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Geodiversity and Ecological Filtering Drive High Local Diversity of Inga (Fabaceae) in Imbabura, Northern Ecuadorian Andes

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Geodiversity and Ecological Filtering Drive High Local Diversity of Inga (Fabaceae) in Imbabura, Northern Ecuadorian Andes

Hugo Orlando Paredes Rodríguez [1,*], Wilfredo Franco [2] and Elio Sanoja [3]

[1] Universidad Técnica del Norte, Ibarra 100105, Ecuador;
[2] Universidad Regional Amazónica IKIAM, Tena 150150, Ecuador
[3] Universidad Nacional Experimental de Guayana, Puerto Ordaz 8051, Venezuela
* Correspondence: hoparedes@utn.edu.ec; Tel.: +593 0997038712

Abstract

The Neotropical genus *Inga* (Fabaceae) is a dominant component of tropical forests and plays important ecological and functional roles; however, its diversity patterns and environmental controls across Andean landscapes remain poorly documented under increasing deforestation pressure. This study quantified the diversity, distribution, and environmental determinants of *Inga* species in the Imbabura Province, northern Ecuador, by integrating field surveys along five elevational transects, herbarium records, and Geographic Information Systems (GIS)-based analyses of climatic and edaphic variables. We recorded 17 species, nearly tripling previous regional findings. Species richness and occurrence were strongly structured by altitude, temperature, and soil properties. Ten species showed narrow altitudinal range and limited thermal tolerance (<2 °C), indicating habitat specialization, whereas *I. densiflora* and *I. insignis* exhibited broader niche breadths and generalist behavior. Edaphically, most species were associated with sandy loam soils, particularly Mollisols and Inceptisols. These results indicate that environmental gradients and soil conditions act as primary filters shaping *Inga* assemblages in heterogeneous montane landscapes. The high level of specialization observed suggests elevated vulnerability to land-use change and highlights the need for habitat-specific conservation strategies in Andean forests.

Keywords: *Inga*; Andean forests; environmental gradients; niche specialization; soil–climate interactions; species distribution modeling; montane biodiversity

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Highlights

- Seventeen Inga species documented in Imbabura, northern Ecuador.
- Species distributions are structured by altitude and soil properties.
- Ten species exhibit narrow thermal and altitudinal specialization, others are generalists.
- Uplift and volcanic substrates generate fine-scale edaphic mosaics.
- Geodiversity likely amplifies ecological filtering in Andean forests.

1. Introduction

Tree diversity is critical to the health of the global ecosystem. While South America is home to remarkable richness with approximately 16,880 tree species, compared to 1,873 in North America, 3,529 in Africa, and 4,560 in Oceania, this biodiversity faces critical threats [1]. Ecuador, distinguished by its high biodiversity, is home to approximately 2,500 recognized tree species [2]. However, the country faces a critical environmental challenge: deforestation. Between 1990 and 2000, the average deforestation rate was approximately 89,944 ha·year^{-1} (-0.71%), and although this rate decreased to 44,497 ha·year^{-1} (-0.37%) between 2008 and 2014, the continued loss of forest cover represents a major challenge for the conservation of biodiversity and the sustainability of ecosystems. [3].

In this context, the genus *Inga* Mill. (Fabaceae) is particularly relevant. It is a diverse group of legumes common in neotropical forests with important socioeconomic value [4]. The genus includes around 300 species distributed from Mexico to northern Argentina, with the highest diversity in the Andes of Peru, Ecuador and Colombia [4]. In Ecuador, publications such as Trees of Ecuador describe representative species [5], while the fundamental work of Pennington and Revelo reports 75 species for the country. However, historically only six species have been reported for the province of Imbabura [6], a figure that contrasts with the heterogeneous relief and the potential for numerous ecological niches of the region. The presence and development of *Inga* species are conditioned by ecological factors such as altitude, precipitation, temperature and life zones [7]. However, anthropogenic factors also play a crucial role. Human occupation in South America has driven the domestication of plants for millennia, modifying landscapes since pre-Columbian times [8,9]. Human activities, such as the consumption of *Inga* fruits (guabas), influence dispersion, with humans acting as vectors along roads and trails. This phenomenon contrasts with the behavior of wild species, which tend to remain confined to forest remains [6]. This duality suggests that the distribution of Inga in Imbabura is driven by a complex interaction between natural ecological filters and anthropogenic history.

