Plant community assembly is predicted by an environmental gradient in high-altitude wetlands in the semiarid western Bolivian Andes

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SUMMARY

The floristic composition and distribution of plant communities is the product of species-specific responses to localized environmental conditions often structured following environmental gradients. Although the importance of Andean high-elevation wetlands (*bofedales*) for provisioning ecosystem services has been critically emphasized in various studies, very little is known about how different micro-environmental factors shape their zonation and community assembly. Here we examined and quantified differences in herbaceous plant composition, alpha diversity, and aboveground biomass within waterlogged and dry habitats in three *bofedales* located in western Bolivia. Our results show that although alpha diversity was similar between both habitats, obligate wetland taxa were more abundant in waterlogged habitats whereas upland graminoids and halophytes were predominant in desiccated habitats. Furthermore, aboveground biomass of obligate wetland graminoids was higher in waterlogged habitats, while saline tolerant forbs exhibited higher aboveground biomass in desiccated habitats. Together these results suggest that soil water and organic matter content largely governs plant composition and biomass production but not alpha diversity in the studied high-altitude Andean wetlands. These results have important consequences for predicting plant species' response to changes in the hydrological cycle due to habitat degradation and aridification caused by land use intensification and global climate change.

KEY WORDS: aboveground biomass, alpha diversity, bofedales, zonation

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INTRODUCTION

Andean high-elevation wetlands, commonly known as *bofedales*, are one of the most productive alpine ecosystems above 3,000 m above sea level. Characteristically, bofedales are subject to extreme environmental conditions, including semiarid and cold weather, intense solar radiation, daily frost, and hypoxic soils (Squeo *et al.* 2006, Beck *et al.* 2010, Otto *et al.* 2011). Bofedales provide key ecosystem services including carbon sequestration, regulation of water flux, soil protection, phytoremediation, and habitat for endemic species (Earle *et al.* 2003, Cooper *et al.* 2010, Miguel *et al.* 2013, Maldonado Fonkén 2014, Servat *et al.* 2018, Valois *et al.* 2020). Moreover, they provide the most productive grazing forage consumed by native (llamas and alpacas) and introduced (sheep and cattle) livestock in the highland Andes and have constituted a central economic resource for traditional pastoralist native communities for at least four millennia (Reiner &

Bryant 1986, Moreau *et al.* 2003, Alzérreca *et al.* 2007, Verzijl & Quispe 2013, Villarroel *et al.* 2014, Gandarillas R. *et al.* 2016, Domic *et al.* 2018, 2019).

While high-altitude Andean wetlands have been understudied in comparison to other upland ecosystems, there has been a growing interest in describing plant richness (Squeo *et al.* 2006, Ruthsatz 2012, Maldonado Fonkén 2014, Meneses *et al.* 2019), compositional patterns (Alzérreca *et al.* 2001, Salvador *et al.* 2014, Loza Herrera *et al.* 2015, Meneses *et al.* 2015), and the impacts of grazing on their vegetation abundance and diversity (García *et al.* 2014, Urbina & Benavides 2015, Danet *et al.* 2017, Carevic *et al.* 2019). Recent estimates have shown that bofedales are distinguished by a high plant taxonomic richness (~120 species), including several endemics and habitat-specialists (Meneses *et al.* 2019, Polk *et al.* 2019). Nevertheless, how the high number of species that characterize these plant communities are able to coexist is still poorly understood. By evaluating the role of abiotic drivers

1

on patterns of species richness and community composition in bofedales, we could identify which factors control species occurrence, diversity patterns and community assembly and predict the potential effects of ongoing global climate change.

Environmental gradients affect the plant communities of wetland ecosystems in various ways (Blom & Voesenek 1996). The physiological and ecological adaptations of individual species determine their ability to survive and tolerate flooding and droughts during their lifespan (Damgaard *et al.* 2017). Empirical studies have shown that hydrological gradients play a major role in the composition and zonation of vegetation, which primarily reflects differential response of wetland taxa to flooding (Blom & Voesenek 1996, Silvertown *et al.* 1999, Valdez *et al.* 2019). Furthermore, the hydrological regime experienced by wetland species at a local scale depends on the interaction between basin hydrology and geomorphology, which can create gradients of flood height and duration, shaping the diversification and distribution of various plant communities.

