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SYNTHESIS



Pastoralism in the high tropical Andes: A review of the effect of grazing intensity on plant diversity and ecosystem services

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Abstract

Aims: Pastoralism is a land-use system that involves the care and use of grazing livestock and has been more common in areas of low resource availability. In this review, we analyze the impact of pastoralism on biodiversity and ecosystem services across the tropical Andes. This region is the most extensive and populated tropical mountain region in the world and presents a high diversity of biomes, livestock types and management histories. Given that pastoralism is a main land use here, understanding its impacts is important for providing appropriate recommendations for sustainable management.

Location: Tropical Andes; Venezuela to the north of Argentina and Chile.

Methods: To understand these impacts, we performed a systematic literature search (August 2021) and obtained 103 articles. We created a conceptual framework to map how available research has contributed to our understanding of the main pastoral systems, their associated management strategies and the impact of different grazing intensities on vegetation cover/diversity and ecosystem services.

Results: We found that research has focused on two leading pastoral systems in the region: bovines in the páramo biome of the northern Andes and camelids in the puna biome of the central Andes. We found important environmental impacts at high grazing intensities for both the puna camelid and páramo bovine pastoral systems, including a decrease in soil organic carbon and an increase in soil compaction, a decrease in aboveground biomass, plant species richness, and graminoid cover, as well as clear changes in the growth-form composition of vegetation.

Conclusions: Given these findings, we recommend coordinated research efforts using common methodologies, documenting current and previous land use, including stocking rates, and combining observational and experimental approaches to develop a more integrated understanding of pastoralism's impacts across this diverse and vulnerable region.

KEYWORDS

biodiversity, camelid, cattle, environmental impact, grazing intensity, pastoral system

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1 | INTRODUCTION

Pastoralism, an extensive land-use system, occurs in ca. 100 countries worldwide and is mostly practiced in areas that do not present the biophysical conditions needed for intensive crop cultivation (FAO, 2001; Box 1). For example, in arid or low-resource regions, pastoralism is used as a subsistence livelihood option (Fratkin, 1997). Traditional pastoralism consists of complex multi-level interactions, including the interaction between biophysical conditions and biogeographic patterns that produce unique phytogeographic locations. In addition, socioeconomic conditions, including historical and present-day use, shape the magnitude and frequency of land use and further structure these socio-ecosystems. To analyze the functioning and impacts of pastoralism as an animal husbandry strategy from a regional perspective, we focused this review on the tropical Andes. The tropical Andes is the most extensive and populated tropical mountain region in the world (Cuesta et al., 2019). Here, pastoralism takes on multiple forms, where this way of life occurs amid a heterogeneous landscape composed of a mosaic of biomes and ecosystems, as well as current and past land uses.

In the tropical Andes, climatic and ecological conditions foster a conducive environment for provisioning, regulating, and supporting ecosystem services (Buytaert et al., 2006; Anderson et al., 2011). For example, high-Andean ecosystems provide and regulate the availability of water (Rolando et al., 2017), and carbon is stored in mineral and organic soils owing to slow decomposition rates due to cold temperatures and large areas of wetlands and peatlands (Hribljan et al., 2016). Moreover, alpine ecosystems in the tropical Andes are outstandingly rich in plant species with a high level of endemism, making it a key global biodiversity hotspot (Myers et al., 2000; Sklenář et al., 2013). The diverse biophysical conditions are linked with extensive elevational and latitudinal gradients, affecting temperature and precipitation ranges (Cuesta et al., 2023). Depending on local climate and elevation, different ecosystems occur in the puna, páramo, and jalca biomes of the tropical Andes (Box 1), including tussock grasslands with or without giant rosette forms, shrublands, peatlands, and other wetlands.

The tropical Andes also comprise a large diversity of pastoral systems that differ along the latitudinal gradient. For example, pastoralism in the northern Andes is mainly dominated by introduced species (e.g., cattle and horses), whereas pastoralism in the central Andes is dominated by wild and domesticated camelids (Molinillo & Monasterio, 2006). Camelids from the genus *Lama* and *Vicugna* evolved in the southern and central Andes (Franklin, 1982). Therefore, the history of traditional pastoralism in this region spans thousands of years, during which the natural vegetation, pastoralist cultures, and camelids co-evolved and shaped the puna landscape (Arzamendia et al., 2021).

Land-use history in the páramo is less documented, and there is less evidence of pastoralism before the Inka conquest (15th century). Vegetation in this region did not co-evolve with human-managed grazing practices, but hunting-gathering activities partly shaped the landscape (Westreicher et al., 2007; White, 2013). After the

BOX 1 Definitions of key concepts used in this review.

