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Ecological impacts of climate change on Peruvian Andean ecosystems

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Keywords: Andes, ecosystem response, modeling, mountains, Peru, ecosystem-process model

Abstract

Studies of climate change in the Andes predict an upward trend in temperatures and increased variability in precipitation patterns. Though these changes in environmental conditions will impact plant species, community assembly, and ecosystem processes, the magnitude of these impacts is still not well understood. To examine these concerns, we analyzed the ecological impacts of climate change in a valley in the Andes of Peru. We used L-Range, a spatially explicit ecosystem-process model, to simulate ecosystems' response to climate change. L-Range simulates monthly primary aboveground production and plant population dynamics. Implementing L-Range required parametrizing 54 climatic, edaphic, and plant variables for cover classes and using landscape and climatic information. We used outputs from three climate models to capture the ecosystems' potential response to changes in temperature and precipitation. The impacts of climate change will vary across cover classes, scenarios, and location. Woodlands will become more productive under future climate conditions (RCP 4.5 and 8.5). Shrublands and grasslands will increase their productivity only under the intermediate emissions scenario (RCP 4.5). In contrast, the productivity of wetlands will decline under future climate conditions (RCP 4.5 and 8.5). Changes in herbaceous plants (forbs, grasses, and graminoids) and shrub cover will be minimal across the cover classes. Bare cover is projected to increase across all cover classes under future climate conditions. The largest increases are expected in wetlands (ranging from 23% to 44%), compared to grasslands and shrublands (each about 8%) and woodlands (12%). Changes of herbaceous plants, shrubs, bare cover and productivity will be spatially heterogeneous across the watershed. We identified the ecological processes, ecosystem attributes, and cover classes that will be more affected by climate change, along with the areas where these changes are likely to occur. In this way, our study provides information that can be used as a basis to develop conservation and restoration strategies, such as identifying priority areas for revegetation and establishing livestock exclusion zones.

1. Introduction

Mountains provide a range of critical ecosystem services to populations worldwide, including carbon sequestration, water supply, climate regulation, and nutrient cycling (Egan and Price 2017). Additionally, mountains play a vital role in the economies of both upstream and downstream communities (Romeo *et al* 2020) and contribute significantly to the sustainability of food systems (Immerzeel *et al* 2020). Moreover, mountain regions are biodiversity hotspots, characterized by high levels of species richness and endemism, making them crucial for global conservation efforts (Korner and Spehn 2024). Nonetheless, mountain regions have experienced increasing impacts of climate change in recent decades. These changes have observable repercussions for both people and ecosystems in these areas (Adler *et al* 2022). The high vulnerability of mountain regions to climate change arises from their topographic complexity, which is characterized by abrupt elevation changes and climatic variability over short distances (Beniston 2003). Furthermore, this vulnerability is exacerbated by the fact that warming rates increase with elevation, causing high-elevation zones to experience more rapid temperature rises than lower areas (Pepin *et al* 2015). As a result, climate change is reshaping mountain ecosystems more quickly than other terrestrial habitats (Pepin *et al* 2015, Adler *et al* 2022), driving substantial biotic and abiotic changes with lasting ecological consequences (Dainese *et al* 2024). This trend is particularly evident in the Andes, where climate-driven shifts in species distributions, vegetation zones, and hydrological cycles reveal these ongoing transformations, threatening the sustainability of both natural systems and the human communities that depend on them (Young *et al* 2017, Pabón-Caicedo *et al* 2020, Tovar *et al* 2022).

The mean temperature in the Andes has increased by approximately 0.09 °C decade^{-1} over the past sixty years (Pabón-Caicedo *et al* 2020). Climate projections indicate that the Andes will continue to undergo an increasing temperature trend, with the lowest increases (less than 3 °C) in extratropical latitudes and the highest increases in the Central Andes (up to 5 °C). Additionally, in the tropical Andes, increasing temperatures are projected to be higher at higher elevations, with an increase of about 4 °C for the 2040–2070 period under the most extreme scenario (CMIP5 RCP8.5). Precipitation patterns are projected to be highly variable (Pabón-Caicedo *et al* 2020), exhibiting marked differences between the eastern and western slopes, but with significant uncertainties for certain regions due to the complex topography of the Andes (Tovar *et al* 2022). Precipitation patterns and temperature changes affect plant species differently, triggering their range expansion or contraction along environmental gradients (Gwate *et al* 2023). Temperature increases will reduce the coolest climatic zones at mountain peaks, modify vegetation belts (Williams *et al* 2007), and alter species composition. These changes will alter the assembly of communities, create novel ecosystems (Williams *et al* 2007), and modify ecosystem processes (Gottfried *et al* 2012).

Climate change is transforming plant communities in mountain regions. Cold-adapted species are declining, while native and non-native plant species adapted to warm environments are colonizing once colder areas (Gottfried *et al* 2012, Zu *et al* 2021, Zhu *et al* 2024). As temperature decreases with altitude by 5 °C–10 °C km^{-1}, rising temperatures will further reduce the extent of the coolest climatic zones at mountain peaks and modify vegetation belts. However, the balance of species' positive and negative responses to temperature increases and changes in precipitation patterns will determine their abundance and survival, which are also influenced by biotic and abiotic factors. For example, while increases in plant productivity can be driven by higher temperatures, they require optimal soil moisture levels and nutrient availability. Furthermore, different plant species and functional groups are expected to respond variably to climate change (Winkler *et al* 2019). Consequently, climate change is likely to alter the distribution and extent of Andean biomes (Tovar *et al* 2022), impacting the area and distribution of glaciers and other ecosystems (Urrutia and Vuille 2009), including Andean wetlands (Otto and Gibbons 2017, Polk *et al* 2017).

Although it is anticipated that the effects of climate change will be significant in the tropical Andes, the extent of these impacts is still not well understood (Tovar *et al* 2022). The main goal of this study is to explore the potential ecological impacts of climate change in a mountain landscape in the Andes of Peru. We analyzed how projected scenarios of future climate conditions would alter ecosystems' structure and functioning. We parameterized the L-Range ecosystem-process model (Boone *et al* 2024) to simulate vegetation dynamics and biogeochemical processes under future climate conditions, quantifying changes in herbaceous plant cover, bare cover, and primary production. To the best of our knowledge, no similar simulation analyses have been conducted to explore the potential impacts of climate change on ecosystems in the Andes of Peru.

2. Study area

The study site is the Arhuaycancha Valley of Huascarán National Park (HNP), located in the north-central Andes of Peru (figure 1). HNP was established in 1975, with a delimiting boundary at 4000 m (Young and Lipton 2006), covers 3400 km^2, and includes the Cordillera Blanca Mountain range (Chimner *et al* 2019). Large daily temperature changes and minimal temperature variations throughout the year characterize the climate in the Cordillera Blanca (Kaser and Georges 1997). The precipitation follows a strong seasonal pattern, with a dry season from May to September and a wet season from October to April, during which about 80% of the annual precipitation occurs (Vuille *et al* 2008). Soils in the area are mainly entisols, inceptisols, and histosols (Polk 2016). The park's landscape is characterized by patches of wetlands, shrubs, and *Polylepis* sp. forests within a grassland matrix, with some areas under ecological succession due to glacier retreat (Young *et al* 2017).

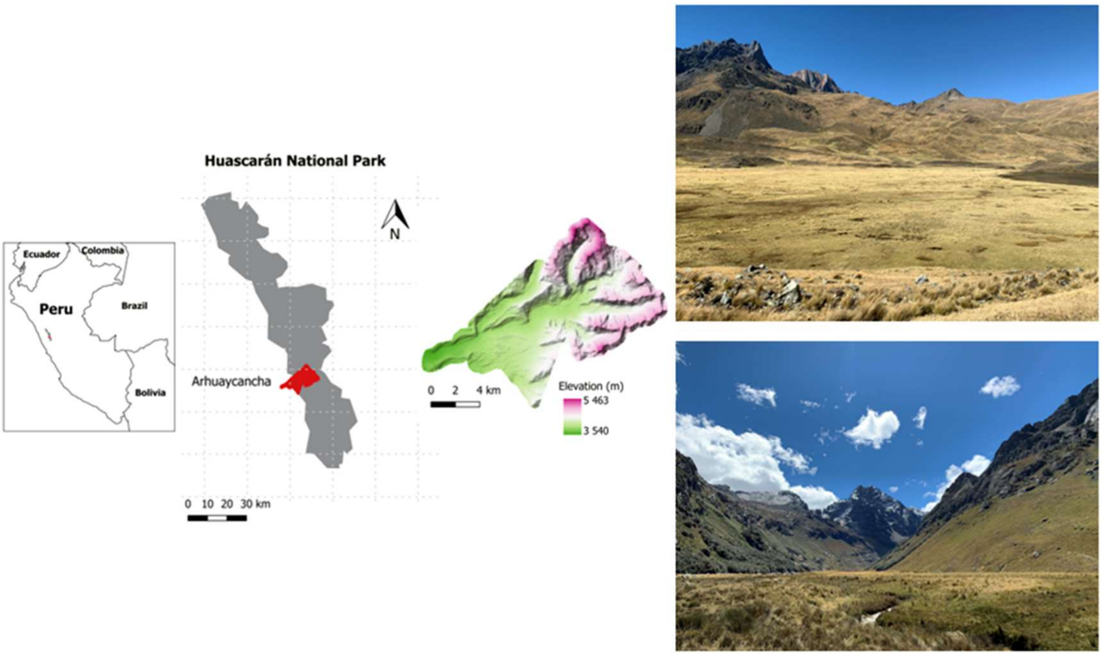

Figure 1. Vegetation of the Arhuaycancha Valley. Top photo: Cushion wet meadows and peatlands in the middle section of the watershed. Bottom photo: Forest patches surrounding graminoid wet meadows and grasslands in the upper left portion of the watershed. Photo credit: the corresponding author.

The Arhuaycancha Valley, associated with the Río Negro (river) within the Rúrec catchment in the province of Recuay, drains to the Santa River. The elevation of Arhuaycancha Valley ranges from 3540 to 5463 masl. Part of the valley lies in HNP, while the other part falls in the lands of the Cordillera Blanca community. The land cover of the Arhuaycancha Valley consists of barren areas (56.4%), which include dispersed vegetation, bare rock, and transitional zones; grasslands (13.4%); graminoid wet meadows (12.6%); peatlands (10.2%); snow/ice (2.4%); woodlands (1.5%); shrublands (1.3%), agricultural lands (1.1%); cushion wet meadows (1.0%); water bodies (0.2%); and developed areas (0.002%) (Chimner *et al* 2019). Vegetation in the Arhuaycancha Valley is patchy and heterogeneous. Wetlands and grasslands are primarily found in flat areas within the watershed, though wetlands can also occur on mountain slopes. In contrast, woodlands and shrublands are predominantly located on these slopes.

