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RESEARCH ARTICLE



Biogeography and climate change threats of supersect. *Tacsonia* (subgenus *Passiflora*), in Peru

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Abstract

Supersection *Tacsonia* (*Passiflora* L.) is a high-Andean lineage whose geographic restriction and environmental specialization make it particularly vulnerable to ongoing climate change. However, broad-scale evidence integrating distribution patterns, endemism, protection coverage, and future habitat stability remains limited for the Peruvian Andes. Here, we assessed the spatial distribution, richness patterns, habitat associations, and climate-driven vulnerability of *Tacsonia* species in Peru. We compiled 1,758 georeferenced occurrence records for 25 *Tacsonia* species (including one unidentified taxon) spanning elevations of 1,500–4,500 m and summarized richness across administrative regions, elevation bands, and latitudinal/longitudinal gradients. We also evaluated protection coverage by intersecting records with the national protected-area system and developed ecological niche models to estimate current suitability and potential losses under climate-change scenarios. Most records occurred between 3,000 and 3,500 m, and 23 species were found between 2,500 and 3,000 m. Cusco concentrated the highest number of observations (543) and species richness (14), followed by Cajamarca (226 records; 11 species). Richness peaks were detected around 6°, 7°, and 13°S and 72°, 75°, and 77°W. Thirteen species are endemic to the Peruvian Andes, including five restricted to Cusco, La Libertad, and Amazonas. *Tacsonia* species occupy multiple Andean ecosystems (Tropical Dry Forest, Páramo, Puna, Yungas, and Andean Dry Forest), with *P. tripartita* occurring across all habitat types. Occurrences were recorded within several protected areas (Alto Mayo, Pui Pui, Manu, Río Abiseo, Huascarán, Yanachaga-Chemillén, Calipuy, Cotahuasi, Pampa de Ayacucho, Machu Picchu, and Ampay), including endemic taxa such as *P. amazonica*, *P. huamachucoensis*, *P. parvifolia*, *P. peduncularis*, *P. trifoliata*, *P. trisecta*, and *P. weigendii*. Niche models indicated high current suitability along northern slopes and across the central and southern eastern Andes (AUC = 0.94), but projected climate change could reduce suitable habitat by ~20%–60% by 2100. Consistent with this vulnerability, the IUCN categorizes *P. kuethiana* as Critically Endangered, 21 species as Endangered, and *P. trifoliata*, *P. mixta*, and *P. tripartita* as Vulnerable. Overall, our results provide a baseline for prioritizing conservation actions by identifying richness hotspots, narrow endemics, and regions expected to experience the greatest future loss of suitability.

Keywords: commercialization; fruit; ethnobotany; Andes; plant genetic resource.

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1. Introduction

Passifloraceae has been recognized as a family of great economic importance due to its uses in food, medicine, and ornamentation (Dhawan et al., 2004; Ulmer & MacDougal, 2004). However, it has been reported as vulnerable to anthropogenic pressures (León et al., 2006; Ocampo et al., 2010). In Peru, this family is represented by the genera *Dilkea*, *Ancistrothyrsus*, *Passiflora*, *Turnera*, *Piriqueta*, and *Malesherbia* (Brako & Zarucchi, 1993; Chase et al., 2016; Killip, 1938; Ulloa Ulloa et al., 2004). The genus

Passiflora has been described as the most important, comprising six subgenera: *Passiflora*, *Astrophea* (DC) Mast., *Deidamioides* (Harms) Killip, *Decaloba* (DC) Rchb., *Tetrapathea* (DC) P.S. Green, and *Tryphostemmatoides* (Harms) Killip (Buitrago et al., 2018; Feuillet & MacDougal, 2003a, 2003b; Krosnick et al., 2009; Muschner et al., 2003; Ocampo et al., 2007; Ocampo & Coppens d'Eeckenbrugge, 2017), which are distributed in the Neotropics from 1,400 to 4,400 m (Ulmer & MacDougal, 2004).

The subgenus *Passiflora* has been subdivided into supersections, sections, and series, comprising approximately 240 species (Feuillet & MacDougal, 2003a, 2003b). Among these, 67 species have been assigned to the supersection *Tacsonia*, which is distributed in the Andes of Venezuela, Colombia, Ecuador, Peru, and Bolivia (Brako & Zarucchi, 1993; Kuethe & Bernal, 2020; Kuethe et al., 2025; León et al., 2006; Ocampo et al., 2007; Ocampo & Coppens d'Eeckenbrugge, 2017). In the taxonomic revision of the supersect. *Tacsonia* by Feuillet & MacDougal (2003a, 2003b), 12 sections were recognized; among them, *Elkea*, *Tacsonia*, *Insignes*, *Boliviana*, *Trifoliata*, *xlnkea*, and *Manicata* were reported for Peru, with the section *Elkea* harboring the two most important species, *Passiflora tarminiana* and *Passiflora tripartita* var. *mollissima*.

Important markets for these species have been identified in Colombia and Ecuador, but they have been scarcely commercialized in Peru (Ocampo et al., 2017; Segura et al., 2003). Their economic relevance is attributed to their adaptability for cultivation, the nutritional quality of their fruits, the ornamental value of their flowers, and their medicinal properties (Coppens d'Eeckenbrugge et al., 2001; Córdova-Ramos et al., 2023). Their fruits are soft, glabrous or pubescent, and exhibit interspecific variation in size, shape, and color (Mayorga et al., 2020). The flower morphology is characterized by an elongated hypanthium, a shortened dentate-to-filamentous corona, and a prominent nectar chamber (Ocampo & Coppens d'Eeckenbrugge, 2017). These species are allogamous and are pollinated by the hummingbird *Ensifera ensifera* (Abrahamczyk et al., 2014; Ocampo, 2011; Ulmer & MacDougal, 2004). Various common names have been recorded according to the geographic region where the species is used, being referred to in the north as "pur-pur," "puru-puru," or "poro-poro," and in the south as "tumbo" or "tumbes" (Castañeda et al., 2019). Colombia exhibits the most incredible diversity, with 34 inventoried species, followed by Peru with 24 (Caicedo, 2021).

Geographic Information Systems (GIS) have become a practical, low-cost, and widely accessible framework for analyzing botanical collections and exploratory datasets on species diversity (Guarino et al., 2009; Ocampo et al., 2010; Ramírez-Barahona et al., 2023; Rodríguez et al., 2005; Scheldeman et al., 2006). By combining climatic, geological, and species-occurrence factors (Guarino et al., 1995), maps have been produced that condense such information, facilitating both comprehension and applicability in conservation efforts (Pearson, 1994; Peterson et al., 2011). Consequently, knowledge of

species-distribution patterns (Hijmans & Spooner, 2001), enhanced planning of explorations and collections (Greene et al., 1999; Jones et al., 1997), research on climate change and adaptability (Berger et al., 2003; Song et al., 2018; Titeux et al., 2017; Tovar et al., 2022), understanding of evolution (Jarvis et al., 2002), detection of underexplored and overexplored areas (Ramírez-Barahona et al., 2023; Reddy & Dávalos, 2003), and the identification of conservation areas (Balogun et al., 2022; Bystriakova et al., 2003; Funk et al., 1999; Kress et al., 1998) have been facilitated, enabling strategies tailored to future needs (Scheldeman et al., 2006).

Climate change has been identified as a significant threat to neotropical plant genetic resources, affecting their distribution, diversity, and adaptive capacity (Sheldon, 2019). According to projections from the Intergovernmental Panel on Climate Change (IPCC), increases in temperature and changes in precipitation patterns are expected to adversely affect biodiversity in these regions (IPCC, 2021). In the medium term, these shifts could lead to species redistribution, whereby some species may find new areas suitable for growth, while others may experience reductions in their natural habitats (Pecl et al., 2017). Over the long term, climate change could accelerate the loss of genetic diversity, which is critical for species' adaptation to changing environmental conditions, thereby limiting their potential contribution to food security and the development of climate-resilient crops (FAO, 2019). Moreover, the effects of climate change on pollinators and plant life cycles may trigger ecological mismatches that jeopardize the reproduction and survival of many neotropical species (Potts et al., 2010). In the medium and long term, these processes could alter ecosystem composition and function, thereby affecting the ecosystem services on which human communities depend for their well-being (Díaz et al., 2019).

In Peru, research on this taxonomic group is limited and yields inconclusive results. Knowledge about biological diversity, conservation status, and potential uses has been connected to current use and trade (Caicedo, 2021; Fuertes et al., 2019; Ocampo et al., 2017). Recently, efforts have focused on improving understanding of *Tacsonia* species (Aliaga et al., 2023; Chañi-Paucar et al., 2024; Chávez-Corcuera et al., 2023; Kuethe & Bernal, 2020; Kuethe et al., 2025; Mayorga et al., 2025). Therefore, this study aims to map the distribution, richness, endemism, and climatic niche patterns of *Tacsonia* in Peru, as well as forecast the impacts of climate change on habitat suitability (CMIP6 SSP1–2.6 and SSP5–8.5), while assessing conservation

status (IUCN) and representation within SINANPE protected areas.

2. Methodology

Study area and database

The study was focused on the Peruvian territory, by the country's department-level political division. The database was constructed using georeferenced occurrence records provided by Segura and Caicedo (Caicedo, 2021; Segura et al., 2003), museum databases, personal data from researchers, and published literature (Fajardo et al., 2014). Additionally, occurrences from TROPICOS, GBIF, and iNaturalist were incorporated after filtering out errors in identification, geospatial accuracy, and biases (Soberón & Peterson, 2004). Peruvian institutions with herbaria were also consulted. Both identified and unidentified specimens were verified and redetermined using the taxonomic keys of Killip (1938), Holm-Nielsen et al. (1988), and Escobar (1987, 1988).

Herbarium specimens whose coordinates were geographically distant from the recorded locality information were corrected using Google Earth Pro-7.3.4.8642 (Google, 2022). Unless otherwise stated, data processing, statistical analyses, and modeling were performed in R (version 4.3.2; R Core Team, 2023) using RStudio as the integrated development environment (Posit team, 2025). Packages used at each step are specified below (*readxl*, *readr*, *sf*, *terra*, *geodata*, and *tidyverse* for data handling and spatial processing).

Spatial analysis

The richness analysis was conducted using DIVA-GIS 7.5 (Hijmans et al., 2012). A point-to-grid parameter of $0.05^\circ \times 0.05^\circ$ was applied (Moraes et al., 2020), and a circular-neighborhood radius of 1° was used (Hijmans & Spooner, 2001; Ocampo et al., 2010; Ocampo et al., 2007).

A principal components analysis (PCA) was performed using the 19 WorldClim variables with *FactoMinerR* (Lê et al., 2008) at a 1 km^2 spatial resolution (Fick & Hijmans, 2017; Hijmans et al., 2005; Hijmans & Spooner, 2001). Based on the variables selected by the PCA, the number of clusters was determined through biological validation using the *clValid* function of the *Mclust* packages (Brock et al., 2008; Scrucca et al., 2023), employing the sections to which each species corresponds. A cladogram was generated with a distance matrix through the "maximum" method and the *Hclust* packages. An analysis of climatic variables was conducted to determine the following parameters for each species: minimum and

maximum temperature, minimum and maximum precipitation, mean annual temperature, and mean annual precipitation.

Climate modeling

Species distribution modeling was performed using the Maxent algorithm (Maintainer & Phillips, 2022), known for its predictive accuracy (Merow et al., 2013), and employing the *dismo*, *terra*, *maxent*, *raster*, and *rJava* packages (Hijmans et al., 2022). To model areas with climatic suitability, presence records of *Tacsonia* were used (Elith et al., 2006; Graham et al., 2008; Hijmans et al., 2005; Soberón, 2007). Duplicate records per species within a 1 km^2 area were removed, and outliers whose normalized values exceeded 3.5 times the standard deviation of the absolute value were also discarded to correct sampling bias (Castro-Llanos et al., 2019; Elith et al., 2011; Newbold, 2010). In addition, pseudo-absences were generated as a random background sample in a 1:1 ratio to non-duplicate presence records to increase model predictive accuracy (Barbet-Massin et al., 2012; Castro-Llanos et al., 2019; Chefaoui & Lobo, 2008; Dudík et al., 2005; Ferrier et al., 2002; Ferrier & Watson, 1997; Graham et al., 2004; Smith et al., 2013; Stockwell, 1992; Stockwell & Peters, 1999; VanDerWal et al., 2009). Sampling error was further minimized by selecting pseudo-absences in a representative way across the entire study area (Manly et al., 2002; Pearce & Boyce, 2006). The climatic variables considered biologically relevant to these species were selected through PCA and expert criteria (Araújo et al., 2005; Austin, 2007; Jiménez-Valverde et al., 2009). The environmental variables used for modeling were consistent with those commonly found in mountainous geography (Ramirez-Villegas et al., 2014; Teixeira et al., 2016). The model was trained using the selected variables, and 25-fold cross-validation was employed to assess model performance (Fielding & Bell, 1997; Ramirez-Villegas et al., 2014; Warren et al., 2013). For each species, the k-fold value varied according to the number of records. Finally, the model's performance was evaluated using the area under the receiver operating characteristic curve (AUC) (Bunn et al., 2015; Hand & Till, 2001; Radosavljevic & Anderson, 2014; Thuiller et al., 2004).

Climate change

Eleven global climate models (GCMs) from the IPCC's Sixth Assessment Report (Tokarska et al., 2020) were employed to analyze future scenarios (ACCESS-CM2, CMCC-ESM2, EC-Earth3-Veg, GISS-E2-1-G, HadGEM3-GC31-LL, INM-CM5-0, IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, MRI-

ESM2-0, UKESM1-0-LL) of the sixth phase of the Coupled Model Intercomparison Project (CMIP6) (Tokarska et al., 2020), which incorporate the Shared Socioeconomic Pathways (SSP) (Van Vuuren et al., 2012). The low-mitigation scenario (2.6 W/m²) (Van Vuuren et al., 2007, 2011, 2012) and the high-emissions scenario, leading to 8.5 W/m² (Riahi et al., 2007, 2011; Van Vuuren et al., 2012), were employed. By selecting multiple models, intermodal uncertainty was better managed (Iqbal et al., 2021; Lutz et al., 2016; Nashwan & Shahid, 2020).

