996–2019). Linear regression equations were calculated separately for each month (Tymkiv and Kasiyanchuk 2019; Table S1) and used to reconstruct monthly averages of the depth of the water table (expressed in decimeters: dm) for 1996–2019 of TPZ-2 A. This provided information for the subseries 1997–2000, 2001–2004, 2011–2015, and 2016–2019.

Dynamics of Permanent and Temporary Vegetation Cover Zones

Determination of Wetland Vegetation

A total of 329 satellite images with a spatial resolution of 30 m were downloaded from the Thematic Mapper (TM) sensor onboard the Landsat 5 satellite and the Operational Land Imager (OLI) sensor onboard the Landsat 8 satellite for the period between 1985 and 2019, obtaining the monthly frequency (Table S2). The images were transformed to surface reflectance and subjected to radiometric (using image metadata in ENVI) and atmospheric corrections (Dark Object Subtraction-DOS) to obtain images suitable for multitemporal analysis (Chavez 1996; Chander et al. 2009).

The surface covered by azonal vegetation was delineated and its area was determined using the Normalized Difference Vegetation Index (NDVI), which uses the visible red (Red) and infrared (NIR) bands, respectively. NDVI values of 0.13 and 0.18 were considered thresholds for Landsat 5 and Landsat 8 images, respectively, to ensure compatibility across long sequences from different sensors in hyperarid areas (Holden and Woodcock 2016; Zhu et al. 2016; Khosravi et al. 2017; Soto et al. 2019). This analysis was complemented with a visual analysis of real-color images.

Determination of Permanent Vegetation Cover

For the historical series (1985–2019) and six subseries (Table 1), a frequency analysis was applied to determine the pixels with the greatest permanence of azonal vegetation cover over time ($\geq 95\%$ of the time) (Danilova et al. 2012; Wulder et al. 2020; Moumane et al. 2022). Results of the permanent vegetation cover were compared with those of

the accumulated deviation in precipitation to determine the influence of dry or wet cycles on stable surfaces.

Subsequently, each pixel detected with permanent vegetation was identified with respect to the total number of pixels in the scene, maintaining the same order in the grid, and comparisons were made between the different subseries analyzed (Table 1). This allowed the construction of a confusion matrix from which the overall precision and Kappa coefficient could be determined (Bosquilia and Muller-Karger 2021; Su et al. 2021). The Kappa coefficient indicated the proportion of pixels that remained stable over time and those that changed. The value ranges between 0 and 1, with values closer to 1 indicating greater permanent cover (Monserud and Leemans 1992; Zekarias et al. 2021).

Determination of Temporary Vegetation Cover

The temporary vegetation cover (<95% of the time) within the Tilopozo wetland system was identified by subtracting the surface with permanent vegetation obtained from the historical series (1985–2019) from the total area covered with vegetation for each month. Then, the temporary vegetation cover was correlated with the average monthly precipitation, evapotranspiration, and water table using Spearman correlation, considering various time lags (ranging from 0 to 4 months) where each environmental factor subsequently influences the temporary vegetation cover (Otto et al. 2011; Dangles et al. 2017; Wulder et al. 2020). Significance levels (0.10, 0.05, and 0.01) were assessed using student's t-test (Haque et al. 2022). For months without available satellite images, the surfaces covered with vegetation (temporary vegetation cover zones) were completed using the monthly average of each time subseries.

Dominant Vegetation in Areas of Permanent and Temporary Vegetation Cover

For the 2016–2019 subseries, a cross-reference was conducted between areas of permanent and temporary vegetation cover and existing land use and vegetation maps, enabling the identification of vegetation formations and plant species. The cartography was developed by “Gestión Ambiental Consultores” (GAC 2019) and was built from 20 transects and 155 floristic plots, with multiple field visits for updating and verification from 2016 to 2019. This was complemented by field visits by the research team during the same period, as well as verification using freely accessible high-definition satellite images (Google Earth Pro ©) between 2003 and 2015.

Results

Environmental Factors

Monthly precipitation varied in magnitude over the study period. In the historical series of 1975–2019, precipitation was highly variable and mainly concentrated in the summer–autumn period (January to June), with a maximum in February at 7.04 mm (± 12.30 mm), followed by March at 5.76 mm (± 15.06 mm) (Fig. 2a). On the contrary, evapotranspiration peaked in December at 189.56 mm (± 5.79 mm) and was the lowest in June in the Southern Hemisphere winter, at 79.15 mm (± 4.46 mm) (Fig. 2a).

Analysis of the environmental factors by subseries revealed differences. During pre-extraction subseries (1985–1989 and 1989–1992; Fig. 2b and c), the maximum precipitation occurred during February, with earlier occurrences in December in the 1989–1992 subseries. In contrast, the transition subseries (1997–2000 and 2001–2004; Fig. 2d and e), the maximum precipitation shifted to March, with late precipitation events occurring until August. In the aftereffects series (2011–2015 and 2016–2019; Fig. 2f and g), a reduction in the magnitude of precipitation events was observed, with a maximum observed during February and events observed until September.

In all subseries, the minimum evapotranspiration was observed in June, with values ranging from 77.36 to 82.37 mm. However, the maximum evapotranspiration varied between January and December, ranging from 187.31 mm in the 2001–2004 subseries (Fig. 2e) to 193.47 mm in the 2016–2019 subseries (Fig. 2g), the latter being the warmest period. In accordance with the evapotranspiration patterns, the water table exhibited seasonal variation, with the shallowest depths (−4.70 to −6.15 dm; Fig. 2d and g) occurring between July and September (lowest evapotranspiration) and the greatest depths observed in February and March (−7.34 to −7.86 dm; Fig. 2d and g). An increase in the depth of the water table was observed, with the after effects subseries having the greatest depths; however, seasonal variation remained (Fig. 2d and g).