Given that Andean wetlands are being replaced by grasslands or saltpans characterized by contrasting plant communities and soil properties due to aridification processes (Minckley *et al.* 2013, Yager *et al.* 2019), it is critical to assess the mechanism involved on niche separation and variation in plant community structure and composition. To understand the link between plant community assemblage, diversity and above-ground biomass and environmental conditions, we studied the composition of plant communities and measured environmental factors, soil water content, and organic matter content in surface samples from three highland wetlands in western Bolivia. These factors are expected to vary along the wetland micro-topography, which is characterized by a network of small streams intermixed with shallow ponds with some areas saturated with water and others with low water availability. We compare abundance, alpha diversity and aboveground biomass between waterlogged and desiccated habitats in three closely located bofedales. Assuming that environmental heterogeneity has an important effect on plant niche separation, this study addressed the following hypotheses: 1) Environmental heterogeneity produces different plant diversity patterns in Andean wetlands, evidenced by contrasting plant vegetation communities; 2) Habitats with desiccated soils and low organic matter content exhibit lower abundance of obligate wetland forbs and graminoids due to their sensitivity to soil desiccation; and 3) desiccation-tolerant plants (e.g. halophytes and upland taxa) that

exploit water more efficiently exhibit higher aboveground biomass in comparison to obligate wetland plants in habitats with desiccated soils and low-organic matter content.

METHODS

Study area

We conducted our research in three Andean high-altitude wetlands located in the Charaña municipality of the western Bolivian Andes, near the tripartite border with Chile and Peru (16° 59' – 18° 09' S, 68° 36' – 70° 06' W) (Figure 1). The studied wetlands are part of the tributary streams that flow into the Mauri River and eventually into Lake Poopo by means of the Desaguadero River. The climate is semiarid and cold, with an average mean annual temperature of 6.3 °C and an average total annual precipitation of 312 mm (SENAMHI 2016). Seasonal variation in precipitation produces changes in the water table with a reduction of water availability during the dry season between May and August (Agua Sustentable 2016). The rainy season occurs between November and April and 90 % of the total annual precipitation is concentrated during this time. The surrounding vegetation cover is scarce and typical of the xerophytic *puna* landscape including tussock grasslands (*Deyeuxia*, *Festuca* and *Poa*), sclerophylous shrubs (*Baccharis* and *Parastrephia*), and a few patches of *Polylepis tarapacana* woodlands (Ibisch *et al.* 2003, Beck *et al.* 2010).

Field surveys

Field surveys were conducted between the end of the dry season and the beginning of the wet season (November) of 2013 in three bofedales locally known as Jalaru, Kurajpucho, and Putani (Figure 1). On each wetland, we randomly selected waterlogged areas and desiccated areas for floristic surveys and above ground biomass estimation.

Floristic survey

We used the line-intercept method to conduct vegetation assessments (Naoki *et al.* 2014). On each study site, we randomly installed 15 transects, specifically 7 in waterlogged areas (Figure 1b) and 8 in desiccated areas (Figure 1c). We used 200-cm long transects and registered the presence of a species every 20 cm at point intercepts (100 points total per transect).

Specimens were identified using reference collections and taxonomic guides at the Herbario Nacional de Bolivia (LPB). We used the Bolivia Catalogue of Vascular Plants as the official source on the taxonomy of plant species (Jørgensen *et al.* 2014).
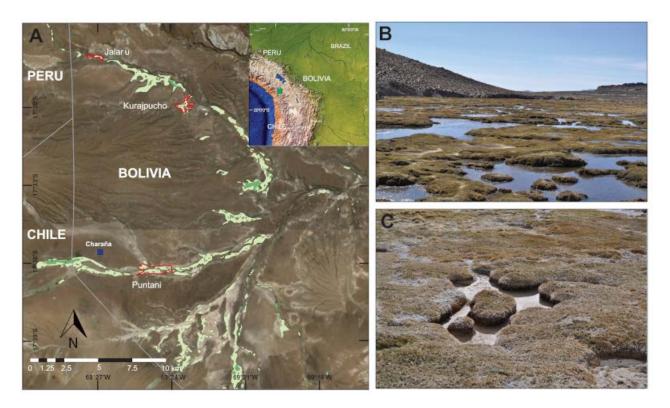
Figure 1. Research area including A) location of studied wetlands and typical examples of B) a waterlogged, and C) a desiccated habitat of Andean high-altitude wetland in the western Bolivian Altiplano.

