Climate change effects on Peruvian Lomas plant distribution

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Abstract

The Lomas ecosystem, situated along the arid coast of Peru, is a key refuge for biodiversity. Lomas vegetation has evolved diverse adaptive mechanisms to thrive in this unique environment, strongly influenced by fog masses during winter months while allowing vegetation growth in the dry season. However, climate change poses a threat to this fragile ecosystem. Despite species' resilience to drought, changing rainfall patterns and soil moisture reduction from aridification have led to population declines in recent decades, affecting various taxa. Understanding changes in habitat suitability and species distribution is crucial for mitigating increased extinction risks due to climate change. Urgent research is needed to comprehend these impacts on Peruvian Lomas, especially amidst urbanization and population growth, threatening their survival. In this study, Species Distribution Models (SDMs) predicted Lomas plant species distribution within the Andes and Lomas regions under two future (SSP1-2.6 and SSP3-7.0) scenarios. Both regions were expected to experience declines in habitat suitability, with Lomas being the most vulnerable, particularly under the SSP3-7.0 scenario. Endemic species were anticipated to migrate upslope, utilizing their unique adaptations, while non-endemic species might move downslope. High-elevation species were projected to undergo larger range shifts, while low-elevation species could face more pronounced habitat alterations, influenced by key traits and vegetation interactions. Due to the discontinuous distribution of Lomas systems along the coast, certain species already face threats that could alter these responses in the future. Urgent conservation efforts are necessary to mitigate habitat loss and fragmentation's impacts on vulnerable plant species, especially with increasing urbanization and desertification in the region.

1. Introduction

1.1. The Lomas ecosystem

In Peru, the Lomas stands out as a remarkable ecosystem, resiliently enduring in the arid coastal regions amidst rapid urban expansion. This distinctive habitat, characterized by its arid conditions and the isolation of populations within mesic islands (Ferreyra, 1961; Péfaur, 1982), hosts a rich array of native and endemic species. Vegetation in this region has evolved various adaptive survival mechanisms, including bulbs, rhizomes, and extended seed dormancy (Gonzales et al., 2023). Lomas are dominated by fog, which is the primary source of vegetation growth. Particularly during the humid season, fog predominates between 300 and 1,000 meters due to a thermal inversion layer (Péfaur, 1982) and it plays a crucial role in sustaining the delicate natural balance of the region.

Various hypotheses have been proposed to understand vegetation patterns in water-limited ecosystems like Lomas (Borthagaray et al., 2010). Factors such as climate, terrain, soil properties, and the species' ability to endure drought play an important role. Climatic and physical barriers, such as the Abancay Deflection and the Atacama Desert, have led to distinct floristic partitions in Peru and Chile (Gonzales et al., 2023). Despite peak productivity occurring during the foggy months in winter, occasional humidity from phenomena such as El Niño-Southern Oscillation (ENSO) also contributes to the unique

composition of Lomas vegetation, largely consisting of ephemeral herbs (Gonzales et al., 2023; Manrique et al., 2010; Muenchow, et al., 2013; Tovar et al., 2018). The interaction between individuals and the environment enhances the possibility of growth and survival, as demonstrated by trees and shrubs intercepting humidity to foster the growth of certain species (herbs, epiphytes), while also contributing to soil moisture preservation (Rolando et al., 2017; Sotomayor & Lortie, 2016; Tovar et al., 2018). However, negative effects, primarily attributed to competition for resources, can also reduce populations during dry periods. Nonetheless, there are many species that can thrive even in dry scenarios (Borthagaray et al., 2010).

However, the rapid and unprecedented changes brought about by climate change pose a serious threat to this fragile ecosystem (Borthagaray et al., 2010; Gonzales et al., 2023; Moat et al., 2021). Changes in evapotranspiration rates have the potential to intensify aridification in the future, which could reduce soil moisture and lead to diverse forms of vegetation decline including increased plant dieback, diminished density and reduced vitality of plant species (Intergovernmental Panel on Climate Change, 2023; Pinto & Kirberg, 2005; Rundel et al., 1997). Research conducted in the Lomas of Atacama in Chile has shown changes in rainfall intensity and frequency over time (Schulz, et al., 2011). Although many species in the Lomas ecosystem show adaptability to prolonged droughts, there has been a decline in vegetation and a decline in several taxa in recent decades (Pinto & Kirberg, 2005; Rundel et al., 1997; Schulz, Richter, et al., 2011). Plants are expected to undergo physiological and fitness changes in response to changing climates, yet these responses remain largely underexplored in this ecosystem (Sotomayor & Lortie, 2016). This knowledge void is especially critical given the region's crucial coastal location, making it one of the areas worldwide most affected by the El Niño-Southern Oscillation (ENSO) and thus experiencing heightened climate variability (Muenchow, et al., 2013; Ruhm et al., 2022).

Globally, vegetation has been observed to migrate upslope in response to changing conditions; however, the unique characteristics of Lomas challenges conventional migration patterns in other ecosystems (Dillon et al., 2009; Manrique, 2011; Muenchow, et al., 2013). It is crucial to understand whether the habitat of this ecosystem will contract, leading to reduced species distribution ranges and heightened risks of extinction. High-elevation species are particularly vulnerable, as they exhibit lower photosynthetic acclimation to warmer temperatures than plants from lower elevations (Hernández-Fuentes et al., 2023). Similarly, endemics identified by various studies in the Mediterranean and Alpine ecosystems are particularly sensitive to climate change due to their small and fragmented populations, reducing habitat suitability and reproductive success (González-Mancebo, 2022; Mendoza-Fernández et al., 2022). Despite global studies on climate change effects, extensive research is urgently needed to understand the specific impacts of climate change on the Peruvian Lomas ecosystem.

In the face of these challenges and recognizing the significant impacts of climate change on the Lomas ecosystem, we employed Species Distribution Models (SDMs) as a quantitative tool to generate invaluable insights into how environmental factors shape habitat suitability and influence distributional responses. SDMs allow us to predict the potential shifts in the distribution of Lomas plant species within the Andes and Lomas regions. Additionally, we aimed to identify the response of specific vegetation

types, classified by elevation and endemic status, and highlight plant species most vulnerable to these environmental changes. Through this study, we clarify potential implications for extinction and proposals for the conservation status of the unique Lomas ecosystems.

2. Materials and Methods

2.1. Species and study areas considered

Our primary focus was on species of the Lomas ecosystems, situated at the base of the Andean Mountain range along the coast of Peru. To compile an initial list of Lomas species, we thoroughly reviewed literature, including journal articles, local floristic books, and handouts, reporting botanical and floristic site-specific data for Lomas localities, primarily in Peru. Taxa identified only to the genus level were excluded from our analysis. Moreover, we categorized the species based on their native and endemic status and elevation preferences. Elevation preferences were determined using the average height of occurrence records for the studied regions (see section 2.2), aligning with delineations such as South America, Andes, Peru, and Lomas. The categorization process involved defining elevation ranges based on quantile thresholds within the Andes. These thresholds, established at the 0.33 and 0.66 quantiles (584 m and 2382 m, respectively) of the altitudinal data, served as benchmarks to classify species according to their median height of occurrence. Tailored to accommodate non-normal distributions, this approach allowed us to investigate how plant species at specific elevation ranges might respond to changing habitat conditions.

2.2. Species occurrence data

Following the compilation of the species list, geo-referenced occurrence data were obtained from various databases, including the Global Biodiversity Information Facility (GBIF), iNaturalist, Integrated Digitized Biocollections (IDigBio) using the spocc package (Owens et al., 2023) and Botanical Information and Ecology Network (BIEN) with the BIEN package (Maitner, 2023). Additional data were sourced from the National Forestry and Wildlife Service of Peru (SERFOR). Given that some of these species also inhabit other areas in South America than the Lomas, we collected occurrence data from this broader region to correctly model the species niche. Several cleaning and filtering steps were employed to ensure data quality. We restricted coordinate uncertainty to 1 km and filtered observations by the year of occurrence, excluding records from before 1975. Records from botanical gardens and museums were eliminated using the CoordinateCleaner package (Zizka et al., 2019). Duplicate entries were removed, and centroids were detected, as poorly geo-referenced occurrences are often mistakenly attributed to the centroid of the country or its capital (Serra-Diaz et al., 2017). Utilizing the rgdal package (Bivand et al., 2023), records were assigned the EPSG:4326 coordinate reference system, and points outside the South American region were excluded. Finally, species with a sample size fewer than 30 occurrence points were excluded from the analysis (Wisz et al., 2008). This rigorous filtering process resulted in a final dataset comprising 149 species from the initial list of 587 species (Table S1). Our

occurrence dataset was limited by the scarcity of reported occurrences, as more than 74% of the total species list could not be included in the analysis.

2.3. Environmental data

Forty-one predictor variables at a 30 arcsec resolution (~ 1km) were preselected to characterize the study environment. This set includes 19 bioclimatic variables obtained from CHELSA version 2.1 (Information S1; Karger et al., 2017), representing the average macroclimate over 1981–2010 ('current' conditions). The topographic data (elevation, slope, aspect) utilized in this study were retrieved from the digital elevation model products of the 250 m Global Multi-resolution Terrain Elevation Data 2010 dataset (GMTED2010) (Danielson & Gesch, 2011). Sine and cosine transformations were applied to maintain a continuous representation of circular variables. These transformations integrated landscape orientation, particularly southwest orientation in this coastal region, aligning with expectations of landscape features facing seaward (Hesse, 2012; Moat et al., 2021). Five soil variables, i.e. organic carbon, sand fraction, electrical conductivity (EC), coarse fragments, and pH, were extracted from the SoilGrids database (Poggio et al., 2021). Remote sensing-derived cloud observations at 1 km² resolution, representing fog, were obtained from EarthEnv (Wilson & Jetz, 2016). Cloud cover was selected considering August as the representative month for Lomas fog (Ruhm et al., 2022). The Topographic Wetness Index (TWI), as a proxy for topography-driven soil moisture, was calculated using the System for Automated Geoscientific Analyses (SAGA) GIS software, as per Kopecký et al. (2021). This calculation was based on Digital Elevation Models (DEM) obtained from the United States Geological Survey (USGS) through their EarthExplorer tool. We employed the Multiple-flow FD8 algorithm to achieve precision and incorporated a flow dispersion close to 1.0 while considering the local slope gradient. Moreover, to assess aridity in this region, we utilized the Global Aridity Index, according to Zomer et al. (2022). All predictors were projected to a 1 x 1 km² grid (EPSG:4326) using the raster package (Hijmans, 2023). Environmental values were extracted at 10,000 points within a 2 km buffer around occurrence points, chosen for their relevance to the specific Lomas environment.

To mitigate overfitting in our model, we conducted a pairwise Spearman correlation test on the predictor variables (using values extracted at 10,000 points within a 2 km buffer around occurrence points; Figure S1). Variables with high correlation (Spearman's coefficients > 0.7) were systematically removed from the analysis, selecting the ecologically most relevant variables to include in the model, ensuring it remained concise and effective (Dormann et al., 2013). This process resulted in a final set of 18 predictor variables, including bioclimatic factors (BIO1, BIO2, BIO3, BIO5, BIO9, BIO12, BIO15, BIO19), topographic attributes (elevation, slope, aspect), cloud cover metrics (mean cloud cover in August, interannual variability of cloud cover), and soil properties (organic carbon at a depth of 5–15 cm, sand fraction at a depth of 0-5cm, cation exchange capacity at a depth of 0–5 cm, fraction of coarse fragments at a depth of 0–5 cm).

