universität wien

MASTERARBEIT | MASTER'S THESIS

Titel | Title

Hotspots of Alpine Vascular Plants of the Andes and Their Conservation Status

verfasst von | submitted by

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angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2025

Studienkennzahl lt. Studienblatt | Degree programme code as it appears on the student record sheet:	UA 066 879
Studienrichtung lt. Studienblatt | Degree programme as it appears on the student record sheet:	Masterstudium Naturschutz und Biodiversitätsmanagement
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Abstract (Deutsch)

Die Anden, die längste Gebirgskette der Welt, beherbergen eine außergewöhnlich hohe Anzahl an endemischen Pflanzenarten, die zunehmend durch Klimawandel, Landnutzung sowie Habitat-Fragmentierung bedroht sind. Analysen auf Basis von Schutzgebietsdaten aus der World Database on Protected Areas (WDPA) zeigen, dass nur 15,8 % der Fläche der Anden unter Schutz stehen, was deutlich unter dem 30%-Schutzziel des Kunming-Montreal Global Biodiversity Framework liegt. Ziel dieser Arbeit ist es, Biodiversitätshotspots alpiner Gefäßpflanzen in den Anden zu identifizieren und ihren aktuellen Schutzstatus zu bewerten.

Vorkommensdaten aller alpinen Gefäßpflanzen der Anden wurden von GBIF bezogen, wodurch insgesamt 107.410 georeferenzierte Datensätze innerhalb der Andenregion, definiert durch das GMBA Mountain Inventory v2.0, vorlagen. Das Untersuchungsgebiet wurde in 50 × 50 km große Rasterzellen unterteilt, in jeder Rasterzelle wurden vier Biodiversitäts- und Endemismus-Indizes berechnet. Die Zellen wurden für jeden Index nach Reichtum geordnet und eine Zelle wurde als Hotspot klassifiziert, wenn sie zu den obersten 5 %, 5–10% oder 10–20% der reichsten Zellen in mindestens einem Index gehörte. Schutzgebiete wurden anhand der WDPA-Daten integriert; Zellen wurden als geschützt gewertet, wenn mindestens 10% ihrer Fläche von Schutzgebieten der IUCN-Kategorien I–IV überlappt wurden. Die übrigen Zellen wurden als Schutzlücken identifiziert. Liegt der Schutzgebietanteil unter 10%, wurde der Hotspot als Schutzlücke eingestuft.

Von insgesamt 1.459 alpinen Arten sind 1.370 endemisch für die Anden (94 %), 585 kommen in weniger als 1% des Untersuchungsgebiets vor (43 % der Endemiten). Insgesamt wurden 70 Zellen als Top 5% Hotspots, 101 Zellen als Top 5–10% Hotspots und 149 Zellen als Top 10–20% Hotspots identifiziert. Diese Hotspots befinden sich überwiegend in der zentralandinen Puna, den Páramos in den nördlichen Anden sowie in den bolivianischen und peruanischen Yungas. Allerdings sind derzeit nur 27 %, 23 % bzw. 19,5 % der Hotspots der Top 5%, 5–10% und 10–20% durch Schutzgebiete abgedeckt. Die übrigen Gebiete stellen somit deutliche Schutzlücken dar.

Diese Ergebnisse verdeutlichen, dass große Schutzlücken in den Anden bestehen, was die Notwendigkeit unterstreicht, den Schutz in diesen biodiversitätsreichen Regionen zu verbessern.

Abstract

The Andes, the longest mountain range in the world, harbour an exceptionally high number of endemic plant and animal species, which are increasingly threatened by ongoing climate change, land-use and habitat fragmentation. Recent analyses, based on protected area data from the World Database on Protected Areas (WDPA), indicate that only 15.8% of the Andes are protected, which is significantly below the 30% conservation target set by the Kunming-Montreal Global Biodiversity Framework. This study aims to delineate alpine plant biodiversity hotspots across the Andes and evaluate their current conservation status. Occurrence data for all alpine vascular plant species of the Andes were obtained from GBIF, resulting in 107,410 georeferenced records within the Andean region, as defined by the GMBA Mountain Inventory v2.0. The study area was divided into 50 × 50 km cells, and four indices (species richness, endemic richness, range-restricted endemic richness, and range rarity richness) were calculated. Cells were ranked and grouped into richness percentiles. A grid cell qualified as a hotspot if it fell within the uppermost 5%, 5–10%, and 10–20% richest cells for at least one index. Protected areas were integrated using the WDPA data, with cells classified as protected if at least 10% overlapped with IUCN categories I–IV, and the rest were identified as Conservation Gaps (CGs). From a total of 1,459 alpine species, 1,370 were endemic to the Andes (94%), and 585 species were range-restricted, i.e. occurring in less than 1% of the study area (43% of the endemics). A total of 70 cells were identified as top 5% hotspots, 101 cells as top 5–10% hotspots, and 149 cells as top 10–20% hotspots. These hotspots were mostly found in the Central Andean Puna, northern Andean Páramos, and Bolivian and Peruvian Yungas ecoregions. However, only 27%, 23%, and 19.5% of the top 5%, 5–10%, and 10–20% hotspots, respectively, are currently protected, while the remaining areas represent CGs. These patterns highlight significant CGs in the Andes, emphasizing the urgent need to enhance protection efforts in these biodiversity-rich regions.

1. Introduction

Mountains are widely recognized as global biodiversity hotspots (Antonelli et al., 2018; Hoorn et al., 2018; Rahbek et al., 2019), harbouring a high proportion of range-restricted species (Hobohm, 2014; Spehn et al., 2011). This is because their steep environmental gradients, complex topography and climatic heterogeneity create a dense mosaic of ecological niches, which promotes high species richness (Perrigo et al., 2020). Geographic isolation of mountain regions promotes speciation and therefore creates centres of endemism (Muellner-Riehl, 2019). As endemism increases with elevation, high-elevation ecosystems contain disproportionately many unique species in small areas yet are highly vulnerable to climate change, therefore the conservation of mountain systems is especially important (Steinbauer et al., 2016).

The Andes, extending over a length of about 7,000 km along the West of South America, constitute the longest mountain range in the world. Due to their extreme elevational range and complex topography, the Andes exhibit pronounced environmental gradients that strongly influence climate, vegetation, and species distribution patterns (Särkinen et al., 2012). Abiotic factors such as precipitation, temperature, solar radiation, and soil conditions vary with elevation, latitude, and proximity to the ocean, which creates distinct habitat zones along mountain slopes (Garreaud, 2009). These strong environmental gradients shape species distributions and lead to high biodiversity across elevational ranges (McCain and Grytnes, 2010). Another major driver of rich endemism in this mountain range is geographic isolation, creating evolutionarily persistent “islands” of habitats that promote high endemism (Särkinen et al., 2012).

As a result of these combined factors, the Andes harbour an exceptionally high number of endemic plant and animal species (Myers et al., 2000). Covering only about 0.6% of the Earth's land surface, the Andes is home to approximately 30,000 vascular plant species, which is about 10% of the world’s vascular plant diversity (Pérez-Escobar et al., 2022). A wide range of climatic and geographic conditions has led to distinct alpine biomes, such as the Páramo and Puna, each exhibiting significant floristic heterogeneity along latitudinal and elevational gradients (Cuesta et al., 2017).

Species richness reaches its peak in the Central Andes, where the high levels of endemism and unique biogeographic characteristics further solidify the region’s status as a global biodiversity hotspot (Figueroa et al., 2021). Furthermore, the Andes also act as a key source and sink of Neotropical plant diversity, facilitating species interchange

with Central America, Amazonia, and other neighbouring regions over evolutionary timescales (Pérez-Escobar et al., 2022).

The alpine regions of the Andes, particularly the Páramo and Puna, are highly sensitive ecosystems that are increasingly threatened by climate change and human activities (Cuesta et al., 2017). Key anthropogenic pressures include grazing, mining, species exploitation and urban expansion (Edison and Mejía, n.d.). In the Páramos of the northern Andes, human impacts on species composition exceed those of natural factors, as ecosystem services such as crop production and livestock grazing intensify the land-use pressures on biodiversity (Vásquez, Balslev and Sklenář, 2015). These disturbances lead to habitat fragmentation and reduce the resilience of ecosystems, and accelerate species loss, particularly in ecologically fragile mountain regions (Young, 2009). Combined with ongoing climate change, this contributes to habitat degradation, biodiversity decline, and desertification (Alba Mejía, n.d.). Sustainable land management and restrictions on intensive human use are therefore crucial to maintain biodiversity and ecosystem functioning in these areas.

Recent analyses, based on protected area data from the World Database on Protected Areas (WDPA), managed by UNEP-WCMC and IUCN, indicate that only 15.8% of the Andes are protected, which is significantly below the 30% conservation target set by the Kunming-Montreal Global Biodiversity Framework (Theobald et al., 2024).

This thesis aims to identify alpine biodiversity hotspots in the Andes through a grid-based spatial analysis of alpine vascular plant diversity, using four biodiversity indices and examining the ecological factors to explain these patterns. In a second step, the conservation status of these hotspots is assessed by analysing their overlap with protected areas. Identifying hotspots is crucial because biodiversity is unevenly distributed and conservation resources are limited.

The Andes are widely recognized for their exceptional biodiversity, and the Tropical Andes are officially listed as one of the 36 global biodiversity hotspots (Myers et al., 2000). In such large and heterogeneous regions, biodiversity is not evenly distributed, and conservation therefore requires identifying “hotspots within a hotspot”, meaning smaller areas that concentrate disproportionally high levels of endemism and therefore represent priority sites for conservation (Cañadas et al., 2014).

The central research question of this study is: *Where are the centres of endemism and highest species richness of alpine vascular plants in the Andes, and to what extent are these hotspots represented within the current protected area network?*

Based on previous research and ecological theory, the following hypotheses were formulated:

(1) The richness indices are strongly correlated with each other, and all richness indices show positive correlations with ecological variables (topographic heterogeneity and elevational difference).

(2) Stricter hotspot thresholds (e.g., 5% richest cells) exhibit a higher proportion of protected area coverage compared to less restrictive thresholds (e.g., 10–20%), suggesting that areas of exceptionally high diversity are more likely to fall within existing protected zones.

(3) Biodiversity hotspots are primarily located in the alpine regions of the Andes, particularly within the Páramo and Puna ecoregions.

(4) Despite the extensive network of protected areas across the Andes, a considerable proportion of biodiversity hotspots is expected to remain insufficiently protected.

2. Material and Methods

This section outlines the data sources, spatial framework, and analytical methods used to assess patterns of alpine plant biodiversity to identify hotspots and their conservation coverage across the Andes.

2.1. Study Area

This section defines the spatial extent of the study area, focusing on the Andes Mountain system as delineated by the GMBA Mountain Inventory v2.0 by Snethlage et al. (2022). This delineation provides the geographic framework for the subsequent hotspot analysis and conservation assessment conducted in this study. Figure 1 shows a digital elevation model (DEM) of South America, the blue triangles mark the 99 peaks higher than 6,000 m a.s.l. The DEM provided by Stanford University Library (2006) was used, and shapefiles from Geofabrik GmbH (n.d.) were applied for the South American borders. Coordinates of the peaks were extracted from Peakbagger.

