Effects of grazing pressure on plant species composition and water presence on bofedales in the Andes mountain range of Bolivia

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SUMMARY

Bofedales are high-Andean peatland plant communities with high capacity for water retention, which are regarded as oases of biodiversity. These areas have great social and economic value for livestock grazing, which plays an important role in their vegetation dynamics. However, the effects of increased livestock pressure on vegetation composition and surface water have not yet been clarified. The goal of this study was to assess the impact of current grazing practices on bofedal vegetation, species diversity and function. Specifically, the study aimed to (1) quantify carrying capacity and stocking rate in grazed bofedales and (2) quantify the effects of grazing pressure on plant composition and the extents of bare soil and surface water. Biomass and stocking rate estimates for 25 bofedales along the Cordillera Real (Tropical Andes, Bolivia) showed that all bofedales were overgrazed (carrying capacity/stocking rate (CC/SR) <1). Regression analyses showed significant decreases in number of plant species, species dominance, diversity and percent surface water as CC/SR declined ($p < 0.05$). Bofedales are negatively affected by increased grazing pressure and potentially affected by changes in livestock species. These pressures, combined with land use changes and climate change, could result in long-term negative effects for the ecological functioning and sustainability of bofedales.

KEY WORDS: carrying capacity, high Andean wetlands, overgrazing, stocking rate, vegetation diversity

INTRODUCTION

High Andean peatlands, also known as Puna wetlands or bofedales (hereafter ‘bofedales’), are wetland plant communities with high capacity for water retention and development of an organic layer (Squeo *et al.* 2006, Maldonado Fonkén 2014). They develop along streams and can be regarded as biodiversity oases in a matrix of predominantly dry landscape (Ruthsatz 2012, Maldonado Fonkén 2014). This makes bofedales important ecosystems for the conservation of endemic plant species, key environmental services, habitat for wildlife and resources for livestock production (Squeo *et al.* 2006, Verzijl & Guerrero Quispe 2013, Salvador *et al.* 2014, Loza Herrera *et al.* 2015). They harbour a number of rare and endemic species including small mammals and birds that use these areas for food, water and reproduction (Ruthsatz 2012, Maldonado Fonkén 2014). Bofedales act as important reservoirs and sources of water, as well as carbon sinks which contribute significantly to carbon sequestration (Segnini *et al.* 2010, Buytaert *et al.* 2011, Zimmer *et al.* 2014, Hribljan *et al.* 2015). Located at altitudes of 4,000–5,000 m a.s.l. within the tropical Andes, they are found at the edge of the hydrological and altitudinal limits for plant life in South America, mainly in Argentina, Bolivia, Chile and Perú (Squeo *et al.* 2006). They are regarded as native pastures and have constant water supplies, which make them highly productive as well as biologically and ecologically diverse (Squeo *et al.* 2006, Villarroel *et al.* 2014). Bofedales are also important to local communities in the Andes as sources of livestock fodder (Alzérreca *et al.* 2001, Zorogastúa-Cruz *et al.* 2012).

Bofedales have great social and economic value as they are part of the agricultural production system,

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providing grazing for the llama (*Lama glama*), alpaca (*Vicuña pacos*), vicuña (*Lama guanicoe*) and sheep (*Ovis aries*) which provide a source of income for the families and communities living around these areas (Genin & Alzerreca 2006, Meza Aliaga & Díaz Villalobos 2014, Salvador *et al*. 2014, Villarroel *et al*. 2014). Livestock have grazed bofedales for the last 9,000 years and grazing plays an important role in their vegetation dynamics (García *et al*. 2014). Grazing of bofedales usually continues year-round due to the perennial availability of green forage (Cooper *et al*. 2010, Benavides *et al*. 2013, Cooper *et al*. 2015). However, since bofedales are small areas within low-productivity landscapes, they can be vulnerable to fragmentation if subjected to excessive disturbance (Loza Herrera *et al*. 2015, Dangles *et al*. 2017).

Bofedales are considered to be fragile ecosystems which can be disturbed by livestock overgrazing, as well as by changes in drainage systems for crop production, mining and/or extraction of peat for use in urban gardens (Buttolph & Coppock 2004, Verzijl & Guerrero Quispe 2013, Salvador *et al*. 2014, Raevel *et al*. 2018). These disturbances and constraints in a rapidly changing environment can negatively impact on species diversity, long-term sustainability of grazing activities and the ecological functions of bofedales (Hole *et al*. 2011, Vuille 2013). Bofedales influenced by the presence of glaciers may be even more impacted due to accelerated glacial retreat, which will provide more water to bofedales in the short term but far less in the long term, and ultimately increase bofedal fragmentation (Dangles *et al*. 2017). Due to increased demand for resources such as water and forage, bofedales are now exposed to increases in land use change as well as in the other disturbances mentioned above, with potentially negative impacts on ecological functions and ecosystem services for local communities (Benavides *et al*. 2013, Cooper *et al*. 2015, Raevel *et al*. 2018).

