LIVERWORTS IN A CHANGING WORLD: VULNERABILITY AND EXTINCTION RISK OF SPECIALIST SPECIES UNDER CLIMATE CHANGE IN A TROPICAL COUNTRY (COLOMBIA)

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The various effects of climate change pose major threats to biodiversity, increasing the risk of local and regional extinction of species. This study evaluates the effect of climate change on the risk of extinction and vulnerability of 18 species of epiphyllous (leaf-inhabiting) liverworts, a guild sensitive to environmental changes. The area of environmental suitability for typical Neotropical epiphyllous liverworts was evaluated under optimistic (SSP126) and pessimistic (SSP585) future climate scenarios (2080–2100) using bioclimatic variables and the MaxEnt algorithm, with a focus on Colombia. The vulnerability analysis was performed by integrating spatial and climate niche metrics, while the risk of extinction was based on the potential and projected distribution in future scenarios using the values of relative loss of extent of suitability area and area of occupancy (AOO), according to the IUCN Criterion A3(c). Climate change will have significant impacts on the community because the area of environmental suitability of most of the species evaluated (89%) will have declined in future scenarios. An extreme example is *Bromeliophila helenae*, which will lose 97.12% of its total area of suitability, and the proportion of suitable area protected within Protected Areas (PAs) will be reduced by ca. 80%. Although only five species are currently found within PAs, these PAs play an important role because the area of environmental suitability will increase in future scenarios, particularly in the Caribbean and Orinoco regions. The risk of extinction of almost all species (95%) evaluated will increase in future scenarios, especially in the Andes, a region with potential to act as a refuge for specialist liverwort species. The results of this study highlight the urgent need to develop conservation strategies that include the expansion of the number of PAs and greater efficiency in the management of the existing PAs.

Key words: bryophytes, climate model, environmental suitability, epiphytes, Neotropics

Introduction

Climate change caused by increased greenhouse gas emissions represents one of the main factors driving biodiversity extinction processes (Hutter et al., 2017; Bhuiyan et al., 2018). Scientific studies have repeatedly shown that global warming is exacerbating the vulnerability of species to extinction, modifying their geographic distribution ranges and, therefore, altering the composition and functioning of ecosystems (Pecl et al., 2017; Ruklani et al., 2021; Hao & Chu, 2022). Faced with the growing impacts of climate change, the UN 2030 Agenda for Sustainable Development (UN, 2019) stresses the need for urgent actions to conserve biodiversity and mitigate human and environmental pressures, including the protection and restoration of ecosystems, the sustainable use of natural resources and the integration of conservation into development policies (UN, 2019).

The vulnerability of species to climate change and risk of extinction vary according to habitat specialisation and tolerance to environmental variations (Gradstein et al., 2008; Pacifici et al., 2015; Foden et al., 2019; Glime, 2019). Thus, quantifying the ecological niche of species has gained importance in the context of climate change due to the possibility of predicting the species' distribution range under various future climate scenarios (Thuiller et al., 2005; Broennimann et al., 2006; Cianfrani et al., 2018) and identifying potential climate refuges, that is, places that will remain suitable for the species despite global warming (Dong et al., 2024). In addition, ecological niche analyses may reveal gaps in the network of Protected Areas (PAs), indicating key area sites that deserve greater protection to ensure the survival of the species (Li et al., 2022), particularly in megadiverse regions.

Colombia, recognised as one of the most biodiverse countries in the world, is home to

approximately 33 000 plant species (ColPlantA, 2024), including 1500 bryophyte species, of which 708 species (47.2%) are liverworts (Bernal et al., 2020; Gradstein, 2021). The combination of tropical forests, Andean mountain ranges, and varied microclimates provides ideal conditions for the development of these plants (Gradstein & Pócs, 1989; Frahm & Gradstein, 1991; Gradstein, 1995; Bernal et al., 2020). Although other Neotropical countries also exhibit diverse liverwort floras and even higher rates of endemism for this group, the overall richness of Colombia's flora and the ongoing threats to its ecosystems stemming from deforestation due to agricultural expansion, illegal mining, and drug trafficking, compounded by climate change make the country a focal point for conservation studies (Álvarez, 2003; Armenteras et al., 2003; Etter et al., 2008; González et al., 2011; Sánchez-Cuervo et al., 2012; Bonilla-Mejía & Higuera-Mendieta, 2019; Clerici et al., 2020). In response to conservation challenges, many countries, especially developing ones, have significantly expanded their PAs in recent decades, making them a pillar of environmental policies (Anderson & Ohlemüller, 2011; Watson et al., 2014; Bonilla-Mejía & Higuera-Mendieta, 2019). In the case of Colombia, although PAs and indigenous reserves have proved to be effective in reducing deforestation (Defries et al., 2005; Bonilla-Mejía & Higuera-Mendieta, 2019; Coad et al., 2019), the success of these efforts has been limited by the structural fragility of the management of these areas (Clerici et al., 2020).

Bryophytes exhibit limited capacity to adapt to rapid climate change due to their physiological constraints and habitat specialisation, a pattern well-documented in tropical ecosystems (Gignac, 2001; Bates et al., 2005; Tuba et al., 2011; Glime, 2019; Zanatta et al., 2020; Dai et al., 2023). While some epiphytic species, such as high-Andean bryophytes, may temporarily mitigate warming impacts through altitudinal migration (Jácome et al., 2011), this strategy is ineffective for highly specialised groups like epiphyllous liverworts. Focusing on epiphyllous liverworts specifically, these species can be subdivided into two ecological categories, namely typical epiphylls, which grow almost exclusively on living leaves, and facultative epiphylls, which colonise leaves but also occur on other substrates (Gradstein, 1997). Typical epiphylls exhibit prostrate growth with strong adhesion to leaf surfaces via rhizoidal discs, short life cycles, and frequent asexual reproduction traits that optimise survival on ephemeral substrates but limit adaptability to environmental shifts (Glime & Pócs, 2018; Gradstein, 2021). In contrast, facultative epiphylls display broader niche plasticity, reducing their extinction risk compared to strict specialists (Gradstein & Sporn, 2009). This dichotomy in adaptive strategies explains why typical epiphylls face disproportionate threats from synergistic environmental pressures.

The synergistic effects of forest conversion and climate change disproportionately threaten typical epiphylls. Their reliance on stable microclimates and short-lived leaves makes them acutely vulnerable to habitat fragmentation and altered precipitation regimes (Glime & Pócs, 2018). In Colombia, only 7% of liverwort species (approximately 50 taxa) are classified as typical epiphylls (Gradstein, 2021), a group prioritised in this study due to their high extinction risk and value as bioindicators of forest health (Jiang et al., 2014; Tang et al., 2018).

In this study, our main objective was to understand how climate change could affect the vulnerability and risk of extinction of epiphyllous liverwort species in Colombia at various scales: the country as a whole, the Colombian biogeographic regions and within PAs. We also calculated and used vulnerability indices at the species and community level, spatially mapping the susceptibility of these communities to climate change. Our hypothesis is that future climatic conditions will cause considerable contraction in areas in Colombia with suitable habitats for epiphyllous liverworts, increasing the risk of extinction in the country, and that PAs and sites at higher altitudes will constitute climate refuges.

Material and Methods

Study area

This study was developed considering the limits of Colombia (12.51278° N, -4.225° S, 66.84833° E, -79.0425° W). Colombia is divided into five biogeographic regions: Amazon, Andean, Caribbean, Orinoco and Pacific, each with distinct climatic and phytogeographic characteristics (Rangel-Ch, 1995). The Amazon region has an equatorial climate with minimum temperatures of 18.7°C and maximum of 28°C on average and annual rainfall of 1800 mm to 3750 mm, dominated by humid tropical forests.

The Andean region has a significant altitude gradient and shows climatic variations with mean annual daytime temperatures varying from 20°C to 25°C in low areas (1000–2500 m a.s.l.) and from 0°C to 18°C in high areas (> 3000 m a.s.l.) (Castro et al., 2016), including páramos and fog forests. The Caribbean region has a dry tropical climate and rainfall between 846 mm and 3000 mm and is characterised by dry tropical forests and mangroves. In the Orinoco region, the temperature ranges between 18°C and 28°C and the vegetation consists of savannas and gallery forests. The Pacific region, with a humid tropical climate and annual rainfall that can reach up to 12 000 mm, is dominated by humid tropical forests (Bernal et al., 2020; Gradstein, 2021; Lombo-Sanchez et al., 2024).