We classified taxa into nine groups based on a Wetland Indicator Status based on species responses to flooding and geographic origin (Table 1). Obligate wetland forbs and graminoids include species that occur almost always (99 %) in wetlands; facultative wetland forbs include species that are usually found in wetlands (67–99 %) but occasionally are found in non-wetland habitats; subaquatic forbs are species found always submerged in shallow ponds and streams (99 %); facultative upland graminoids are species that usually occur in non-wetlands but are occasionally found in wetlands (1–33 %); and saline tolerant forbs and graminoids are species usually found in saltpans (33–50 %) but can be found occasionally in non-saltpan habitats (Beck *et al.* 2010, Meneses *et al.* 2019).

Estimating aboveground biomass
To quantify aboveground biomass, we installed 10 linear transects 100-cm long on each wetland during the wet season of January of 2014, from which 5 were installed in waterlogged areas and 5 in desiccated areas. We extracted five samples with live vegetation along each transect using a metallic 10 cm deep cylinder with a 94 cm² surface area. Samples were subdivided by species, including leaves and inflorescences. Samples were oven dried to a constant temperature at 80 °C for 24 h and weighed. Plant

samples were processed at the Herbario Nacional de Bolivia in La Paz. Due to scarce plant material, we were unable to estimate aboveground biomass of facultative graminoids, generalist graminoids, obligate upland forbs, and subaquatic forbs.

Estimating soil characteristics
We collected a total of 30 superficial soil samples (15 samples in waterlogged areas and 15 samples in dry areas). We homogenized soils by hand, removed plant material and sieved them to remove particles larger than 2 mm (including roots). We employed the gravimetric method to quantify soil moisture content. Each sample was weighed immediately after collection, dried at 80 °C between 72 and 96 hours until they were completely dry, and reweighed. We quantified organic matter content of the sediment by using the loss on ignition method (LOI). Each sample was burned in a muffle furnace at 480° C for 7 h and reweighed.

Data analysis
We performed two-way ANOVAs to determine differences in soil moisture content and organic content between waterlogged and dried areas. We performed linear mixed effect models to test if plant cover and aboveground biomass was different between wetland type and study sites, wetland type

Table 1. Wetland indicator status groups and characteristics of species found in waterlogged and desiccated habitats in Andean high-altitude wetlands in western Bolivian Altiplano (Ruthsatz 2012, Jørgensen *et al*. 2014, Meneses *et al*. 2019).

Wetland Indicator Status	Species
Facultative wetland forb (FF)	*Gentiana sedifolia* *Hypochaeris taraxacoides* *Lachemilla pinnata* *Ouricia muscosa* *Plantago tubulosa*
Facultative upland graminoid (FG)	*Festuca rigescens*
Obligate upland forb (OUF)	*Aciachne pulvinata* *Astragalus sp.* *Azorella diapensoides* *Baccharis caespitosa* *Gentiana minima* *Mancoa hispida* *Tarasa tenella*
Obligate upland graminoid (OUG)	*Deyeuxia deserticola* *Deyeuxia spicigera* *Festuca orthophylla*
Obligate wetland forb (OWF)	*Arenaria compacta* *Cotula Mexicana* *Cuatrecasasiella argentina* *Distichia muscoides* *Myrosmodes paludosa* *Oritrophium limnophilum* *Oxychloe andina* *Werneria pygmaea*
Obligate wetland graminoid (OWG)	*Carex maritima* *Deyeuxia rigescens* *Juncus stipulates* *Phylloscirpus deserticola* *Zameioscirpus atacamensis* *Zameioscirspus muticus*
Saline tolerant forb (STF)	*Baccharis acaulis* *Sarcocornia pulvinata*
Saline tolerant graminoid (STG)	*Distichlis humilis* *Triglochin concinna*
Subaquatic forb (Sub)	*Lachemilla diplophylla* *Lilaeopsis macloviana* *Lobelia oligophyla* *Ranunculus uniflorus*

and study site were treated as fixed factors and transect as random and nested within study sites. To estimate ecological diversity indices (alpha diversity index and species evenness), we used the *Vegan* package in the statistical environment R version 3.4.2 (copyright 2001, The R Development Core Team). Linear mixed effect models were conducted using *lme4* package also in the R environment.

