Article:

Mills, S.C., Parra Sanchez, E., Socolar, J.B. et al. (6 more authors) (2023) Avian biodiversity losses from grazing of high Andean páramo. Biological Conservation, 286. 110298. ISSN: 0006-3207

https://doi.org/10.1016/j.biocon.2023.110298

Biological Conservation 286 (2023) 110298

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Avian biodiversity losses from grazing of high Andean páramo

Simon C. Mills[a], Edicson Parra Sanchez[a], Jacob B. Socolar[b], Chris Bousfield[a], Bryn Coffey[a], Jos Barlow[c], Jose Manuel Ochoa Quintero[d,e], Torbjørn Haugaasen[f], David P. Edwards[a,g,*]

[a] *Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, UK*
[b] *NCX, 2443 Fillmore St. #380-1148, San Francisco, CA 94115, United States of America*
[c] *Lancaster Environment Centre, Lancaster University, Lancaster, UK*
[d] *Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia*
[e] *Universidad Federal de Mato Grosso do Sul, Campo Grande, Brazil*
[f] *Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway*
[g] *Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge CB2 3EA, UK*

ARTICLE INFO

Keywords:
Páramo
Tropical grasslands
Tropical alpine ecosystem
Bird community

ABSTRACT

Páramos are high-elevation grassland-dominated ecosystems of the northern Andes that harbour large numbers of small-ranged and endemic species and provide important ecosystem services. Though páramos are increasingly managed with a conservation focus, they remain ecologically threatened, in part due to overgrazing. Here, we assess the impacts of grazing on bird communities using data collected from three páramo complexes in the Eastern Andes of Colombia. We (1) assess how densities of shrubs and frailejones—a keystone group of plants in the páramo—are impacted by grazing, (2) determine the influence of these vegetation features on bird occupancy, and (3) examine how bird species richness and community composition are impacted by páramo grazing. We find that grazing status strongly influences the vegetation characteristics of the páramo, resulting in large reductions in the abundance of shrubs and frailejones. These vegetation changes have significant impacts on páramo bird communities, with reduced shrub abundance resulting in lower occupancy for most species (4 out of 48). As a consequence, grazed páramo communities contain fewer bird species and vary in composition relative to those of natural páramo. However, the magnitudes of these differences are modest and it is possible that low-intensity grazing remains compatible with conservation management. We suggest that it is important to consider how páramo conservation may interact with management of adjacent montane forests and the potential for leakage effects resulting in increased deforestation outside of protected areas.

1. Introduction

Páramos are unique high-elevation grassland-dominated ecosystems that occur above the treeline of high mountains in the northern Andes and into Panama and Costa Rica. Occupying an area of 25–36,000 km^2 (Hofstede et al., 2003, Jiménez-Rivillas et al., 2018; Peyre et al., 2021), they harbour a unique and highly specialised biota (Sklenář et al., 2014; Correa et al., 2020) with large numbers of endemic and small-ranged vertebrate (Astudillo et al., 2017) and plant species (Luteyn, 1999; Cruz and Lasso, 2021). In addition to their high biodiversity value, they also play important roles in ecosystem service provisioning, especially below-ground carbon sequestration (Thompson et al., 2021) and hydrological regulation (Correa et al., 2020). Though there is growing interest in management of páramos for conservation, reflected in recent legislative changes in countries that contain large areas of páramo (Colombia, Ecuador), the biodiversity benefits of different land uses and agricultural activities remain poorly quantified and the empirical basis for making management decisions lacking (Farley et al., 2013; Llambí et al., 2020).

With a long history of human modification (Rodríguez and Behling, 2012; White, 2013), significant areas of páramo today exists in a highly modified state, particularly across the Eastern Cordillera of Colombia (Burbano-Girón et al., 2020). Within Colombia, 15–20 % of páramos are considered heavily altered (Llambí et al., 2020; Peyre et al., 2021), with figures as high as 50 % in some Colombian páramo systems (García et al., 2019; Ungar, 2021). Though the dominant human activities have varied through time in response to legislative changes and agricultural reforms (Hofstede et al., 2002; López-Sandoval and Maldonado, 2019),

---

* Corresponding author.
E-mail address: dpe29@cam.ac.uk (D.P. Edwards).

https://doi.org/10.1016/j.biocon.2023.110298
Received 30 January 2023; Received in revised form 11 September 2023; Accepted 15 September 2023

the primary activities in páramos have generally focussed on agricultural production (mainly potato crops; Robineau et al., 2010) and livestock grazing (Astudillo et al., 2017). More recently several of the countries that contain significant areas of páramo have made a number of legislative changes to limit activities that can be carried out in the páramo, preventing agriculture, grazing, and mining (López-Sandoval and Maldonado, 2019; Joslin, 2021; Ungar, 2021). Nevertheless, grazing remains widespread, as does the occurrence of human-set fires to maintain forage quality for livestock (Borrelli et al., 2015). Developing a stronger understanding of the effects of grazing impacts on páramo biodiversity is central to informing management of páramos and better defining low impact activities based on biodiversity responses.

Livestock directly impacts páramo vegetation via grazing and trampling (Molinillo and Monasterio, 1997; Urbina and Benavides, 2015), and indirectly through the periodic burning (traditionally on a 2–3 year cycle) that is used to maintain forage quality (Verweij and Kok, 1992; Hofstede et al., 1995). Structural recovery of shrubby plants can take 20 years from cessation of burning (Williamson et al., 1986), and compositional differences remain for at least 15 years (Zomer and Ramsay, 2021). Recovery following burning is in turn influenced by grazing pressure and topography (Matson and Bart, 2013), with heavily grazed páramos tending to more slowly accumulate biomass following burning (Sarmiento, 2006). Heavily grazed páramos tend to have areas of bare soil and an altered plant community (Janzen, 1973; Matson and Bart, 2013), with native vegetation often replaced by introduced grasses (Urbina and Benavides, 2015). One of the dominant groups of páramo plants, Frailejones (subtribe Espeletiinae, family Asteraceae; Diazgranados, 2012), experience increased mortality in heavily grazed and burned locations, resulting in fewer frailejón species and an age distribution shifted towards younger plants (Verweij and Kok, 1992; Horn and Kappelle, 2009). While the impacts of grazing and associated burning on páramo vegetation can be stark, without periodic burning, and particularly at low stocking rates that allow recovery of páramo vegetation following grazing and trampling, impacts on the plant community can be relatively minor (Hofstede et al., 1995).

While it is likely that vegetation changes from grazing and associated burning result in changes to the faunal community of the páramo, these impacts have not been thoroughly characterised to date. Koenen and Koenen (2000) found that bird species richness increased following cessation of burning, with páramos that have been unburnt for at least 8 years tending to contain approximately twice as many species as páramos that have been recently burnt. Though these changes were not linked to differences in vegetation, corresponding increases in woody vegetation suggest that they at least partly owe to increasing shrub cover. Similarly, Astudillo et al. (2017) found that overall abundance of páramo bird specialists tends to be greatest in páramos that also display low levels of grazing, but these changes were not strongly related to vegetation features. Thus, while there is some evidence that the bird community responds to vegetation changes resulting from grazing and burning, the role of vegetation in mediating the response of the bird community remains unclear.