To assess the distribution of the species in the context of climate change (Allen et al., 2018), the CMIP6 SSP1-2.6 and SSP5-8.5 emission scenarios were applied for the years 2021-2100 (Tokarska et al., 2020). These scenarios were used at a spatial resolution of 1 km², given the heterogeneity of climates in the Andes (Garreaud, 2009; Pérez-Escobar et al., 2022; Ramirez-Villegas et al., 2014; Rivas-Martinez & Tovar, 1983; Tovar et al., 2022). The means of the 11 models for each SSP and year range were used to derive a general interpretation of each future scenario (Ramirez-Villegas et al., 2014). Finally, the response to climate change was evaluated against the potential climatic model (current climate) to quantify the persistence and loss of climatic suitability (Loehle & LeBlanc, 1996; Peterson et al., 2001; Ramirez-Villegas et al., 2014). The gain or loss of suitability was calculated as the percentage of predicted areas that remain or become unsuitable under future scenarios (Broennimann et al., 2006; Castro-Llanos et al., 2019; Ramirez-Villegas et al., 2014).

An assessment of elevation and climatic suitability was conducted to correlate these parameters across the climate-change models analyzed. A Digital Elevation Model (DEM) was employed, along with climate-change models for each time range and SSP, and the resolution was interpolated bilinearly (Robert & Hijmans, 2024).

Conservation

The *Tacsonia* species were evaluated using the IUCN threat category criteria (IUCN Species Survival Commission, 2003). To determine the area of occupancy (AOO) and extent of occurrence (EOO) for each species (Bachman et al., 2011), the GEOCAT platform (<https://geocat.iucnredlist.org/>) was used. Additionally, the ecogeographical division scheme for Peru proposed by Brack & Mendiola (2000) and the protected natural areas belonging to the National System of Protected Natural Areas (SINANPE) (SERANP, 2012) were adopted. The intersection of potential distribution layers with protected natural areas (PNA) was evaluated.

3. Results and discussion

Database and georeferencing

A total of 1,758 occurrence records of *Tacsonia* were compiled for Peruvian territory. It was possible to identify 25 species, one of which is at the sp. level (Figure 1). Of the georeferenced records, 38% were contributed by Segura and Caicedo, 29% by non-digitized herbarium specimens from Peru, 33% by iNaturalist, TROPICOS, and GBIF. Photographic documentation was available for all endemic species except *P. amazonica*. Records were observed across 19 of Peru's 24 departments (Figure 2). Nine endemic species presented fewer than 15 records (Figure 3). A total of 409 records were excluded as duplicates per species in areas smaller than 1 km², and due to outlier filters based on climatic variables. Using iNaturalist records, we were able to identify the presence of *P. glaberrima*, *P. mandonii*, *P. runa*, *P. salpoense*, *P. anastomosans*, *P. peduncularis*, *P. lanceolata*, and the fruit of *P. pinnatistipula* (Figure 1).

A principal drawback of data gathered from iNaturalist is the inaccuracy of taxonomic determinations (Callaghan et al., 2022; Unger et al., 2021). This issue was not the focus of the present analysis. However, it is inferred that the error rate diminishes as the academic and non-academic communities adopt an updated taxonomic and phylogenetic framework. On the other hand, these records exhibit strengths in geographic locations, owing to the use of portable electronic devices or dedicated applications for that purpose.

A total of 67 *Tacsonia* species have been recognized (Caicedo, 2021; Escobar, 1988; Esquerre-Ibanez, 2015; González & Evangelista, 2015; Killip, 1938; Kuethe & Bernal, 2020; Kuethe et al., 2025; Ocampo et al., 2007; Ulmer & MacDougal, 2004). The highest diversity of this supersect. is found in Colombia (Escobar, 1988; Ocampo et al., 2010), followed by Peru (Caicedo, 2021). Ecuador ranks third (Holm-Nielsen et al., 1988), whereas Bolivia and Venezuela harbor lower diversity (Jorgensen & Vasquez, 2009; Roa Delgado et al., 2009). Consequently, Peru is considered an important center of diversity for these species.

In Peru, a broad elevational distribution between 1,600 and 4,500 m above sea level (a.s.l.) has been documented, while in Colombia, it has been reported above 2,500 m (Ocampo et al., 2010; Ocampo et al., 2007). The greatest elevational richness in the Americas is noted between 2,500 and 3,000 m above sea level (Bonilla, 2014), which matches the pattern observed for those distributed in Peru. Bonilla (2014) reported species diversity in

the Americas between 3° and 8°N latitude, 1° and 4°S latitude, and 77° and 73°W longitude.

In Peru, elevational distributions by species have varied since **Bonilla (2014)** and **Caicedo (2021)**, primarily due to increases in the number of recent occurrence records and in collection efforts. While *P. tripartita* in Peru occurs between 1,600 and 4,500 m above sea level, an elevational amplitude of 2,000 to 3,500 m. has been reported for the Americas (**Bonilla, 2014**). The same situation applies to *P. mixta*, *P. tarminiana*, and *P. gracilens*, as their

elevational ranges in Peru extend more broadly. Among the species with restricted elevational ranges, *P. huamachucoensis* was reported at 3,900 m by **Bonilla (2014)** and then at elevations between 3,500 and 4,000 m by **Caicedo (2021)**. However, it is now known to survive at elevations up to 4,500 m above sea level, the highest elevation recorded for the supersect. For *P. runa*, which occurs between 2,500 and 3,500 m above sea level, similarities persist despite an increase in records (**Bonilla, 2014; Caicedo, 2021**)

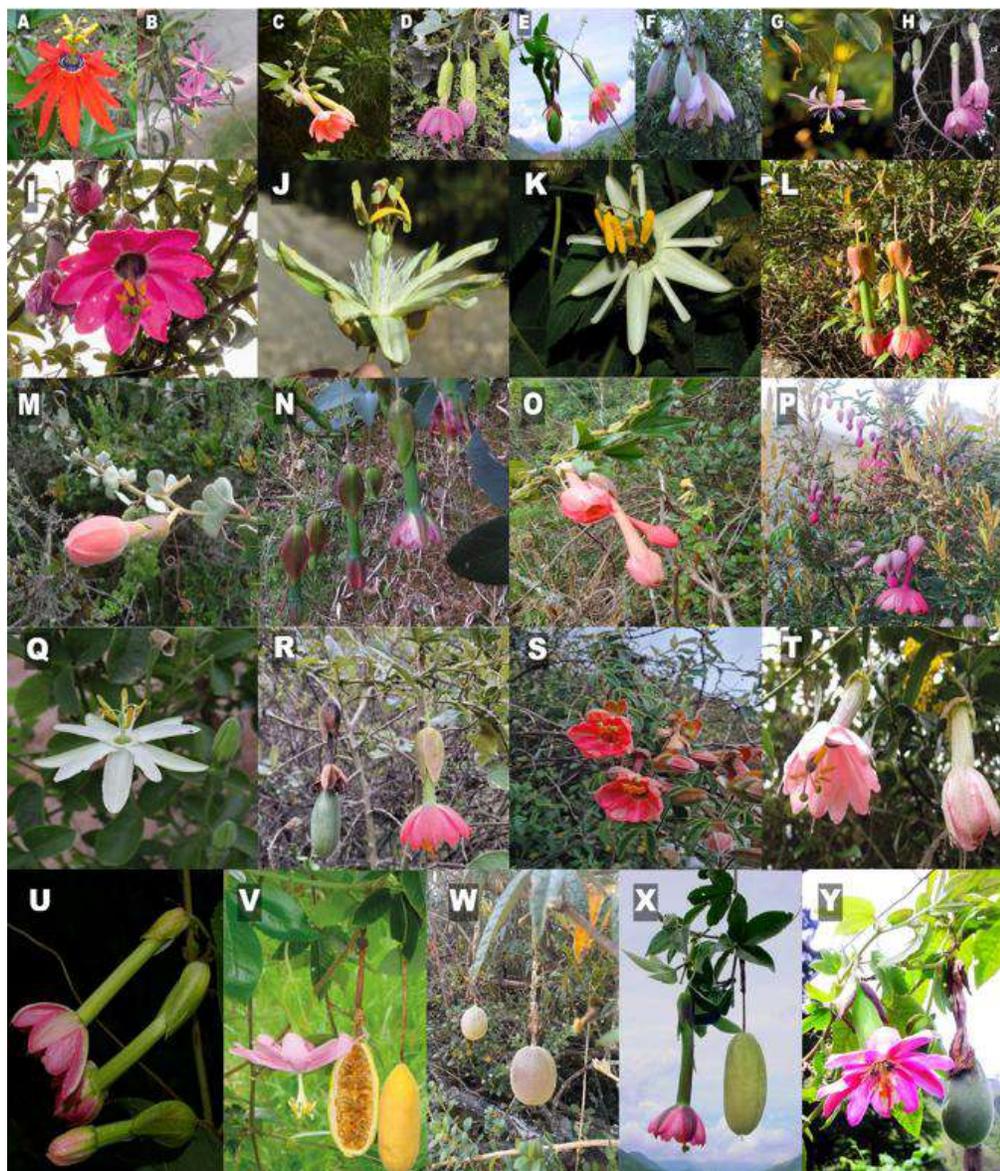


Figure 1. Diversity of supersect *Tacsonia* is distributed in Peru. Non-endemic: A) *P. manicata* (Juss.) Pers., B) *P. gracilens* (A. Gray) Harms, C) *P. mixta* L.f., D) *P. glaberrima* (Juss.) Poir., E) *P. mathewsii* (Mast.) Killip, F) *P. pinnatistipula* Cav., G) *P. mandonii* (Mast.) Killip, H) *P. cumbalensis* (H. Karst.) Harms. Endemic: I) *P. huamachucoensis* L.K. Escobar, J) *P. weberbaueri* Harms, K) *P. trisecta* Mast., L) *P. runa* L. K Escobar, M) *P. salpoense* S. Leiva & Tantalean, N) *P. kuethiana* B. Esquerre, O) *P. anastomosans* (Lamb. Ex Dc.) Killip, P) *P. parvifolia* (DC.) Harms, Q) *P. peduncularis* Cav., R) *P. sp.*, S) *P. trifoliata* Cav., T) *P. lanceolata* (Mast.) Harms, U) *P. weigendii* T. Ulmer & Schwerdtfeger, Marketed fruits: V) *P. tarminiana* Coppins y V. E. Barney, W) *P. pinnatistipula* Cav., X) *P. tripartita* (Juss.) Poir., Y) *P. x rosea* (H. Karst.) Killip. Photos: S by Elky Alfaro; I and R by Miguel A. Caicedo-Baltodano; B, F, O, Q, and U by Gonzalo Chávez; H and N by Boris Esquerre; P by Lizzet Luis; A, C, E, V, X, and Y by John Ocampo; K by Mario Sanchez; J by Anthony Yuca. Note. Photos D, G, L, M, and T were taken from iNaturalist (**Birdernaturalist, 2011; Herzog, 2023; Jrkuethe, 2025; Manuelroncal, 2012; Martinwettges, 2022**).

The species *P. lanceolata*, documented in only three records (Caicedo, 2021), was previously considered possibly extinct but was recently rediscovered by Chávez-Corcuera & Fernández-Hilario (2019). It was also observed and reported on iNaturalist in a new locality (<https://www.inaturalist.org/observations/196295458>),

encouraging further collection efforts and re-population initiatives for this rare species. Likewise, *P. weigendii* aligns with previous reports prior to this study. On the other hand, *P. sp.* has been recorded at elevations between 3,000 and 4,000 m, similar to those of the closely related *P. glaberrima*, *P. cumbalensis*, *P. loxensis*, and *P. luzmarina*.