The Colombia's shapefile was extracted from the Colombian Environmental Information System (SIAC) (https://geonetwork.minambiente.gov.co/geonetwork) and the Agustín Codazzi Geographic Institute (IGAC) (https://geoportal.igac.gov.co/contained/open-data-cartography-y-geography) using the WGS 1984 datum (World Geodetic System, 1984), ensuring consistency and proper integration of the geospatial data used in our analysis.

Database – species occurrences

A database of species distribution was prepared according to the following criteria: 1) typical epiphylls, 2) Neotropical distribution and 3) presence of at least four points of occurrence, including Colombia (Heming et al., 2019; Cerrejón et al., 2022). Geographic coordinates were compiled for each species as obtained from the online platforms GBIF (https://www.gbif.org) and Tropicos (https://tropicos.org). The studies of Gradstein (1997, 2021) and Gradstein & Uribe (2016) were consulted to confirm the nomenclature and occurrence of the species on the surface of living leaves. Also, the records of each species were first of all manually cleaned to remove exact duplicates and any clearly erroneous points, yielding a high-quality subset of occurrences. These cleaned records were then filtered to retain the maximum number of occurrences at least 0.5 km apart using the «spThin» R package (Aiello-Lammens et al., 2015), thereby reducing spatial sampling bias and improving model performance (Boria et al., 2014) (Table S1). The database comprised a list of 18 species with geographic co-ordinates (yjlombo, 2024) (Fig. 1).

Database – environmental variables

A set of 19 bioclimatic variables was obtained from the WorldClim database version 2.1 with a spatial resolution of 0.30 seconds (Fick & Hijmans, 2017). A correlation matrix of the current climate data was calculated using Pearson's correlation coefficients, applying a 75% cutoff value to reduce collinearity issues. The variable selection was performed using the «select_vars» function of the ENMwizard R package (Heming et al., 2019). The results of the correlation were extrapolated to future scenarios. Each variable was evaluated based on its biological relevance, according to the species of interest (Table S2).

Ecological niche modelling

Ecological niche modelling was performed using occurrence data from across the Neotropics to model the native distribution of epiphyllous liverwort species, and then projections were made specifically for Colombia. Species suitability areas were estimated using the MaxEnt algorithm (version 3.4.1; Phillips et al., 2017), which applies the principle of maximum entropy with presence-only data and environmental variables. This algorithm was chosen because it generally outperforms others, even when occurrence data are limited (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008; Cerrejón et al., 2022). The «ENMwizard» package (Heming et al., 2019) was used to establish the calibration area for each species, creating a minimum convex polygon around all occurrences and surrounded by a 1.5° buffer, which reflects the areas potentially accessible to the species and increases environmental diversity, improving niche prediction (Anderson & Raza, 2010; Barve et al., 2011; Boria et al., 2014, 2016; Mota et al., 2022).

The cross-validation of the model was performed with the «ENMevaluate_b» function, and the «ENMeval» package was implemented to optimise the parameters of the MaxEnt (Muscarella et al., 2014), allowing to adjust different combinations of Feature Classes (FCs) and Regularisation Multipliers (RMs). Classes included L (linear), P (product), Q (quadratic), H (hinge), and combinations such as LP, LQH, among others, with multipliers ranging from 0.5 to 5.0. To evaluate the candidate models, we applied the «calib_mdl_b» function from the «ENMwizard» package, following an Ensemble

of Best-Performing Models (EBPM) approach (Heming et al., 2019). Model selection was based on multiple criteria, including statistical significance (partial ROC), lower omission rates (OR), and the lowest corrected Akaike Information Criterion (AICc) (Boria et al., 2016; Cobos et al., 2019; da Costa-Pinto et al., 2024; Sanchez et al., 2025). The evaluation was performed using a jackknife n-1 cross-validation approach, which is particularly suitable for datasets with limited occurrence records. This method iteratively excluded one occurrence point at a time for validation while using the remaining points for model calibration (Veloz, 2009; Hijmans, 2012; Sanchez et al., 2025). Finally, we generated the best-performing model for each species using the «proj_mdl_b» function, producing a suitability map in «Cloglog» format, where values range from 0 to 1, indicating relative climatic suitability. To enhance robustness, we integrated a consensus model by averaging the top 10% of selected models based on the same evaluation criteria (Boria et al., 2016; Cobos et al., 2019).

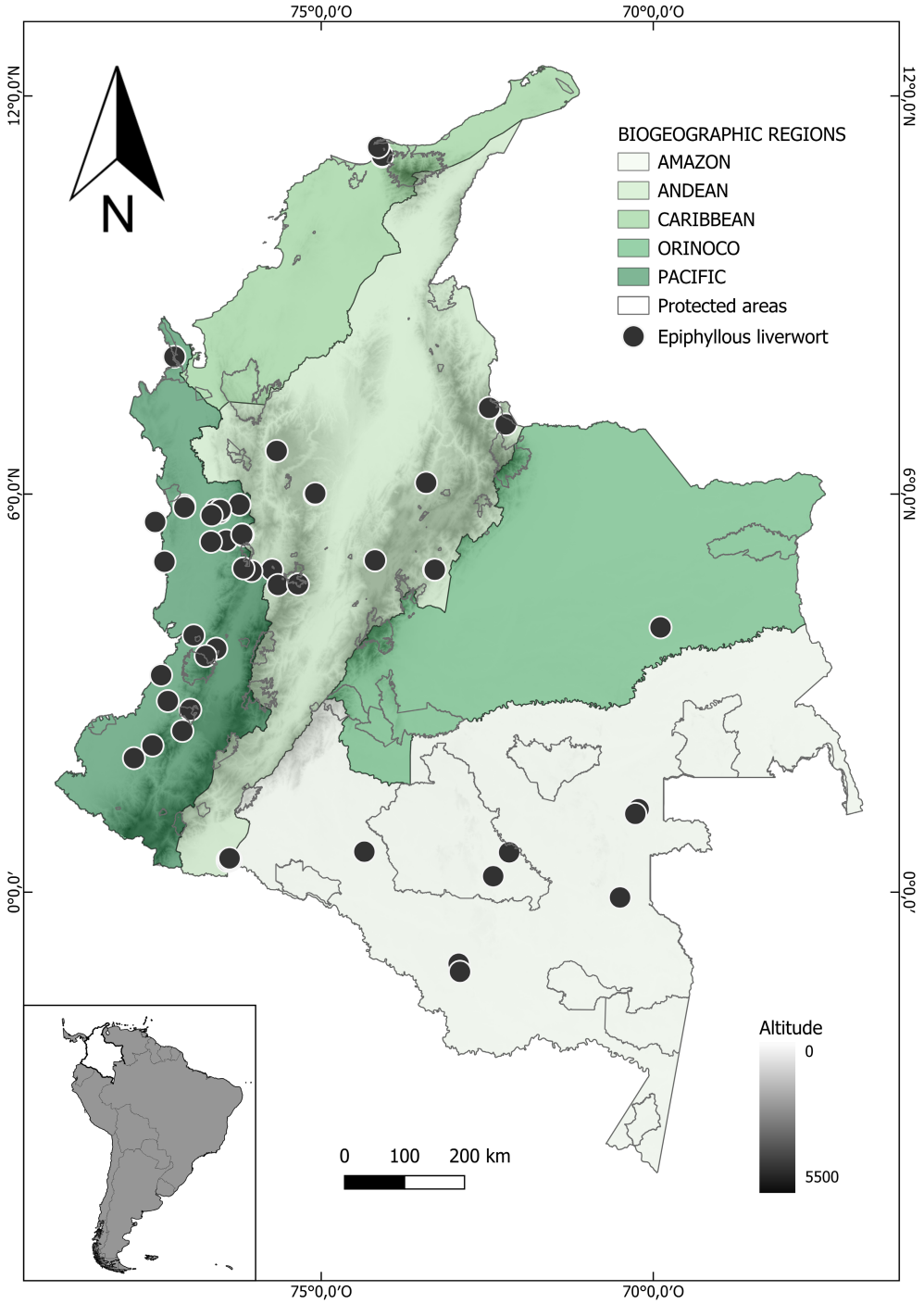

Fig. 1. Occurrence of epiphyllous liverwort species in Colombia and distribution of Environmental Protection Areas.