Here we assess the species- and community-level impacts of intensive páramo grazing on the avifaunal community using data collected from three páramo complexes in the Eastern Cordillera of Colombia (La Rusia, Iguaque, Chingaza). We focus on birds because they have not been comprehensively studied in the context of páramo degradation, play important roles in ecosystem functioning by providing services such as pollination and seed dispersal (Kraemer, 2001; Melcher et al., 2000; Sekercioglu, 2006), are good indicators of patterns of land-use change impacts on other taxonomic groups (Barlow et al., 2007), and are cost effective to study (Gardner et al., 2008). In quantifying the impacts of heavily grazed páramo relative to ungrazed páramo controls, we have three key objectives. (1) To assess how densities of woody shrubs and frailejones are impacted by páramo grazing; (2) to determine how these vegetation features in turn influence bird occupancy; and (3) examine how bird species richness and community composition are impacted by páramo grazing. We discuss the conservation implications of these results, namely the potential for low levels of grazing to be compatible with conservation goals, and the risk of leakage effects if grazing pressure is simply offset to unprotected areas adjacent to páramo.

2. Methods

2.1. Study area

Fieldwork was carried out at 74 points across three páramo complexes in the Eastern Andes of Colombia: La Rusia, Iguaque, and Chingaza (situated in the departments of Santander, Boyaca, and Cundinamarca; Fig. S1). All three complexes fall in the same phytogeographic province (Londoño et al. 2014), with minimal biogeographic turnover in the bird community across them (Hilty and Brown, 2021). Climatically they share similar thermal profiles with low average temperatures (12 °C at midday) and wide diurnal temperature ranges of 5–13 °C (Morales Rivas et al., 2007; Londoño et al., 2014). The complexes vary somewhat in their average precipitation: Chingaza experiences a precipitation gradient, ranging from around 4500 mm annually on the southeastern edge to 1200 mm on the western edge, while La Rusia on average experiences 1950 mm annually. Iguaque is the driest of the three complexes, with on average 810 mm of rain a year (Morales et al. 2007).

Points were visited over the course of three field seasons (August 2018, Feb-Mar 2019, and July 2019; Table S1). Surveyed points span an elevational range of 3170–3880 m.a.s.l., and are broadly categorised as sub- and mid-páramo, with vegetation predominantly comprised of tussock grassland and low shrubland (around 1–2 m in height), with patches of stunted elfin forest towards lower elevations. Survey points were placed exclusively in tussock grassland or at heavily grazed (‘pasture’) points, and all fall within areas legally delimited as páramo. The sampling design followed Gilroy et al. (2014), with points placed in clusters of three, with 200 m between points and with at least 500 m between each cluster.

2.2. Bird sampling

Each point received four 10-min point counts over four consecutive days, apart from three páramo points that received three counts due to logistical constraints (resulting in 292 point counts in total). Point counts were carried out between 05:30 am and 14:00 pm, varying the visit order each day so that all points received early and late counts. Point counts were run by experienced observers (SCM, JBS, DPE), with all birds observed or heard within a 100 m radius recorded, excluding flyovers. The area falling within the point count radius was always homogeneous in classification (i.e. did not include a mix of grazed and ungrazed pasture). Point counts were additionally recorded (Olympus LS10 or Tascam DR100 mk III with Sennheiser ME-62 microphone) for subsequent identification of unknown vocalisations through cross-comparison across observers and use of online reference material (www.xeno-canto.org). Flyovers and non-breeding long-distance migrants were excluded from analyses, as were three species of aquatic bird (detected on three páramo points), with the latter excluded on the basis that their presence owed to large water bodies on the peripheries of the point rather than the condition of the páramo surveyed.

2.3. Vegetation sampling

Vegetation surveys were carried out by EPS from January 2019 to November 2020, with vegetation sampling run concurrently with bird surveys, save for 6 points in Iguaque PNN which were revisited in 2020. There were no significant changes in habitat composition over this period, as confirmed by DPE revisiting these points during 2019 and 2020. We established sampling plots of 10 × 30 m centred on the bird sampling point. We recorded the number of standing frailejones and shrubs with a diameter > 5 cm and a height > 50 cm. We consider frailejones as adult and immature individuals of species in the subtribe Espeletiineae (Asteraceae) of the genera *Carramboa*, *Espeletia*, *Coespeletia*, and *Espeletiopsis*. Páramo shrubs were individuals with hard stems and healthy leaves (adult individuals belonging to botanical families such as Asteraceae, Berberidaceae, Brunelliaceae, Cunoniaceae Ericacae, and Melastomataceae). Shrub and frailejon abundance was calculated as the number of individuals of each group within the sampling plot.

2.4. Defining pasture points

Across our 74 surveyed points, we identified 15 points with evidence of recent or current grazing and/or burning to maintain pasture. Pasture points comprise: (1) six points in central páramo La Rusia that had cattle and/or horses on during our sampling period which have been maintained as pasture, containing dry-stone walling and/or fencing and resembling semi-improved grassland; (2) three points also in páramo La Rusia but that retain low páramo vegetation, having been burnt for grazing 2 years prior (in 2017), and in 2019 contained only ankle-height vegetation with occasional frailejones that were able to survive the burning, as well as evidence of recent grazing; (3) three pasture points on the fringe of Iguaque PNN with semi-improved grassland and dry-stone walling; and (4) three points within Chingaza, in an area that has historically been used for mining but is used as pasture in the present day, with cattle present at time of sampling. We contrasted these with 59 points that have experienced limited or infrequent grazing within the last 30-years, based on verbal histories from National Natural Parks and local residents. Though we cannot exclude the possibility that some points classified as páramo have experienced low-levels of grazing, verbal histories indicated that they have not been significantly grazed within at least 30 years, and have not been burnt in the last 10–15 years, and in most cases much longer. We discuss the implications of imperfect classification of grazing pressure more fully in the Discussion.

2.5. Statistical analysis

We hypothesised that the effects of grazing pressure and associated burning on bird occupancy are mediated via compositional changes to the vegetation on each point. Vegetation composition additionally varies with elevation, with upper elevations of the mid-páramo tending to be increasingly dominated by grassland and frailejones, while lower elevations will naturally tend to contain more woody vegetation. The impacts of grazing are therefore likely to vary elevationally, mediated via compositional changes to habitat that occur independently of grazing (Fig. 1). Differences in the vegetation structure (due to either elevation or grazing status) may also influence our ability to detect species, with reduced detection on points with substantial three-dimensional vegetation structure. To address this potential confounding effect, we used a hierarchical occupancy-detection model that allows us to model the effects of vegetation on both detection and occupancy simultaneously, while also accommodating other sources of detection-side variation (observer, time of day; MacKenzie et al., 2002; Socolar et al., 2022). To capture the hypothesised pathway by which grazing influences bird occupancy, we further embed this within a piecewise Structural Equation Model (Lefcheck, 2016) that relates grazing status to the abundance of shrubs and frailejones on a point, which in turn influences bird species' occupancy (Fig. 1).