3. Methodology

The simulation of ecosystem processes was performed using L-Range (Boone *et al* 2024), the local version of the global rangeland model G-Range (Boone *et al* 2018). The foundation of the biogeochemical modeling of L-Range is the CENTURY model (Parton *et al* 1993), while other aspects of the ecosystem-process model come from the SAVANNA model (Coughenour 1992). L-Range spatially explicitly represents ecosystems. The biogeochemical processes that L-Range simulates are decomposition, N and C cycling, transpiration, primary production, and plant population dynamics for three types of plant functional groups or facets: herbaceous plants (forbs, grasses, and graminoids), shrubs, and trees. However, it does not represent the hydrological processes of glaciers and underground water sources, such as meltwater flow and aquifer storage and flow.

The vegetation facets represent the model's hierarchical structure and determine the vegetation cover dynamics. The herbaceous plant facet includes a vegetation layer of herbaceous plants, a layer of herbaceous plants under shrubs, and a layer of herbaceous plants under trees. The shrub facet comprises a layer of shrubs and a layer of shrubs under trees (figure A1). The tree facet consists only of a layer of trees. The plant parts of the herbaceous plants facet consist of leaves and fine roots. The shrub and tree facets include those parts plus fine branches, coarse branches, and coarse roots.

L-Range works with spatial surfaces and a set of soil, climatic, and plant parameters that determine plant growth, and other ecological attributes of the ecosystems. L-Range consists of core state variables, plant, climatic, and soil parameters, and 'hard-wired' parameters and variables derived from CENTURY and SAVANNA. These variables and parameters are assigned by landscape or grid cells, vegetation facets, or plant parts for simulating ecosystem processes. For example, plant growth is determined by soil nutrient availability, plant reproduction is limited by seed production and soil moisture, and water loss is estimated based on transpiration and evaporation rates (Boone *et al* 2024).

3.1. Model parametrization and implementation

Implementing the L-Range model required the parametrization of 54 climatic, edaphic, and plant variables. We also provided L-Range with spatial surfaces that contain landscape information, such as fractional vegetation cover, topographic features, and soil properties. The tree, shrub, and herbaceous plants fractional cover were obtained from the EarthEnv 1-km dataset (Tuanmu and Jetz 2014). Soil physical and chemical properties data, e.g., texture, coarse fragments, and soil organic carbon, was derived from the SoilGrids250m database (Hengl *et al* 2017). The slope layer was obtained from the United States Geological Survey's (USGS) Shuttle Radar Topography Mission (SRTMGL1, Version 3) imagery, which consists of a fine-resolution (30 m) topographic map. The land cover map of the study area was obtained from Chimner *et al* (2019). All these layers were resampled to 50 m, i.e., the spatial resolution of the analysis, and were georeferenced to the WGS84 datum, UTM projection Zone 18, using the free open-source QGIS Geographic Information System software (version 3.20 Odense, QGIS Development Team 2021).

Critical variables of L-Range are monthly mean minimum and maximum temperature and monthly precipitation. This data was obtained from the Climatologies at high resolution for the earth's land surface areas (CHELSA version 1.2) dataset. CHELSA provides high resolution (~1 km) and long-term climate data, from 1979 onwards, with global coverage. Climate data from CHELSA are based on a quasi-mechanistical statistical downscaling of the ERA-Interim global circulation model with Global Precipitation Climatology Centre (GPCC) and a Global Historical Climatology Network (GHCN) bias correction (Karger *et al* 2017). Additionally, CHELSA data has topographic adjustments based on the surface altitude and orography from the Global Multi-resolution Terrain Elevation Data (*GMTED2010*). We downloaded historical (1970 to 2005) and projected (2006 to 2100) monthly mean minimum and maximum temperatures (K) and precipitation (kg m^{-2}) raster data from CHELSA. Climate data was extracted to a reference region via a Python script. Subsequent processing in R (version 4.1.1) (R Core Team 2022) and RStudio (version 1.4.17.17) (RStudio Team 2016) involved projecting the data, resampling it to 1 km, and converting units to Celsius for temperature and millimeters for precipitation. All resampling used nearest neighbor methods.

3.2. Scenarios under analysis

We downloaded climate projection data from CHELSA from the Representative Concentration Pathways (RCP) 4.5 and 8.5 of three global circulation models: the Australian Community Climate and Earth System Simulator (ACCESS1.3) model, the Community Earth System Model version 1.0 with Biogeochemistry (CESM1-BGC), and the Euro-Mediterranean Center on Climate Change Climate Model (CMCC-CM). The climatic scenarios under analysis also included ecosystems' responses to projected atmospheric carbon dioxide (CO_2) enrichment for the RCP 4.5 and RCP 8.5 projections used by the IPCC (Meinshausen *et al* 2011). We included the atmospheric CO_2 enrichment projections to analyze vegetation responses to changes in CO_2 concentration. L-Range can estimate plant productivity in response to CO_2 fertilization, which originally was implemented in the CENTURY model by Parton *et al* (2001). Changes in plant productivity are calculated using a production correction factor:

$$1 + \frac{\mathrm{CO_2ipr} - 1}{(\log_{10}(2) \times \log_{10}(\mathrm{CO_2concentration}/350))}$$

Where CO_2ipr is the multiplier on plant production of doubling the atmospheric CO_2 concentration from 350 ppm to 700 ppm and was 1.25. Also, we used 2006 as the baseline year to capture CO_2 enrichment effects and additional corrections to plant productivity respected the CENTURY model (e.g., a correction factor for proportion of live material per vegetation layer), and therefore a constant (0.20) was subtracted from the values. The CO_2 concentration values for the RCP 4.5 ranged from 0.8 historically to 0.915 in 2070 while for the RCP 8.5 spanned from 0.8 to 1.008. The scenarios analyzed include the RCPs 4.5 and 8.5 for the three global circulation models. We used historical data from 1970 to 2020 and copied this data to create a 'Current Conditions' scenario for 2021 to 2070, which does not incorporate changes in precipitation, temperature, and CO_2 concentrations.

3.3. Model calibration and assessment

The calibration of L-Range involved adjusting the various plant facets and soil parameters for the different vegetation cover classes. Some parameters adjusted were the death rate of shoots, leaves, and roots, seed production, herbaceous plants and wood cover effect on plant establishment, soil drainage affecting anaerobic decomposition, and plant temperature production. The two 'hard-wired' parameters of L-Range that were modified were heat accumulation and temperature effect on decomposition.

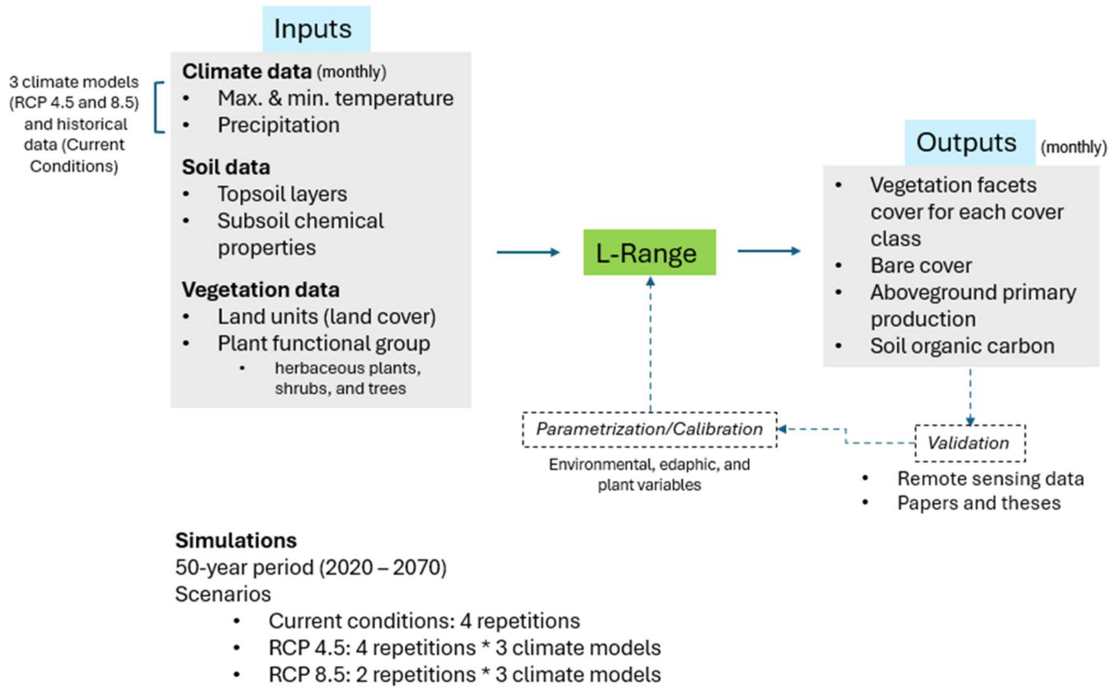

Figure 2. Workflow for parametrization and validation of L-Range and simulations performed. L-Range requires climate, soil, and vegetation data to estimate ecosystem processes for different cover classes (e.g., grasslands and wetlands). The model is parametrized and calibrated using information from peer-reviewed journals and remote sensing data.

Since our main goal was to model vegetation dynamics and ecosystem processes, we adjusted the L-Range parameters until the variables of interest, i.e., Aboveground Net Primary Productivity (ANPP) ($\mathrm{g\ m^{2}\ yr^{-1}}$), soil organic carbon ($\mathrm{g\ m^{2}\ yr^{-1}}$), facet cover (%), and bare cover (%), were similar to estimations from peer-reviewed articles and theses and surfaces derived from MODIS data (Myneni *et al* 2015) (figure 2). We validated the ANPP using MODIS data from 2000 to 2020 for the different cover classes. We downloaded the MODIS data using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS Team 2022). Nonetheless, accurate estimations of primary production through remote sensing require ground validation that incorporates site-specific features and detailed *in situ* data (Abdelmajeed and Juszczak 2024).

All simulations included a 100-year spin-up period from 1970 to 2069, allowing the model's state variables to reach equilibrium. We conducted four repetitions for the 'Current Conditions' and 'RCP4.5' scenarios, and two repetitions for the 'RCP8.5' scenario for each climate model (ACCESS, CMCC, and CESM1). The simulations were run over a 50-year period (2020 to 2070). We estimated the coefficient of variation across repetitions for each model and across all models, finding minimal variations. Thus, we calculated the mean value across all climate model repetitions. Additionally, to analyze spatial structural and functional changes in the ecosystems, we created average raster layers in QGIS using the raster calculator, focusing on variables such as herbaceous plant cover and ANPP.

4. Results

4.1. Changes in ecosystem productivity

4.1.1. Aboveground net primary production (ANPP)

Woodland ecosystems are predicted to become more productive under future climate conditions (RCP 4.5 and 8.5) in the modeling, becoming the most productive ecosystem. Shrublands and grasslands will also respond positively to climate change, but only to the intermediate scenario (RCP 4.5). In fact, under the most extreme climatic scenario (RCP 8.5), shrubland productivity will decline from 2050 onwards. On the contrary, all three wetland types are expected to be less productive under all future climate conditions (RCP 4.5 and 8.5) (figure 3). Additionally, from 2040 onwards, graminoid wet meadows and peatlands will exhibit a marked decrease in ANPP of about 50% compared to 2020, under future climate conditions.

