Ecohydrology and ecosystem services of a natural and an artificial *bofedal* wetland in the central Andes

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HIGHLIGHTS

- The expansion of bofedales by herders is a long-standing practice in the central Andes.
- The natural and the artificial bofedal show similar ecohydrological properties and ecosystem services.
- Soil organic carbon and soil water electric conductivity are related to plant species composition.
- Highly nutritious plant species show low correlation with environmental variables due to grazing.
- Artificial wetland creation enhances community livelihoods in a sustainable way.

GRAPHICAL ABSTRACT
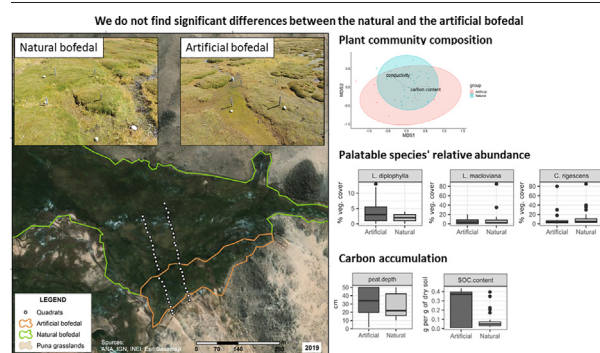
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ABSTRACT

High-altitude wetlands of the Central Andes, locally known as *bofedales*, provide important ecosystem services, particularly carbon storage, forage provisioning, and water regulation. Local communities have artificially expanded bofedales by irrigating surrounding grasslands to maximise areas for alpaca grazing. Despite their importance, biophysical processes of both natural and artificial bofedales are still poorly studied, which hinders the development of adequate management and conservation strategies. We analyse and compare the vegetation composition, hydrological variables, groundwater chemistry, and soil characteristics of a natural and an artificial bofedal of at least 10 years old in southern Peru, to understand their interrelations and the consequences for ecosystem service provisioning. We do not find statistically significant differences in the soil, water, and

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vegetation characteristics. Soil organic carbon (SOC) content, which we use as a proxy for carbon storage, is negatively correlated to dissolved oxygen, pH, and soil water temperature. In addition, Non-Metric Multidimensional Scaling analysis shows a positive relation between plant community composition, SOC content, and water electric conductivity. Our results suggest a three-way interaction between hydrological, soil, and vegetation characteristics in the natural bofedal, which also holds for the artificial bofedal. Vegetation cover of two of the most highly nutritious species for alpaca, *Lachemilla diplophylla* and *Lilaeopsis macloviana* with 19–22% of crude protein, are weakly or not correlated to environmental variables, suggesting grazing might be obscuring these potential relationships. Given the high economic importance of alpaca breeding for local communities, expanding bofedales artificially appears an effective strategy to enhance their ecosystem services with minimal impact on the ecohydrological properties of bofedales.

1. Introduction

The upper regions of the tropical and subtropical Andes above 3000 m are characterized by extensive grassland-dominated biomes that occur between the upper forest line and the permanent snowline (Buytaert et al., 2011). They range from the perennially humid *páramo* in Colombia, Ecuador, and northern Peru to the seasonal, semiarid *puna* of southern Peru and Bolivia (Josse et al., 2009). These regions also host abundant wetland areas, which contribute to different ecosystem services such as water supply (Buytaert et al., 2011; Ramsar Convention, 2005), carbon storage due to its potential to accumulate peat (Dise, 2009; Hribljan et al., 2015), and forage provision (Squeo et al., 2006), thus sustaining Andean wildlife and the welfare of human inhabitants (Salvador et al., 2014). In the highlands of Peru, Bolivia and northern Chile and Argentina, these wetland ecosystems are known as "*bofedales*", and are particularly important for water supply and grazing lands (Loyola-Gonzales, 2015; Squeo et al., 2006). Because of the arid climate, bofedales are only present as patches in the headwaters and along the water courses and springs, mostly above 3100 m altitude (Tapia-Núñez and Flores-Ochoa, 1984). Although bofedales research has recently increased due to their ecological and social importance (e. g. Chimner et al., 2019; Cooper et al., 2019; Hribljan et al., 2016; Valois et al., 2020), the characteristics and functions of these ecosystems are still poorly described.

The existence, characteristics, and functioning of wetlands are the result of very specific interactions between the local hydrology, soils, and biotic communities (Fennessy et al., 2007; Mitsch and Gosselink, 2000). Bofedales are mostly fed by precipitation but may also get contributions from groundwater and glacier melt (Cooper et al., 2010, 2019; Polk et al., 2017). As in other wetlands, their contribution to the water cycle will depend on their storage capacity and hydrological connectivity (Acreman, 2012; Acreman and Bullock, 2003). However, hydrological processes will in turn affect soil properties and influence underground water availability and temperatures (Cooper et al., 2010). Bofedales soils can also store significant amounts of carbon in the form of partially degraded organic matter (peat) and both soil properties and hydrological properties can influence peat deposition and decomposition rates (Chimner et al., 2020; Hribljan et al., 2015). Particularly plant species such as *Distichia muscoides* and *Oxychloe andina*, have been linked to the accumulation of large amounts of peat (Cooper et al., 2015; Oyague and Cooper, 2020). In turn, species composition and richness are related to the chemical properties of soil water, such as pH (Cooper et al., 2010).

Soil, water, and biotic conditions will also determine the resulting ecosystem services provided by bofedales. Globally it is estimated that peatland soils can store almost one third of the world's soil carbon even though they cover only 3% of the Earth's land area (Limpens et al., 2008). But the specific contribution of the tropical mountain peatlands to carbon storage and the main drivers of peatland accumulation has been insufficiently quantified (but see Hribljan et al., 2015, 2016; Planas-Clarke et al., 2020). In addition to carbon storage, forage provision is a very important ecosystem service of the bofedales, especially for local communities that depend on alpaca breeding among other animals (Maldonado-Fonkén, 2014; Squeo et al., 2006). For example, it was estimated that at least 1.5 million people living on the Peruvian Andean highlands depended

on alpaca breeding as their principal economic activity (CONACS, 2005 in Schmid, 2006). Bofedales provide a higher ratio of nutritious and palatable species to livestock than the surrounding dry grasslands (Tapia-Núñez and Flores-Ochoa, 1984). Animals grazing in low quality forage may be prone to slow development or pregnancy problems (Van Saun, 2013). For that reason, the amount of nutritious and palatable species can be used as an estimator of forage provision.

The Andean highlands of Peru have been inhabited by humans for at least the last 11,500 years (Engel, 1976; Rademaker et al., 2014). Hydrological alterations of the landscape have long been a part of agricultural practice, including the creation of terraces (Wei et al., 2016) and canals for irrigation and artificial recharge to increase dry season flows (Ochoatocachi et al., 2019) or fodder production (Verzijl and Guerrero, 2013). The expansion of bofedales by irrigating surrounding grasslands using canals, is also a common and long-standing practice among traditional camelid herder communities. Evidence suggests that agropastoralist communities have implemented these practices for the last 500–1000 years (Lane, 2006). However, few studies have documented the ecological, hydrological and soil dynamics of these artificially-expanded bofedales (Verzijl and Guerrero, 2013), or compared their ecological value and related ecosystem services to those of natural bofedales (Murillo-Pacheco et al., 2016). Such evidence base is necessary to support strategies for sustainable management and conservation of these ecosystems (Chimner et al., 2011). This is particularly relevant as bofedales have suffered from rapid and dramatic degradation in the last decades, especially as a result of mining, peat harvesting, road construction and overgrazing (Maldonado-Fonkén, 2014; Salvador et al., 2014). Alterations to their hydrological connectivity due to on-going climate change has also been observed (Polk et al., 2017).

To address these knowledge gaps and support bofedales management, this study aims to (1) identify the ecohydrological interactions (hydrological processes, soil characteristics, and vegetation) in a bofedal of southern Peru; (2) understand the consequences of these interactions for carbon storage and fodder provision, and (3) compare these characteristics between a natural and an artificial bofedal.

2. Materials and methods

2.1. Study site

The study site consists of a bofedal that spans between 71°17′10"W and 71°20′40"W and 15°38′30"S and 15°40′20"S, at 4413 masl in the community of Chalhuanca within the department of Arequipa in the southern Peruvian Andes (Fig. 1). Annual precipitation fluctuates between 200 mm and 590 mm and occurs mostly between January and March. Annual mean temperature ranges between 3 °C and 8 °C, while thermal fluctuations and frosts are common (Coaguila et al., 2010).