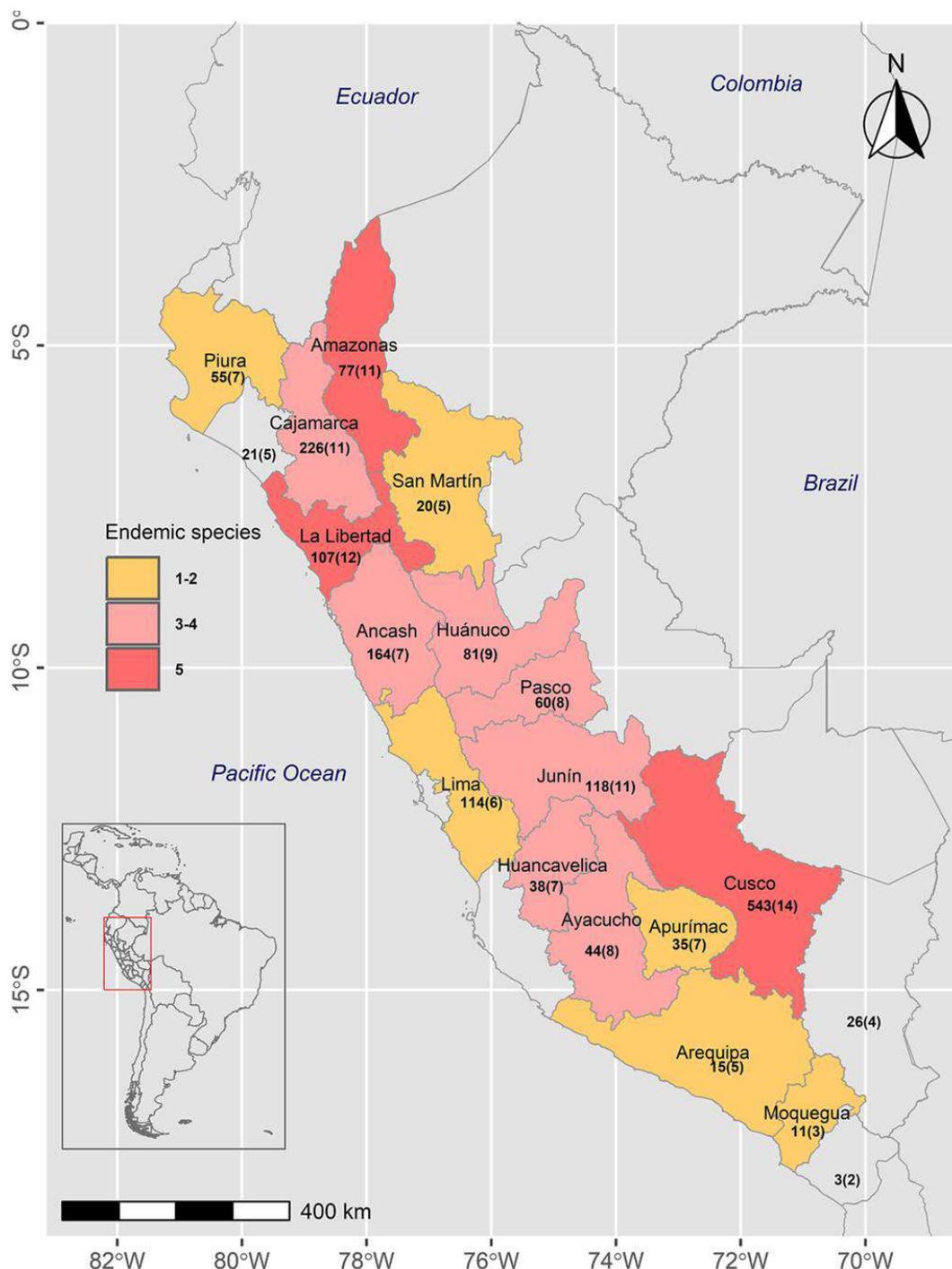


Figure 2. Number of endemic species by department. Numbers outside the parentheses correspond to occurrences, and numbers inside the parentheses correspond to the number of species.

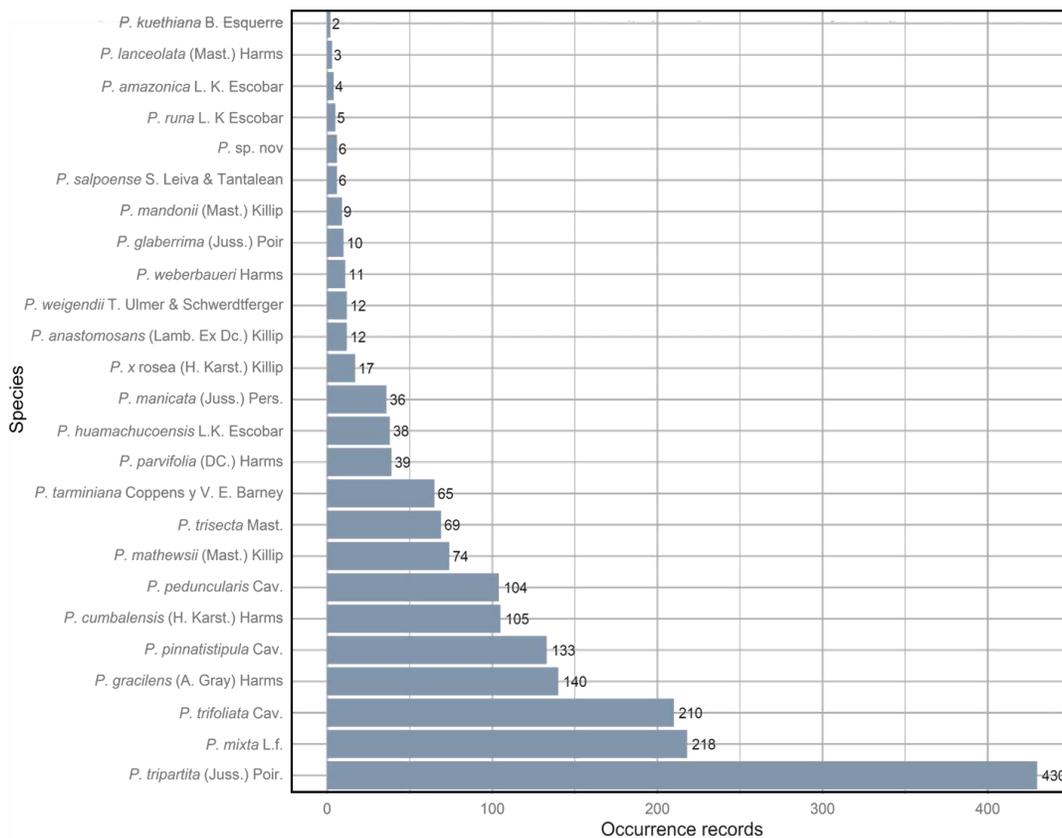


Figure 3. Number of occurrence records per species of the supersect *Tacsonia* in Peru.

Geographic patterns of species richness

The 3,000–3,500 m elevational range has shown the most incredible abundance, with 561 records (Figure S1). The highest diversity has been observed near 13°S and between 6° and 7°S, with 15 and 13 species, respectively (Figure S2). The greatest elevational range of 1,500 to 4,500 m was documented for *P. tripartita*, *P. mixta*, *P. tarminiana*, and *P. gracilens*, followed by *P. cumbalensis* and *P. mathewsii* at 1,500 to 4,000 m (Figure S3). In contrast, endemic species exhibited restricted elevational ranges.

The species richness analysis demonstrated that Peru contains areas with more than 10 species, contradicting Bonilla's (2014) findings. However, the diversity patterns in areas holding 7 to 9 species remain the same (Bonilla, 2014). Moreover, Ecuador's highest species richness is in the south of the country, bordering northern Peru (Bonilla, 2014). The decrease in diversity from southern Ecuador to northern Peru has been attributed to the depression in the cordillera at Huancabamba, Piura (Hazzi et al., 2018). Nevertheless, the species richness in that lower portion of the cordillera in Peru remains higher compared to other departments in the central and southern regions.

The richness values observed in this study are similar to those reported by Bonilla (2014) and Segura et al. (2003) for potential distribution. Additionally, the species richness documented in Cusco (Figure 9) is similar to that recorded in the Eastern Cordillera of Colombia and the central and southern regions of Ecuador (Bonilla, 2014).

Distribution and richness by ecoregions

It has been observed that supersect *Tacsonia* is distributed across two biogeographical domains, five biogeographical provinces, and five ecoregions (Figure 4 and Figure S4). Observations have been recorded for the Andean–Patagonian domain (59%) and the Amazonian domain (41%). Within the Andean–Patagonian domain, 827 records have been assigned to the Puna biogeographical province and 208 to the Occidental Slope province. In turn, 643 records have been attributed to the Yungas province of the Amazonian domain, 61 to the Pacific province (Dry Forests and Northern-Forested Steppes), and 14 to the Paramo province. Overall, 47% of the total records have been associated with Puna, 37% with Yungas, 12% with the Andean Dry Forest, 3.5% with the Equatorial Dry Forest, and 0.5% with the Paramo.

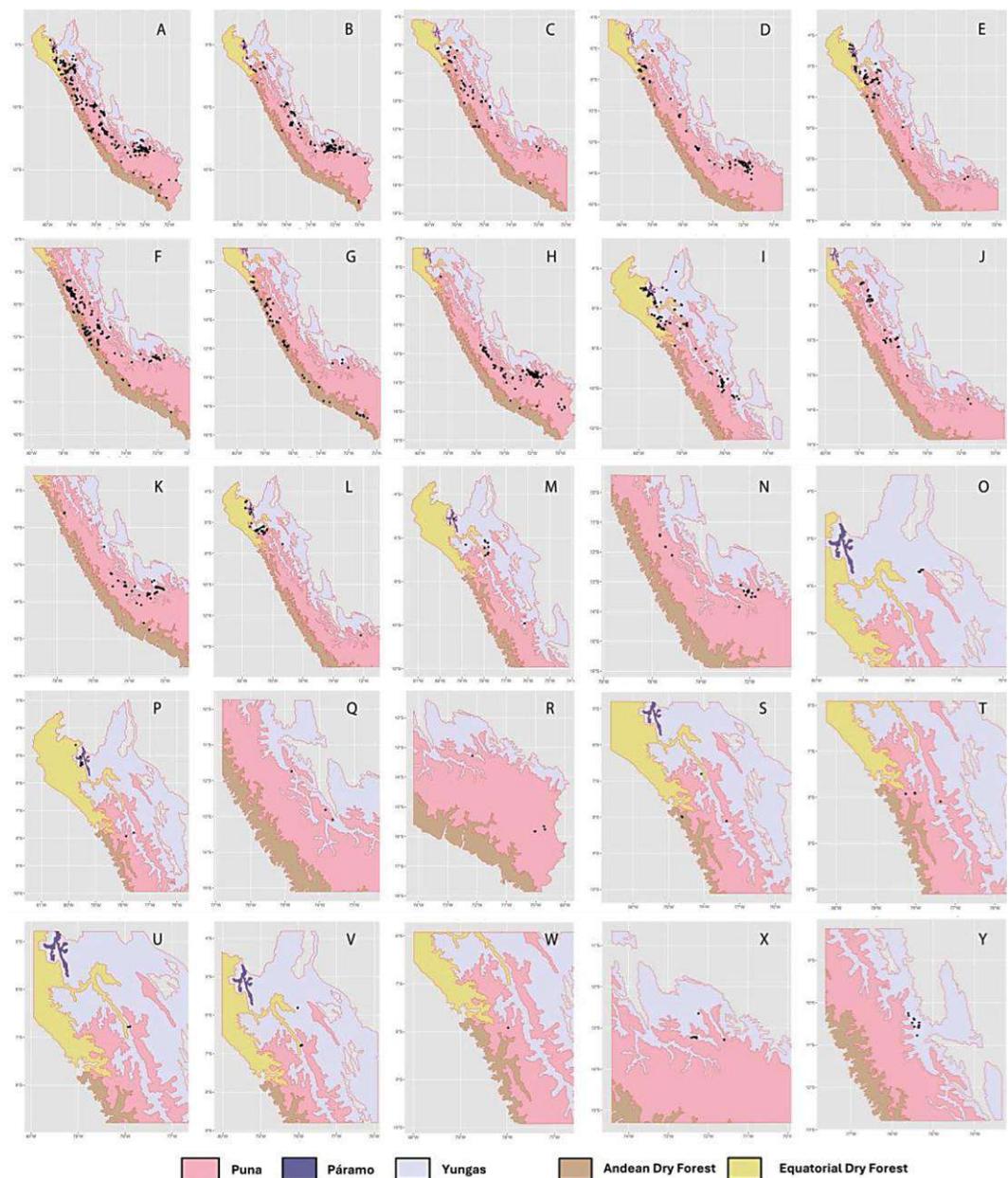


Figure 4. Distribution maps for the 24 *Tacsonia* species and an unidentified specimen. A). *Passiflora tripartita*, B). *P. mixta*, C). *P. tarminiana*, D). *P. gracilens*, E). *P. mathewsii*, F). *P. trifoliata*, G). *P. peduncularis*, H). *P. pinnatistipula*, I). *P. cumbalensis*, J). *P. parvifolia*, K). *P. trisecta*, L). *P. manicata*, M). *P. anastomosans*, N). *P. x rosea*, O). *P. amazonica* L. K. Escobar, P). *P. glaberrima*, Q). *P. lanceolata*, R). *P. mandonii*, S). *P. salpoense*, T). *P. huamachucoensis*, U). *P. kuethiana*, V). *P. runa*, W). *P. sp.*, X). *P. weigendii*, Y). *P. weberbaueri*.

Within the Andean-Patagonian domain, 24 species have been documented, except for *P. weigendii*, whereas 23 species have been recorded in the Amazonian domain, excluding *P. huamachucoensis* and *P. sp.* In the Andean-Patagonian domain, the Puna province contains 24 species, and the Occidental Slope province only 10. Conversely, in the Amazonian domain, the Yungas province has been reported to harbor 23 species. In comparison, the Pacific province (Dry Forests and Northern-Forested Steppes) comprises nine species. In con-

trast, the Paramo province contains five species, specifically *P. cumbalensis*, *P. glaberrima*, *P. anastomosans*, *P. mathewsii*, and *P. tripartita* (Table 5). In total, 24 species have been recorded in the Puna, 23 in Yungas, 10 in Andean Dry Forest, 9 in Equatorial Dry Forest, and 5 in Paramo. Among the species with more than 100 records, *P. tripartita* has been documented in all these ecosystems. In Puna, this species is recorded 218 times, followed by 148 in Yungas, 51 in the Andean Dry Forest, 13 in the Equatorial Dry Forest, and 1 in the Paramo ecosystem.

Likewise, *P. mixta* has been recorded in 122 locations in Yungas, 94 in the Puna, 1 in the Andean Dry Forest, and 1 in the Equatorial Dry Forest. In the same abundance category, *P. trifoliata* displays 126 records in the Puna, 61 in the Andean Dry Forest, and 23 in Yungas. For *P. gracilens*, the highest abundance has been noted in the Puna (67 records), followed by the Yungas (55 records), the Equatorial Dry Forest (11 records), and the Andean Dry Forest (7 records). *P. pinnatistipula* shows 100 records in the Puna, 27 in Yungas, and 4 in the Andean Dry Forest. *P. cumbalensis* has been most abundant in the Yungas, with 70 records, followed by 18 in the Puna, 9 in the Paramo, and 8 in the Equatorial Dry Forest. Lastly, among the most abundant species, *P. peduncularis* was recorded in 59 locations in the Andean Dry Forest, 23 in the Puna, 16 in the Equatorial Dry Forest, and 6 in the Yungas.