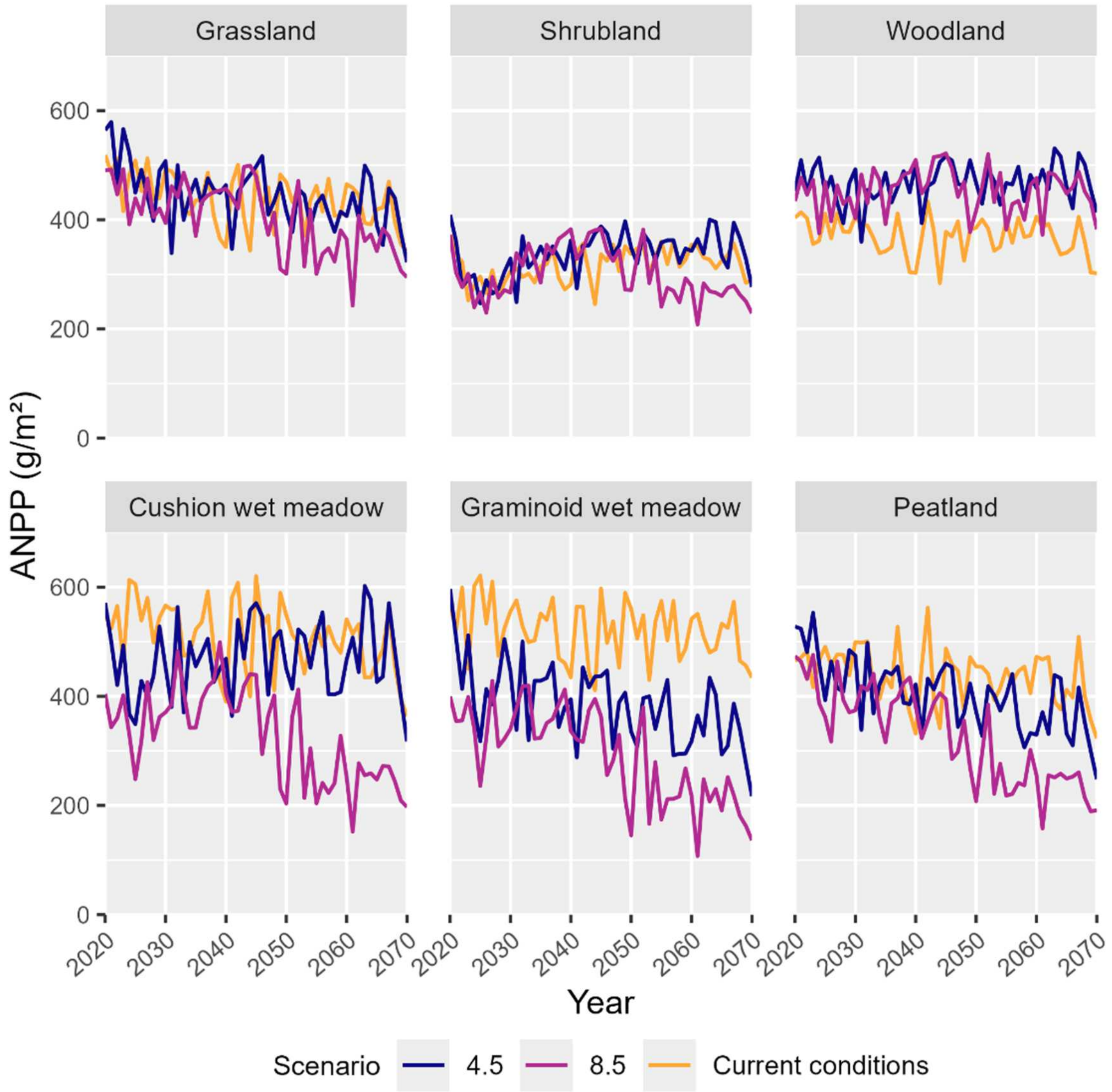

Figure 3. Average change in Aboveground Net Primary Production (ANPP) (g/m^2) by cover class and scenario from 2020 to 2070.

4.2. Changes in vegetation facets cover

4.2.1. Herbaceous plant cover

Changes in herbaceous plant cover (forbs, grasses, and graminoids) did not vary largely across cover classes (figure 4). While herbaceous plants cover in the three wetland classes showed a slight declining trend across all scenarios, changes in other vegetation classes were more variable, particularly in shrublands. Although the herbaceous plants cover of shrublands exhibited a dynamic pattern, its overall range of change (whether an increase or decrease) was minimal. In grasslands, a slight increase in herbaceous cover is projected, while a modest decrease is expected in woodlands.

4.2.2. Shrub and tree cover

Shrub cover changes in grasslands were more dynamic than in other vegetation classes, showing a consistent decline from 10% to approximately 4% by 2050 across all scenarios (figures A2 and A3). In comparison, shrub cover in graminoid wet meadows and peatlands exhibited a slight decrease under the RCP4.5 and RCP8.5 scenarios relative to the 'Current Conditions' scenario. Shrub cover in cushion wet meadows remained relatively stable across all scenarios. Similarly, the shrub cover in shrublands and woodlands showed little temporal variation. Changes in tree cover were minimal across all vegetation classes (figures A4(a) and (b)).

4.3. Changes in bare ground cover

The amount of bare cover across different vegetation classes showed an upward trend in all scenarios, with a marked increase in wetlands (figures 5 and A5). Generally, bare cover in the climate change scenarios was higher than in the 'Current Conditions' scenario for all cover classes, except for cushion wet meadows and graminoid

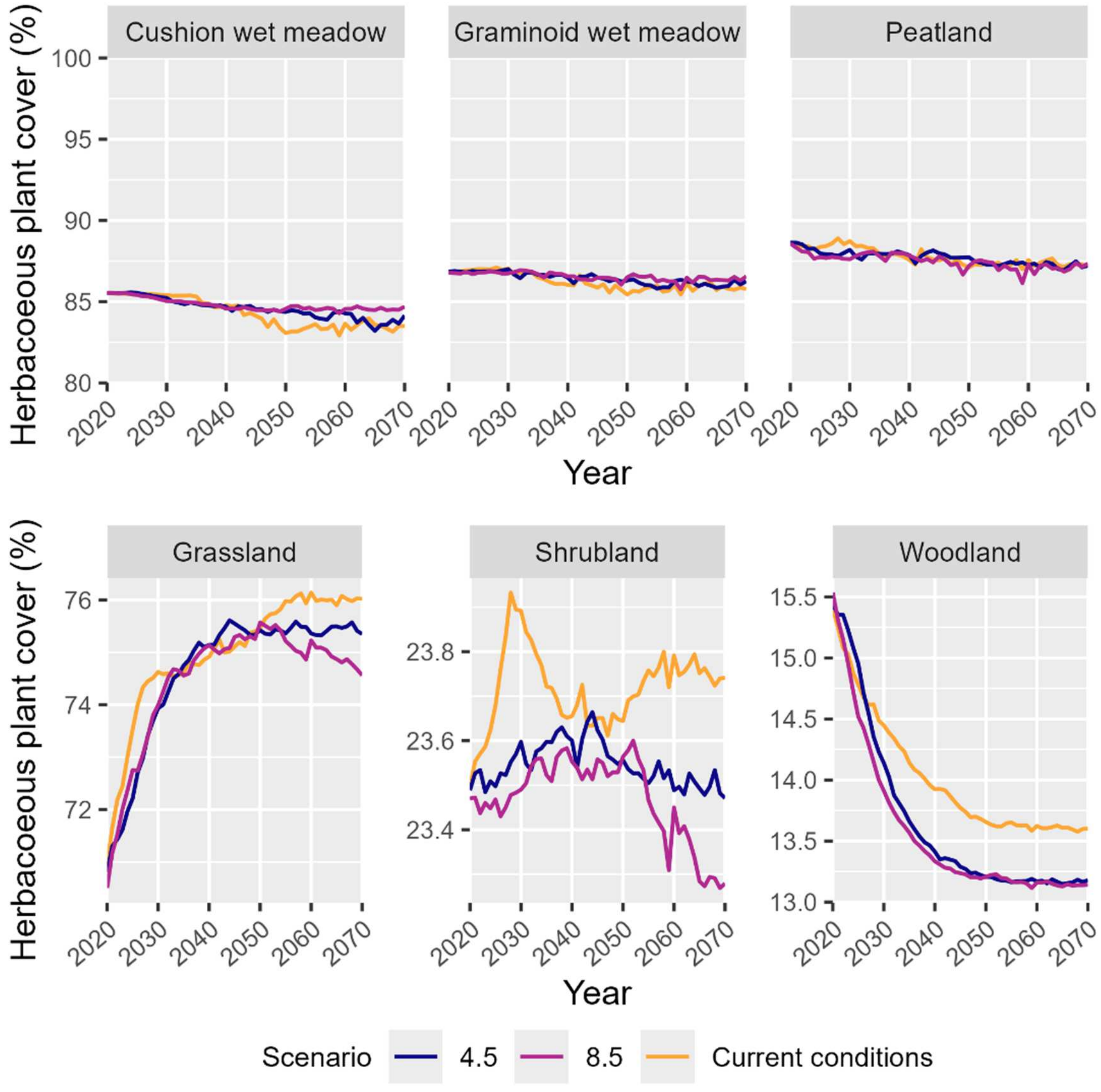

Figure 4. Average change in herbaceous plant cover (%) by scenario from 2020 to 2070.

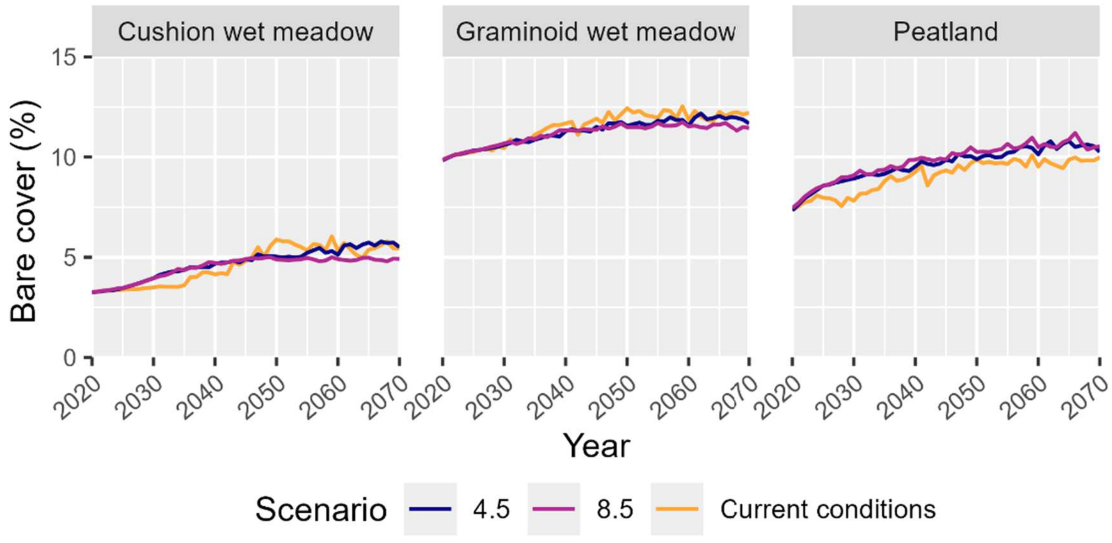

Figure 5. Average changes in bare cover (%) for wetlands by scenario from 2020 to 2070.