To project changes in species distribution under future climatic scenarios, bioclimatic variables were extrapolated for 2071–2100 ('future' conditions) using data from CHELSA. We focused on two SSP scenarios, encompassing a fusion of Representative Concentration Pathways (RCPs) and Shared

Socioeconomic Pathways (SSPs). The SSP1-2.6 scenario represents a strong mitigation scenario, exploring the impact of limiting global warming to 2°C by the century's end. In contrast, SSP3-7.0 reflects a no-additional-climate-policy scenario, projecting high greenhouse gas emissions doubling from current levels by 2100 (Arias et al., 2021). These scenarios were established by integrating global climate models within the Coupled Model Intercomparison Project Phase 6 (CMIP6) framework. They are derived from five CMIP6 General Circulation Models (GCMs): GFDL-ESM4/3, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL, providing a comprehensive representation of potential future climatic conditions (Zhou et al., 2023). Unlike the macroclimate variables, no estimated future data is available for the edaphic, topographic and cloud cover variables. Therefore, we assumed that these variables remained constant in all models.

2.4. Species distribution model

This study employed the MaxEnt (Maximum Entropy) algorithm to model the impact of environmental drivers on the geographic distribution and habitat suitability of Lomas plant species (Phillips & Dudik, 2008). MaxEnt utilizes species presence-only location data and environmental predictor data as input. MaxEnt predicts the Relative Occurrence Rate (ROR) per grid cell, representing the relative probability of a species being present in each cell and indicating the suitability of each cell as a habitat. The algorithm begins with a uniform distribution, assuming an equal probability of presence in all cells. It then identifies the distribution with maximum entropy that aligns with observed occurrence data while respecting environmental constraints. This resulting distribution is translated into a map with ROR values, providing insights into habitat suitability across the landscape. Operating as a presence-only algorithm, it necessitates background locations where presence is unknown. These background points were generated using a 2D kernel-density estimate via the MASS package (Venables & Ripley, B., 2002), with 10,000 background points sampled around known species presence locations. This approach, suggested by Lake et al., 2020 and Vollering et al., 2019, aimed to align the spatial density of background points with species occurrences, mitigating the risk of sampling points too far from species locations and reducing spatial bias. The resulting 2D kernel-density layer ensured that background points accurately reflected the observed spatial distribution of species presence data.

To address bias and optimize model complexity, hyperparameters were fine-tuned using the package ENMeval2.0 (Kass et al., 2021). Tuning parameters involved selecting linear, quadratic, and product feature classes, which is crucial in determining constraints on environmental predictors during model training and influencing the potential shape of the marginal response curve. A linear feature was chosen to align the mean of the predictor at the predicted species occurrence approximately with the observed mean, while a quadratic feature matched the variance (Merow et al., 2013). The product feature constrained the covariance of two pairs of predictors, corresponding to an interaction term in regression. Regularization was performed with coefficients 0.5, 1, and 2 to mitigate overfitting risk, minimizing the Akaike Information Criterion (AIC) among competing models. Smaller coefficients (e.g., 0.5) provide less regularization, allowing for more complex relationships, whereas larger coefficients (e.g., 2) encourage stronger regularization, favoring simpler relationships. AIC aids in model selection by favoring models

that fit the data well while maintaining simplicity. To evaluate model performance, we employed spatially blocked 10-fold cross-validation using the blockCV package (Valavi et al., 2019). This approach partitions data into training and test subsets for evaluation (Merow et al., 2013). The Continuous Boyce Index (CBI) served as our primary assessment metric, chosen for its accuracy when utilizing only presence data, outperforming the Area Under the Receiver-operating Characteristic Curve (AUC) (Jiménez & Soberón, 2020). The CBI reflects the correlation between predicted habitat suitability and the distribution of occurrence records. In addition to predicted-to-expected ratio curves, the CBI provides insights into robustness, habitat suitability resolution, and deviation from randomness (Hirzel et al., 2006). Its values range between − 1 and 1, where values > 0 indicate a better-than-random fit, with higher CBI values generally corresponding to more reliable predictions (Hirzel et al., 2006). This rigorous evaluation strategy ensures a comprehensive assessment of model accuracy and reliability.

The final model was utilized to project current and future habitat suitability trends across the western side of the Andes Mountains and Lomas regions under two different climate scenarios and for the five GCMs using the package dismo (Hijmans et al., 2023). The predictions included the Andes but were specifically limited to the Lomas regions, with the ultimate boundary being the Peruvian desert (latitudes between 5°8' and 21°25' S). To address considerable variability among alternative models (Araújo & New, 2007), the final model prediction was derived as the unweighted average of the five GCMs. To estimate occurrence probability, we applied a complementary log-log transformation, converting continuous ROR values into a probability-like scale (Phillips et al., 2017). This transformation facilitated thresholding, creating binary (presence-absence) maps (Saupe et al., 2015; Syfert et al., 2014). Cells in the raster with modeled probabilities exceeding the threshold were considered suitable, with the choice of threshold significantly impacting inferred extinction risks (Nenzén & Araújo, 2011). To ensure the robustness of our analysis, we initially explored two threshold selection methods: a fixed 10% probability threshold and a prevalence-based threshold set equal to the ratio of presence points to total observations, resulting in a 50% probability threshold. The choice of threshold for converting logistic maps to binary maps significantly influenced the assessment of species distribution and extinction risk. Higher threshold values (50%) led to more projected extinctions. In light of these outcomes, we opted to proceed with the 10% threshold for our scenarios comparison and for comparing species endemic status and elevations.

Within the Andean and Lomas ecosystems, we identified species with the highest absolute horizontal and elevational distribution shifts (Figure S2) and species that are expected to lose their habitat under future SSP scenarios (Table S2). Moreover, we used binary maps to examine the effects of habitat change on characteristic Lomas species, including *Heliotropium arborescens*, *Oziroe biflora*, *Solanum peruvianum*, *Stenomesson flavum*, *Tillandsia latifolia*, and *Trixis cacalioides*. These species are present in the Lomas of Lima and play a crucial role in the ecological structure of the region (Table S3). By highlighting the current threats that these species face, particularly in the context of urbanization pressures, this analysis helps us identify plants with potential applications in urban green strategies.

2.5. Statistical analysis

To quantify changes in habitat suitability of all 149 species, we utilized centroid detection along latitude, longitude, and elevation dimensions. Employing the dismo package (Hijmans et al., 2023), we determined the center of gravity for current and future modelled distributions, enabling subsequent distance and angle calculations. The raster package (Hijmans, 2023) facilitated the derivation of total change and percentage between current and future suitable areas. To explore the projected range shifts in both the Andes and Lomas regions, we separately analyzed vertical (elevational) and horizontal shifts under each climate scenario. Our aim was to discern significant differences between scenarios, highlighting their critical impact on species distribution. Due to the non-normal distribution of our data, we opted for the Wilcoxon signed-rank test, considering a specific paired experimental design in this case. Additionally, to evaluate the expected changes in species distribution between low-, middle-, and high-elevation species, we employed the Kruskal-Wallis test and Dunn's post hoc test with Benjamini-Hochberg adjustment to correct for false discovery rates. Similarly, with respect to endemic status, we investigated the range shift distances for both endemic and non-endemic species using the Mann-Whitney test. These analyses, considering both elevation and endemic status, were conducted separately for each scenario and each region (Andes and Lomas). Finally, we assessed habitat suitability changes under a 10% occurrence threshold, calculating total changes in suitable habitat area (and percentage change) for the Andes and Lomas under the two future scenarios using the Wilcoxon signed-rank test for paired designs. This analysis of suitable habitat changes also considered species elevation and endemic status in both regions, employing Kruskal-Wallis and Mann-Whitney tests, respectively. We used a significance level ($\alpha = 0.05$) for all analyses in this study. All aspects of the analysis, from statistical tests to visualizations, were conducted in RStudio (version 4.3.0), and binary map arrangements were performed with QGIS (version 3.28.2).

3. Results

3.1. Model performance

The selected model had a CBI value of 0.38 ± 0.2 (standard deviation). Although for the majority of the species (84.6%), there is a positive CBI value, there were some negative values (2%) and missing data (13.4%, Table S4). This information helped us understand which species are better or worse (than random) predicted by the model, especially for those with small occurrence data.

3.2. Shift of species distribution

3.2.1. Species distribution over the Andes and Lomas regions

Considering the entire Andes region, species distributions were not significantly different between climate scenarios ($p = 0.75$, Fig. 1a). Under both scenarios, the median species distribution shift is projected to be approximately 80.6 km (Table S5). Most species are projected to move to the east and southeast with median migration angles of 142º and 155º (Fig. 2, Table S5). Nevertheless, the move in

elevation was significantly different ($p = 0.03$) between scenarios (Fig. 1b). The median species shift is projected to move down 0.02 km under the SSP1-2.6 and 0.005 km under the SSP3-7.0 scenario (Table S5).

Significant differences were found between the two SSP scenarios for horizontal ($p < 0.001$) and elevation ($p < 0.02$) range shifts for the Lomas region (Fig. 1c,d). We found a median horizontal range shift of approximately 63.5 km and a downslope elevation shift of about − 0.08 km for the SSP1-2.6. In contrast, in the SSP3-7.0, the median distance was 170.1 km with an elevation shift of -0.08km (Table S5). Most species' migration angles and scenarios were southeast (from 120º to 180º, Fig. 2). However, some species moved northwest (322º). The extent of species shifts displayed significant variability, with certain species exhibiting substantial alterations in horizontal distance and elevation. For instance, under the SSP1-2.6 scenario, *Gamochaeta purpurea* demonstrated the most extensive potential range shift, spanning 1293.7 km, while *Solanum tuberosum* exhibited the greatest elevational shift, ascending approximately 3588 m. In contrast, the SSP3-7.0 scenario featured *Cylindropuntia tunicate* with the largest projected range shift of 1279.2 km and *Caiophora cirsiifolia* undergoing the most pronounced elevational change, descending 1753.6 m under both scenarios (Figure S2a-b). This diversity underscores the individualistic responses of various species to climate change. In the Lomas region, under both SSP scenarios, *Caiophora cirsiifolia* exhibited the most substantial shifts (3226 km) in both distance and elevation (Figure S2c-d). These findings highlight the unique potential adaptive strategies employed by different species in response to environmental shifts, while not considering landscape dispersal or connectivity factors.

3.2.2. Species distribution based on their preferred elevation and endemic status

In the Andes, contrary to the elevation changes, the horizontal projected range shift of species was significantly influenced ($p < 0.001$) by the vegetation's elevation preference under both SSP scenarios (Fig. 3a,b). High-elevation species displayed a more extensive range shift, with a median horizontal shift of 276.5 km and elevation moves exceeding 100 m downslope for both scenarios. Middle and low-elevation species had median horizontal and vertical shifts below 76 km and 5 meters, respectively (Fig. 3a-d, Table S6). Significant findings were observed in Lomas for horizontal and vertical range shifts in both scenarios, except for horizontal distance under the SSP3-7.0 scenario ($p = 0.40$, Fig. 3f). High-elevation species in Lomas exhibited the most substantial shifts, with median distance ranges of 161.3 km and 182 km for both SSP scenarios, respectively, and an overall 0.7 km shift downslope (Fig. 3e-h, Table S6). Similar to the Andes region, middle and low-elevation species in Lomas displayed comparable horizontal movement ranges, featuring median projected horizontal shifts of around 50 km under SSP1-2.6 and about 168 km under the SSP3-7.0 scenario. However, elevation shifts showed notable contrasts between scenarios. Middle and low-elevation species displayed downslope movements, with shifts of 5 and 4 meters under SSP1-2.6 and 53 and 17 meters under SSP3-7.0 scenarios, respectively (Fig. 3, Table S6).