- Pastoralism: a type of extensive land-use system that involves the care and use of grazing livestock by rural populations. Typically, pastoralists do not provide feed for the animals, which graze freely with limited or no management of pastures (e.g., fertilization). Another characteristic of pastoralism is herd mobility, which ranges from little migration and transhumance (seasonal migration), to nomadic pastoralism, in which not only animals, but also homesteads are frequently moved.
- Grazing intensity: a type of pressure exerted by grazing animals on the ecosystem. It is often understood and measured as stocking rate and/or evidence of impact. Stocking rate is typically measured by quantifying animals (typically using standardized animal units) per period per area or by estimation through interviews with local pastoralists. Levels of impact can be estimated quantitatively or qualitatively by observing/recording evidence of trampling, browsing, or droppings.
- Carrying capacity: can be measured as the number or density of organisms (e.g., grazers) that a given region/ ecosystem can support without environmental degradation. Hence, to evaluate whether a given stocking rate has the potential to degrade the ecosystem's forage provision, it is important to compare it with the carrying capacity. Carrying capacity, however, is challenging to measure because of the complexities of ecosystem processes that influence primary productivity and forage availability and its dynamics, including biotic interactions and environmental spatial-temporal variability (Shaofeng, 2004).
- Páramo: An open, alpine grassland biome found in the humid northern-most part of the Andes, between 6°S at 10°N (Venezuela, Colombia, Ecuador, and northern Peru; Hofstede & Llambí, 2020).
- Puna: An open, alpine grassland biome in the central part of the Andes. It is drier than the páramo and ranges from 6°S to 23°S (encompassing most of Peru, Bolivia, and the northern Andean parts of Chile and Argentina) (Cuesta et al., 2019).
- Jalca: A transition zone that shares climatic characteristics between the northern and Central Andes. This zone presents endemic species but shares similarities with the northern páramos and the puna in the central Andes (Josse et al., 2009).
- Pastoral system: System characterized by including, (a)
 the livestock type (e.g., bovine, camelid, ovine); (b) the
 biome (puna, páramo); (c) the management strategy (e.g.,
 burning, animal rotations, trenching-irrigation); and (d)

BOX 1 (Continued)

the type of economic activity that pastoralism is used for (e.g., subsistence vs market-oriented production, agropastoralism). The pastoral system is expected to be modulated by the climate and topography of each region as well as legacy effects from previous activities on the landscape, which should, in turn, modulate the degree of environmental impact.

Spanish colonization, exotic animals such as *Bos taurus* (cows), *Ovis aries* (sheep), and *Capra hircus* (goats) were introduced as livestock in the late 16th century and are estimated to have reached the higher páramos in the 19th century. Although this form of pastoralism does not use native animals, it is still considered such, given the similar forms of management—with few to no enclosures, no provision of fodder or supplements, and no controlled breeding in most cases of cattle raising in the high páramos (McCarthy, 1997). Hence, although it is recognized that camelids dominate pastoralist landscapes in the central Andes, the concept of pastoralism with exotic animals and the merging of customs that came with colonialism have been less explored in the global literature (Dong et al., 2016).

The environmental impacts of grazing in the high Andes have been documented since at least the 1970s, when researchers highlighted its importance to local livelihood strategies (Webster, 1973). Previous literature reviews on this topic have focused on páramo hydrology and the ecosystem services of grazed ecosystems in punas (Buytaert et al., 2006; Rolando et al., 2017; Patino et al., 2021). However, at a regional level, important knowledge gaps remain and. to the extent of our knowledge, there are no previous reviews that analyze the impacts of pastoralism across the tropical Andes in an integrated way, considering both puna and páramo biomes, different pastoral systems (Box 1), and multiple response variables including biodiversity and ecosystem services. Moreover, key conceptual frameworks, such as the intermediate disturbance hypothesis (Gao & Carmel, 2020), which evaluates the way herbivory intensity (understood as disturbance) modifies biodiversity, have not been evaluated comprehensively in the tropical Andes.

From an applied perspective, the effects of pastoral systems on landscapes and their ecological processes can inform appropriate management, conservation, and restoration practices for these biomes, which are considered global biodiversity hotspots and ecosystem services providers for more than 60 million rural and urban inhabitants across the region (Myers et al., 2000; Anderson et al., 2011). A thorough understanding of changes in ecosystem services in response to different livestock systems is particularly important in the face of climate change that, combined with shifting land-use pressures, has put these fragile ecosystems and vulnerable livelihoods at risk (Verzijl & Quispe, 2013; Postigo, 2014; Cuesta et al., 2020). Therefore, to promote conservation, sustainable management and design appropriate adaptation strategies in this naturally and culturally diverse region, it is important to understand the

role pastoralism has played and the impacts it has had in these socioecological systems. For example, it is unclear how different levels of grazing intensity by native camelids and exotic livestock could differentially affect multiple ecosystem indicators.

Our objective in this review is to analyze the impact of different types of grazing (in terms of the types of animals, grazing intensity, and management strategies) on biodiversity and ecosystem services in the main pastoral systems that have been studied in the tropical Andes. We address the complexities of pastoralist systems across the region by describing their environmental context and prevalent management strategies, using that to analyze their ecosystem impacts. To do this, we reviewed peer-reviewed publications to evaluate the main pastoral systems in the region and systematically recorded the types and effects of different levels of grazing intensity.

Hence, we considered four main aspects in this systematic review: (a) a description of the most common and most investigated pastoral systems in the tropical Andes; (b) these studies' research methods; (c) whether grazing pressure evaluations were included and if so, which ones; and (d) the indicators of biodiversity and ecosystem services impacted and the metrics used to measure them. Based on the results of this analysis, we discuss implications for the conservation and management of these unique and diverse ecosystems as well as ways to improve current research, identifying what we consider to be the main open challenges that future research could address.

2 | METHODS

2.1 | Review structure

We assessed the effects of pastoralism on ecosystems by determining (a) the level of grazing intensity/animal loads (sometimes in relation to the carrying capacity of the ecosystem, Box 1); (b) the history of land use, including possible co-evolution of livestock with humans and the spatiotemporal extent of pastoralism; and (c) the climatic and environmental changes the ecosystem is undergoing. To quantify these effects, ecosystem indicators such as hydrologic regulation, vegetation coverage, plant diversity metrics, forage palatability, and ecosystem services (e.g., carbon storage, above- and below-ground biomass) can provide information on how grazing modifies the relationship between biodiversity and ecosystem functioning.