The effects of increased pressure from livestock on vegetation, water and land management in bofedales have not yet been studied in detail. They require more attention so that we may better understand how management and conservation can effectively help local communities conserve and maintain these resources (Squeo *et al*. 2006). Although there are some anecdotal observations, very little information has been published on pasture management, livestock stocking rates and carrying capacity of these natural pastures (Verzijl & Guerrero Quispe 2013, Hartman *et al*. 2016). Moreover, bofedales are poorly known ecosystems, and there is a need to improve our understanding in the face of traditional and modern management approaches as well as challenges due to climate change (Salvador *et al*. 2014). Because of their high economic, social, and ecological values, there is a fundamental need to develop strategies for their sustainable management and conservation (Ruthsatz 2012). A first step towards developing such strategies is to gain new knowledge about the existing relationship between carrying capacity and multiple-species stocking rates in these ecosystems, as well as potential effects on plant species diversity. Such an analysis will provide local farmers, decision makers and conservationists with an information baseline that can be used as a starting point for the implementation of practices which promote conservation, restoration and sustainability of bofedales. It could also serve as a model for other regions facing similar ecological, agricultural and social challenges. Therefore, the aim of this study was to assess the impact of current grazing practices on the phytodiversity and functions of bofedales. The specific objectives were to:

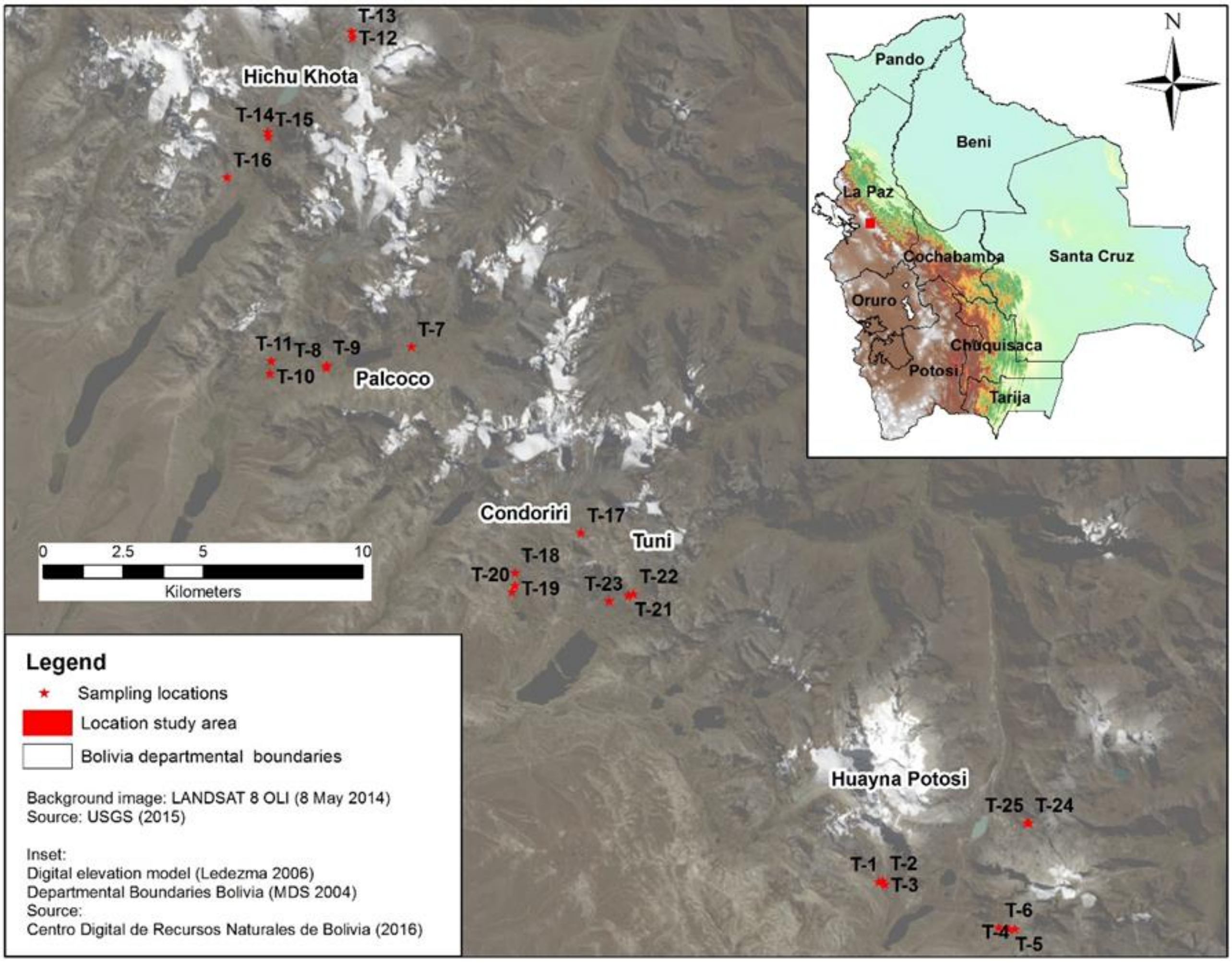
1. quantify the carrying capacity and stocking rates of bofedales subject to grazing; and
2. determine how grazing pressure may affect plant diversity and surface water area in these systems.