Different responses were observed in the projected range shifts' distance (horizontal and vertical) between endemic and non-endemic species in both Andes and Lomas under both SSP scenarios. In the Andes, similar horizontal distance shifts were identified among endemic and non-endemic species under both scenarios (Fig. 4a,b). Particularly, endemics were forecasted to exhibit greater horizontal mobility, with median distances of approximately 130 km, in contrast to the 76 km projected for non-endemic species, consistently under both scenarios. Conversely, in terms of elevation, a significant contrasting pattern emerged: endemics were anticipated to ascend by a median projection of 75 m. In comparison, non-endemics were predicted to significantly shift downslope by 119 m under the SSP1-2.6 scenario ($p = 0.002$). A similar pattern was observed under the SSP3-7.0 scenario ($p = 0.03$), with median horizontal shifts of approximately 113 km and 15 km for endemics and non-endemics, respectively (Fig. 4c,d, Table S7). No significant differences in horizontal distance were observed in the Lomas region based on endemic status. Both endemic and non-endemic species were projected to undergo horizontal shifts, covering similar distances of ~ 65 km and 58 km, respectively, under the SSP1-2.6 scenario. Under the SSP3-7.0 scenario, the distances increased to 193 km and 165 km for both vegetation types (Table S7). As in the Andes, elevation shifts indicated a significant ($p = 0.01$) upslope movement of 111 m for endemics and a downslope shift of 235 m for non-endemics under the SSP1-2.6 scenario. Similarly, under the SSP3-7.0 scenario ($p = 0.03$), endemics exhibited an upslope movement of 661 m, while non-endemics shifted downslope by 179 m (Fig. 4g,h, Table S7).

3.3. Habitat suitability

3.3.1. Change in Habitat suitability for the Andes and Lomas region

We observed a decline in habitat suitability in both the Andes and Lomas regions under the examined climate scenarios. In the Andes, this change exhibited no significant difference ($p = 0.12$) across SSP scenarios. The projected median reduction in suitable habitat area was 501,498 km² for the SSP1-2.6 scenario. Under SSP3-7.0, the reduction was approximately 52,498 km² (Fig. 5a). Conversely, in the Lomas region, a significant ($p = 0.002$) reduction in projected suitable habitat area was noted between future SSP scenarios. Under the SSP1-2.6 scenario, the median reduction was approximately 257 km², while under SSP3-7.0, there was a reduction of 229.1 km² (see Fig. 5b, Table S8). The percentage of habitat change averaged 15% in the Andes, with higher median changes (reduction ~ 5%) in SSP1-2.6 compared to SSP3-7.0 (Table S8). In the Lomas region, the habitat change was about 50%, although median values indicated reductions of less than 10%.

Furthermore, notable statistical distinctions emerged regarding the alteration in habitat suitability among low-, mid-, and high-elevation species in the Andes under the SSP1-2.6 scenario ($p = 0.03$). Conversely, a contrasting pattern manifested under the alternative SSP scenario. In the context of the SSP1-2.6 scenario, low-elevation species exhibited a more substantial change in suitability (median values of -55.4%) compared to their mid- and high-elevation counterparts (Fig. 6a). A parallel trend was observed for the SSP3-7.0 scenario, albeit with median values registering below (12%, Fig. 6b). In the Lomas

region, a similar trend was observed, although changes in suitability were not significantly different based on species' elevation preferences ($p = 0.28$ and 0.83 for SSP1-2.6 and SSP3-7.0 scenarios, respectively; Fig. 6c,d). Habitat changes were observed across all species, with a more pronounced reduction for low-elevation species and a subtle expansion in habitat highlighted for high-elevation species (Table S9).

Significant differences based on endemic status were found in both the Andes ($p = 0.002$) and Lomas regions under the SSP1-2.6 scenario ($p < 0.001$). In the Andes, endemic species showed a higher median (104.61%) compared to non-endemic species (-16.5%, Fig. 7a). In the Lomas, endemic species also exhibited a higher median (108.3%) compared to non-endemic species (-15.38% Fig. 7c). Under the SSP3-7.0, just like in the Andes, no significant differences were observed between endemic and non-endemic species (Table S10).

3.3.2. Habitat dynamics and species responses in the Lomas region

Habitat suitability outcomes from the binary map outputs revealed distinct patterns for the selected species (Fig. 8). In general, the projections indicated that 23 species under the SSP1-2.6 scenario and 28 species under the SSP3-7.0 scenario are anticipated to completely lose their habitat, spanning both the Andes and the Lomas region. Notably, two species within this subset were endemic (Table S2).

Most of our selected Lomas species exhibited similar responses under both SSP scenarios, with the exception of *Tillandsia latifolia* (Fig. 8). Certain species, such as *Solanum peruvianum*, *Stenomesson flavum*, and *Trixis cacalioides*, were forecasted to maintain and even expand their habitat beyond the boundaries of the coastal Lomas. *Tillandsia latifolia* stood out as an exception, projected to lose habitat under the SSP1-2.6 scenario; however, a portion of the Lomas region became suitable under the SSP3-7.0 scenario. Conversely, species like *Heliotropium arborescens* and *Oziroe biflora* were predicted to lose the majority of their suitable habitat under both future SSP scenarios (Fig. 8).

4. Discussion

4.1. Adverse climate change scenarios impact Lomas ecosystems

Our study highlights the potential impact of climate change scenarios on Lomas species distribution across the Andes and Lomas regions. Predictions under two SSP scenarios reveal significant shifts in species distribution. While the Andes exhibit consistent horizontal and downslope movements eastward, spanning approximately 81 km, the Lomas region encounters greater challenges under the SSP3-7.0 scenario. These challenges arise due to the unique environmental conditions, such as the fragmented structure and comparatively smaller geographic extent compared to the extensive Andean region (Garreaud, 1999; Ruhm et al., 2022). Additionally, drought risk projections indicate that under SSP1-2.6,

drought risk remains low until 2060 but increases after that. In contrast, SSP3-7.0 reveals a substantial and sustained increase in global average drought risk (Zhou et al., 2023). This future scenario, marked by low international priority for environmental concerns, accentuates environmental degradation, particularly in vulnerable regions like Lomas (Bond & Scott, 2022). Contrary to existing literature suggesting an upward shift in species elevation (Jump & Peñuelas, 2005; Rubenstein et al., 2023; Wadgymar et al., 2019), our findings reveal a predominant downslope migration, particularly towards the east, with certain movement to the northwest. This migration pattern is related to the dynamics of the Lomas ecosystem, where the fog presence, vital for vegetation, is influenced by the thermal inversion phenomenon. The thermal inversion, induced by the subtropical Pacific Anticyclone and intensified by the Humboldt current, limits fog presence above 1000 masl, impacting vegetation distribution (Del Río et al., 2018; Dillon & Rundel, 1990; Muenchow, et al., 2013; Ruhm et al., 2022). Studies demonstrate that the dense fog contributes to water availability at higher elevations before the thermal inversion, fostering a higher concentration of vegetation within the typical ecosystem range 500–800 masl (Moat et al., 2021; Muenchow, et al., 2013).

However, the persistence and interaction of vegetation, including trees and shrubs, alongside rock outcrops are pivotal in capturing soil moisture and facilitating vegetation growth at lower elevations (Borthagaray et al., 2010; Dillon & Rundel, 1990). In the future, the dynamics of species interactions will be shaped by the varying abilities of species to survive, migrate, and engage with each other, influencing the composition of the Lomas ecosystem (Moat et al., 2021). Incorporating biological interactions and dispersal limitations into SDMs could enhance our understanding of species responses to environmental change.

4.2. Low-elevation species lose their habitat, while high-elevation species move further to expand their habitat

In both the Andes and Lomas regions, high-elevation species are projected to undergo larger shifts than their middle or low-elevation counterparts. This involves greater displacements in the Andes and more pronounced downslope elevation shifts in the Lomas. Low-elevation species, in general, exhibited more substantial changes in habitat suitability, while high-elevation species demonstrated a subtle expansion in habitat. In our analysis, high-elevation species are unexpectedly found above the thermal inversion layer (> 2300 m) within the Lomas region. While this elevation marks a transition zone where vegetation characteristic of montane environments may coexist with Lomas flora, the climate tends to be cooler than in typical Lomas habitats, with varying precipitation levels (Castro et al., 2021). These findings raise questions about the ecological dynamics between the Andean and Lomas ecosystems. Considering the projected increase in temperatures, particularly in high-elevation areas, these species are likely to face warmer conditions in the future. As a response, there may be a need for these species to migrate downslope, seeking cooler temperatures and suitable habitat conditions. Moreover, high-elevation species, often situated at the trailing edge of their ranges, can be susceptible to population decline due to limited gene flow from better-adapted populations (Davis & Shaw, 1994; Sexton et al., 2016).

It is important to recognize that the thermal inversion layer can significantly impact vegetation persistence, potentially limiting suitable habitats and necessitating extensive range shifts to lower elevations. High-elevation species may face a particularly challenging scenario, requiring significant migratory efforts to access projected suitable habitats. In contrast, low and middle-elevation species, such as shrubs and herbs thriving within the fog layer's interaction with vegetation, may not face the same migration imperative. However, at these lower elevations, there is a risk as these plants may encounter areas with sandy soils lacking water retention capacity, thus making the environment less optimal. Successful colonization of these very low-elevation areas may only be feasible for species highly adapted to aridity, as observed in certain Lomas ecosystems currently (Dillon & Rundel, 1990; Muenchow, et al., 2013).

4.3. Endemic species are the exception

The distribution shift trend reveals a significant contrast when considering our species' endemic status. In both regions, endemic species were anticipated to move upslope, while non-endemic species were projected to move downslope. Furthermore, endemics demonstrated a more substantial and positive change in habitat suitability, gaining habitat, in contrast to non-endemics experiencing smaller yet negative changes. Globally, endemic species are often seen as more vulnerable to climate change due to their small populations, limited dispersal capabilities, and confinement to specific geological formations (Dirnböck et al., 2011; Zera & Denno, 1997). However, in the unique Lomas ecosystem, where species have evolved to persist in extreme arid conditions, endemic Lomas species possess traits that may require fewer or less drastic adaptations to thrive in the future. As observed in other studies, endemic species could tolerate new conditions or evolve to avoid extinction (Wadgymar et al., 2019). Several endemic species in our study, particularly those within the Cactaceae family, showcase traits commonly associated with desert environments, such as succulence (Revilla et al., 2015; Arce, 2019). Moreover, species with deep roots, such as *T. cacalioides* or *C. spinosa*, demonstrate the ability to access water from deeper layers of the soil. Additionally, certain species, like *Tillandsia spp.*, display morphological adaptations, including rosette leaves for water accumulation and CAM metabolism, enabling survival even in the absence of functional roots (Pauca-Tanco et al., 2020). This positive response could also be linked to occasional ENSO events, which may provide bridging conditions enabling populations to expand beyond their typically restricted distribution areas (Dillon & Rundel, 1990). While recognizing the resilience and adaptability of several Lomas species to environmental changes, predicting the extent of these changes is challenging due to the escalating extremity of factors in this region. High-resolution climatological studies tailored to the complex topography and climatic processes are needed (Tovar et al., 2022). Microclimatologies capturing fine-scale variations could enhance the accuracy and ecological authenticity of SDMs, particularly for species with narrow ecological niches (Haesen et al., 2023).