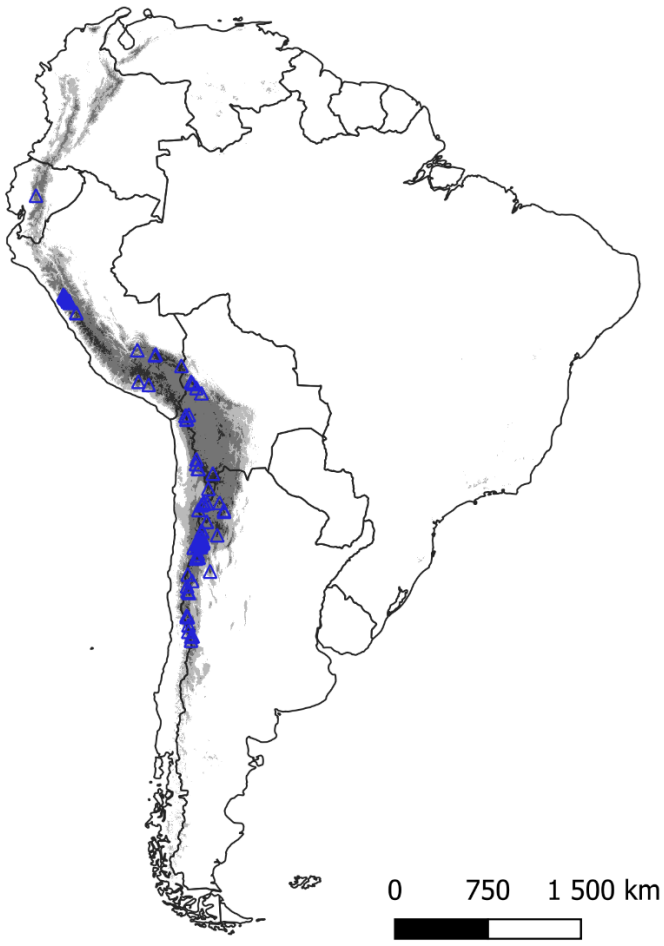

Figure 1: DEM of South America. In the DEM, the elevation is classified into five zones: 0–1500 m, 1500–3000 m, 3000–4500 m, 4500–6000 m, and 6000 m up to the highest summit. The blue triangles mark the 99 peaks higher than 6,000 m a.s.l.

2.1.1. The Andes

The Andes span across seven countries (Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, and Chile), and also cover a broad latitudinal range from approximately 10° N to 53° S (Garreaud, 2009). Numerous peaks exceed 5,000 m above sea level (Luebert and Weigend, 2014), 99 peaks rise above 6,000 m a.s.l. (Peakbagger, n.d.). The highest treeline occurs at 4,810 m a.s.l. on the Sajama Volcano in the Central Andes, which is also the highest known treeline worldwide (He et al., 2016), while the lowest, at 625 m a.s.l., is found in southern Chile in Karukinka in the Tierra del Fuego (Fajardo and Piper, 2017).

2.1.2. Delineating the Andes

To delineate the Andes, the “Broad” version of the GMBA Mountain was used, as this version extends beyond the standard GMBA definition by including areas that are considered mountainous according to alternative global definitions such as the World Conservation Monitoring Centre (WCMC) and the United States Geological Survey (USGS) as featured in the Global Mountain Explorer. This approach was chosen to include also high-elevation plateaus and transitional zones like the Altiplano or Puna region which are for example excluded by the “standard” version of the GMBA Mountain Inventory. Figure 2 shows the standard version of the GMBA Mountain Inventory in red. It can be seen, that the altiplano and Puna region were excluded in the standard version despite high elevation and importance for biodiversity.

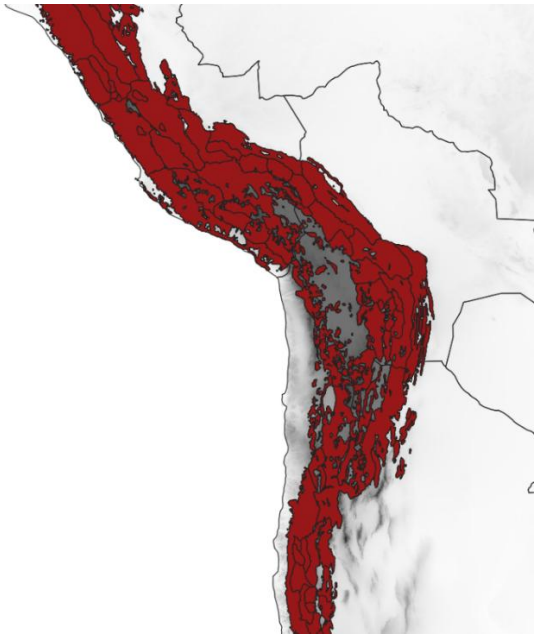

Figure 2: Standard version of the GMBA Mountain Inventory. High-elevation plateaus such as the Altiplano are excluded in this version.

The Broad Inventory was not intersected with these alternative layers, as minor extensions into lower areas are unlikely to influence the identification of biodiversity hotspots in alpine regions at this regional scale. Figure 3 shows the final research area in green.

Figure 3: Final research area delineated based on the GMBA Mountain Inventory.

2.1.3. Alpine Zones of the Andes

Páramo: The Páramo is a high-elevation ecosystem found above the treeline in the mountains of Venezuela, Colombia, Ecuador, and northern Peru (Peyre et al., 2018). It extends between 6° S and 10° N (Duchicela et al., 2024) and the altitudinal range lies above 3000 m a.s.l. (Herzog et al., 2011, based on Josse et al., 2009). Figure 4 shows the location of the Páramos. It is primarily a humid grassland and shrubland system, usually forming a relatively narrow belt along the upper slopes of the northern Andes (Cresso et al., 2020). Moving south, Páramo vegetation becomes more and more fragmented, occurring in smaller and more isolated patches. This ecosystem is characterized by cool, moist conditions, strong diurnal temperature variations, and frequent cloud cover (Brück et al., 2023). Páramos harbour exceptionally high levels of endemism and are considered the floristically richest tropical alpine ecosystem with about 5,000 plant species in more than 500 plant communities (Sklenář et al., 2014). The ecoregion plays a crucial role in regional hydrology by capturing and storing water through their sponge-like soils and dense vegetation. Typical plant taxa *include Espeletia* spp. (Asteraceae), *Jamesonia* (Pteridaceae), *Azorella* (Apiaceae), *Stipa, Calamagrostis* and *Festuca* (Poaceae), and *Werneria* (Asteraceae), as well as *Baccharis* and *Loricaria* (Asteraceae), *Hypericum* (Hypericaceae), *Valeriana* (Caprifoliaceae), and *Puya* (Bromeliaceae) (Ansaloni et al., 2022; Brück et al., 2023), along with a rich diversity of mosses, lichens, and ferns. These species are well adapted to intense radiation, low temperatures, and nutrient-poor soils (Brück et al., 2023).

Puna: The Puna is an open, alpine grassland that lies in the Central Andes (Duchicela *et al.*, 2024). Figure 4 shows the extent of the Puna region, from the southern part of Peru to the north of Chile and Argentina and it stretches from 6° S to 23° S (Duchicela et al., 2024). It extends roughly between 2,000 and 6,000 m a.s.l., forming the dominant high-elevation ecosystem south of the Páramo region. The vegetation is dominated by tussock grasses and also shrubs and cacti (Herzog et al., 2011, based on Josse et al., 2009). The Puna replaces the Páramo where precipitation becomes lower and seasonally concentrated, it is therefore drier than the Páramo (Duchicela et al., 2024). It can be divided into two different phytoregions, along a gradient of duration of the rainy season and decreasing precipitation. Annual precipitation in the Wet Puna ranges from 500 to 1,000 mm and is characterized by strong temperature fluctuations, seasonal rainfall, and extensive grassland plateaus. Further south, in the Dry Puna the annual precipitation ranges between 300 and 500 mm (Rolando et al., 2017).

Figure 4: Páramo (red) and Puna (orange) ecoregion

2.1.4. Ecoregions of the Study Regions

The ecoregion boundaries were obtained from the *Terrestrial Ecoregions of the World* dataset (Resolve, 2017). In total there are 67 ecoregions present within the research area.

2.2. Species Data

Occurrence data for alpine plant species was systematically compiled, cleaned, and classified to provide a robust basis for the hotspot analyses. The process included extracting species lists from a published dataset, downloading and filtering their occurrence records from Global Biodiversity Information Facility (GBIF), cleaning the data, and classifying species according to their biogeographic distributions, with a focus on identifying Andean endemics. The steps are described in the following section.

2.2.1. Compilation of Alpine Plant Species Data

Alpine species, which occur in the biogeographic region of South America were extracted from the dataset provided by Figueora et al. (2021), resulting in a species list of ca. 1,500 alpine species. Species occurrence data of these species was obtained from the Global Biodiversity Information Facility (GBIF; GBIF.org, 2025) using the rgbif package in R. The dataset comprises 2,871 individual datasets and was published by 792 institutions across 80 countries (DOI: https://doi.org/10.15468/dl.nf44qm).

Five species could not be downloaded due to missing GBIF keys, and four species were excluded due to lacking coordinate information. During the download process, species names were matched to the GBIF backbone taxonomy, which led to the merging of 27 species that were either synonyms or subspecies of others. For instance, *Festuca loricata*, *F. villipalea*, and *F. weberbaueri* were consolidated under *F. fiebrigii*. In addition, 155 species names were corrected to their accepted synonyms according to the GBIF backbone taxonomy. After these steps, the dataset contained 1,464 species with a total of 2,161,359 occurrence records.

2.2.2. Data Cleaning and Spatial Filtering

All downloaded occurrence records contained only those with coordinates, which were filtered using the predicate pred("hasCoordinate", TRUE). Further data cleaning was conducted using the CoordinateCleaner package (Zizka et al., 2019), which flagged a total of 595,049 records due to various coordinate-related issues. Specifically, 2,363 records were flagged because they had identical latitude and longitude values, 2,397 records got flagged because they had zero coordinates, 13,909 records were located at country capitals, 4,451 records were positioned at country centroids, and 582,768 records were flagged because they only matched the country identity (EQ = 0.28). After removing these flagged records, 1,566,310 records remained. In the final cleaning step, duplicates, defined as identical records of the same species at the same coordinates, were removed, resulting in 942,960 unique records. From these, 111,807 occurrences were located within the biogeographic region of South America, based on the Global Mountain Biodiversity Assessment (GMBA) mountain delineation (hierarchy level 2). All records situated in the lowlands were subsequently excluded, as these were likely not correct due to imprecise georeferencing or misidentifications. Additionally, *Urtica gracilis subsp*. *mollis* was excluded to avoid overrepresentation, as it had been merged with *Urtica gracilis*, resulting in an inflated number of occurrences.

Figure 5 shows all 111,807 records of alpine plant species in South America. Out of these, 107,410 occurrences were within the research area.

Figure 5: All occurrence records (n = 111,807) of alpine plant species in South America.

This low number of species in South America compared to all downloaded records can be explained with the presence of highly distributed cosmopolitan species, such as *Deschampsia cespitosa* (847,340 occurrences), *Empetrum nigrum* (414,489 occurrences), and *Plantago maritima* (134,894 occurrences), which also occur in the Andes.

2.2.3. Classification of South American Endemics

All 1,464 species were then classified according to their distribution, distinguishing between species endemic to South America and those occurring across multiple continents. This classification was primarily based on the distribution information provided by the *Plants of the World Online* (POWO) database (Royal Botanic Gardens, Kew, 2024) and complemented by occurrence records from GBIF to verify patterns. Based on these criteria, 1,381 species out of the 1,464 species were classified as endemic to

South America, while the remaining species were categorized according to their continental distribution patterns, including combinations such as South and North America, South America and Europe, South America and Antarctica, as well as species with cosmopolitan distributions.

2.2.4. Identification of Andean Endemics

In a second step, the South American endemic species were further assessed to determine whether they were endemic to the Andes. All occurrence records were clipped to the GMBA mountain regions in South America, which included the Andes, South American Coastal Ranges, South American Interior Highlands, Brazilian Highlands, and the Guayana Shield. This resulted in 107,851 occurrence records across these regions, representing 1,463 species, after the removal of one species that only occurred in the lowlands. Figure 6 shows the mountain regions as defined by the GMBA mountain inventory.