Specifically, occupancy at the *i*th point and for the *k*th species, $\psi_{i,k}$, is modelled as a function of site and site × species intercepts, $\gamma_{site[i],k}$ (i.e. allowing average occupancy to vary between páramos, and for each species to vary in their average occupancy between páramos), species intercepts, $\beta_{0,k}$, plus the effects of elevation, $\beta_{1,k}\text{elevation}_i$, frailejón abundance, $\beta_{2,k}\text{frailejones}_i$, and shrub abundance, $\beta_{3,k}\text{shrubs}_i$. By fitting species-specific slopes, individual species can have habitat and elevation associations that vary around the overall average effect across species. Site effects were fitted as fixed effects, with all other effects modelled as random slope or intercept terms. The occupancy model is therefore:

$$logit(\psi_{i,k}) = \gamma_{site[i],k} + \beta_{0,k} + \beta_{1,k}\text{elevation}_i + \beta_{2,k}\text{frailejones}_i + \beta_{3,k}\text{shrubs}_i$$

Detection, $\theta_{i,j,k}$, is also allowed to vary across visits (indexed by *j*), and is modelled as a function of a varying observer intercept, $\omega_{observer[i,j]}$, (observer at the *i*th point on the *j*th visit), a varying species intercept, $\delta_{0,k}$, plus the effects of time of day, frailejón abundance and shrub abundance, with all covariates modelled via random slopes on species, save for the observer effect (which was fitted as a fixed effect):

$$logit(\theta_{i,j,k}) = \omega_{observer[i,j]} + \delta_{0,k} + \delta_{1,k}\text{time}_{i,j} + \delta_2\text{frailejones}_i + \delta_3\text{shrub}_i$$

Observations, y_{ijk}, are then modelled as a function of detection and occupancy components:

$$z_{i,k} \sim Bernoulli(\psi_{i,k})$$

$$y_{i,j,k} \sim Bernoulli(z_{i,k}\cdot\theta_{i,j,k})$$

Abundance of frailejones and shrubs were modelled as a function of site, elevation and grazing status:

$$\text{frailejones}_i \sim ZINB(exp(\eta_{1,site[i]} + \alpha_1\text{elevation}_i + \alpha_2\text{grazing}_i))$$

$$\text{shrubs}_i \sim ZINB(exp(\eta_{2,site[i]} + \alpha_3\text{elevation}_i + \alpha_4\text{grazing}_i))$$

where ZINB indicates Zero-inflated negative binomial distribution, with elevation additionally included in the zero-inflation term.

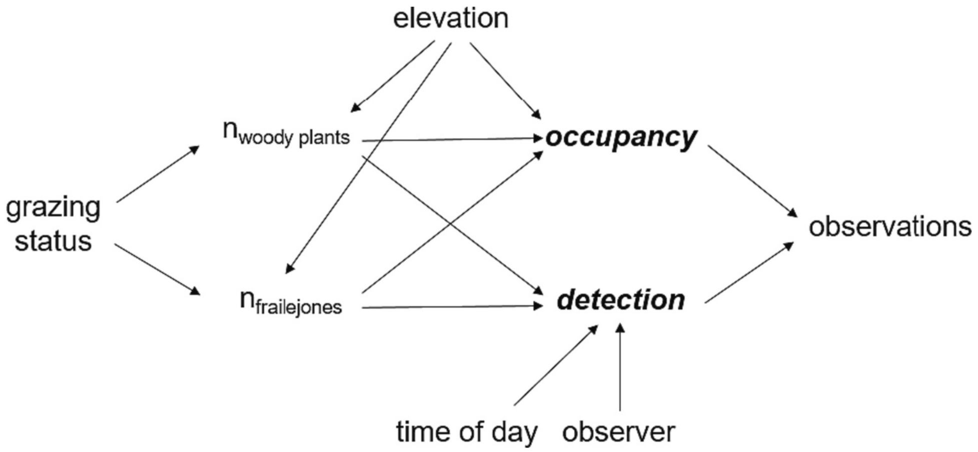

Fig. 1. Conceptual diagram of the model relating grazing status of a point to bird observations.

All parameters were given weakly informative priors which do not entertain a priori implausible effect sizes and avoid issues with push-forward densities that are strongly concentrated around 0 and 1 in the occupancy-detection component of the model (Banner et al., 2020), while also entertaining substantially larger uncertainty about effects than we have prior to model fitting. The model was fitted in Stan (version 2.27; Stan Development Team, 2021) via flocker (0.1–0; Socolar and Mills, 2023) and brms (2.16.2; Bürkner, 2017). The model was run with 4 chains, each with 1000 warmup and 1000 sampling iterations per chain. Convergence diagnostics were monitored and models checked with posterior predictive checks.

Community-level impacts (objective 3) were measured in two ways: (1) the species richness of the community at grazed vs. ungrazed points, and (2) changes in community composition. To address (1), we derived species richness from the SEM model directly, as the expected species richness on grazed and ungrazed points, while propagating uncertainty in parameters through the model. To address (2), we used an Analysis of Similarity (ANOSIM) on the raw detection/non-detection data, using 9999 permutations. Non-metric multidimensional scaling (NMDS) was used to visualise differences between communities in reduced dimensions. Code for all analyses is available at: github.com/SimonCMills/paramo_bird_community.