Among the species with fewer than 100 records, *P. mathewsii* has been observed 48 times in the Yungas, 15 times in the Puna, and 5 times each in the Andean Dry Forest and Equatorial Dry Forest, with one record in the Páramo. Likewise, *P. trisecta* has been recorded in 33 locations in the Puna, 32 in the Yungas, and 4 in the Andean Dry Forest. *P. tarminiana* has been represented by 32 records in the Puna, 16 in Yungas, 14 in the Andean Dry Forest, and 3 in the Equatorial Dry Forest. Similarly, *P. parvifolia* has been recorded in 25 locations in Puna and 14 locations in Yungas. *P. huamachucoensis* has appeared 38 times in the Puna. Lastly, *P. manicata* has been recorded in 29 locations in Yungas, 4 in the Puna, and 3 in the Equatorial Dry Forest.

According to the ecological classification by **Brack & Mendiola (2000)**, *Tacsonia* species exhibit adaptations to the climates of the Puna (24 species), Yungas (23 species), Andean Dry Forest (10 species), Equatorial Dry Forest (9 species), and Páramo (5 species). In addition to the number of records per ecosystem, species appear to be established in certain zones based on climatic conditions and biotic factors, such as pollinators (**Abrahamczyk et al., 2014; Abrahamczyk & Kessler, 2015**). For instance, *P. tripartita*, *P. trifoliata*, *P. gracilens*, *P. pinnatistipula*, *P. trisecta*, *P. tarminiana*, *P. parvifolia*, *P. huamachucoensis*, *P. x rosea*, *P. mandonii*, *P. sp.*, and *P. lanceolata* have shown the most significant number of records in the Puna ecosystem.

Under the Puna concept by **Brack & Mendiola (2000)**, this ecosystem is represented by elevations above 3,500 m and is characterized by reduced atmospheric pressure, low mean temperatures, sharp differences between day and night, and varied terrain. Between 4,000 and 5,000 m, average annual

precipitation is approximately 700 mm, with a mean annual temperature of about 6 °C. Meanwhile, the species adapted to the Yungas include *P. mixta*, *P. cumbalensis*, *P. mathewsii*, *P. manicata*, *P. anastomosans*, *P. weigendii*, *P. glaberrima*, *P. weberbaueri*, *P. runa*, *P. kuethiana*, and *P. amazonica*, which generally display average temperatures of 15 °C and precipitation exceeding 1,000 mm. This ecosystem is characterized by a very humid sub-warm climate (800-2,500 m) with annual precipitation over 2,000 mm and temperatures averaging 22 °C, and a cold climate (2,500-3,800 m) where annual precipitation is about 700 mm and temperatures average 12 °C (**Brack & Mendiola, 2000**).

Only two species, *P. peduncularis* (59 records) and *P. salpoense* (3 records), demonstrated adaptability in the Andean Dry Forest. Although other species also occupy this ecosystem, such as *P. trifoliata* (61), *P. tripartita* (51), *P. tarminiana* (14), *P. gracilens* (7), *P. mathewsii* (5), *P. pinnatistipula* (4), *P. trisecta* (4), and *P. mixta* (1), their higher abundance in other ecosystems suggests that they are less specialized in the Andean Dry Forest. A similar situation was observed in the Páramo, where only five species (*P. cumbalensis*, with 9; *P. glaberrima*, with 2; *P. anastomosans*, with 1; *P. mathewsii*, with 1; and *P. tripartita*, with 1) were documented, with *P. cumbalensis* being the most abundant. Lower abundance was also registered for the Equatorial Dry Forest, which contained *P. tripartita* (51), *P. mixta* (1), *P. gracilens* (11), *P. cumbalensis* (8), *P. peduncularis* (16), *P. mathewsii* (5), *P. tarminiana* (3), *P. manicata* (3), and *P. glaberrima* (1). Occurrences in the Equatorial Dry Forest correspond to the Marañon Valley, with maximum elevations of 2,800 m above sea level, annual precipitation of around 500 mm, and temperatures ranging from 23 to 24 °C (**Brack & Mendiola, 2000**). These parameters represent the upper and lower limits for species distributed in that ecosystem (**Table 2**).

Regarding maximum and minimum temperature and precipitation, some species have adapted to both the Puna and Yunga ecosystems. *P. gracilens* has shown minimum temperature and precipitation values of 5.25 °C and 282 mm, and maximum values of 19.01 °C and 1,485 mm, reflecting adaptability to both ecosystems. Indeed, it has been recorded 67 times in Puna and 55 times in Yungas. Similarly, *P. trisecta* is characterized by a temperature range of 1.72 to 20.13 °C, with precipitation ranging from 264 to 1,707 mm, supported by its 33 occurrences in Puna and 32 in Yungas. Other species in this group include *P. cumbalensis*, *P. mathewsii*, *P. mixta*, *P. parvifolia*, *P. tarminiana*, and *P. tripartita*. In contrast, a higher

degree of climatic specificity has been noted for *P. amazonica*, *P. glaberrima*, *P. huamachucoensis*, *P. kuethiana*, *P. lanceolata*, *P. runa*, *P. sp.*, *P. weberbaueri*, and *P. weigendii*. Adaptation to these climatic conditions is demonstrated by their narrower maximum and minimum values for temperature and precipitation, as well as by their limited number of occurrences, which are confined to one specific ecosystem or strongly favor it. For example, *P. huamachucoensis* occurs solely in the Puna, whereas *P. weigendii* is limited to the Yungas. Because of multiple approaches, efforts, and methodologies used for determining Peru's biogeographical zones (Beraún Chaca & Villanueva Fernández, 2016; Brack & Mendiola, 2000; Britto, 2017; Cabrera & Willink, 1973; León et al., 2007; MINAM, 2015, 2018; Morrone, 2001; Olson et al., 2001; Pease García Yrigoyen, 1984; Pulgar Vidal, 2014; Rivas-Martínez & Tovar, 1983; Sarmiento, 1975; Zamora, 1996), adopting some of them is conceptually intricate and not feasible for spatial analysis at the time of this research. Nevertheless, the proposal by Brack & Mendiola (2000) was used, since it integrates climate, soils, hydrology, flora, and fauna to delineate Peru's ecological regions and is also readily available for GIS-based research. León et al. (2007) classified species of *Passiflora* L. ecologically, following Zamora (1996). Accordingly, only *P. amazonica*, *P. cumbalensis*, *P. huamachucoensis*, *P. parvifolia*, *P. peduncularis*, *P. runa*, *P. trifoliata*, *P. weberbaueri*, and *P. weigendii* were categorized (León et al., 2007). Meanwhile, *P. lanceolata* remained unclassified due to insufficient data and unknown elevation (León et al., 2007). The ecological regions identified for *Tacsonia* included Montane Very Humid Forests (BMHM) between 1,500 and 2,500 m, Páramo (PAR) between 3,500 and 4,200 m, Montane Rain Forests (BPM) between 2,500 and 3,500 m, Meso-Andean (MA) between 2,500 and 3,500 m, and Humid and Dry Puna (PSH) between 3,800 and 4,200 m. (León et al., 2007). Hence, according to León et al. (2007), *P. huamachucoensis*, *P. cumbalensis*, *P. parvifolia*, *P. runa*, *P. weberbaueri*, and *P. weigendii* occur in BMHM. However, *P. parvifolia* and *P. runa* are additionally classified in BPM. Furthermore, *P. huamachucoensis* was reported in PAR, *P. peduncularis* in MA, and *P. trifoliata* in both MA and PSH. However, the results obtained in this research indicate that *P. huamachucoensis* does not occur in the Páramo.

Among the countries where *Tacsonia* is distributed, efforts in Colombia have included a family-level (Passifloraceae) taxonomic study (Escobar, 1988) and based on Hernández-Camacho et al. (1992), a

biogeographical approach (Ocampo et al., 2007). Both endemic and widespread *Tacsonia* species in the Americas were designated within the Andes and Caribbean regions (Ocampo et al., 2007). Those authors later reported that these two regions had higher collection efforts than other biogeographical areas (Ocampo et al., 2010), laying the groundwork for improved use and conservation of these species (Ocampo et al., 2021). In Ecuador, Holm-Nielsen et al. (1988) provided a taxonomic treatment of Passifloraceae, with general descriptions of geography but little specific climatic detail, aside from mentioning high and extreme precipitation for *P. cumbalensis* (Holm-Nielsen et al., 1988). In Bolivia, despite some targeted work on these species (Espinoza, 2014), studies at the genus level (*Passiflora* L.) have also been conducted (Justiniano Suárez, 2019). In the latter study, *Tacsonia* species are found in Montane Cloud Forests, Montane Humid Forests, the Andes, the Yungas, and Humid Puna (Justiniano Suárez, 2019). Finally, in Venezuela, species at the genus level have been documented in the Llanos biogeographical region (Delascio-Chitty, 2006), although specific treatments for *Tacsonia* are lacking. A morphological atlas of *Passiflora* L. seeds from that country include *Tacsonia* species (Pérez-Cortéz, 2007), indicating their elevation, but does not provide a detailed biogeographical report. Furthermore, Van der Plank (1991) asserted that *Passiflora* L. species in South America predominantly occupy rainforests. For Peru, this biogeographical classification and climatic characterization provide a foundation for conservation and future applications to improve cultivated species, particularly in countries that host *Tacsonia*. When the diversity of ecosystems is examined by grouping species according to their sections and principal ecosystems (those with the highest number of occurrences), it becomes apparent that the *Boliviana*, *Trifoliata*, x *Inkea*, and *Insignes* sections are highly specialized in the Puna ecosystem (Table 5) (Figure 8). These sections exhibit low ecosystem diversity and contain species adapted to high-mountain conditions with low temperatures and moderate precipitation. High ecological specificity and limited capacity for adapting to different climatic conditions are thus indicated (Parmesan, 2006). In contrast, the *Elkea* section exhibited the greatest ecosystem diversity, with species adapted to the Yungas, Páramo, and Puna environments. Such elevated diversity suggests a pronounced adaptability of this section's species to different climatic conditions, likely reflecting greater phenotypic plasticity and colonization capability in varied habitats. The *Manicata* and *Tacsonia* sections

exhibited moderate diversity, with species present in Yungas and Páramo, thus indicating an intermediate level of adaptability.

These outcomes carry important ecological and biogeographical implications. The high specialization observed in sections such as *Boliviana* and *Insignes*, which are primarily confined to a single ecosystem, suggests that these species may be more vulnerable to climatic changes and environmental disturbances due to a narrow range of adaptability (Parmesan, 2006). By contrast, the broad ecosystem diversity observed in the *Elkea* section highlights heightened resilience and adaptability to diverse environmental conditions, potentially conferring evolutionary and survival advantages under climate change scenarios (Sheldon, 2019). Additionally, moderate biological validation suggests that, while the groups exhibit significant ecological relationships, limitations remain in resolving climatic adaptations, likely due to the biological complexity of interactions and the phenotypic variability observed within species (Ocampo & Coppens d'Eeckenbrugge, 2017). This underlines the importance of more detailed analyses and the inclusion of additional ecological and genetic data to refine the accuracy of clustering models subjected to biological validation.

Species richness

Four ranges of species richness were identified. The first range (1-3 species) was observed in lower areas of the eastern and western slopes of the Andes (Figure S5). This range was more commonly noted in the central-northern and central-southern

regions of Peru. The second richness range (4-6 species) was observed uniformly along the eastern slope of the Andes, with greater representation in northern Peru. The third range (7-9 species) was found in the northern, central, and southern parts of the mountain range: in the north, in Cajamarca, Amazonas, and La Libertad; in the center, in Huánuco and Junín; and finally, in the south, in Cusco. The fourth and highest richness range (10-13 species) was documented along the boundaries of Cajamarca, Amazonas, and La Libertad in northern Peru. In the south, only Cusco exhibited a richness of 10-13 species.

Analysis of climatic variables

A PCA was conducted, with 91.7% of the cumulative variance observed in the first four components (Table 1). Components 1 and 2 were selected because they accounted for 74.4% of the total explained variance.

A map was constructed to plot the species coordinates along with the variables that contributed most to components 1 and 2 (Figure 5). In this map, the taxonomic assignment of the species by section present in Peru was distinguished by color. Differences and similarities among the species were revealed on the central plane. Component 1, which is related to temperature variables, displayed a distribution from lower to higher temperature on the central plane. The species of the section *Elkea* shared similarities with those of the section *Tacsonia*. In contrast, *Inkea*, *Boliviana*, *Manicata*, and *Insignes* were found to be similar among themselves but more distant from *Elkea* (Table 2).