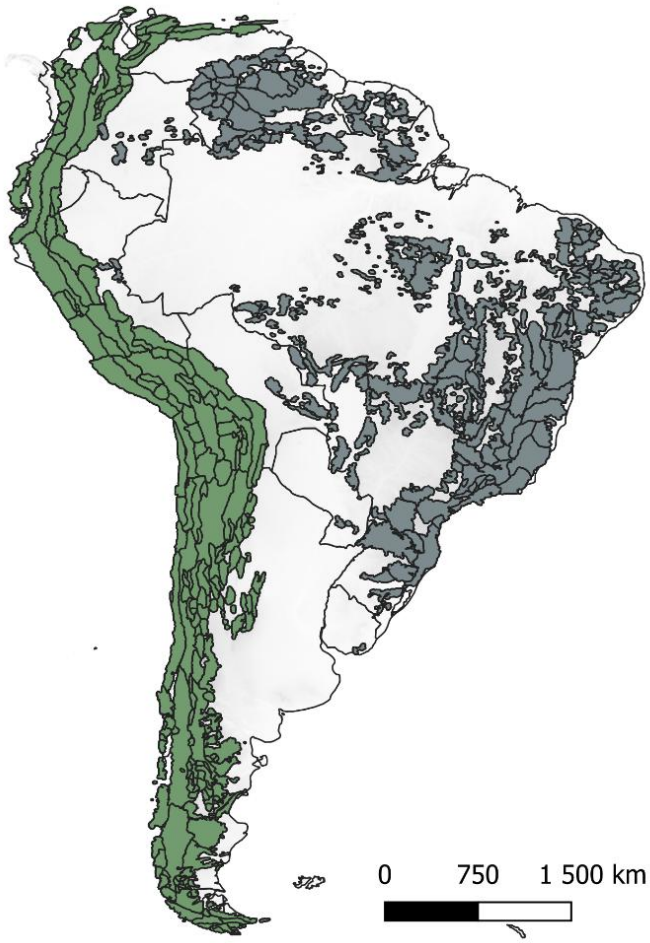

Figure 6: GMBA mountain inventory layer showing mountain regions in South America. The research area, which includes the South American Coastal Ranges, South American Interior Highlands, and the Andes (in green), is highlighted, while the Brazilian Highlands and Guayana Shield are shown in grey.

To refine the classification of Andean endemics, species occurrences within the Andes were compared to those in the Brazilian Highlands and the Guayana Shield. There was only one species present in mountain areas outside of the Andean region (*Callianthe schenckii*). In total, 35 species with 441 occurrences were found in the Brazilian Highlands or Guayana Shield, 24 of them with only one observation and two with only two observations. These 26 species were then cross-checked with POWO to determine if they are native to regions outside of the Andes. This was the case for two species (*Stenoptera acuta* and *Cyperus xanthostachyus*), while the remaining 24 species were classified as endemic to the Andes, as POWO confirmed they are native only to Andean countries. Species with more than two occurrences in mountainous regions outside of the Andes were also classified as not endemic to the Andes.

The following eight species were identified as not endemic to the Andes, as they showed multiple occurrence records in both the Brazilian Highlands and Guayana Shield and were classified as native to these regions according to POWO: *Perezia multiflora, Drimys winteri, Clematis millefoliolata, Verbena hispida, Callitriche lechleri, Polypogon exasperatus, Cyperus xanthostachyus,* and *Stenoptera acuta*. Furthermore, in this step, two species were removed as they were considered non-alpine: *Dioscorea piperifolia* and *Callianthe schenckii*. The final dataset therefore contains 1,459 species with jointly 107,410 occurrence records, 1,370 species being endemic to the Andes.

2.3. Spatial Analysis and Conservation Assessment

To assess the conservation status of biodiversity hotspots a spatial analysis was performed using QGIS 3.34 (QGIS.org, 2024). The analysis involved identifying hotspots based on four indices and overlaying these hotspots with protected area data to identify CGs. The individual steps of this analysis are described in the following sections.

2.3.1. Projection and Grid

The spatial analysis was done in QGIS using the Albers Area Conic projection (ESRI: 102033) which is an equal area projection to ensure accurate area calculations and to minimize distortions. This choice follows recommendations by Budic et al. (2016), who emphasize the importance of using equal area projections for ecological applications that involve area-based indicators. Therefore, it can be considered suitable for regions

that span a wide range of latitudes, like the Andes. The study area was divided into equal-area grid cells measuring 50 × 50 km and laid over the Andes region based on the delineation described in section 2.1. This grid can be seen in Figure 7.

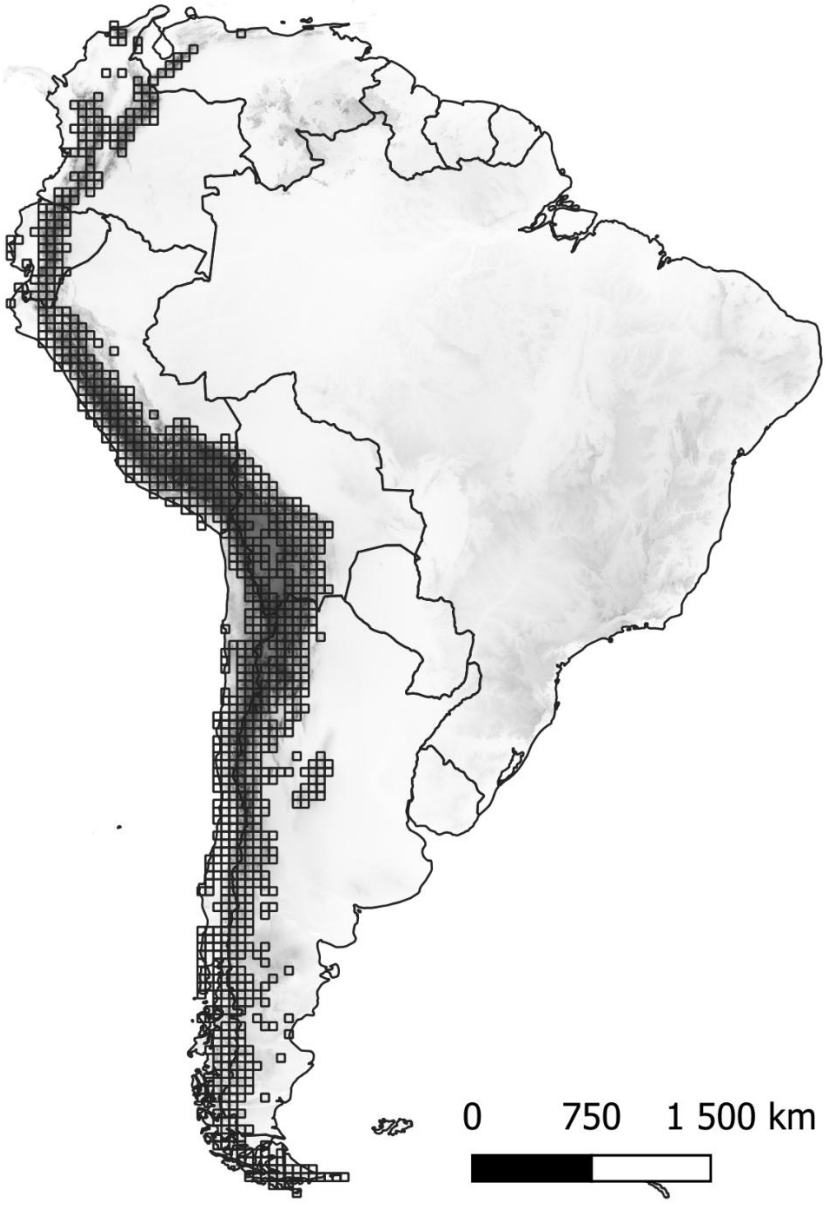

Figure 7: 50 × 50 km grid of the research area in an Albers Equal Area Conic projection (ESRI: 102033), showing only grid cells containing more than two species (n = 1,007).

2.3.2. Biodiversity Indices

To analyse species distribution patterns and quantify biodiversity, four biodiversity indices were calculated for each grid cell, including Species Richness (SR), Endemic Richness (ER), Range-Restricted Endemic Richness (RER), and Range-Rarity Richness (RRR). Only grid cells with more than 2 species were included in the study (n = 1,007).

Species Richness (SR): Represents the total number of different species occurring within a single grid cell.

Endemic Richness (ER): Refers to the number of endemic species occurring within a single grid cell.

Range-Restricted Endemic Richness (RER): Indicates the number of endemic species per grid cell that occur in less than 1% of the study area (i.e. fewer than 10 cells in this study) as described by Noroozi et al. (2023).

Range-Rarity Richness (RRR): A weighted index that assigns higher values to species occurring in fewer grid cells. The index is calculated for each grid cell as the sum of species scores, where each species is weighted inversely to the number of cells it occupies, following Noroozi et al. (2023), originally introduced by Crisp et al. (2001).

2.3.3. Hotspot Classification

Hotspot cells were identified for each of the four biodiversity indices separately by ranking all grid cells and selecting the top 5%, 5–10% and 10–20% richest cells for each indicator. Subsequently, the hotspot layers of the individual indicators were combined into composite hotspot maps for each richness threshold. A cell was classified as a hotspot if it was ranked within the respective threshold for at least one of the indicators. For this reason, the hotspot classes do not represent strictly additive groups (e.g., a cell classified as a top 5% hotspot for one indicator could simultaneously fall within the 5–10% or even 10–20% class for another index). Therefore, the number of cells classified as top 5–10% hotspots do not necessarily complement the number of top 5% cells to exactly match the number of top 10% cells.

2.3.4. Integration of Protected Areas Data

To assess the effectiveness of the current conservation network, a protected areas dataset, based on the WDPA shapefile (UNEP-WCMC and IUCN, May 2025) was incorporated. This dataset was overlaid with the hotspots in the alpine regions of the Andes to evaluate their proportion currently under protection. Areas with high levels of endemism but low protection coverage were identified, highlighting priority regions for conservation efforts.

In total, 2,435 protected areas exist across the Andes. 28 in Category I, 177 in Category II, 40 in Category III, 27 in Category IV. 58 in Category V, and 1,673 in Category

VI. 468 of the protected areas have unreported/unassigned status. Only the IUCN Categories I–IV were used to analyse the conservation status as they represent the strictly protected classes and are generally considered more effective for safeguarding biodiversity. In contrast, Categories V and VI allow multiple use and therefore provide weaker protection, therefore making them less suitable for evaluating the conservation of biodiversity hotspots (Shafer, 2015). Therefore the 272 protected areas, belonging to categories I—IV were used (Figure 8). To analyse the conservation status of a cell, a cell was classified as protected when at least 10% of the cell was covered by an IUCN conservation area. When less than 10% were covered, it was identified as a CG cell.

Figure 8: Protected areas as defined by the WDPA. In total, 272 protected areas, classified under IUCN categories I–IV were included within the study area. Protected areas are shown in blue, and the research area is outlined in brown.

2.3.5. Distribution Across the Ecoregions

The top 5%, 5—10% and 10—20% hotspots were analysed with respect to their spatial distribution across ecoregions as described in section 2.1.4. to provide ecological context. The coverage of each ecoregion within each hotspot class was calculated, and the corresponding percentages were derived to compare the distribution across the different richness classes. In total there are 67 ecoregions within the study area. Table 1 shows a list of all ecoregions within the research area.

2.3.6. Ecological Factors

To explain biodiversity patterns, topographic heterogeneity and elevational range were quantified. Topographic heterogeneity, representing the ruggedness and complexity of the terrain, was measured for each grid cell. The three-dimensional surface area of each 50 × 50 km grid cell was estimated from a DEM using the r-package terra. Slope was derived in radians, planimetric cell area obtained with cellSize(), and true surface area approximated as planimetric area divided by cos(slope). These values were summed per grid cell using zonal statistic. The elevational range was calculated as the difference between the maximum and minimum elevation per cell, also using the same DEM. Both ecological factors were then correlated to the four richness using Pearson's correlation coefficient.

3. Results

This section describes the results of each index and the corresponding hotspot patterns. Furthermore, it presents the overlap of protected areas with these hotspots, as well as the relationships between the ecological factors and the indices and the ecoregions share per hotspot class.

3.1. Biodiversity Patterns

3.1.1. Species and Indices Overview

Out of the 1,459 species, a total of 1,370 were identified as endemic to the study area (94%). Table 1 shows the results of the distribution of all 1,459 species classified to different distribution categories. A total of 585 species were range-restricted endemics, i.e., occurring in less than 1% of the study area (43% of the endemics), 16 of them were only present in 1 cell.

Table 1: Summary of the 1459 species classified into distribution categories (S=South America; N=North America).

Distribution	Count
Endemic	1370
S+N	42
S+N, Asia, Europe	9
S	8
Cosmopolite	6
S, Europe	5
S+N, Africa, Asia, Europe	4
S, Australia, Europe	3
S+N, Australia, Asia, Europe	2
S+N, Europe	2
S, Australia	2
S+N, Africa, Europe	1
S+N, Antarctica	1
S+N, Australia, Europe	1
S, Antarctica	1
S, Asia, Australia	1
S, Asia, Australia, Europe	1

Only cells with more than two species were included, resulting in 1,007 cells. Species richness ranged from 3 to 439 species per grid cell; endemic richness ranged from 1 to 397 endemic species. Range-restricted endemic richness (RER) ranged from 1 to 115 species per cell. Range-restricted species were present in 630 cells. The richest cell contained 115 range-restricted species, while the second richest held 74. Range-rarity richness (RRR) ranged from 0.0625 to 35.051, with the second richest cell having a value of 21.428. Figure 9 shows the richest cells for each index.