The local community has artificially expanded bofedales by irrigating some of the dry puna grasslands that surround the natural bofedales to increase fodder availability for alpacas (Fig. 1). We studied a natural bofedal and the adjacent artificial bofedal created after the construction of a canal. Although the exact date of the construction is difficult to be determined, the local herders assured that this canal was built at least 10 before the
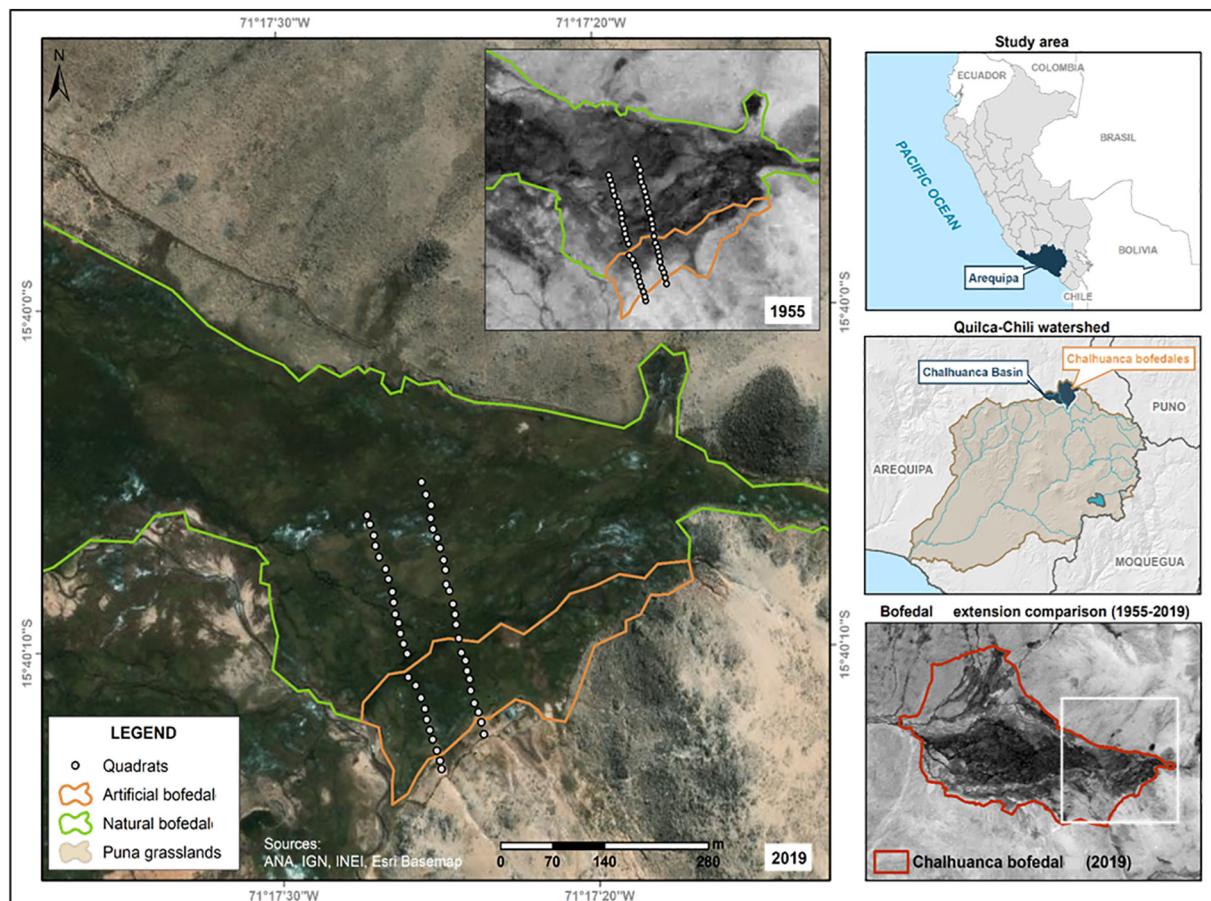
Fig. 1. Study area in Chalhuanca, Caylloma, Arequipa, Peru. Satellite image is from WorldView02, picture from November 27, 2019 (Image ID = 103001009E8A7100). Black and white aerial picture is from July 15, 1955 (Instituto Geografico del Peru). Dark tones reflect the presence of wetland in 1955. Satellite and aerial images were taken during the dry season.

fieldwork visit took place. Grazing fields that are used by the community are composed of a combination of bofedales (10% of the area) and puna grasslands (90%). Land management techniques include fertilization of the puna grasslands using alpaca excretions, agricultural field rotation between the puna grassland slopes and the bofedales, and bofedales irrigation (Descosur, 2018; Struelens et al., 2017). Alpaca herding is the main economic activity of the Chalhuanca community with 13,581 alpacas in 2016 (99.7% of all livestock; Descosur, 2018). This reflects the importance of Arequipa for alpaca breeding, the third most important department after Puno and Cusco with 12.7% of all alpacas recorded for Peru in 2011/2012 (INEI, 2012). In addition to local fodder provision, the area is also important regionally as it is located in the headwaters of the river basin that provides water to the city of Arequipa, Peru's second largest city (1,121,500 inhabitants).

2.2. Sampling design

We implemented fieldwork during the dry season (June) of 2019. We sampled along two transects, which both crossed the natural and the adjacent artificial bofedal (Fig. 1). We placed 1 m² quadrats every 10 m in alternating sides of each transect, totaling 44 quadrats (28 in the natural bofedal and 16 in the artificial bofedal). Each quadrat corresponded to a sampling point in which we collected information about vegetation, soil, and hydrological characteristics. In each quadrat we estimated total species richness (number of species), species composition (full list of all vascular plants) and visually determined the percent of vegetation cover for each species in the whole quadrat.

2.2.1. Soil characterization

We measured volumetric soil moisture (%) at 9 different points along the diagonals of each quadrat with an HH2 moisture meter and an ML3 Theta Probe sensor (15.8 cm long) that was inserted vertically. The first point was located at the center of the quadrat and the subsequent points were placed in each of the diagonals at 30 cm and 60 cm from the center respectively. We did each round of measurements twice and, if the measurements of the same point differed by more than 10%, the point was measured again. We took all measurements at approximately 15.8 cm depth and then averaged them per quadrat.

2.2.2. Soil organic carbon content

We collected one soil core of 50 cm depth close to each quadrat using a Russian D-section soil corer. After estimating peat depth (cm) with a ruler, based on colour and texture, we extracted the soil from the whole core to analyse carbon content (g per g of dry soil). Soil samples were analysed using the Walkley Black method (Walkley and Black, 1934) at the soil laboratory of the Universidad Nacional Agraria La Molina (UNALM, Peru). Quadrats with 50 cm of peat depth most likely have deeper peat, therefore those measurements should be read as "at least 50 cm".

2.2.3. Fodder characterization

We selected three palatable species according to what local herders considered that was preferred by their alpacas: *Calamagrostis rigescens* J. Presl, *Lachemilla diplophylla* (Diels) Rothm., and *Lilaeopsis macloviana*

(Gand) A. W. Hill from the Poaceae, Rosaceae, and Apiaceae family respectively. We collected approximately 10 g of leaves from each of these species and sun-dried the samples for 2 days before sending them to the laboratory of the UNALM for food nutritional assessment. We collected the leaves manually from outside the quadrats. Following the protocols of AOAC (2005), we measured four nutritional parameters of the samples: moisture content (%), ash content (%), crude protein (%) and crude fibre (%).

2.2.4. Hydrology and water quality characterization

We installed piezometers in the same cavity where soil cores were taken to manually measure water table depths. We used PVC tubes of 1.5 m length and a diameter of 7.6 cm, perforated every 5 cm and surrounded by a filter fabric to avoid the lateral entry of solids. The tubes were open at their bottom but tapped at their opening above the soil surface. All monitoring wells were at least 50 cm deep into the soil and water depth was measured from soil surface level. After overnight stabilization, we measured the water table depth manually once between 11 h00 and 16 h30 the following day. A water table depth close to the surface resulted in a value of 0, whereas the deeper the water table, the larger the negative value of water table depth. Additionally, we measured 4 water quality parameters: pH, electrical conductivity (µs/cm), dissolved oxygen (DO in %) and temperature (°C), using a Hanna HI 98194 multiparameter.