4.4. Changing habitats drive divergent responses of Lomas species

Climate change induces ecological and evolutionary responses, affecting species migration and potentially reducing colonization success and increasing extinction risk, particularly for high-elevation

and non-endemic species. However, populations located at intermediate elevations in Lomas may enhance adaptability through improved water capture and genetic variability from pollen and seed exchange with better-suited sources (Davis & Shaw, 1994). In the Andes, species responded differently between scenarios: *Gamochaeta purpurea* and *Solanum tuberosum* are projected to undergo the most significant horizontal and vertical shifts, respectively, under the SSP1-2.6 scenario, while *Cylindropuntia tunicate* and *Caiophora cirsiifolia* were identified for the SSP3-7.0 scenario. However, in the Lomas region, only one species appears to be most influenced, *Caiophora cirsiifolia*, emphasizing distinct adaptive strategies. While most of these species exhibit traits conducive to this response, such as succulence and endurance in dry environments, as well as widespread distribution in Lomas (exceptional case, *S. tuberosum*, a cultivated species; Dillon (2005)), others like *C. tunicate* face current threats (Arana, 2019). However, accurately predicting species movements remains challenging, particularly given the rapid pace of projected climate change, which hampers successful responses. This challenge is compounded by habitat fragmentation and degradation resulting from human activities (Halpin, 1997; Honnay et al., 2002). Urban and agricultural land use globally poses obstacles to distributional changes and gene flows between populations (Davis & Shaw, 1994), with pronounced impacts on Lomas systems characterized by a discontinuous and fragmented distribution along the coast (Arakaki & Cano, 2003; Manrique et al., 2014; Rundel & Dillon, 1998). Increasing urbanization puts Lomas ecosystems at higher risk from climate change and desertification, particularly given their proximity to millions of coastal city dwellers (Alonso & Jesús, 2021; Flood & Niewiadomski, 2022; PNUD, 2018).

Consequently, the Lomas ecosystem faces significant habitat loss, particularly affecting at least 23 species. Non-migratory species may encounter higher extinction risks (Wadgymar et al., 2019), while endemics may possess adaptations for resilience. As a result of chronic water limitations and precipitation variability, species use a variety of strategies in order to cope with these challenges, including drought tolerance and avoidance (Ogle & Reynolds, 2004; Reynolds et al., 1999). Concerning our selected Lomas species for supporting urban green ecosystems, *Solanum peruvianum*, a genetic resource related to tomatoes, *Trixis cacalioides* and *Stenomesson flavum*, are projected to expand their habitat beyond coastal Lomas. *T. cacalioides* and *S. peruvianum* are both prominent in the Lomas of Lima and can grow all year round (Del Castillo, 2016; Trinidad et al., 2012). As middle-elevation shrubs, these species can effectively seek water, mitigating drought challenges (Rolando et al., 2017; Sotomayor & Lortie, 2016; Tovar et al., 2018). Although the endemic geophyte bulbous *S. flavum*, located at medium elevation, is forecasted to be less affected by climate warming, it is currently in decline, likely due to urbanization (Paraskevopoulou et al., 2020). Nevertheless, there is a latent risk of extinction for this unique vegetation. Among the selected species, *Heliotropium arborescens*, *Oziroe biflora*, and *Tillandsia latifolia* under SSP1-2.6 face habitat loss. *H. arborescens* is a dominant shrub in Lomas that influences water retention and provides shade to lower-elevation herbaceous species like other shrubs (Paraskevopoulou et al., 2020; Sotomayor & Lortie, 2016; Velásquez, 2014). *Oziroe biflora*, a bulbous species with deciduous leaves found at low elevations, is at risk of habitat loss, as population decline has been reported (Cuba-Melly & Odar, 2018; Paraskevopoulou et al., 2020). Despite adaptive strategies, these species are vulnerable. *T. latifolia*, reliant on coastal fog, may lose habitat under moderate

scenarios but may be able to improve in severe scenarios. In more severe future scenarios, environmental changes, including global water cycle intensification, may provide temporary water availability (Tschirschwitz et al., 2024), helping species adapt. In light of future uncertainty, research is needed to understand habitat dynamics and resilience as more complex interactions might influence them.

Furthermore, the exclusion of certain Lomas species highlights their rarity and imminent threat, underscoring the urgent need for comprehensive research (Flood & Niewiadomski, 2022). Experimental studies are vital to grasp their response under local conditions (Flores & Van Meerbeek, 2024) while ensuring holistic conservation measures, including their integration into urban green design, are essential for sustainability (Segar et al., 2022). Addressing these gaps is crucial for Lomas preservation amid urbanization and climate change.

5. Conclusion

Our study emphasizes the significant impact of climate change on Lomas plant species, revealing downslope distribution shifts in response to changing environmental conditions. Both the Andes and Lomas regions are experiencing declines in habitat suitability, with the Lomas region being the most vulnerable, particularly under the most drastic SSP scenario. Endemic species are predicted to migrate upslope, utilizing their unique adaptations, while non-endemic species are expected to move downslope.

As climate change intensifies, there is a crucial need to protect the Lomas ecosystems. Endemic Lomas species show a somewhat positive response to habitat expansions. High-elevation species are projected to undergo larger range shifts, while low-elevation species experience more pronounced habitat alterations. The differences between species, which are driven by key traits and vegetation interaction, play a vital role in their migration response. However, some species are already facing threats that could alter this response in the future.

The omission of rare and endangered Lomas species highlights the need for extensive research. Conservation strategies must be tailored to the distinct characteristics of Lomas ecosystems and the unique adaptation mechanisms of endemic and non-endemic species. Implementing conservation measures that also consider urbanization and climate change is vital for maintaining ecological balance, with urban design and green infrastructure strengthening the future resilience of Lomas species.

Declarations

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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Author Contribution

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Sarah Bracke and Sofia Flores. Modeling was supervised by Stef Haesen and Koenraad Van Meerbeek. The first draft of the manuscript was written by Sofia Flores and all authors commented on previous versions of the manuscript. All authors reviewed and approved the final manuscript.

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References

1. Alonso C, Jesús R (2021) Problemática socioambiental de las lomas costeras de Lima: una revisión. Revista de Ciencias Sociales 2(2):18–28
2. Arakaki M, Cano A (2003) Composición florística de la cuenca del río Ilo-Moquegua y Lomas de Ilo, Moquegua, Perú. Revista Peruana de Biol 10(1):5–19. https://doi.org/10.15381/rpb.v10i1.2472
3. Arana A (2019) Ecología y biogeografía de las plantas vasculares de las lomas del Perú Central. Universidad Nacional Mayor de San Marcos
4. Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22(1):42–47. https://doi.org/10.1016/j.tree.2006.09.010
5. Arce R (2019) Efecto del cambio climático y uso del suelo en la distribución de los taxones endémicos de Cactaceae Juss. en la región Arequipa, 2017–2018. Universidad Nacional de San Agustín de Arequipa
6. Arias PA, Bellouin N, Coppola E, Jones RG, Krinner G, Marotzke J, Naik V, Palmer MD, Plattner G, Rogelj J, Rojas M, Sillmann J, Storelvmo T, Thorne PW, Trewin B, Achuta Rao K, Adhikary B, Allan RP, Armour K, Zickfeld K (2021) Technical Summary. Climate Change 2021 – The Physical Science Basis. Cambridge University Press, pp 35–144. https://doi.org/10.1017/9781009157896.002
7. Bivand R, Keitt T, Rowlingson B (2023) rgdal: Bindings for the Geospatial Data Abstraction Library. https://r-forge.r-project.org/projects/rgdal/

8. Bond TC, Scott CE (2022) Aerosol and precursor gas emissions. In Aerosols and Climate (pp. 299–342). Elsevier. https://doi.org/10.1016/B978-0-12-819766-0.00006-7
9. Borthagaray AI, Fuentes MA, Marquet PA (2010) Vegetation pattern formation in a fog-dependent ecosystem. J Theor Biol 265(1):18–26. https://doi.org/10.1016/j.jtbi.2010.04.020
10. Castro A, Davila C, Laura W, Cubas F, Avalos G, López-Ocaña C, Villena D, Valdez M, Urbiola J, Trebejo I, Menis L, Marín D (2021) Climas del Perú [Climates of Peru]. In Senamhi (RED ACTIVA, Vol. 53, Issue 9)
11. Cuba-Melly N, Odar J (2018) Lima – Perú Biologist 16(2):237–250. https://doi.org/10.24039/rtb2018162245. Diversidad De Flora Vascular De Las Lomas De Granados Y Posibles Amenazas a Su Conservación, Provincia De Huaral
12. Danielson JJ, Gesch DB (2011) Global multi-resolution terrain elevation data 2010 (GMTED2010). https://pubs.usgs.gov/of/2011/1073/pdf/of2011-1073.pdf
13. Davis MB, Shaw RG, Beer J, Mende W, Stellmacher R (1994) Quat Sci Rev (369). Smithsonian Institution Press. www.sciencemag.org
14. Del Castillo J (2016) Estudio de la variación espacio-temporal de la comunidad vegetal de las lomas de Carabayllo (Lima, Perú) durante el 2013 como contribución a su gestión
15. Del Río C, Garcia JL, Osses P, Zanetta N, Lambert F, Rivera D, Siegmund A, Wolf N, Cereceda P, Larraín H, Lobos F (2018) ENSO influence on coastal fog-water yield in the Atacama desert, Chile. Aerosol Air Qual Res 18(1):127–144. https://doi.org/10.4209/aaqr.2017.01.0022
16. Dillon M (2005) The Solanaceae of the Lomas formations of coastal Peru and Chile. A Festschrift for Willian G. D'Arcy, September, pp 131–156
17. Dillon M, Tu T, Xie L, Silvestre Q, V., Wen J (2009) Biogeographic diversification in Nolana (Solanaceae), a ubiquitous member of the Atacama and Peruvian deserts along the western coast of South America. J Syst Evol 47(5):457–476. https://doi.org/10.1111/j.1759-6831.2009.00040.x
18. Dillon M, Rundel PW (1990) The botanical response of the Atacama and Peruvian desert floras to the 1982-83 El Niño event. Elsevier Oceanogr Ser 52(C):487–504. https://doi.org/10.1016/S0422-9894(08)70047-3
19. Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob Change Biol 17(2):990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x
20. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, Mcclean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1):27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x
21. Ferreyra R (1961) Lomas costaneras del extremo sur del Perú. Boletín de La Sociedad Argentina de Botánica 9:87–120

22. Flood Chávez DI, Niewiadomski P (2022) The urban political ecology of fog oases in Lima, Peru. Geoforum, 129(December 2021), 1–12. https://doi.org/10.1016/j.geoforum.2022.01.001
23. Flores S, Van Meerbeek K (2024) Endangered Lomas plant communities and their potential on green roofs in Peru. Landsc Urban Plann 247:105061. https://doi.org/10.1016/j.landurbplan.2024.105061
24. Garreaud R (1999) Multiscale Analysis of the Summertime Precipitation over the Central Andes. Am Meteorological Soc 127:901–921
25. Gonzales FN, Craven D, Armesto JJ (2023) Islands in the mist: A systematic review of the coastal lomas of South America. Journal of Arid Environments, 211(July 2022), 104942. https://doi.org/10.1016/j.jaridenv.2023.104942
26. González-Mancebo JM, Bello-Rodríguez V, Cubas J, Parada-Díaz J, Bañares A, Palomares A, Martín-Esquivel J, Arco M (2022) Assessing global warming vulnerability of restricted and common plant species in alpine habitats on two oceanic islands. 32(14):4831–4851. https://doi.org/10.21203/rs.3.rs-2312185/v1
27. Haesen S, Lenoir J, Gril E, De Frenne P, Lembrechts JJ, Kopecký M et al (2023) Microclimate reveals the true thermal niche of forest plant species. Ecol Lett 26:2043–2055. https://doi.org/10.1111/ele.14312
28. Halpin PN (1997) Global Climate Change and Natural-Area Protection: Management Responses and Research Directions. Ecol Appl 7(3):828. https://doi.org/10.2307/2269436
29. Hernández-Fuentes C, Galmés J, Bravo LA, Cavieres LA (2023) Plant Biol 25(5):793–802. https://doi.org/10.1111/plb.13539
30. Hesse R (2012) Spatial distribution of and topographic controls on Tillandsia fog vegetation in coastal southern Peru: Remote sensing and modelling. J Arid Environ 78:33–40. https://doi.org/10.1016/j.jaridenv.2011.11.006
31. Hijmans RJ (2023) raster: Geographic Data Analysis and Modeling. https://cran.r-project.org/package=raster
32. Hijmans RJ, Phillips S, Leathwick J, Elith J (2023) dismo: Species Distribution Modeling. https://cran.r-project.org/package=dismo
33. Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199(2):142–152. https://doi.org/https://doi.org/10.1016/j.ecolmodel.2006.05.017
34. Honnay O, Verheyen K, Butaye J, Jacquemyn H, Bossuyt B, Hermy M (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecol Lett 5(4):525–530. https://doi.org/10.1046/j.1461-0248.2002.00346.x
35. Intergovernmental Panel on Climate Change (2023) Technical Summary. In Climate Change 2021 – The Physical Science Basis (pp. 35–144). Cambridge University Press. https://doi.org/10.1017/9781009157896.002
36. Jiménez L, Soberón J (2020) Leaving the area under the receiving operating characteristic curve behind: An evaluation method for species distribution modelling applications based on presence-

only data. Methods Ecol Evol 11(12):1571–1586. https://doi.org/10.1111/2041-210X.13479