3. Results

(1) Effects of grazing on densities of woody plants and frailejones

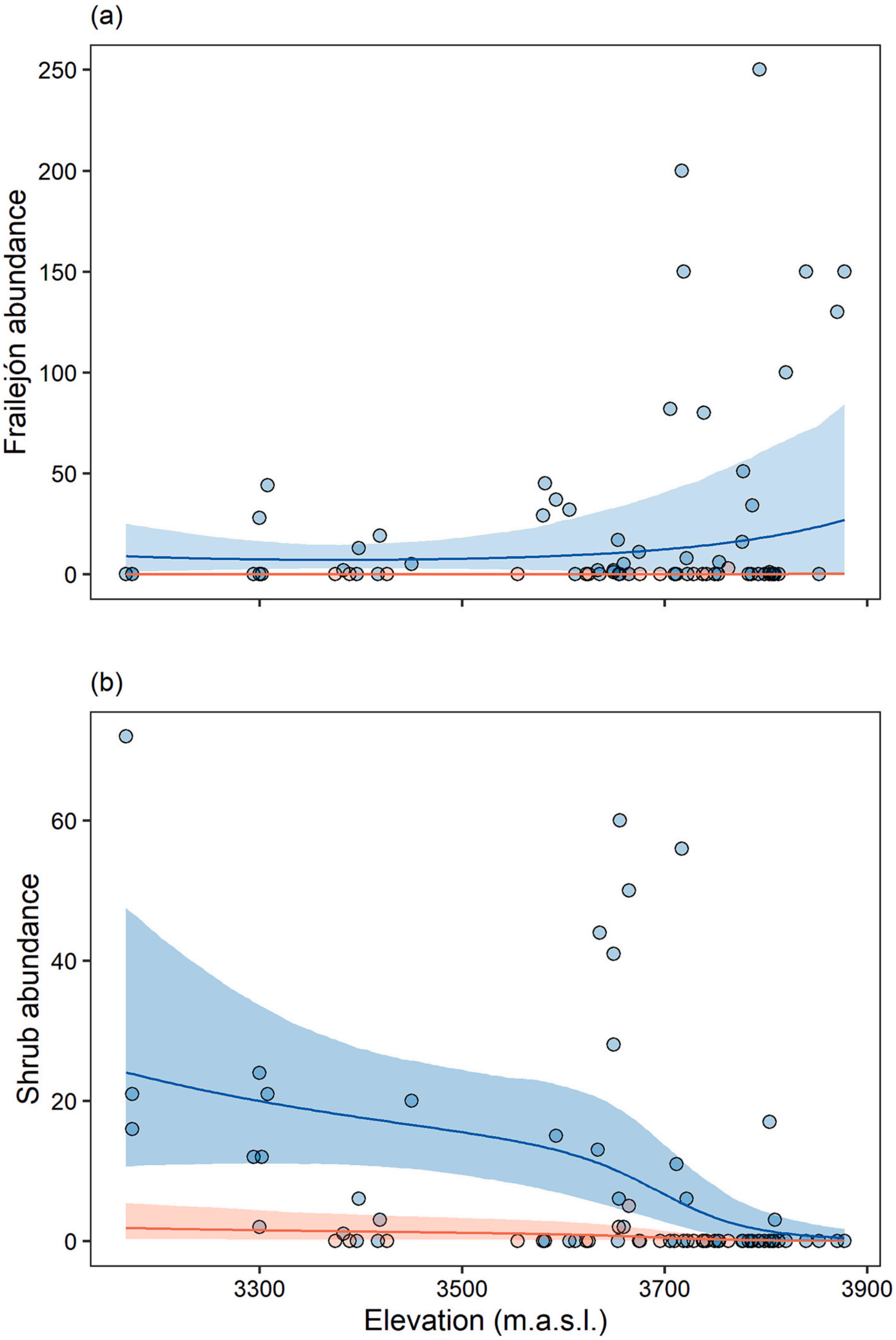

Fig. 2. Frailejón (a) and shrub abundance (b) in natural páramo (blue) and pasture (orange). Shaded areas represent the 90 % credible interval of the fitted model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Grazed points differed strongly in their abundances of shrubby plants and frailejón relative to natural páramo points (Fig. 2). Frailejón were recorded in low numbers on just a single pasture point (Fig. 2a), and only a few shrubs were found on a minority of the pasture points (Fig. 2b). Correspondingly, the modelled effect of grazing was strongly negative for both frailejón (mean = −2.52, 95 % CI: −1.46, −3.42) and shrub abundance (mean = −1.48; 95 % CI: −0.60, −2.28). While there was a weak tendency for frailejón abundance to increase towards higher elevations, and shrub abundance tended to decline with elevation (Fig. 2), both shrubs and frailejón were frequently found in high numbers at ungrazed páramo points across the majority of the elevational gradient surveyed.

(2) Effect of vegetation features on bird occupancy

In total, we detected 48 bird species across our surveyed points, with the majority of these observed at páramo points (where our surveying effort was greatest; $n_{\text{páramo}} = 44$; $n_{\text{pasture}} = 24$). There was a strong effect of shrub abundance on occupancy (mean = 0.55, 95 % CI: 0.13–0.98), but no observed effect of frailejón abundance on occupancy (mean = 0.00, 95 % CI: −0.36, 0.31; Fig. 3). The majority of species exhibited increased occupancy with increasing abundance of shrubs, with just four species displaying reduced occupancy at higher levels of shrub abundance (though note that CIs substantially overlap 0; Fig. 3). Conversely, there were negligible effects of frailejón abundance on occupancy, and