Our main hypothesis was that grazing above carrying capacity will negatively affect plant species composition and reduce the amount of surface water area in bofedales.

METHODS

Study area

The study area is situated in the Cordillera Real, a tropical Andean mountain range peaking at 6,432 m a.s.l., between Lake Titicaca and the city of La Paz-El Alto in Bolivia. Our study sites were located in the central part of the Cordillera Real, between the valleys of Hichu Khota (68° 18' 3.86" W, 16° 03' 44.78" S) and Milluni (68° 6' 37.36" W, 16° 16' 55.70" S) (Figure 1). Temperatures in this region range between -7.2 °C and 21.1 °C, solar radiation is 5.4–5.7 KWh m^{-2} and the average relative humidity is 49 % (Montes de Oca 2005, Zeballos *et al*. 2014). Rainfall occurs mostly between November and May with an average annual rainfall of 700 mm (Hribljan *et al*. 2015). Depending on the hydrological regime, the sampled bofedales were classified as hydromorphic and mesic (Troncoso 1983, Alzérreca *et al*. 2001). Hydromorphic bofedales have water throughout the year while mesic bofedales have dry and wet periods. Vegetation communities in these areas are largely dominated by *Distichia muscoides*,



Background image: LANDSAT 8 OLI (8 May 2014)
Source: USGS (2015)

Inset:
Digital elevation model (Ledezma 2006)
Departmental Boundaries Bolivia (MDS 2004)
Source:
Centro Digital de Recursos Naturales de Bolivia (2016)

Figure 1. Locations of the 25 bofedales evaluated for grazing in the Andes Mountain range in Bolivia (MDS 2004, Ledezma 2006).

Distichia filamentosa, *Oxychloe andina*, *Plantago tubulosa* and *Phylloscirpus deserticola* (Loza Herrera *et al.* 2015). The vegetation consumed by livestock is mainly composed of grasses such as *Festuca dolichophylla*, *Deyeuxia* sp., *Juncus* sp., *Lachemilla pinnata*, *O. andina* and *D. muscoides* (Genin & Alzérreca 2006). Pasture management follows a community-based land share system (Hoffmann *et al.* 2014). The most frequent livestock species are llama, alpaca, sheep, cattle (*Bos taurus*), donkeys (*Equus asinus*) and horses (*Equus caballus*) (Alzérreca *et al.* 2001). Within the study area, 13 sites containing 25 bofedales (Table A1 in Appendix) were selected using the following criteria:

(1) bofedales located at > 4,350 m a.s.l.;

(2) bofedales identified as grazing areas by local communities;

(3) size of bofedal large enough to be representative of the study area; and

(4) area of the bofedal homogeneous and representative within the sampling area (Cochi *et al.* 2014).

Data collection and analysis

Presence of surface water and dominant species (*e.g.* *F. dolichophylla* or *Deyeuxia rigescens*) were used to determine the type of bofedal to be sampled. Each bofedal was defined as hydromorphic (wet throughout the year) or mesic (dry and wet seasons) according to Troncoso (1983) and Alzérreca *et al.* (2001). If the two types of bofedal were found in the same area, they were delineated and analysed separately (Cochi *et al.* 2014). For each type of bofedal, a representative transect (30–50 m in length) based on the bofedal size and type was sampled (Cochi *et al.* 2014). Within each transect, samples were collected every four metres. For each point sampled, vegetation composition, percent surface water, percent manure, percent organic soil layer and percent bare soil were determined using the point intercept cover technique with a ten-pin frame (Goodall 1953, Cochi *et al.* 2014). At each sampling point, plants and cover that came in contact with the pins were identified and quantified. Plant composition data were collected with emphasis on species grazed by livestock (Table A2). Standing biomass was collected using sampling rings (diameter = 0.10 m). Rings were placed randomly along the transect line and ten samples were collected within each transect. For each ring sample, available forage was harvested with a pair of scissors simulating bites made by livestock when foraging (Cochi *et al.* 2014). Green vegetation was weighed (*i.e.* green weight), bagged and dried at 65 °C for 48–72 hours until a constant weight (*i.e.* dry matter; DM) was reached (Alzérreca *et al.* 2001, Flachier *et al.* 2009). Mean DM values *per* m² for each transect were multiplied by the corresponding bofedal area to estimate total dry matter (kg). Bofedales were delineated in the field using a Garmin GPS unit and following the boundaries of what was considered to be a hydromorphic or mesic bofedal. This information was used to estimate annual carrying capacity within each bofedal.

The llama, with a mean weight of 72 kg (Condori 2000), was selected as the reference species to determine carrying capacity (see details in Cochi *et al.* 2014). The following factors were used to estimate the amount of dry biomass required *per* animal unit *per* year: dry matter requirement (2.2 % of animal weight *per* day for llamas; San Martin 1996), number of grazing days in bofedal (300 days, local community data; M. Andrade, personal communication) and percentage of time *per* day spent grazing within bofedales (37.5 %). This percentage was calculated by estimating the average number of grazing hours spent daily in a bofedal (3 hours) and the total number of hours spent grazing *per* day (8 hours), as reported by local communities. The reference annual DM forage requirement *per* animal unit was calculated as 178.2 kg. The total forage DM (kg) in each bofedal was divided by this reference value to estimate the carrying capacity animal unit equivalent (AUE). Stocking rate was calculated by adding the AUE of all animals present in each bofedal (Table A1) and dividing this number by our animal unit reference weight (178.2 kg AU^{-1} $year^{-1}$). Carrying capacity (CC) values were divided by stocking rate (SR) values; if the CC/SR quotient was >1, then the bofedal was undergrazed; on the other hand, if this value was < 1, the bofedal was considered to be overgrazed. The smaller the value of CC/SR, the more overgrazed the site.