RESULTS

Soils of waterlogged habitats exhibited significantly higher gravimetric water content (345.9 ± 120.4 %) than desiccated habitats (54.9 ± 10.7 %) (type $F = 31.6$ df = 1 $P < 0.001$, site $F = 0.27$ df = 2 $P = 0.76$, type*site $F = 2.05$ df= 2 $P = 0.15$). Organic matter content was also three times higher in soils from waterlogged habitats (27.7 ± 2.9 %) than from soils of desiccated habitats (7.8 ± 1.6 %) (type $F = 17.2$ df = 1 $P < 0.01$, site $F = 1.24$ df = 2 $P = 0.4$, type*site $F = 0.1$ df= 2 $P = 0.9$).

We observed a total of 42 taxa, from which we identified 40 to the species level and two to the genus level. The number of species found in each wetland was comparatively similar in waterlogged and desiccated habitats (range: 21–16 species); except for desiccated habitats in Kurajpucho, where we registered only 12 species. We found a similar alpha diversity in both habitats (*H'* waterlogged: 2.7, desiccated: 2.5). Alpha diversity was also comparatively higher in the waterlogged and desiccated habitats of Jalaru in comparison to those from Kurajpucho and Putani (Table 2). The desiccated habitats from Kurajpucho and Putani also exhibited the lowest alpha diversity.

Species evenness was very alike between habitats and between study sites (Table 2), but there were differences in the number of species based on wetland indicator status. For example, obligate wetland forbs accounted for 7 species in waterlogged habitats and 4 species in desiccated habitats (Table 3). In general, we found low species evenness values (waterlogged: 0.45, desiccated: 0.38) suggesting that Andean wetlands are mostly dominated by very few species and that most of the species are rare.

We found a strong differentiation in species assemblage composition among waterlogged and dry habitats (Figure 2). Two subaquatic forbs (*Lilaeopsis macloviana* and *Ranunculus uniflorus*) and three obligate wetland forbs (*Cotula mexicana*, *Distichia muscoides*, and *Oxychloe andina*) were found exclusively in waterlogged habitats. In contrast, one saline tolerant graminoid (*Distichlis humilis*), two obligate upland graminoids (*Deyeuxia spicigera* and

Table 2. Species diversity indexes in the studied desiccated and waterlogged habitats in Andean high-altitude wetland in western Bolivian Altiplano.

	Jalaru		Kurajpucho		Putani	
	waterlogged	desiccated	waterlogged	desiccated	waterlogged	desiccated
Number of species	21	20	19	12	18	16
Alpha diversity	4.70	4.65	4.27	2.81	3.84	3.58
Evenness	0.28	0.29	0.27	0.33	0.27	0.30

Table 3. Vegetation composition in the studied desiccated and waterlogged habitats in Andean high-altitude wetland in western Bolivian Altiplano. Statistical significant differences are flagged (*$P < 0.05$, **$P < 0.001$, *** $P < 0.0001$).