Analysis of the historical precipitation series of 1975–2019 revealed an average annual precipitation was 20.00 mm (± 19.71 mm). A slight decreasing trend in precipitation was observed over the 44 years (−0.06 mm; Fig. 3), but this was not statistically significant. In contrast, an analysis of accumulated precipitation deviations for the different subseries studied showed a significantly downward trend in the wet years, which decreased in magnitude and temporal extension. In contrast, the magnitude and intensity of dry periods increased steadily, being notorious in the aftereffects subseries (2011–2015 and 2016–2019; Fig. 4).

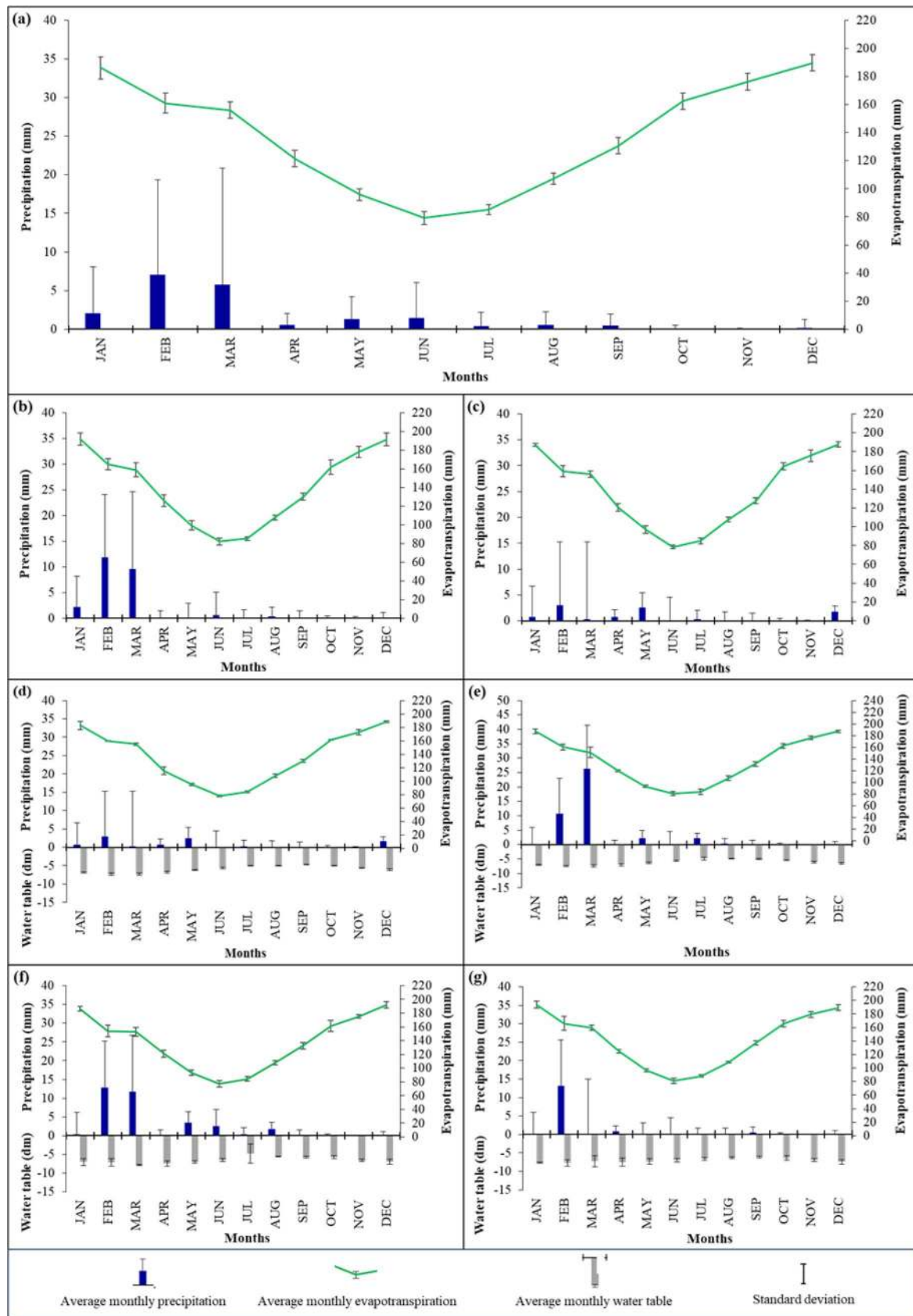


Fig. 2 Monthly averages of precipitation, evapotranspiration, and water table depth for the historical series 1975–2019 (a); pre-extraction subseries 1985–1989 (b) and 1989–1992 (c); transition subseries 1997–2000 (d) and 2001–2004 (e); aftereffects subseries 2011–2015 (f) and 2016–2019 (g)