Therefore, it is necessary to deepen the knowledge of the distribution and ecology of *Inga* species in this Andean region to improve their conservation and sustainable use. The objective of this study is to determine the geographic distribution of *Inga* species in the province of Imbabura-Ecuador by evaluating their presence in different ecosystems and analyzing key environmental factors such as altitude, temperature, precipitation and soil type.

2. Materials and Methods

2.1. Study Area

The study was carried out in the province of Imbabura, located in the northern inter-Andean region of Ecuador, covering the western foothills of the Royal and Western mountain ranges. The region is characterized by a heterogeneous relief composed of slopes, hills and plateaus, shaped by drainage networks and tectonic processes. This geomorphological complexity creates a mosaic of environmental conditions that favor high plant diversity and provides differentiated ecological niches for the *Inga* genus.

2.2. Data Collection and Sampling Strategy

The research methodology was divided into two phases: field sampling and laboratory analysis. For the field sampling phase, five strategic routes were defined to cover the floral diversity of the province:

1. Ibarra–Lita (73.13 km) and San Gerónimo–Buenos Aires (22.77 km);
2. Ibarra–Pimampiro (51 km);
3. Ibarra–Otavalo–Cajas (37.88 km);
4. Otavalo-Intag (116.7 km);
5. Las Golondrinas (19.53 km).

In total, the exploration route covered 321 km. Imbabura has an area of 4785 km2 (Figure 1).

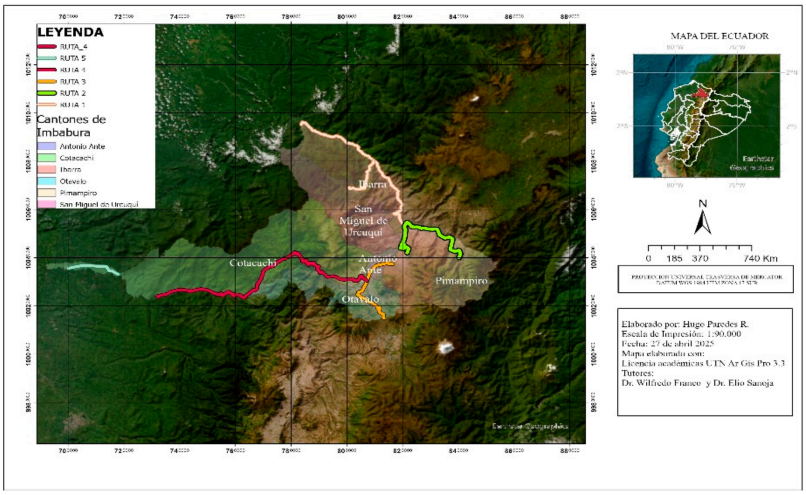

Figure 1. Sampling areas in the province of Imbabura.

Sampling was conducted on adult individuals located within a 50 m buffer zone on each side of the road. Collection protocols followed the standards of the Herbarium of the Universidad Técnica del Norte (HUTN). Field data were recorded using the KoBoToolbox application [45], parameterized to capture variables specific to the genus *Inga*.

In addition to primary data, secondary data from the Global Biodiversity Information Facility (GBIF) [21,22] and national herbarium databases (QCNE, MO, AAU, F, HUTN) were compiled to identify historical records of Inga in Imbabura. Sites with historical records of species were reviewed for verification. This study was carried out under research permit No. MAATE-ARSFC-2023-0036, granted by the Ministry of Environment, Water and Ecological Transition of Ecuador (MAATE). [23]

2.3. Taxonomic Identification

Botanical samples were processed using traditional phytaxonomic techniques. Taxonomic identification was carried out using specialized keys for the genus, specifically those proposed by Pennington & Revelo [6] and Pennington [12], and validated through consultation with specialists (Eng. Nixon Revelo). Valid specimens for 12 species (including duplicates) were deposited in the HUTN herbarium. The identification of the four remaining species was confirmed through consultation with the National Biodiversity Institute (INABIO) and digital herbaria (Tropicos, WFO).

2.4. Geospatial and Ecological Analysis

Geospatial analysis was performed using ArcGIS Pro-3. The precise location of each specimen was integrated with the provincial and cantonal administrative limits [13]. To determine the ecological zoning of *Inga* species, point data overlaid with geopedological shapefiles containing the following variables:

- Climatic: Temperature, precipitation and ombrothermal index [16].
- Edaphic: soil type (order), texture, pH and slope [14].
- Land Use: Current vegetation cover and types of land use [15].