To achieve this, first we used the study area described in the publications to extract a description of the pastoral systems and their main characteristics. We then characterized the research methods by determining the type of study (observational, experimental, or literature review) and whether grazing pressure was evaluated regarding grazing intensity and/or the ecosystem's carrying capacity to sustain grazing (Box 1).

To analyze the environmental impacts that have been addressed along a grazing intensity gradient, we used environmental indicators and their metrics. We searched for articles that related pastoralism to ecosystem services focusing on water regulation, erosion control, soil fertility, climate regulation (e.g., carbon/biomass accumulation) and provision of palatable forage. The metrics for plant biodiversity and functional diversity indicators were percent cover of either species or traits, species diversity indices, and the cover of vegetation, plant growth forms or target/indicator species.

In the case of water regulation, we looked for soil water retention and infiltration (generally measured at the plot level), but also indicators that are more relevant at a watershed level, such as base flow. We also searched for carbon stock and biomass accumulation as potential indicators for multiple ecosystem services. Furthermore, we extracted information on forage provision as an ecosystem service, as measured directly by above-ground biomass (AGB) of palatable species and through nutrient analysis.

2.2 | Literature search methodology

We first selected 25 articles that clearly addressed our objective for this study (based on our background knowledge) and used them as our "gold standard" to develop our keyword search phrase (Appendix S1). We performed a literature search in Web of Science (August 2021) based on the keywords listed in Appendix S2. We obtained 1,506 articles. Using the abstracts of this initial search, we filtered the list using the following additional inclusion criteria: (a) regional, restrained to the tropical Andes (Venezuela to northern Argentina and Chile); and (b) elevation, restrained to alpine ecosystems (páramos, punas, jalcas). Using these restrictions, we obtained a total of 243 articles, 103 that contained potential comparable data on the characteristics of pastoral systems and their grazing impacts, and a separate 141 articles that could be used to describe the regional context.

2.3 | Analysis/counts

To quantify the pastoral system characteristics, we counted each animal type, biome, manipulation and livelihood type, where each item was counted separately even when found in the same article (e.g., for mixed herds, we quantified each animal type separately). Therefore, the total number of tallies was greater than the total number of articles. Furthermore, Andean ecosystems were grouped into overarching biome categories (e.g., peatlands and grasslands in páramos were categorized as páramo studies).

We selected all the articles that measured grazing intensity (quantified stocking rate or determined use through evidence of impact) and categorized intensities into four levels—none, low, medium and high—using the grazing descriptions in each study (Appendix S3; Step 1 in Appendix S4). In most articles, the grazing intensity "none" is obtained through exclusion (fencing) and corresponds to a control treatment. To analyze how the selected impact variables change with grazing pressure, we then built a comparative table by selecting variables that were studied in multiple articles. Studies were

kept if there were at least two that analyzed the same variable. We sorted these data into the four grazing intensity levels (Step 2 in Appendix S4). Lastly, we compared the indicators in each intensity level with the next lowest level, noted if they reported statistical significance for differences in the indicator values and created a summary of the results (Step 3 in Appendix S4).

3 | DIVERSITY OF PASTORAL SYSTEMS ACROSS THE TROPICAL ANDES

To describe their study sites, authors in most articles mentioned the biome where the study was located and the livestock type, so we used this information to describe the pastoralist system. We found that this intersection was indicative of the main pattern of livestock distribution across the tropical Andes. Camelid (*Vicugna* sp. and *Llama* sp.) and bovine livestock (29% and 32%, respectively) were the most common forms of pastoralism analyzed. Within the biome types, puna and páramos were the most studied (48% and 47%, respectively), whereas studies in the transitional Peruvian jalca were less common (5%; Figures 1 and 2).

To describe the livestock systems, the type of animal (154 mentions within the main group of papers) and livelihood/management options (extensive vs. intensive, land tenure, etc., 118 mentions) were more frequently addressed, whereas biome (87 mentions) and management strategies (e.g., fire, rotational systems, afforestation, 83 mentions) were used less (Figure 2). The use of extensive grazing (37%) was the most prevalent management strategy described, as systems tend to be found on community-owned lands, or in "páramo grazing rights" systems in the northern Andes, in which large pasture areas are distributed between individual families.

The pastoral systems in Colombian and Venezuelan páramos were mainly composed of bovines (71% and 83%, respectively). Some studies in Colombia and Venezuela also mentioned mixed herds with *Equus caballus* (horses), sheep and goats (17% in Venezuela, 7% in Colombia).

All livestock types were found in the páramos of Ecuador, which encompass wetland, grassland and shrubland ecosystems. Fifty percent of studies focused on bovines and 21% included sheep and goats within mixed herds (Figure 1). Further south, this diversity of livestock types remained, with camelids becoming prevalent in the puna of Peru, Bolivia and the north of Argentina and Chile (varying from 35% in Argentina to 78% in Chile, Figure 1).