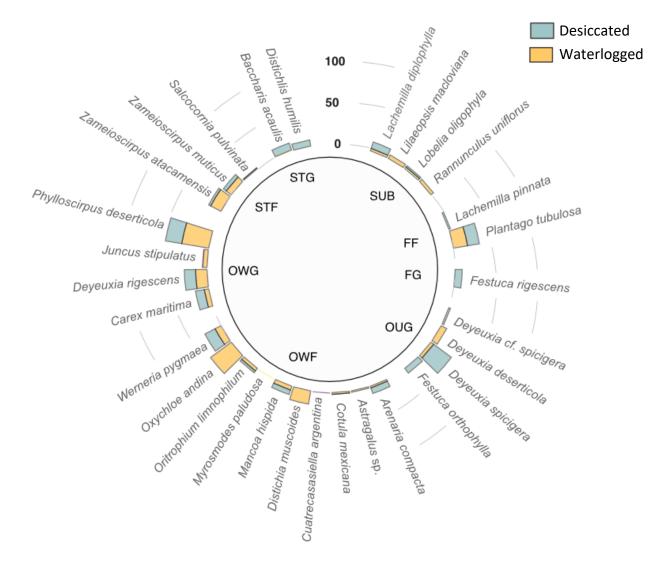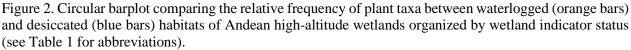| Characteristics		Desiccated habitats	Waterlogged habitats
Facultative wetland forb (FF)	No species	2	1
	Abundance (%)	12.4 ± 1.6	17.2 ± 2.1
	Aboveground biomass (g m^2)	37.4 ± 6.9	19.1 ± 4.1
Facultative upland graminoid (FG)	No species	1	0
	Abundance (%)	8.4	0
	Aboveground biomass (g m^2)	---	35.8 ± 9.8
Obligate upland forb (OUF)	No species	4	2
	Abundance (%)	3.6 ± 0.06	5 ± 0.09
	Aboveground biomass (g m^2)	54.8 ± 39.2	---
Obligate upland graminoid (OUG)	No species	2	2
	Abundance (%)	**23.7 ± 6.9**	**4.6 ± 1.6*** **
	Aboveground biomass (g m^2)	---	---
Obligate wetland forb (OWF)	No species	4	7
	Abundance (%)	10.5 ± 3.4	12.8 ± 2.7
	Aboveground biomass (g m^2)	18.1 ± 5.2	24.9 ± 4.5
Obligate wetland graminoid (OWG)	No species	6	6
	Abundance (%)	12.5 ± 2.3	16.8 ± 2.7
	Aboveground biomass (g m^2)	**11.4 ± 2.5**	**26.9 ± 3.7** **
Saline tolerant forb (STF)	No species	1	2
	Abundance (%)	9.2 ± 3.1	1.1 ± 0.1
	Aboveground biomass (g m^2)	35.5 ± 20.6	---
Saline tolerant graminoid (STG)	No species	1	0
	Abundance (%)	7.4 ± 2.5	0
	Aboveground biomass (g m^2)	**21.4 ± 5.4**	**10.4 ± 3.8***
Subaquatic forb (SF)	No species	2	4
	Abundance (%)	4.4 ± 1.6	3.4 ± 0.05
	Aboveground biomass (g m^2)	4.3 ± 1.4	6.55 ± 1.44

Festuca orthopylla), and two facultative plants (*Lachemilla pinnata* and *Festuca rigescens*) were found solely in desiccated habitats. A small group of species was found in both wetland types, including one facultative forb (*Plantago tubulosa*) and three obligate wetland taxa (*Phylloscirpus deserticola*, *Carex maritima*, and *Deyeuxia rigescens*).

Plant abundance was similar for most of the wetland indicator groups, except for obligate upland graminoids that showed 20 % higher abundance in desiccated habitats (Figure 3) ($\chi^2 = 13.4$, $P < 0.05$). Aboveground biomass of obligate wetland graminoids was two times higher in waterlogged habitats in comparison to desiccated habitats (Figure 4) ($\chi^2 = 521.3$, $P < 0.001$). Saline tolerant graminoids also exhibited significantly higher biomass in desiccated habitats ($\chi^2 = 99.425$, $P < 0.0001$), which was particularly higher in Kurajpucho.

DISCUSSION

We found evidence that environmental heterogeneity of Andean high-altitude wetlands was associated with specific vegetation composition and biomass production, probably linked to differences in soil humidity and organic matter content. Soils from desiccated habitats exhibited comparatively lower water and organic matter content, which can be partially attributed to sediment characteristics. Desiccated habitats are possibly less likely to hold moisture during the dry season, decreasing the capacity of hydrophytes to survive drought conditions (Reddy & DeLaune 2008, Urbina & Benavides 2015). The scarcity of cushion-forming forbs (*Distichia muscoides* and *Oxychloe andina*) in desiccated wetlands may further decrease soil water retention capacity because compact cushions reduce

Figure 2. Circular barplot comparing the relative frequency of plant taxa between waterlogged (orange bars) and desiccated (blue bars) habitats of Andean high-altitude wetlands organized by wetland indicator status (see Table 1 for abbreviations).