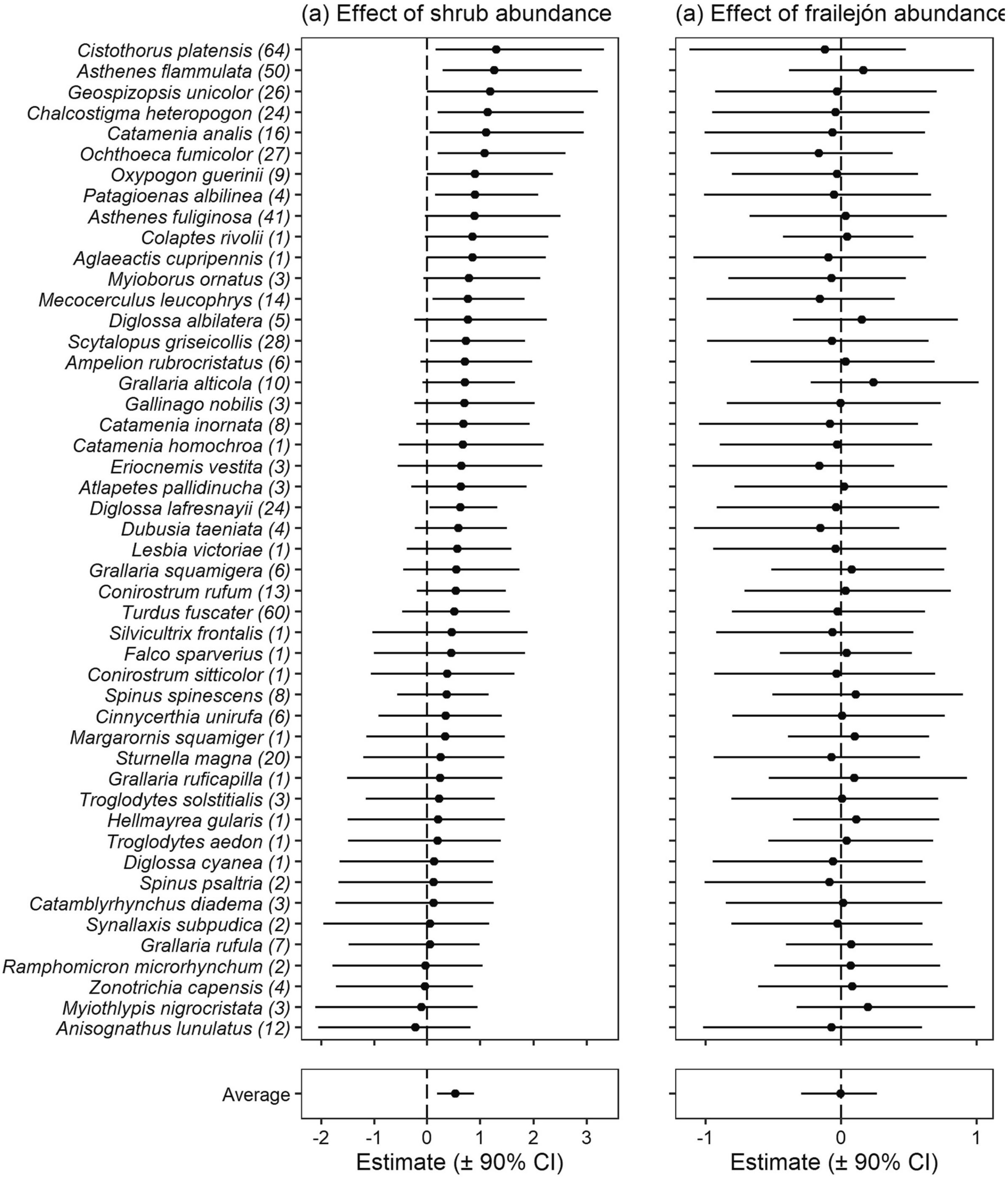

Fig. 3. Effect of páramo degradation on occupancy for each species in the dataset (upper panel), and overall effect (lower panel), with 90 % credible interval overlaid. Numbers next to species names indicate the number of points each species was detected on.

all 48 species had CIs that strongly overlapped 0.

(3) Effect of páramo grazing on species richness and community composition

Mediated via changes to shrub abundance on heavily grazed points, there were significant differences in the species richness of bird communities on heavily grazed páramo (Fig. 4). These differences were largest towards lower elevations where the differences in shrub abundance between grazed and ungrazed points was highest, with an average loss of four species from grazed páramo points relative to the more undisturbed baseline. Though the effect of grazing remained negative across the entire surveyed gradient, the magnitude of species loss declined with elevation, with an average loss below one above 2750 m. This effect arose partly due to the elevationally varying effect of grazing on shrub abundance, as well as the tendency for species' average occupancy to decline towards higher elevations, such that there are fewer species present in the community at the highest elevations. In addition to differences in species richness, communities on grazed and ungrazed páramo additionally varied compositionally, with significant differences in the composition of the bird communities encountered on pasture and páramo points (Fig. 5; $R_{ANOSIM} = 0.14$; $p = 0.04$).

4. Discussion

Páramo ecosystems are increasingly being managed with a conservation focus, but the responses of many taxonomic groups to different management regimes remains poorly characterised (Farley et al., 2013; Llambí et al., 2020). Here, we find that livestock grazing has a strong negative effect of grazing on frailejón and shrub abundance, which in turn mediates significant differences in the bird community present. Vegetation differences between grazed and natural páramo were stark, with frailejón species almost entirely absent in grazed páramo and shrubs present infrequently in highly reduced abundance. Differences to the bird community were more subtle, but the majority of species benefitted from increased shrub abundance, resulting in a smaller and compositionally different community on heavily grazed páramo. Overall, these results are consistent with previous work on the response of páramo birds to grazing and disturbance (e.g. Koenen and Koenen, 2000; Astudillo et al., 2014; Astudillo et al., 2017), and also highlight the potential for low levels of grazing pressure to be consistent with conservation goals.

Points with shrubby vegetation tend to be structurally more complex, providing habitat for species that are not pure grassland specialists and are reliant on some degree of woody vegetation for foraging or nesting

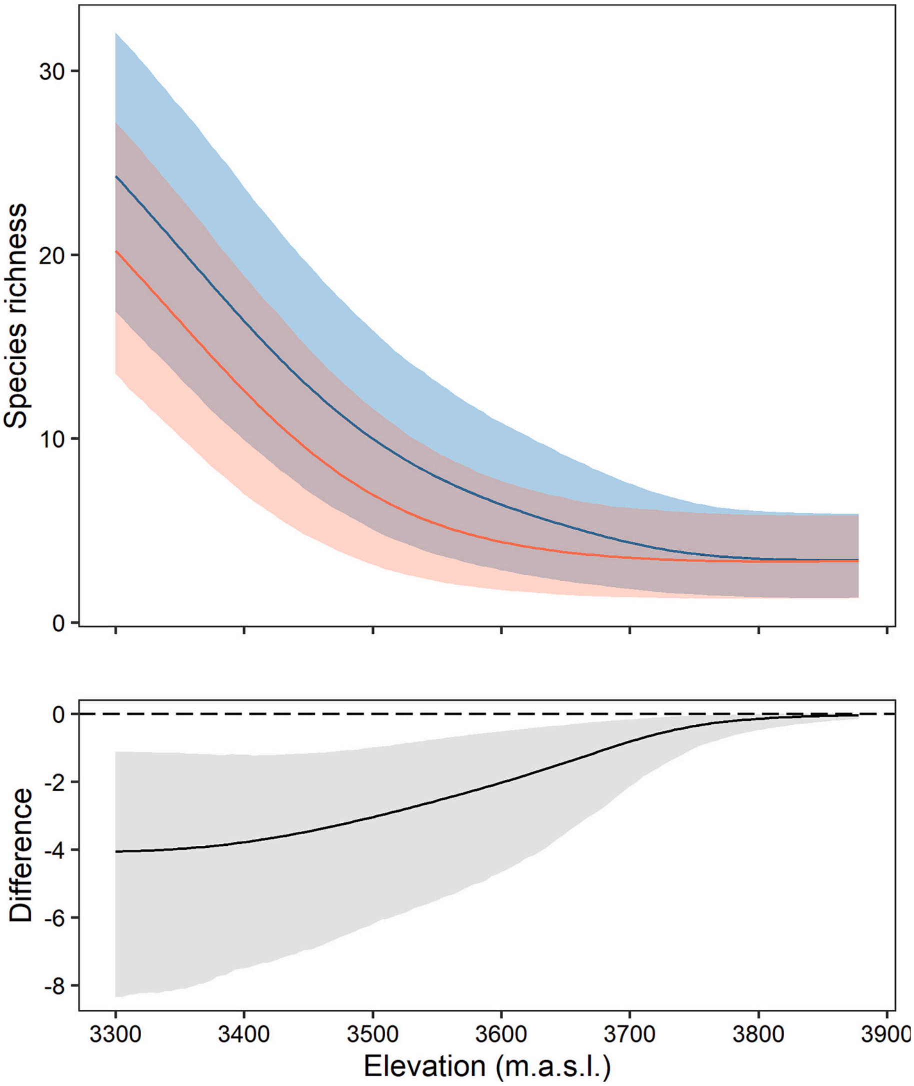

Fig. 4. Bird species richness in páramo (blue) and pasture (orange; upper panel), and difference in species richness between páramo and pasture points (lower panel). Shaded areas represent the 90 % credible interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