Data sources included the Ministry of Agriculture and Livestock (MAG) (SIGTIERRAS), the Ministry of the Environment (MAATE) and the National Institute of Meteorology and Hydrology (INAMHI). These variables were analyzed to generate distribution maps and determine the specific ecological niche for each species.

3. Results

3.1. Floristic Composition and Diversity

The review of national and international herbaria databases (QCNE, MO, AAU, F, HUTN), combined with field expeditions, confirmed the presence of 17 species of the genus *Inga* in the province of Imbabura [21,22]. A total of 52 samples were collected and identified. Confirmed species include *Inga acuminata* Benth., *I. cinnamomea* Spruce ex Benth., *I. cocleensis* Pittier, *I. densiflora* Benth., *I. edulis* Mart., *I. feuillei* DC., *I. insignis* Kunth, *I. marginata* Kunth, *I. multijuga* (Benth.) Kuntze, *I. oerstediana* Benth., *I. punctata* Wi-lld., *I. sapindoides* Willd., *I. silanchensis* T.D.Penn., *I. spectabilis* (Vahl) Willd., *I. striata* Benth., *I. velutina* Willd. and *I. vera* Willd. [Table A1. A1].

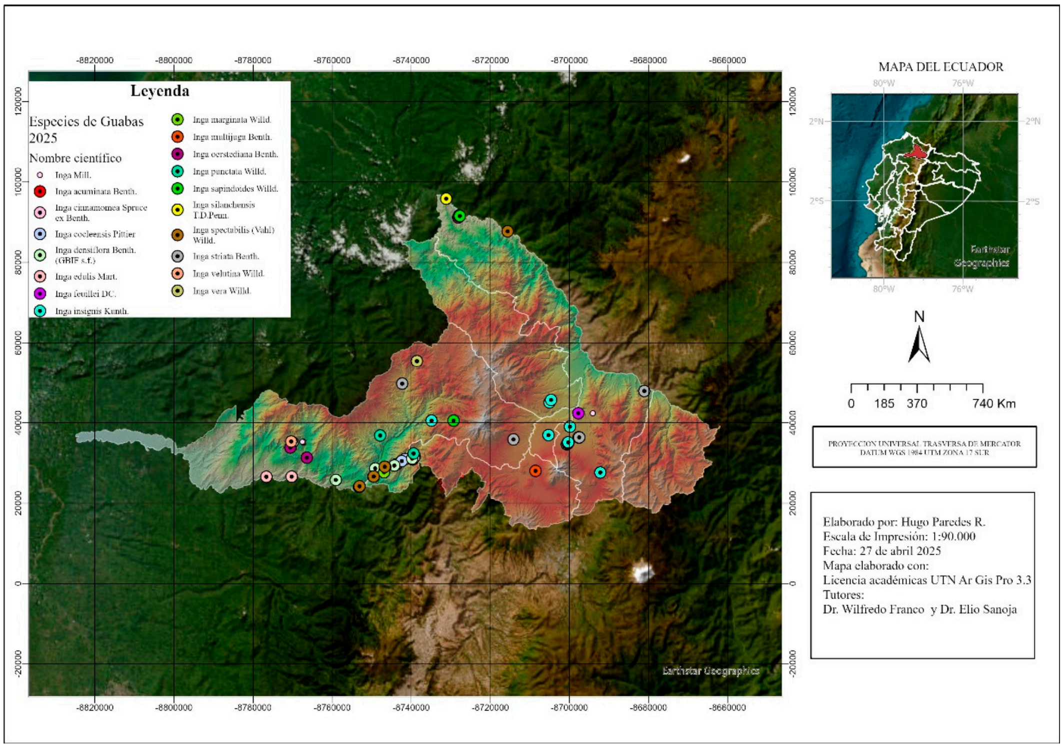

Figure 2. Species of the genus *Inga* in Imbabura.

3.2. Thermal and Altitudinal Distribution Patterns

The analysis of the altitudinal distribution reveals two different ecological behaviors among the identified species [Table 1].