The current potential distribution consensus model was used to estimate the percentage change in distribution size relative to future climate scenarios. Four General Circulation Models (GCMs) were selected to generate the future projections from 2080–2100: BCC-CSM2-MR (Wu et al., 2021), CMCC-ESM2 (Cherchi et al., 2019), HadGEM3-GC31-LL (Williams et al., 2018) and IPSL-CM6A-LR (Boucher et al., 2020). These models were selected because they span the full range of equilibrium climate sensitivity (ECS 2.9–5.5°C; Zelinka et al., 2020) and have demonstrated skill in reproducing historical temperature and precipitation patterns in South America with low bias (Eyring et al., 2016; Zelinka et al., 2020; Hodnebrog et al., 2022; Scafetta, 2023) (Table S3). Climate projections were performed using two Shared Socioeconomic Pathways (SSPs): SSP126, as an optimistic scenario, and SSP585, as a pessimistic scenario for greenhouse gas emissions. The study area was delimited to Colombia, with an additional buffer of 1.5°. We used the consensus of the selected GCMs to generate the projections in the future scenarios, ensuring a robust representation of the possible climatic variations.

The contraction of the species distribution area or the loss of suitable areas between current and future climatic conditions was calculated using the «thrshld_b» function of the «ENMwizard» package. We used the 10th percentile training presence criterion (10.percentile.training.presence), which is a method commonly used in ecological niche modelling to define potentially suitable areas (Heming et al., 2019). This method is based on the 10th percentile of presences observed during model training, thus establishing a limit that excludes the 10% of the least suitable places of presence (Boria et al., 2016; Heming et al., 2019). An analysis of variance (ANOVA) and the Tukey post hoc test («stats» package) were applied to test the significant difference in the contraction of the species distribution area between climate scenarios (Kembel et al., 2010; Crawley, 2013). The «common_spatial_metric» function of the «ENMwizard» package was used to calculate community richness (Heming et al., 2019). All analyses were performed using R v.4.1.1. (R Core Team, 2024).

Suitable areas and Protected Areas

The percentage of climatically suitable areas covered by PAs was estimated for each climate scenario (SSP126 and SSP585) using the «mask_thr_projs_mscn_b» function of the «ENMwizard» package (Heming et al., 2019). We chose to use the National System of Protected Areas (SINAP) for our analysis due to its comprehensive coverage and official designation by the government (Parques Nacionales Naturales de Colombia, 2014). Within SINAP, we focused on Colombia's 42 National Natural Parks (PNN), which are formally established areas and are managed for conservation purposes (Parques Nacionales Naturales de Colombia, 2014). The shapefile of the spatial distribution of PAs was obtained through the Colombian Environmental Information System (SIAC) (https://geonetwork.minambiente.gov.co/geonetwork) and the Agustín Codazzi Geographic Institute (IGAC) (https://geoportal.igac.gov.co/contenido/datos-abiertos-cartografia-y-geografia). An ANOVA and Tukey's post hoc test («stats» package) were applied to test whether there was a significant difference in suitable areas covered by PAs between each climate scenario (Kembel et al., 2010; Crawley, 2013). All analyses were performed using R v.4.1.1. (R Core Team, 2024).

Niche hypervolume species (NHSVI) and community (NHCVI) vulnerability indices

The vulnerability index was calculated by integrating spatial and ecological niche metrics to assess the susceptibility of species to environmental changes. To represent the ecological niche, n-dimensional hypervolumes were used, while spatial metrics described the potential geographic distribution of the species. The calculated spatial metrics were: Range Size (total area occupied by the species (km^2), obtained from its potential distribution), Spatial Position (distance between the centroid of each suitable area for the species and the centroid of all suitable areas (km)), and Spatial Overlap (mean overlap between the suitable areas of the species) (Hespanhol et al., 2022).

The n-dimensional hypervolume was calculated using the «hypervolume_Gaussian» function of the «Hypervolume» package (Blonder et al., 2014, 2018), fitting a Gaussian distribution to the ecological niche of each species, based on the selected climatic variables. After obtaining the hypervolume for each species, the following metrics were calculated: Niche Position (distance between the centroid of the hypervolume of the species and the centroid of the hypervolume of all species

records), Niche Overlap (mean overlap between the hypervolumes of the species), and Niche Amplitude (measure of tolerance to environmental conditions) (Hespanhol et al., 2022).

The species vulnerability index (NHSVI) was calculated based on the integration of the abovementioned metrics, according to the approach described by Hespanhol et al. (2022). After calculating the index, the values were normalised within the range of 0 to 1, resulting in the final vulnerability score of each species. It is noteworthy that a score of zero does not indicate the absence of vulnerability. This value stems from the normalisation process, which adjusts vulnerability scores in relation to other species in the community. Therefore, a zero score reflects that the species is relatively less vulnerable within the context of the analysed community (Hespanhol et al., 2022).

To generate the community vulnerability index (NHCVI), a spatial representation was developed that combined individual vulnerability metrics with their potential distributions. Initially, the final vulnerability score of each species (NHSVI, normalised between 0 and 1) was multiplied by its binary presence/absence model and habitat suitability, obtained from the environmental suitability models. It was assumed that the initial environmental suitability models had a scale of 0 to 1. To scale the individual vulnerability values to a potential range of 0 to 1000, the results of this multiplication were multiplied by 1000. This process eliminated the unsuitable sites for the species and allowed greater vulnerability in areas with more favourable environmental conditions (Hespanhol et al., 2022). Calculations were performed at the pixel level for each species in the community. For each species, a set of vulnerability maps was generated in which each pixel represented a distribution of vulnerability values for the entire community. From this spatial representation, the values were aggregated pixel by pixel to calculate the following community metrics: average community vulnerability value (NHCVIav); maximum level of vulnerability within a locality (NHCVImx); and standard deviation (NHCVIstd), as a measure of dispersion of community vulnerability ratings (Hespanhol et al., 2022).

The spatial correlations between species richness and various community vulnerability indices (NHCVIav, NHCVImx, NHCVIstd) were analysed using Pearson's local correlation coefficients, calculated with the 'raster' package (Hijmans, 2024), using a focal radius of 5 km (Hespanhol et al., 2022). All analyses were performed using R v.4.1.1. (R Core Team, 2024).

Risk of extinction of species

The analysis of risk of extinction of species was based on the potential distribution and projected in the different future scenarios, using the relative loss values of the extent of the suitable area and the Area of Occupancy (AOO), according to Criterion A3(c) of the IUCN Red List (IUCN, 2024). Criterion A3 considers a «population reduction projected or suspected to be met in the future», and sub-criterion (c) refers to «a decline in area of occupancy (AOO), extent of occurrence (EOO), and/or habitat quality». Thus, we classified the species as follows: Extinct (EX): species that lose 100% of the suitable habitat; Critically Endangered (CR): species that lose more than 80%; Endangered (EN): species that lose between 50% and 80%; Vulnerable (VU): species that lose between 30% and 50%; Near Threatened (NT): species that lose less than 30%; and Little Concern (LC): species that have no projected loss (Pomoim et al., 2022). For the current extinction risk status, we classified species based on the modeled extent of suitable habitat: CR < 100 km^2, EN < 5000 km^2, VU < 20 000 km^2, NT < 30 000 km^2 and LC > 30 000 km^2 (IUCN, 2024). The suitable habitat was estimated by binarising the continuous species distribution models, using the 10^{th} percentile training presence threshold to define presence/absence areas. This threshold reduces commission errors by excluding the most extreme occurrence points while maintaining ecological realism in the predicted distribution. All analyses were performed using R v.4.1.1 (R Core Team, 2024).

Results

The 18 epiphyllous liverwort species modelled presented omission rates moderately close to the expected values, with satisfactory performance in the ecological niche models. The models showed satisfactory predictive performance, with AUC values ranging from 0.71 to 0.99. Specifically, 63% of the models had AUC values above 0.85, indicating excellent predictive ability, while 34% fell within the range of 0.71–0.85, reflecting acceptable performance. No models had AUC values below 0.71, suggesting a generally robust predictive capacity (Table S2).