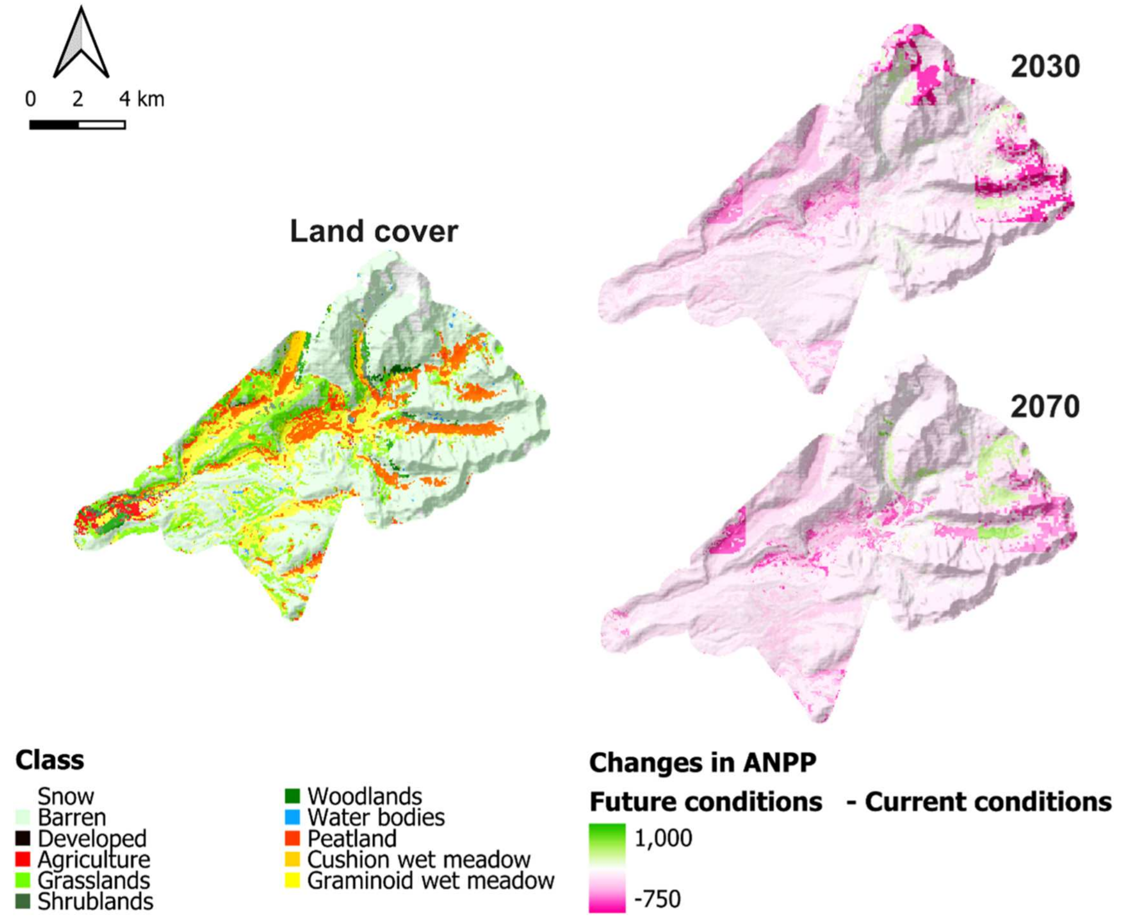

Figure 6. Spatial variation in ANPP (g/m^2) for 2030 and 2070 to 2020. This figure illustrates the difference in ANPP between the RCP 4.5 scenario (average of three climate models) and the 'Current Conditions'. Shades of green indicate areas with higher ANPP, while fuchsia represents areas with lower ANPP.

wet meadows. Changes in the bare cover of grasslands, shrublands, and woodlands were much less variable. By 2050, bare cover in cushion wet meadows, peatlands, and graminoid wet meadows is projected to increase by approximately 44%, 33%, and 23%, respectively, compared to 2020. In contrast, the bare cover of grasslands and shrublands is projected to increase by approximately 8%, while the bare cover of woodlands will rise by about 12%.

4.4. Spatial changes in ANPP

Flat areas on the eastern side of the watershed will have higher ANPP under future climate projections, indicating that the vegetation in this area will become more productive (figure 6). The cover classes that will benefit from these increases will be shrublands and peatlands. In contrast, wetlands and grasslands in the middle of the watershed will exhibit a reduction in ANPP.

4.5. Spatial changes in herbaceous and shrub cover

The difference in herbaceous cover between the average RCP 4.5 climate scenarios and the 'Current Conditions' scenario is projected to be positive in the western and middle zones of the watershed, indicating an increase in herbaceous cover (figure A6). Grasslands, cushion wet meadows, graminoid wet meadows, and peatlands are the cover classes positively affected by these changes. In contrast, herbaceous cover in the middle and lower zones of the eastern part of the watershed is expected to decrease, impacting grasslands, peatlands, and graminoid wet meadows. Additionally, some patches of barren areas in the lower-eastern part of the watershed are projected to experience an increase in herbaceous cover.

Regarding shrub cover, a decrease is expected in the upper northern part of the watershed, especially on mountain slopes. Conversely, shrub cover will increase in the middle of the watershed, where grasslands and graminoid wet meadows are located (figure A7).

4.6. Spatial changes in bare cover

The bare cover is expected to increase under future climate conditions in the west and middle zones of the watershed, negatively impacting grasslands, cushion wet meadows, graminoid wet meadows, and peatlands (figure A8). These increases will occur both in flat areas and on mountain slopes. Additionally, bare cover will rise in the middle of the watershed and in high-elevation zones on the northeast side, near glaciers. Conversely, the lower areas on the southeast side of the watershed will see a decrease in bare cover, while the high-elevation zones in this area are projected to experience an increase.

4.7. Soil Organic Carbon (SOC)

Although the L-Range model was validated with the most reliable data available for Andean ecosystems, we approach the SOC estimations cautiously and recognize that wetland SOC will be highly constrained by local hydrology. The SOC of grasslands, shrublands, and woodlands will increase over time across all scenarios, with higher values for both climate projection scenarios than the 'Current Conditions' scenario (figure A9). In the case of wetlands, only graminoid wet meadows will have a positive trend on SOC accumulation, with higher values for the 'Current Conditions' scenario. Peatlands and cushion wet meadows will exhibit a decreasing SOC accumulation trend over time.

5. Discussion

Although climate change is altering mountain ecosystems globally, its effects are uneven and shaped by local environmental conditions. Our modeling results indicate that under the RCP4.5 scenario, all cover classes are projected to become more productive. However, this will not be the case under the most extreme scenario (RCP8.5), where all cover classes except for woodlands will be less productive. Changes in herbaceous plants and shrub cover are projected to be minimal, while bare cover is expected to increase across all vegetation classes over time. These shifts in ecosystem structure and processes carry significant implications for biodiversity conservation and the long-term sustainability of agropastoral systems that support local communities.

5.1. Changes in ANPP

The complex topography and climate of the Andes, with a diversity of biomes, suggest different vulnerabilities and responses of ecosystems to climate change would be expected (Young *et al* 2011, Tovar *et al* 2013). We found that future climate conditions will positively impact woodlands (RCP 4.5 and 8.5) and shrublands (only RCP 4.5), i.e., these ecosystems will become more productive. Nonetheless, under the most extreme climate scenario (RCP 8.5), all ecosystems except for woodlands will be less productive, particularly from 2050 forward. Though no past studies in the Peruvian Andes have estimated future trends in ANPP, Polk *et al* (2020) used the Normalized Difference Vegetation Index (NDVI) as a proxy to assess vegetation changes in the study region from 2000 to 2017. They found that greening (a positive trend in NDVI, related to increased vegetation) outpaced browning (a negative trend in NDVI, related to decreased vegetation), with 15.1% of the Andean highlands categorized as highest greening and 4.1% as highest browning. These findings indicate that vegetation biomass increased from 2000 to 2017, aligning with our simulation results that Andean ecosystems will become more productive. Choler *et al* (2021) similarly found that upland areas of the European Alps experienced increased greening from 2000 to 2020, with high-elevation ecosystems responding positively to summer warming. The strongest responses occurred in sparsely vegetated, north-facing slopes with prolonged snow cover.

Additionally, Chen *et al* (2020) conducted a meta-analysis of 65 studies on alpine grasslands in the Tibetan Plateau to quantify the effects of warming on ecosystem carbon and nitrogen cycles. They found that warming significantly increased both aboveground and belowground plant biomass, with mean increases of 11.0% and 24.3%, respectively. Similarly, Shi *et al* (2022) conducted a global meta-analysis of 64 studies to evaluate how warming and management practices, such as grazing, fertilization, and mowing, affect carbon fluxes in grasslands. Warming increased gross primary productivity and ecosystem respiration by 9.8% and 16.4%, respectively. Fertilization also enhanced gross primary productivity, ANPP, and ecosystem respiration, whereas grazing and mowing reduced ANPP by 19.9% and 22.8%, respectively.

Our findings of increasing productivity under future climate conditions also align with studies conducted in the Qinghai-Tibetan Plateau. Gao *et al* (2016) found that net primary production in alpine ecosystems (>4000 m) of the Qinghai–Tibetan Plateau is projected to increase by 79% and 134% under the RCP 4.5 and RCP 8.5 scenarios, respectively, between 2020 and 2080, with spatial variation across the region. Gao *et al* (2016) attribute these changes to a positive response of vegetation to increasing precipitation, temperature, and CO_2 concentrations. Moreover, vegetation found in more favorable hydrothermal conditions, primarily coniferous and broadleaf forests, had the highest net primary production under the RCP8.5 scenario. Similarly, Li *et al* (2024) found that gross primary production in the Qinghai–Tibetan Plateau is projected to increase throughout the 21st century under all climate scenarios (RCP 2.6, 4.5, 7.0, and 8.5), with regional variation. By 2100, annual gross primary production is expected to reach approximately 1011.98, 1032.67, 1044.35, and 1055.50 Tg C under the respective scenarios, corresponding to increases of 0.4%, 4.0%, 5.6%, and 5.7% relative to 2021 levels.

We found that spatial changes in ANPP will be variable across the watershed. Flat areas in the east-upper part of the watershed, consisting of peatlands, will become more productive, according to the modeling. In contrast, wetlands and grasslands in the middle of the watershed will be less productive. Moreover, in general, mountain slopes of the watershed will become more productive over time. These findings can be supported by Polk *et al* (2020), who found that greening trends in the Peruvian Andes occurred with higher frequency in high-elevation areas (>5000 m.a.s.l.) while browning was dominant in areas below 5000 masl. Nonetheless, analyzing the factors that drive ANPP changes is crucial. For instance, the impact of a grassland becoming more productive due to shrub expansion will differ significantly from a case where its production increases due to enhanced herbaceous plant growth. Both scenarios carry distinct ecological and land management implications. In the first case, shrub expansion would indeed increase primary production but simultaneously decrease the availability of palatable forage for livestock.