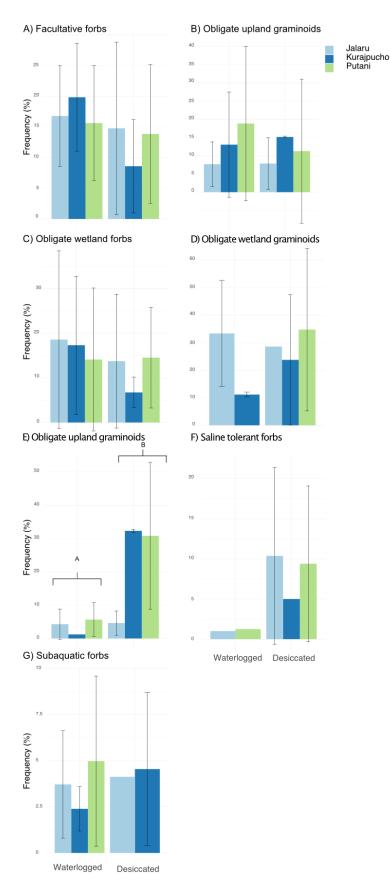Figure 3. Barplot comparing mean (± 1 SE) relative abundance of A) facultative forbs, B) obligate upland graminoids, C) obligate wetland forbs, D) obligate wetland graminoids, E) obligate upland graminoids, F) saline tolerant forbs, and G) subaquatic forbs between waterlogged and desiccated habitats of Andean high-altitude wetlands in western Bolivian Altiplano. Different letters indicate significant differences (*P* < 0.05).

soil evaporation and contribute with dead plant material (Ruthsatz 2012, Benavides *et al.* 2013, Cooper *et al.* 2015).

We found a small difference in species richness and alpha diversity between desiccated and waterlogged habitats. Obligate wetland forbs and subaquatic forbs made up the greatest number of species in waterlogged habitats whereas obligate upland forbs were commonly present in desiccated habitats. Higher water content in waterlogged habitats allows subaquatic forbs and obligate wetland forbs to germinate and establish in water saturated soils, while hypoxic conditions inhibits germination of upland species (Casanova & Brock 2000).

The abundance of wetland indicator groups was distinctly different among habitats. We found evidence that supported our hypothesis stating that desiccated habitats exhibit lower abundance of obligate wetland forbs due to their sensitivity to soil desiccation. The cushion-forming species *D. muscoides* and *O. andina* were very rare in

desiccated habitats and were found almost exclusively in waterlogged habitats. The restricted local distribution of both species could be associated with habitat requirements, particularly oxygen-deficient fluvial surfaces where soils are saturated by almost constant stream flow or groundwater (Ruthsatz 2012, Loza Herrera *et al.* 2015). Alternatively, low desiccation tolerance or a lack of dormant propagules in desiccated habitats from which active plants could emerge and establish after surface water returns could influence their distribution and abundance (Grillas *et al.* 1993, Leck & Brock 2000, Brock *et al.* 2003, Fernandez 2018). Further research is required to identify the role of resistance mechanisms of hydrophytes to drying, such as dormant seedbanks and physiological traits required to tolerate complete desiccation (Fernandez 2018, Casanova & Brock 2000).

The results from this study also show that desiccation-tolerant plants were comparatively more abundant in desiccated habitats. Reduced soil water
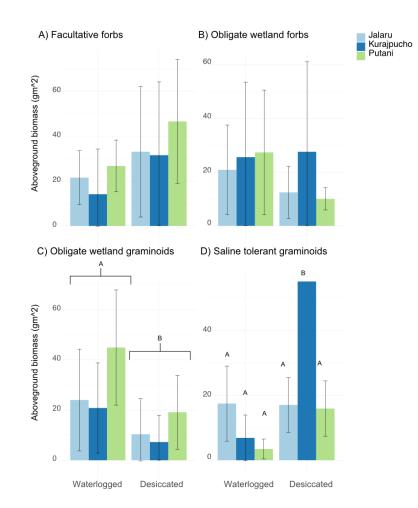
Figure 4. Barplot comparing the mean (± 1 SE) aboveground biomass of A) facultative forbs, B) obligate wetland forbs, C) obligate wetland graminoids, and D) saline tolerant graminoids between waterlogged and desiccated habitats of Andean high-altitude wetlands in western Bolivian Altiplano. Different letters indicate significant differences ($P < 0.05$).

humidity and low organic matter content simultaneously provided conditions that favoured the establishment of obligate upland graminoids like *Distichlis humilis* and saline-tolerant forbs such as *Baccharis acaulis*. The accumulation of salt on the surface of soils could be a product of changes in water flow regime, which has created favourable conditions for colonization of desiccation-tolerant species (Yager 2009, Ruthsatz 2012). Salinization constitutes a major threat to the ecological health of Andean wetlands (Domic *et al.* 2019) and increasing salt accumulation could induce large shifts in wetland communities by inducing physiological stress in wetland biota and by favouring the establishment of halophytes.