Table 1

Components, correlation eigenvalues, total variance, and cumulative variance of the four components that determine the distribution of *Tacsonia* in Peru

Climatic variables	Code	Components			
		1	2	3	4
Annual Mean Temperature	bio_1	0.81954	0.53772	0.15531	0.01631
Mean Diurnal Range	bio_2	-0.52277	0.40910	0.52801	-0.08536
Isothermality	bio_3	0.71725	-0.17515	-0.42862	0.34221
Temperature Seasonality	bio_4	-0.77620	0.20540	0.38031	-0.22896
Max Temperature of Warmest Month	bio_5	0.66610	0.65148	0.34688	-0.04043
Minimum Temperature of Coldest Month	bio_6	0.93539	0.29953	-0.06642	0.11530
Temperature Annual Range	bio_7	-0.69081	0.34769	0.55918	-0.24327
Mean Temperature of Wettest Quarter	bio_8	0.76960	0.59352	0.16406	0.01553
Mean Temperature of Driest Quarter	bio_9	0.87502	0.46035	0.08311	0.05383
Mean Temperature of Warmest Quarter	bio_10	0.76003	0.59383	0.21506	-0.01060
Mean Temperature of Coldest Quarter	bio_11	0.87768	0.45593	0.08081	0.05858
Annual Precipitation	bio_12	0.53492	-0.67997	0.43079	-0.01770
Precipitation of the Wettest Month	bio_13	0.30122	-0.63320	0.60749	0.28817
Precipitation of the Driest Month	bio_14	0.72403	-0.52297	-0.03778	-0.38158
Precipitation Seasonality	bio_15	-0.61672	0.43601	0.14420	0.40481
Precipitation of the Wettest Quarter	bio_16	0.28192	-0.58943	0.70430	0.22143
Precipitation of the Driest Quarter	bio_17	0.72857	-0.54156	0.00910	-0.36823
Precipitation of Warmest Quarter	bio_18	0.09082	-0.79943	0.13093	0.31141
Precipitation of the Coldest Quarter	bio_19	0.66730	-0.43783	0.02883	-0.31447
% Total variance		47.80995	26.59472	12.03274	5.24324
% Cumulative variance		47.80995	74.40468	86.43742	91.68066

Table 2Climatic preferences of the *Tacsonia* species

Species	Temperature	Temp. Min.	Temp. Max.	Precipitation	Prec. Min.	Prec. Max.
<i>P. amazonica</i>	16.86 (±1.58)	15.20	18.48	1,130.00 (±38.81)	1,090.00	1,183.00
<i>P. anastomosans</i>	14.28 (±2.05)	10.32	17.67	1,042.50 (±184.11)	823.00	1,431.00
<i>P. cumbalensis</i>	13.93 (±2.32)	5.63	19.21	966.46 (±213.61)	515.00	1,585.00
<i>P. glaberrima</i>	13.44 (±1.03)	11.90	15.45	958.00 (±73.01)	795.00	1,042.00
<i>P. gracilis</i>	12.81 (±2.43)	5.25	19.01	673.71 (±227.51)	282.00	1,485.00
<i>P. huamachucoensis</i>	7.53 (±0.61)	6.65	8.21	1,227.40 (±121.96)	1,057.00	1,340.00
<i>P. kuethiana</i>	10.98	10.98	10.98	1,344.00	1,344.00	1,344.00
<i>P. lanceolata</i>	11.44 (±1.43)	10.11	12.95	1,031.33 (±29.37)	1,005.00	1,063.00
<i>P. mandonii</i>	10.77 (±2.67)	9.12	14.76	722.50 (±153.22)	544.00	918.00
<i>P. manicata</i>	15.47 (±1.61)	10.04	17.68	890.35 (±144.19)	511.00	1,233.00
<i>P. mathewsii</i>	13.34 (±2.54)	6.25	19.54	908.05 (±249.97)	211.00	1,465.00
<i>P. mixta</i>	12.85 (±2.95)	3.18	19.90	848.95 (±299.44)	116.00	2,884.00
<i>P. parvifolia</i>	11.41 (±2.35)	5.45	18.12	1,124.25 (±205.28)	542.00	1,419.00
<i>P. peduncularis</i>	12.20 (±2.66)	6.20	18.94	449.51 (±270.76)	24.00	1,554.00
<i>P. pinnatistipula</i>	10.55 (±2.02)	2.39	16.55	737.31 (±178.29)	134.00	1,466.00
<i>P. runa</i>	13.38 (±1.30)	11.71	14.87	1,176.25 (±118.90)	1,022.00	1,287.00
<i>P. salpoense</i>	12.72 (±2.83)	9.80	15.47	589.75 (±384.88)	219.00	988.00
<i>P. sp.</i>	9.08	9.08	9.08	1,187.00	1,187.00	1,187.00
<i>P. tarminiana</i>	13.46 (±2.83)	5.08	19.24	678.91 (±248.15)	102.00	1,065.00
<i>P. trifoliata</i>	8.60 (±2.79)	2.92	18.08	657.08 (±182.5)	155.00	1,261.00
<i>P. tripartita</i>	12.72 (±2.37)	6.41	21.42	756.99 (±252.81)	37.00	1,695.00
<i>P. trisecta</i>	14.42 (±3.29)	1.72	20.13	850.24 (±308.50)	264.00	1,707.00
<i>P. weberbaueri</i>	14.66 (±1.03)	13.00	16.13	715.10 (±235.92)	301.00	1,006.00
<i>P. weigendii</i>	16.70 (±0.99)	15.25	18.85	1,023.92 (±211.65)	795.00	1,586.00
<i>P. x rosea</i>	11.95 (±1.10)	10.59	14.02	625.19 (±143.85)	403.00	955.00

Three groupings were validated. In the first grouping, the sections *Elkea* and *Tacsonia* were combined (Figure 6). The number of clusters was determined by biological validation of the sections using the Self-Organizing Tree Algorithm (SOTA) (BHI, 0.4670) and the Maximum distance metric (Silhouette, 0.4908). Likewise, the second grouping included the sections *Elkea*, *Tacsonia*, *Insignes*, and *Manicata*. The remaining grouping encompassed the diversity of sections. Some correspondence to hybridization was identified at the species level, as exemplified by *P. tripartita* and *P. pinnatistipula*, which give rise to the spontaneous hybrid *P. x rosea*. Principal component analysis revealed correlations between these components and precipitation and temperature, consistent with reports by Bonilla (2014) and Ocampo et al. (2010). Component 1 correlated with temperature variables, whereas Component 2 correlated with precipitation, mirroring the findings of Bonilla (2014) for *Tacsonia* species. Seasonal temperature and precipitation variations do not appear to dictate the distribution of *Tacsonia* from the Venezuelan to the Bolivian Andes (Bonilla, 2014). A similar pattern was shown for the genus *Passiflora* L. in Colombia (Ocampo et al., 2010). The differences between the component variables reported by Bonilla (2014) for the entire Andes and those reported in this study for Peru were attributable to discrepancies in the structure of the climatic information between the two studies. Furthermore, the number of Peruvian records analyzed here is more than three times higher than

the dataset examined by Bonilla (2014). Nevertheless, the relevant temperature variables are the same, except for the mean temperature of the wettest and warmest quarters reported by Bonilla (2014). Greater divergence was found in precipitation variables. The distribution of *Tacsonia* species in Peru appears to be determined primarily by annual mean precipitation, precipitation during the wettest period, and precipitation during the warmest quarter (Table 1). An analysis of the climatic variables of the genus *Passiflora* L. in Colombia revealed a similar pattern for *Tacsonia* species across the Americas (Bonilla, 2014; Ocampo et al., 2010). This could indicate that *Passiflora* L. species share an established climatic niche in which the different subgenera have evolved adaptive traits related to climate and biotic factors in these same environments (Abrahamczyk et al., 2014; Abrahamczyk & Kessler, 2015; Ocampo, 2007; Ocampo et al., 2010; Ocampo & Coppens d'Eeckenbrugge, 2017). However, climatic niches have not yet been delineated by subgenus in the Americas, nor has overlap been analyzed within these areas. In Brazil, De Giovanni & Bernacci (2015) modeled the distribution of *P. ischnoclada* under the following environmental parameters: diurnal temperature range, average maximum temperature of the warmest period, average minimum temperature of the coldest period, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter some of which coincide

with those reported for *Passiflora* by **Bonilla (2014)** and **Ocampo et al. (2010)**.

A study using 19 climatic variables likewise revealed three clusters, although based on climatic differences among countries (**Bonilla, 2014**). In this study, however, the clusters appear to provide a better explanation for the adaptations exhibited by the various sections and their species in response to Peru's specific climatic conditions.

Climate modeling

A reduction of 391 *Tacsonia* records was observed after duplicate coordinates were filtered out within a 1 km² area. With these clean records, 1,367 pseudo-absences were randomly distributed. The mean AUC across the cross-validation folds was 0.94 (range, 0.88 - 0.98). On average, the variables showed the following: bio_1 was 12 °C (±3), with a minimum of 2 °C and a maximum of 20 °C. Bio_13 averaged 140 mm (±39), ranging from 4 mm to 272 mm. The bio_18 averaged 258 mm (±82), with a minimum of 12 mm and a maximum of 535 mm. Bio_6 was 3 °C (±4), from 10 °C to 12 °C. Bio_9 averaged 11 °C (±3), ranging from 0.3 °C to 20 °C. Bio_5 was 20 °C (±3), from 10 °C to 29 °C. Lastly, bio_11 was 11 °C (±3), with a minimum of 0.3 °C and a maximum of 20 °C.

High levels of uncertainty were found along the Pacific slope in the central and southern ranges of the Peruvian Andes, as well as in the northern parts of the Amazonas and Cajamarca departments (Figure S6). Areas below 1,500 m, including parts of the Amazon region, and sections of the Pacific and

eastern slopes above that altitude in the northern, central, and southern Andes also showed elevated uncertainty. The highest predicted climatic suitability was observed in the northern and central parts of Peru on both slopes, with values exceeding 0.75. Greater suitability for current climate conditions was indicated as elevation decreased (below 4,000 m). By contrast, areas above 5,000 m. in the southern range were associated with lower climatic suitability. The potential distribution modeling indicated 100% climatic suitability in the northern region, on both the western and eastern slopes, as well as in the central and southern regions on the eastern slope of the Andes. Conversely, niche modeling indicated 100% suitability on the range's northwestern slope, decreasing to 75% and 50% on the eastern slope. Predicted areas for the model ranged from 0% to 25% (light-colored areas) in coastal zones, the rainforest, and at elevations above 4,500 m above sea level (a.s.l.), covering an area of 2,537,494 km². The 25-50% interval covered 223,400 km², while the 50-75% climatic suitability accounted for 155,463 km². Finally, the model predicted 163,923 km² in the high-suitability range for *Tacsonia*, corresponding to the dark green areas.

Maxent is a machine-learning algorithm commonly used for modeling climatic and ecological niches, noted for its efficient output sizes relative to other methods (**Phillips et al., 2006**). In the context of this study, improvements beyond presence-only records lie in methodologies that assess performance using independent, well-structured presence-absence (or pseudo-absence) data (**Elith et al., 2006**).

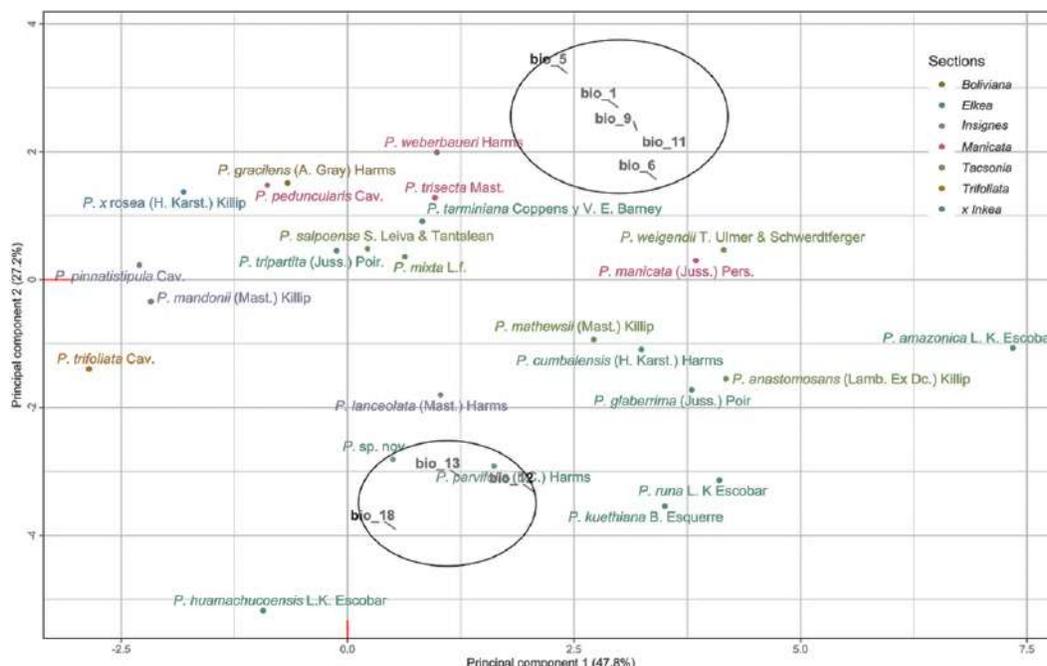


Figure 5. Biplot of variables and species in components 1 and 2. The legend Section groups the species by colors.

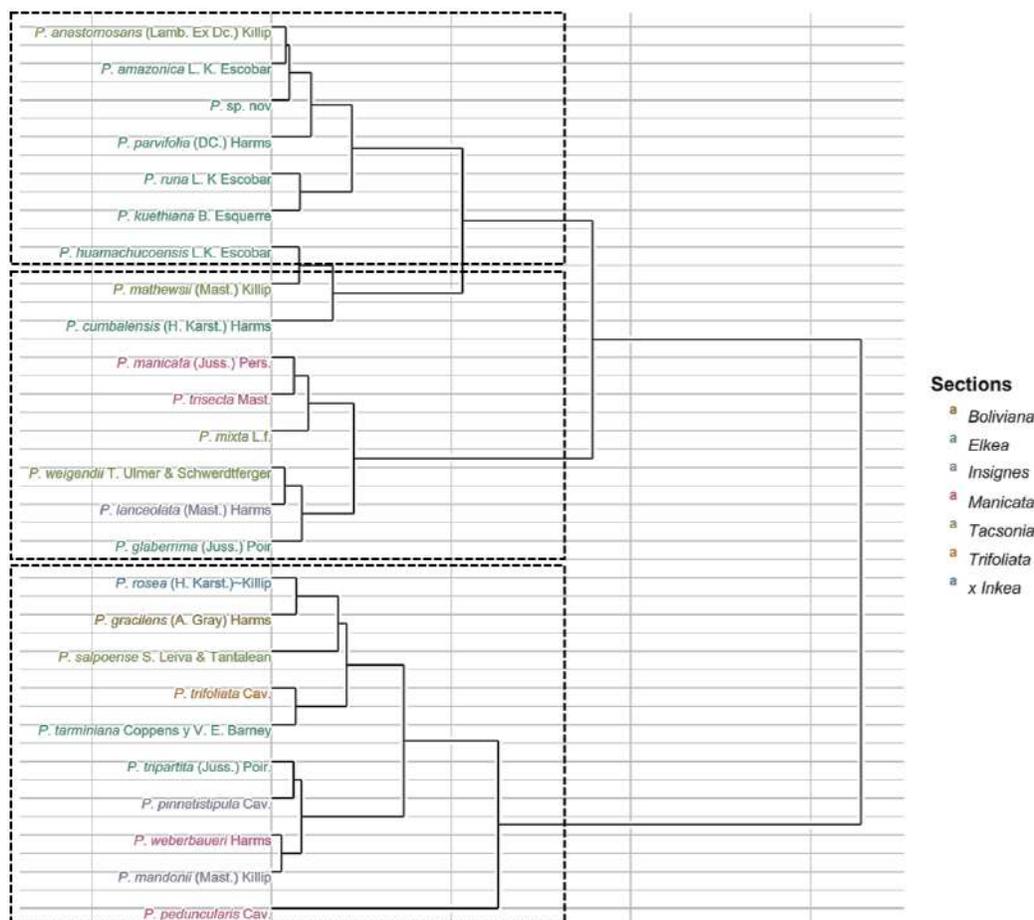


Figure 6. Climate relationship tree for the supersect. *Tacsonia*.