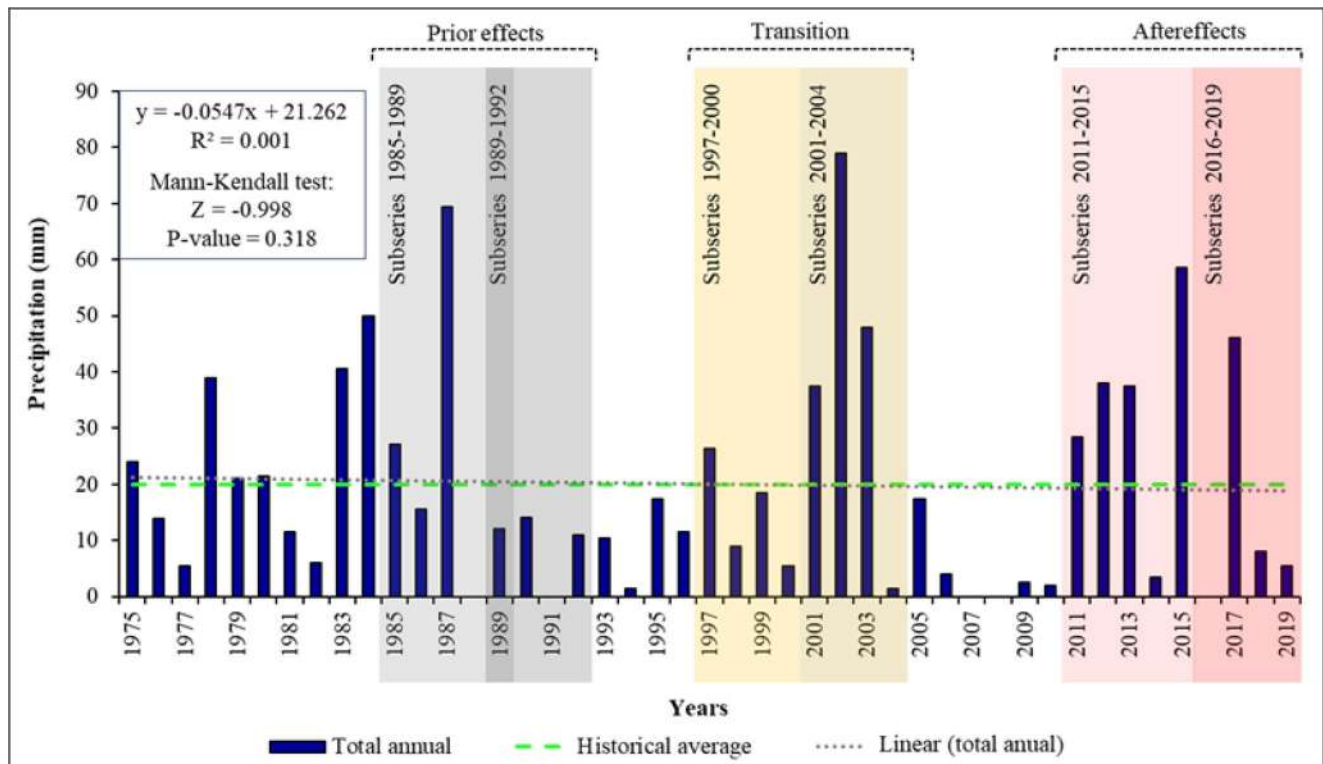


Fig. 3 Historical annual rainfall histogram series 1975–2019, considering the pre-extraction subseries 1985–1989 and 1989–1992; transition subseries 1997–2000 and 2001–2004; aftereffects subseries 2011–2015 and 2016–2019

Dynamics of Permanent and Temporary Vegetation Cover Zones

Permanent Vegetation Cover

The historical series from 1985 to 2019 showed a permanent vegetation cover area of 57.87 ha, with 308 of the 324 analyzed images (months) displaying consistent permanent vegetation pixels, regardless of the seasonality, precipitation patterns and the observed effects of the water table (Fig. 4). It should be noted that images from August, September, and October 2009 and October and November 2017 were excluded from the analysis because of visual detection of fire events that significantly affected the vegetated surface.

When disaggregated by subseries, different patterns in vegetation cover were observed. During pre-extraction subseries (1985–1989 and 1989–1992) an extremely humid period was observed. The permanent vegetation covered 62.46 ha, with vegetation observed in 39 of 41 images (Figs. 4 and 5a) and then decreased to 56.07 ha, with vegetation observed in 42 of 44 images (Figs. 4 and 5b). In the transition subseries (1997–2000 and 2001–2004), showed an increase to 66.06 ha (39 of 41 images; Fig. 5c), and then a reduction to 60.57 ha (30 of 32 images; Fig. 5d). During this period, climatic conditions were contrasting, ranging from extremely dry to extremely humid (Fig. 4). During

aftereffects subseries (2011–2015 and 2016–2019), the coverage was 63.63 ha (35 of 37 images; Fig. 5e), and then went to 59.31 ha (42 of 44 images; Fig. 5f); with a climate that transitioned from slightly dry to slightly humid conditions (Fig. 4).

Comparison of permanent vegetation across the different subseries revealed that the overall accuracies ranged from 92.66% to 97.53%, with an average of 94.72% ($\pm 1.59\%$; Table 2). The Kappa coefficient for comparisons between subseries varied from 0.79 to 0.93 (Table 2), indicating a classification between “very good” and “excellent” according to the criteria established by Monserud and Leemans (1992). These results suggest that the permanent vegetation identified in each subseries showed little variability, both in numerical terms and in specific areas within the wetland system, remaining stable over time (Fig. 4; Table 2).

Temporary Vegetation Cover

The temporary vegetation cover in the Tilopozo wetland system exhibited significant variation within and between years, with areas covered by vegetation ranging from 7.67 ha to 64.18 ha. In the historical series (1985 to 2019), the largest area of temporary vegetation cover was recorded in June, with an average of 44.11 ha (± 12.43 ha; Fig. 6a; Table 3).