Camelids include domesticated *Vicugna pacos* (alpacas) and *Llama glama* (Ilamas), and wild *Vicugna vicugna* (vicuñas) and *Llama guanicoe* (guanacos). In the Argentine puna, transhumant subsistence raising of camelids plus introduced species such as cattle, sheep, goats and equines, is a main type of economic activity (Navarro et al., 2020). However, sheep were the largest domestic livestock in this country, although it has been showing a decreasing trend in importance with the growth of urbanization (Izquierdo & Ricardo Grau, 2009). Through changes in laws and international agreements, there has been a recovery of wild herbivores and, therefore, an increase in

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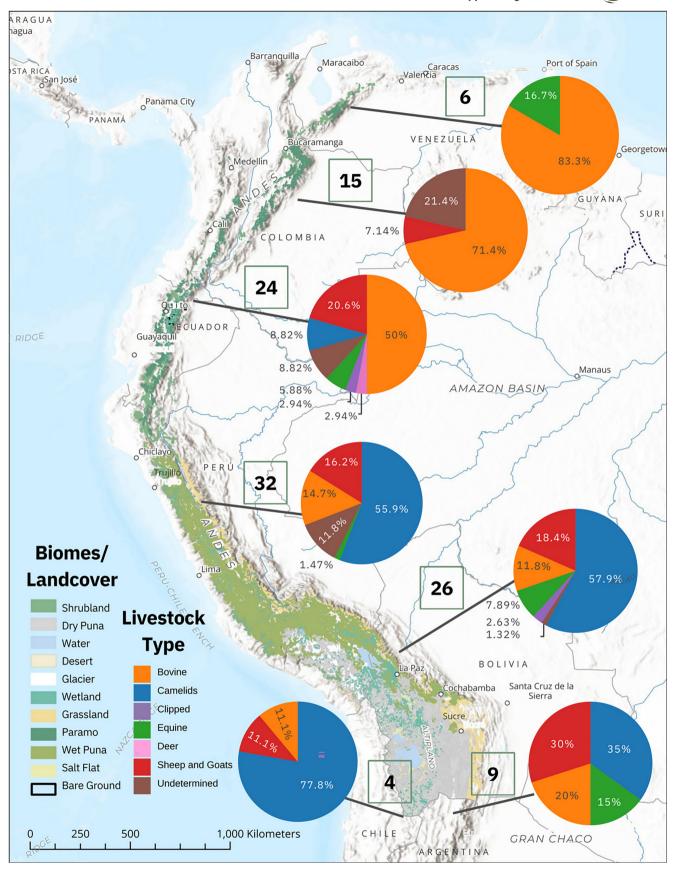


FIGURE 1 Map of the target region analyzed in our systematic review, the tropical Andes. The main biomes/land-cover types were based on grouped phytoregions following Josse et al. (2009). Pie charts show the proportion of studies related to each livestock type in the studies within each country within the tropical Andes.

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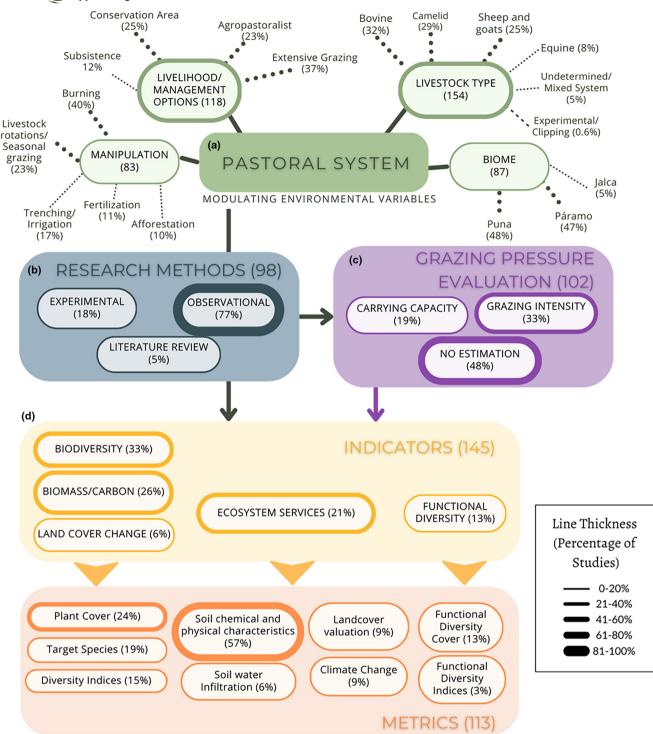


FIGURE 2 Conceptual diagram reflecting and expanding upon the prevalent themes found in 103 articles included in the review. The four main components are: (a) a description of the management strategies/livestock system, (b) the study methods, (c) the grazing pressure evaluation methods, and (d) indicators of grazing impact analyzed to show trends in the available literature.

vicuña populations (Navarro et al., 2020). In Bolivia, camelids correspond mainly to alpacas and llamas, families typically owning an average of 200 animals. Seasonal rotation is reported as a common strategy, where alpacas graze in the wetlands for most of the year, but the llamas graze the highlands during the wet season and the wetlands during the dry season (Molinillo & Monasterio, 2006).

The páramo bovine livestock system occurs in different ecosystems. In Ecuador, grass-dominated páramos are part of a landscape with high-Andean forests, pine plantations—typically planted over grazed páramo-and managed pastures (Hofstede et al., 2002). Private property exists in several protected areas in Ecuador and grazing takes place with varying levels of intensity. For example, in

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the Reserva Ecológica Antisana parts of the grassland páramo are heavily degraded because of past sheep grazing, which was only recently excluded. In the Cotopaxi and Cayambe-Coca National Parks, cattle is freely roaming in low densities on private and communal lands (Cierjacks et al., 2008). This is also characteristic of several páramos in protected areas in Venezuela and Colombia (Hofstede et al., 2003; Hofstede & Llambí, 2020).