2.3. Statistical analysis

2.3.1. Interactions between hydrological, soil and vegetation variables

After testing for normal distributions using the Shapiro-Wilk test, we estimated a Spearman correlation matrix to identify which of the hydrological, soil and vegetation (species richness) variables interact. We then used a Non-Metric Multidimensional Scaling (NMDS) to evaluate the effect of environmental variables on plant communities by visualizing the ordination of communities' species composition. We appraised the effect of environmental variables on these communities through the envfit function of the R package "vegan", performing 10,000 permutations. The envfit function fits vectors of environmental variables to the ordination (Oksanen et al., 2019) using maximum correlation between the points and the corresponding environmental variables.

2.3.2. Influence of environmental variables and vegetation on ecosystem services

To determine the influence of environmental variables on fodder provision, we fitted the relative abundance of palatable species in a generalised linear model (GLM) with the relative cover of each species as the response variable and environmental variables (soil organic carbon –SOC– content, soil moisture, water table, water temperature, water pH, water dissolved oxygen –DO– and water electric conductivity) were used as explanatory variables. We fitted the GLM of *L. diplophylla* using the Poisson family while the quasi-Poisson family was used for the other species to correct for overdispersion. We used a null model to assess the contribution of transect or quadrat as random effects, but since these explained less than 2% of the variation, they were not used in the final model. We used a backward stepwise regression to eliminate variables, selecting only those that contributed to the model with minimal loss of fit. We assessed the normality of the residuals and homogeneity of variances through model plots.

We used peat depth as a proxy for carbon storage. The correlation between this proxy and hydrological, soil and vegetation (only species richness) variables was analysed in 2.3.1. To determine how community composition is related to carbon storage, we created Euclidean-distance matrices of community composition and peat depth and compared them through a Mantel test with 10,000 permutations. In addition, to determine which species were more related to peat accumulation, we constructed boxplots of peat depth by species. We used a Kruskal Wallis

test and the post-hoc Dunn test to compare between all species, using a Bonferroni correction to account for multiple comparisons.

2.3.3. Differences between the natural and the adjacent artificial bofedal

Lastly, we used a permutational multivariate analysis of variance to assess differences in community composition between the natural and the artificial bofedal. For this, we used 10,000 permutations, fitting the Bray-Curtis dissimilarity matrix as a response variable and the type of bofedal as an explanatory variable. In the same way, we used unpaired two-samples Wilcoxon-Mann-Whitney tests to compare environmental variables, richness of species, and the provision of ecosystem services between the two types of bofedal. We corrected for multiple comparisons using the Bonferroni correction and we report our results with 95% confidence. We performed all statistical analyses with the statistical software R version 3.6.1 using the core, lme4 and vegan packages (Oksanen et al., 2019; R core team, 2019).

3. Results

3.1. Vegetation composition

We identified a total of 29 plant species in the bofedal (Table A1). The most diverse botanical family is Asteraceae, followed by Poaceae. The most abundant species in the bofedal is the rush *Distichia muscoides* with a mean cover of 31.5% (SD = 32.7%), followed by the grass *C. rigescens* (mean coverage of 10.5%, SD = 17.9%), which was also the most frequent (present in 41 out of 44 plots). We also found 19 species that were only present in the grassland area, and that will be used as reference for future studies (Table A1).

3.2. Interaction between soil, water, and vegetation

The correlation matrix shows that seven soil and hydrological variables (SOC content, peat depth, water dissolved oxygen, water pH, water table and soil water temperature) have statistically significant correlation between them, while species richness is not correlated with any of the other variables (Fig. 2A). The NMDS combined with the envfit analysis showed that community composition is related mainly to SOC and to the electric conductivity of the soil water (Fig. 2B).

3.3. Relations between environmental variables and ecosystem services

3.3.1. Fodder provision

Lachemilla diplophylla had the best nutritional values of the compared species but the least mean vegetation cover among them (2.3% per quadrat). This species had the highest content of crude protein (22.18%) and ash (17.14%) and the lowest values of raw fibre (6.99%). *Lilaeopsis macloviana* had similar nutritional values, with high contents of protein (18.5%) and ash (16.77%) and low fibre content (10.86%). The moisture content was similar for all species, ranging typically between 6% and 8% but slightly higher in L. *diplophylla* and L. *macloviana* (Table A2). The relative abundance of L. *diplophylla* was negatively related to soil moisture and positively correlated to the water table depth (the higher the relative abundance the closer to the surface the water table) (Fig. 3A). *Calamagrostis rigescens* was negatively related to carbon content and water table (higher relative abundance at deeper water table) (Fig. 3C), while L. *macloviana* did not show any significant relations (Fig. 3B).

3.3.2. Peat accumulation

Peat depth was negatively related to water temperature, and positively correlated to SOC (Fig. 2A). Although species richness did not affect peat depth in the soil, we found a significant relation between plant community composition and peat accumulation ($r = 0.138, p < 0.005$). We did not find statistically significant association between single species and peat depth ($H = 36.477$, df = 28, $p = 0.131$). However, some of the most frequent species are present in quadrats with a median peat depth > 30 cm. Of
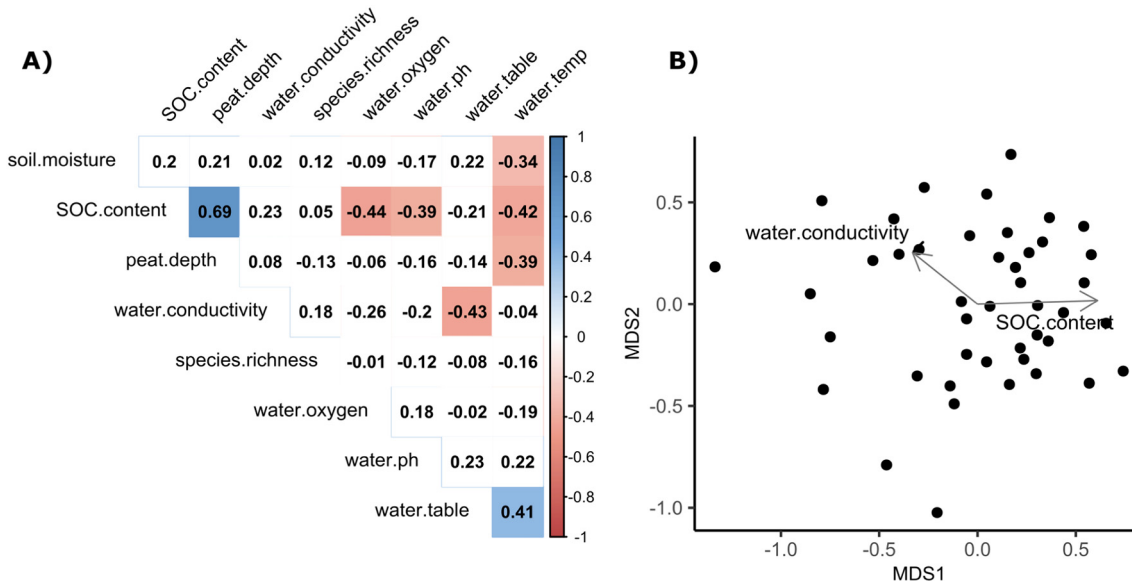
Fig. 2. Interactions between hydrology, soils and vegetation. **A)** Spearman correlation between hydrological, soil and vegetation variables, significant correlations (*p*-value <0.05) are shown as coloured squares. **B)** Nonmetric multidimensional scaling (NMDS) ordination showing the association between species composition and hydrological and soil variables. Black circles represent plant communities organised along the identified environmental gradients. Arrows represent the effect of significant environmental variables (envfit correlations) with *p* < 0.05. Only the significant variables are presented in the plot and the length of the arrows is proportional to the correlation.

these species, *Distichia muscoides*, *Phylloscirpus acaulis*, *Ourisia mucosa* and *Ranunculus flagelliformis* are present in areas with the deepest peat (50 cm of peat at least) (Fig. 4).

3.4. Differences between the natural and the artificial bofedal

We did not find any significant differences in the environmental conditions, species richness, nor in the ecosystem services between the natural and the artificial bofedal (Fig. 5). Plant community composition in the natural and the artificial bofedal did not differ from each other as shown in the NMDS plot where plant communities and species from both types of bofedales are not clearly separated (Fig. 6).