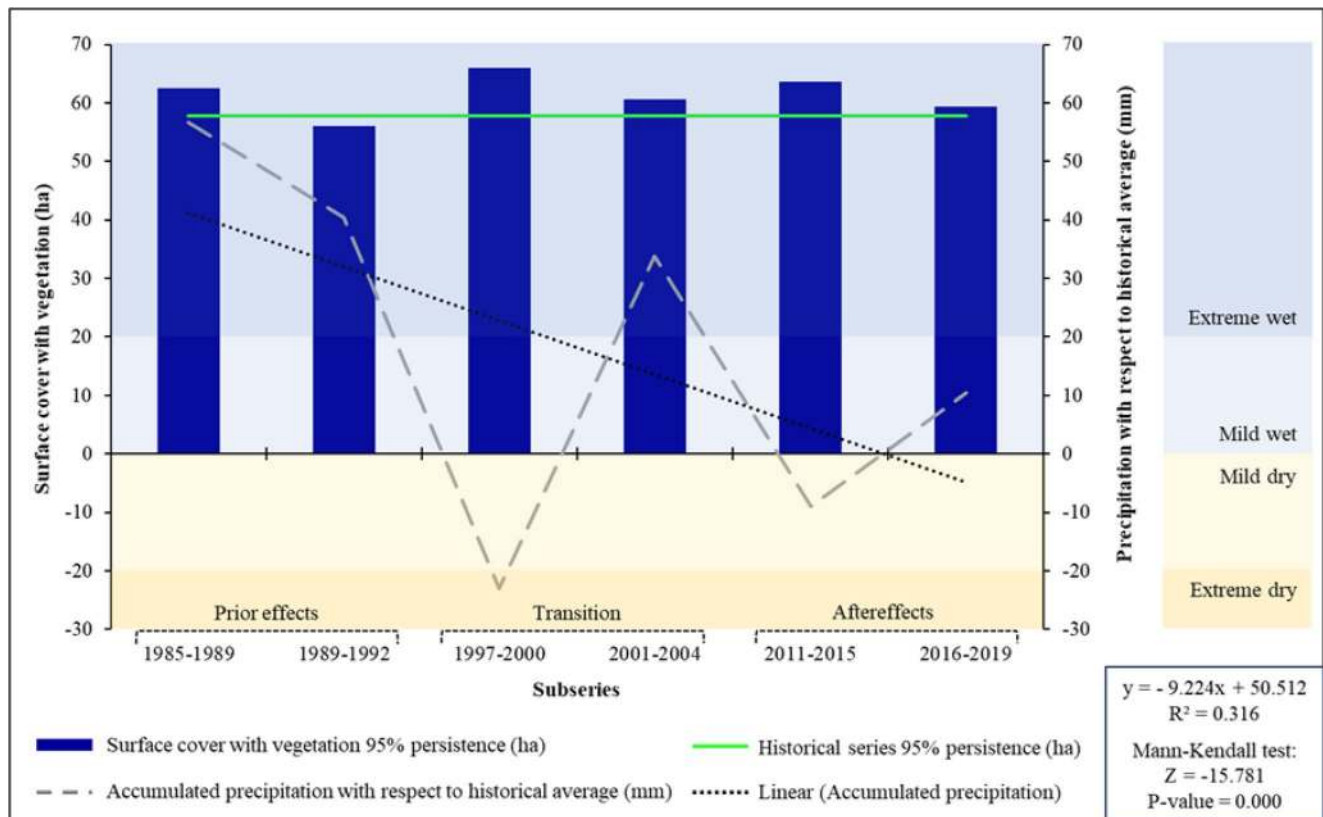


Fig. 4 Permanent vegetation cover in the Tilopozo wetland system, with a 95% probability for the historical series (1985–2019) and pre-extraction subseries 1985–1989 and 1989–1992; transition subseries

1997–2000 and 2001–2004; aftereffects subseries 2011–2015 and 2016–2019, with respect to the wet and dry climate cycles

The month of peak temporary vegetation cover varied across the different time subseries. In the 1989–1992 (pre-extraction) and 2001–2004 (transition) subseries, the maximum areas of temporary vegetation cover were observed in February, at 41.23 ha (± 8.96 ha; Fig. 6c) and 49.44 ha (± 31.73 ha; Fig. 6e), respectively. In contrast, in the 1985–1989 (pre-extraction), 1997–2000 (transition), and 2011–2015 (aftereffects) subseries, the peak temporary vegetation cover occurred in April, with areas of 64.18 ha (± 9.29 ha; Fig. 6b), 53.95 ha (± 14.80 ha; Fig. 6d), and 39.65 ha (± 18.23 ha; Fig. 6f), respectively. In the 2016–2019 (after-effects) subseries, the maximum area was observed in June, with 44.11 ha (± 12.43 ha; Fig. 6g).

The temporary vegetation cover was influenced by evapotranspiration and precipitation but was not sustainedly influenced by the water table variation. Evapotranspiration affected the temporary vegetation cover with a 4-month lag, while precipitation induced the responses more quickly, with a 2-month lag. During pre-extraction (1985–1989 and 1989–1992) and aftereffects (2011–2015) subseries, precipitation showed strong climatic control with higher correlations, but the influence of evapotranspiration was lower. In contrast, in the transition (1997–2000 and 2001–2004), and

aftereffects (2016–2019) subseries, evapotranspiration had a greater impact than precipitation (Fig. 6; Table 3; Table S3). In comparison, the water table had a low influence on the temporary vegetation cover in the different subseries, except for the period 2001–2004 (transition), where it had a moderate influence (Fig. 6; Table 3; Table S3).

Dominant Vegetation in Areas of Permanent and Temporary Vegetation Cover

When integrating the permanent vegetation cover detected in the 2016–2019 subseries with the vegetation maps, the largest proportion of the surface area was composed of strictly hygrophilous species, reaching 79.31%, represented by vegetation formations dominated by grasslands of *S. americanus* and *B. juncea*. Transitional hygrophilous species covered 16.53% of the surface area, dominated by *D. spicata* grasslands and *T. absinthoides* scrubs (Table 4). In contrast, the temporary vegetation cover zone was essentially represented by transitional hygrophilous species, reaching 66.62%, dominated by *D. spicata* grasslands and *T. absinthoides* and *L. humile* shrublands (Table 4). Co-dominance of strict and transitional hygrophilous species,