All species evaluated showed changes in their distribution, although the area of environmental suitability was not significantly different between the scenarios (F = 1.963; p = 0.15). *Cololejeunea antillana* Pócs and *Leptolejeunea tridentata* Bischl. were the only species that had a gain in their area of environmental suitability in both scenarios, while *Leptolejeunea radicosa* (Mont.) Grolle only had an increase in the optimistic scenario (Fig. 2). The distribution area of *Cololejeunea antillana* increased by 512.29% (optimistic) and 572.84% (pessimistic) and that of *Leptolejeunea tridentata* increased by 32.52% (optimistic) and 40.25% (pessimistic). Most species had losses in their areas of environmental suitability under both climate scenarios, with reductions varying from 7.67% to 85.53% (optimistic) and from 14.07% to 97.12% (pessimistic). *Bromeliophila helenae* Gradst., *Leptolejeunea serratifolia* Schiffn., and *Drepanolejeunea polyrhiza* (Nees) Grolle & R.L.Zhu were the species with the largest reductions, with losses ranging from 49.67% to 85.53% in the optimistic scenario and from 78.34% to 97.12% in the pessimistic scenario (Fig. 2, Fig. S2–S19, Table S2, Table S4, Table S5).

The biogeographic regions with the highest species richness were the Pacific region, with 13 species, and the Andean region, with nine species, followed by the Amazon (four species), the Caribbean (two species) and the Orinoco (one species). Moreover, the area of potential environmental suitability for the occurrence of the epiphyllous community in Colombia is projected to shrink under both future scenarios (Fig. 3).

There was a significant difference between climate scenarios in terms of area of environmental suitability inserted in PAs (F = 4.29; p = 0.014), with a decrease in the pessimistic scenario in relation to the current scenario (diff = 126.31; p = 0.01) (Fig. 3; Fig. 4a). However, there was no significant difference between the optimistic and the pessimistic scenario (diff = -68.49; p = 0.25) and between the current and the optimistic scenario (diff = 57.81; p = 0.37). The percentage of area of environmental suitability inserted in PAs increased in most regions, especially in the Caribbean and Orinoco, where protection reached up to 98.55% and 51.63%, respectively (Fig. 4b, Table S6).

When evaluated for each species, the area of environmental suitability inserted in PAs did not vary significantly (F = 0.012; p = 0.988) between scenarios. Currently, *Radula mammosa* Spruce has the highest percentage of environmental suitability within PAs (16.22%), while *Leptolejeunea tridentata* has the lowest (1.66%). Nine species are expected to have their suitable area within PAs expanded in both future scenarios, two species only in the optimistic scenario, five species only in the pessimistic scenario, and finally, two species are expected to have a lower percentage of area of environmental suitability within PAs in both scenarios (Fig. 5, Table S7).

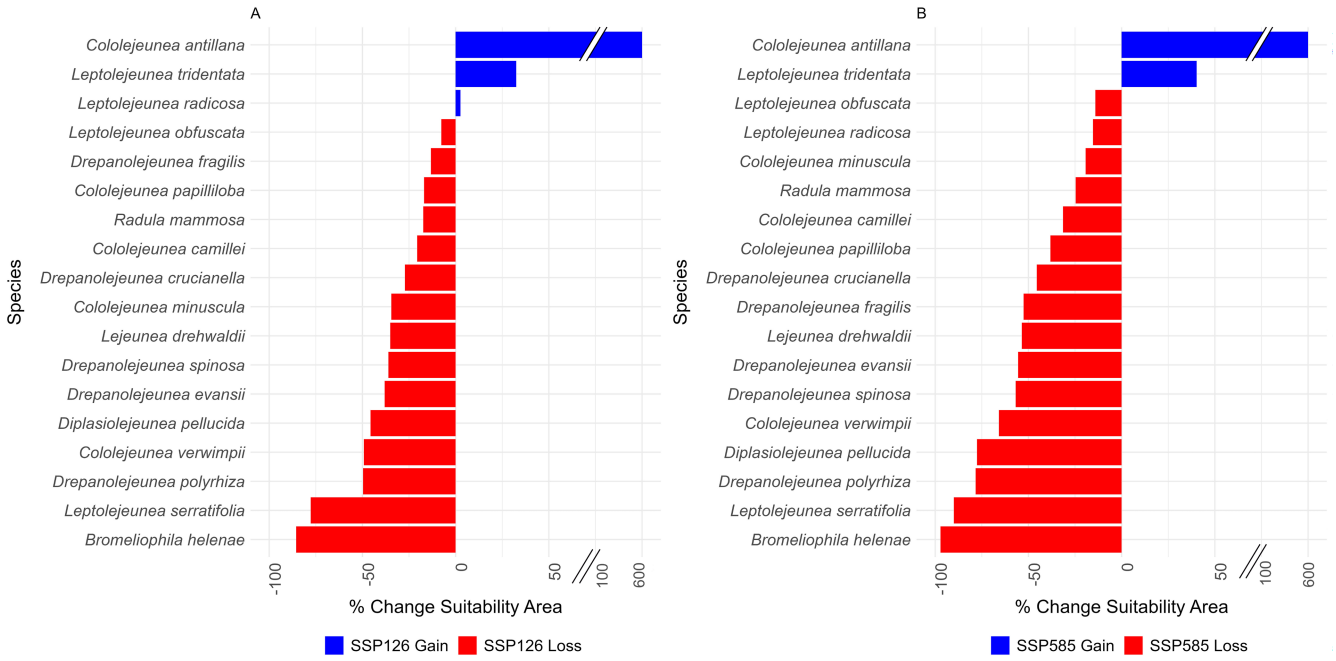

Fig. 2. Percentage of change in the area of environmental suitability for epiphyllous liverworts in future climate scenarios in Colombia, showing loss and gain of area of suitability under (A) optimistic (SSP126) and (B) pessimistic (SSP585) future scenarios in Colombia.

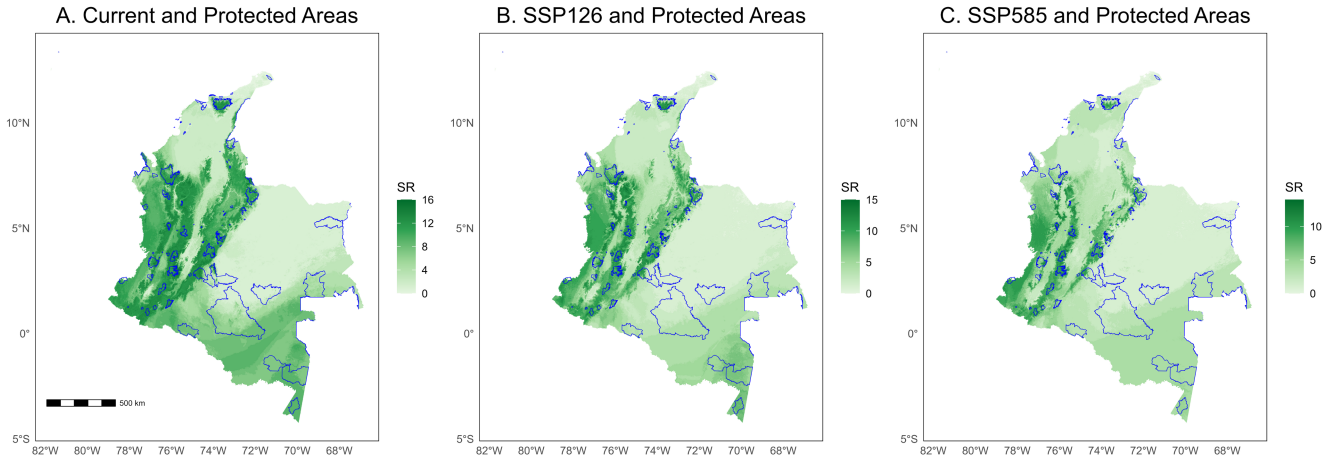

Fig. 3. Potential area of environmental suitability for epiphyllous liverworts in Colombia under (A) current, (B) optimistic (SSP126) and (C) pessimistic (SSP585) future climate scenarios and environmental protection areas (blue contour). Designations: SR – Species Richness (predicted number of species per grid cell). The colour bar values represent the number of species, ranging from 0–16 (current), 0–15 (SSP126), and 0–14 (SSP585).