Both types of bofedal showed high variation associated with SOC (Fig. 5), potentially due to the topography and geology (bedrock) associated with the transects, where steeper areas had lower SOC, and less steep areas tended to accumulate higher SOC (Fig. A1).
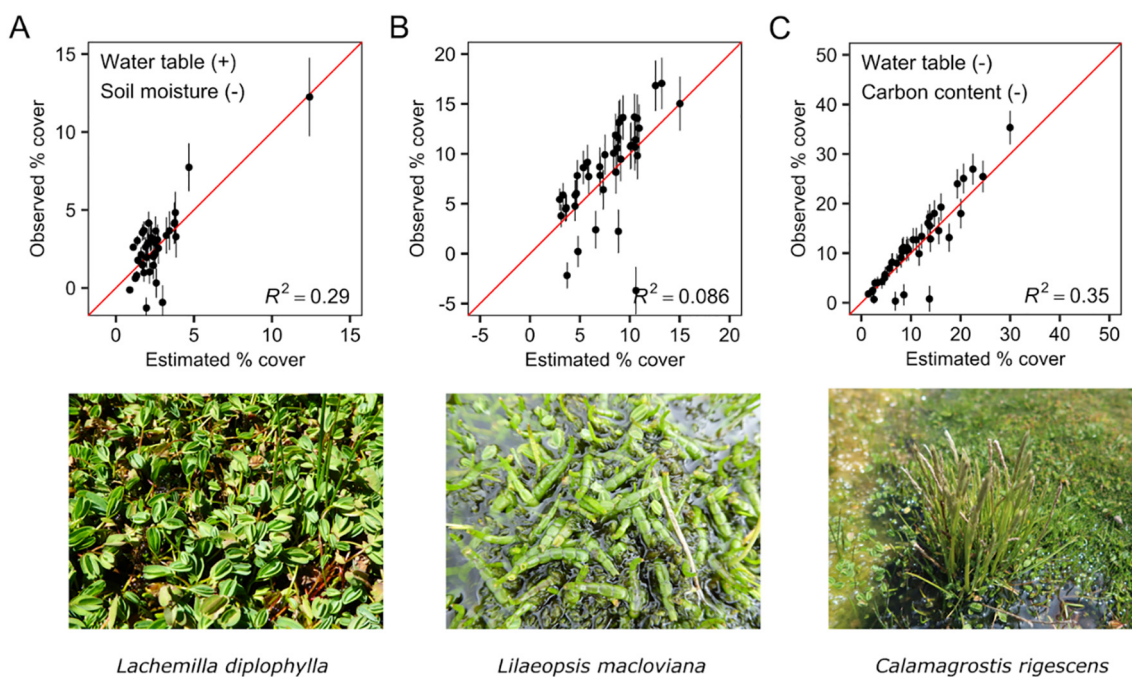
Fig. 3. Linear regression results for the vegetation cover percentage of three species that provide forage against soil characteristics and hydrological variables. Variables that had a significant effect (p < 0.05) are shown in each graph with their respective effect. The red line shows a 1:1 fit of the estimated values vs the observed values of the model. Pictures by Daniel Montesinos.
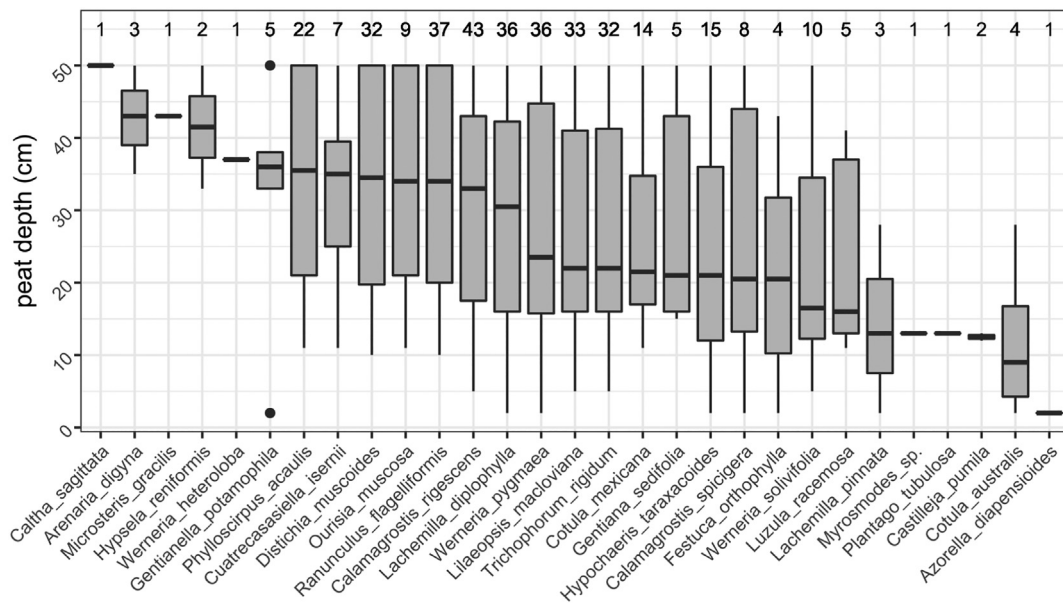
Fig. 4. Peat depth by species. The boxplots summarise the peat depth of all quadrats where a given species is present. Numbers at the top represent the number of quadrats for each species. The boxplots are ordered from highest mean peat depth (left) to lowest (right).

4. Discussion

4.1. Biogeochemical functioning

The development and functioning of bofedales is governed by the specific hydroclimatic and geological boundary conditions, which in turn will determine the specific ecosystem services, such as carbon storage,

forage provision and water regulation. We have conceptualized these influences and interactions in a diagram with stocks and flows (Fig. 7), which guides our discussion here.

Bofedales wetlands are located in the alpine grasslands from northern Peru to central Chile and Argentina, usually between 3200 and near 5000 masl (Squeo et al., 2006). While this region has a wide range of total annual average precipitation (200–1300 mm), the range of annual potential
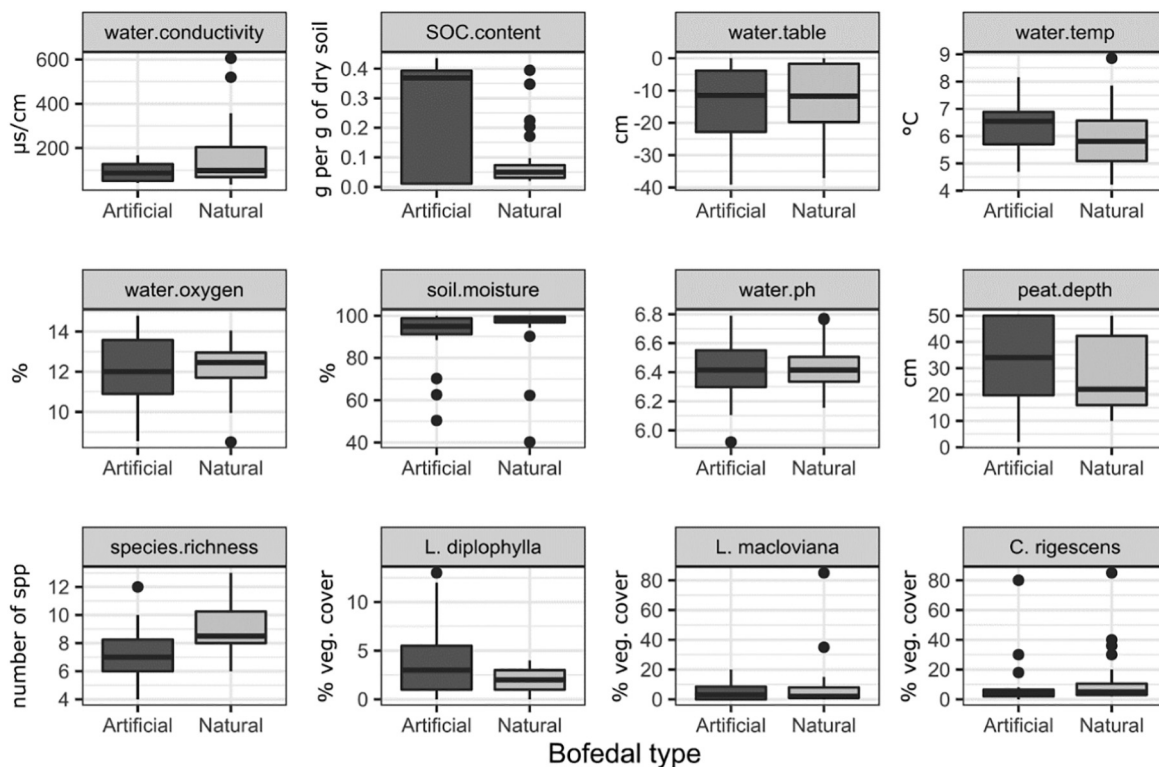