37. Jump AS, Peñuelas J (2005) Running to stand still: Adaptation and the response of plants to rapid climate change. Ecol Lett 8(9):1010–1020. https://doi.org/10.1111/j.1461-0248.2005.00796.x
38. Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Sci Data 4:1–20. https://doi.org/10.1038/sdata.2017.122
39. Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla-Buitrago GE, Boria RA, Soley-Guardia M, Anderson RP (2021) ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods Ecol Evol 12(9):1602–1608. https://doi.org/10.1111/2041-210X.13628
40. Lake TA, Runquist RDB, Moeller DA (2020) Predicting range expansion of invasive species: Pitfalls and best practices for obtaining biologically realistic projections. Divers Distrib 26:1767–1779. https://doi.org/https://doi.org/10.1111/ddi.13161
41. Maitner B (2023) BIEN: Tools for Accessing the Botanical Information and Ecology Network Database. https://cran.r-project.org/package=BIEN
42. Manrique R (2011) El Niño Southern Oscillation and its effect on fog oases along the Peruvian and Chilean coastal deserts [Università di Bologna]. https://amsdottorato.unibo.it/3436/
43. Manrique R, Ferrari C, Pezzi G (2010) The influence of El Niño Southern Oscillation (ENSO) on fog oases along the Peruvian and Chilean coastal deserts. 5th International Conference on Fog, Fog Collection and Dew Münster, Germany, July. https://doi.org/10.13140/2.1.2522.7207
44. Manrique R, Ricotta C, Ferrari C, Pezzi G (2014) Latitudinal pattern in plant composition along the Peruvian and Chilean fog oases. Plant Biosystems 148(5):1002–1008. https://doi.org/10.1080/11263504.2014.918059
45. Mendoza-Fernández AJ, Fernández-Ceular Á, Alcaraz-Segura D, Ballesteros M, Peñas J (2022) The Fate of Endemic Species Specialized in Island Habitat under Climate Change in a Mediterranean High Mountain. Plants 11:3193. https://doi.org/10.3390/plants11233193
46. Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species ' distributions: what it does, and why inputs and settings matter. https://doi.org/10.1111/j.1600-0587.2013.07872.x. March 1–12
47. Moat J, Orellana-Garcia A, Tovar C, Arakaki M, Arana C, Cano A, Faundez L, Gardner M, Hechenleitner P, Hepp J, Lewis G, Mamani JM, Miyasiro M, Whaley OQ (2021) Seeing through the clouds – Mapping desert fog oasis ecosystems using 20 years of MODIS imagery over Peru and Chile. Int J Appl Earth Obs Geoinf 103. https://doi.org/10.1016/j.jag.2021.102468
48. Muenchow J, Bräuning A, Rodríguez EF, von Wehrden H (2013) Predictive mapping of species richness and plant species' distributions of a Peruvian fog oasis along an altitudinal gradient. Biotropica 45(5):557–566. https://doi.org/10.1111/btp.12049
49. Muenchow J, Hauenstein S, Bräuning A, Bäumler R, Rodríguez EF, Von Wehrden H (2013) Soil texture and altitude, respectively, largely determine the floristic gradient of the most diverse fog oasis in the

Peruvian desert. J Trop Ecol 29(5):427–438. https://doi.org/10.1017/S0266467413000436

50. Nenén HK, Araújo MB (2011) Choice of threshold alters projections of species range shifts under climate change. Ecol Model 222(18):3346–3354. https://doi.org/10.1016/j.ecolmodel.2011.07.011
51. Ogle K, Reynolds JF (2004) Plant responses to precipitation in desert ecosystems: Integrating functional types, pulses, thresholds, and delays. Oecologia 141(2):282–294. https://doi.org/10.1007/s00442-004-1507-5
52. Owens H, Barve V, Chamberlain S (2023) spocc: Interface to Species Occurrence Data Sources (R package version 1.2.2). https://cran.r-project.org/package=spocc
53. Paraskevopoulou AT, Tsarouchas P, Londra PA, Kamoutsis AP (2020) The Effect of Irrigation Treatment on the Growth of Lavender Species in an Extensive Green Roof System. Water 12(3):863. https://doi.org/10.3390/w12030863
54. Pauca-Tanco GA, Villasante-Benavides F, Villegas-Paredes L, Luque-Fernández CR, Quispe-Turpo JP (2020) Distribución y caracterización de las comunidades de Tillandsia (Bromeliaceae) en el sur de Perú y su relación con la altitud, pendiente y orientación. Ecosistemas 29(3):1–11
55. Péfaur JE (1982) Dynamics of Plant Communities in the Lomas of Southern Peru. In Source: Vegetatio (Vol. 49, Issue 3)
56. Phillips S, Dudik M (2008) Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. Ecography, 31(161)
57. Phillips SJ, Anderson RP, Dudik M, Schapire RE, Blair ME (2017) Opening the black box: An open-source release of Maxent. Ecography 40:887–893
58. Pinto R, Kirberg A (2005) Conservation status of Eriosyce (Cactaceae) in northernmost Chile. Bradleya 23(23):7–16. https://doi.org/10.25223/brad.n23.2005.a3
59. PNUD (2018) Retos y oportunidades en la conservación de las lomas de Lima Metropolitana. Programa de Las Naciones Unidas Para El Desarrollo, 1, 15. https://www.undp.org/content/dam/peru/docs/Publicaciones medio ambiente/Brochure_24PP_FINAL.pdf
60. Poggio L, de Sousa LM, Batjes NH, Heuvelink GBM, Kempen B, Ribeiro E, Rossiter D (2021) SoilGrids 2.0: producing soil information for the globe with quantified spatial uncertainty. SOIL 7:217–240. https://doi.org/10.5194/soil-7-217-2021
61. Revilla I, Fernández R, Crespo S, Astocaza M (2015) Candes 1(November):38–39. http://candes.net/wp-content/uploads/2018/11/8.-RN-Lachay-interactivo.pdf Diversidad y Distribución de la Familia Cactaceae y Avifauna Asociada en la Reserva Nacional de Lachay [versión PDF]
62. Reynolds JF, Virginia RA, Kemp PR, De Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. Ecol Monogr 69(1):69–106. https://doi.org/10.1890/0012-9615(1999)069[0069:IODODS]2.0.CO;2
63. Rolando JL, Castillo D, Padilla JD, Quinteros D, Z., Sánchez E (2017) Annual seasonality and diversity patterns of the plant community in a fog oasis ecosystem in the city of Lima. Trop Ecol 58(4):781–

791

64. Rubenstein MA, Weiskopf SR, Bertrand R, Carter SL, Comte L, Eaton MJ, Johnson CG, Lenoir J, Lynch AJ, Miller BW, Morelli TL, Rodriguez MA, Terando A, Thompson LM (2023) Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. In Environmental Evidence. BioMed Cent Ltd 12(1). https://doi.org/10.1186/s13750-023-00296-0
65. Ruhm J, Böhnert T, Mutke J, Luebert F, Montesinos-Tubée DB, Weigend M (2022) Two Sides of the Same Desert: Floristic Connectivity and Isolation Along the Hyperarid Coast and Precordillera in Peru and Chile. Front Ecol Evol 10:1–17. https://doi.org/10.3389/fevo.2022.862846
66. Rundel PW, Dillon MO (1998) Ecological patterns in the Bromeliaceae of the lomas formations of Coastal Chile and Peru. Plant Syst Evol 212(3–4):261–278. https://doi.org/10.1007/BF01089742
67. Rundel PW, Palma B, Dillon M, 0, Sharifi MR, Nilsen ET, Boonpragob K (1997) Re vista Chilena de. In Historia Natural (Vol. 70)
68. Saupe EE, Qiao H, Hendricks JR, Portell RW, Hunter SJ, Soberón J, Lieberman BS (2015) Niche breadth and geographic range size as determinants of species survival on geological time scales. Glob Ecol Biogeogr 24(10):1159–1169. https://doi.org/10.1111/geb.12333
69. Schulz N, Aceituno P, Richter M (2011) Phytogeographic divisions, climate change and plant dieback along the coastal desert of Northern Chile. Erdkunde 65(2):169–187. https://doi.org/10.3112/erdkunde.2011.02.05
70. Segar J, Callaghan CT, Ladouceur E, Meya JN, Pereira HM, Perino A, Staude IR (2022) Urban conservation gardening in the decade of restoration. Nat Sustain 5(8):649–656. https://doi.org/10.1038/s41893-022-00882-z
71. Serra-Diaz JM, Enquist BJ, Maitner B, Merow C, Svenning JC (2017) Big data of tree species distributions: how big and how good? For Ecosyst 4(1). https://doi.org/10.1186/s40663-017-0120-0
72. Sexton JP, Hufford MB, Bateman AC, Lowry DB, Meimberg H, Strauss SY, Rice KJ (2016) Climate structures genetic variation across a species' elevation range: A test of range limits hypotheses. Mol Ecol 25(4):911–928. https://doi.org/10.1111/mec.13528
73. Sotomayor D, Lortie CJ (2016) Direct and indirect consequences of dominant plants in arid environments. Figshare, September. https://doi.org/10.6084/m9.figshare.3315961.v1
74. Syfert MM, Joppa L, Smith MJ, Coomes DA, Bachman SP, Brummitt NA (2014) Using species distribution models to inform IUCN Red List assessments. Biol Conserv 177:174–184. https://doi.org/10.1016/j.biocon.2014.06.012
75. 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., … Hollingsworth, P. M. (2022). Understanding climate change impacts on biome and plant distributions in the Andes: Challenges and opportunities. Journal of Biogeography, 49(8), 1420–1442. https://doi.org/10.1111/jbi.14389