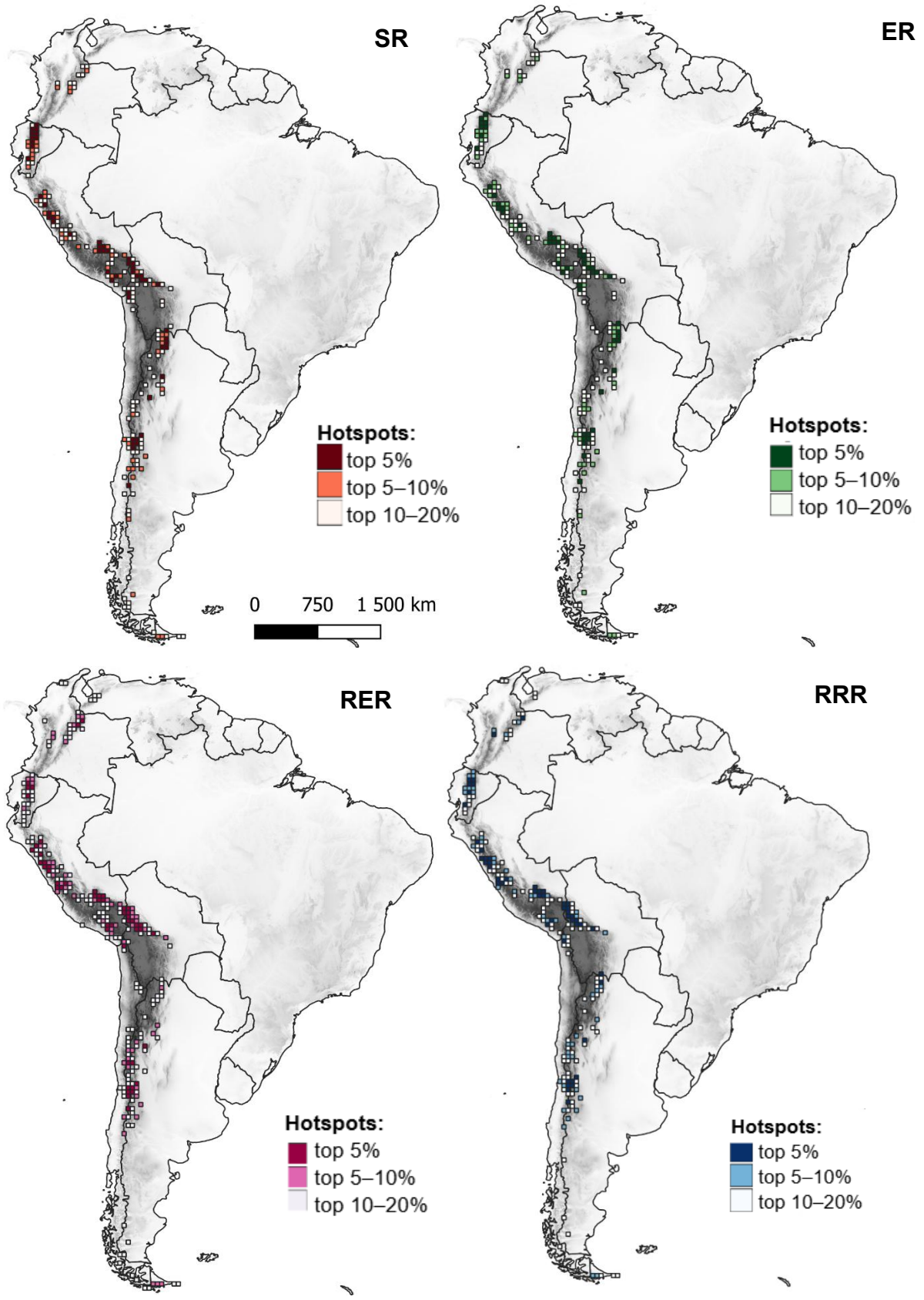

Figure 9: Hotspot areas representing the top 5%, 5–10%, and 10–20% richest cells for each biodiversity index (SR, ER, RER, RRR).

3.1.2. Correlation Between the 4 Indices

All four indices were strongly positively correlated with each other, the correlation coefficients ranging from 0.84 to 0.99. This means that cells that have a high number of species also have a high number of endemics and show high values in the other indices as well.

In particular, SR and ER are almost perfectly correlated, with a coefficient of about 0.996. RRR also shows a high degree of agreement with the other indices (correlation values above 0.84). This can be seen in Table 2. Overall, this indicates that the different measures of species and endemic richness are closely related.

Table 2: Correlation between the richness indices

	ER	RER	RRR
SR	0.9964	0.8427	0.9418
ER		0.8580	0.9514
RER			0.9670

3.2. Hotspots

3.2.1. Hotspot Distribution Across the Andes

A total of 70 cells were identified as top 5% hotspots, 101 cells as top 5–10% hotspots, and 149 cells as top 10–20% hotspots. These hotspots can be seen in Figure 10.

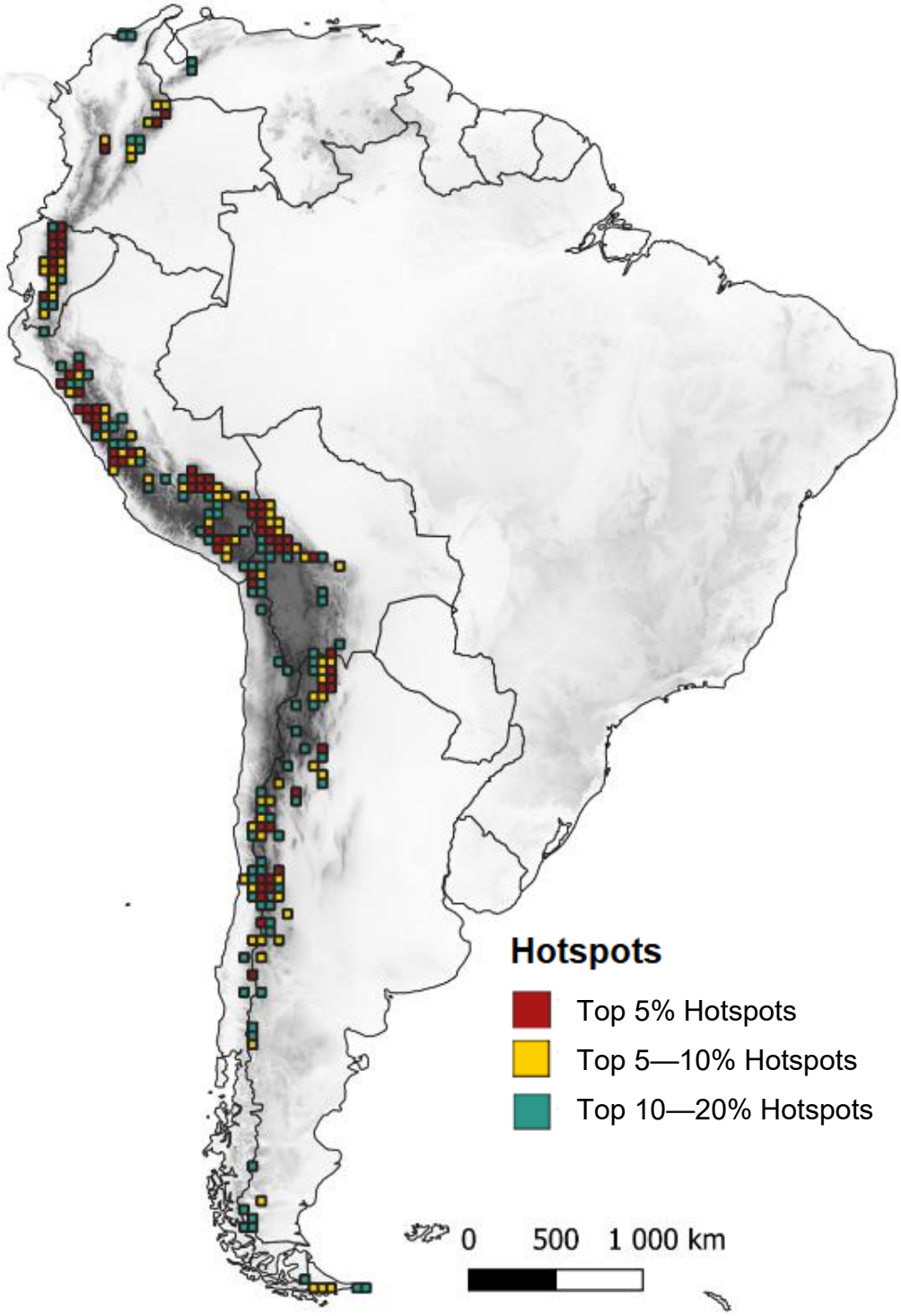

Figure 10: Spatial distribution of biodiversity hotspots.

It can be observed that the second and third hotspot classes mainly cluster around the top 5% hotspots. A large hotspot is in Ecuador, corresponding to the Páramos of the northern tropical Andes. In Peru, clusters of hotspots are found in both the northern and southern parts, with the latter connecting to the northern region of Bolivia. Additional hotspots occur in northern Argentina and along the border between Argentina and Chile.

3.2.2. Overlap Among Richness Indices Within Hotspot Classes

Among the top 5% richest cells, 50% contained all four indices, indicating a strong overlap among richness measures. In the 5–10% hotspot class, this overlap decreased, with only 8.9% of cells containing all indices. However, in the 10–20% hotspot class, the proportion of cells containing all four indices increased again to 36.2% (Table 3).

Table 3: Number of indices present within a cell for the top 5%, top 5—10% and top 10—20% hotspots respectively

Hotspots	Total cells	4 indices	3 indices	2 indices	1 index
Top 5%	70	35	6	18	11
Top 5–10%	101	9	20	40	32
Top 10–20%	149	54	15	67	13

Figure 11 shows, how many indices are present per grid cell for each hotspot class. Black indicates that all four indices are present, violet means three indices are present, pink means two are present and yellow indicates that only one index is present in this cell.