- **Specialized species**: A group of species, including *I. cinnamomea*, *I. silanchensis*, *I. edulis*, *I. spectabilis*, *I. marginata*, *I. punctata*, *I. velutina* and *I. feuillei*, occupy narrow altitudinal ranges with variations of less than 500 m. These species are restricted to specific microhabitats [Table 1; Figure A2].
- **Generalist species**: In contrast, *I. sapindoides*, *I. oerstediana*, *I. densiflora*, *I. insignis* and *I. striata* exhibit extensive plasticity and thrive across broad elevation gradients [Figure 3]. For example, *I. densiflora* was recorded between 800 and 2,075 m a.s.l., and I. *sapindoides* between 600 and 2,800 m a.s.l. [Table 1; Figure 3].

Regarding thermal niches, 70.6% of the species (12 species) inhabit areas with narrow thermal fluctuations (average annual variation <2 °C) [Table 1]. On the contrary, species such as *I. oerstediana* and *I. insignis* tolerate broader thermal ranges (variation from 5 to 11 °C), which correlates with their broader altitudinal distribution [Table 1].

Table 1. Edaphoclimatic characteristics of the *Inga* species in Imbabura.

Species	Altitude (m a.s.l.)	Temp. (°C)	Precip. (mm)	Soil Order	Soil Texture	pH
I. edulis	700–1000	21–22	1500–2000	Mollisol	Clay-Loam	Slightly Acidic
I. feuillei	2000–2200	15–16	500–750	Mollisol	Sandy Loam	Alkaline
I. multijuga	2600–2800	12–13	750–1000	Inceptisol	Loam	Neutral
I. marginata	1600–1700	17–19	1750–3000	Inceptisol	Sandy Loam	Neutral
I. oerstediana	700–1800	18–23	2000–2500	Incept.+Entisol	Loam	Med. Acidic
I. insignis	1100–2800	11–21	500–1500	Incept.+Mollisol	Loam/Sandy	Variable
I. sapindoides	600–2800	12–23	750–2500	Inceptisol	Clay-Loam	Slightly Acidic
I. striata	1800–2200	15–17	250–1750	Incept.+Mollisol	Sandy Loam	Neutral
I. silanchensis	600–700	22–23	3000–3500	Inceptisol	Loam	Acidic
I. spectabilis	800–900	21–22	1750–2000	Mollisol	N/A	N/A
I. densiflora	800–2075	14–21	1000–3000	Incept.+Mollisol	Clay-Sandy	Slightly Acidic
I. cinnamomea	600	22–23	3000–3500	Inceptisol	Loam	Acidic
I. vera	2400–2600	13–14	1250–1500	Incept.+Entisol	Clay-Loam	Slightly Acidic
I. cocleensis	1600	17–18	2500–3000	Inceptisol	Sandy Loam	Neutral
I. acuminata	1400–1900	16–18	1750–2000	Incept.+Entisol	Sandy Loam	Med. Acidic
I. velutina	1600-1800	17-18	2500-3000	Incept.+Entisol	Clay-Loam	Slightly Acidic
I. punctata	1600-1700	17-18	2500-3000	Inceptisol	Sandy Loam	Neutral

3.3. Soil Preferences and Precipitation Regimes

Among the variables related to soil categories, a marked preference for specific soil conditions is indicated. The distribution of species according to soil order and texture is summarized in Table 1.

1. **Soil texture: Most species prefer sandy loam soils.** *I. feuillei*, *I. marginata* and *I. punctata* were predominantly found in these textures, while *I. densiflora* showed adaptation to sandy clay soils.
2. **Soil taxonomy:** The genus in Imbabura is mainly associated with Inceptisols and Mollisols. *I. edulis* and *I. striata* are notably associated with Mollisols, while *I. multijuga* and *I. silanchensis* are restricted to Inceptisols.
3. **pH tolerance:** most species (approx. 94%) thrive in neutral to slightly acidic soils (pH ≈ 6.5–7.0). However, *I. insignis* and *I. silanchensis* tolerate acidic conditions, while *I. feuillei* was the only species recorded in alkaline soils.

Regarding precipitation, *I. feuillei* and *I. multijuga* demonstrate resistance to dry conditions (500–750 mm/year), while most of the genus species requires humid regimes ranging between 1250 and 3000 mm/year. [Figure A2].