5.2. Changes in herbaceous cover

Changes in herbaceous cover will be minimal, remaining relatively constant across cover classes and scenarios, indicating that climate change may not trigger rapid major changes in herbaceous cover. Tovar *et al* (2013) created multiple logistic regression models to determine the distribution of Andean biomes using climate data from the Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model. They found that at the biome level, i.e., not considering plant physiology and species composition, most Andean biomes will remain with the same general distribution, not what is predicted for species distribution modeling. Though gradual changes in species composition will not cause immediate alterations at the biome level, these changes, e.g., alterations in understory vegetation or vertical structure, can alter ecosystem structure and functioning (Tovar *et al* 2013). For example, soil chemical properties and processes are affected by the quality and quantity of litter inputs (Vivanco *et al* 2024). Cuesta *et al* (2023) analyzed data from permanent plots on 45 mountain summits across the high Andes of South America and found evidence of ongoing vegetation change, including an overall increase in species richness (mean = 0.38 species m^{-2} yr^{-1}). Subalpine areas showed gains in vegetation cover, whereas alpine, subnival, and nival zones experienced losses. Species changes were positively associated with increases in minimum air and soil temperatures. At the community level, species composition shifted toward endemic and cosmopolitan taxa with broader thermal niches.

We also found that the herbaceous cover of wetlands and grasslands varied the most across years compared to the other vegetation classes. The high variability in the herbaceous cover of wetlands can be associated with alteration in their water inputs. A critical environmental driver determining the occurrence of Andean wetlands within a watershed is the mean annual rainfall. However, wetlands can also receive water inputs from glacier melt and underground water sources (Otto and Gibbons 2017, Chimner *et al* 2019, Duhalde *et al* 2024). Projected decreases in mean annual rainfall and increased variability in spatial rainfall patterns might affect the spatial distribution of Andean wetlands (Otto and Gibbons 2017). Moreover, temperature increases and glacial shrinkage over the next decades will alter the inputs to wetlands from water runoff from melting glaciers, affecting wetlands' hydrological balance and altering their extent and number (Young *et al* 2011). We also found that changes in herbaceous cover in the watershed will not be uniform. The location of Andean ecosystems in various landscape settings (valley areas and mountain slopes) and their composition (species taxonomy and physiology) create the conditions for different ecosystem responses to climate change and, therefore, different climate change impacts on them (Young *et al* 2011).

5.3. Changes in shrub cover

Shrub cover did not broadly vary across climate scenarios. The shrub cover of grasslands decreased from 10% to approximately 4% by 2050. The shrub cover of wetlands exhibited a negative trend over time, with reductions of 5.6% for cushion wet meadows, 20% for graminoid wet meadows, and 33% for peatlands. Spatial changes in shrub cover in the watershed will not be uniform.

There is a global trend of conversion of semi-arid and mesic grasslands to shrub-dominated areas and shrub encroachment of wetlands. These vegetation shifts have been attributed to climate warming, shrub expansion into water-limited environments such as grasslands, and elevated atmospheric CO_2 concentrations (Saintilan and Rogers 2015). However, this trend was not evident in our modeling results for the Arhuaycancha Valley. Under future climate scenarios, our models project a reduction in shrub cover across both wetlands and grasslands. This contrasts with Aide *et al* (2019), who reported significant increases in woody vegetation in grasslands above 4000 m a.s.l. in the tropical Andes between 2001 and 2014. That expansion was likely driven by rising temperatures and drier conditions, which may have facilitated shrub encroachment and tree growth beyond the historical treeline. Nevertheless, our results suggest that some areas within the Arhuaycancha Valley could experience localized increases in shrub cover.

Shrub expansion across regions is driven by a combination of biotic, abiotic, and land management factors. In the Arctic, for example, warming accelerates the release of nitrogen and phosphorus from soils, fertilizing historically nutrient-limited landscapes and increasing the abundance of deciduous shrubs and herbaceous species (Prager *et al* 2020). In arid and semiarid ecosystems of Argentina, Romero-Ovalle *et al* 2024 found that shrub expansion between 1970 and 2018 primarily occurred in areas with high pre-existing shrub density and followed a heterogeneous spatial pattern. In alpine grasslands, changes in shrub and tree cover are constrained by low temperatures, limited precipitation, and grazing pressure (Snell *et al* 2022), while also being influenced by broader climatic and topographic factors. For instance, Bayle *et al* (2024) found that elevation, slope, and aspect, factors limiting water availability, affect the distribution of Ericaceae-dominated shrublands in the European Alps. Similarly, the upper elevational limits of shrublands are influenced by low temperatures. In the Central Apennines of Italy, De Toma *et al* (2022) found that the distribution of dwarf shrubs from 1960 to 2020 was strongly influenced by fine-scale topography, microclimate, soil characteristics (e.g., fertility and aridity), and grazing pressure. Dwarf shrubs showed limited ability to invade grasslands compared with woody areas and were mainly associated with harsh, resource-limited conditions.

In addition, factors such as fire and grazing intensity influence shrub expansion. For example, using high-resolution satellite imagery from Alaska and western Canada, Liu *et al* (2022) found that shrub expansion in the tundra between 1984 and 2014 was driven primarily by seed dispersal and fire rather than environmental suitability. They further showed that when models incorporate seed dispersal along with projected fire and climate conditions, shrubs are expected to expand into 25% of non-shrub areas by 2100, compared with 39% when environmental suitability alone is considered.

Grazing intensity is also a key factor in regulating shrub expansion. Shi *et al* (2023) found that livestock grazing exclusion led to shrub encroachment, as evidenced by a three- to eight-fold increase in shrub growth and reproduction characteristics. This pattern was observed in exclosure experiments conducted over three, nine, and seventeen years in the alpine grasslands of the Qinghai-Tibetan Plateau. Also, shrub expansion depends on the physiological response of shrub species. For instance, Venn *et al* (2021) analyzed the temperature range for germination of Australian alpine shrubs. They found that while some shrub species can successfully germinate at high temperatures, others appear to be limited by inherent seed dormancy. Shrub expansion in alpine areas was associated with conditions that influence seed germination at the microsite scale.

5.4. Changes in bare cover

We found that bare cover increased across all scenarios and cover classes, with marked increases for the three wetland classes. Cuesta *et al* (2023) reported an average annual loss of vegetation cover (mean $= -0.26\%/\mathrm{yr}$) across the high Andes of South America, particularly affecting alpine, subnival, and nival areas. In the Peruvian Andes, more specifically in Huascarán National Park, Young *et al* (2017) found varying land cover changes from 1987 to 2010. From 1987 to 1999, some tropical alpine vegetation areas contracted, creating new barren sites. From 1999 to 2010, the cover of alpine vegetation increased due to plant succession in barren lands and the expansion of grasses and shrubs, mainly on the north-and northeast-facing slopes.

Though we found increases in bare cover in areas next to glaciers, our analysis scale (50 m, including climate surfaces resampled from much coarser surfaces) may have hindered the detection of finer-scale ecological changes. For instance, glacier retreat creates conditions conducive to ecological succession, as newly exposed barren lands are prone to colonization by forbs and graminoids (Young *et al* 2017). However, this early plant succession is not a stochastic process; rather, it is influenced by the local ecological context (Bayle *et al* 2024).

5.5. Changes in Soil Organic Carbon (SOC)

Although we validated the L-Range model with the best available data for Andean ecosystems, it is necessary to indicate that we are cautious about the SOC estimations. The complexity of ecosystems, the limited understanding of soil ecological processes in ecosystems such as Andean peatlands, and the limited information available for these high-elevation areas could affect the model estimations. For example, Chimner *et al* (2023) found significant differences in the carbon stocks between peatlands and wet meadows in Huascarán National Park. Carbon stocks in peatlands varied from 278 to 4,740 Mg C ha^{-1} with a mean of 1092 Mg C ha^{-1}. In contrast, carbon stocks in wet meadows ranged from 3 to 181 Mg C ha^{-1} with a mean of 30 Mg C ha^{-1}. This broad range of SOC highlights the challenges for the initialization and parametrization of the soil carbon processes of L-Range.

Moreover, information about SOC is site-specific, especially in areas with highly variable topography, such as the Andes. Therefore, SOC from a different region or quantified at different elevations cannot be directly compared with our estimations. For instance, we only found one study that estimated SOC near the study area. Vivanco *et al* (2024) estimated SOC for *Polylepis* sp. forest in Ulta Valley at Huascarán National Park. They found that through an elevation gradient (3500 to 4500 masl), *Polylepis* sp. forests soils located at intermediate elevations (~4000 masl) had a thicker soil organic layer and, therefore, higher soil organic carbon stock (154.2 Mg C ha^{-1}), than those located at higher (26.2 Mg C ha^{-1}) and lower elevations (34.8 Mg C ha^{-1}).

5.6. L-Range model generalizability and applications

The L-Range ecosystem process model (Boone *et al* 2024) is a recently developed tool designed to perform the same processes as the global rangeland model G-Range (Boone *et al* 2018), but at a finer spatial scale. The first documented application of L-Range (Warrier *et al* 2024) simulated ecosystem processes to estimate plant biomass accumulation in Kenyan rangelands. Because L-Range is derived from G-Range, its generalizability builds upon insights gained from previous G-Range applications. At the global scale, Godde *et al* (2020) used G-Range, coupled with spatially explicit economic, demographic, and livestock datasets, to analyze how pastoral families may be affected by vegetation changes under future climate conditions. At the regional scale, Liu *et al* (2024) applied G-Range to simulate changes in vegetation cover, ANPP, and SOC density on the Tibetan Plateau under RCP 4.5 and RCP 8.5 scenarios. At a finer scale, Su *et al* (2022) coupled G-Range with an agent-based model to explore the effect of environmental protection policies on alpine grassland dynamics in Sanjiangyuan National Park, China.

The applicability of L-Range to other regions or ecosystems depends on the ecological processes under analysis and the availability of data for calibration and validation, as its accuracy is constrained by the spatial resolution of input data. Fine-scale applications, such as those focused on specific valleys, allow for tailored calibration and validation that can capture localized processes and responses to climate change. In contrast, applying L-Range across broader areas, such as the entire Peruvian Andes, would yield insights only at coarser spatial scales.

5.6.1. Caveats

The heterogeneous landscape of the Arhuaycancha Valley, characterized by high variability in vegetation and soil properties, poses challenges for accurately modeling ecosystem processes. The accuracy of the L-Range outputs is constrained by the spatial resolution of the input data. A lack of high-resolution data for climate projections and herbaceous plants, shrubs, and tree cover may have impacted the L-Range estimations. Furthermore, field studies on vegetation dynamics and ecosystem processes in the Andes, such as ANPP and nitrogen and carbon cycling, are limited, which hinders model parameterization and calibration. Therefore, implementing field assessments and experiments, such as vegetation surveys and CO_2 flux measurements across cover classes and elevation gradients, can improve model parameterization and validation.