PREVALENT RESEARCH METHODS FOR ANALYZING GRAZING IMPACTS

The three overarching research method types were: (a) literature reviews; (b) observational studies, in which the comparative design (e.g., between areas with different existing grazing intensities) involved no manipulation of the system; and (c) experimental studies, which included some type of manipulation, for example, fencing, nutrient addition or clipping to simulate grazing. Only 18% of the articles were experimental, whereas 77% were observational. There were three literature reviews that compared impacts of different land-use systems including grazing/pastoralism on the general hydrology (Buytaert et al., 2006) or hydro-physical soil properties of páramos (Patino et al., 2021), and the ecosystem services of high-Andean punas (Rolando et al., 2017).

Studies that assessed grazing pressure or the system's capacity to sustain it (53 of 102 papers) mostly determined grazing intensity through evidence of impact or stocking rates (34 articles). By using evidence of impact, authors graded grazing intensity on a scale from no grazing to very high grazing. Grading was done by observing altered physical characteristics of the landscape, such as evidence of biomass consumption by browsing, signs of trampling or feces droppings per area. Also, word-of-mouth was used, in which local people provided information on estimated animal densities.

We found that grazing intensity was mostly qualitatively assessed using expert and/or local knowledge. A few studies quantified it by explicitly measuring stocking rates. For example, Sarmiento (2006) compared agricultural fallow areas that were experimentally grazed at a stocking rate of 0.4 cows per hectare, with paired adjacent areas excluded from grazing. Other measures consisted of indirect evidence of grazing; for example, Molinillo and Brener (1993) divided areas of low grazing intensity from areas of high grazing intensity using the density of herding trails (Appendix S3).

Fewer articles (35% of 53 studies) focused on measuring carrying capacity (also including impact variables in some cases). These studies (Machaca et al., 2018; Zuniga et al., 2018; Yaranga, 2020) employed plant composition to extract the density and/or percent cover of palatable species. These data, plus plant vigor indices, using plant height as proxy, provided the ecological condition of the study site in terms of forage provision. However, only one study compared carrying capacity (CC) with stocking rate (SR) to obtain a quotient (CC/SR) that allowed evaluation of overgrazing (Machaca et al., 2018).

The indicators used to determine the impacts of grazing mostly focused on biodiversity (33%) or structural biomass/ carbon stock (26%) and less on analyzing changes in ecosystem services (21%), functional diversity (13%) and land-cover change due to pastoralism using remote sensing (6.2%). The metrics used for biodiversity, biomass/carbon and land-cover change included plant cover, where studies analyzed target species or used total plant cover as a proxy for AGB. In some cases, plant cover was combined with species composition and 17 studies used diversity indices for all vascular plants present (e.g., Shannon or Hill). Functional diversity metrics included percent cover of functional types (plant growth- forms), and functional diversity indices (e.g., Shannon Index based on functional trait community matrices). The metrics used to analyze ecosystem services were the physical and chemical characteristics of soil, soil water infiltration, financial returns on land use or payments for ecosystem services, and metrics related to climate change mitigation (e.g., greenhouse gas exchange).

EFFECTS OF GRAZING INTENSITY ON **BIODIVERSITY AND ECOSYSTEM SERVICES**

Puna camelid systems

We found 10 articles that measured grazing intensity on puna camelid systems. From these, we extracted information on six variables measured in more than one study (Appendices \$3 and \$5); species richness, graminoid cover, total plant cover, soil organic matter (SOM)/soil organic carbon (SOC), AGB and below-ground biomass (BGB). Although trends were difficult to quantify because of the small number of studies, differences in the way analyses were reported and differences in context (e.g., samples were collected in grasslands on valley slopes vs wetlands), we were able to identify several clear patterns.

Five articles analyzed species richness (Becerra, 2006; Catorci et al., 2016; Duchicela et al., 2019; Barros et al., 2014; Machaca et al., 2018; Table 1a). Three of them also measured total plant cover and/or graminoid plant cover. For species richness and the Shannon Index, only Machaca et al. (2018) found a significant decrease with an increase in grazing intensity. The other studies that measured species diversity did not report significant differences between treatments. However, within each study there seemed to be a threshold at which species richness increased and then decreased again (the response had a bell-curved relationship, but the fit of the data to this response model was not evaluated). Regarding functional diversity, Catorci et al. (2014) analyzed changes in community structure between high and low grazing pressure using community similarities via plant traits. The authors found that high intensity grazing affects species composition and the growth-form structure of the community.

Only Barros et al. (2014) reported a significant effect of grazing on graminoid cover, showing an increase at medium intensity and a

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TABLE 1 Effects of grazing intensity for two predominant livestock systems present in the tropical Andes.