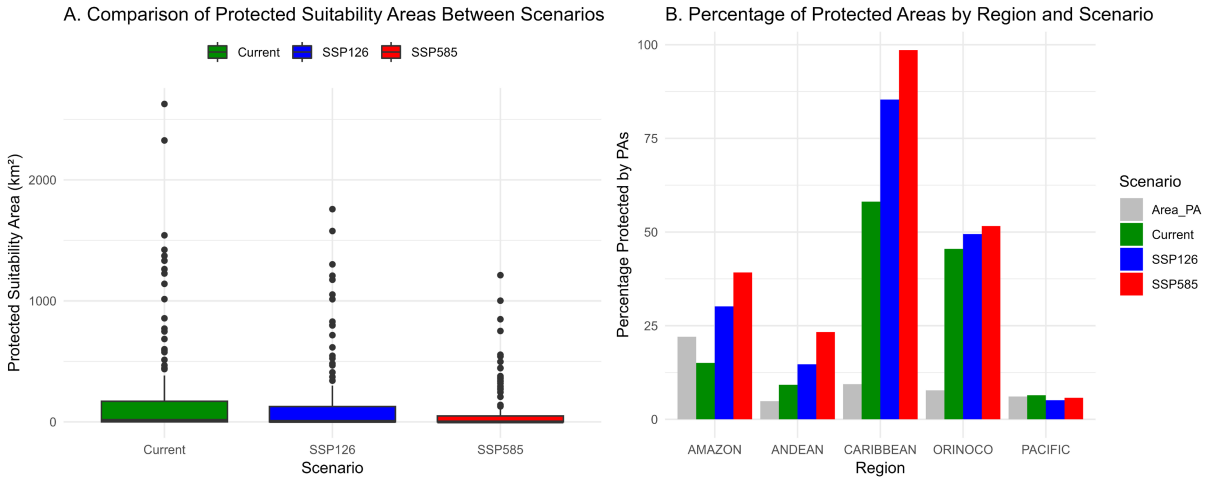

Fig. 4. Comparison of protection of areas of environmental suitability under various climate scenarios in Colombia. Designations: A – Boxplot of the distribution of suitable areas (in km^2) inside Protected Areas (PAs) under current and optimistic (SSP126) and pessimistic (SSP585) future climate scenarios; B – Percentage of suitable areas protected within PAs in the biogeographic regions of Colombia: Amazon, Andean, Caribbean, Orinoco and Pacific. Gray bars indicate the percentage area of PAs in each region and coloured bars show the percentage of suitable areas protected in each scenario.

The vulnerability analyses revealed that all species were susceptible to climate change, with seven (36%) having NHSVI equal to or greater than 0.50 (Fig. 6, Table S8). *Bromeliophila helenae*, *Drepanolejeunea polyrhiza*, *D. fragilis*, and *D. crucianella* were the species with the highest scores. Community vulnerability metrics (NHCVIav, NHCVImax, and NHCVIsd) showed high values across the Andes. The overall correlation between species richness and vulnerability at the community level was significantly high and positive (NHCVIav, r = 0.96; NHCVImx, r = 0.88; NHCVIstd, r = 0.93) (Fig. 7).

Risk of extinction

The analysis of the risk of extinction of epiphyllous liverworts in Colombia under various climate scenarios revealed a worrying trend as climate conditions become more severe. Our results showed that currently all species are classified as Least Concern (LC). In the optimistic scenario (SSP126), 61% of the species shift to higher risk categories, with species classified as Near Threatened (NT) and Vulnerable (VU) increasing notably (Fig. 8a). In the pessimistic scenario (SSP585), most species (44%) were classified as EN, followed by Near Threatened (NT, 17%) and Vulnerable (VU, 22%) (Fig. 8a). *Bromeliophila helenae* in special was predicted to change from LC to Critically Endangered (CR) in both scenarios. In addition, *Leptolejeunea serratifolia* is expected to change from LC to EN in the optimistic scenario and to CR in the pessimistic scenario.

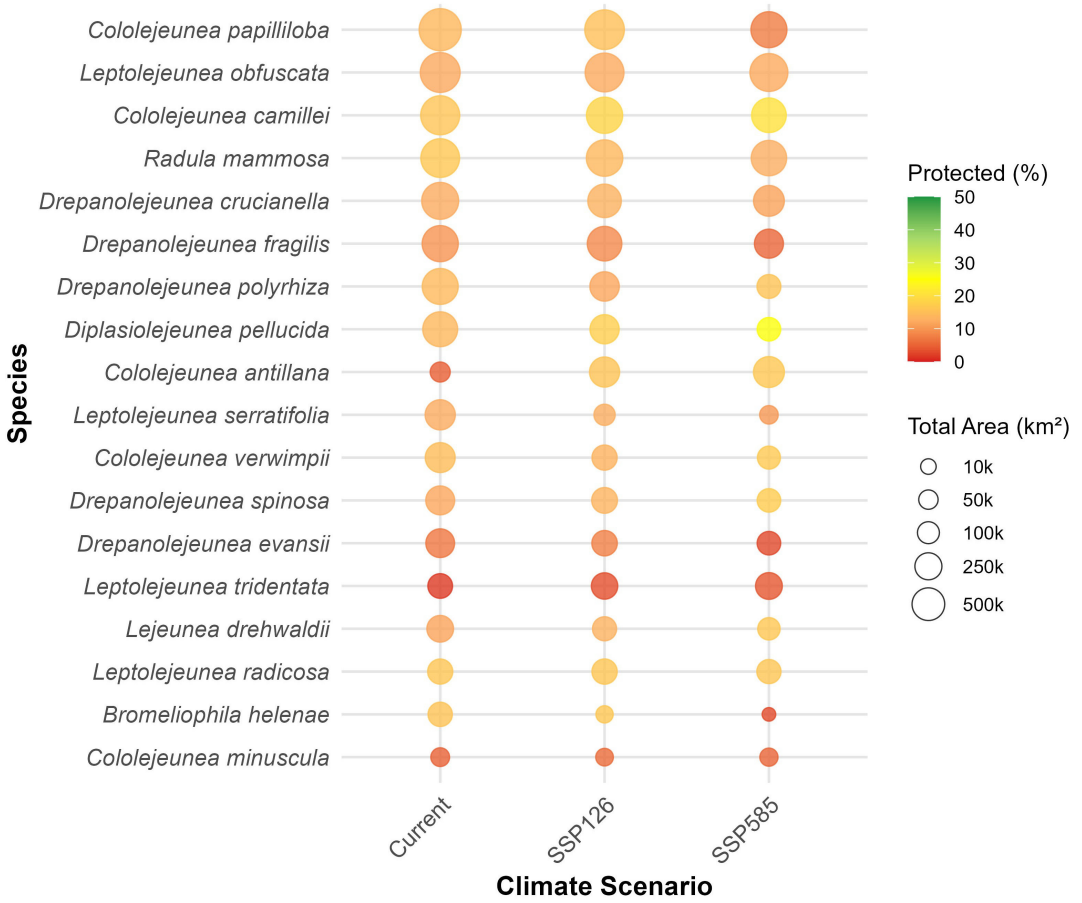

Fig. 5. Percentage of environmental suitability area for epiphyllous liverwort species within Protected Areas under the current climate scenario and projected changes under optimistic (SSP1-2.6) and pessimistic (SSP5-8.5) future climate scenarios in Colombia. The colour of the circles represents the percentage of the species' environmentally suitable area that falls within Protected Areas, according to the colour gradient. The size of the circles represents the total area (km^2) of environmental suitability for each species under each climate scenario, according to the size legend.