76. Tovar C, Infantas ES, Roth VT (2018) Plant community dynamics of lomas fog oasis of Central Peru after the extreme precipitation caused by the 1997-98 El Niño event. PLoS ONE 13(1):1–19. https://doi.org/10.1371/journal.pone.0190572
77. Trinidad H, Huamán-Melo E, Delgado A, Cano A (2012) Flora vascular de las lomas de Villa María y Amancaes, Lima, Perú. Revista Peruana de Biol 19(2):149–158. https://doi.org/10.15381/rpb.v19i2.834
78. Tschirschwitz J, Werner M, Gao Q, Sime L, Brunello CF (2023) Moisture source changes of precipitation in Europe under SSP1-2.6 and SSP3-7.0 warming. EGU General Assembly 2023, Vienna, Austria, 24–28 Apr 2023, EGU23-17506 https://doi.org/10.5194/egusphere-egu23-17506
79. Valavi R, Elith J, Lahoz-Monfort JJ, Guillera-Arroita G (2019) blockCV: An R package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. Methods Ecol Evol 10(2):225–232. https://doi.org/10.1111/2041-210X.13107
80. Velásquez M (2014) Variación de la composición florística de las lomas de Tacahuay desde el Pleistoceno hasta la actualidad. Tacna-Perú)
81. Venables WN, Ripley B (2002) D. Modern Applied Statistics with S (fourth). Springer. https://www.stats.ox.ac.uk/pub/MASS4/
82. Vollering J, Halvorsen R, Auestad I, Rydgren K (2019) Bunching up the background betters bias in species distribution models. Ecography 42(10):1717–1727. https://doi.org/10.1111/ecog.04503
83. Wadgymar S, MacTavish R, Anderson J (2019) Evolutionary consequences of climate change. In Ecosystem Consequences of Soil Warming: Microbes, Vegetation, Fauna and Soil Biogeochemistry (pp. 29–59). Elsevier. https://doi.org/10.1016/B978-0-12-813493-1.00003-X
84. Wilson AM, Jetz W (2016) Remotely Sensed High-Resolution Global Cloud Dynamics for Predicting Ecosystem and Biodiversity Distributions. PLoS Biol 14(3):e1002415. https://doi.org/10.1371/journal.pbio.1002415
85. Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x
86. Zera AJ, Denno RF (1997) Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology, 42(February 1997), 207–231. https://doi.org/10.1146/annurev.ento.42.1.207
87. Zhou Z, Zhang L, Chen J, She D, Wang G, Zhang Q (2023) Projecting Global Drought Risk Under Various SSP-RCP Scenarios Earth's Future. 1–20. https://doi.org/10.1029/2022EF003420
88. Zizka A, Silvestro D, Andermann T, Azevedo J, Duarte Ritter C, Edler D, Farooq H, Herdean A, Ariza M, Scharn R, Svanteson S, Wengstrom N, Zizka V, Antonelli A (2019) CoordinateCleaner: standardized cleaning of occurrence records from biological collection databases. Methods Ecol Evol 10:7. https://doi.org/10.1111/2041-210X.13152
89. Zomer RJ, Xu J, Trabucco A (2022) Version 3 of the Global Aridity Index and Potential Evapotranspiration Database. Sci Data 9(1):1–15. https://doi.org/10.1038/s41597-022-01493-1

Figures

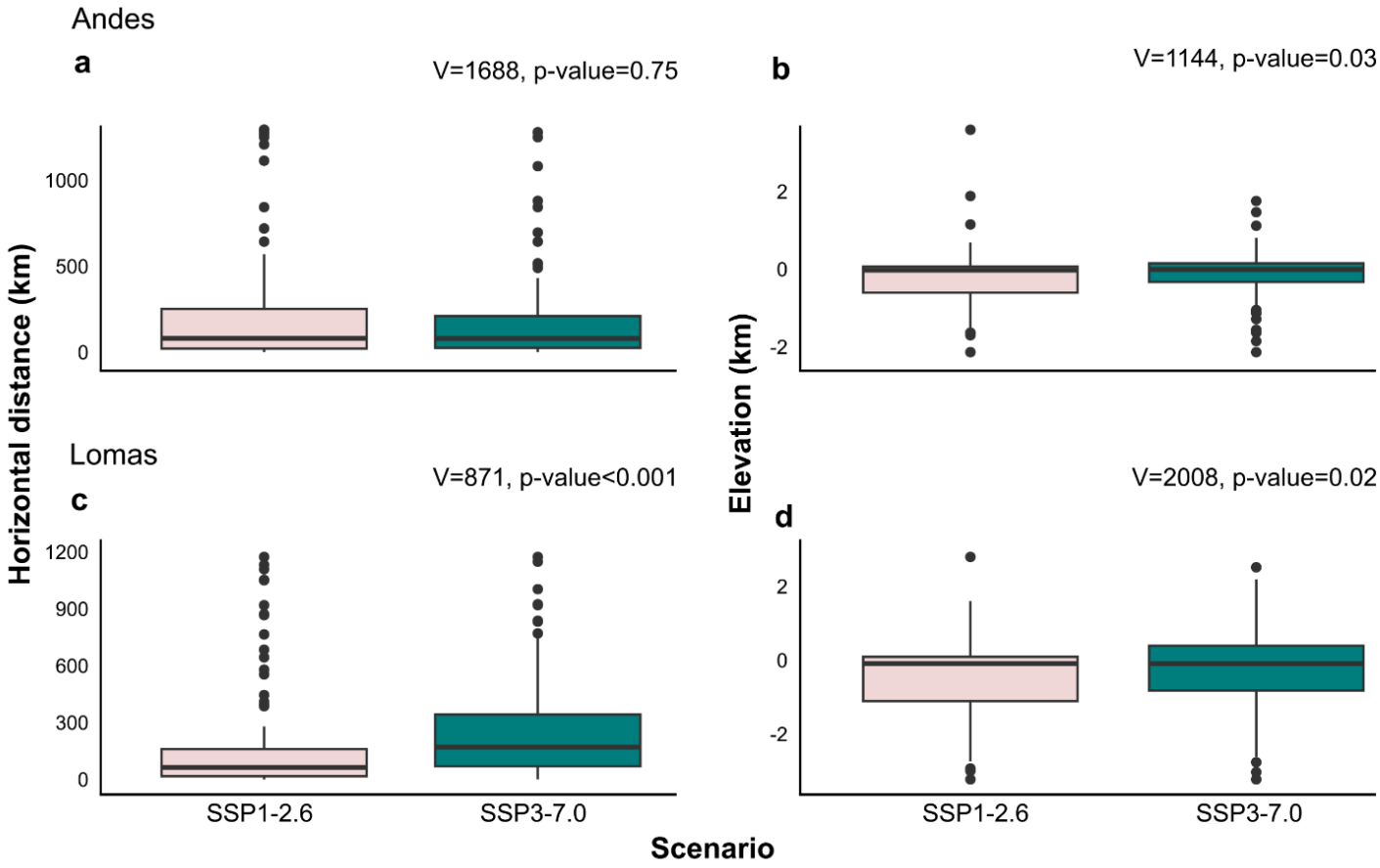

Figure 1

Horizontal (in longitude and latitude direction) distances of projected range shifts for 149 species in the Andes (a) and Lomas region (c), alongside vertical (elevation) shifts in the Andes (b) and Lomas (d) under two SSP (SSP1-2.6 and SSP3-7.0) scenarios. Differences between scenarios were tested using the Wilcoxon signed-rank (V) test

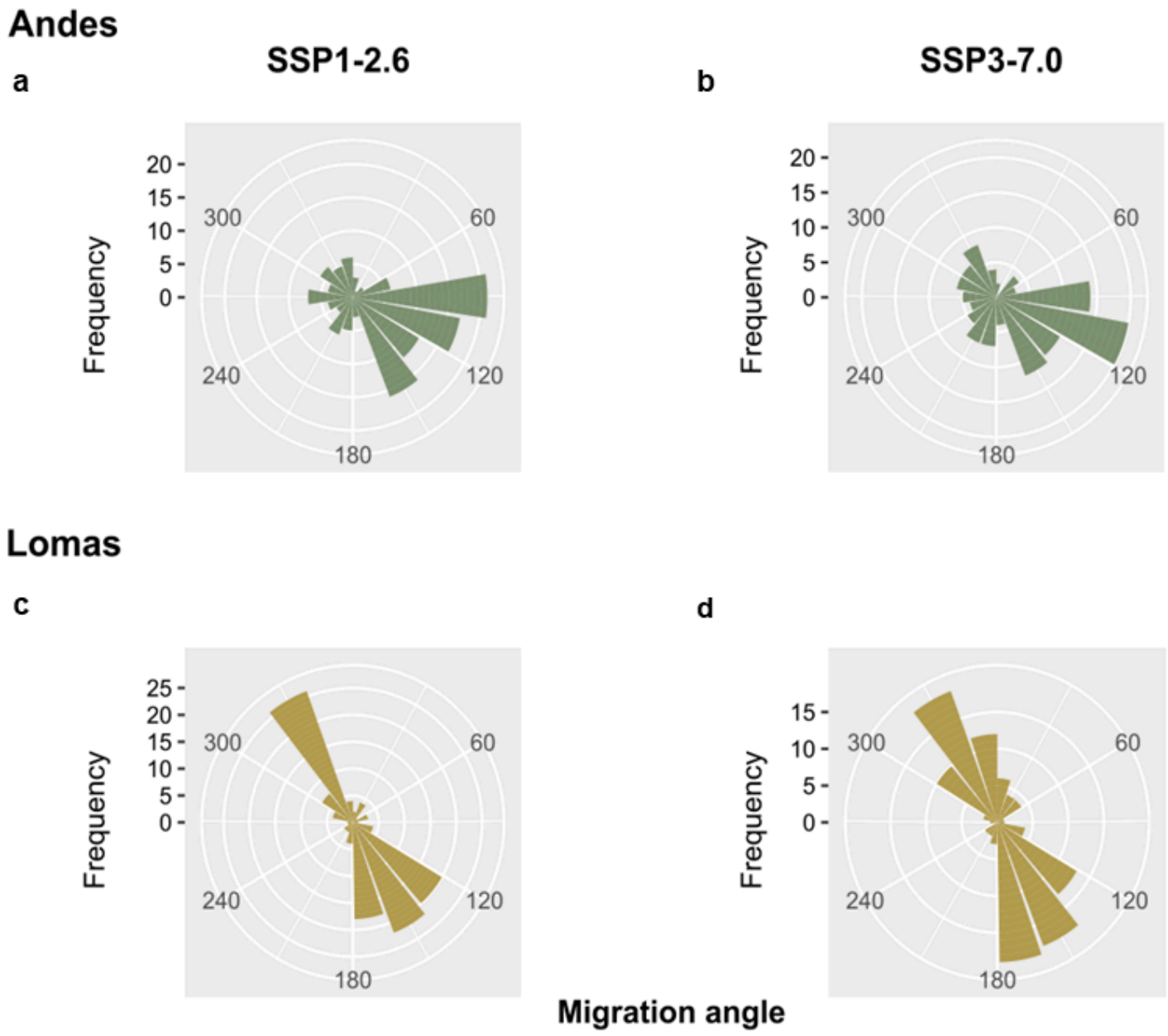

Figure 2

The directions of the projected range shift in two future SSP scenarios in the Andes (green bars) and Lomas regions (yellow bars). The frequency indicates the number of species belonging to each 20-degree interval