Although we used NDVI as an indicator of vegetation production, the analysis could not capture the effects of different climate scenarios on plant composition, such as changes in the cover of palatable and unpalatable species for grazing. Therefore, we cannot determine whether increases in landscape productivity are driven by increases in palatable or unpalatable plants. However, developing species distribution models can complement the analysis and enhance understanding of how future climate conditions may influence changes in ecosystem composition.

In addition to the aforementioned considerations, it is important to note that L-Range does not model glacier dynamics; therefore, the effects of glacier retreat and groundwater changes on ecosystem process simulations remain uncertain. Although supported in the modeling framework, wildfires were not incorporated into L-Range due to limited data on their occurrence and triggering factors, such as litter accumulation, moisture content, and wind patterns. Finally, because GCM cannot capture extreme storm events at fine spatial resolutions, the assessment of their localized impacts on ecosystem processes remains unknown.

6. Conclusion

Climate change will affect the structure and functioning of Andean ecosystems. The modeling analysis shows that increases in temperature and changes in precipitation patterns will create conditions for woodlands and shrublands to become more productive. However, these conditions will not be favorable for wetlands. Nonetheless, the productivity of all cover classes will be negatively impacted under the most extreme climate conditions scenario. Changes in the cover of herbaceous plants (forbs, grasses, and graminoids) will be minimal. However, the herbaceous cover of wetlands and grasslands will be the most variable across cover classes. Model results indicate that wetlands will undergo a reduction in herbaceous plant cover from 2050 onwards, a reduction that can be associated with the temporal and spatial alteration of water inflows, i.e., precipitation, underground water, and glacier retreat water inputs. Changes in shrub cover will also be minimal, with the shrub cover of grasslands being the most variable across cover classes. Under future climate conditions, bare cover will increase in all cover classes. However, this increase will be larger for wetlands. Furthermore, the spatial distribution of bare cover will broadly vary across the watershed. For instance, it will increase in flat areas and some mountain slopes but decrease in low-elevation areas in the basin mouth. In contrast, bare cover will increase in areas close to glaciers.

Our spatially explicit analysis identified the ecological processes, ecosystem attributes, and cover classes most vulnerable to climate change. In this way, our study provides information that can serve as a basis for developing ecosystem conservation and restoration strategies. For instance, wetlands, identified as highly sensitive ecosystems to climate change impacts, should be prioritized for specialized management measures, such as revegetation and, in degraded areas, grazing exclusion to reduce or prevent further degradation. Beyond ecological shifts, such as alterations in aboveground primary production and increases in bare cover, changes in the structure and functioning of Andean ecosystems will also have significant socioeconomic repercussions for local communities that rely on mountain ecosystem services. Therefore, it is equally critical to develop adaptation strategies that enable local communities to adjust to these changes, safeguard their livelihoods, and promote sustainable land management.

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Conflict of interest statement

The authors certify that they have no financial interest in the subject matter discussed in the manuscript.

Data availability statement

The data that support the findings of this study will be openly available following an embargo at the following URL: https://mountainscholar.org/home. Data will be available from 1 June 2026.

Appendices

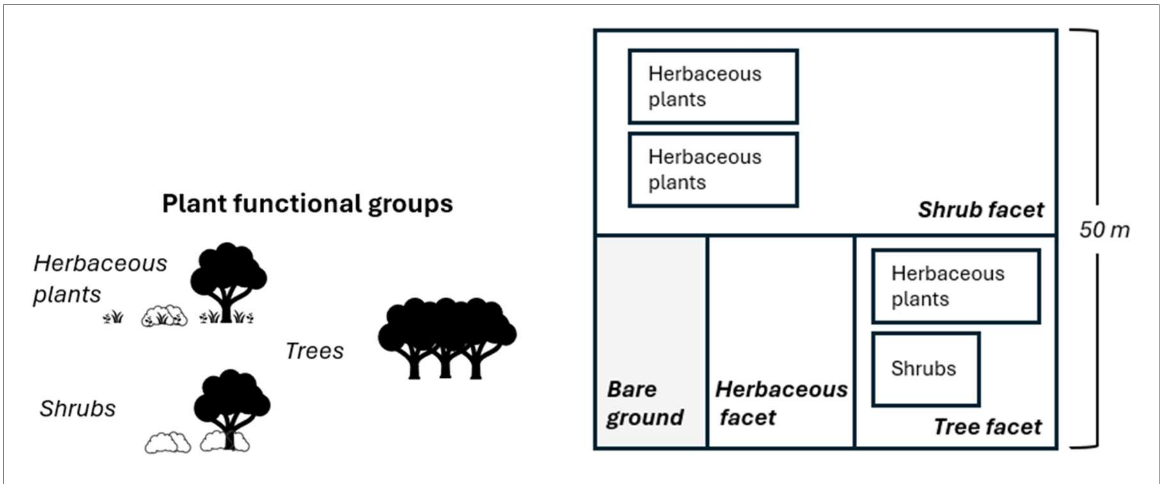

Figure A1. Representation of vegetation layers by facet in L-Range. The L-Range includes three plant functional groups: (i) herbaceous plants, (ii) shrubs, and (iii) trees. The herbaceous facet comprises vegetation layers of herbaceous plants alone, under shrubs, or under trees; the shrub facet includes shrub layers alone or under trees; and the tree facet consists solely of a tree layer. In the Arhuaycancha Valley application, each pixel (50 × 50 m) of the different cover classes (e.g., grasslands and shrublands) may contain one or more of these facets, as well as bare ground. Source: corresponding author's own elaboration.

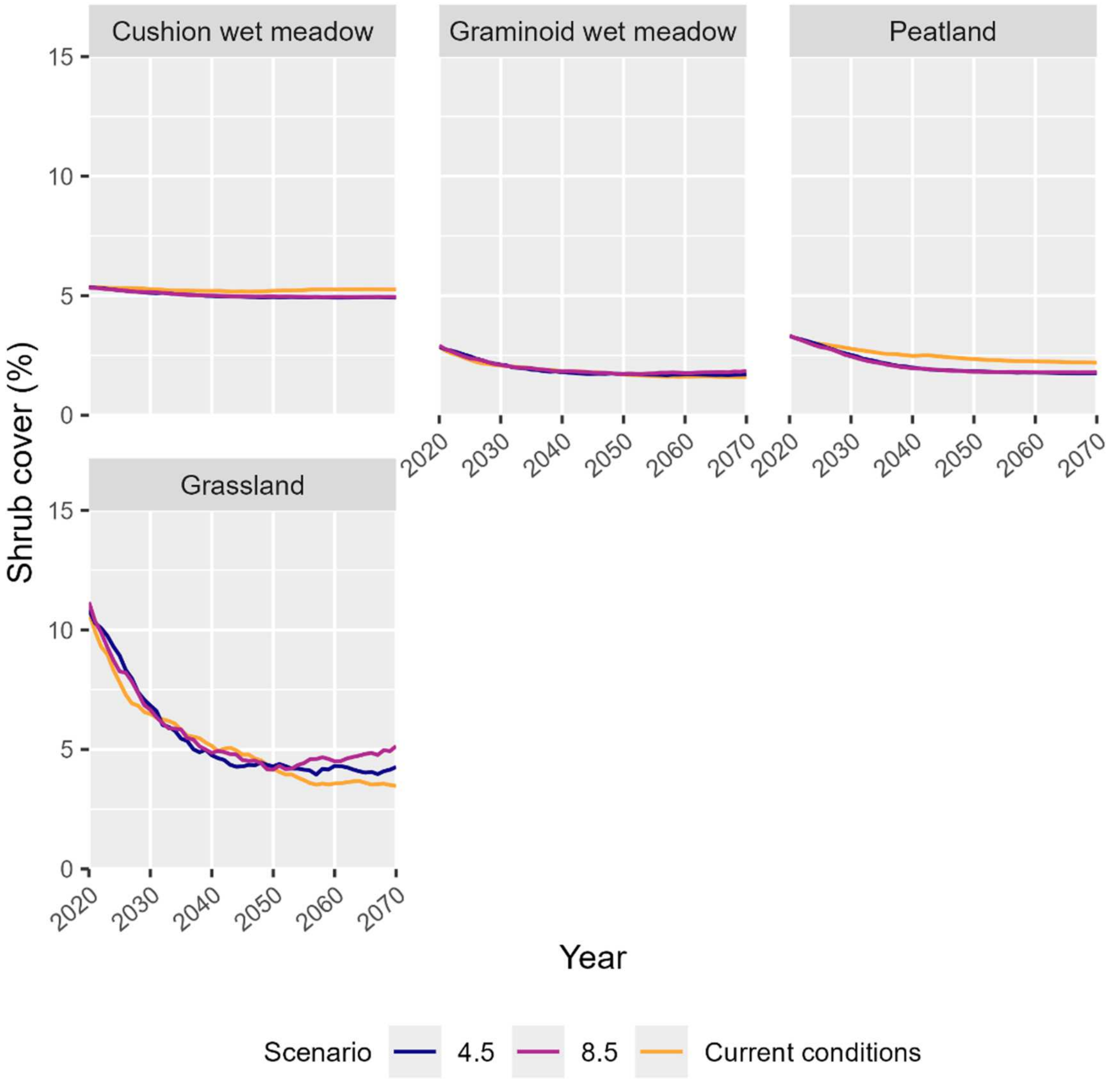

Figure A2. Average change in shrub cover (%) in wetlands and grasslands from 2020 to 2070 under different climate scenarios and 'Current Conditions'.

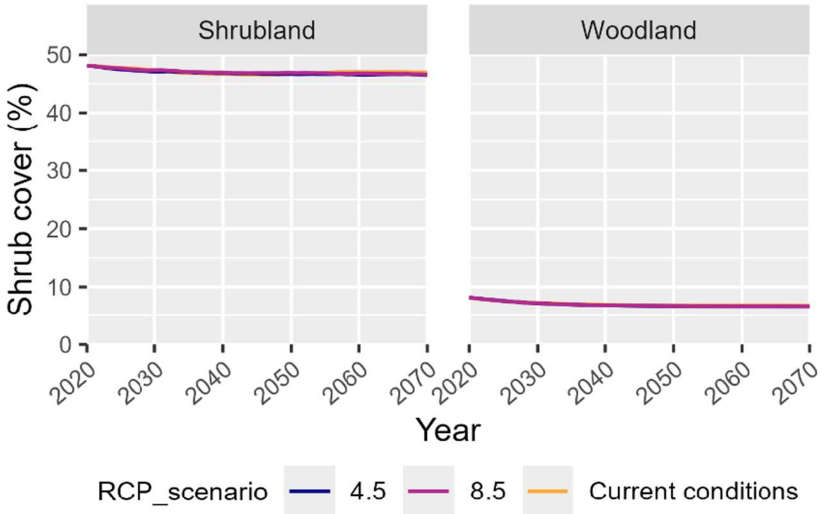

Figure A3. Average change in shrub cover (%) in shrublands and woodlands from 2020 to 2070 under different climate scenarios and 'Current Conditions'.