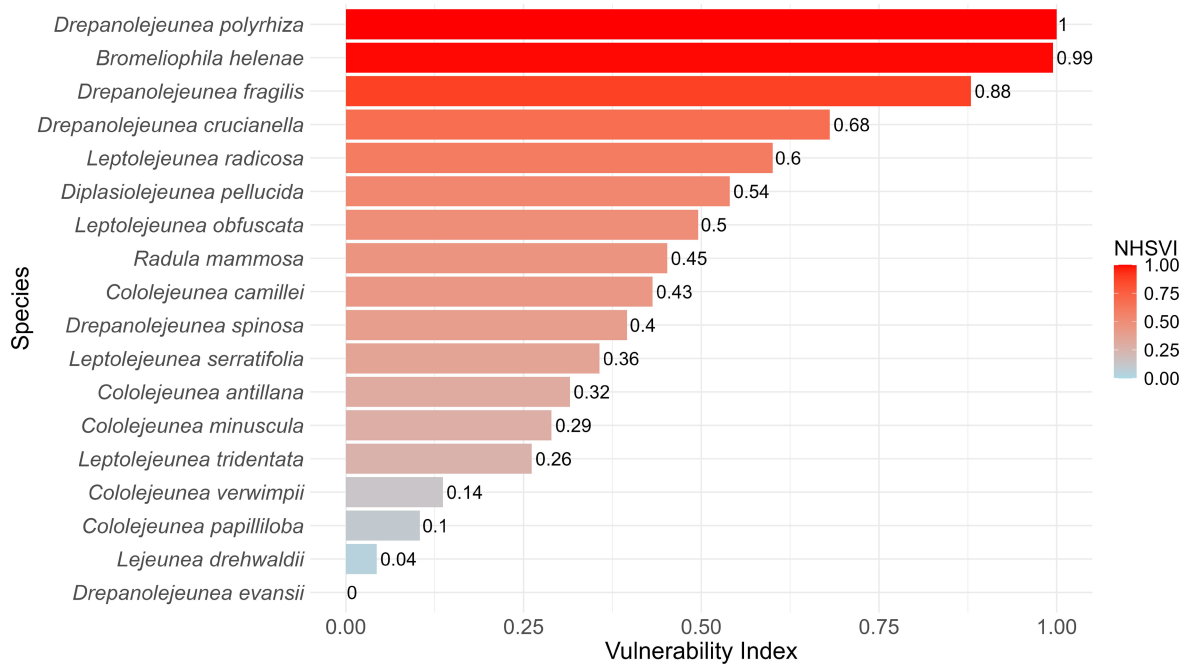

Fig. 6. Niche Hypervolume Species Vulnerability Index (NHSVI, x-axis) for epiphyllous liverworts in Colombia. Values for the NHSVI index are normalised between 0 and 1, where higher values (warmer/redder colours) indicate greater relative vulnerability within the analysed epiphyllous liverwort community in Colombia. Lower values (cooler/bluer colours) represent lower vulnerability. The colours of the bars indicate the magnitude of the NHSVI, as per the legend.

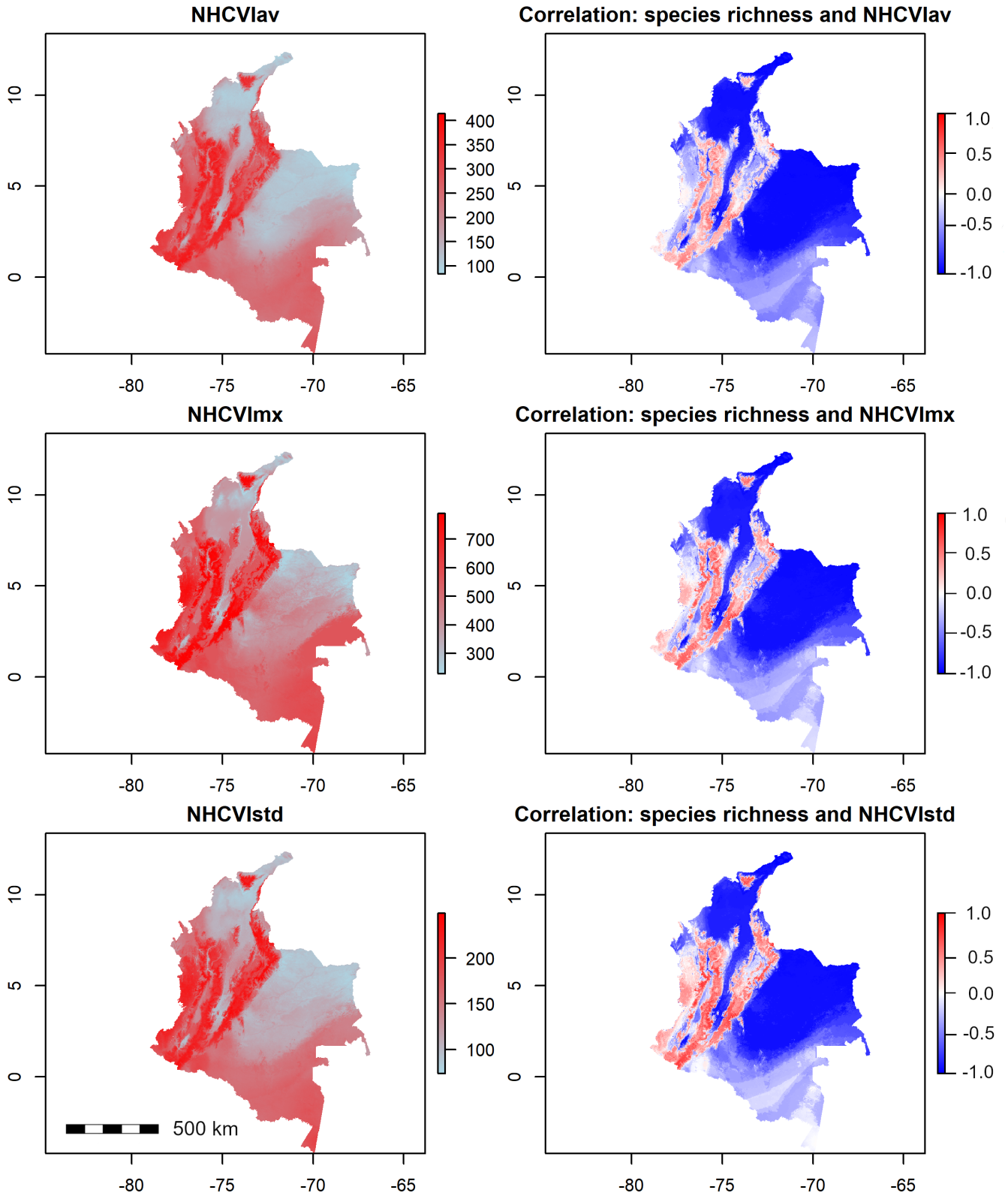

Fig. 7. Spatial patterns of niche hypervolume community vulnerability indices (NHCVI) for epiphyllous liverworts in Colombia and their local correlation with species richness. The maps on the left side represent the distribution of NHCVIav – average community vulnerability (values range approximately from 100 to 400, reflecting the average of individual species' vulnerabilities scaled by habitat suitability (0–1000)); NHCVImx – maximum community vulnerability (values range from 0 to 1000); NHCVIstd – standard deviation of community vulnerability. The colours in these maps indicate the magnitude of vulnerability (see individual legend of each map). The maps on the right side show the local Pearson correlation coefficients between species richness and each NHCVI index, where red colours indicate positive correlation, blue colours indicate negative correlation, and white colours indicate correlation close to zero (see individual legend of each map).