Based on the vegetation composition data collected in each transect, the number of individuals, number of species, dominance, Shannon index and Buzas and Gibson's evenness were estimated for each bofedal (Harper 1999). Dominance is an estimate of the dominance of taxa whose value ranges from 0 (all taxa equally present) to 1 (one taxon dominates the community). Shannon index measures diversity taking into account number of species as well as evenness of species; for this metric, the higher the value, the higher the species diversity. Buzas and Gibson's evenness is calculated by dividing the Shannon index by the number of species (Harper 1999, Jost 2010). First, these variables were compared to test for differences between hydromorphic and mesic bofedales following the methodology of Alzérreca *et al.* (2001). Levene’s test was used to check equality of variances. If no significant differences were observed with this test, we assumed equal variances and we were able to compare differences with a t-test (alpha = 0.05). Because no statistical differences between hydromorphic and mesic bofedales were found (except for organic matter and bare soil), the CC/SR quotient observed in each bofedal was compared using linear regression (SPSS, IBM Corporation, Armonk, New York), with the following variables: number of individuals, number of species, dominance, Shannon index, Buzas and Gibson’s evenness, percent surface water, percent manure, percent organic layer and percent bare soil cover. The goal was to assess whether CC/SR would affect the selected factors. This was potentially a more robust analytical approach than the comparison between hydromorphic and mesic bofedales. For each comparison we ran a linear regression analysis, and we reported the constant, intercept, r² and the significance at alpha < 0.05. We finally conducted a k-means cluster analysis (Jain 2010) with the species composition recorded in each transect (43 × 25, n = 1,075). Data clustering is a useful technique to gain further insight into data and identify further noticeable features. In this case, the botanical composition of each site was an integrating variable that could be used to assess the ecological function of the bofedales (Danet *et al.* 2017). The number of classes and their centroids (k) were randomly determined, then 50 iterations and determinant criterion were applied. Once the classes were identified, these were compared to the CC/SR values in order to determine whether there were similarities between the two variables (species composition and CC/SR). Data K-means clustering was conducted in R software (R Core Team 2016).

RESULTS

Hydromorphic ($_h$) and mesic ($_m$) bofedales were not significantly different in terms of number of species, number of individuals, dominance, Shannon index, Buzas and Gibson's evenness indices, water presence or manure ($p > 0.05$; Table 1). Significant differences between the two types of bofedal were observed for percent organic matter (OM_h = 7.06 % ± 2.39; OM_m = 22.3 % ± 11.25; p = 0.004) and percent bare soil ($bare_h$ = 2.13 % ± 0.10; $bare_m$ = 29.4 % ± 5.13; p = 0.004). No significant differences in CC/SR were observed between hydromorphic and mesic bofedales. The quantification of CC/SR showed that all bofedales with livestock production had quotients < 1. The lowest values, or highest overgrazing rates, were found in Condoriri (bofedal 17; CC/SR = 0.02) and Alto Milluni (bofedales 2 and 3; CC/SR = 0.08) (Table 2). The highest values were observed in Alto Milluni (bofedales 5 and 6; CC/SR = 0.94 and 0.58, respectively) and Umapalca (bofedal 12; CC/SR = 0.66). For all other bofedales CC/SR ranged between 0.11 and 0.56. Regression analyses between CC/SR and bofedal variables showed significant positive linear trends for number of species, dominance, Shannon index, percent surface water area and percent manure (Table 3). The number of species (slope = -7.168, intercept = 18.792, r^2 = 0.319, p = 0.008), Shannon index (slope = -0.698, intercept = 2.416, r^2 = 0.299, p = 0.010) and percent manure (slope = -21.662, intercept = 16.636, r^2 = 0.230, p = 0.028) decreased as CC/SR increased (lower grazing pressure). Dominance (slope = 0.135, intercept = 0.125, r^2 = 0.236, p = 0.026) and percent water cover (slope = 23.798, intercept = 2.778, r^2 = 0.225, p = 0.030) increased as CC/SR increased.

The cluster analysis grouped the 25 bofedales into three classes on the basis of species composition (Table 4). The most observed species in Class 1 were *Oxychloe andina*, *Festuca dolichophylla*, *Deyeuxia spicigera*, *Zameoscirpus muticus* and *Distichia muscoides*. Bofedales in Class 1 had the highest CC/SR quotients or lowest grazing pressures. Class 2 included the bofedales with the lowest CC/SR quotients or highest grazing pressures. Predominant species in Class 2 included *Plantago tubulosa*, *Festuca dolichophylla*, *Eleocharis albitracteata*, *Phylloscirpus deserticola*, *Werneria pygmaea* and *Carex* sp. The most common species in Class 3 were *Distichia filamentosa*, *Werneria pygmaea*, *Deyeuxia spicigera* and *Werneria heteroloba*. The values of CC/SR ranged from 0.29 to 0.66 in Class 3. No hydromorphic or mesic bofedales were related to specific classes, which is consistent with our findings in Table 1.