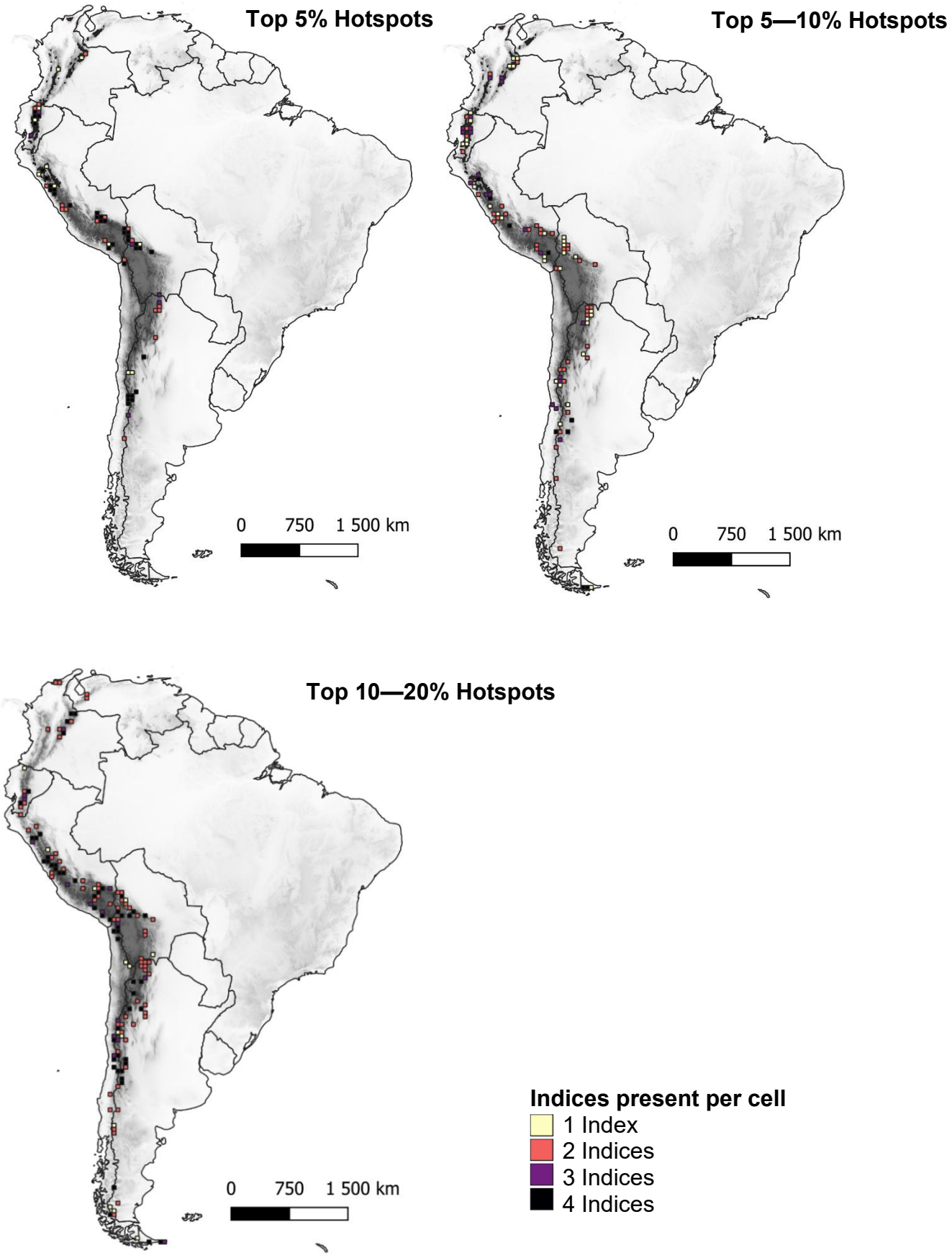

Figure 11: Distribution of the number of biodiversity indices per cell within the top 5%, 5–10%, and 10–20% hotspots.

3.2.3. Hotspots Distribution Across Ecoregions

In total there are 67 ecoregions present in the study area as defined by the Resolve Dataset (2017). The hotspots are predominantly located in the alpine regions of the Puna and Páramos ecoregions. To maintain readability, only ecoregions that overlap with ≥5% of the hotspot area are highlighted, as smaller overlaps are numerous and ecologically uninformative.

More specifically: For the 5% hotspots the cells are distributed across 23 ecoregions, 17.4% of the top 5% hotspots are located in the Central Andean Wet Puna ecoregion, 10.8% in the Peruvian Yungas, 9.4% in the Sechura Desert, 9.0% in the Central Andean Puna, 8.0% in the Southern Andean Steppe, 6.5% in the Northern Andean Páramos, and 6.1% in the Bolivian Yungas and 5.6% in the Northwest Andean montane forests . These distributions are shown in Figure 12.

The 5—10% richest cells are distributed across 25 ecoregions. Their spatial distribution shifts slightly, with 12.7% of hotspots in the Central Andean Puna, 10.2% in the Central Andean Wet Puna, 9.8% in the Peruvian Yungas, 7.1% in the Southern Andean Steppe, 6.5% in the Sechura Desert, 6.3% in the Northern Andean Páramo, 6.2% in the Bolivian Yungas, and 5.3% in the Eastern Cordillera Real Montane Forests. Fourteen additional ecoregions each contribute less than 5% to this category.

The 10—20% richest cells are distributed over 34 ecoregions, with the highest proportions found in the Central Andean Puna (12.4%), Southern Andean Steppe (10.9%), Peruvian Yungas (9.6%), Central Andean Wet Puna (8.9%), Central Andean Dry Puna (7.0%), and Bolivian Yungas (5.8%).

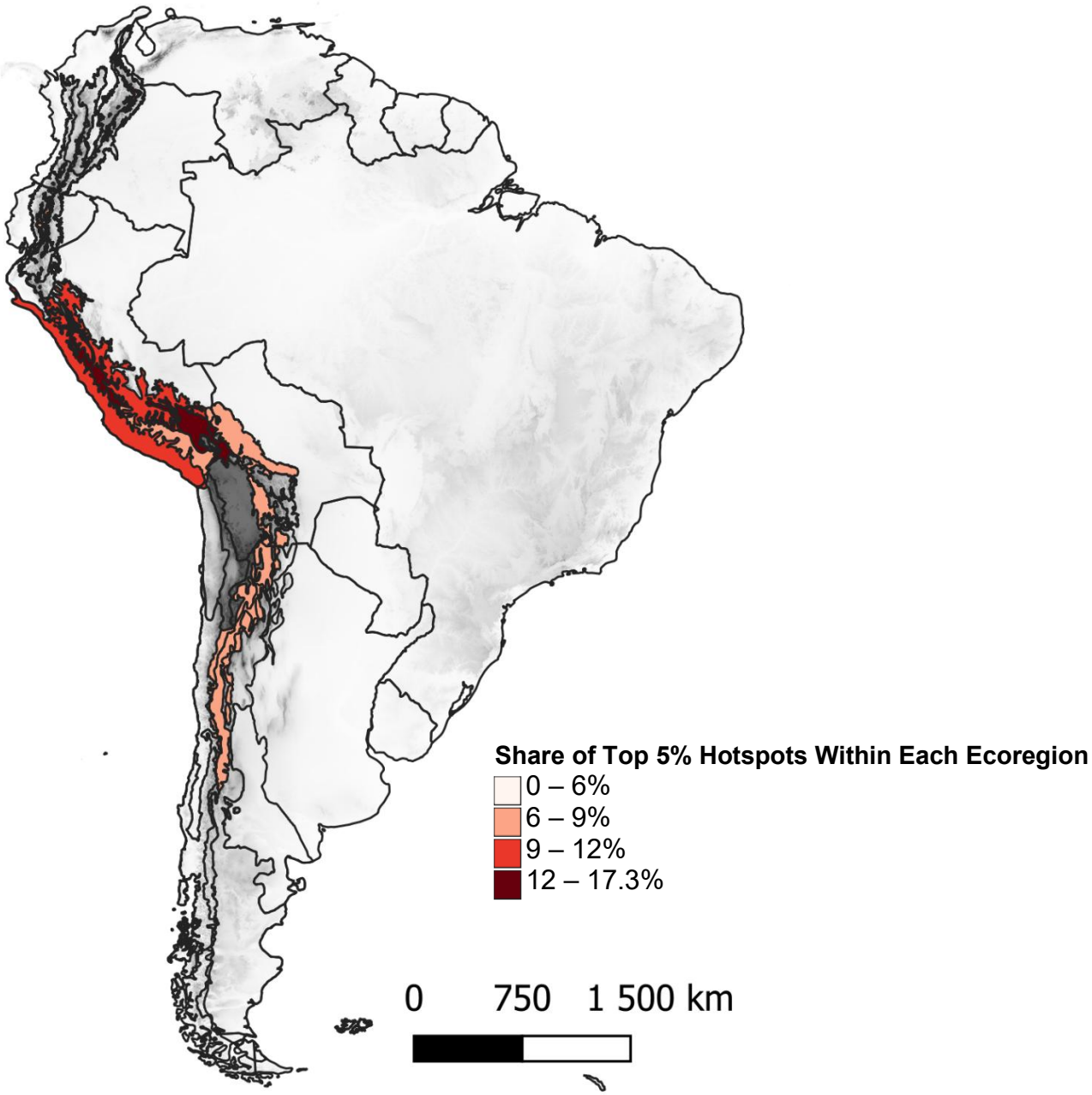

Figure 12: This map illustrates the percentage of overlap between the area of the top 5% hotspots and the ecoregions.

3.3. Ecological Factors

The following sections shows the results of the two ecological factors that were analysed which are the topographic heterogeneity and the elevational amplitude per cell. Both factors were correlated with all four richness indices.

3.3.1. Topographic Heterogeneity

The topographic heterogeneity shows positive correlations with all four biodiversity indices, being strongest for ER (r = 0.196), followed by SR, RRR, and RER (Table 4).

3.3.2. Elevational Amplitude

The correlation between the elevational difference and the richness indices is positive. This indicates that the greater the difference between the lowest and highest point within a cell, the higher the species richness. The correlation coefficients range from 0.339 to 0.386. RRR showing the highest (0.386), followed by ER and SR. RER has the lowest correlation with the elevational difference (Table 4). The elevational difference per cell can be seen in Figure 13.

Table 4: Correlation between the four indices and the topographic heterogeneity

Index	Topogrpahic Heterogeneity	Elevational Amplitude
ER	0.196	0.367
SR	0.192	0.361
RRR	0.168	0.386
RER	0.129	0.339

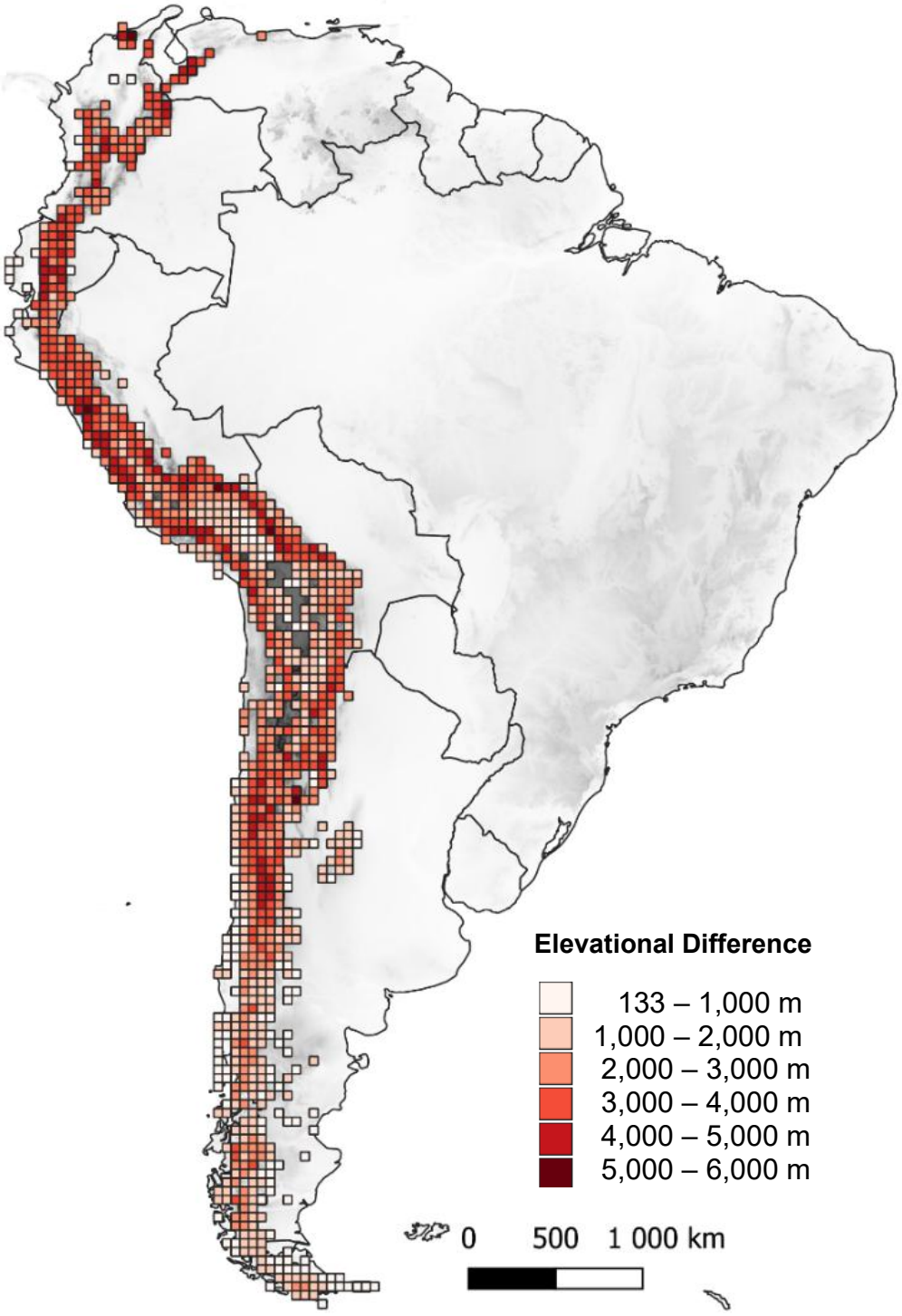

Figure 13: Elevational difference within a cell

3.4. Conservation Status

3.4.1. Protected Areas Category

A total of 272 protected areas within the study region are assigned to IUCN protection categories I–IV. Most protected areas in the Andes are classified as Category II (177), with relatively few strict reserves (6 classified as Ia and 22 as Ib). The remaining protected areas are distributed among Category III (40 protected areas) and IV (27 protected areas).