Colonization of upland plant taxa into desiccated habitats may be further assisted by human-mediated disturbance, in particular grazing by domestic camelids (llamas and alpacas). Disturbance often increases resources (e.g., space, nutrients, etc.) and creates opportunities of non-native taxa to invade wetlands. Surveyed wetlands were used as traditional grazing areas, mostly for llamas and alpacas that feed on local plants through the entire year (Villarroel *et al.* 2014). We found evidence of overgrazing as some cushions were intensively browsed and we recorded the presence of *Aciachne pulvinata*, a grazing-tolerant species (Salvador *et al.* 2014, Meneses *et al.* 2019). Furthermore, grazing could be an important disturbance factor altering species diversity through the direct addition of organic matter and macronutrients (nitrates and phosphorous) from manure (Urbina & Benavides 2015). A clearly favoured species is *Mancoa hispida*, which is abundant near camelid dung piles (Beck *et al.* 2010), but other taxa also benefit from livestock inputs.

We also found evidence that partially supported our third hypothesis stating that desiccation-tolerant plants (e.g. halophytes and upland taxa) that exploit water more efficiently exhibit higher aboveground biomass in comparison to obligate wetland plants in desiccated habitats. Aboveground biomass of saline tolerant graminoids was higher in only one desiccated habitat, where soil moisture and organic matter content were comparatively very low. The results also showed that obligate wetland graminoids were less productive in desiccated habitats, where biomass production was probably controlled by water, nitrogen and carbon availability (Wilson & Keddy 1985, van den Brink *et al.* 1995).

Our findings have implication for the potential impacts of climate change and habitat degradation of high-altitude wetlands in the tripartite region. Recent research suggests that this region is experiencing increasing temperatures, changes in precipitation patterns, and longer droughts as a consequence of global climate change (Agua Sustentable 2016, Yager *et al.* 2019). This process could exacerbate the desiccation of wetlands with the potential to modify the biomass production of hydrophytes by inducing desiccation stress and preventing plants from recovering after soils dry out. The impacts of wetland drying may, in contrast, encourage biomass productivity of halophytes as they are able to effectively withstand increasing levels of reduced soil humidity and perform better under drained conditions.

CONCLUSIONS

This study focused on identifying niche separation of plant communities in high-altitude Andean wetlands among an environmental gradient. We found that soil moisture and organic matter content play a critical role in determining plant community assembly and aboveground biomass production. Obligate wetland taxa inhabited areas with high soil moisture and organic matter, contrastingly saline tolerant forbs and upland plants colonized habitats with low soil moisture and organic matter content. For herbaceous plant communities, there was a species turnover along the environmental gradient, consistent with species having distinct hydrological niches. These findings suggest that obligate wetland and drought tolerant herbaceous communities will respond differently to shifting hydrological regimes under ongoing habitat degradation and will be exacerbated by global climate change.

Andean wetlands are sensitive to changes in the hydrological cycle and our results highlight a series of issues that should be considered in conservation and sustainable development and management programs in the tripartite border between Bolivia, Chile and Peru. Because wetlands are composed of a diversity of obligate native wetland plants, critical measures should be implemented to reduce the negative effects of desiccation due to a reduction in water levels and increasing droughts. For example, the construction of irrigation canals and herd size control could help to raise (or at least help to mitigate the decrease) of wetland water tables, reduce pressure on vegetation and facilitate plant recovery. Additional efforts should be implemented to revert the desiccation of wetlands and restore the native vegetation by limiting water diversion and conducting soil enrichment and revegetation programs. Traditional knowledge and management of Andean pastoralists can help restore and reverse the negative effects of habitat degradation, thus

engaging local communities in the decision-making process and in the implementation of programs should further facilitate the recovery of wetlands and bring benefits both to people and the ecosystems they inhabit.

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AUTHOR CONTRIBUTIONS

Conceptualization: PP & AID; Data curation: AID & RIM; Formal analysis: AID & JMC; Funding acquisition: PP; Investigation: AID & RIM; Methodology: AID & RIM; Project administration: PP; Resources: PP & RIM; Software: AID; Supervision: PP; Visualization: AID & JMC; Writing - original draft: AID; Writing - review & editing: AID, JMC, PP.

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12