Table 1. Comparison of variables between hydromorphic and mesic bofedales. Statistical differences are shown with (*). Equal variances were assumed as Levene’s test for equality of variances showed no statistical differences between hydromorphic and mesic bofedales.

Variable	Mean and CI hydromorphic bofedal	Mean and CI mesic bofedal	*t*	P-value
Number of species	16.2 ± 14.44	15.7 ± 13.36	0.382	0.706
Number of individuals	239.07 ± 204.91	203.90 ± 180.35	1.646	0.110
Dominance	0.16 ± 0.13	0.17 ± 0.12	-0.060	0.952
Shannon index	2.18 ± 2.03	2.16 ± 1.92	0.159	0.875
Buzas and Gibson’s evenness	0.56 ± 0.50	0.57 ± 0.48	-0.071	0.944
Percent surface water (%)	15.2 ± 9.04	11.2 ± 0.17	0.755	0.457
Manure (%)	8.27 ± 2.85	9.3 ± 1.72	-0.251	0.804
Organic matter	7.06 ± 2.39	22.3 ± 11.25	-3.193	0.004*
Bare soil (%)	2.13 ± 0.10	29.4 ± 5.13	-3.119	0.004*
CC/SR	0.33 ± 0.21	0.35 ± 0.13	-0.174	0.863

Table 2. Calculation of carrying capacity (CC), stocking rate (SR) and CC/SR for each bofedal. The values of AUE were calculated using the annual dry matter (DM) forage requirement of llama (178.2 kg).

Transect	Peatland type	Carrying capacity (CC)				SR (AUE) from Table A1	CC/SR quotient
		DM (m^{-2})	Area (m^2)	Total DM	AUE (CC)		
T-1	H	0.369	50,260	18,551.0	104.1	305.7	0.34
T-2	M	0.088	10,680	939.4	5.3	65.0	0.08
T-3	H	0.092	5,652	520.0	2.9	34.3	0.08
T-4	H	0.122	20,940	2,554.7	14.3	36.6	0.39
T-5	M	0.292	31,560	9,215.5	51.7	55.2	0.94
T-6	M	0.180	22,240	4003.2	22.5	38.9	0.58
T-7	M	0.226	64,490	14574.7	81.8		
T-8	H	0.047	83,360	3,917.9	22.0		
T-9	H	0.135	43,920	5929.2	33.3		
T-10	H	0.094	210,200	19,758.8	110.9	245.2	0.45
T-11	H	0.102	205,600	20,971.2	117.7	239.9	0.49
T-12	H	0.338	35,330	11,941.5	67.0	101.6	0.66
T-13	M	0.194	13,370	2,593.8	14.6	38.4	0.38
T-14	H	0.263	72,510	19,070.1	107.0	282.6	0.38
T-15	M	0.360	17,310	6,231.6	35.0	67.4	0.52
T-16	H	0.178	44,180	7,864.0	44.1	402.0	0.11
T-17	M	0.090	23,150	2,083.5	11.7	590.0	0.02
T-18	H	0.144	52,450	7,552.8	42.4	272.3	0.16
T-19	M	0.161	39,010	6,280.6	35.2	202.5	0.17
T-20	H	0.083	109,600	9,096.8	51.1	568.9	0.09
T-21	H	0.186	144,900	26,951.1	151.2	269.6	0.56
T-22	M	0.090	96,960	8,726.4	49.0	180.4	0.27
T-23	H	0.175	10,660	1,865.5	10.5		
T-24	H	0.153	12,420	1900.3	10.7	36.9	0.29
T-25	M	0.111	22,610	2,509.7	14.1	67.1	0.21

Table 3. Intercept, constant, r^2 and p values from linear regression analysis between CC/SR (x) and variables measured in the field (y). Statistical differences are shown with (*).

Variable	Intercept	Constant	R^2	P-value
Number of individuals	48.504	207.579	0.037	0.407
Number of species	-7.618	18.792	0.319	0.008^*
Dominance	0.135	0.125	0.236	0.026^*
Shannon index	-0.698	2.416	0.299	0.010^*
Buzas and Gibson’s evenness	-0.133	0.611	0.081	0.210
Percent surface water	23.798	2.778	0.225	0.030^*
Manure	-21.662	16.636	0.230	0.028^*
Organic matter	6.232	11.253	0.010	0.669
Percent bare soil	-38.141	27.453	0.107	0.149

Table 4. Botanical composition of 25 peatlands in the Bolivian Andes. Results of K-means clustering into three classes based on species composition (n=1075). The central object of each class is shown in **bold red** type.