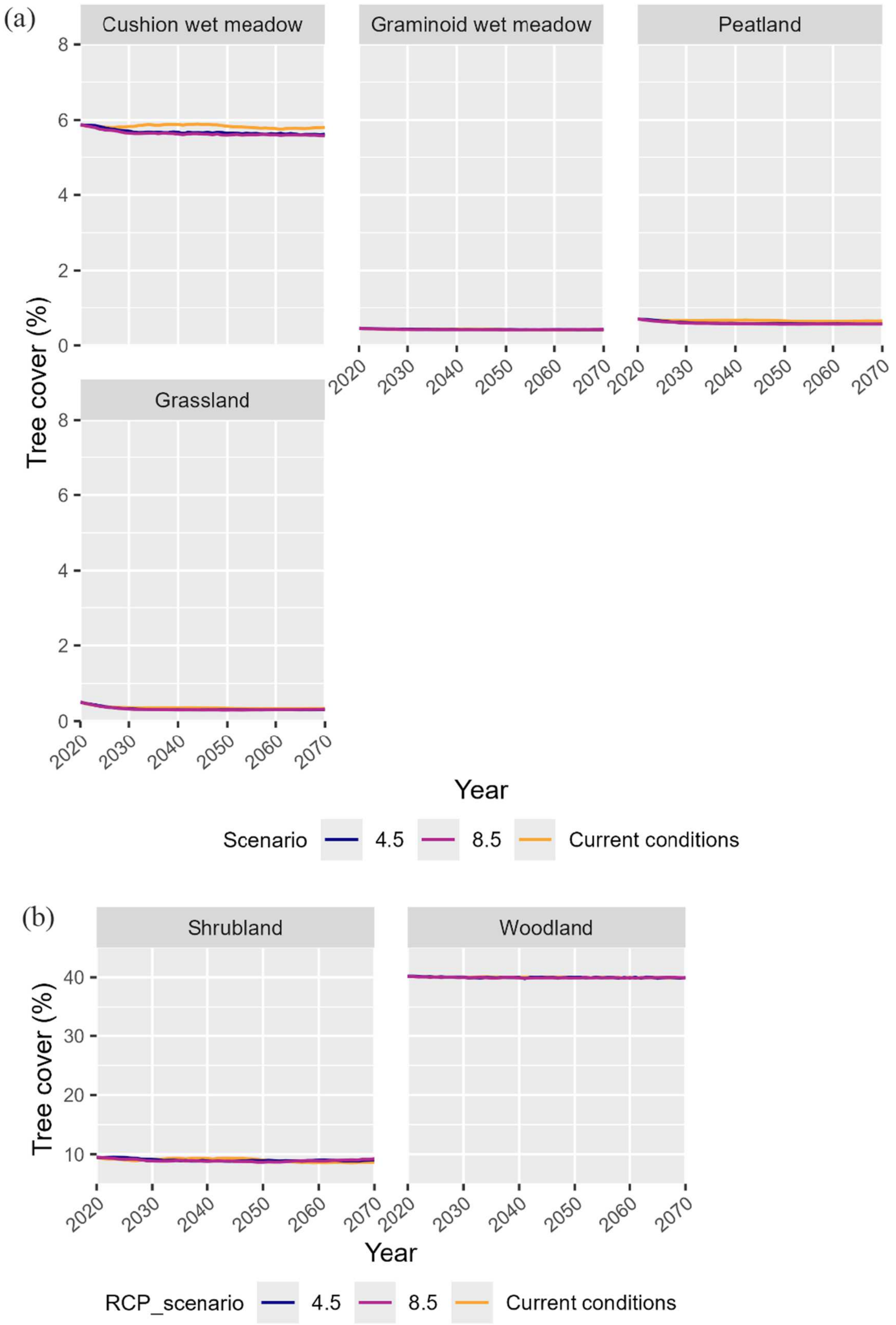

Figure A4. (a). Average change in tree cover (%) across wetlands classes from 2020 to 2070 under different climate scenarios and 'Current Conditions'. (b). Average change in tree cover (%) in shrublands and woodlands from 2020 to 2070 under different climate scenarios and 'Current Conditions'.

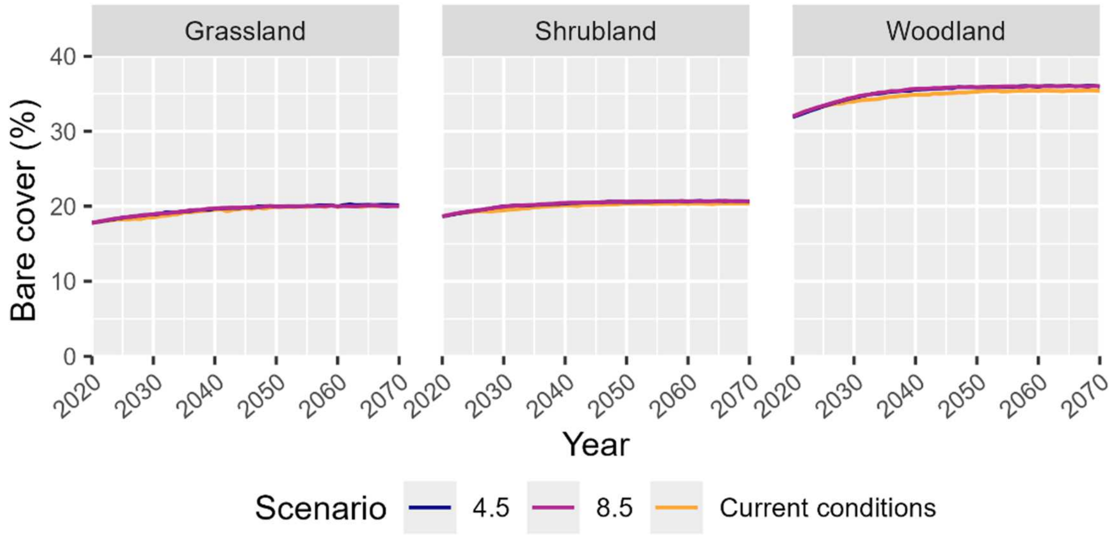

Figure A5. Average change in bare cover (%) in grasslands, shrublands, and woodlands from 2020 to 2070 under different climate scenarios and 'Current Conditions'.

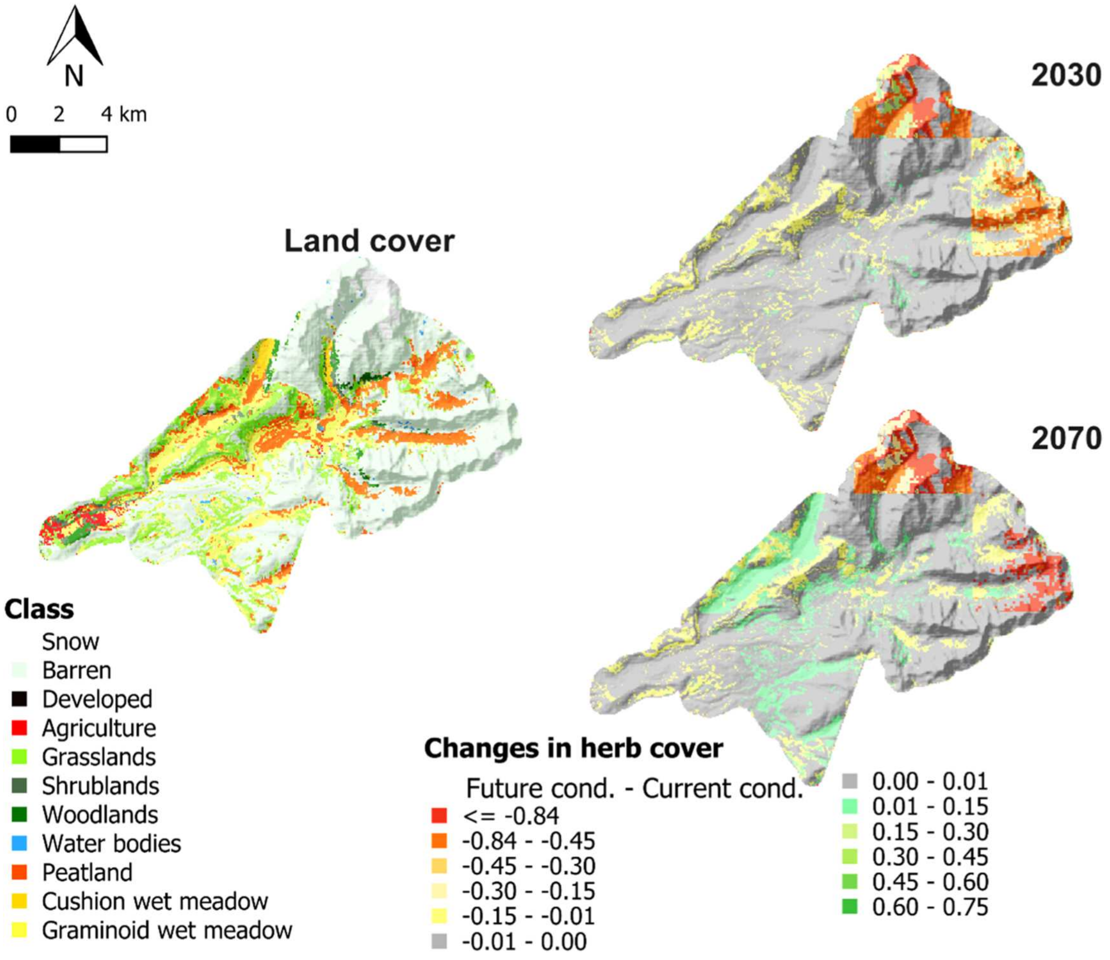

Figure A6. Differences in herbaceous plant cover for 2030 and 2070 relative to 2020 under the RCP 4.5 scenario (mean of three climate models) compared with the 'Current Conditions' scenario. Shades of green indicate areas with increases in herbaceous cover, whereas shades of yellow, orange, and red represent decreases. For example, in the 2070 map, most of the watershed consists of light green areas corresponding to increases in herbaceous cover of up to 0.15 (15%) relative to 2020, while orange and red areas indicate decreases ranging from 0.45 to 0.84 (45%–84%) over the same period.