4. Discussion

4.1. Ecological Filters: Altitude and Climate Differentiation

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The high local richness of *Inga spp*. recorded in Imbabura (17 species within ~4,800 km^2) can be framed primarily within the Humboldtian perspective of plant geography, where climatic gradients act as primary ecological filters. We identify two different adaptive strategies:

- **Specialists:** 58.8% of the species occupy restricted altitudinal floors. This pattern supports recent findings in Andean tropical forests, where the rate of thermal gradient restricts the distribution of trees to specific thermal floors [45]. These limited-range species are particularly susceptible to biotic attrition driven by climate change [30].
- **Generalists and Distribution Changes:** Species such as *I. densiflora* and *I. sapindoides* exhibited extensive plasticity. Notably, our data show that I. *densiflora* reaches 2075 m a.s.l., an altitude higher than the limit of 1900 m reported in Peru [12]. This upward extension could indicate thermophilization of Andean forests, where lowland species migrate upslope in response to increasing temperatures, a phenomenon widely documented in the tropical Andes [31,32]. Conversely, ecotonal barriers could be preventing the migration of less adaptable species, creating strong barriers to distribution [33].

4.2. Edaphic Influence, Nitrogen Fixation and Functional Traits

Edaphic factors play a fundamental role in the distribution of *Inga*. While traditional lite-rature often describes *Inga* habitats generally, our study correlates specific species with soil texture and taxonomy (Mollisols/Inceptisols). As nitrogen-fixing legumes, *Inga* species present a competitive advantage in nitrogen-poor soils [34]; however, its distribution in montane forests could be more strongly limited by soil phosphorus (P) availability or acidity than by nitrogen [35,36]. The specificity of *I. insignis* for acidic soils and of *I. feuillei* for alkaline conditions supports the habitat filtering hypothesis. Additionally, the balance between growth and defense is crucial in this genre. Species that invest heavily in chemical defenses (saponins, phenolics) tend to be specialists in resource-poor environments, while fast-growing generalists may invest less in defense [42,43].

4.3. Geological and Evolutionary Multi-Scale Drivers of Local Inga Richness in Imbabura

Our results lead us to relate the high diversity found in the genus *Inga spp*. in Imbabura to multiple geological and climatic drivers in the last 10 million years. Those that have generated exceptional topographic and edaphic heterogeneity in a relatively small area.

At the macroevolutionary scale, Miocene–Pliocene uplift of the northern Andes established steep elevational gradients, reorganized drainage, and reshaped precipitation regimes, creating juxtaposed montane, cloud-forest, and inter-Andean environments over short distances [1,2]. Phylogenetic evidence indicates that much of Inga's species-level diversification is relatively recent (late Neogene–Quaternary), consistent with rapid radiations unfolding within landscapes already structured by Andean orogeny [3,4]. Superimposed on this tectonic template, Neogene–Quaternary climatic oscillations repeatedly shifted vegetation belts upslope and downslope, modulating population connectivity along elevation and potentially producing cycles of isolation and secondary contact that can reinforce lineage divergence [5]. Finally, persistent volcanism in northern Ecuador adds a disturbance–renewal dynamic: eruptions periodically restructure forests and, through repeated tephra inputs, create stratified soils and buried paleosols that increase fine-scale soil mosaics over time [6,7]. Together, these nested processes provide a coherent framework for understanding why present-day ecological filters alone are unlikely to explain the documented richness.

Elevation, climate, and connectivity under Quaternary dynamics are another determinants of diversity. Across the tropical Andes, elevational gradients impose strong thermal and moisture constraints on tree distributions, and specialized communities can show limited capacity to track warming compared with more generalist assemblages [8,9]. In this context, glacial–interglacial oscillations likely acted as recurrent "connectivity switches" for montane populations: cooler phases displaced forest belts downslope, while warmer interglacials promoted upslope expansion and compression of montane habitats [5]. Such repeated belt shifts can fragment populations along steep gradients and later reconnect them, increasing genetic structuring and creating opportunities for ecological divergence. Modern observations of upslope compositional change (“thermophilization”) and elevational migration of Andean trees further support the plausibility of strong, elevation-linked demographic dynamics that can operate on ecological timescales and accumulate over Quaternary times [8,10]. For Inga in Imbabura, the coexistence of narrow-range taxa and broader-elevation generalists is consistent with a landscape in which connectivity has fluctuated repeatedly, and where dispersal and establishment have been filtered by both climate and habitat discontinuities.