Fig. 5. Comparisons between hydrological, soil and vegetation variables between natural and artificial bofedales using Wilcoxon-Mann-Whitney tests. No significantly differences were found.
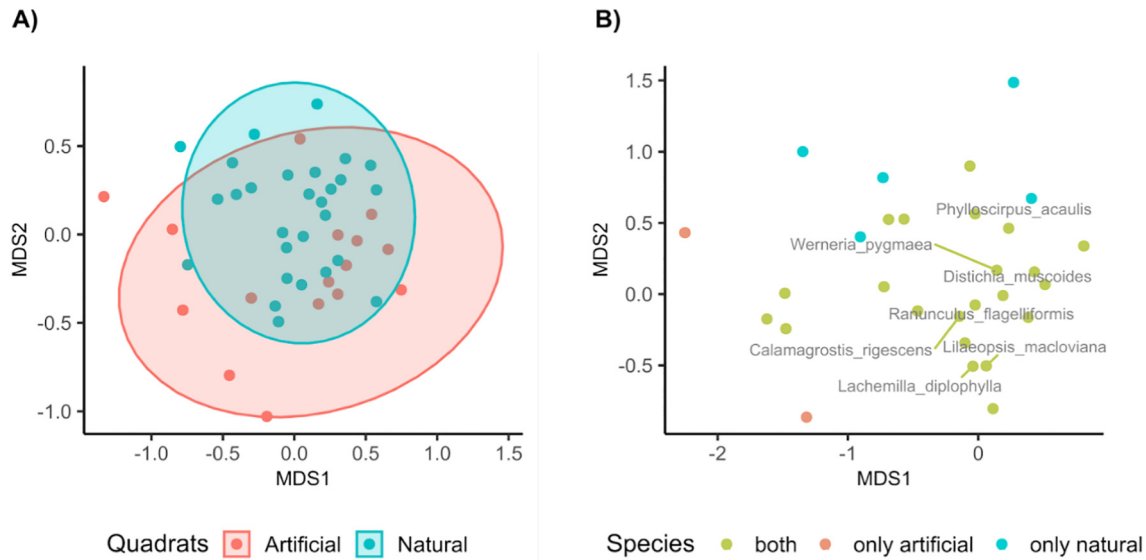
Fig. 6. Nonmetric multidimensional scaling (NMDS) ordination of plant communities in natural and artificial bofedales. A) Quadrats position in the NMDS axes. B) Species position in the NMDS axes. Species names are shown only for key species (for carbon or forage).

evapotranspiration is much narrower (500–1000 mm) (Aybar et al., 2017, 2020; Fig. 8). The precipitation regime of Chalhuanca is situated in the dry end of this spectrum and is representative of southern Peru, while bofedales in northern Peru are situated at the wetter extreme (Cooper et al., 2010). Seasonal variations in both precipitation and temperature are high (Fig. 8) but decrease along a South to North gradient, which makes southern bofedales, and particularly, those without glacier melt contributions, more vulnerable to seasonal trends in precipitation. The dry and seasonal climate is the main factor that differentiates bofedales located in the puna from wetlands located in wetter-grassland systems such as the paramos from the northern Andes (Josse et al., 2009). Compared to wetlands in the paramos, bofedales tend to have a lower accumulation of organic matter in the soils, and a different yet highly endemic species composition.

These characteristics are reflected in the properties of the Chalhuanca bofedal.

The dry conditions of the study region may be responsible for the particular species composition in these bofedales, with a lower abundance of *Distichia muscoides* and other cushion plants, and higher pH values compared to bofedales from Central Peru (Fuentealba and Mejía, 2016). Management activities may also play a role; however we believe that this is unlikely because of the high plant species richness (i.e. number of species), compared to other studies of nearby bofedales (Alvis-Ccoropuna, 2018; Coaguila et al., 2010; León-Tinoco, 2016). With a mean of 8 species/m^2 its richness is also higher than the 3.1 species/m^2 recorded in Huascaran National park in Central Peru under wetter conditions (Polk et al., 2019).
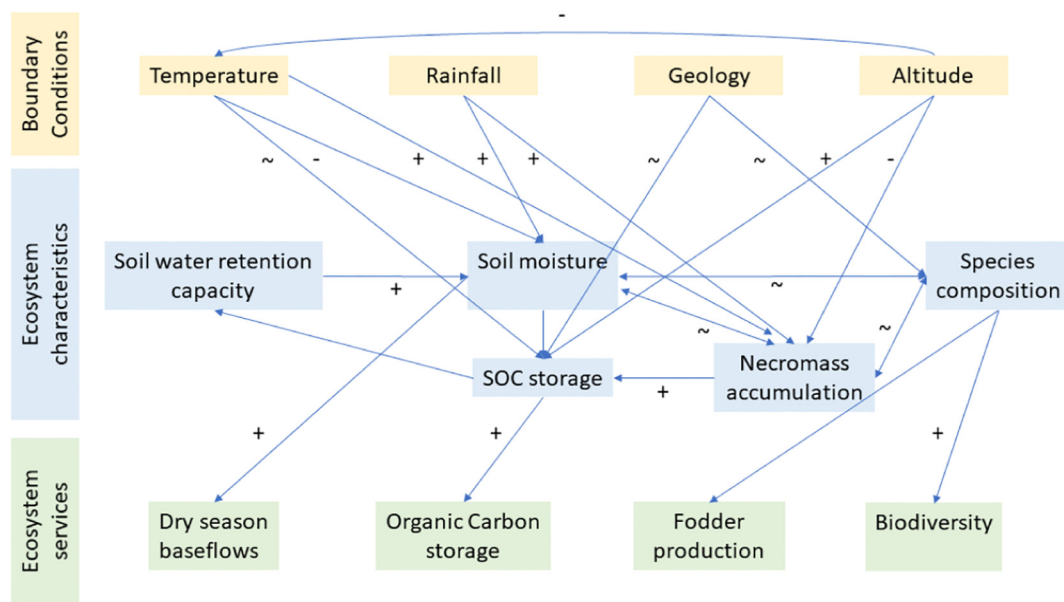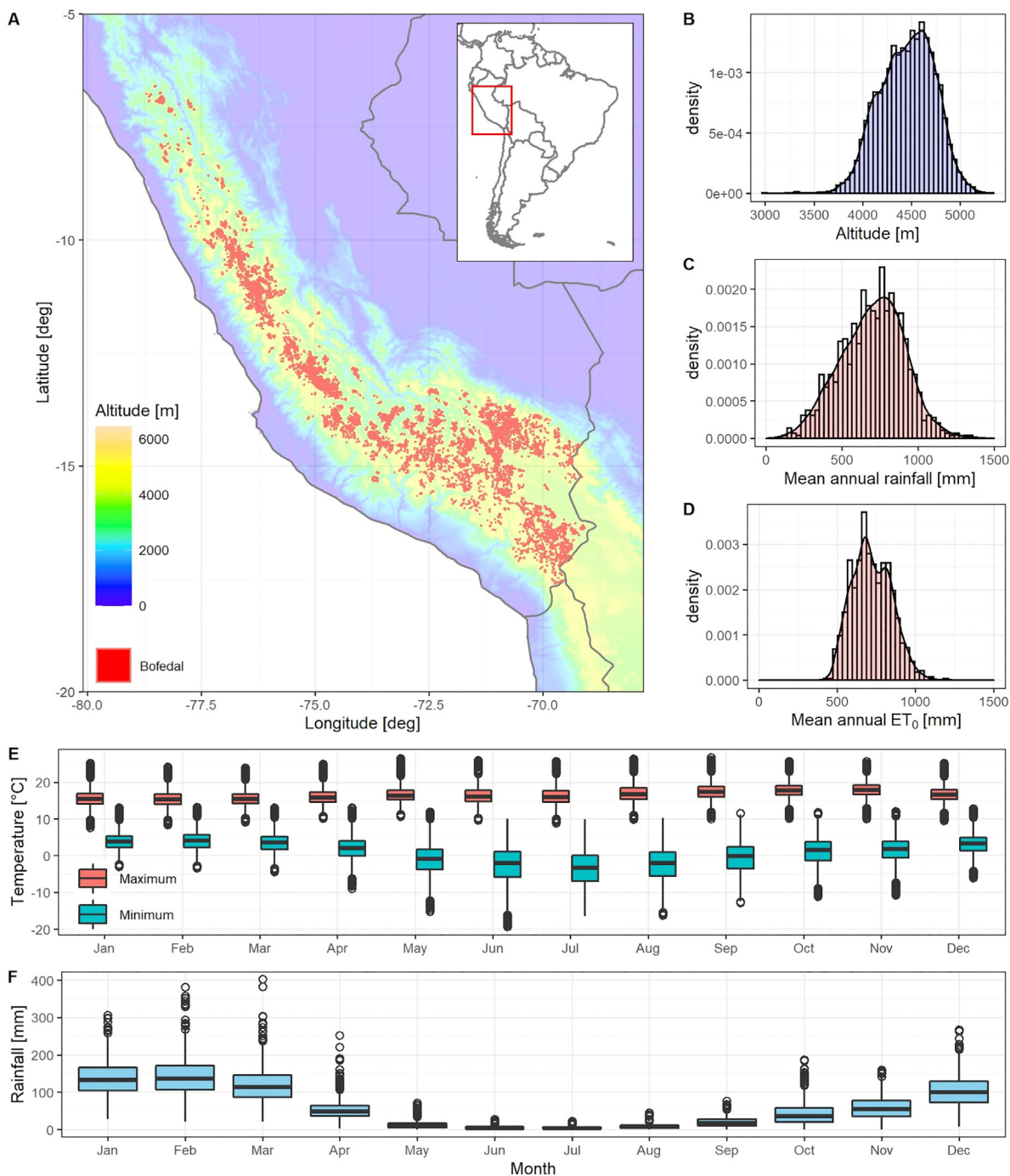