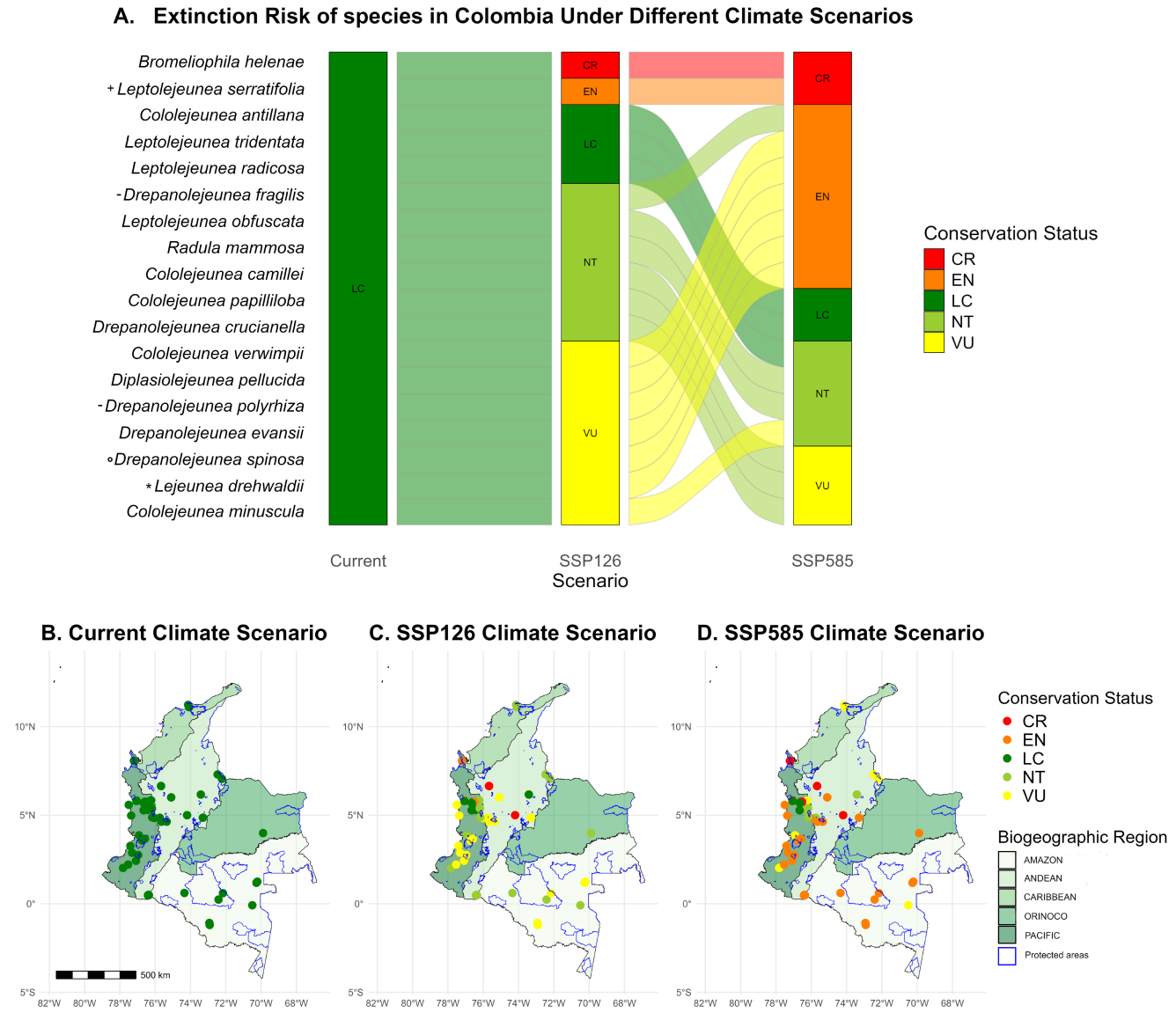

Fig. 8. Extinction risk and geographic distribution of epiphyllous liverworts in Colombia under various climate scenarios. The Sankey graph (A) illustrates the changes in the conservation status of species under current and optimistic (SSP126) and pessimistic (SSP585) future climate scenarios. The conservation states are Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT) and Least Concern (LC). The maps (B, C, D) show the geographic distribution of the species in each scenario, with the conservation status of the species in the Amazon, Andean, Caribbean, Orinoco and Pacific biogeographic regions. Species inserted in Protected Areas are indicated with the following symbols: (+) Darien National Protective Forest Reserves, (-) Serrania de Chiribiquete National Natural Park, (°) Los Nevados National Natural Park, (*) Munchique National Natural Park.

Regarding the biogeographic regions, the conservation status of the species in the Andean and Pacific regions was aggravated in various climate scenarios, particularly in the pessimistic one (Fig. 8b). Although the Amazon region showed less risk in the current scenario, in future scenarios it experiences a strong increase of EN species, which makes it a region of high concern. On the other hand, although the Orinoco region showed fewer changes, it also showed a pattern of increased risk of extinction in more extreme scenarios (Fig. 8b,c,d, Table S9).

Of the 18 species evaluated, only five (*Leptolejeunea serratifolia*, *Lejeunea drehwaldii*, *Drepanolejeunea fragilis*, *D. polyrhiza*, and *D. spinosa*) occur in four PAs in Colombia, and important variations in their conservation status are observed under various climate scenarios. Currently, all of these species are in the LC category. However, it is projected that, in future climate scenarios, these species may face a greater risk of extinction, with their status changing to VU, EN and even CR (Fig. 8a,b,c,d, Table S9).

Discussion

Climate change has the potential to cause a drastic contraction of suitable habitats for most species of epiphyllous liverworts in Colombia, especially in the pessimistic scenario. Furthermore, most of the species studied are vulnerable and will face a high risk of extinction in the future. This trend of decline in suitable habitats is particularly evident in regions such as the Amazon, where the area of suitability for species richness may drastically be reduced by 91.4% despite the proportional increase in PAs. Although PAs maintain relatively constant coverage, their effectiveness in preserving suitable habitats decreases under the extreme climate projections. Similar trends are observed in the other regions, suggesting that, even if PAs are expanded, their ability to preserve suitable habitats may be insufficient in the face of future climate conditions. Climate change not only reduces the extent of suitable habitats, but also directly affects several ecological processes essential for epiphyllous liverworts, such as spore dispersal, colonisation of new substrates and nutrient cycling in ecosystems (Hao & Chu, 2022). Climate change can also compromise important ecosystem functions such as microclimate regulation and moisture retention, which are key elements to maintain the ecological stability of the forest communities where these species live (Hao & Chu, 2022).

Our findings reinforce patterns previously described in the literature on the impact of climate change (Tuba et al., 2011). Higher temperatures in future scenarios are likely to have a negative effect on humidity patterns, directly affecting the growth, reproduction and survival of species (Gignac, 2001; Anderson & Ohlemüller, 2011; Ruklani et al., 2021). For example, higher temperatures can increase the evapotranspiration rates of leaves, affecting their ability to keep hydrated (Wagner et al., 2014). Alatalo et al. (2020) demonstrated that long-term warming negatively affects bryophytes, they recorded a significant decrease in coverage and species richness after 18 years of experimental heating. Jiang et al. (2014) identified that epiphyllous liverwort species in particular are less likely to occur under conditions that involve temperature seasonality above 7°C, annual thermal amplitude greater than 28°C, temperatures of the driest quarter less than 6.5°C, temperatures of the coldest quarter less than 5°C, and annual rainfall less than 1100 mm. Our results indicate that epiphyllous liverworts, for the most part, require environments with precipitation rates greater than 2000 mm and within the optimal temperature range from 15°C to 25°C (Fig. S1), which coincides with the ranges identified by Jiang et al. (2014). This congruence is crucial for the conservation of the species and for predicting how they might respond to climate change.

In this study, we found that some species of epiphyllous liverworts are distributed in specific areas at low altitudes (> 500 m a.s.l.), such as the biogeographic Chocó (Pacific) and the Amazon. These regions will face severe climate change, with rising temperatures, resulting in reduced suitable areas and lower overall richness of species. Thus, unfavourable conditions can drastically reduce the geographic distribution of epiphyllous liverworts, negatively affecting their survival (Jiang et al., 2014). Zotz & Bader (2009) observed that many tropical bryophytes are reaching their limits of thermal tolerance, which increases respiration and, consequently, the loss of water and essential nutrients. This phenomenon is especially critical for epiphylls, since, living at the interface between vegetation and the atmosphere, they are particularly sensitive to microclimatic variations (Benzing, 1998; Jácome et al., 2011; Jiang et al., 2014; Tang et al., 2018). Furthermore, recent studies show that in the Amazonian forests climate change is causing the loss of tree species, which significantly reduces the area and connectivity of evergreen forests (for example, a decrease in the diversity and abundance of trees in the region has been observed) (Miles et al., 2004; Esquivel-Muelbert et al., 2019; Morais et al., 2024). Jiang et al. (2014) and Tang et al. (2018) also demonstrated that the presence of epiphytic liverworts is strongly associated with vegetation cover, evidencing that forest degradation and fragmentation negatively impacts the microenvironmental conditions necessary for its development (Jiang et al., 2014; Tang et al., 2018). Taken together, these findings suggest that, in future scenarios, reducing suitable areas in the Amazon and Pacific could increase the vulnerability and risk of extinction of these species, which, in turn, would compromise key ecosystem functions such as moisture retention and nutrient cycling (Benzing, 1998; Zotz & Bader, 2009; Jácome et al., 2011).

In addition, species with narrow ranges of distribution were found to have a high risk of extinction and high vulnerability to

environmental changes (Dee et al., 2019; Vincent et al., 2020). The results of our study indicate that *Bromeliophila helenae*, currently classified as LC, will face a critical risk due to the drastic reduction of suitable habitats. This suggests that as climate change advances, drier areas will exacerbate the vulnerability of these species, accelerating extinction events. Although *Bromeliophila helenae* grows on bromeliad leaves that are widely distributed across the Colombian mountains, Males et al. (2023) show that epiphytic bromeliads are highly sensitive to extreme climate conditions. Even if the substrate of the bromeliad remains available, adverse microclimatic changes, such as increased temperatures and prolonged droughts, can affect the physiological performance of *Bromeliophila helenae*, reducing habitat quality and increasing its risk of extinction. Therefore, vulnerability of this species to climate change is likely not due to the scarcity of its host bromeliads, but rather to the degradation of the microenvironment in which it thrives. While some drought-resistant species, such as *Cololejeunea antillana* and *Leptolejeunea tridentate* (the latter being reported in almost all forest microhabitats, including areas exposed to full sunlight (Benavides & Sastre-De Jesús, 2011)), may adapt to these changes, most species in regions such as the Pacific and the Amazon (which already face environmental pressures) will be particularly affected under future climate change scenarios. These regions have historically been biodiversity refuges (Benavides & Sastre-De Jesús, 2011; Azevedo et al., 2020; Ruiz-Agudelo & Gutiérrez-Bonilla, 2023) and as they have a high number of threatened species, they may become areas with significant biodiversity losses.