(a) Camelids	in puna					
Grazing intensity	Soil organic carbon (Oliveras et al., 2014)	Above-ground biomass (Oliveras et al., 2014)	Species richness (Cochi Machaca et al., 2018)	Graminoid percent cover (Barros et al., 2014)	t Plant percent cover (no significant tre	biomass (Olivera
None	Lowest level	Lowest level	N/A	Lowest level	Lowest level	Lowest level
Low	\downarrow	\downarrow	Lowest level	\downarrow	\downarrow	↑
Medium	↓	\downarrow	\downarrow	↑	\downarrow	↓
High	N/A	↓	\downarrow	\downarrow	\downarrow	N/A
(b) Bovines in Grazing intensity	Soil organic carbon/ matter (Avellaneda- Torres et al., 2018)	Above-ground biomass (Molinillo & Monasterio, 1997; Vargas et al., 2002; Sarmiento, 2006)	Species richness (Alzerreca et al., 2006; Sarmiento, 2006	(Molinillo & M Sarmiento, <mark>20</mark>	onasterio, 1997;	Bulk density (Hofstede et al., 2002 Cierjacks et al., 2008; Valero, 2010)
None	N/A	Lowest level	Lowest level	Lowest level		N/A
Low	Lowest level	\downarrow	\downarrow	1		Lowest level
Medium	\downarrow	\downarrow	1	\downarrow		\uparrow
High	\downarrow	\downarrow	\downarrow	↓		↑

Note: Distinctions in intensity levels per publication can be found in the Appendix S3. Arrows (pointing upwards for increases, downwards for decreases) show general trends found in publications for that intensity level compared with the next lower intensity level. If statistical significance was found for each variable the articles that report a significant result are cited at the beginning of each column. NA: not applicable.

strong decrease at high intensity. Becerra (2006) reported an increase in graminoid cover at high intensity, but it was not statistically significant. Only Becerra (2006) and Duchicela et al. (2019) measured total plant cover and did not find significant differences between grazing levels, although they found a general decreasing trend in plant cover with increasing grazing intensity.

Four studies compared SOC stocks (Heitkamp et al., 2014; Oliveras et al., 2014; Machaca et al., 2018; Duchicela et al., 2019). Oliveras et al. (2014) showed a slight reduction in SOC from no grazing to low-intensity grazing, and a significant reduction from low to medium intensity. The other studies did not report clear trends: Heitkamp et al. (2014) compared soil properties of not grazed grasslands, forests and rangeland, and found that grasslands and forests had lower SOC values than rangelands, but the differences were not significant. Machaca et al. (2018) used a linear regression to determine if the carrying capacity/stocking rate quotient affected SOM (no significant effects).

Three studies measured the effect of camelids on AGB and two also measured BGB (Table 1a). Oliveras et al. (2014) showed significant decreases of AGB at higher grazing intensity. Barros et al. (2014) did show a decrease in biomass with grazing presence (grazed-not grazed) but did not find a significant relationship with grazing intensity. Duchicela et al. (2019) only compared no grazing with high intensity in wetlands and grassland puna, and no significant differences were found. Results for BGB showed a bell-shaped curve (Oliveras et al., 2014), although Duchicela et al. (2019) only compared no grazing with high intensity and no significant differences were found.

5.2 | Páramo bovine systems

We found 14 articles that analyzed the effect of grazing intensity for páramo bovine systems (Appendices S3 and S6). From these, we extracted variables that were reported in more than one article: species richness, SOM or SOC, AGB, graminoid cover and soil bulk density (Table 1b).

Alzerreca et al. (2006) found a bell-shaped relationship for both Shannon Index and species richness with grazing intensity. In turn, Sarmiento (2006) found a consistent decrease in species richness in successional old fields under low grazing intensity compared with areas with no grazing. Regarding SOM or SOC, across six studies we found a decreasing trend along grazing intensities. Avellaneda-Torres et al. (2018) found significant differences between the low and medium intensities (Table 1b), but other studies did not report significant differences.

Eight articles analyzed the impact of grazing of AGB in páramo. Comparisons were challenging because AGB was not estimated in the same way across studies. For example, Hofstede et al. (1995) reported total AGB, whereas Molinillo and Monasterio (1997) divided AGB into high and low herbaceous layers. On the other hand, Sarmiento and Smith (2011), Valero (2010) and Vargas et al. (2002) used biovolume (the sum of plant cover over vertical vegetation strata) as an estimator. Nevertheless, in general, AGB decreased with increasing grazing intensity; for example, comparing lowintensity grazing vs no grazing in fallow fields (Sarmiento, 2006), in wetlands (Valero, 2010) and after moderate grazing when measuring total herbaceous biomass (Molinillo & Monasterio, 1997). Sarmiento

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and Smith (2011) found much lower plant biovolume (and species richness) in páramo shrubland areas that were severely degraded by historic grazing and wheat cultivation compared with undegraded páramo areas. However, the authors note that degradation in this case was mainly associated with wheat cultivation, because a cattle exclusion experiment showed no significant effects under presentday grazing loads. They conclude that previous land use can be a strong factor in determining the current impact of grazing.

Four studies measured impact of bovine grazing on graminoid cover in páramo (Appendix S3). Cardenas-Arevalo and Vargas-Rios (2008) found a significant increase in graminoids cover with low grazing intensities owing to new open soil availability created by disturbance. By contrast, Sarmiento (2006) and Molinillo and Monasterio (1997) found significant decreases in graminoid cover at moderate and high grazing intensities (Table 1b).

Three studies in the páramo reported decreases in the relative abundance of different plant growth forms as a result of cattle grazing. Vargas et al. (2002) reported a decrease in tall tussock grasses and bamboos and an increase in short grasses and small herbs/forbs with increasing grazing intensity. Similarly, Valero (2010) found a decrease in tall grasses, mosses and giant rosettes and an increase in cushion-forming grasses in grazed vs ungrazed wetland areas. However, no studies in the paramo explicitly quantified changes in functional diversity.