Fig. 7. Synthesis of the state of the art of our understanding of bofedales functioning. The different components of boundary conditions, ecosystem characteristics and the ecosystem services are shown where feedback can be positive (+), negative (−) or not well studied and yet to know its direction (~).

Fig. 8. Bofedales distribution in the Peruvian Andes and their climatic conditions. A) Spatial distribution of bofedales (MINAM, 2019) shown as red polygons. B) Altitude was derived from *elevatr* package (Hollister et al., 2021) at (approximate resolution 240mx240m pixel size). Significant outliers (altitude < 2000 masl) were removed. C) and D) Mean annual rainfall and mean annual evapotranspiration derived from PISCO v2.0 (Aybar et al., 2020) and PISCO v1.1 (Aybar et al., 2017) monthly datasets respectively for the period 1981–2016. E) Monthly maximum and minimum temperature for the period 1981–2016 (Aybar et al., 2020) F) Accumulated monthly rainfall for the period 1981–2016 (Aybar et al., 2020). Climatic variables are calculated by spatial joint with the *bofedales* shapefile; they represent local values and not contributing or catchment variables.

As in other types of wetlands, the accumulation of soil water is key to the production and accumulation of soil organic carbon and peat formation (Joosten and Clarke, 2002). Bofedales may form in local topographic depressions fed by small streams, as is the case for Chalhuanca. However, because of the seasonal nature of the precipitation regime (Fig. 8), a minimum contribution of dry-season streamflow or subsurface runoff is required to sustain bofedales during the dry season. The main source of water for the Chalhuanca bofedal is a small stream (18.3 km^2 of catchment area) but the geographical positioning of the bofedal suggests that it receives some subsurface contribution from nearby hillslopes.

The dynamics of subsurface flow patterns in high mountain regions, and how they determine the development and location of bofedales, are still poorly understood. Research on páramo wetlands has shown that the topographic index, which combines upslope contributing area with the local slope, is a good predictor for the occurrence of saturated

areas (Buytaert and Beven, 2011). However, as the topographic index is derived from a digital elevation model, it cannot account for the contribution of deep subsurface flow or subsurface flows that do not follow surface flow lines. In addition, it does not account for both surface and subsurface connectivity. Evidence suggests that these are important processes in bofedales, as a result of the presence of lateral moraines on hillslopes, talus or bedrock, as well as resurfacing glacier meltwater in glacierized areas (not the case in Chalhuanca), could be substantial water sources for bofedales (Cooper et al., 2010, 2019; Polk et al., 2017). This has implications for the sensitivity of bofedales to variations in the seasonal weather cycle. The lack of seasonal snow cover in these regions means that bofedales will only exist in locations where the local topography and subsurface flow contributions can sustain perennially wet conditions, despite the high atmospheric evaporative demand. Changes in the water balance, for example an increase in evaporative demand or an intensification of the seasonal cycle as a result of global warming, may affect this ability negatively.

A three-way ecohydrological interaction between vegetation, soils and hydrology appears to exist (Fig. 7). Studies in other high-altitude wetlands have shed light on the positive feedback between soil water retention capacity and organic carbon accumulation (Buytaert et al., 2007, 2006). As plants are the main source of organic carbon, vegetation may be a further cause of differential soil development between wetlands and the surrounding areas; however, available evidence on this process is much more limited (Benavides et al., 2013).

Here we find indeed that plant community composition is related to SOC. The bofedal area has a predominance of species that have been associated with peatland accumulation, for example the cushion-forming species *D. muscoides* (Cooper et al., 2010). Although we did not measure water retention in this study, the positive correlation between cushion-forming species and soil organic carbon, nutrients and soil moisture is documented elsewhere (Anthelme et al., 2012; Hupp et al., 2017). Frequent species present generally in the quadrats with the deepest peat include *Phylloscirpus acaulis, Distichia muscoides,* and *Ranunculus flagelliformis.*

According to our results, water electric conductivity and soil organic carbon are the main environmental variables that determine plant community composition in the bofedal. Previous studies have also found that groundwater chemistry is an important driver of floristic composition (Cooper et al., 2010; Tovar et al., 2012). SOC is often considered a key determinant of soil fertility and plant growth (Ontl and Schulte, 2012). Soil organic matter improves soil quality by increasing water and nutrient retention and thus it improves the productivity of plants (Herrick and Wander, 1997). Similarly, soil organic carbon content is related to the transfer of carbon from the plant to microbial symbionts, hence higher values of SOC could be considered an indicator of good functioning (Ontl and Schulte, 2012). Likewise, electric conductivity is determined by the quantity of mineral salts and it is an important factor for assessing water quality (Tutmez et al., 2006). Higher electric conductivity corresponds to higher osmotic pressure around the roots, which may cause oxidative stress (Wang et al., 2003) and even the denaturation of functional structures and proteins (Smirnoff, 1998).

4.2. Implications for ecosystem services provision

Since Chalhuanca is located in a high-altitude area, where agricultural land is scarce and the only source of income comes from alpaca breeding (Descosur, 2018), forage provision, mainly for alpacas, is one of the most important ecosystem services for the local community. Analyses of the nutritional composition of the diet selected by free-ranging alpacas are scarce (López-López, 2004), but it has been reported that L. *diplophylla* has an average of 21.0% crude protein, 12.1% ash and 19.9% fibre in wet season (Alzérreca et al., 2001). These values are comparable to our results, and small differences could be attributed to seasonal effects (Reiner and Bryant, 1986; Van Saun, 2013). L. *diplophylla* and L. *macloviana* have both high nutritional values in our results

(e.g., >18% of crude protein). It has been reported that their nutritional value is higher than that of *D. muscoides* in the same season (Alzérreca et al., 2001). Given that alpacas select the composition of their diet in order to get a better nutritional balance (Tapia-Núñez and Flores-Ochoa, 1984) and that they change their diet according to the season (Arana-Ccencho, 2014; Castellaro et al., 2004), it may be valuable to compare the nutritional values of palatable species in both seasons. The shift in diet may be caused by seasonal nutritional changes rather than by availability of the species.

The vegetation cover of L. *diplophylla* can be explained statistically by soil moisture and water tables but with confounding effects, while the cover of L. *macloviana* is not explained by the measured environmental variables. Alpaca grazing may be responsible for the low explanatory values of the two highly nutritious species since much of their cover would be removed during grazing. This is in line with the observation that all three forage species studied here are present in more than half of the quadrats but the more nutritive ones (L. *diplophylla* and L. *macloviana)* with a much lower cover (2–6%) than the less nutritive *C. rigescens* (10%).