Volcanism, edaphic mosaics, and niche partitioning likely contributed to diversification and coexistence via two non-exclusive mechanisms: (i) episodic disturbance that resets forest structure and creates spatial discontinuities, and (ii) long-term generation of edaphic heterogeneity through tephra deposition and soil profile stratification. Ecuadorian volcanism has been persistent from the Late Pliocene to the present, with repeated explosive activity capable of producing extensive tephra blankets and geomorphic disturbance [6]. In northern Ecuador, tephra stratigraphy studies show that volcanic ash soils can comprise multiple discrete tephra units and exhibit strong vertical and lateral variation in physical and chemical properties [7]. Such variability is particularly relevant for nutrient dynamics in volcanic and strongly weathered tropical soils, where phosphorus availability and fixation processes can strongly constrain plant distributions [11,12]. Fine-scale edaphic mosaics can therefore promote habitat specialization and local-scale niche partitioning, especially where soil differences interact with biotic pressures such as herbivory [13]. Although our dataset does not include phylogeographic or tephrostratigraphic tests, the observed coexistence of specialist and generalist Inga species across heterogeneous substrates is compatible with long-term landscape renewal and soil-driven ecological divergence.

4.4. Biotic Interactions and Human-Mediated Landscapes

Within this geodynamic context, biotic interactions and anthropogenic landscapes can further shape realized distributions. Inga is well known for strong biotic interactions (e.g., herbivory pressures and defense syndromes), and diversification in the genus has been linked to trait divergence associated with species coexistence and niche differences [4,14,15]. In addition, Neotropical forests are increasingly recognized as historically influenced by human management and landscape domestication, which can alter local abundance patterns and dispersal opportunities for useful taxa [16,17].

Many Inga species (including cultivated or managed forms) are prominent in agroforestry systems, where they provide shade, biomass inputs, and soil fertility services; these systems can act as semi-natural habitat networks that maintain gene flow and facilitate persistence across fragmented landscapes [18–20]. The predominance of *I. edulis* (local name: guaba) in agricultural mosaics in Imbabura confirms its status as a domesticated or semi-domesticated species, widely dispersed by humans for its fruit pulp [37,38]. This species, along with *I. insignis*, plays a vital role in local agroforestry systems [39,40]. Unlike wild species confined to forest remnants (*I. oerstediana*), these "anthropogenic" species benefit from human disturbances. Recognizing this dual function—ecological keystones in forests and productive assets on farms—is essential for landscape-scale conservation [41].

5. Conclusions

This study increases the documented richness of Inga in Imbabura from six to seventeen species, revealing exceptionally high local diversity in a relatively small but environmentally heterogeneous Andean landscape. The geographical distribution of the genus Inga in Imbabura is driven by a complex interaction of altitudinal gradients, precipitation patterns and specific edaphic properties, particularly soil texture and pH. This environmental heterogeneity supports a significantly higher species richness (17 species) than previously recorded, organized in a discontinuous pattern where specialist species are restricted to specific microhabitats while generalists occupy broader ranges.

We interpret this richness as emerging from the interaction of (i) Miocene–Pliocene Andean uplift that generated steep climatic and topographic gradients [1,2], (ii) late Neogene–Quaternary climatic oscillations that repeatedly altered elevational connectivity and demographic structure [5,8,10], and (iii) persistent volcanism that periodically reset forest structure while producing long-term edaphic mosaics via tephra stratification and soil profile complexity [6,7]. These drivers likely amplified ecological filtering and niche partitioning, consistent with the observed coexistence of elevational and edaphic specialists alongside broad-tolerance generalists.

These findings highlight the vulnerability of specialized populations to habitat fragmentation and climate change. Therefore, conservation strategies must be tailored to protect these critical ecological niches rather than applying generic forest management policies. From a conservation and management perspective, maintaining Inga diversity in Imbabura will likely require protecting elevational corridors and microrefugia across soil mosaics, while also accounting for ongoing climate-driven compositional shifts in Andean forests [8,10]. Because several Inga species are integral to agroforestry and restoration systems, strengthening landscape connectivity through well-managed shade-tree networks may provide complementary benefits for biodiversity persistence and ecosystem services [18–21].

Finally, given the observed presence of domesticated species in agricultural mosaics, future research should integrate ethnobotanical approaches to quantify the role of local human communities in the conservation and dispersal of *Inga* species in the Andean region.