The impact of climate change on biodiversity results from a complex combination of habitat loss and displacement of areas of occurrence, due to the emergence of new susceptible areas (Warren et al., 2013; Dai et al., 2023). This process forces species to adapt to new environments or move towards suitable areas, changing their geographic distribution range, many move towards higher latitudes and altitudes (Anderson & Ohlemüller 2011; Bellard et al., 2012). For example, Chen et al. (2011) observed that many terrestrial organisms are moving northward at a rate of 17 km per decade and ascending to higher altitudes at a rate of 11 m per decade. Notably, despite their limited dispersal capacity, epiphyllous bryophytes are also shifting poleward, as documented in Tianmushan (China), where recent warming has enabled Lejeuneaceae species to colonise higher latitudes through microclimatic amelioration (Tang et al., 2018). Our results also indicate a clear trend of species displacement to higher altitudes under current and future climatic conditions, especially in the Andes, in search of more favourable climatic conditions. These zones act as climate refuges (Feeley et al., 2011), maintaining a greater richness of epiphyllous liverworts compared to lowlands. However, such refuges face dual threats: climatic instability and anthropogenic disturbances (e.g. ecotourism), which may degrade the humid microhabitats critical for epiphyll survival (Tang et al., 2018). These refuges are crucial for the preservation of biodiversity and survival of these species in the face of climate change, but their long-term efficacy depends on integrating habitat protection with strict regulation of human activities in sensitive areas (Jiang et al., 2014; Tang et al., 2018).

Regarding the effectiveness of PAs in Colombia under various climate scenarios, our study revealed disparities in their ability to conserve the richness of epiphyllous liverwort species in the various biogeographic regions. In some regions, such as the Amazon, the proportion of PAs increases despite the reduction in total habitat suitability, suggesting a greater efficiency of the remaining PAs to conserve the species in future climatic conditions. However, in other regions, such as the Andean and Pacific regions, both habitat suitability and proportion of PAs are expected to decrease. In the Andean region, for example, the drastic reduction of suitable habitats under climate scenarios combined with high levels of community vulnerability is a threat to the stability of the community of epiphyllous liverworts. Although the region is a home to 56 PAs, which cover only 4.8% of its surface, the projected decrease in habitat suitability is alarming, suggesting that these areas may not be sufficient to preserve local biodiversity. Similarly, in the Pacific region, where there are 24 PAs corresponding to 6.08% of the total surface area, the loss of suitable habitats of the species is also worrying, and the projected climate changes will compromise the survival of the species.

These results underscore the critical importance of the existing PAs and the urgent need to expand them to mitigate future habitat losses (Bonilla-Mejía & Higuera-Mendieta, 2019; Lombo-Sanchez et al., 2024). However, the creation of

new conservation areas does not automatically guarantee the preservation of biodiversity because approximately 63% of PAs in Colombia are under some degree of transformation, degradation or habitat loss due to human activities (Armenteras et al., 2003; Bonilla-Mejía & Higuera-Mendieta, 2019; Clerici et al., 2020). Besides that, the effectiveness of PAs varies considerably depending on the institutional context, as observed in many tropical countries (Bonilla-Mejía & Higuera-Mendieta, 2019). Researchers highlight that, although PAs contribute significantly to reducing deforestation in Colombia, their effectiveness is more pronounced in areas close to urban centres, especially in municipalities with better public services and lower rates of violence. In contrast, in remote areas, national PAs are particularly vulnerable to the expansion of illicit crops such as coca and illegal gold mining (Bonilla-Mejía & Higuera-Mendieta, 2019).

In short, our results show the negative impacts of climate change on suitable habitats for epiphyllous liverworts, underscoring the importance of PAs as potential refuges. However, most of these species face serious threats of extinction, especially in the central Andes and southwestern Colombia, regions of high biodiversity under strong anthropogenic pressure (Lombo-Sanchez et al., 2024). To mitigate these impacts, it is essential to expand the PA network and strengthen the management of these zones with plans for continuous monitoring and adaptation to climate change (Watson et al., 2014; Bonilla-Mejía & Higuera-Mendieta, 2019; Lombo-Sanchez et al., 2024). Measures such as habitat restoration, creation of ecological corridors and promotion of connectivity between PAs can increase the resilience of the species (Leverington et al., 2010; Eklund et al., 2016). Reviewing and adjusting conservation policies in the light of future climate scenarios is crucial to ensuring the long-term effectiveness of these actions.

Conclusions

Epiphyllous liverworts across Colombia are broadly at risk under twenty-first-century climate change, with most species projected to lose large fractions of their currently suitable habitat. Only a handful of species show potential range expansion, and overall community vulnerability is the highest in the Andean and Pacific regions. While existing PAs will continue to harbour a portion of remnant suitable habitats, their static boundaries will be insufficient to conserve many species under more severely warming scenarios.

To safeguard this imperiled group, conservation planning must integrate dynamic climate projections: expanding and connecting Protected Area networks into emerging climate refugia, and targeting microhabitat restoration to maintain humidity and temperature regimes critical for liverwort survival. Without rapid adaptation of both policy and on-the-ground management, many of Colombia's unique epiphyllous liverworts face greatly elevated extinction risk by mid-century.

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Supporting Information

Additional data for the paper may be found in the **Supporting Information**.

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ПЕЧЕНОЧНИКИ В МЕНЯЮЩЕМСЯ МИРЕ: УЯЗВИМОСТЬ И РИСК ИСЧЕЗНОВЕНИЯ ВИДОВ-СПЕЦИАЛИСТОВ В УСЛОВИЯХ ИЗМЕНЕНИЯ КЛИМАТА В ТРОПИЧЕСКОЙ СТРАНЕ (КОЛУМБИЯ)

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Различные последствия изменений климата представляют серьезную угрозу биоразнообразию, увеличивая риск локального и регионального исчезновения видов. В данном исследовании оценивается влияние изменений климата на риск исчезновения и уязвимость 18 видов эпифильных (обитающих на листьях растений) печеночников, как группы организмов, чувствительных к изменениям окружающей среды. Область пригодности окружающей среды для типичных неотропических эпифильных печеночников оценивалась в рамках оптимистичного (SSP126) и пессимистичного (SSP585) сценариев будущего климата (2080–2100 гг.) с использованием биоклиматических переменных и алгоритма MaxEnt на примере Колумбии. Анализ уязвимости проводился путем интеграции пространственных и климатических показателей ниши вида. Риск исчезновения основывался на потенциальном и прогнозируемом распространении в сценариях будущего климата с использованием значений относительной утраты степени пригодности территории и область обитания (AOO) в соответствии с критерием A3(c) Красного списка МСОП. Изменения климата окажут значительное воздействие на печеночников, поскольку в будущих сценариях область экологической пригодности большинства оцененных видов (89%) сократится. Ярким примером является *Bromeliophila helenae*, вид, который потеряет 97.12% своей общей площади пригодности, а доля пригодной площади, находящейся под охраной в пределах особо охраняемых природных территорий (ООПТ), сократится примерно на 80%. Хотя в настоящее время в пределах ООПТ встречается только пять видов, эти ООПТ играют важную роль, поскольку в сценариях будущего климата площадь экологически пригодной среды обитания увеличится, особенно в регионах Ориноко и Карибского бассейна. Риск исчезновения почти всех оцененных видов (95%) возрастет в сценариях будущего климата, особенно в Андах, регионе, который может стать убежищем для специализированных видов печеночников. Результаты данного исследования подчеркивают острую необходимость разработки стратегий охраны природы, включающих расширение числа ООПТ и повышение эффективности управления существующими ООПТ.

Ключевые слова: климатическая модель, мохообразные, Неотропика, пригодность окружающей среды, эпифиты