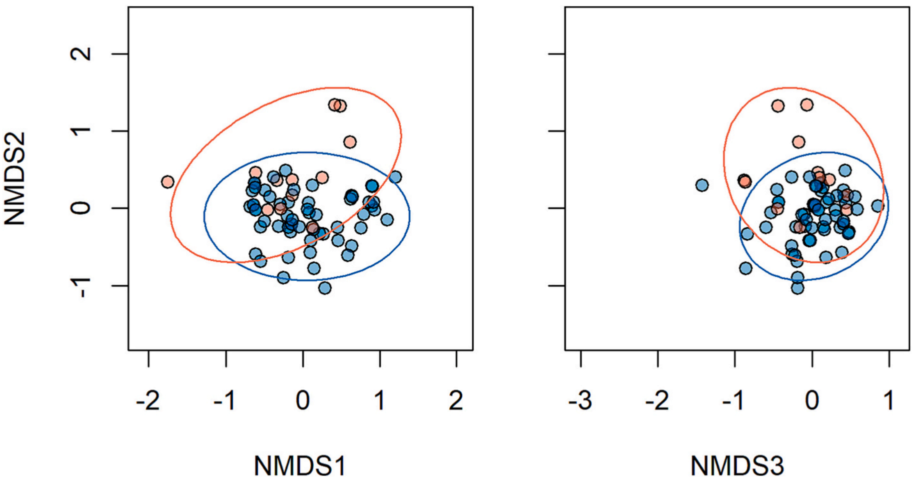

Fig. 5. NMDS ordination of páramo bird communities at points in grazed (orange) and natural páramo (blue). Ordination analyses were run on raw detection/non-detection data. Ellipses display 95 % confidence intervals. Stress = 0.15. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(e.g. *Ochthoeca fumicolor*, *Atlapetes pallidinucha*, *Mecocerculus leucophrys*). While this effect partially contributes to the increased species richness in ungrazed páramo, we also found that species that are associated with grasslands and frequently occur on points without any shrub presence (e.g. *Cistothorus platensis*, *Asthenes flammulata*, *Catamenia analis*) also tend to increase in occupancy with increasing shrub abundance. Patterns of increased species richness therefore do not purely emerge through the addition of non-grassland species, as they also appear to benefit grassland-associated species. These benefits potentially arise through (1) increased foraging opportunities that arise in structurally complex vegetation, and (2) structural complexity provided by shrubby vegetation providing a greater variety of microclimates, in particular helping to buffer low temperatures that occur during the night (Scheffers et al., 2014; Pérez-Ordoñez et al., 2022).

Though we observed consistent differences in the bird communities of grazed and ungrazed páramo (with CIs not overlapping 0), these effects were typically fairly small in magnitude, amounting to a maximum loss of four species from heavily grazed points in which shrubs are largely absent. Towards the upper end of the elevational gradient, where the potential bird community is small and shrubs tend to be absent regardless of grazing status, the differences between bird communities in grazed and ungrazed páramo are marginal. These results therefore permit that some level of light grazing may be compatible with conservation goals (Matallana-Tobón et al., 2018). Several previous studies indicate that low stocking rates combined with a cessation of burning may be capable of maintaining páramo vegetation in a near-natural state (Hofstede et al., 1995; Sarmiento, 2006). Indeed, in the high-elevation puna grasslands of Peru, areas in which cattle have been fully excluded have seen the treeline encroach into what was previously grassland (Lutz et al., 2013). Low levels of grazing may therefore even be desirable to prevent woody encroachment and thereby maintain a páramo bird community, as opposed to a high elevation forest community (Matson and Bart, 2013). Conversely, in situations where páramo is capable of supporting high elevation *Polylepis* or stunted elfin forest (Fjeldså, 2002), it may instead be desirable to explore the regeneration of forest at some locations (Lloyd and Marsden, 2008).

A difficulty faced by observational studies such as ours is that it is typically difficult to perfectly resolve land-use history (see also Astudillo et al., 2017). The main consequence of this is that points that we characterise as grazed are likely to represent the extreme end of the spectrum of grazing intensity as they are, by definition, points that are being actively maintained as pasture, rather than intermittently grazed at low intensities. The effects that we observe therefore likely correspond to intensive grazing pressure, and it is probable that lower grazing intensities (particularly in the absence of burning) would result in a bird community that was more marginally affected. Conversely, due to our inability to perfectly resolve land-use history, we cannot rule out the possibility that there is some level of grazing at points we classified as natural páramo. Verbal histories were able to delimit areas as definitely grazed and/or burnt in recent history, but the reverse (not recently grazed) is more fuzzily defined. Imperfect classification of grazing status would act to dilute the effect of grazing on bird communities, resulting in underestimates of the influence of grazing status on occupancy (McInerny and Purves, 2011). Future work to develop remote sensing products that allow for better resolution of burning and grazing impacts on páramo would also be highly useful (e.g. Borrelli et al., 2015).

While we focus on changes to the páramo grassland, páramo conservation should not be considered in isolation, but instead take a wider perspective that also considers the status of areas outside the páramo at lower altitudes. Conservation interventions within the páramo that are offset by increased loss or degradation of higher diversity montane forests (leakage effects; Moilanen and Laitila, 2016) are unlikely to achieve a net positive impact on biodiversity and ecosystem services. High-elevation tropical forests sequester large quantities of above-ground carbon (Cuni-Sanchez et al., 2021) and stabilise soils and reduce landslide risk (Grima et al., 2020). They additionally harbour animal communities that are more diverse than those in páramo, and are comprised of species that are highly dependent on forest (Terborgh, 1977; Fjeldså, 1993; Mills et al., 2022). Rural populations living in the vicinity of páramos are likely to continue to have livestock that require grazing irrespective of the current legal status of páramo, resulting in conflict with local and indigenous land users (Garrido Corredor et al., 2021; Ungar, 2021). A narrow focus on páramo conservation that does not consider the potential for leakage effects risks perverse conservation outcomes through offset deforestation outside of páramo areas.

5. Conclusion

Grazing has a substantial influence on páramo vegetation, which is likely to be largely mediated through the practice of regular burning to maintain good foraging for livestock. These vegetation changes have knock-on impacts on the bird community, with heavily grazed páramo tending to have lower occupancy probabilities, resulting in a less species rich community that also varies compositionally. Effects are fairly small, however, and it remains possible that conservation goals are compatible with low levels of grazing, which might even be considered a conservation management strategy to prevent encroachment of forest into páramo areas. While additional work is required to more fully resolve the mechanisms of biodiversity change in the páramo, it is important that páramo conservation is not considered in isolation from the surrounding montane landscape. If perverse conservation outcomes are to be avoided, it must instead be embedded within a wider perspective that encompasses displaced human activity outside of the páramos.