Class	1	2	3
Objects	12	10	3
Within-class variance	3832.9	2914.7	5189.7
Average distance to centroid	52.0	50.3	58.2
	T-1	T-2	T-12
	T-4	T-3	T-13
	T-5	T-8	**T-24**
	T-6	T-9	
	T-7	T-10	
	T-11	T-17	
	T-14	T-18	
	T-15	**T-20**	
	T-16	T-22	
	T-19	T-25	
	T-21		
	T-23		

DISCUSSION

Heavy grazing pressure is degrading bofedales in the tropical high Andes. Our study found that all sites were overgrazed (CC/SR < 1). This negatively impacted plant species composition (lower number of species) and relative abundance (reduced number of individuals and dominance), which are important for ecological functions and ecosystem services such as water provision and CO_2 capture. To our knowledge, this is the first study to quantify stocking rates, carrying capacity and the impact of grazing on bofedales, and the potential impact on ecosystem function in these areas. Our findings confirm previous anecdotal observations from Bolivia (Hartman *et al.* 2016), Chile (Squeo *et al.* 2006) and Peru (Salvador *et al.* 2014), where overgrazing has been reported as one of the leading causes for bofedal degradation. Salvador *et al.* (2014) reported that most bofedales in Peru were highly disturbed and grazing was the most common source of disturbance due to excessive stocking rates. In particular, overgrazing had a negative impact on vegetation and the soil surface, with potential to alter hydrological function (Salvador *et al.* 2014). Bofedales are sensitive to hydrological changes since reduction of vegetation cover can lead to increased runoff at the expense of infiltration and groundwater recharge, which causes stress for wetland plants (Hartman *et al.* 2016). This is consistent with our results showing increased overgrazing of bofedales reducing the amount of surface water present. This negative impact can potentially have an important effect on biogeochemical functions in terms of water flow and accumulation of organic matter (Cooper *et al.* 2010). This could cause changes in soil oxygen and decomposition of organic matter with reduced carbon accumulation and increased release of CO_2 (Delarue 2016). Our results suggest that these effects may be exacerbated by the introduction of cattle, horses and sheep. Overgrazing also affects plant composition by shifting plant communities. In our study, the number of species increased and dominance decreased with increased overgrazing. García *et al.* (2014) hypothesise that grazing will change vegetation composition and structure, and can also have a species-specific effect on dominant plant species.

Although studies reporting the impacts of grazing on bofedales are scarce, Salvador *et al.* (2014) observed that *Deyeuxia rigescens*, *E. albibracteata*, and an abundance of *Aciachne pulvinata* could be used as indicators of overgrazing in Peruvian bofedales. This is consistent with our results which show *E. albibracteata*, *F. dolichophylla* and *P. tubulosa* as the predominant species in the most overgrazed bofedales of our study area. We also observed the presence of *A. pulvinata* and *D. rigescens* in areas with the highest grazing pressures. On the other hand, areas with less overgrazing have species such as *Distichia filamentosa* and *O. andina*. These two species, along with *Distichia muscoides*, play an important role in bofedal ecosystem function and are considered endangered species in Bolivia (Ruthsatz 2012, Loza Herrera *et al.* 2015). Danet *et al.* (2017) observed that the percentages of *D. muscoides* and *O. andina* were significantly lower in grazed areas than in non-grazed areas. The replacement of cushion species (*e.g. O. andina*) by graminoid species (Figure 2) has been reported as an indicator of bofedal degradation in the Bolivian Andes (Loza Herrera *et al.* 2015). These changes can be exacerbated by other activities in the region (Buttolph & Coppock 2004, Verzijl & Guerrero Quispe 2013, Salvador *et al.* 2014).

Bofedales are being affected by increased grazing pressure, changes in livestock species, and high rates of land use change, all of which have potentially negative long-term effects for biodiversity and the livelihoods of local communities. Bofedales have been grazed by domesticated llamas and alpacas for centuries and this is regarded as the basis of the economy of local communities (Postigo *et al.* 2008). However, Hribljan *et al.* (2015) report that, due to the increased number of animals, bofedales in Bolivia are being grazed every day with no resting periods; and more importantly, grazing species have shifted from the traditional llama and alpaca to sheep and cattle. This shift can increase vegetation trampling and soil compaction, and is very likely to increase runoff. Cole & Spildie (1998) and Deluca *et al.* (1998) found that animals with hooves (*e.g.* horses, cattle) have a higher potential to disturb vegetation and increase sediment yields, and impose longer-term disturbance, than animals with feet (*e.g.* llamas). In our study areas, bofedales with cattle and sheep were observed in Milluni (bofedales 1, 2 and 3; cattle), Villa Andino (bofedales 11 and 12; cattle and sheep), Alto Peñas (bofedal 16; cattle and sheep) and Condoriri (bofedales 18, 19 and 20; cattle and sheep) (Table A1). Bofedales with high cattle and/or sheep AUE values had CC/SR ≤ 0.17 (Table 2) which indicates high rates of overgrazing. Therefore, a change in species or a reduction in cattle and sheep numbers to reduce stocking rate may be important to maintain bofedal ecosystem function. Furthermore, peat extraction and mining have been observed in bofedales across the region (Verzijl & Guerrero Quispe 2013, Salvador *et al.* 2014) and we were able to find evidence of mining activities in at least one of the sites visited for this study.