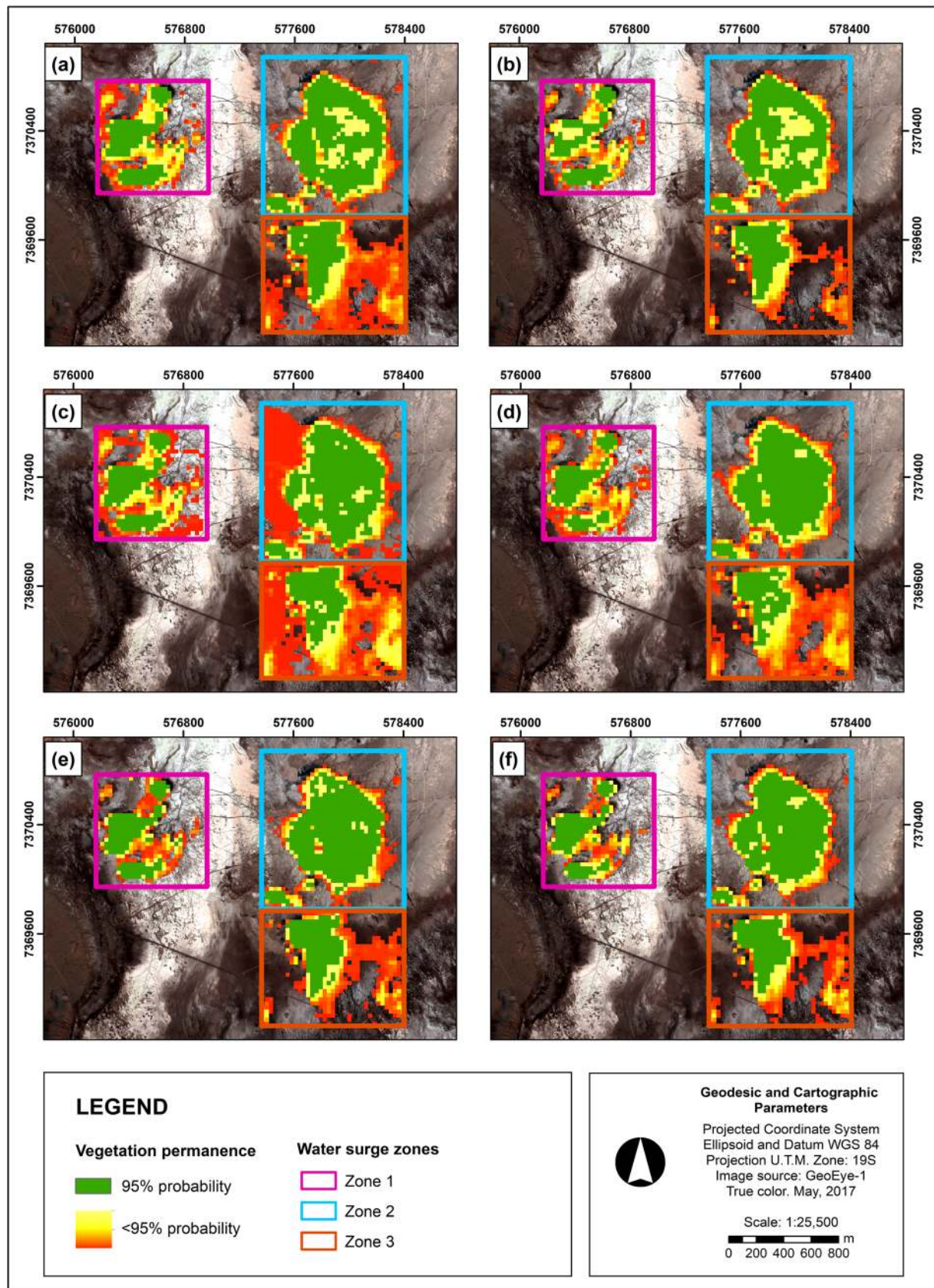


Fig. 5 Permanent vegetation cover in the Tilopozo wetland system, with a 95% probability: considering the pre-extraction subseries 1985–1989 (a) and 1989–1992 (b); transition subseries 1997–2000 (c) and 2001–2004 (d); aftereffects subseries 2011–2015 (e) and 2016–2019 (f)

Table 2 Overall accuracy (%) and kappa coefficient of permanent vegetation cover with 95% permanence compared by pairs between the Temporal subseries analyzed in the Tilopozo wetland system

Overall accuracy (%)						
Subseries	1985–1989	1989–1992	1997–2000	2001–2004	2011–2015	2016–2019
1985–1989	-	97.53	93.75	93.45	94.18	93.25
1989–1992		-	92.66	93.68	93.81	93.35
1997–2000			-	94.90	95.56	94.17
2001–2004				-	96.84	97.04
2011–2015					-	96.58
2016–2019						-
Kappa coefficient						
Subseries	1985–1989	1989–1992	1997–2000	2001–2004	2011–2015	2016–2019
1985–1989	-	0.93	0.83	0.81	0.84	0.81
1989–1992		-	0.79	0.81	0.82	0.80
1997–2000			-	0.86	0.88	0.84
2001–2004				-	0.91	0.91
2011–2015					-	0.90
2016–2019						-

referred to as “mixed composition” (grasslands of *J. bal-ticus* and *D. spicata*), had the lowest participation but was observed in areas with permanent (4.08%) and temporary cover (14.70%; Table 4).

Discussion

Dynamics of Permanent and Temporary Vegetation Cover

Despite vegetation in wetland systems in hyperarid environments typically being considered azonal, recent studies have identified variations in vegetation responses to precipitation events, depending on whether the vegetation is strictly or transitionally hygrophilous (Campbell 2010; Zhang et al. 2013; Sieben 2019).

Our findings demonstrate that vegetation within the Tilopozo wetland system exhibits contrasting responses to environmental drivers, particularly precipitation, evapotranspiration, and groundwater level. A portion of the vegetation-covered area (approximately 60 ha) remained stable over time, regardless of the subseries analyzed or changes in environmental factors, including precipitation, evapotranspiration, and groundwater level (Figs. 4 and 5). These areas exhibited a high degree of spatial and temporal invariability, with Kappa coefficients ranging from “very good” to “excellent” (Table 2), representing a stable core of vegetation over time and serving as an indicator of ecosystem health (Zhang et al. 2013). However, the lowest Kappa coefficient values were observed in the comparison between the pre-extraction (1997–2000) and transition (2001–2004) subseries, which may be related to the increased climatic variability and not to the water table, whose effects are more evident in

terms of depth in the aftereffects subseries (2011–2015 and 2016–2019).