Alzerreca et al. (2006) reported a decrease in palatable species and total vegetation cover under higher grazing pressure and concluded that moderate grazing apparently favored plants with taller growth forms and that in degraded wetlands the growth of smaller species was favored. Vargas et al. (2002) also reported a decrease in biovolume of tall, more palatable tussock grasses with increasing grazing intensity and an increase in less palatable short grasses. Furthermore, Valero (2010) found the same shift in the biovolume of tussock vs cushion-forming grasses in fenced vs grazed wetlands. Cierjacks et al. (2008) found that areas with more trampling were positively associated with an increase in seedling numbers of their target species. They attributed this trend to the reduction in litter depth, which was negatively associated with trampling.

Three studies (Table 1b) found a significant increase in soil bulk density with increasing grazing intensity. Hofstede et al. (2002) concluded that trampling resulted in soils becoming denser, drier and less acidic. Valero (2010) found a significant decrease in bulk density and a very marked increase in soil water retention after 4-5 years of cattle exclusion in two páramo wetlands in Venezuela (especially in more humid sectors within wetlands).

5.3 Camelids in páramo systems

We found two articles that studied the effects of grazing in camelid páramo systems, which were introduced as a low-impact strategy by private landowners (Appendix S3). Harden et al. (2013) found that afforestation or grassland burning affected páramo soil moisture more than camelid grazing. However, Farley et al. (2013) found that the unburned, alpaca-grazed sites had less soil carbon at 0-10cm depth, being significantly different from the unburned and ungrazed treatment (which showed the highest soil carbon).

5.4 Other livestock systems

We found two studies that measured livestock intensity in systems focused on sheep and goats in puna (Becerra, 2006; Molinillo & Monasterio, 2006). One of Molinillo and Monasterio's (2006) study sites in Argentina, was mostly associated with sheep and bovine livestock. They analyzed plant composition along a grazing intensity gradient and found that, for all their case studies, there were no significant differences for species richness under variable grazing pressures. However, for their case studies that included sheep and cattle (in Argentina and Venezuela) moderate to heavy grazing was associated with an increase in the number of weeds and exotic species.

Synthesis or overall trends in páramo and puna pastoral systems

Grazing by camelids in the puna, particularly at low intensities, where there has been a co-evolution of pastoralism with the ecosystem, would be expected to have a lower impact on biodiversity and ecosystem services, or even a positive impact in their long-term maintenance (as mentioned in Molinillo & Monasterio, 2006 and Machaca et al., 2018 for wetland, bofedal systems) compared with bovine grazing (both in páramos and Punas), because bovines were only introduced in these systems in the past 500 years.

Our review indicates that cattle in the paramo can compact soils, modify the growth-form structure of the plant community, reduce grass cover and AGB, and reduce plant diversity, especially at high grazing intensities. Negative impacts from camelids are also reported on graminoid cover, AGB, SOC and plant diversity, although the evidence is less consistent in this case, with fewer studies reporting statistically significant effects. This could be partially due to camelid characteristics, such as having pads instead of hooves, which are softer and cause less damage, as well as their foraging behavior (e.g., they tend to consume only the upper part of the plant), which tends to result in lower impacts on vegetation. Moreover, it could be linked with the co-evolution of native camelids and vegetation in the central Andes.

Trampling and browsing are important disturbances for community assembly and structure. In puna camelid systems, biodiversity decreased in most of the studies. One study, however, showed the opposite trend (Duchicela et al., 2019), in which species richness increased when compared with no grazing. The authors discussed that grazing resulted in the dominant species, a palatable bunchgrass, to be restricted and therefore, caused competitive release, allowing other species to encroach on the newly cleared areas. Other biodiversity measures along with species richness, such as the Shannon or Hill indices showed decreases at high grazing intensities. In some

studies (Alzerreca et al., 2006 in a bovine páramo system), diversity increased when no grazing was compared with low intensity levels and then decreased again at high intensity. For this indicator, as well as in graminoid percent cover for camelids in the puna, the trend showed a bell curve, which could be expected from the intermediate disturbance hypothesis (Gao & Carmel, 2020).

We found a decreasing trend along the grazing intensity gradient in SOC or total SOM and AGB in puna camelid and páramo bovine pastoral systems. In general, trampling can be associated with decreased organic matter in the top 10cm of soil, may cause compaction and is, therefore, related to higher bulk density and with lower water retention capacity (e.g., see Valero, 2010 for páramo wetlands). Moreover, in camelid puna systems we found that BGB increased at lower grazing intensities and then decreased. This shows that whereas at lower grazing intensities a shift in biomass allocation may occur, there is a potential threshold above which there is less plant productivity in general.

6 | IMPLICATIONS FOR MANAGEMENT AND CONSERVATION

In general, our results indicate that low grazing levels can be compatible with maintaining both biodiversity and key ecosystem services while sustaining pastoralist systems, which can play diverse roles in the local/regional economy. In the case of the paramo, especially when grazing by exotic bovines occurs within protected areas, there is a need to critically evaluate the role that this productive activity plays in the rural socioeconomic and cultural context vis-à-vis its ecological impacts (e.g., the regulation of water provision for agriculture and human consumption), and to explore sustainable management alternatives and their effectiveness (e.g., management of grazing pressures through fencing and rotation, cattle exclusion from critical areas such as wetlands, genetic improvement of animal herds, pasture management). There are, in fact, examples of community-led initiatives to protect high páramo wetlands from grazing to guarantee water provision for irrigation in the agricultural belt (see Acevedo et al., 2019). Also, several protected areas are included in water protection projects, funded by Municipal water funds, that compensate high country farmers for reducing cattle (Farley & Bremer, 2017).