Figure 2. Bofedal with *Oxychloe andina* being overtaken by *Festuca dolichophylla*. Note that as *F. dolichophylla* density increases (upper left) the cover of surface water decreases. This shift in plant community is an indicator of bofedal degradation. Photo: H.L. Perotto-Baldivieso.

The increased pressure, combined with species shifts and changes in climate patterns, could result in long-term negative effects for the ecological functioning and sustainability of bofedales. Analysis of rainfall observations in the region show a trend of decreasing precipitation (Vuille *et al.* 2003). Otto & Gibbons (2017) found that rainfall is significantly correlated with bofedal density and bofedales located on the western slopes (250–470 mm rainfall) of the tropical Andes mountain range are more sensitive to rainfall than bofedales on east-facing slopes (1,000 mm rainfall). Our study area has a mean annual rainfall of 700 mm. If the projection reported by Vuille *et al.* (2003) holds for our study area, the number and size of bofedales could decrease, with direct impacts on biodiversity and negative effects on the livelihoods of local communities. More recently, Dangles *et al.* (2017) observed that while the overall areas of bofedales may increase due to changes in climate patterns, fragmentation of individual bofedales will increase, hence the area and connectivity of vegetation communities will decrease. Changes in temperature and rainfall patterns as well as glacier cover are promoting the upward migration of structuring bofedal species. However, these migrations seem to be particularly slow, generating a time lag between the changing climatic trends and the speed of bofedal succession (Dangles *et al.* 2017, Zimmer *et al.* 2018).

Finally, while the classification of hydromorphic and mesic bofedales proposed by Troncoso (1983) and Alzérreca *et al.* (2001) may have been useful in defining these areas, we were not able to quantitatively separate these two types of bofedal. We hypothesise that using visual assessment of water and species dominance to classify bofedales may be subjective and the separation not sensitive enough for statistical analysis. Our analysis using CC/SR quotients provides a solid quantitative approach and generates values that can be related to the variables evaluated in this study. We were able to assess the effect of stocking rate on vegetation composition, dominance, surface water and other variables that are important in understanding the ecological functioning of bofedales. The use of remote sensing platforms and vegetation indices (*e.g.* normalised difference vegetation indices) could provide greater insights into the future evolution of these peatlands.

CONCLUSION

Bofedales play an important role in regulating hydrological cycles, improving water quality, providing forage for domestic livestock and habitat for wildlife, increasing carbon accumulation, and enhancing local livelihoods. This study provides valuable information on the level of impact that livestock impose on plant composition and surface water in bofedales along the Cordillera Real in the Tropical Andes. Our results show that all bofedales are currently overgrazed and this is negatively impacting water retention and species composition, by altering vegetation dynamics. Moreover, the introduction of sheep and cattle has increased stocking rates and thus intensified grazing pressure in these areas. These pressures combined with bofedal fragmentation due to climate change and land use changes is likely to have more negative long-term effects on bofedal ecological functions for biodiversity, community livelihoods and sustainability.

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Appendix

Table A1. Number of animals and Animal Unit Equivalent (AUE) for each bofedal.

Site	Transect	Peatland type	Stocking rates (number of animals)					Stocking rates (AUE)					
			Llama	Alpaca	Sheep	Cattle	Equine	Llama	Alpaca	Sheep	Cattle	Equine	Total
Alto Milluni	T-1	H	135.85	75.47		11.32		135.85	56.62		113.20		305.7
	T-2	M	28.87	16.04		2.41		28.87	12.03		24.10		65.0
	T-3	H	15.28	8.49		1.27		15.28	6.37		12.70		34.3
	T-4	H	22.98	18.21				22.98	13.66				36.6
	T-5	M	34.63	27.45				34.63	20.59				55.2
	T-6	M	24.39	19.34				24.39	14.51				38.9
Villa Andino	T-7	M											
	T-8	H											
	T-9	H											
	T-10	H	101.10	50.55	30.33	7.58		101.10	37.92	30.33	75.80		245.2
	T-11	H	98.90	49.45	29.67	7.42		98.90	37.10	29.67	74.20		239.9
Umapalca	T-12	H	29.02				7.26	29.02				72.60	101.6
	T-13	M	10.98				2.74	10.98				27.40	38.4
Suriquiña	T-14	H	40.37			12.11	12.11	40.37			121.10	121.10	282.6
	T-15	M	9.63			2.89	2.89	9.63			28.90	28.90	67.4
Alto Peñas	T-16	H	2.00	80.00	230.00	10.00	1.00	2.00	60.02	230.00	100.00	10.00	402.0
Condoriri	T-17	M	590.00					590.00					590.0
	T-18	H	30.00	16.96	151.32		7.83	30.00	12.72	151.32		78.30	272.3
	T-19	M	22.31	12.61	112.52		5.82	22.31	9.46	112.52		58.20	202.5
	T-20	H	62.69	35.43	316.16		16.35	62.69	26.58	316.16		163.50	568.9
Tuni	T-21	H	59.91			11.98	8.99	59.91			119.80	89.90	269.6
	T-22	M	40.09			8.02	6.01	40.09			80.20	60.10	180.4
	T-23	H						0.00					
Llaullini	T-24	H	22.69			1.42		22.69			14.20		36.9
	T-25	M	41.31			2.58		41.31			25.80		67.1

Table A2. Plant species composition by bofedal.