3.4.2. Protected Areas by Country

The number and distribution of protected areas vary significantly across countries in the Andes (Table 5). Colombia contains 90 out of the 272 protected areas, followed by Argentina with 65, Venezuela with 53, Ecuador with 37 and Peru with 26. Only one protected area was present in Bolivia.

Table 5: Number of protected areas by country

Country	Number of Protected Areas
Colombia	90
Argentina	65
Venezuela	53
Ecuador	37
Peru	26
Bolivia	1
Total	272

3.4.3. Conservation Status of Hotspots

For the top 5% hotspots, 19 cells (27.1%) were protected with more than 10% overlap with IUCN protected areas, while 51 cells (72.9%) were identified as CGs. For the top 5–10% hotspots, 23 cells (22.8%) were protected, and 78 cells (77.2%) were CGs. For the top 10–20% hotspots 29 cells (19.5%) were sufficiently protected, while 120 cells (80.5%) were CGs. Figure 14 provides a spatial overview of protection status of the top 20% richest cells and showing whether they are sufficiently protected or not (CGs). Yellow cells indicate sufficient protection, while red cells represent CGs.

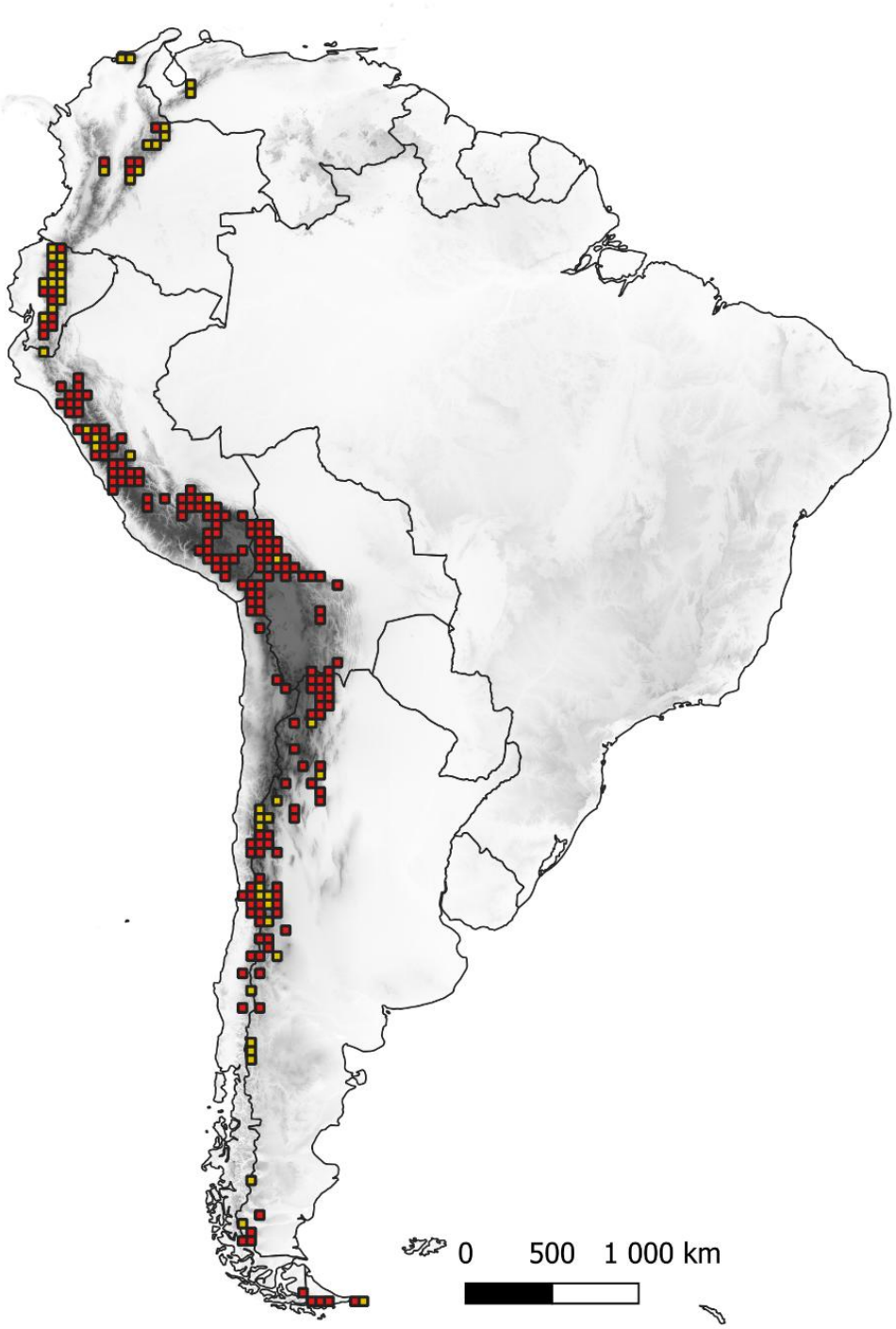

Figure 14: Conservation status of the 20% richest cells.

When increasing the protection threshold to ≥30%, only 8 cells (11.4%) of the top 5% hotspots, 13 cells (12.9%) of the top 5–10% hotspots, and 16 cells (10.7%) of the top 10–20% hotspots reach this stricter level of protection.

Figure 15 gives an overview of the three hotspots classes and their conservation status. A black dot in the cell indicates, that the cell is protected with a 10% threshold.

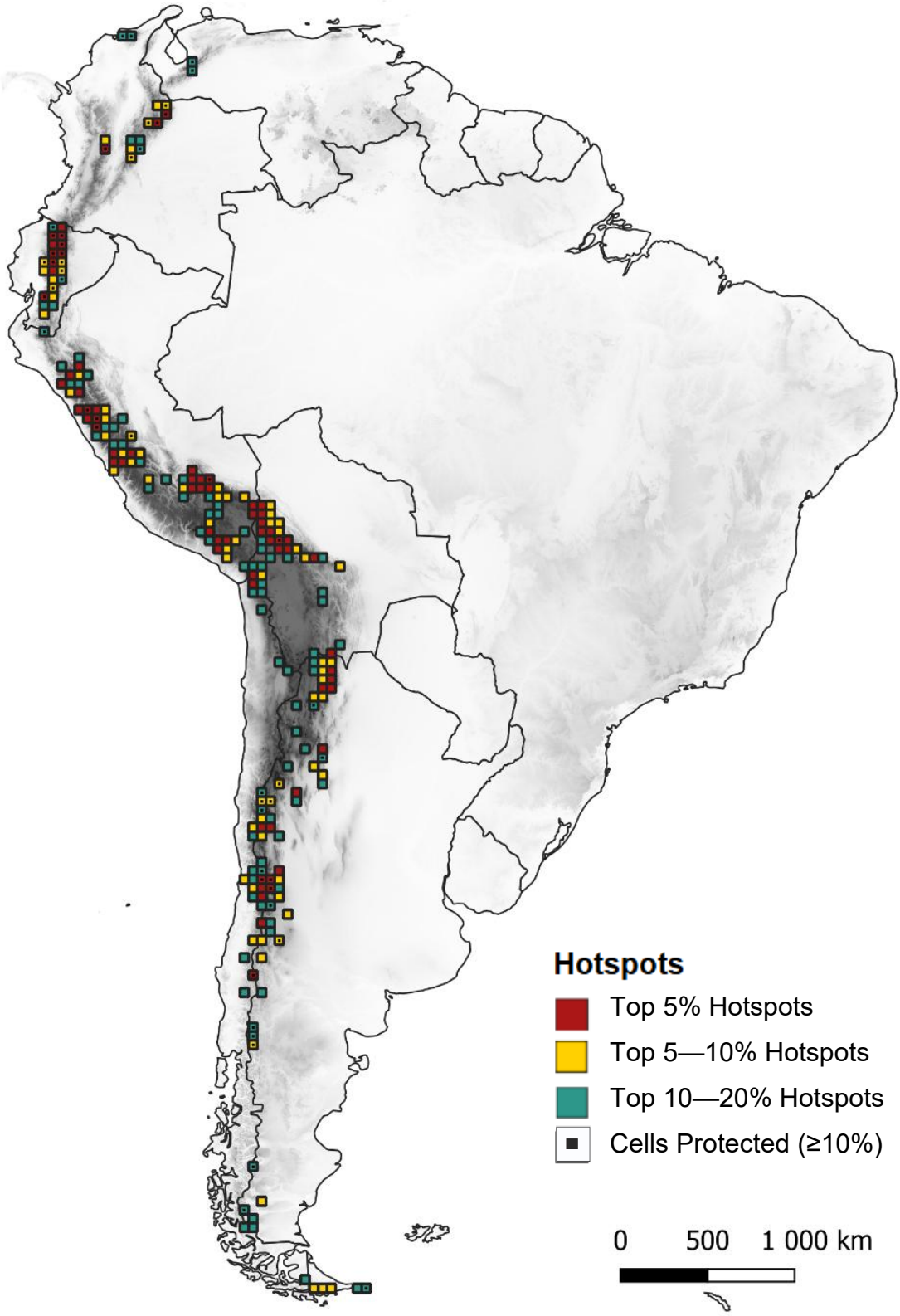

Figure 15: Top 5%, top 5—10% and top 10—20% Hotspots and their Conservation status. A black dot within the cell means the hotspot is protected.

4. Discussion

4.1. Overview of the Key Findings

The analysis highlights the exceptional level of endemism within the Andean region. Of all recorded species, 94% are endemic, and 43% of all endemics were also range-restricted. These high levels of localized endemism, combined with pronounced biodiversity hotspots, underline the global conservation importance of this mountain system. The four richness indices showed very similar patterns. By combining them into one composite hotspot map, a total of 70 cells were identified as top 5% hotspots, 101 cells as top 5–10% hotspots, and 149 cells as top 10–20% hotspots. However, protection was low, with 27% of the top 5% hotspots, 23% of mid-ranked, and 20% of lower-ranked hotspots categorized as protected. Hotspots mainly occurred in the Puna, Páramo, Southern Andean steppe, and Yungas ecoregions. The indices were positively correlated with elevational range and topographic heterogeneity. The 272 protected areas were very unevenly distributed over the seven Andean countries. While Colombia had 90 protected areas, Bolivia only had one.

4.2. Ecological Interpretation of Patterns (Hypotheses 1)

The spatial distribution of hotspots can be partly explained by ecological factors, namely elevational range and topographic heterogeneity per grid cell, both of which show positive correlations with all four richness indices. However, the correlations are relatively weak, suggesting that additional factors may influence biodiversity patterns. Potential drivers of mountain biodiversity include climatic variables such as temperature, precipitation, and seasonality, as well as erosion rates and soil heterogeneity (Rolando et al., 2017). The Andes have been profoundly shaped by geological and climatic forces, such as orogeny, volcanism, sea-level fluctuations, and especially Pleistocene glaciations like the Last Glacial Maximum, which helped form today's patterns of species richness and endemism (Antonelli et al., 2018).

4.3. Distribution of Hotspots Across Ecoregions (Hypothesis 2)

Most biodiversity hotspots are in the main alpine regions, which are the Puna, Páramo and Southern Andean Steppe and ecoregions, confirming Hypothesis 2. Specifically, the top 5% hotspots are concentrated in the Central Andean Wet Puna (17.3%), Peruvian Yungas (10.8%), Sechura Desert (9.4%), Central Andean Puna (9.0%), Southern

Andean Steppe (8.0%), Northern Andean Páramos (6.5%), and Bolivian Yungas and Northwest Andean montane forests (5.6%). Given that several ecoregions are very narrow, some of the occurrences outside alpine zones may be due to inaccurate GBIF data coordinates. Data limitations are discussed in section 3.6.