Declaration of competing interest

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

Data availability statement

Data are available at: https://figshare.com/s/d9af8b47f4f917708196.

Acknowledgements

We thank the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt for logistical support and acquiring fieldwork permissions, and local assistants that contributed to fieldwork. Funding was provided to D.P.E. and J.B. from the Natural Environment Research Council (grant number NE/R017441/1) and to T.H. and D.P.E. by the Research Council of Norway (grant number 208836), respectively supporting SCM and JBS. This is article #39 of the Biodiversity, Agriculture and Conservation in Colombia/Biodiversidad, Agricultura, y Conservacion en Colombia (BACC) project.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110298.

References

Astudillo, P.X., Samaniego, G.M., Machado, P.J., Aguilar, J.M., Tinoco, B.A., Graham, C. H., Latta, S.C., Farwig, N., 2014. The impact of roads on the avifauna of páramo grasslands in Cajas National Park, Ecuador. Stud. Neotropical Fauna Environ. 49, 204–212.

Astudillo, P., Barros, S., Siddons, D., 2017. Influence of habitat modification by livestock on páramo bird abundance in southern Andes of Ecuador. Stud. Neotropical Fauna Environ. 53, 1–9.

Banner, K.M., Irvine, K.M., Rodhouse, T.J., 2020. The use of Bayesian priors in ecology: the good, the bad and the not great. Methods Ecol. Evol. 11, 882–889.

Barlow, J., Gardner, T.A., Araujo, I.S., vila-Pires, T.C.A., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. 104, 18555–18560.

Borrelli, P., Armenteras, D., Panagos, P., Modugno, S., Schütt, B., 2015. The implications of fire management in the Andean paramo: a preliminary assessment using satellite remote sensing. Remote Sens. 7, 11061–11082.

Burbano-Girón, J., Berbeo, M.A.M., Montoya, C.G., Cruz-Rodríguez, C.A., Ochoa Quintero, J.M., 2020. Estado de conservación de los páramos en Colombia. Humboldt Institute, Colombia.

Bürkner, P.-C., 2017. brms : an R package for Bayesian multilevel models using Stan. J. Stat. Softw. 80.

Correa, A., Ochoa-Tocachi, B.F., Birkel, C., Ochoa-Sánchez, A., Zogheib, C., Tovar, C., et al., 2020. A concerted research effort to advance the hydrological understanding of tropical páramos. Hydrol. Process. 34, 4609–4627.

Cruz, M., Lasso, E., 2021. Insights into the functional ecology of páramo plants in Colombia. Biotropica 53, 1415–1431.

Cuni-Sanchez, A., Sullivan, M.J.P., Platts, P.J., Lewis, S.L., Marchant, R., Imani, G., et al., 2021. High aboveground carbon stock of African tropical montane forests. Nature 596, 536–542.

Diazgranados, M., 2012. A nomenclator for the frailejones (Espeletiinae Cuatrec., Asteraceae). PhytoKeys 16, 1–52.

Farley, K.A., Bremer, L.L., Harden, C.P., Hartsig, J., 2013. Changes in carbon storage under alternative land uses in biodiverse Andean grasslands: implications for payment for ecosystem services. Conserv. Lett. 6, 21–27.

Fjeldså, J., 1993. The avifauna of the Polylepis woodlands of the Andean highlands: the efficiency of basing conservation priorities on patterns of endemism. Bird Conserv. Int. 3, 37–55.

Fjeldså, J., 2002. Polylepis forests- vestiges of a vanishing ecosystem in the Andes. Ecotropica 8, 111–123.

García, V.J., Márquez, C.O., Isenhart, T.M., Rodríguez, M., Crespo, S.D., Cifuentes, A.G., 2019. Evaluating the conservation state of the páramo ecosystem: an object-based image analysis and CART algorithm approach for central Ecuador. Heliyon 5, e02701.

Gardner, T.A., Barlow, J., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., Da Silva, M.N.F., Motta, C.D.S.M., Peres, C.A., 2008. The cost-effectiveness of biodiversity surveys in tropical forests. Ecol. Lett. 11, 139–150.

Garrido Corredor, A.M., Cottyn, H., Martínez-Medina, S., Wheatley, C.J., Sanchez, A., Kirshner, J., et al., 2021. Oso, Osito ¿A Qué Venís? Andean bear conflict, conservation, and campesinos in the Colombian Páramos. Sustainability 13, 10489.

Gilroy, J.J., Edwards, F.A., Medina Uribe, C.A., Haugaasen, T., Edwards, D.P., 2014. Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. J. Appl. Ecol. 51, 1337–1346.

Grima, N., Edwards, D., Edwards, F., Petley, D., Fisher, B., 2020. Landslides in the Andes: forests can provide cost-effective landslide regulation services. Sci. Total Environ. 745, 141128.

Hilty, S.L., Brown, W.L., 2021. Birds of Colombia. Lynx Edicions, Barcelona.

Hofstede, R., Coppus, R., Vásconez, P.M., Segarra, P., Wolf, J., 2002. El estado de conservación de los páramos de pajonal en el el Ecuador. Ecotropicos 15, 3–18.

Hofstede, R.G.M., Castillo, M.X.M., Osorio, C.M.R., 1995. Biomass of grazed, burned, and undisturbed páramo grasslands, Colombia. I. Aboveground vegetation. Arct. Alp. Res. 27, 1–12.

Hofstede, R.P., Segarra, P., Menavasconex, P.M., 2003. Los Paramos del Mundo. Proyecto Atlas Mundial de los Paramos. Global Peatland Initiative /NC-IUCN/ Ecociencia, Quito, Ecuador.

Horn, S.P., Kappelle, M., 2009. Fire in the páramo ecosystems of Central and South America. In: Cochrane, M.A. (Ed.), Tropical Fire Ecology: Climate Change, Land Use, and Ecosystem Dynamics, Springer Praxis Books. Springer, Berlin, Heidelberg, pp. 505–539.

Janzen, D.H., 1973. Rate of regeneration after a tropical high elevation fire. Biotropica 5, 117–122.

Jiménez-Rivillas, C., García, J.J., Quijano-Abril, M.A., Daza, J.M., Morrone, J.J., 2018. A new biogeographical regionalisation of the Páramo biogeographic province. Aust. Syst. Bot. 31, 296–310.

Joslin, A., 2021. Intersections of conservation, cattle, and culture in Ecuador's páramo grasslands. mred 41, R1–R7.

Koenen, M.T., Koenen, S.G., 2000. Effects of fire on birds in paramo habitat of northern Ecuador. Ornitologia Neotropical 11, 155–163.