In contrast, the surrounding temporary vegetation cover, located between the core and the adjacent dry environment, was dominated by temporary hygrophilous vegetation and displayed consistently statistically significant responses to precipitation and evapotranspiration, but not to groundwater fluctuations (Figs. 4 and 5, and 6; Table S3). In the pre-extraction (1985–1989 and 1989–1992) and aftereffects (2011–2015 and 2016–2019) subseries, variations in the temporal vegetation cover were affected by precipitation, with 2-month lags (Fig. 6; Table 3; Table S3). These findings align with those of studies from other arid wetland systems, such as Otto et al. (2011) and Dangles et al. (2017) in the Puna arid biome of the Andes, who found that the vegetation response exhibited a 3-month lag. In addition, research conducted by Puig (2015) in hot-arid environments and Chen et al. (2020) in cold-arid environments reported a 2-month lag.

No significant correlations between precipitation and the vegetation response were observed in the transition (1997–2000 and 2001–2004) subseries (Fig. 6; Table 3; Table S3). This could be related to the high variability in the magnitude of precipitation in both time subseries (Fig. 2c, d). Such continuous variability likely enhanced soil moisture in temporary vegetation cover areas, thus improving the growth of transitional vegetation, with greater permanence over time (Lowman et al. 2018; Sieben 2019). This was evident in the varied coverage peaks for both subseries (Fig. 6c, d). Furthermore, both subseries showed an abrupt change in precipitation from an extremely dry cycle to an extremely humid one, which could influence the responses of the vegetation cover (Figs. 4 and 5). This variability underlines that vegetation responses depend not only on precipitation

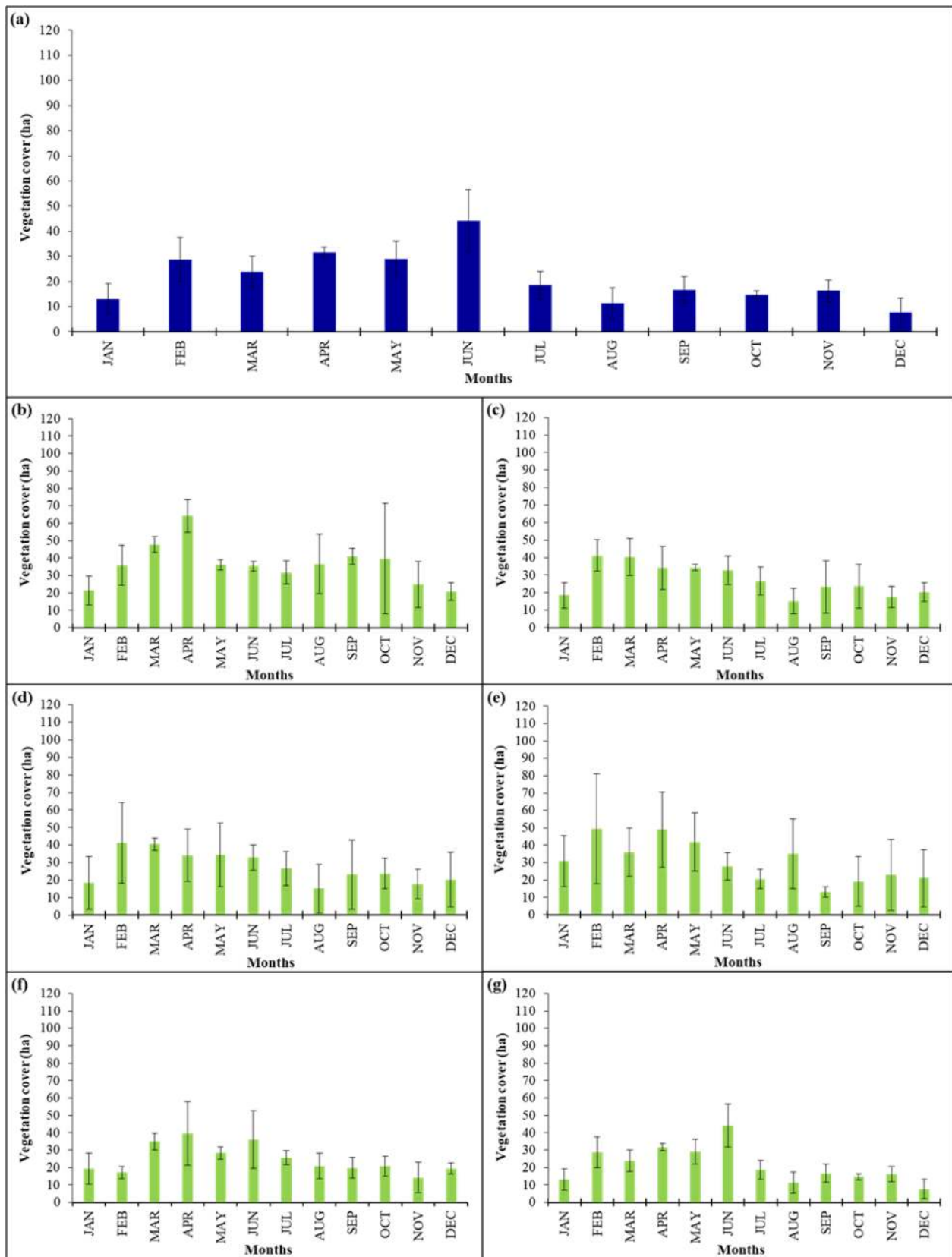


Fig. 6 Average monthly temporary vegetation cover (ha) in the Tilo-pozo wetland system, considering historical series 1985–2019 (a) and pre-extraction subseries 1985–1989 (b) and 1989–1992 (c); transition

subseries 1997–2000 (d) and 2001–2004 (e); aftereffects subseries 2011–2015 (f) and 2016–2019 (g)