At a regional scale, bofedales are considered important for downstream water supply. However, water-related ecosystem services constitute a trade-off between water storage capacity, and increased evaporation. A high-water storage capacity in bofedales tends to support subsurface runoff and base flows in rivers descending from the puna. This may be crucial for downstream water supply systems, which often depend on surface runoff from the highlands, especially in arid regions such as the Peruvian coast. However, the high-water storage capacity of bofedales will also cause a higher evaporative flux compared to the surrounding landscape, thus reducing the overall runoff from the catchment. The significance of either process will depend on the regional hydrological setting; however, as the total area of bofedales is limited, the impact of increased evaporation is thought to be negligible in most cases.

More recently, bofedales have received attention for their carbon storage capacity (Maldonado-Fonkén, 2014). We find a mean peat depth of 30 cm, which is below the threshold used to classify bofedales as peatlands (> 40 cm) or wet meadows (< 40 cm) (Chimner et al., 2019). Mean soil organic carbon content of the 50 cm soil core was also low (0.22 g per g of dry soil (22%) in natural bofedales) compared to other wetter bofedales, such as those located in Cajamarca (18–35% measured in 0–40 cm depth; Cooper et al., 2010) or in the seasonally flooded bofedales in Puno (63.4% measured in the first 30 cm of soil; Segnini et al., 2010). These low values are however not uncommon in nearby bofedales (Coaguila et al., 2010). This may result from a more seasonal precipitation in our study area but also potentially from the dilution effect caused by the accumulation of mineral material. Bofedales may trap dust or be prone to deposition of erosion from higher parts of the landscape. These processes may also be responsible for the high spatial variation in soil organic carbon content that we observe between the samples. However more studies are needed to understand these regional and local patterns, and to account for any potential grazing effect on SOC.

The anaerobic conditions caused by high water levels (Planas-Clarke et al., 2020) make that biomass production rates exceed decomposition rates (Chimner and Ewel, 2005). This is consistent with our findings of a negative correlation between water dissolved oxygen and SOC. However, we do not observe a significant relationship between SOC and water table. Water table values range from 0 to −40 cm, which are similar to those observed in the same dry season in bofedales from Lima and Junin, around 600 km northwest of our study area (Oyague-Passuni, 2021). The limited number of observations to the driest period may play a role in this lack of significance. The negative correlation between SOC content and peat depth with soil water temperature may be caused by soil heat capacity: soils with high SOC content and peat depth will have a higher water storage capacity. As a result of the high heat capacity of water, these soils will heat up more slowly during the day.

4.3. Natural vs artificial bofedal

The creation of artificial bofedales by means of irrigation canals is an ancient practice (Lane, 2006; Verzijl and Guerrero, 2013). At the time of study, the artificial bofedal studied here was reported to be at least 10 years old, however, expansions and contractions in the larger bofedal area may have occurred at least throughout the last 70 years (Fig. 1). Contractions were likely influenced by dry periods, for example those occurring in the Andean region as a result of the El Niño Southern Oscillation. Whereas long-term overall expansion of the bofedal is most likely the result of human management. This is not surprising given the importance of expanding bofedales for alpaca breeding, whose population in Arequipa has increased in 103% between 1994 and 2012 (INEI, 2012). Alpaca breeding is a key economic activity in the Arequipa highlands for textile, meat, and leather production. For example, an average of 300 t/month of alpaca fibre were exported just from Arequipa, 1 of the 17 departments of Peru with alpaca populations, between 2012 and 2018, with an export free on board (FOB) price ranging between $11 and $20 per kilo, depending on the fibre quality and treatment (MINAGRI - DGPA - DEEIA, 2019).

Human management may affect the interactions between vegetation, soil, and hydrology, with potential implications for the ecosystem services. However, our results show that the natural and the artificial bofedal have similar levels of abundance of palatable species and carbon accumulation. We were expecting less developed soils in the artificial bofedal; however, its similarity in soil characteristics, including SOC and peat depth, to the natural bofedal suggests that carbon storage is occurring. Moderate management does not seem to impact any of the two major ecosystem services identified above.

The use of irrigation canals to rewet the bofedales can be applied also for their restoration. For example, inspired by this ancient practice in Chalhuanca, SEDAPAL, a Peruvian water state company has started its first project in the bofedal of Milloc (Lima, Peru) to recover its ecosystem services (Gammie et al., 2021). Ancient techniques can therefore contribute to nature-based solutions aiming to improve, forage, carbon storage and water security.

5. Conclusions

High-altitude wetlands are a key landscape element of mountain regions such as the Andes and the Himalayas because of their potential for carbon storage and the provision of local ecosystem services. Yet, studies on their traditional management and functioning, which are necessary for their conservation, remain limited. This study contributes to a better understanding of these wetlands in the Andes (bofedales) and particularly the beneficial impact of artificial expansions.

Our results suggest interactions between hydrological, soil and vegetation characteristics. These interactions are indicative of potential feedback loops between those components. The clearest of those loops is between soil organic carbon, water retention, and vegetation. Based on our results, we hypothesize that soil organic carbon accumulation supports soil water retention, which determines the species composition and enhances biomass production, thus enhancing further carbon accumulation. This is reflected in the significant relation between plant species composition and SOC. Therefore, further studies should integrate these components to better understand the dynamics of these interactions, for example by looking at the temporal co-evolution of plant species, soil properties, and soil humidity in artificial bofedales.

Carbon storage and fodder provision, measured as peat depth and nutritional content and vegetation cover of three species respectively, show variable associations with different hydrological and soil properties, which could be influenced by the grazing regime. Among the most frequent species, *Distichia muscoides, Phylloscirpus acaulis* and *Ranunculus flagelliformis* occur in quadrats with the deepest peat. However, Chalhuanca bofedales have lower peat accumulation (mean of 30 cm) than those in the northern bofedales, potentially due to the high precipitation seasonality found in the

region and grazing activities. *Lachemilla diplophylla* and *Lilaeopsis macloviana* have high protein content (> 18%) and are frequent but more studies are needed to analyse nutritional variation between wet and dry season. When comparing the natural and the artificial bofedal, we found that the provision of carbon storage and fodder, the soil-water properties, and species composition are similar between them. This suggests that moderate management conducted by local communities has successfully expanded bofedales, increasing their ecosystem services and creating new areas to offset the grazing pressure on natural bofedales. Local communities recognize the importance of the bofedal as a provider of fodder and water for their domestic herds (Fuentealba and Mejía, 2016). Therefore, in order to increase the interest of local communities in bofedal conservation, restoration strategies should really emphasize the provision of these ecosystem services.

Conserving and restoring high-altitude wetlands is of utmost importance not only for carbon storage and forage provision but also to ensure water security for the millions of people living in mountains worldwide. Moderate management using irrigation canals can help restore the water-soil-vegetation interactions in these wetlands leading to increased or improved ecosystem services. A better understanding of other ancient practices in mountain regions can help in identifying nature-based solutions to urgent problems their populations are currently facing.

Our study is one of the first studies to analyse the eco-hydrological impact of artificial expansions of Andean wetlands and how these artificial expansions can contribute to the provision of ecosystem services. We hope that this study can serve as a base line for future long-term studies about the ecology and succession of natural and artificial bofedales. In the same way, we hope to bring light to the work that the local community can do to protect the water sources, and the benefits of this practice, manifested as increased ecosystem services. For future studies, we suggest including other bofedales with different water balances but similar management regimes, sampling during both wet and dry season periods, and considering other water quality variables such as nutrients content.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

María J. Monge-Salazar: Conceptualization, Methodology, Software, Validation, Formal analysis, field work, Data Curation, Writing - Original

Appendix A

Table A1

List of species found in Chalhuanca using 44 x 1m² quadrats in the bofedales and 4 in the adjacent dry Puna grassland. Mean cover, standard deviation and frequency considered the 48 quadrats.