Kraemer, M., 2001. On the pollination of Bejaria resinosa Mutis ex Linné f. (Ericaceae), an ornithophilous Andean páramo shrub. Flora 196, 59–62.

Lefcheck, J.S., 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579.

Llambí, L., Becerra, M., Peralvo, M., Avella, A., Baruffol, M., Flores, L., 2020. Monitoring biodiversity and ecosystem services in Colombia's high Andean ecosystems: toward an integrated strategy. Mt. Res. Dev. 39, A8–A20.

Lloyd, H., Marsden, S.J., 2008. Bird community variation across Polylepis woodland fragments and matrix habitats: implications for biodiversity conservation within a high Andean landscape. Biodivers. Conserv. 17, 2645–2660.

Londoño, C., Cleef, A., Madriñán, S., 2014. Angiosperm flora and biogeography of the páramo region of Colombia, Northern Andes. Flora 209, 81–87.

López-Sandoval, M., Maldonado, P., 2019. Change, collective action, and cultural resilience in páramo management in Ecuador. mred 39, R1.

Luteyn, J.L., 1999. Paramos, a checklist of plant diversity, geographical distribution, and botanical literature. Mem. N. Y. Bot. Gard. 84, 1–278.

Lutz, D.A., Powell, R.L., Silman, M.R., 2013. Four decades of Andean timberline migration and implications for biodiversity loss with climate change. PLoS ONE 8, e74496.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255.

Matallana-Tobón, C.L., Santamaria, M., Tapias, A.A., Solano, C., Galán, S., 2018. Rethinking nature conservation in Colombia: a case study of other effective area-based conservation measures. Parks 24, 89–98.

Matson, E., Bart, D., 2013. Interactions among fire legacies, grazing and topography predict shrub encroachment in post-agricultural páramo. Landsc. Ecol. 28, 1829–1840.

McInerny, G.J., Purves, D.W., 2011. Fine-scale environmental variation in species distribution modelling: regression dilution, latent variables and neighbourly advice. Methods Ecol. Evol. 2, 248–257.

Melcher, I.M., Bouman, F., Cleef, A.M., 2000. Seed dispersal in páramo plants: epizoochorous and hydrochorous taxa. Plant Biol. 2, 40–52.

Mills, S.C., Socolar, J.B., Edwards, F.A., Parra, E., Martínez-Revelo, D.E., Ochoa Quintero, J.M., et al., 2022. High sensitivity of tropical forest birds to deforestation at lower altitudes. Ecology 104, e3867.

Moilanen, A., Laitila, J., 2016. FORUM: indirect leakage leads to a failure of avoided loss biodiversity offsetting. J. Appl. Ecol. 53, 106–111.

Molinillo, M., Monasterio, M., 1997. Pastoralism in paramo environments: practices, forage, and impact on vegetation in the Cordillera of Merida, Venezuela. Mt. Res. Dev. 17, 197–211.

Morales Rivas, M., García, J.O., van der Hammen, T., Perdigón, A.T., Vargas, C.E.C., Peñaloza, C.A.P., Eraso, N.R., Aguilera, C.A.F., Suárez, J.C.B., Ospina, E.O., Gilede, E.P., Valencia, L.C., 2007. Atlas de Paramos de Colombia. Bogota, Colombia, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt.

Pérez-Ordoñez, D., Titulaer, M., Correll, M., Strasser, E., Baeza-Tarin, F., Martin, R., et al., 2022. The role of temperature and microclimate in the survival of wintering grassland birds. Avian Conserv. Ecol. 17.

Peyre, G., Osorio, D., François, R., Anthelme, F., 2021. Mapping the páramo land-cover in the Northern Andes. Int. J. Remote Sens. 42, 7777–7797.

Robineau, O., Châtelet, M., Soulard, C.T., Michel-Dounias, I., Posner, J., 2010. Integrating farming and páramo conservation: a case study from Colombia. Mt. Res. Dev. 30, 212–221.

Rodríguez, F., Behling, H., 2012. Late Quaternary vegetation, climate and fire dynamics, and evidence of early to mid-Holocene Polylepis forests in the Jimbura region of the southernmost Ecuadorian Andes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 350–352, 247–257.

Sarmiento, L., 2006. Grazing impact on vegetation structure and plant species richness in an old-field succession of the Venezuelan Páramos. In: Spehn, E., Liberman, M., Körner, C. (Eds.), Land Use Change and Mountain Biodiversity. CRC Press LLC, Boca Raton FL, USA, pp. 119–135.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E., Evans, T.a., 2014. Microhabitats reduce animal's exposure to climate extremes. Glob. Chang. Biol. 20, 495–503.

Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.

Sklenář, P., Hedberg, I., Cleef, A.M., 2014. Island biogeography of tropical alpine floras. J. Biogeogr. 41, 287–297.

Socolar, J.B., Mills, S.C., 2023. flocker: flexible occupancy estimation in R. R package version 0.1-0. https://github.com/jsocolar/flocker/.

Socolar, J.B., Mills, S.C., Haugaasen, T., Gilroy, J.J., Edwards, D.P., 2022. Biogeographic multi-species occupancy models for large-scale survey data. Ecol. Evol. 12, e9328.

Stan Development Team, 2021. Stan Modeling Language Users Guide and Reference Manual, v. 2.28. https://mc-stan.org.

Terborgh, J., 1977. Bird species diversity on an Andean elevational gradient. Ecology 58, 1007–1019.

Thompson, J.B., Zurita-Arthos, L., Müller, F., Chimbolema, S., Suárez, E., 2021. Land use change in the Ecuadorian páramo: the impact of expanding agriculture on soil carbon storage. Arct. Antarct. Alp. Res. 53, 48–59.

Ungar, P., 2021. Assembling an ecosystem: the making of state Páramos in Colombia. Conserv. Soc. 19, 119–129.

Urbina, J.C., Benavides, J.C., 2015. Simulated small scale disturbances increase decomposition rates and facilitates invasive species encroachment in a high elevation tropical Andean peatland. Biotropica 47, 143–151.

Verweij, P.A., Kok, K., 1992. Effects of fire and grazing on *Espeletia hartwegiana* populations. In: Baslev, H., Luteyn, J.L. (Eds.), Páramo: An Andean System Under Human Influence. Academic Press, London.

White, S., 2013. Grass páramo as hunter-gatherer landscape. The Holocene 23, 898–915.

Williamson, G.B., Schatz, G.E., Alvarado, A., Redhead, C.S., Stam, A.C., Sterner, R.W., 1986. Effects of repeated fires on tropical páramo vegetation. Trop. Ecol. 27, 62–69.

Zomer, M.A., Ramsay, P.M., 2021. Post-fire changes in plant growth form composition and diversity in Andean páramo grassland. Appl. Veg. Sci. 24, e12554.