Such methodologies are compatible with machine-learning algorithms because they allow the implementation of pseudo-absences or conditional models (Phillips et al., 2006). They also facilitate performance evaluation using various metrics, including the AUC (Elith et al., 2006, 2011; Phillips et al., 2006).

Climatic distribution modeling is informed by the findings of Araújo et al. (2005), who reported excellent predictive performance based on AUC values. The mean AUC value for the 25 cross-validation partitions was 0.94, within a range of 0.88 to 0.98. These values are considered excellent and indicate a strong capacity of the model to distinguish and assign climatic suitability with the variables used for supersect. *Tacsonia*. According to Swets (1988), AUC values between 0.75 and 0.90 are considered reliable when assessing climatic predictions. Furthermore, as noted by Fielding & Bell (1997), averaging AUC across multiple partitions reduces overestimation of actual error rates, since the evaluation is not dependent on a single partition. The species-specific potential distribution models showed predictive performance with AUCs above

0.91 (Table 3). It was found that the number of occurrence records is not uniformly related to the model's predictive capacity (Elith et al., 2006). For instance, *P. parvifolia* exhibited an AUC value of 0.98, the highest obtained, with 36 records. *P. peduncularis* followed this with 82 records and an AUC of 0.97, *P. tripartita* with 297 records and an AUC of 0.97, and other species with 16 or more records, including *P. x rosea*. The lowest AUC value among this group was for *P. mathewsii*, with 62 records and an AUC of 0.91. However, some reports indicated that larger record sets sometimes adversely affect prediction (Pearce & Ferrier, 2000; Stockwell & Peterson, 2002).

Species with fewer than 16 records exhibited AUC values ranging from 0.3 to 1. Nonetheless, *P. huamachucoensis* and *P. weberbaueri* presented AUC values of 1 with 5 and 11 records, respectively. Likewise, *P. weigendii* had an AUC of 0.92, *P. glaberrima* 0.88, *P. anastomosans* 0.75, *P. mandonii* 0.75, *P. salpoense* 0.75, and *P. sp.* 0.7.

According to Araújo et al. (2005), these values reflect moderate predictability. However, they also suggest the model may generate areas of suitability

that are unlikely and thus should be discounted in favor of increasing the number of field records (Figure 7). This trend was reported by Elith et al. (2006). In those species, with limited distributions and a low number of records, higher AUC values were produced than in more widely distributed species. In contrast, *P. amazonica*, with an AUC of 0.5 and just two records, yielded a model no better than random chance, lacking the power to discriminate between presence and absence (Araújo et al., 2005). Similarly, *P. lanceolata* and *P. runa*, both with three records and an AUC of 0.3, revealed poor model performance due to the low number of records (Araújo et al., 2005; Fielding & Bell, 1997). Moreover, Araújo et al. (2005) showed that evaluations using non-independent data are more optimistic than those using independent data when measuring model performance. The dataset used in this study was sourced from various sources, including museums, community science initiatives, and targeted field collections.

Few modeling studies have been conducted on *Passiflora* L. species. Wyckhuys et al. (2012) modeled the distribution of *Daiops inedullis* in Colombia using MaxEnt and GARP but did not report model performance evaluations. Bezerra et al. (2019a, 2019 b) reported overlaps between passion fruit and its pollinators in present and future climate change scenarios in the Americas. Cristina Giannini et al. (2013) modeled the current and future distribution of plants and pollinators associated with *Passiflora*

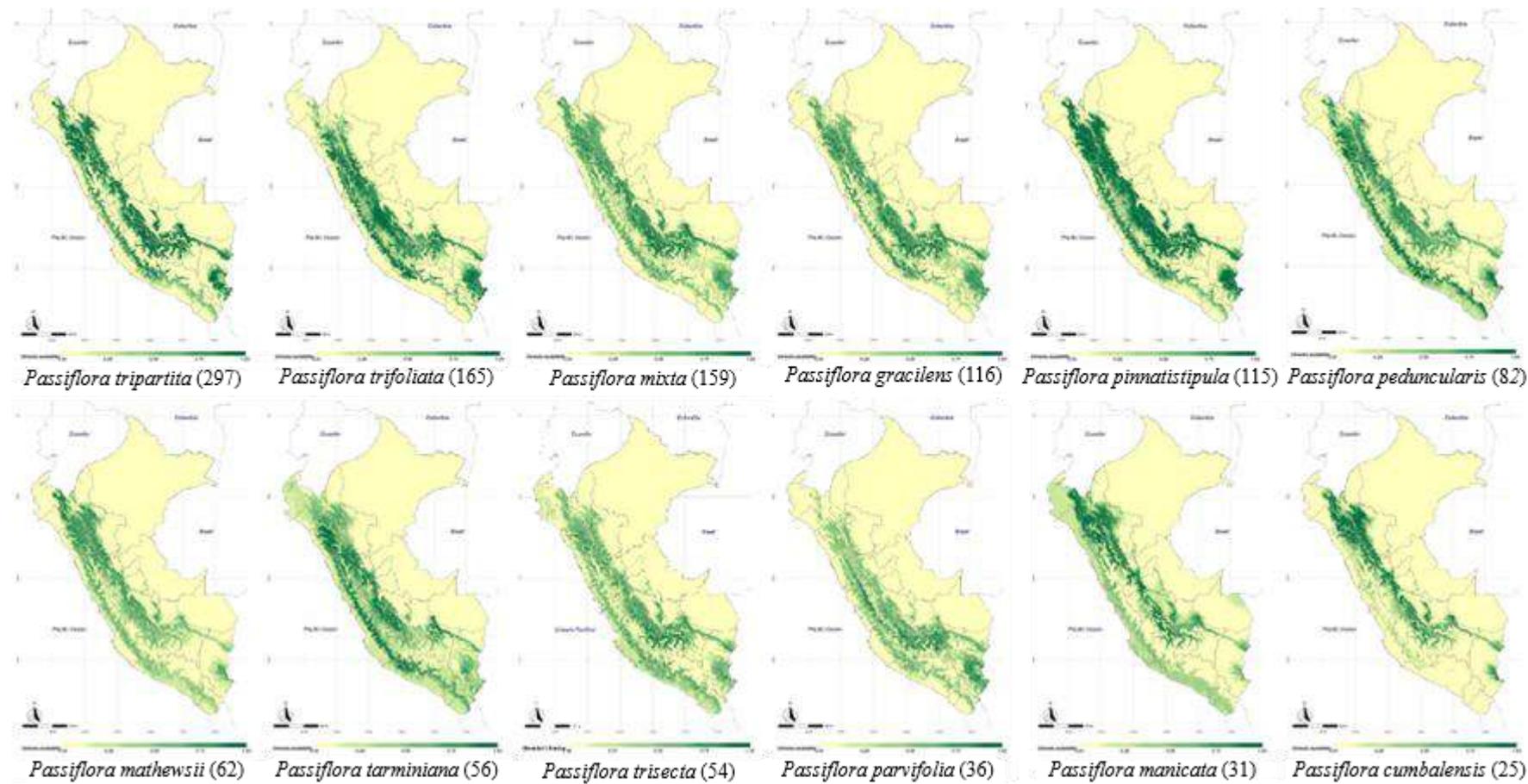
L. in the Brazilian Tropical Savanna (BTS). De Giovanni & Bernacci (2015) modeled the distribution of *P. ischnoclada* Harms using a single record. Teixeira et al. (2016) evaluated the potential effects of future climate change on *P. actinia* in the Atlantic Forest of Brazil. Halsch et al. (2020) modeled the distribution of *Passiflora* L. species that serve as hosts for the Gulf Fritillary Butterfly (*Agraulis vanillae*) to explain the butterfly's geographic range expansion.

Only Segura et al. (2003) modeled species of supersect. *Tacsonia*, but without any evaluation of predictive capacity. This work is the closest antecedent to the present study. Recently, efforts have been made to determine the potential distribution of *Tacsonia*; however, as noted by Segura et al. (2003), no model evaluation has been reported (Caicedo, 2021). However, the projected potential distribution areas are similar, predicting higher suitability in northern and central Peru but differing in the high southern ranges of the Andes. Caicedo (2021) also predicted a low probability of species occurrence along the western slope of the Peruvian Andes, while the potential and climatic niche distribution in the present study estimated high suitability in these areas. The discrepancy stems from the methodology used by Caicedo (2021), as BIOCLIM only characterizes the environmental space using existing records and does not infer novel areas that differ from them (Beaumont et al., 2005; Busby et al., 1991; Elith et al., 2006).

Table 3

Performance metrics (AUC) and the most influential bioclimatic variable for potential distribution models of *Tacsonia* species

Species	Records	AUC mean	AUC range	Main variable	Contribution
<i>P. cumbalensis</i>	89	0.94	0.3–1	bio_12	57%
<i>P. gracilis</i>	116	0.96	0.76–1	bio_1	74%
<i>P. huamachucoensis</i>	5	1	—	bio_1	89%
<i>P. manicata</i>	31	0.96	0–1	bio_12	—
<i>P. mathewsii</i>	62	0.91	0.5–1	bio_12	43%
<i>P. mixta</i>	159	0.94	0.7–1	bio_13	57%
<i>P. parvifolia</i>	36	0.98	0.8–1	bio_1	56%
<i>P. peduncularis</i>	82	0.97	0.7–1	bio_12, bio_1	53%, 57%
<i>P. pinnatistipula</i>	115	0.93	0.8–0.99	bio_1	70%
<i>P. tarminiana</i>	54	0.96	0.5–1	bio_12	62%
<i>P. trifoliata</i>	165	0.95	0.8–1	bio_13	76%
<i>P. tripartita</i>	297	0.97	0.8–1	bio_1	75%
<i>P. trisecta</i>	56	0.93	0.2–1	bio_13	68%
<i>P. x rosea</i>	16	0.94	0–1	bio_13	87%
<i>P. lanceolata</i>	3	0.3	0–1	bio_6	73%
<i>P. mandonii</i>	4	0.75	0–1	bio_6	75%
<i>P. runa</i>	3	0.3	0–1	bio_13	45%
<i>P. salpoense</i>	3	0.75	0–1	bio_6	98%
<i>P. sp.</i>	5	0.7	0–1	bio_12	99%
<i>P. weberbaueri</i>	11	1	—	bio_13	86%
<i>P. weigendii</i>	12	0.92	—	bio_6	49%
<i>P. anastomosans</i>	10	0.75	0–1	bio_13	81%
<i>P. glaberrima</i>	8	0.88	0–1	bio_12	55%
<i>P. amazonica</i>	2	0.5	—	—	—



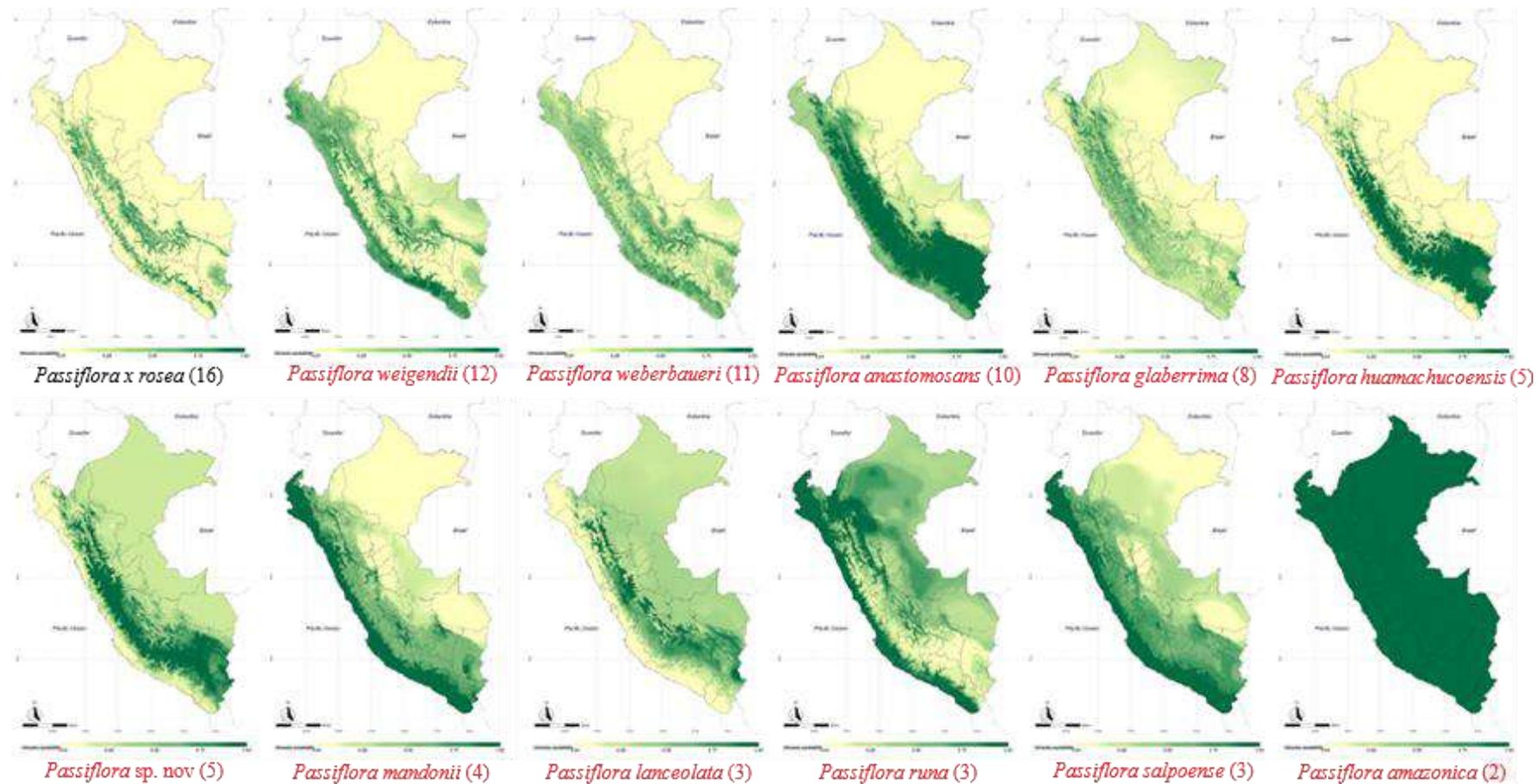


Figure 7. Climatic potential models for *Tacsonia* species in Peru. Number of occurrence records in parentheses. Species in red with fewer than 16 records.