Species	T-1	T-2	T-3	T-4	T-5	T-6	T-7	T-8	T-9	T-10	T-11	T-12	T-13	T-14	T-15	T-16	T-17	T-18	T-19	T-20	T-21	T-22	T-23	T-24	T-25
Aciachne pulvinata	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	3	0	0	7	0	0	0
Acuatica 2	0	0	0	0	0	0	0	3	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alga filamentosa	0	0	2	0	0	0	0	4	0	1	0	0	0	0	0	0	0	3	0	8	0	0	0	0	0
Astragalus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
Baccharis acaulis	6	0	0	0	0	0	3	0	0	0	0	0	0	8	17	4	0	0	7	1	14	1	5	2	3
Carex sp.	3	26	0	0	2	2	6	15	14	9	2	6	6	2	1	2	0	13	4	13	1	7	0	11	16
Deyeuxia chrysantha	8	0	0	0	10	10	14	0	43	0	1	21	0	7	0	0	34	0	0	0	0	0	0	11	0
Deyeuxia curvula	18	17	2	2	10	10	10	11	0	2	4	0	55	39	58	21	5	0	8	0	44	13	34	24	30
Deyeuxia ovata	3	1	0	0	0	0	0	0	16	20	0	0	1	0	0	0	0	29	1	22	0	0	0	0	0
Deyeuxia vicunarum	0	0	0	0	0	0	7	2	0	0	0	0	0	0	0	0	1	0	0	0	0	27	0	0	5
Distichia filamentosa	0	0	0	0	0	0	0	0	0	0	0	106	29	0	0	0	0	0	0	0	0	0	0	25	0
Distichia muscoides,	6	0	38	73	7	7	0	0	0	0	5	14	0	0	0	6	2	0	0	0	5	0	21	38	3
Eleocharis albibracteata	28	25	27	7	8	8	3	38	14	16	4	0	3	7	5	12	2	19	3	19	4	8	4	17	3
Festuca dolichophylla	66	44	3	10	49	49	44	19	80	22	1	0	0	55	43	35	19	13	44	14	6	9	12	0	0
Festuca regisens	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gentiana sedifolia	7	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	7	2	1	20	0	0	2
Hypochoeris sp.	16	7	0	6	7	7	0	0	0	0	6	0	0	13	6	11	2	0	11	2	23	0	24	14	1
Juncus sp.	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lachemilla diplophylla	0	10	2	0	0	0	0	8	1	0	0	0	0	0	0	3	1	8	5	4	0	0	0	0	5

continued overleaf .....

Table A2, continued

Species	T-1	T-2	T-3	T-4	T-5	T-6	T-7	T-8	T-9	T-10	T-11	T-12	T-13	T-14	T-15	T-16	T-17	T-18	T-19	T-20	T-21	T-22	T-23	T-24	T-25
Lachemilla pinnata	6	6	1	0	0	0	0	10	6	0	0	0	3	0	0	0	16	4	0	0	0	24	0	0	15
Lilaeopsis andina	0	0	0	0	0	0	0	45	2	7	0	0	0	0	0	0	0	21	0	11	0	0	0	0	0
Musgo cf.sciaronium	5	5	4	15	5	5	5	0	0	1	0	15	11	11	22	2	8	3	6	5	8	8	8	7	20
Nostoc	0	2	1	0	0	0	0	3	0	1	3	0	0	0	0	0	0	2	0	1	0	0	0	0	0
Ophioglossum crotalophoroides	1	0	0	0	0	0	0	0	6	0	0	0	0	4	0	0	2	9	11	10	0	0	0	1	0
Oxychloe andina	209	24	12	64	78	78	91	0	0	37	70	0	0	107	110	81	18	7	69	9	55	0	52	43	1
Phylloscirpus aff. boliviana	5	5	27	0	0	0	0	0	0	44	10	0	9	0	0	0	0	25	0	34	27	0	20	12	3
Phylloscirpus deserticola	0	1	0	0	1	1	0	7	0	10	9	3	2	2	1	0	0	9	1	5	2	0	3	3	0
Phylloscirpus sp.	0	0	0	5	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plantago sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Plantago tubulosa	3	40	3	1	16	16	0	21	27	35	12	0	0	0	0	3	5	43	9	39	0	2	0	4	19
Polipogon sp.	0	0	0	0	0	0	3	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Potamogeton filiformis	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranunculus sp.	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
Taraxacum sp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
Werneria heteroloba	0	0	0	0	0	0	0	9	2	0	0	40	12	0	0	5	11	3	9	0	0	2	0	2	6
Werneria pygmaea	0	15	4	9	6	6	0	13	0	14	8	15	58	5	0	4	12	30	10	33	7	12	7	28	4
Werneria sp.	6	0	0	0	0	0	14	14	7	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15
Zameoscirpus muticus	0	0	0	47	5	5	0	0	0	8	6	4	0	0	0	5	0	0	0	0	37	0	47	12	7