4.4. Protection Coverage of Hotspots and IUCN Categories (Hypotheses 3 & 4)

The IUCN protected area categories provide a framework for conservation, ranging from strict protection (Ia–Ib, Wilderness and Strict Nature Reserves) to categories allowing human use (V–VI, Protected Landscapes/Seascapes and Areas with Sustainable Use). Categories I–IV are generally considered more effective in conserving highly sensitive biodiversity elements, such as range-restricted endemic species, while V and VI integrate human activity and are often less effective for strict biodiversity protection (Dudley, 2008; Shafer, 2015).

In total, 2,435 protected areas exist across the Andes, but only 272 belong to the stricter categories (I–IV). Only 27.1% of the 5% richest cells, 22.8% of the 5–10% richest cells, and 19.5% of the 10–20% richest cells fall within these strictly protected areas. These results confirm Hypotheses 3 and 4: stricter hotspot thresholds are slightly better protected than less restrictive ones, but a substantial proportion of biodiversity hotspots remains insufficiently protected. While Theobald et al. (2024) report that 15.8% of the Andes are under protection (I–VI), hotspot-focused analyses reveal coverage of 19.5–27% in stricter categories (I–IV), highlighting critical CGs.

4.5. Threats in Alpine Ecosystems

4.5.1. Human Disturbances

Although Páramo vegetation is strongly shaped by elevation, Vásquez et al. (2015) found that human impacts have an even stronger influence on species composition. Disturbances, such as agriculture, settlement, livestock grazing, and fire, are largely driven by accessibility and significantly affect plant diversity.

Beyond their biodiversity value, Páramo ecosystems are crucial for water supply. Large populations in Venezuela, Colombia, and Ecuador depend on them for drinking water; in Colombia alone, they provide around 70% of the country's freshwater (Murad et al., 2024). Their regulation of the hydrological cycle is the most critical ecosystem service,

yet often conflicts with agriculture and livestock farming, intensifying human pressures (Vásquez et al., 2015). Since 1984, two Colombian Páramos have lost about 48% and 60% of their native vegetation to pastures, crops, and plantations, reducing their capacity as water sources and carbon sinks and posing regional to global risks (Murad et al., 2024).

Habitat fragmentation and land-use change further weaken ecosystem resilience to anthropogenic pressures and environmental shifts (Young, 2009). In the Jalca grasslands, agriculture expanded rapidly, causing high natural habitat loss (1.5% per year) and fragmentation, while mining and exotic plantations increased patch isolation and threatened biodiversity and water supply functions (Tovar et al., 2013). Land-use change also strongly shapes how Andean plant species respond to warming: under common climate scenarios, all species are predicted to suffer major population declines regardless of migration ability (Feeley & Silman, 2010). Thus, land-use change amplifies extinction risk by reducing habitat and limiting species' ability to track suitable climates. Tourism also threatens sensitive alpine vegetation, as even brief off-trail trampling damages plants, compacts soils, and alters species composition, with long-lasting effects due to slow recovery (Barros et al., 2015).

4.5.2. Climate Change

The Andes are highly sensitive to climate change, which affects them through rising temperatures, altered precipitation patterns and shrinking snow cover that is critical for water availability (Al-Yaari et al., 2024). As a result, plant communities may shift in distribution, composition and abundance, especially in ecoregions where water is already a limiting factor (Al-Yaari et al., 2024). Climate change is therefore likely to reshape mountain biodiversity by altering species ranges and biome composition (Tovar et al., 2022). According to the Climatic Variability Hypothesis, species near the equator tend to have narrow thermal niches, which makes equatorial Andean species and the communities they form especially vulnerable to warming, as they risk losing suitable thermal habitat (Cuesta et al., 2020). Future climate change between 2040 and 2070 is projected to be strongest at high elevations in the tropical Andes, with temperature increases of up to 4 °C under RCP 8.5, while the temperate Andes are expected to warm by up to 2 °C (Tovar et al., 2022).

4.6. Conservation Planning Implications

To conserve Andean alpine ecosystems, biodiversity hotspot data must be translated into actionable strategies. Many species-rich and endemic areas, especially in the sensitive Páramo and Puna, remain underprotected and continue to face the threats outlined in the previous section. Improving the protected area network could involve upgrading existing areas to stricter categories and expanding the network, prioritizing the strictest hotspots. Addressing national disparities and strengthening cross-border cooperation will also be essential. These strategies are discussed in the following chapters.

4.6.1. Upgrading Categories of Existing Protected Areas

Many protected areas across South America (2,435 in total) are currently classified as IUCN categories V (58), VI (1,673), or have unreported or unassigned status (468). While these areas already provide some level of protection, they offer considerable potential for upgrading to stricter IUCN categories I–IV to better conserve range-restricted and highly sensitive species. This is particularly relevant in the northern Andes, where limiting human impacts is crucial, as noted in section 3.5.1. Since activities such as agricultural practices are partially allowed under IUCN categories V and VI, upgrading these areas to stricter protection could be highly beneficial.

4.6.2. Transnational Cooperation and Connectivity

Given that 57% of ecoregions in the Tropical Andes are shared by two or more countries, effective biodiversity conservation requires strong cross-border coordination (Castillo et al., 2020). Globally, about 15% of the terrestrial surface is protected under IUCN categories I–VI, yet only 7.5% to 9.3% of this area forms well-connected networks. Another study showed that less than half of strictly protected areas (I–IV) are effectively connected (Castillo et al., 2020).

This study showed that the distribution of protected areas across Andean countries is highly uneven. Addressing these national disparities is therefore essential to ensure an effective conservation planning across the Andes and to also prevent critical gaps in underrepresented regions.

4.7. Limitations

4.7.1. Sampling Bias and Working with GBIF Data

Several limitations of this analysis should be acknowledged. Some species were recorded only rarely, which may bias biodiversity patterns. These rare occurrences may reflect true scarcity but can also result from sampling bias, as many regions of the Andes remain underexplored. High-elevation environments are among the least surveyed globally, with sampling coverage below 1% for most taxa above the treeline. Accessibility bias is strong: over 80% of all terrestrial records occur within 2.5 km of a road, indicating that citizen science efforts are heavily shaped by accessibility (Hughes et al., 2021). As a result, remote or high-altitude Andean regions are likely underrepresented, potentially leading to underestimated species richness and endemism.

Although taxonomic harmonization followed the GBIF backbone, residual inconsistencies cannot be fully excluded. Misidentifications or unresolved synonyms in GBIF data may occasionally affect species counts within grid cells.

4.7.2. Spatial and Temporal Resolution

Furthermore, the spatial resolution used in this analysis (50 × 50 km grid cells) provides a suitable compromise between computational feasibility and regional coverage but could overlook fine-scale biodiversity patterns. Consequently, local micro-hotspots might not be fully captured (Rahbek, 2005).

Also, there could be a temporal bias because occurrence data span multiple decades. Species distributions may have shifted over time due to land-use changes and climate warming, meaning that some records no longer reflect current distributions.

4.7.3. Accuracy of Protected Area Data

Castillo et al. (2020), further mention some limitation regarding the accuracy of the World Database of Protected Areas due to reported areas by the government not meeting the criteria of the IUCN.

4.8. Future Research and Recommendations

To address the gaps and biases associated with GBIF data, future research should include additional field surveys, especially in poorly sampled regions, to obtain more representative occurrence data. Combining fieldwork with targeted sampling would

help capture rare and range-restricted species more effectively. Expanding data coverage in this way would reduce uncertainty and improve the accuracy of biodiversity assessments, strengthening conservation planning and prioritization across the Andes.

5. Conclusions

In summary, the Andes host exceptionally high alpine plant endemism, especially in the Páramo and Puna ecoregions, yet protection across these biodiversity hotspots remains insufficient and uneven. Despite coverage of 19.5% to 27%, substantial CGs persist, and alpine vegetation continues to face severe pressures from land use, tourism, resource extraction and climate change. This study enhances the understanding of alpine biodiversity patterns and provides spatially explicit guidance for prioritizing areas of high conservation importance. Addressing the remaining gaps—particularly in Bolivia—through improved connectivity, transnational cooperation and systematic conservation planning will be essential to safeguard alpine plant diversity and support progress toward the global 30×30 conservation targets.

6. References

Al-Yaari, A., Condom, T., Anthelme, F., Cauvy-Fraunié, S., Dangles, O., Junquas, C., Moret, P. and Rabatel, A. (2024) 'Warming-induced cryosphere changes predict drier Andean eco-regions', *Environmental Research Letters*, 19, 104030. Available at: https://doi.org/10.1088/1748-9326/ad6ea6.

Ansaloni, R., Izco, J., Amigo, J. and Minga, D. (2022) 'Analysis of the páramo vascular flora in the Cajas National Park (Central Andes, Ecuador)', *Mediterranean Botany*, 43, e76491. Available at: https://doi.org/10.5209/mbot.76491.

Antonelli, A. et al. (2018) 'Geological and climatic influences on mountain biodiversity', *Nature Geoscience*, 11(10), pp. 718–725. Available at: https://doi.org/10.1038/s41561-018-0236-z.

Barros, A. and Pickering, C.M. (2014) 'Non-native plant invasion in relation to tourism use of Aconcagua Park, Argentina, the highest protected area in the Southern Hemisphere', *Mountain Research and Development*, 34(1), pp. 13–26. Available at: https://doi.org/10.1659/MRD-JOURNAL-D-13-00054.1.

Barros, A., Monz, C. and Pickering, C. (2015) 'Is tourism damaging ecosystems in the Andes? Current knowledge and an agenda for future research', *AMBIO*, 44(2), pp. 82–98. Available at: https://doi.org/10.1007/s13280-014-0550-7.

Brück, S.A., Torres, B.D.M. and de Moraes Polizeli, M.L.T. (2023) 'The páramo in danger: Characteristics, ecosystem services and threats of Ecuadorian páramos', *Global Ecology and Conservation*, 47, e02639. Available at: https://doi.org/10.1016/j.gecco.2023.e02639.

Budic, L., Didenko, G. and Dormann, C.F. (2015) 'Squares of different sizes: Effect of geographical projection on model parameter estimates in species distribution modeling', *Ecology and Evolution*, 6(1), pp. 202–211. Available at: https://doi.org/10.1002/ece3.1838.

Castillo, L.S., Correa Ayram, C.A., Corzo, G., Areiza, A., González-M., R., Matallana Tobón, C.L., Serrano, F., Chalán Briceño, L., Sánchez Puertas, F., More, A., Franco, O., Bloomfield, H., Aguilera Orrury, V.L., Rivadeneira Canedo, C., Morón-Zambrano, V., Yerena, E., Papadakis, J., Cárdenas, J.J., Golden Kroner, R.E. and Godínez-Gómez, O. (2020) 'Connectivity of protected areas: Effect of human pressure and subnational contributions in the ecoregions of tropical Andean countries', *Land*, 9, 239. Available at: https://doi.org/10.3390/land9080239.

Cresso, M., Clerici, N., Sanchez, A. and Jaramillo, F. (2020) 'Future climate change renders unsuitable conditions for páramo ecosystems in Colombia', *Sustainability*, 12(20), 8373. doi: 10.3390/su12208373.

Crisp, M.D., Laffan, S., Linder, H.P. and Monro, A. (2001) 'Endemism in the Australian flora', *Journal of Biogeography*, 28(2), pp. 183–198. Available at: https://doi.org/10.1046/j.1365-2699.2001.00524.x.

Cuesta, F., Muriel, P., Llambí, L.D., Halloy, S., Aguirre, N., Beck, S., Carilla, J., Meneses, R.I., Cuello, S., Grau, A., Gámez, L.E., Irazábal, J., Jácome, J., Jaramillo, R., Ramírez, L., Samaniego, N., Suárez-Duque, D., Thompson, N., Tupayachi, A., Viñas, P., Yager, K., Becerra, M.T., Pauli, H. and Gosling, W.D. (2017) 'Latitudinal and altitudinal patterns of plant community diversity on mountain summits across the tropical Andes', *Ecography*, 40(12), pp. 1381–1394. Available at: https://doi.org/10.1111/ecog.02567.