However, the available studies showed that at high grazing loads both camelid and bovines can have significant negative impacts on both biodiversity and ecosystem services (including the provision of palatable forage, C storage in biomass and soils, soil water retention capacity), although the available evidence was more conclusive in the case of páramo bovine systems. This points to the need to promote strategies to clearly identify degradation thresholds and identify alternatives with local communities to reduce grazing loads and promote more-sustainable management options in these cases. For example, in more arid regions, like the dry puna, where pastoralism is usually done with camelids in extensive stretches of land, fencing off some areas could function as "reserve areas" for when conditions have not allowed vegetation regrowth. The same is true

in key páramo areas for water regulation and provision subjected to overgrazing (e.g., small páramo wetlands). Complementing these strategies with active restoration of degraded areas could also help mitigate some of the impacts using an integrated landscape approach.

Finally, we found that grazing impacts were somewhat similar across ecosystems but when considering pastoralist systems as a whole, taking into account sociocultural conditions, situations may vary. For example, in páramos grazing is mostly associated with agriculture, whereas in punas, pastoral systems tend to make use of wetlands and to be subsistence orientated. Therefore, it is important to consider communities' needs, rights and goals when creating and taking management decisions.

7 | RESEARCH STRATEGIES: LIMITATIONS, CHALLENGES AND FUTURE DIRECTIONS

There is continued interest for research on this topic given the compounded effects of climate change and land-use change on these fragile ecosystems and vulnerable ways of life. Based on our review of the literature, we have three main recommendations for future studies. First, grazing intensity is often explicitly considered in intensive agropastoral systems, but not in more extensive pastoral systems. Either quantifying or describing systematically (through direct observation or interviews with local people) the stocking rate/ evidence of impact and animal type in the study area, is essential for future studies, allowing to derive more robust conclusion and to perform regional meta-analyses. Second, providing landscape descriptions and information on current management and previous land use would also help to increase the comparability between studies, and to correctly interpret their conclusions and implications in a regional context. Evaluating in detail the management and disturbance regimes, such as evaluating whether the area has been burned recently, whether there is seasonal rotation, and what is the land tenure type are examples of crucial questions. In this context, an open topic for further analysis is considering the complex interactions that can result from burning and grazing. In this review, we did not explicitly compare burned vs unburned treatments or situations to avoid complicating the interpretation of our results (hence, we excluded burned treatments when assessed in the available studies), but this needs to be considered because many pastoral systems, especially in bovine systems in the páramo, use burning as part of the strategies for pasture management. Third, even though the environmental impacts of the two main pastoral systems in the tropical Andes—cattle in the paramos and camelids in the puna—have been documented, they have not been explicitly compared in coordinated experiments. Coordinated studies using standardized methodologies, would help comparison between multiple grazing systems. For example, studies could use the methods in Machaca et al. (2018) as a model to quantify environmental impacts of grazing according to stocking rate and carrying capacity ratios. Comparative long-term studies at a regional scale using common protocols and combining

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experimental and observational strategies, would greatly increase our ability to understand how contrasting socio-environmental contexts across the tropical Andes modify grazing impacts and how they interact with other drivers of change such as global warming (e.g., as has been done in climate change monitoring networks in the region such as GLORIA-Andes; see Cuesta et al., 2019).

From our perspective, conservation and sustainable management programs should also consider these three recommendations for future research as key aspects of their management plans, using a more adaptive approach in which monitoring is an integral part of the management cycle. The implementation of alternative cattle management strategies can be interpreted as "field experiments", in which careful monitoring and communication of impacts would provide invaluable information for regional comparative studies and for developing more-sustainable pastoral systems.

CONCLUSIONS

To our knowledge, this review is the first to systematically describe pastoralist systems and assess their impacts across the tropical Andean region. We found that high intensity grazing consistently decreases biodiversity and impacts important ecosystem services such as above-ground/below-ground C accumulation and soil water retention capacity in the two main pastoral systems that have been more extensively studied, bovines in the paramo and camelids in the puna (although there was more conclusive evidence available in the first case). Based on our review of the available evidence, three main conclusions emerge: (a) high-elevation tropical Andean ecosystems show diverse and complex pastoralist systems using diverse management strategies; (b) there is a varying grazing intensity threshold, above which biodiversity and the provision of ecosystem services decrease, although the evidence for this is stronger in the case of bovine systems in the páramos; and (c) the implementation of grazing vs no grazing experiments helps to evaluate environmental impacts, but we can only find clear grazing impact thresholds using differing, and explicitly quantified, grazing intensity levels. Hence, we advocate for the development of coordinated comparative studies across the region combining observational and experimental approaches, including a detailed analysis of pastoral management strategies and an explicit analysis of the stocking rate/carrying capacity.

AUTHOR CONTRIBUTIONS

LDL, VB, FR and SAD conceived the study and structure of the review; SAD carried out the literature review and data analyses; SAD and LDL led the writing of the paper; VB and FR revised and commented on the different versions of the manuscript.

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DATA AVAILABILITY STATEMENT

All the information and metadata systematized to generate the analyses included in the review are available upon request from the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of 25 articles used as standard for keywords in literature search

Appendix S2. Web of Science Search for Keywords.

Appendix S3. Table summarizing grazing intensity evaluations by author.

Appendix S4. Example of grazing intensity data collection process.

Appendix S5. Intensity data per study for camelid and puna.

Appendix S6. Intensity data per study for bovine and páramo.

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