Table 3 Best spearman rank correlation between average monthly temporary vegetation cover (ha) and average precipitation (mm), evapotranspiration (mm), and water table (dm) in the Tilopozo wetland system, considering pre-extraction subseries 1985–1989 and 1989–1992; transition subseries 1997–2000 and 2001–2004; and aftereffects subseries 2011–2015 and 2016–2019

Subseries		Average precipitation (mm)	Average evapotranspiration (mm)	Water table (dm)
Pre-extraction	1985–1989	0.62**	0.29	-
	1989–1992	0.77***	0.74***	-
Transition	1997–2000	0.03	0.66**	0.27
	2001–2004	0.06	0.80***	0.50*
Aftereffects	2011–2015	0.73***	0.63**	0.40
	2016–2019	0.53*	0.75***	0.45
Lag condition		2-months	4-months	4-months

*: Statistical significance to $\alpha=0.10$; **: Statistical significance to $\alpha=0.05$; ***: Statistical significance to $\alpha=0.01$

magnitude but also on its temporal distribution and seasonality, introducing uncertainty in statistical associations. These results highlight that this type of wetland is structured into distinct zones, each governed by different environmental factors.

The peak in temporary vegetation cover showed a temporal shift. In the pre-extraction (1985–1989 and 1989–1992) subseries, the highest values were observed between February and April (Fig. 6b, c). In contrast, in the aftereffects (2011–2015 and 2016–2019) subseries, the peaks were observed between April and June (Fig. 6f, g). This effect may be attributed to changes in precipitation patterns and temperature variations in the area (Anderson et al. 2021). In addition, evapotranspiration played a significant role in the temporal vegetation in all subseries except 1985–1989 (pre-extraction), with positive correlations observed. This contrasts with findings from other arid environments, such as Dai et al. (2022), who observed an inversely proportional relationship between evapotranspiration and vegetation cover; however, this was compensated by increased moisture availability from sources such as glacial or permafrost melt. Although Tilopozo lacks these specific characteristics, as a phreatogenic discharge wetland, its water table is close to the soil surface (Brinson 1993), suggesting that increased evapotranspiration can aid in mobilizing moisture toward the soil surface through capillarity (Kyei-Baffour 2005; Yang et al. 2011), making it available for vegetation in the wetland edges (Fig. 5). This indicates that the increase in evapotranspiration that started in November played a crucial role in the development of the temporary vegetation cover observed in March (Figs. 2 and 6; Table S3).

Meanwhile, variation in the water table did not show a consistent effects on the behavior of temporary vegetation cover across; not even in the aftereffects subseries, where

Table 4 Composition of surface covered with vegetation in the permanent and temporary vegetation cover of the Tilopozo wetland system for the 2016–2019 subseries

Permanent vegetation cover				
Hygrophilous type	Vegetation formation	Total for formation	Total for type	Percentage by type
Transitional hygrophilous	Grassland of <i>Distichlis spicata</i>	8.96 ha	9.80 ha	16.53%
	Scrub of <i>Tessaria absinthioides</i>	0.85 ha		
Mixed composition	Grassland of <i>Juncus balticus</i> and <i>Distichlis spicata</i>	2.42 ha	2.42 ha	4.08%
Strict hygrophilous	Grassland of <i>Schoenoplectus americanus</i> and <i>Baccharis juncea</i>	8.85 ha	47.09 ha	79.39%
	Grassland of <i>Schoenoplectus americanus</i>	38.24 ha		
Total		59.31 ha	59.31 ha	100.00%
Temporary vegetation cover				
Hygrophilous type	Vegetation formation	Total for formation	Total for type	Percentage by type
Transitional hygrophilous	Grassland of <i>Distichlis spicata</i>	18.69 ha	42.12 ha	66.62%
	Scrub of <i>Tessaria absinthioides</i>	23.04 ha		
	Scrub of <i>Lycium humile</i>	0.39 ha		
Mixed composition	Grassland of <i>Juncus balticus</i> and <i>Distichlis spicata</i>	9.29 ha	9.29 ha	14.70%
Strict hygrophilous	Grassland of <i>Schoenoplectus americanus</i> and <i>Baccharis juncea</i>	1.10 ha	11.81 ha	18.68%
	Grassland of <i>Schoenoplectus americanus</i>	10.71 ha		
Total		63.21 ha	63.21 ha	100.00%

a deepening of the water table was observed. This behavior could be attributed to the high evaporation rates in the system, which facilitate the mobilization of moisture through capillarity (Kyei-Baffour 2005; Yang et al. 2011), especially in the wetland edges (Figs. 5 and 6; Table S3).

Dominant Vegetation in Areas of Permanent and Temporary Vegetation Cover

Evapotranspiration can lead to increased salinity at the soil surface (Kyei-Baffour 2005; Yang et al. 2011), particularly

in edge areas where water outcrops are absent and the vegetation cover is temporary (Fig. 5). The accumulated salts can subsequently be leached by precipitation events (Jorenush and Sepaskhah 2003; Guida-Johnson et al. 2017), creating a delicate balance between the accumulation of surface salts and their leaching, with precipitation playing a crucial role. The plant species present in Tilopozo are halophytes or halo-tolerant plants, exhibiting adaptations in their development mechanisms, structure, physiology, and/or metabolism to survive saline conditions (Alzérreca and Cardozo 1991; Degano 1999; Pelliza et al. 2005; Qian et al. 2007; Leal et al. 2023).

Temporary vegetation zones were dominated by transitional hygrophilous species (66.62%; Table 4), particularly *D. spicata* and *T. absinthioides*. This distribution is likely related to the ecosystem's humidity instability because of summer precipitation and the effect of evapotranspiration, which promote sprouting and growth in the wetland edges (Sieben 2019). Transitional species were observed in unsaturated soils with variable rooting depths, depending on the depth of the water table. This observation is consistent with reports on transitional hygrophilous species, such as *D. spicata* (Kray et al. 2012), *T. absinthioides* (Nester et al. 2007), and *L. humile* (Palchetti et al. 2021). In contrast, permanent vegetation cover was dominated by strictly hygrophilous species, particularly *S. americanus* and *B. juncea* (79.39%; Table 4). This composition is likely related to the preference of strictly hygrophilous species for areas where soils are flooded or permanently saturated, with direct contact with the water table, as described in past studies for *B. juncea* (Murray et al. 2007), *J. balticus* (Montemayor et al. 2015), and *S. americanus* (Montejo-Mayo et al. 2015).