Climate change modeling

Future projections for *Tacsonia* species indicated reductions and increases in areas of climatic suitability (Figures 8, S7-S14). Under the future scenario with SSP1-2.6 for 2021-2040, a loss of climatic suitability is projected in low-elevation areas of the northern range and across the entire eastern slope of the Andes, as well as in the northern portion of the western slope (Figure S7). Conversely, a gain in climatic suitability is projected in the central and southern regions of Peru, on both the eastern and western slopes of the southern range. However, only a moderate (10%) gain is expected in the central region. For the period 2041-2060, losses of climatic suitability are projected to persist in the same areas of the northern range and at low elevations on both the eastern and western slopes (Figure S8). By contrast, gains are expected to become more pronounced in the central and southern parts of the range, thus increasing the extent of suitable areas. From 2061-2080, an accentuated loss is projected in the northern range and on the eastern slope (Figure S9). In contrast, slight increases in suitability are anticipated in the central and southern parts of the cordillera. Finally, for the period 2081-2100, losses of climatic suitability are projected in the northern zone and on the eastern slope, in similar proportions to those observed in earlier periods (Figure S10). A slight reduction in suitable areas is expected during that time interval under this scenario. Under SSP5-8.5, for the period 2021-2040, losses of climatic suitability are projected in low-elevation areas of the northern range, specifically in the northern portion of the western slope. Along

the entire eastern slope of the Andes (Figure S11). Meanwhile, gains are expected in the higher-elevation zones of the northern, central, and southern range, with more pronounced increases in the central and southern regions. For 2041-2061, a greater loss of suitable areas is projected in the low-elevation zones of the northern range, extending throughout the eastern slope (Figure S12). Gains in suitable areas are again anticipated in the central and southern cordillera. Between 2061 and 2080, a loss of climatic suitability is projected along the lower elevations of both slopes, with a pronounced effect in the north. Conversely, new suitable zones are projected in the central and southern range, particularly in higher-elevation areas toward the south (Figure S13). Likewise, for 2081-2100, a decline in suitability is expected in low-elevation areas along the eastern and western slopes, with a more substantial impact in the northern sector (Figure S14). By contrast, an increase in suitability is anticipated in the central and southern portion of the cordillera.

A scatter analysis of points relating present climatic suitability to elevation in the Andes was conducted, and a high concentration was observed between 1,500 and 4,500 m above sea level (a.s.l.), with coefficients greater than or equal to 0.75. Points reflecting climatic suitability above 5,000 m. were also noted, although at low density. For coefficients below 0.75, low predictability of suitable climates for *Tacsonia* was observed from sea level to elevations above 6,000 m, with the predictability increasing gradually but then declining again above 3,500 m (Figure S15).

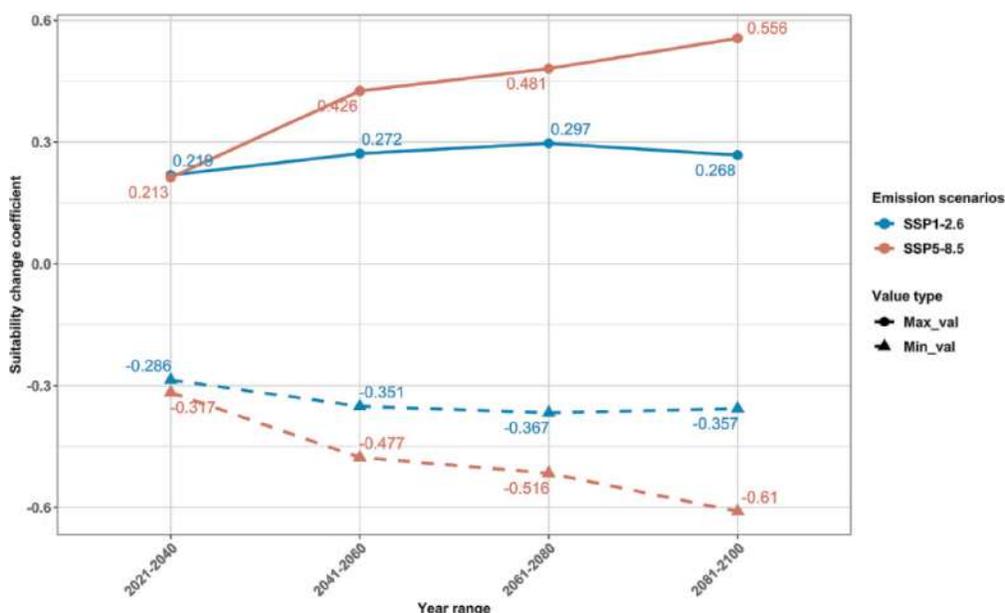


Figure 8. Maximum and minimum values of loss and increase in suitability of *Tacsonia* for the SSP1-2.6 and SSP5-8.5 scenarios in four ranges of years in Peru.

Climate-change models project temperature increases up to 4 °C and shifts in precipitation by 2100 (Thuiller, 2007). The First Assessment Report of the United Nations Intergovernmental Panel on Climate Change (IPCC) highlighted that species at risk include specialists, those less tolerant of ecological changes, and poor dispersers (IPCC, 1990). Furthermore, drastic temperature shifts will be most pronounced at the poles, while the tropics will experience local monthly extreme temperatures of 1-2 °C, depending on the specific tropical and subtropical ecoregion (Beaumont et al., 2011). As a result, research and literature reviews have traditionally focused on biotic impacts at mid- and high latitudes (Feeley et al., 2017). Although one-third of Earth's surface lies in the tropics, tropical ecosystems are notably absent from almost all climate-change studies and reviews (Feeley et al., 2017), even though tropical species match the IPCC's identified risk profile (Forister et al., 2015; IPCC, 1990; Janzen, 1967).

Climatic modeling approaches are useful for assessing the effects on future species distributions (Hijmans & Graham, 2006; Plissock et al., 2014; Teixeira et al., 2016). However, uncertainty arises in future climate-change modeling when selecting which variables to include (Plissock et al., 2014). In addition, a model's current performance does not guarantee similarly optimal performance under past or future climates, which can lead to overly optimistic evaluations unless data independence and appropriate variable selection are carefully considered (Araújo et al., 2005; Plissock et al., 2014; Thuiller, 2004). Current distribution models are often akin to near-term projections, whereas later projections can differ substantially (Araújo et al., 2005). Over or underestimating changes in response to climate change may thus lead to errors (Araújo et al., 2005).

Few studies have evaluated the loss and gain of climatic suitability. Bezerra et al. (2019a, 2019 b) reported a 36.56% loss in 2060 and up to 64.80% by 2080 under RCP 8.5, with AUC values of 0.89 or higher. Those authors also predicted that, in Brazil, a spatial mismatch of up to 42.80% could emerge between *P. edulis* and its bee pollinator species by 2060, accompanied by reductions in the climatic suitability areas for passion fruit and its pollinators (Bezerra et al., 2019a, 2019 b). Those reductions could reach 31.90% and 54.90% in 2060 and 2080, respectively (Bezerra et al., 2019a, 2019b). Additionally, Cristina Giannini et al. (2013) modeled the future distribution of *Passiflora* L. pollinators in Brazil's Tropical Savanna (BTS) by 2050, reporting AUC values above 0.9. Prior to this research, no

studies on climate change for *Passiflora* L. species in the Andes, or specifically for the supersect *Tacsonia*, had been reported.

The climate-change outcomes for *Tacsonia* in this study revealed scenario-specific severity under the SSP1-2.6 and SSP5-8.5 scenarios. On average, the SSP1-2.6 scenario indicates a 26.4% gain in climatic suitability by 2100 (2021-2040, 2041-2060, 2061-2080, 2081-2100), along with a 34% loss. Under SSP5-8.5, the gain could reach 42% over the same time intervals, whereas the loss of climatic suitability could be as high as 48%. Moderate gains and losses were noted in all periods for SSP1-2.6. In contrast, under SSP5-8.5, both increases and decreases in climatic suitability were more pronounced (Figure S15), with notable differences from the current climate. However, for the 2021-2040 period, the losses and gains for both climate-change scenarios appeared similar.

In both scenarios, losses of climatic suitability were concentrated in the northern region and along the slopes on both sides of the cordillera. However, these were more severe and widespread under SSP5-8.5. Conversely, new areas of climatic suitability would be moderate under SSP1-2.6 in the central and southern sectors of Peru, but more extensive under SSP5-8.5, particularly at higher elevations. In addition, the northern part of the cordillera and low-lying *Tacsonia* occurrences appear consistently more vulnerable, given the losses of suitability across both scenarios. By contrast, the central and southern cordillera display areas of future suitability, potentially indicating a shift toward higher latitudes and elevations (Figs. S7-S14). As the century progresses, particularly during 2061-2080 and 2081-2100, the patterns of suitability gains and losses in both scenarios diverge markedly, particularly in SSP5-8.5. Although the changes appear more gradual under SSP1-2.6, absent the necessary measures to avoid the SSP5-8.5 scenario, changes could be more drastic and rapid.

Species adaptation to climate change is commonly predicted to involve migrations in search of suitable habitats for survival (Feeley et al., 2017; Thuiller, 2007). Studies have documented upslope movement in many species in response to warming in lower-altitude areas (Parmesan, 2006; Sheldon, 2019). When analyzing these losses and gains in climatic suitability with respect to elevation, the digital elevation model for Peru was interpolated bilinearly to match the resolution of the climate model outputs. Although resolution cannot be truly enhanced by this method, it becomes more realistic (Phillips et al., 2006). Higher elevations within the cordillera are potential climate refuges for *Tacsonia* species

(Figure S15). Under present conditions, elevations between 1,500 and 4,500 m show a high density of pixels with suitability coefficients above 0.75, thus being the most favorable for this group. Additionally, elevations above 5,000 m also contain suitable pixels, albeit at a low density, potentially due to the occurrence of particular species (e.g., *P. huamachucoensis*) above 4,000 m.

When the pixel distributions in both SSP1-2.6 and SSP5-8.5 are examined, elevations between 1,500 and 2,500 m above sea level (a.s.l.) are expected to experience considerable reductions in climatic suitability. In SSP1-2.6, these declines range from 30% to 35%, whereas more drastic reductions are projected under SSP5-8.5. Conversely, increases in suitable areas from 2,000 to 6,000 m above sea level are observed in both scenarios. Climatic suitability appears to rise between 3,500 and 4,500 m. under SSP1-2.6, and between 3,500 and 5,500 m. under SSP5-8.5. These patterns suggest that optimal climatic conditions for *Tacsonia* may shift toward higher elevations, with greater severity under the SSP5-8.5 scenario. Losses of suitable areas between 1,500 and 3,000 m. became especially pronounced in SSP5-8.5, potentially exceeding 50%-60% by the end of the century. Meanwhile, SSP5-8.5 indicates notable increases in suitability at elevations from 4,000 to 5,500 m.

These findings suggest a temporal dimension of change in both scenarios. A rapid decrease in mid-elevation suitable areas is expected from the present to 2100 within the 1,500-2,500 m range. This temporal pattern indicates that these areas face higher short-term risk, necessitating immediate conservation efforts (Fajardo et al., 2014). On the other hand, sustained but gradual increases may occur at higher elevations. Overall, climate change is likely to have a profound and differential impact on *Tacsonia* distributions in the Andes, resulting in substantial losses of suitable areas at mid-elevations and a potential expansion at higher elevations (Beaumont et al., 2011; Zhao et al., 2013). Even a slight rise in temperature in the tropics can significantly affect the climatic suitability of species (Deutsch et al., 2008). The dispersal capability of pollinators and the colonization potential of newly suitable areas will be critical in the face of climate change. There is evidence that birds also tend to move to higher elevations in search of climatic equilibrium (Forero-Medina et al., 2011; Freeman et al., 2018). However, the major challenge lies in the physiological adaptation of *Tacsonia* species to these new elevations and climatic conditions. One piece of evidence for phenological changes in the tropics comes from shifts in the timing of plant

flowering and fruiting (Zhao et al., 2013). Asynchronous phenological changes may lead to trophic mismatches in tropical communities (Sheldon, 2019). Among *Tacsonia* species, those with extensive latitudinal and elevational ranges may be better equipped to respond to changing climate conditions through plasticity or inherent evolutionary traits (Sheldon, 2019).