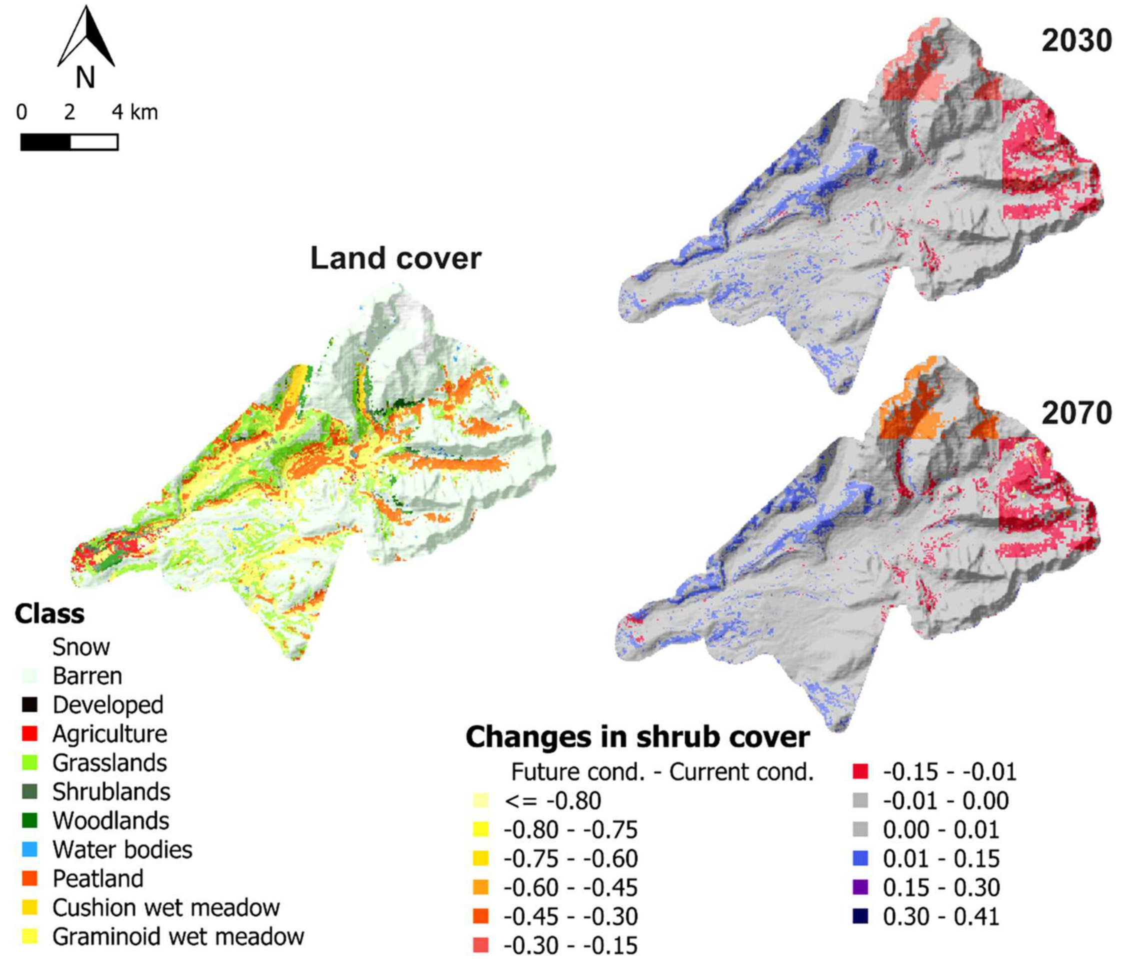

Figure A7. Differences in shrub cover for 2030 and 2070 relative to 2020 under the RCP 4.5 scenario (mean of three climate models) compared with the 'Current Conditions' scenario. Shades of blue, purple, and black represent increases in shrub cover, whereas shades of yellow and red indicate decreases. For example, in the 2070 map, the upper right portion of the watershed (orange areas) shows a reduction in shrub cover from 0.30 to 0.60 (30%–60%) relative to 2020.

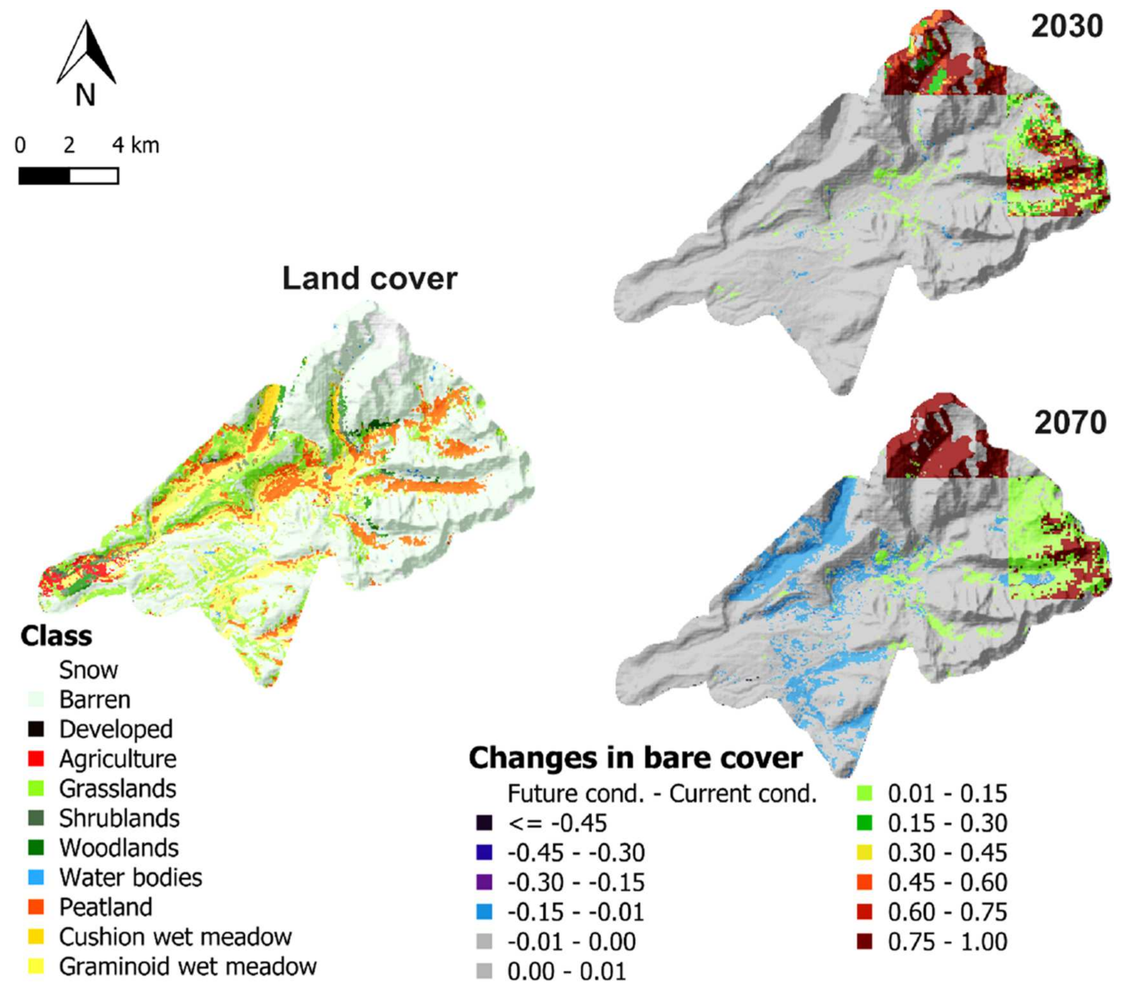

Figure A8. Differences in bare cover for 2030 and 2070 relative to 2020 under the RCP 4.5 scenario (mean of three climate models) compared with the 'Current Conditions' scenario. Shades of green, yellow, and red indicate areas with increases in bare cover, whereas shades of blue, purple, and black represent decreases. For example, in the 2070 map, red and brown areas correspond to increases in bare cover from 0.45 up to 1.00 (45%–100%) relative to 2020, while blue and purple areas indicate decreases from 0.15 to 0.45 (15%–45%) over the same period.

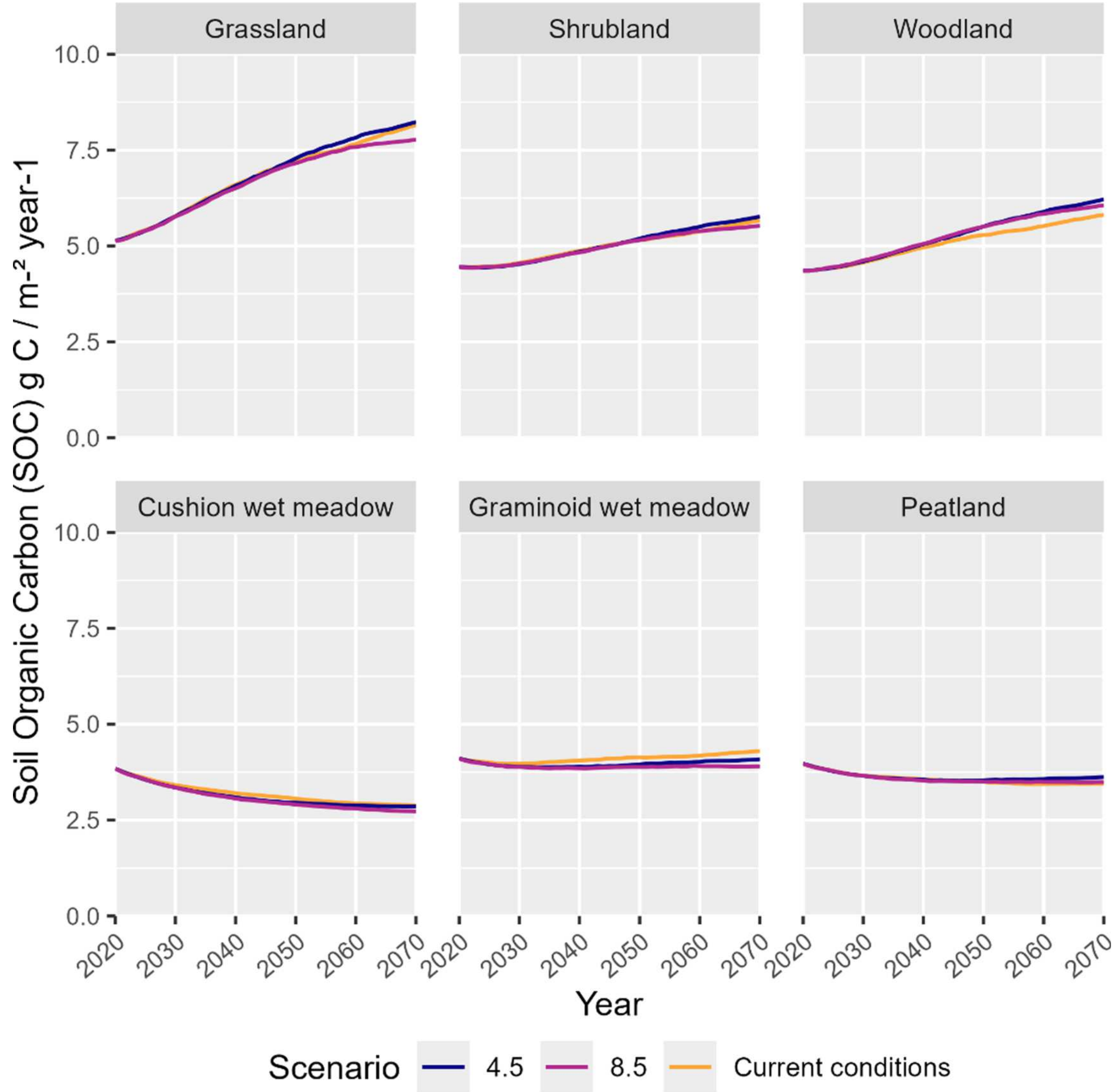

Figure A9. Average change in Soil Organic Carbon (SOC) g C/m^{-2} year^{-1} by cover class under different climate scenarios and 'Current Conditions'.

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