Author Contributions: Conceptualization, H.P.-R.; Methodology, H.P.-R.; Validation, W.F.; Formal Analysis, H.P.-R. and W.F. Research, H.P.-R.; Resources, HP-R.; Data Curation, HP-R.; Writing: preparation of original draft, H.P.-R., W.F and E.S..; Review and Editing, W.F. Visualization, HP-R.; Supervision W.F. and E.S. All authors have read and accepted the published version of the manuscript.

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Conflicts of interest: The authors declare that they have no conflict of interest.

Appendix A

The MaxEnt program was used to generate models for each species of the genus *Inga* in the province of Imbabura. The results will be presented in a new article.

- **A1.- Herbariums reviewed in their databases and contained information on the genus *Inga* in Imbabura.**

Inga cocleensis: 11/8/1990; Rubio y Quelal, [1]; 604 (MO); ***Inga densiflora***: 11/8/1990 y 15/6/2025; Rubio, Quelal, Vargas, Defas y Reyes, [2]; 563 y 6284 (MO; QCNE); ***Inga feuillei***: 1988; Madsen, [1]; 84308 (AAU); ***Inga insignis***: 15/8/1949, 3/11/1986, 18/4/1988, 21/4/1993 y 8/3/2002; Jaramillo, Caranqui, Acosta Solís, Pennington, Vargas y Zak, [5]; 577, 13869, 3655, 9244 y 13368 (F, MO, QCNE); ***Inga marginata***: 15/1/1992 y 31/5/2009; Tipaz, Quelal, Edwards y Palacios, [2]; 608 y 16792 (MO, QCNE); ***Inga multijuga***: 14/5/2009; Palacios, [1]; 16736 (QCNE), ***Inga oerstediana***: 1992 y 15/3/2012; Medina, Cardona, Rojas, Viancha, Vega, Prieto, Herrera y Pennington, [4]; 13967, 11966, 11965 y 11964 (MO); ***Inga punctata***: 11/8/1990; Rubio y Quelal, [1]; 579 (MO); ***Inga sapindoides***: 30/5/1949; Acosta Solís, [1]; 12637 (F); ***Inga striata***: 8/12/1990 y 14/1/1991; Cerón, Montesdeoca y Palacios, [2]; 12576 y 6797 (MO); ***Inga velutina***: 27/10/2005; Vargas, Defas y Reyes, [1]; 6290 (QCNE), ***Inga vera***: 18/2/2007; Palacios, [1]; 17536 (MO).

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QCNE Instituto Nacional de Biodiversidad del Ecuador
MO Trópicos
AAU Herbario de la Universidad de Aarhus
F Herbario SQF

Table A1. Field verification and sample collection for the herbarium of the Technical University of the North.

Species	**Number of samples**	**Collection date**
Inga acuminata Benth.	2	2 025
Inga coclensis	7	2 025
Inga densiflora Benth. (GBIF s.f.)	10	2 025
Inga edulis Mart.	4	2 024; 2 025
Inga insignis Kunth.	18	2 025
Inga oerstediana Benth.	3	2 024
Inga sapindoides Willd.	2	2 024
Inga spectabilis (Vahl) Willd.	3	2 025
Inga striata Benth.	2	2 025
Inga punctata Willd.	1	2 025