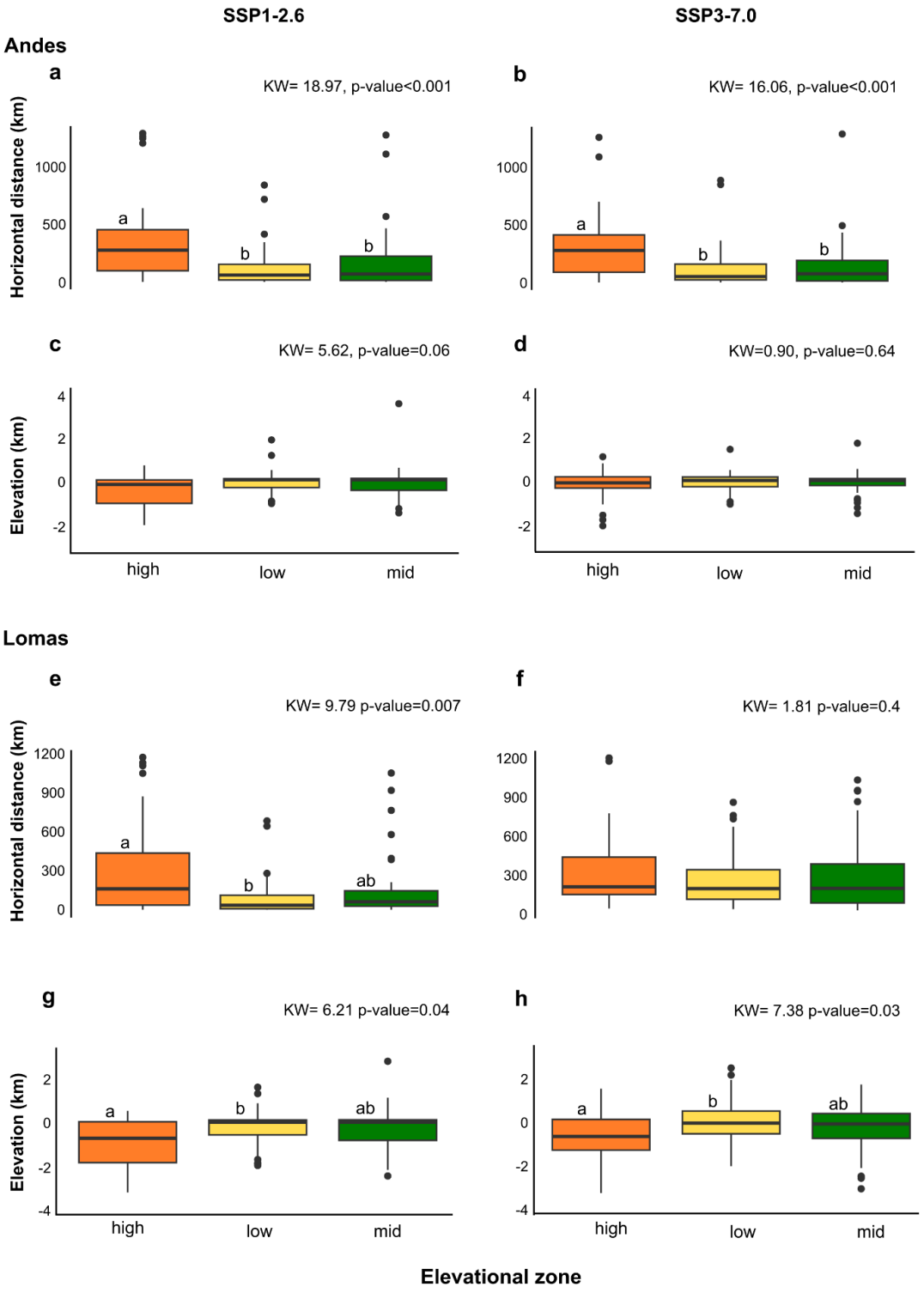

Figure 3

Influence of vegetation elevational zones (high, low, mid) on projected species range shifts under future SSP scenarios. In the Andes, figures (a-b) represent horizontal (latitude and longitude) distances, while figures (c-d) present vertical (elevation) distances under SSP1-2.6 and SSP3-7.0, respectively. Similarly, in Lomas, figures (e-f) depict horizontal distances, and figures (g-h) refer to vertical distances under the

same SSP scenarios. Differences between elevational zones were tested using the Kruskal-Wallis (KW) test and Dunn's post hoc test. Different letters denote significant differences between elevational zones

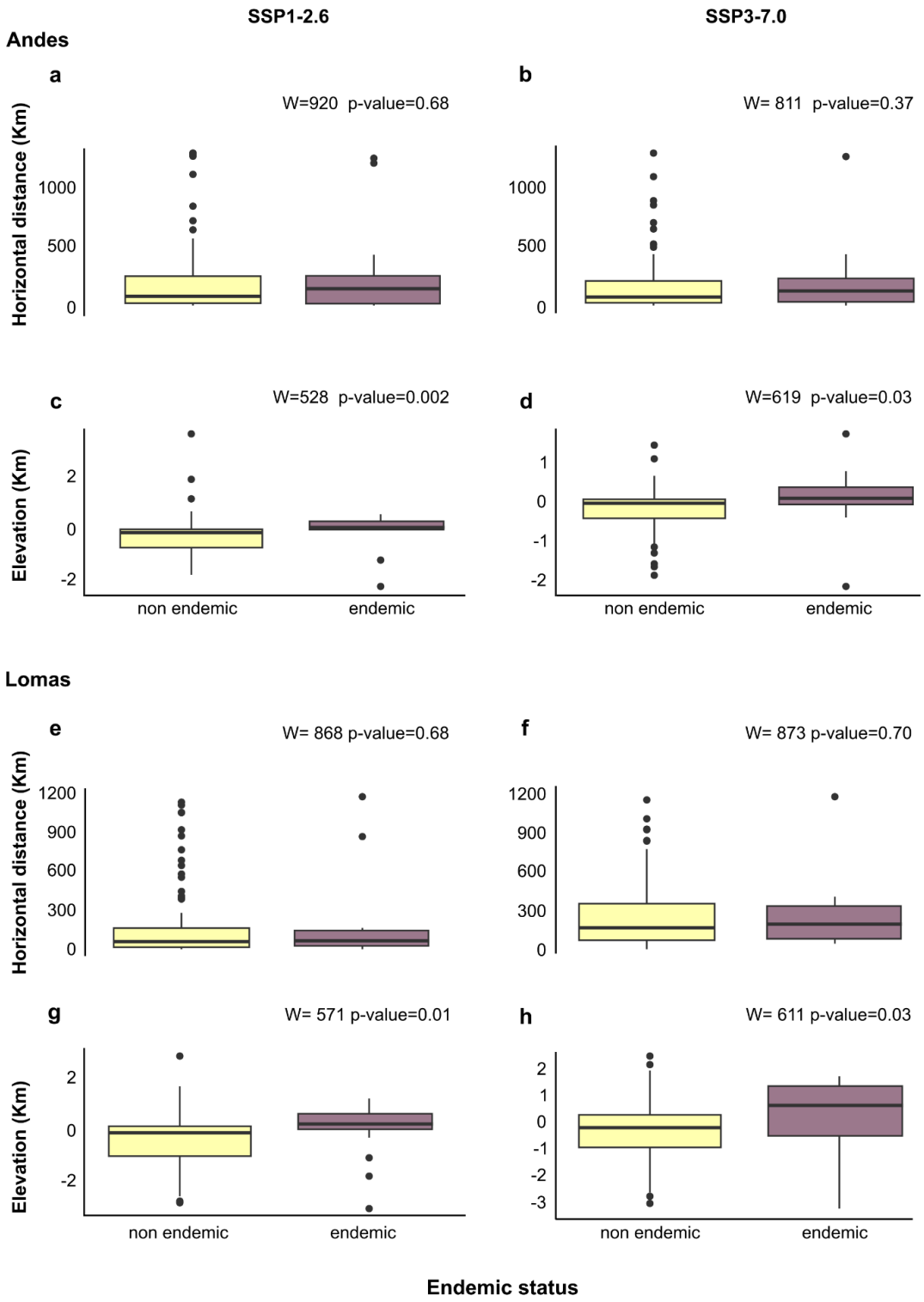

Figure 4

Impact of endemic status on projected species range shifts under future SSP scenarios. In the Andes, figures (a-b) represent horizontal (latitude and longitude) distances, while figures (c-d) present vertical (elevation) distances under SSP1-2.6 and SSP 3-7.0, respectively. Similarly, in Lomas, figures (e-f) depict

horizontal distances, and figures (g-h) refer to vertical distances under the same SSP scenarios. Statistical significance is denoted by p-values and Mann-Whitney (W) statistics for each figure

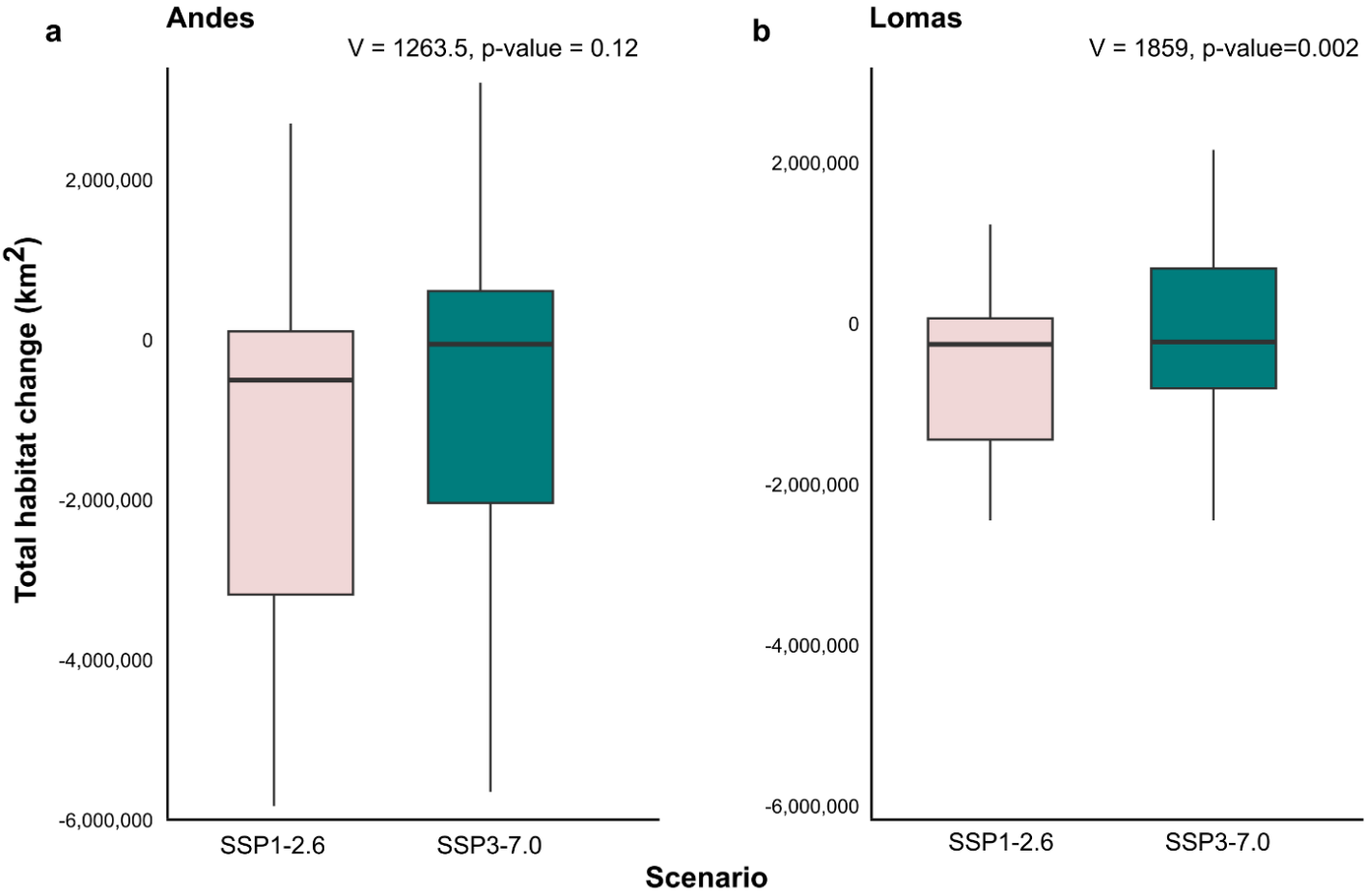

Figure 5

Total habitat change (km^2) in Andes (a) and Lomas (b) under two SSP scenarios. Statistical significance is denoted by p-values and Wilcoxon signed-rank test (V) statistics for paired samples for each figure.