Cuesta, F., Tovar, C., Llambí, L.D., Gosling, W.D., Halloy, S., Carilla, J., Muriel, P., Meneses, R.I., Beck, S., Ulloa Ulloa, C., Yager, K., Aguirre, N., Viñas, P., Jácome, J., Suárez-Duque, D., Buytaert, W. and Pauli, H. (2020) 'Thermal niche traits of high alpine plant species and communities across the tropical Andes and their vulnerability to global warming.' *Journal of Biogeography*, 47(2), pp.408–420. Available at: https://doi.org/10.1111/jbi.13759.

Duchicela, S.A., Llambí, L.D., Bonnesoeur, V. and Román-Dañobeytia, F. (2024) 'Pastoralism in the high tropical Andes: A review of the effect of grazing intensity on

plant diversity and ecosystem services', *Applied Vegetation Science*, 27, e12791. Available at: https://doi.org/10.1111/avsc.12791.

Dudley, N. (ed.) (2008) *Guidelines for Applying Protected Area Management Categories.* Gland, Switzerland: IUCN.

Alba Mejía, J. E. (n.d.) *Grasslands of South America.* [PDF] Available at: (Accessed: May 2025).

Fajardo, A. and Piper, F.I. (2017) 'An assessment of carbon and nutrient limitations in the formation of the southern Andes tree line', *Journal of Ecology*, 105, pp. 517–527. Available at: https://doi.org/10.1111/1365-2745.12697.

Feeley, K.J. and Silman, M.R. (2010) 'Land-use and climate change effects on population size and extinction risk of Andean plants', *Global Change Biology*, 16(12), pp. 3215–3222. Available at: https://doi.org/10.1111/j.1365-2486.2010.02197.x.

Figueroa, H. et al. (2021) 'Alpine, but not montane, seed plants constitute a biogeographically and climatically distinct species pool across the Americas', *Preprints*. Available at: https://doi.org/10.22541/au.161969728.82703460/v1.

GBIF.org (2025) *GBIF Occurrence Download*. Available at: https://doi.org/10.15468/dl.nf44qm (Accessed: April 2025).

Geofabrik GmbH (n.d.) *South America shapefiles (OpenStreetMap data)*. Available at: https://download.geofabrik.de/south-america.html (Accessed: March 2025).

He, W., Zhang, B., Zhao, F., Zhang, S., Qi, W. *et al.* (2016) 'Mass elevation effect of the Central Andes and its implications for the Southern Hemisphere's highest treeline', *Mountain Research and Development*, 36(2), pp. 213–221. Available at: https://doi.org/10.1659/MRD-JOURNAL-D-15-00027.

Herzog, S.K., Martínez, R., Jørgensen, P.M. and Tiessen, H. (eds) (2011) *Climate change and biodiversity in the tropical Andes.* São José dos Campos: Inter-American

Institute for Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE), 348 pp. ISBN 978-85-99875-05-6.

Hobohm, C. (2014) *Endemism in vascular plants*. Dordrecht: Springer.

Hoorn, C., Perrigo, A. L. and Antonelli, A. (eds) (2018) *Mountains, Climate and Biodiversity.* Hoboken, NJ: Wiley. ISBN 978-1-119-15987-2.

Hughes, A. C., Orr, M. C., Ma, K., Costello, M. J., Waller, J., Provoost, P., Yang, Q., Zhu, C., and Qiao, H. (2021). *Sampling biases shape our view of the natural world.* Ecography, 44(9), 1259–1269. Available at: https://doi.org/10.1111/ecog.05926.

Luebert, F. and Weigend, M. (2014) 'Phylogenetic insights into Andean plant diversification', *Frontiers in Ecology and Evolution*, 2, pp. 1–12. Available at: https://doi.org/10.3389/fevo.2014.00027.

Muellner-Riehl, A.N. (2019) 'Mountains as evolutionary arenas: Patterns, emerging approaches, paradigm shifts, and their implications for plant phylogeographic research in the Tibeto-Himalayan region', *Frontiers in Plant Science*, 10, Article 195. Available at: https://doi.org/10.3389/fpls.2019.00195

Myers, N. (1988) 'Threatened biotas: "Hot spots" in tropical forests', *The Environmentalist*, 8(3), pp. 187–208. Available at: https://doi.org/10.1007/BF02240252.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. and Kent, J. (2000) 'Biodiversity hotspots for conservation priorities', *Nature*, 403(6772), pp. 853–858. Available at: https://doi.org/10.1038/35002501.

Noroozi, J., Minaei, M., Khalvati, S., Kaveh, A., Nafisi, H., Nazari, B., Zare, G., Vitek, E., Hülber, K. and Schneeweiss, G.M. (2023) 'Hotspots of (sub)alpine plants in the Irano-Anatolian global biodiversity hotspot are insufficiently protected', *Diversity and Distributions*, 29, pp. 244–253. Available at: https://doi.org/10.1111/ddi.13656.

Peakbagger.com (n.d.) *Andes 6000-meter Peaks.* Available at: https://www.peakbagger.com/list.aspx?cid=38168&hu=1&lid=2201&pt=avg&sort=range&u=m&w=0 (Accessed: August 2025).

Pérez-Escobar, O.A., Zizka, A., Bermúdez, M.A., Meseguer, A.S., Condamine, F.L., Hoorn, C., Hooghiemstra, H., Pu, Y., Bogarín, D., Boschman, L.M., Pennington, R.T., Antonelli, A. and Chomicki, G. (2022) 'The Andes through time: Evolution and distribution of Andean floras', *Trends in Plant Science*, 27(4), pp. 364–378. Available at: https://doi.org/10.1016/j.tplants.2021.09.010.

Peyre, G., Balslev, H. and Font, X. (2018) 'Phytoregionalisation of the Andean páramo', *PeerJ*, 6, e4786. doi: 10.7717/peerj.4786.

Perrigo, A., Hoorn, C. and Antonelli, A. (2020) 'Why mountains matter for biodiversity', *Journal of Biogeography*, 47(2), pp. 315–325. Available at: https://doi.org/10.1111/jbi.13731.

QGIS.org (2025) *QGIS Geographic Information System.* QGIS Association. Available at: http://www.qgis.org.

Rahbek, C. (2005) 'The role of spatial scale and the perception of large-scale species-richness patterns', *Ecology Letters*, 8(2), pp. 224–239. Available at: https://doi.org/10.1111/j.1461-0248.2004.00701.x.

Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J. and Fjeldså, J. (2019) 'Humboldt's enigma: What causes global patterns of mountain biodiversity?', *Science*, 365(6458), pp. 1108–1113. Available at: https://doi.org/10.1126/science.aax0149.

Resolve (2017) *Terrestrial Ecoregions of the World v2017.* Available at: https://developers.google.com/earth-engine/datasets/catalog/RESOLVE_ECOREGIONS_2017 (Accessed: May 2025). Based on Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux,

J.F., Wettengel, W.W., Hedao, P. and Kassem, K.R. (2001) 'Terrestrial ecoregions of the world: A new map of life on Earth', *BioScience*, 51(11), pp. 933–938. Available at: https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2.

Rolando, J.L., Turina, C., Ramírez, D.A., Mares, V., Monerris, J. and Quiroz, R. (2017) 'Key ecosystem services and ecological intensification of agriculture in the tropical high-Andean puna as affected by land-use and climate changes', *Agriculture, Ecosystems & Environment*, 236, pp. 221–233. Available at: https://doi.org/10.1016/j.agee.2016.12.010.

Royal Botanic Gardens, Kew (2024) *Plants of the World Online.* Available at: https://powo.science.kew.org/ (Accessed: February–April 2025).

Särkinen, T., Pennington, R.T., Lavin, M., Simon, M.F. and Hughes, C.E. (2012) 'Evolutionary islands in the Andes: Persistence and isolation explain high endemism in Andean dry tropical forests', *Journal of Biogeography*, 39(5), pp. 884–900. Available at: https://doi.org/10.1111/j.1365-2699.2011.02644.x.

Scott, J.M., Davis, F.W., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'erchia, F., Edwards, T.C. Jr., Ulliman, J. and Wright, R.G. (1993) 'Gap analysis: A geographic approach to protection of biological diversity', *Wildlife Monographs*, 123, pp. 3–41.

Snethlage, M.A., Geschke, J., Spehn, E.M., Ranipeta, A., Yoccoz, N.G., Körner, C., Jetz, W., Fischer, M. and Urbach, D. (2022) *GMBA Mountain Inventory v2.* GMBA-EarthEnv. Available at: https://doi.org/10.48601/earthenv-t9k2-1407.

Shafer, C.L. (2015) 'Cautionary thoughts on IUCN protected area management categories V–VI', *Global Ecology and Conservation*, 3, pp. 331–348. Available at: https://doi.org/10.1016/j.gecco.2014.12.007.

Stanford University Library (2006) *Void-filled digital elevation model of South America at 15 arc-seconds resolution.* Available at: https://earthworks.stanford.edu/catalog/stanford-rm470dn6126 (Accessed: February 2025).

Steinbauer, M.J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H.J.B., Borges, P.A.V., Cardoso, P., Chou, C.-H., De Sanctis, M., de Sequeira, M.M., Duarte, M.C., Elias, R.B., Fernández-Palacios, J.M., Gabriel, R., Gereau, R.E., Gillespie, R.G., Greimler, J., Harter, D.E.V., Huang, T.-J., Irl, S.D.H., Jeanmonod, D., Jentsch, A., Jump, A.S., Kueffer, C., Nogué, S., Otto, R., Price, J., Romeiras, M.M., Strasberg, D., Stuessy, T., Svenning, J.-C., Vetaas, O.R. and Beierkuhnlein, C. (2016) 'Topography-driven isolation, speciation and a global increase of endemism with elevation', *Global Ecology and Biogeography*, 25(9), pp. 1097–1107. Available at: https://doi.org/10.1111/geb.12469.

Spehn, E.M., Rudmann-Maurer, K. and Körner, C. (2011) 'Mountain biodiversity', *Plant Ecology & Diversity*, 4(4), pp. 301–302. Available at: https://doi.org/10.1080/17550874.2012.698660.

Theobald, D.M., Kennedy, C.M., Oakleaf, J.R., Radeloff, V.C., Dubois, N.S. and Jantz, P. (2024) 'Evaluating ecosystem protection and fragmentation of the world's major mountain regions', *Conservation Biology*, 38(3), p. e14240. Available at: https://doi.org/10.1111/cobi.14240.

Tovar, C., Seijmonsbergen, A.C. and Duivenvoorden, J.F. (2013) 'Monitoring land use and land cover change in mountain regions: An example in the Jalca grasslands of the Peruvian Andes', *Landscape and Urban Planning*, 112, pp. 40–49. Available at: https://doi.org/10.1016/j.landurbplan.2012.12.003.

Tovar, C., Carril, A.F., Gutiérrez, A.G., Ahrends, A., Fita, L., Zaninelli, P., Flombaum, P., Abarzúa, A.M., Alarcón, D., Aschero, V., Báez, S., Barros, A., Carilla, J., Ferrero, M.E., Flantua, S.G.A., Gonzáles, P., Menéndez, C.G., Pérez-Escobar, O.A., Pauchard, A., Ruscica, R.C., Särkinen, T., Sörensson, A.A., Srur, A., Villalba, R. and Hollingsworth, P.M. (2022) 'Understanding climate change impacts on biome and plant distributions in the Andes: Challenges and opportunities', *Journal of Biogeography*, 49(7), pp. 1420–1442. Available at: https://doi.org/10.1111/jbi.14389.

UNEP-WCMC and IUCN (2025) *Protected Planet: The World Database on Protected Areas (WDPA) and World Database on Other Effective Area-based Conservation Measures (WD-OECM)* [Online], February 2025. Cambridge, UK: UNEP-WCMC and IUCN. Available at: https://www.protectedplanet.net.

Vásquez, D.L.A., Balslev, H. and Sklenář, P. (2015) 'Human impact on tropical-alpine plant diversity in the northern Andes', *Biodiversity and Conservation*, 24, pp. 2673–2683. Available at: https://doi.org/10.1007/s10531-015-0958-z.

Young, K.R. (2009) 'Andean land use and biodiversity: Humanized landscapes in a time of change', *Annals of the Missouri Botanical Garden*, 96(3), pp. 492–507. Available at: https://doi.org/10.3417/2008035.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V. and Antonelli, A. (2019) 'CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases', *Methods in Ecology and Evolution*, 10(5), pp. 744–751. Available at: https://doi.org/10.1111/2041-210X.13152.