HUTN Herbário Universidad Técnica del Norte

Appendix B

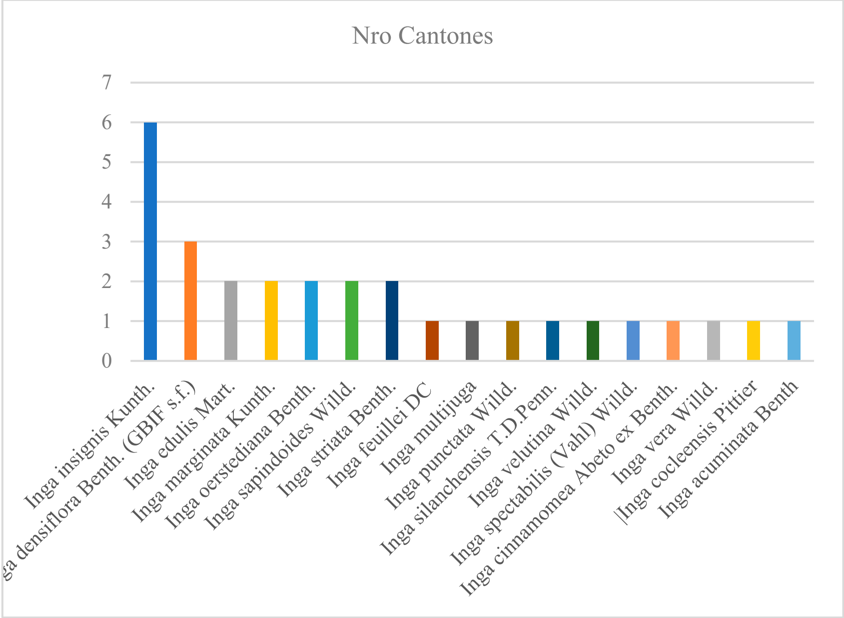

Figure A1. Species of the genus *Inga* in the cantons of Imbabura.

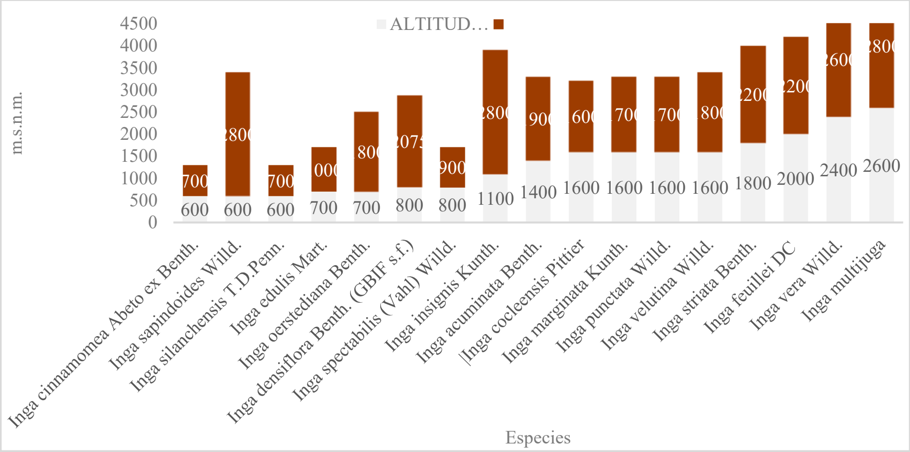

Figure A2. Distribution ranges of species of the genus *Inga* in Imbabura.

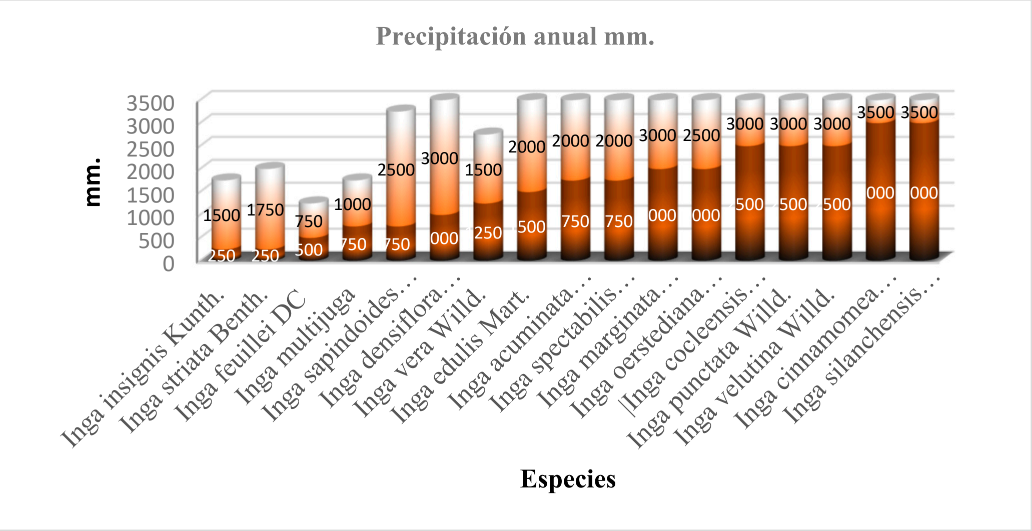

Figure A3. Precipitation ranges of species of the genus Inga in Imbabura.

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