Family	Species	Mean cover (%)	Standard deviation (%)	Frequency (number of plots)	Vegetation unit
Apiaceae	*Azorella diapensioides*	0.48	2.91	2	Bofedal and Puna grassland
Apiaceae	*Lilaeopsis macloviana*	6.67	13.52	31	Bofedal
Asteraceae	*Belloa piptolepis*	0.08	0.45	1	Puna grassland
Asteraceae	*Cotula australis*	0.31	1.31	3	Bofedal
Asteraceae	*Cotula mexicana*	0.58	1.07	8	Bofedal
Asteraceae	*Cuatrecasasiella isernii*	0.23	0.63	3	Bofedal
Asteraceae	*Hypochaeris taraxacoides*	0.56	0.97	9	Bofedal
Asteraceae	*Laennecia artemisiifolia*	0.15	0.71	2	Puna grassland
Asteraceae	*Werneria heteroloba*	0.04	0.29	1	Bofedal
Asteraceae	*Werneria pectinata*	0.04	0.29	1	Puna grassland
Asteraceae	*Werneria pygmaea*	9.48	13.62	33	Bofedal
Asteraceae	*Werneria solivifolia*	0.56	1.20	9	Bofedal
Brassicaceae	*Brayopsis calycina*	0.02	0.14	0	Puna grassland
Brassicaceae	*Mancoa hispida*	0.08	0.40	2	Puna grassland
Campanulaceae	*Hypsela reniformis*	0.04	0.20	0	Bofedal
Caryophyllaceae	*Arenaria digyna*	0.13	0.39	1	Bofedal and Puna grassland
Caryophyllaceae	*Pycnophyllum glomeratum*	0.13	0.87	1	Puna grassland
Cyperaceae	*Phylloscirpus acaulis*	6.35	13.26	20	Bofedal
Cyperaceae	*Trichophorum rigidum*	10.04	17.59	30	Bofedal
Fabaceae	*Astragalus micranthellus*	0.02	0.14	0	Puna grassland
Gentianaceae	*Gentiana sedifolia*	0.15	0.46	2	Bofedal
Gentianaceae	*Gentianella potamophila*	0.13	0.39	1	Bofedal
Geraniaceae	*Geranium sessiliflorum*	0.06	0.32	1	Puna grassland
Juncaceae	*Distichia muscoides*	31.52	32.74	32	Bofedal
Juncaceae	*Luzula racemosa*	0.21	0.65	4	Bofedal
Malvaceae	*Nototriche anthemidifolia*	0.02	0.14	0	Puna grassland
Malvaceae	*Nototriche rugosa*	0.02	0.14	0	Puna grassland
Malvaceae	*Tarasa nototrichoides*	0.04	0.20	0	Puna grassland
Orchidaceae	*Myrosmodes* sp.	0.06	0.43	1	Bofedal
Orobanchaceae	*Castilleja pumila*	0.04	0.20	0	Bofedal
Plantaginaceae	*Bougueria nubicola*	0.13	0.64	2	Puna grassland
Plantaginaceae	*Ourisia muscosa*	0.29	0.71	2	Bofedal and Puna grassland
Plantaginaceae	*Plantago sericea*	0.08	0.35	1	Puna grassland
Plantaginaceae	*Plantago tubulosa*	0.04	0.29	1	Bofedal
Poaceae	*Calamagrostis curvula*	0.33	1.45	3	Puna grassland
Poaceae	*Calamagrostis rigescens*	10.50	17.91	41	Bofedal
Poaceae	*Calamagrostis spicigera*	1.81	9.39	8	Puna grassland
Poaceae	*Dissanthelium calycinum*	0.13	0.64	2	Puna grassland
Poaceae	*Festuca orthophylla*	1.56	6.21	6	Bofedal and Puna grassland
Poaceae	*Muhlenbergia peruviana*	0.08	0.40	2	Puna grassland
Poaceae	*Poa* sp.	0.06	0.43	1	Puna grassland
Polemoniaceae	*Microsteris gracilis*	0.04	0.20	0	Bofedal and Puna grassland
Ranunculaceae	*Caltha sagittata*	0.02	0.14	0	Bofedal
Ranunculaceae	*Ranunculus flagelliformis*	1.40	1.14	20	Bofedal
Rosaceae	*Lachemilla diplophylla*	2.33	2.79	26	Bofedal
Rosaceae	*Lachemilla pinnata*	0.19	0.61	3	Bofedal and Puna grassland
Rosaceae	*Tetraglochin cristatum*	0.27	1.35	2	Puna grassland
Verbenaceae	*Junellia minima*	0.04	0.29	1	Puna grassland

Table A2

Nutritional values of collected fodder species in Chalhuanca.

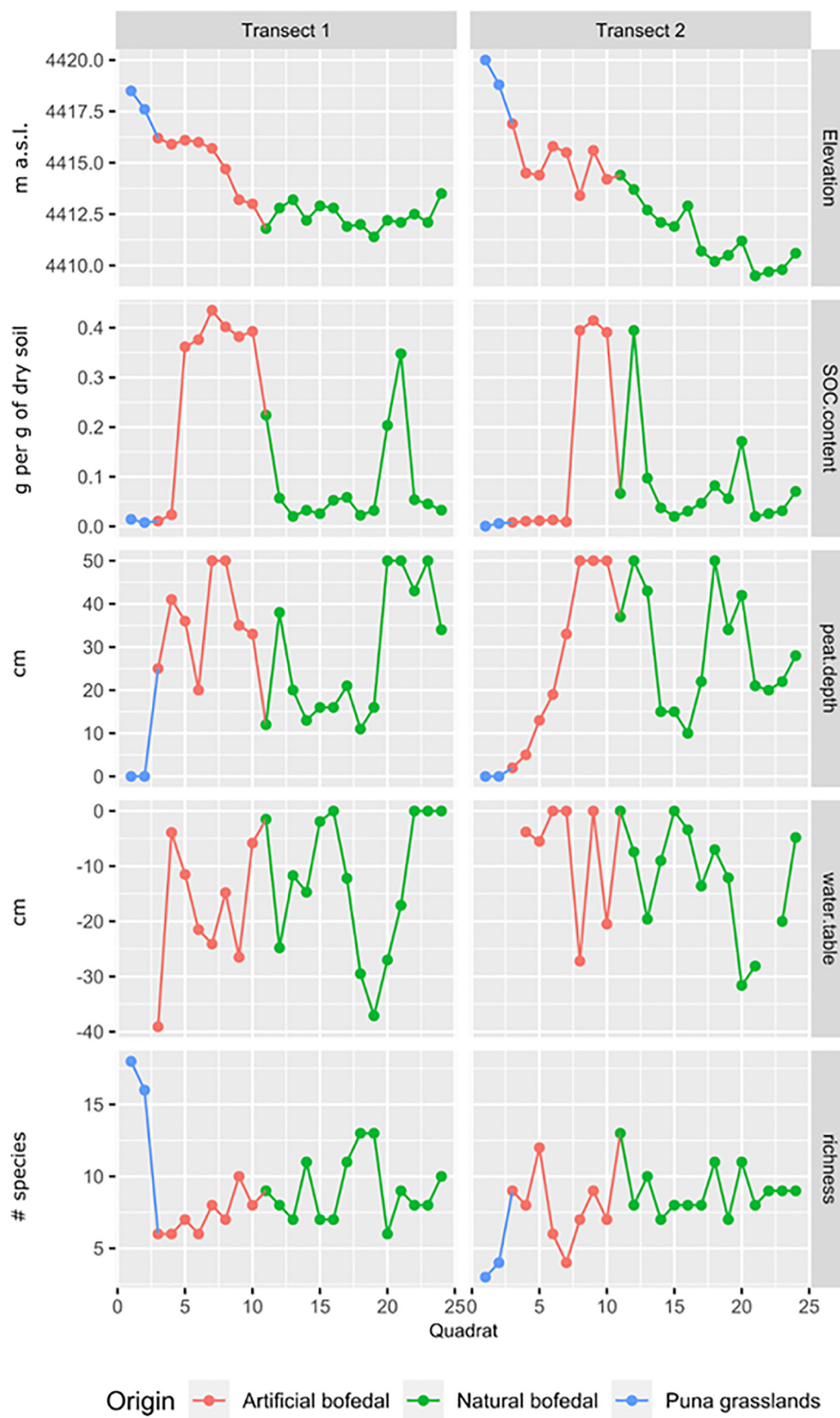| Variable	*Calamagrostis rigescens*	*Lachemilla diplophylla*	*Lilaeopsis macloviana*
Moisture (%)	6.04	8.04	7.28
Crude protein (%)	8.58	22.18	18.5
Raw fibre (%)	22.63	6.99	10.86
Ash (%)	8.08	17.14	16.77

Fig. A1. Changes in elevation, SOC content, peat depth, water table depth and species richness along the two transects. Each point represents a quadrat ordered from outside the border of the bofedal (left) to inside the bofedal (right). Plots taken in puna grassland were included to allow comparison with bofedales, but those plots were not included in the analyses.

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