Furthermore, an ecotone zone was observed within the wetlands, providing a habitat for the interaction between strict and transitional species (Table 4). This interaction may have been influenced by temporary increases (seasonal or interannual) in soil moisture resulting from changes in the water table or evapotranspiration, as well as contributions from precipitation events. The proportion of transitional hygrophilous species present in the permanent vegetation for the 2016–2019 subseries, along with mixed composition formations, is indicative of these dynamics (Table 4). These compositional patterns reinforce the interpretation that wetland cores act as long-term stability areas, while ecotones and transitional zones reflect short-term climatic variability.

Management and Conservation Challenges

Thus, our findings demonstrate that in phreatogenic discharge wetlands, the state and functioning of the permanent vegetation cover largely depend on stable groundwater (Wantzen and Junk 2009; Yin et al. 2015; Chen et al. 2020).

In contrast, transitional vegetation in areas with temporary cover, which could represent the dynamic limits of the wetland, respond to local meteorological behavior, such as precipitation and evapotranspiration, indicating that precipitation is a limiting factor (Ruthsatz 1995; Chen et al. 2020). This provides interesting perspectives related to the management and conservation of wetland ecosystems in hyper-arid areas.

Some studies on wetlands in the arid Puna of the Andes have recommended the use of representative surfaces when evaluating natural systems (Centro de Ecología Aplicada 2006) and new regulations require clear delimitations of wetlands for their conservation and/or application of management plans (Del Fierro 2024). However, uncertainty remains regarding what should be considered representative due to high temporal variability, especially in areas with temporary vegetation cover in wetlands (Roshier et al. 2001; Lowman et al. 2018). Soto et al. (2019) proposed the use of averages between dry and wet season vegetation cover in a long time-series to show the representative vegetation cover, whereas Otto et al. (2011) and Dangles et al. (2017) used point measurements after precipitation and snowmelt events. However, considering only a limited set of measurements (satellite images) is risky and could introduce uncertainty, especially in the presence of meteorological anomalies, such as delayed rains or the occurrence of extreme events, as observed in Tilopozo. Therefore, it is crucial to account for the timing of vegetation peaks across different months to avoid inaccuracies. Additionally, evaluating vegetation during either wet or dry cycles can significantly impact the assessment of vegetated areas. These factors could lead to either over- or underestimations of vegetated surfaces, particularly in arid areas, influencing our understanding of wetland areas and the boundaries between permanent and temporary vegetation cover.

To address these challenges, the present study analyzed the permanence of the vegetation cover, dominant vegetation types, and environmental factors influencing the temporary vegetation cover using a chrono-sequence that encompassed all stages of plant growth. This approach provides a comprehensive view of the natural dynamics within wetlands, enabling the identification of subdivisions within the wetland and dynamic boundaries, which can be used as a threshold for ecosystem management (Coletti et al. 2014). It can also determine the maximum potential area of the wetland, its spatiotemporal probability, and the factors driving changes in temporary vegetation cover (Lowman et al. 2018; Al-Maliki et al. 2022; Wen et al. 2023).

This study also provides information that enables the assessment of the system's natural variability and resilience across different study years, including wetter and drier periods (Fath 2008; Green et al. 2008; Salomon 2008). In this

sense, the proposed framework helps define cores and surrounding temporary vegetation cover, offering practical criteria for conservation planning in hyperarid wetlands where regulatory definitions often assume static boundaries.

However, a limitation of the chrono-sequence study was the availability of field data (floristic composition) only for the most recent time subseries (2016–2019). If historical records had been available for each subseries, a better understanding of the changes in floristic composition based on observed wet and dry cycles could have been provided. Furthermore, the chrono-sequence analysis relied on Landsat images, with a spatial resolution of 30 m, which is less precise compared to other satellites. However, this was mitigated by the incorporation of high-resolution (visible) satellite imagery to corroborate the classifications generated by Landsat. However, Landsat has the advantage of offering an extensive temporal resolution, allowing for the evaluation of long-term vegetation cover stability and changes.

Conclusions

The Tilopozo wetland system, located in a hyper-arid environment of Salar de Atacama, is dependent on groundwater that drains from the MNT aquifer and is categorized as a phreatogenic discharge wetland system. Our results indicated that the proportion of surface covered with vegetation dependent on groundwater discharge acts as a permanent vegetation cover, both in terms of overall surface, which remained stable in the different subseries analyzed (pre-extraction, transition and aftereffects); and in specific areas within the system. This cover is dominated by strictly hygrophilous species, particularly *S. americanus* and *B. juncea*. In contrast, temporary vegetation cover, composed of transitional hygrophilous species such as *D. spicata* and *T. absinthioides*, depends consistently and significantly on precipitation and evapotranspiration behavior, with 2- and 4-month lags, respectively; as observed in different subseries analyzed. Notably, the deepening of the water table did not consistently influence the variation in the temporary vegetation cover, even considering the aftereffects subseries.

Our results demonstrate that the boundaries of the wetland system are not static, but highly dynamic, generating changes in its surface due to climatic factors. Our analysis offers a comprehensive and representative view of the various ecological dynamics observed, to identify stable areas, dynamic areas, and maximum surface potential areas of the wetland, as well as the spatio-temporal probability and environmental factors driving these changes. Such information is crucial for the effective management and conservation of wetland ecosystems. Based on these results, future research on wetlands, differentiating between stable and variable

areas, will enable a better understanding of the ecological dynamics and trends in vegetation cover over time, allowing for the evaluation of the potential effects of climate change on these ecosystems.

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Declarations

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