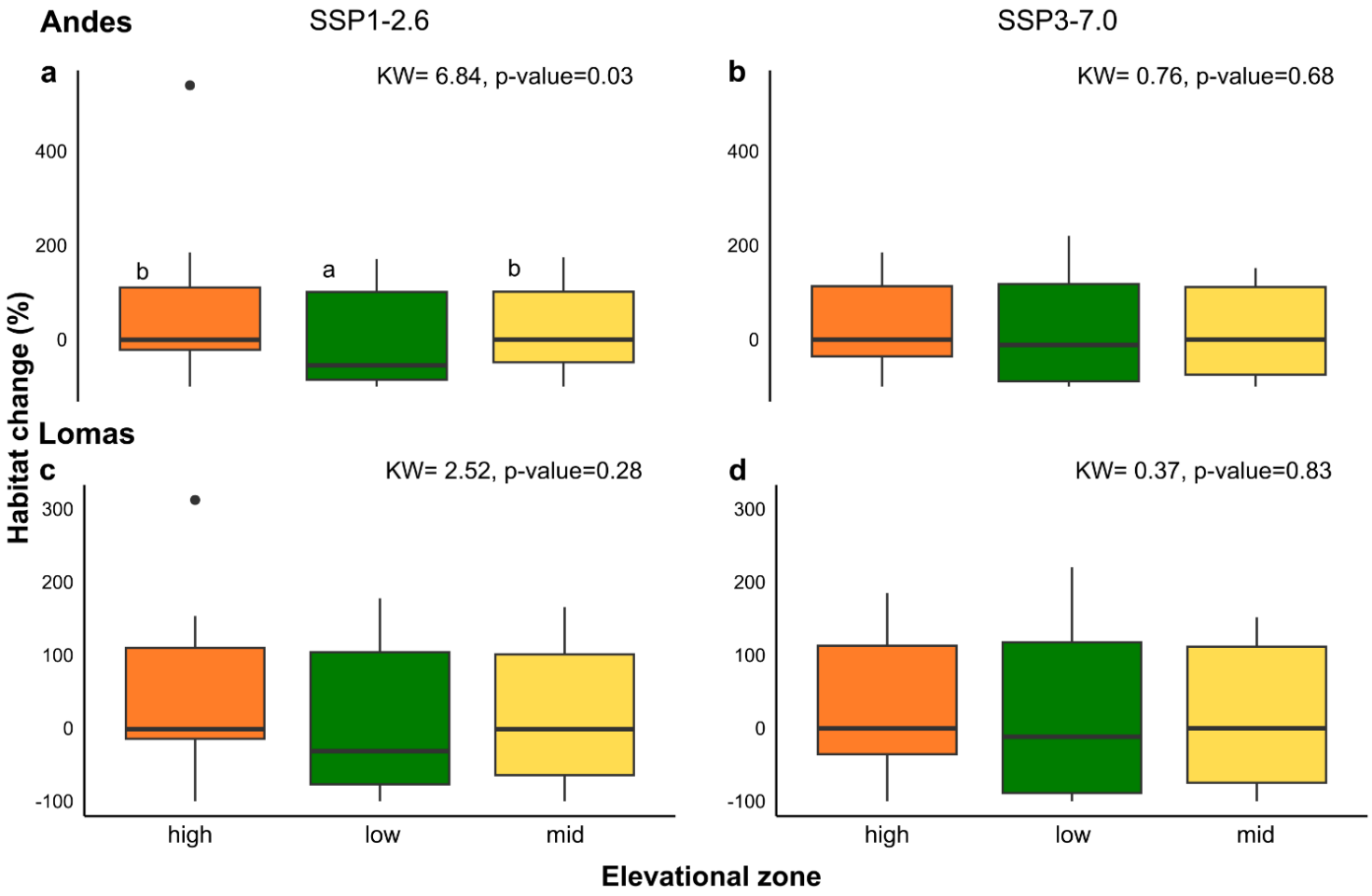

Figure 6

Effect of elevational zone (high, low, mid) preference on total habitat change (%) under SSP1-2.6 and SSP3-7.0 scenarios in the Andes (a-b) and Lomas (c-d) regions. Differences between elevational zones were tested using the Kruskal-Wallis (KW) test and Dunn's post hoc test. Different letters denote significant differences between elevational zones.

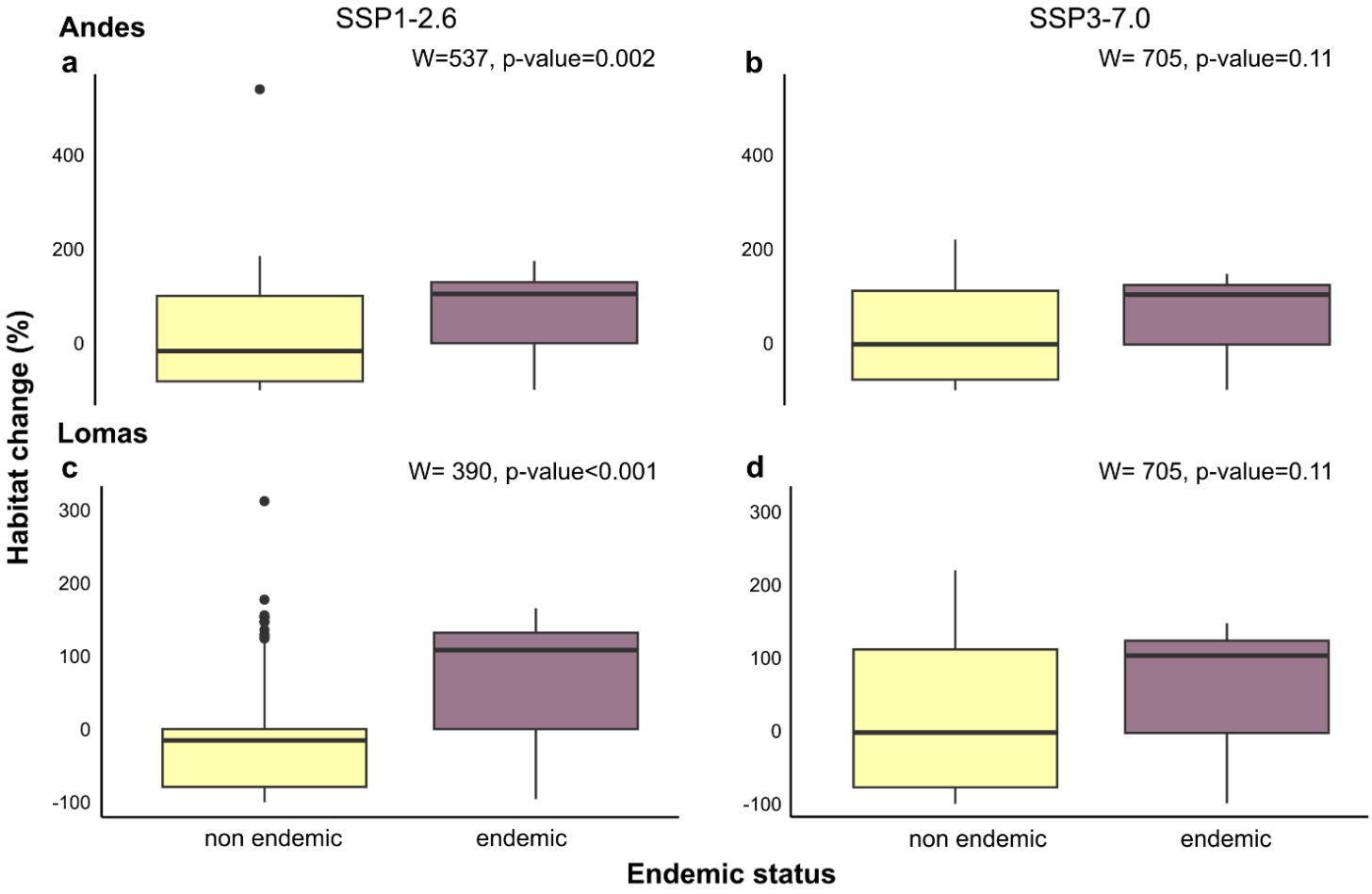

Figure 7

Effect of endemic status on habitat change (%) under SSP1-2.6 and SSP3-7.0 scenarios in the Andes (a-b) and Lomas (c-d) regions. Statistical significance is denoted by p-values and Mann-Whitney (W) statistics for each figure.

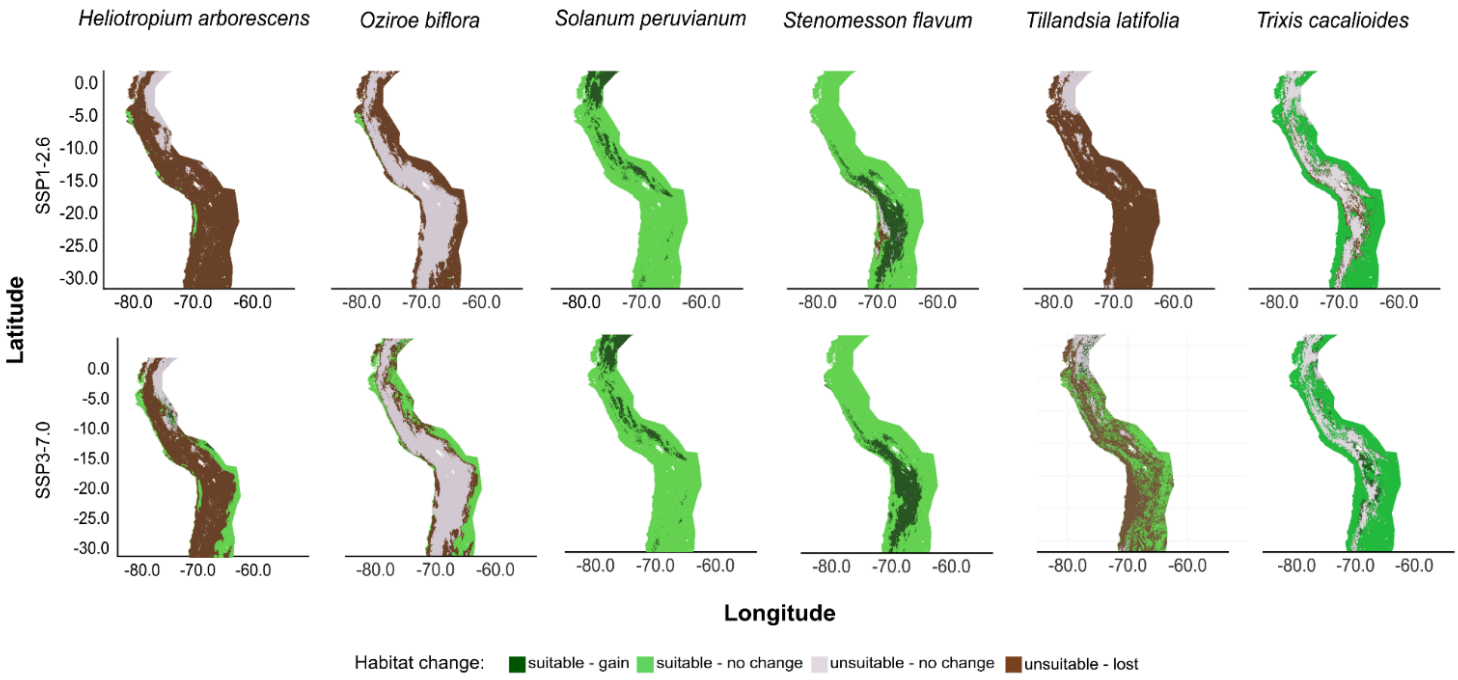

Figure 8

Binary distribution maps indicating the potential suitable area for six selected Lomas species around Lima for the Lomas region's extent under the current climate, SSP1-2.6 and SSP3-7.0 (both for the distant future (2071-2100). Colors on the map denote habitat change

Supplementary Files

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