Conservation status

Of the 25 species, 4% (one species) has been placed in the Critically Endangered (CR) category, 84% (21 species) have been classified as Endangered (EN), and 12% (three species) have been assigned to the Vulnerable (VU) category (Table 4). This indicates that a large majority of these species (88%) are in high-risk categories (CR and EN), reflecting a worrisome situation for their conservation and highlighting the urgent need for protective measures.

Significant increases in both the number of records and in EOO and AOO metrics were observed for some species, leading to either a change in their risk assessment or greater precision in that assessment. Such was the case for *P. huamachucoensis*, which had previously been reported with only one record (Caicedo, 2021), indicating an EOO of 0 km² and an AOO of 4 km². Now, 38 records have been compiled, along with an EOO of 342.725 km² and an AOO of 16 km². A notable change in the available data led to a reclassification of the species from CR to EN, possibly indicating a lesser urgency in its extinction risk. Similarly, *P. runa* underwent a significant increase in records and EOO, rising from 4 records and an EOO of 2,137 km² (Caicedo, 2021) to 5 records and 239.710 km² of EOO. This variation also caused a reclassification from CR to EN. Another species, *P. salpoense*, experienced an increase in records from 3 to 6 and an increase in EOO from 0.004 km² to 9,645.605 km². This data update supported its reclassification from CR to EN. Likewise, *P. amazonica* increased in records from 4 to 6, with an EOO rising from 18.015 km² to 725.037 km². These updates showed a broader distribution than that reported by Caicedo (2021), thus justifying a shift in its risk category.

More moderate increases in records, EOO, and AOO were exhibited by other species, without prompting a change in their risk classification. However, such increases did provide greater precision in their assessment. *P. mixta* and *P. tripartita* provide examples of species that have experienced a considerable rise in records and AOO, resulting in an adjustment from EN to VU in the case of *P. mixta*. Likewise, *P. tripartita* showed an increase in records from 269 to 428 and an AOO from 920 km² to 1,264

km². However, it remained in the Vulnerable category, indicating a stable yet concerning situation for its wild populations. On the other hand, species such as *P. pinnatistipula*, *P. peduncularis*, and *P. gracilens* displayed increases in records and slight increments in EOO and AOO, without altering their EN classification (Caicedo, 2021). These changes highlight improvements in data availability and metric accuracy, both of which are critical for informed management and conservation decisions. For instance, *P. pinnatistipula* rose from 88 to 132 records, with an AOO increasing from 336 km² to 472 km². However, it remained in the EN category because these changes did not significantly alter its extinction risk (Caicedo, 2021).

P. kuethiana remains the only species still classified as CR. This species was placed in the CR category by Caicedo (2021) with a single record, an EOO of 0 km², and an AOO of 4 km², under criteria B1a and D. Although a slight increase in the number of records (from 1 to 2) and in the AOO (from 4 km² to 8 km²) was noted, the species continues to be classified as CR. Despite these small increases in data, its geographic distribution remains extremely limited.

Species richness in protected natural areas

Twelve species have been recorded in National Parks, whereas seven have been recorded in Historic Sanctuaries (Table 5). Although only seven occurrences have been documented in Landscape Reserves and National Sanctuaries, these areas

shelter five and four species, respectively. Among the endemic species, National Parks safeguard five *P. weigendii*, *P. parvifolia*, and *P. trifoliata*, while Historic Sanctuaries protect three endemic taxa: *P. parvifolia*, *P. trifoliata*, and *P. trisecta*. Furthermore, *P. trifoliata* and *P. trisecta* have been reported in both Landscape Reserves and National Sanctuaries. Climatic suitability modeling revealed an increase in the number of protected natural areas where these species could be distributed (Figure S16). This was the case for the Machiguenga Communal Reserve, Titicaca National Reserve, Bahuaja Sonene National Park, Salinas and Aguada Blanca National Reserve, Pampa Hermosa National Sanctuary, Junín National Reserve, and Tabaconas Namballe National Sanctuary, among others. Suitability percentages were found to exceed 75% (0.75).

Analysis of *Tacsonia* species distributions within Peru’s protected natural areas revealed notable patterns in biodiversity and conservation. *P. mixta* emerged as the most widespread species, documented in six Protected Natural Areas. This broad distribution suggests that *P. mixta* may exhibit greater environmental resilience than other species, making it a favorable indicator for conservation.

Several endemic species, *P. weigendii*, *P. trisecta*, *P. trifoliata*, *P. parvifolia*, *P. amazonica*, and *P. peduncularis*, were found in the Protected Natural Areas, underscoring the critical role these areas play in conserving Peru’s endemic biodiversity.

Table 4

Summary of the geographic distribution of *Tacsonia* in Peru. EOO, area of occurrence of a taxon; AOO, area of occupancy of a taxon; CaR, risk category. Sorted by the number of occurrence records. Asterisks show endemic species

Species	Records	EOO (km ²)	AOO (km ²)	CaR
* <i>P. kuethiana</i>	2	0	8	CR, B2ab(iv), D.
* <i>P. lanceolata</i>	4	1.339,051	16	EN, B1, D.
* <i>P. runa</i>	5	239,710	16	EN, B1, D.
<i>P. mandonii</i>	5	7.083,388	16	EN, B2ab(iii), D.
* <i>P. amazonica</i>	6	725,037	24	EN, B1, D.
* <i>P. salpoense</i>	6	9.645,605	16	EN, B2ab(iii), D.
* <i>P. sp.</i>	9	745,364	20	EN, B2ab(iii), D.
<i>P. glaberrima</i>	10	1.444,217	36	EN, B1, D.
* <i>P. weberbaueri</i>	11	3.006,033	40	EN, B1, D.
* <i>P. anastomosans</i>	12	31.561,476	48	EN, B1, D.
* <i>P. weigendii</i>	12	625,816	48	EN, B1, D.
<i>P. x rosea</i>	19	36.882,718	76	EN, B2ab(iii), D.
<i>P. manicata</i>	36	65.814,859	140	EN, B2ab(iii), D.
* <i>P. huamachucoensis</i>	38	342,725	16	EN, B2ab(iii), D.
* <i>P. parvifolia</i>	38	116.051,323	136	EN, B2ab(iii), D.
<i>P. tarminiana</i>	64	276.770,920	236	EN, B2ai(iii), D.
* <i>P. trisecta</i>	70	111.705,728	240	EN, B2ai(iii), D.
<i>P. mathewsii</i>	74	240.972,252	260	EN, B2ai(iii), D.
<i>P. cumbalensis</i>	102	82.290,098	376	EN, B2ai(iii), D.
* <i>P. peduncularis</i>	105	288.200,855	324	EN, B2ai(iii), D.
<i>P. pinnatistipula</i>	132	252.532,554	472	EN, B2ai(iii), D.
<i>P. gracilens</i>	140	227.742,650	436	EN, B2ab(iii), D.
* <i>P. trifoliata</i>	209	186.879,117	664	VU, B2.
<i>P. mixta</i>	221	397.470,275	624	VU, B2.
<i>P. tripartita</i>	428	427.968,725	1.264	VU, B2, C2ai, D1

Table 5Distribution of *Tacsonia* in Protected Natural Areas of Peru. Endemic species are marked with an asterisk

Protected Natural Areas	Number of species	Number of Records	Species
Yanachaga-Chemillén National Park	4	25	<i>P. mixta</i> L.f., * <i>P. weigendii</i> T. Ulmer & Schwerdtfeger, <i>P. cumbalensis</i> (H. Karst.) Harms, <i>P. tripartita</i> (Juss.) Poir.
Machu Picchu Historic Sanctuary	4	37	<i>P. gracilens</i> (A. Gray) Harms, * <i>P. trisecta</i> Mast., <i>P. mixta</i> L.f., <i>P. tripartita</i> (Juss.) Poir.
Huascarán National Park	3	52	* <i>P. trifoliata</i> Cav., <i>P. tripartita</i> (Juss.) Poir., <i>P. tarminiana</i> Coppens y V. E. Barney
Ampay National Sanctuary	3	7	<i>P. mixta</i> L.f., * <i>P. trisecta</i> Mast., <i>P. tripartita</i> (Juss.) Poir.
Abiseo River National Park	2	10	* <i>P. parvifolia</i> (DC.) Harms, <i>P. cumbalensis</i> (H. Karst.) Harms
Nor Yauyos-Cochas Landscape Reserve	2	6	* <i>P. trifoliata</i> Cav., <i>P. tripartita</i> (Juss.) Poir.
Alto Mayo Protection Forest	1	1	* <i>P. amazonica</i> L. K. Escobar
Pui Pui Protection Forest	1	1	<i>P. mixta</i> L.f.
Manu National Park	1	3	<i>P. mixta</i> L.f.
Udima Cloud Forest Wildlife Refuge	1	1	<i>P. cumbalensis</i> (H. Karst.) Harms
Calipuy National Reserve	1	1	* <i>P. peduncularis</i> Cav.
Cotahuasi Sub-basin Landscape Reserve	1	1	<i>P. tripartita</i> (Juss.) Poir.
Historical Sanctuary of the Pampa de Ayacucho	1	1	<i>P. tripartita</i> (Juss.) Poir.

For instance, *P. trifoliata*, which is both endemic and classified as VU, has been observed in three Protected Natural Areas. The prominence of these species in Protected Natural Areas underscores the need to sustain their protection, as these crucial habitats provide vital refuges for endemic and threatened biodiversity.

Peru's Protected Natural Areas play a central role in preserving a broad range of species (Fajardo et al., 2014), many of which are currently designated as VU or EN under IUCN criteria (León et al., 2006). These classifications reflect the species' susceptibility to threats such as habitat loss, fragmentation, and population declines. Yanachaga-Chemillén National Park and Machu Picchu Historic Sanctuary each host species such as *P. weigendii* and *P. trisecta* (both endemic), classified as EN. Huascarán National Park is home to *P. tarminiana* and *P. trifoliata* (endemic), also categorized as EN. *P. amazonica* and *P. peduncularis* are recorded in Alto Mayo Protected Forest and Calipuy National Reserve, where they are also listed as EN. In addition, wild populations of *P. tripartita*, a cultivated *Tacsonia* species, are protected in Huascarán National Park, Machu Picchu Historic Sanctuary, and the Nor Yauyos-Cochas Landscape Reserve. Lastly, Yanachaga-Chemillén National Park and Río Abiseo National Park host *P. cumbalensis* and *P. parvifolia* (the latter endemic), designated as VU. These protected areas not only serve as refuges that allow these species to maintain viable populations but also function as repositories of genetic diversity, which is crucial for

their long-term resilience to environmental change and other stressors. Notably, when the current climatic suitability within these Protected Natural Areas was examined, a considerable expansion of suitable habitat was observed.

Our findings underscore the need for a comprehensive examination of the niche adaptations of *Tacsonia* species. Future studies could investigate the interaction between these species and their pollinators and dispersers, potentially unveiling key mechanisms for conservation. Understanding biotic interaction networks can aid in identifying species at greatest risk of extinction under climate change. Mapping which *Tacsonia*-associated species and areas of diminishing and/or expanding climatic suitability overlap could offer deeper insights into future conservation needs. The marked rise in species records underscores the importance of field collection and monitoring, especially for rare species. Additionally, implementing *ex-situ* conservation strategies for these taxa is essential.

4. Conclusions

The supersection *Tacsonia* is widely distributed across the Peruvian Andes, occurring between elevations of 1,600 and 4,500 m. This study mapped 25 species, including one potentially new to science, with the highest levels of species richness concentrated in the Cusco department, particularly between 2,500 and 3,500 m above sea level. The integration of a new dataset from iNaturalist significantly expanded the available records,

bringing the total to 1,758 georeferenced entries. This dataset represents the most comprehensive and spatially detailed inventory of *Tacsonia* species in Peru to date, substantially improving upon previous assessments and highlighting the value of participatory data for biodiversity and plant genetic resources research.

Distribution models under climate change scenarios suggest that *Tacsonia* species may shift to higher elevations. Significant losses in climatic suitability are projected between 1,500 and 3,000 m above sea level, alongside potential expansion above 3,500 m. This highlights the risks to current populations and underscores the urgent need for effective conservation strategies. Projections of future climate scenarios point to substantial reductions in suitable habitats, with estimated decreases of up to 60% by the end of the 21st century.

A significant proportion of *Tacsonia* species face elevated extinction risk, with numerous taxa classified as Critically Endangered (CR) or Endangered (EN) under IUCN Red List criteria. Endemic species, such as *Passiflora kuethiana*, *P. lanceolata*, and *P. amazonica*, are characterized by narrow geographic ranges and limited occurrence records, which significantly increase their vulnerability to habitat degradation and the impacts of climate change.

These results offer a spatially explicit baseline for prioritizing future research and conservation efforts for *Tacsonia* in the Peruvian Andes. Future work should (i) conduct targeted field surveys in under-sampled regions and areas predicted to remain suitable under climate change scenarios (potential refugia), (ii) implement integrated taxonomic assessments that combine morphology, herbarium revision, and DNA-based methods to confirm the status of the potential new taxon and resolve misidentifications, and (iii) measure population size, demographics, and genetic diversity of narrow endemics to improve extinction-risk assessments beyond the occurrence-based metrics (EOO/AOO). Meanwhile, model refinement should include microclimatic heterogeneity, land-use change, and connectivity to identify elevational corridors, guide restoration priorities, and evaluate the viability of in situ measures (protected-area expansion, corridor design) and ex situ strategies (seed banking and living collections) for the most threatened taxa. Overall, the occurrence database and suitability projections presented here can directly support conservation planning, monitoring efforts, and evidence-based updates of IUCN assessments for *Tacsonia* species in Peru. In this context, our results provide practical guidance for prioritizing investments in surveys, management, and conservation in

Andean landscapes experiencing rapid climatic change.

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