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Araucaria araucana Forests in Argentina: Exploring Floristic and Ecological Variability Along a West-East Transect

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Abstract

In Argentina, the *Araucaria araucana* forest occupies a vast area in the Northwest of Patagonia, following a pronounced gradient of increasing xericity from west to east over a short distance. These forests have been the subject of detailed studies due to their uniqueness and ecological relevance. In this context, an exhaustive investigation was carried out to understand the diversity and structure of these ecosystems. The objective was to study the floristic and ecological differences in humid and xeric areas along a west-east transect where *A. araucana* is distributed. Floristic surveys, geomorphological analyses, and bioclimatic data were examined. In Argentina, *A. araucana* integrates two distinct forest types: mesic and xeric. The xeric *A. araucana* forest constitutes a forest with floristic, genetic, geomorphological, and bioclimatic identity. The results highlight the importance of understanding the local variability of these ecosystems for the design of effective conservation strategies. Furthermore, they highlight the need for further research into the ecology and dynamics of these forests, especially in the context of climate change and human activities.

Keywords

Forest, Floristic Identity, Rocky Outcrops, Xericity

1. Introduction

Understanding the structure and dynamics of *Araucaria araucana* forests in

northern Patagonia, Argentina, has been the focus of numerous scientific studies due to the uniqueness and ecological importance of these ecosystems. In particular, it has been observed that many forest landscapes, including *Araucaria* forests, appear to be fragmented, resulting in the formation of scattered patches in areas that may have previously formed a continuous forest (Ewers et al., 2011; Pert et al., 2012; Tagliari et al., 2021; Guo et al., 2023). It is essential to recognize that this fragmentation can occur as a result of two different processes: fragmentation or expansion, or even a combination of both (Lawes et al., 2004; Matte et al., 2015; Palmero-Iniesta et al., 2020). Fragmentation involves the division of a continuous forest into smaller fragments, while expansion involves the advance of a forest into previously non-forested areas, such as grasslands or shrublands (Duarte, 2011; Pert et al., 2012; Zambrano et al., 2020; Frelich, 2016).

In the context of *A. araucana* forests, rocky outcrops play a crucial role. These outcrops can act as nucleation sites, where local recruitment increases the number of trees and the complexity of the forest structure (Carlucci et al., 2011). Previous studies in southern Brazil have evidenced this phenomenon, highlighting the importance of rocky outcrops as drivers of forest dynamics (Duarte et al., 2006; Müller et al., 2012). In hillslope forests, geomorphological processes play a relevant role, where relief or microrelief act as direct or indirect agents on forest ecology (Pawlik, 2013). Geomorphic variables are of great importance because they are the most stable ecological factor (Meilleur et al., 1994). *A. araucana* forests are distributed in the southwestern Andes of Argentina and central-southern Chile, extending northeastward in Argentina to the Patagonian steppe region (Cabrera, 1953; Hoffmann et al., 2001; González et al., 2013; Hadad et al., 2020). These forests are often associated with isolated rocky outcrops, where *Araucaria* develops in small pure stands (Donoso, 1993; Rechene et al., 2003; Martínez Carretero, 2009). *Araucaria araucana*, with its imposing stature and distinctive morphology, has been of interest both for its ecological value and its cultural significance.

However, the regeneration dynamics of these forests have been the subject of debate. According to recent studies, the recruitment process has been affected by various human activities, such as logging and intentional fires, suggesting a perturbation in the regenerative process over the past centuries (Rechene et al., 2003; Roig et al., 2014; Souza, 2021; Souza-Alonso et al., 2022). Despite its ability to reproduce sexually and asexually, sexual regeneration is hindered by predation and environmental constraints, resulting in a predominance of the agamic regeneration process (Duplancic & Martínez Carretero, 2013; Duplancic et al., 2015).

The adaptive capacity of *A. araucana* to adverse environmental conditions has been the subject of study and speculation. Palaeoecological studies suggest that *Araucaria* has shown a remarkable ability to adapt to natural catastrophes, such as volcanic events and climate change (Mundo et al., 2012; González et al., 2020). However, its past distribution has been modified by several factors, including volcanic and glacial activity, as well as the history of fires in the region (Marchelli et al., 2020; Souza-Alonso et al., 2022).

The presence of *A. araucana* forests in Argentina has been studied for many years, and they are generally considered to be a single ecosystem despite significant differences in their extent and the surrounding environmental characteristics. However, there is a growing understanding that these forests are not homogeneous but show significant differences in their floristic composition and the ecological conditions that define them. The aim of this study was specifically to explore the differences between the humid and xeric zones of *A. araucana* forests, which appear as patches on rocky outcrops near the grassland steppes of northern Patagonia. By analyzing these differences, a deeper understanding of the diversity and dynamics of these ecosystems, as well as their interaction with the surrounding environment, will be sought.

2. Material and Methods

2.1. Study Area

The study was carried out in the localities of Caviahue (37˚50'S-70˚58'W), Chenque-Pehuén (38˚06'S-70˚52'W) and Primeros Pinos (38˚52'S-70˚34'W) (Figure 1) in the province of Neuquén, Argentina. These sites are located in the northern distribution of the forest and are similar in terms of environment and forest structure. The local landscape is made up of many exogenous processes and one endogenous (volcanic) process (González Díaz, 2005). Caviahue: located at an altitude of approximately 1500 masl, in the province of Neuquén. Climate: The climate is subpolar mountainous. The average annual temperature is around 4˚C.
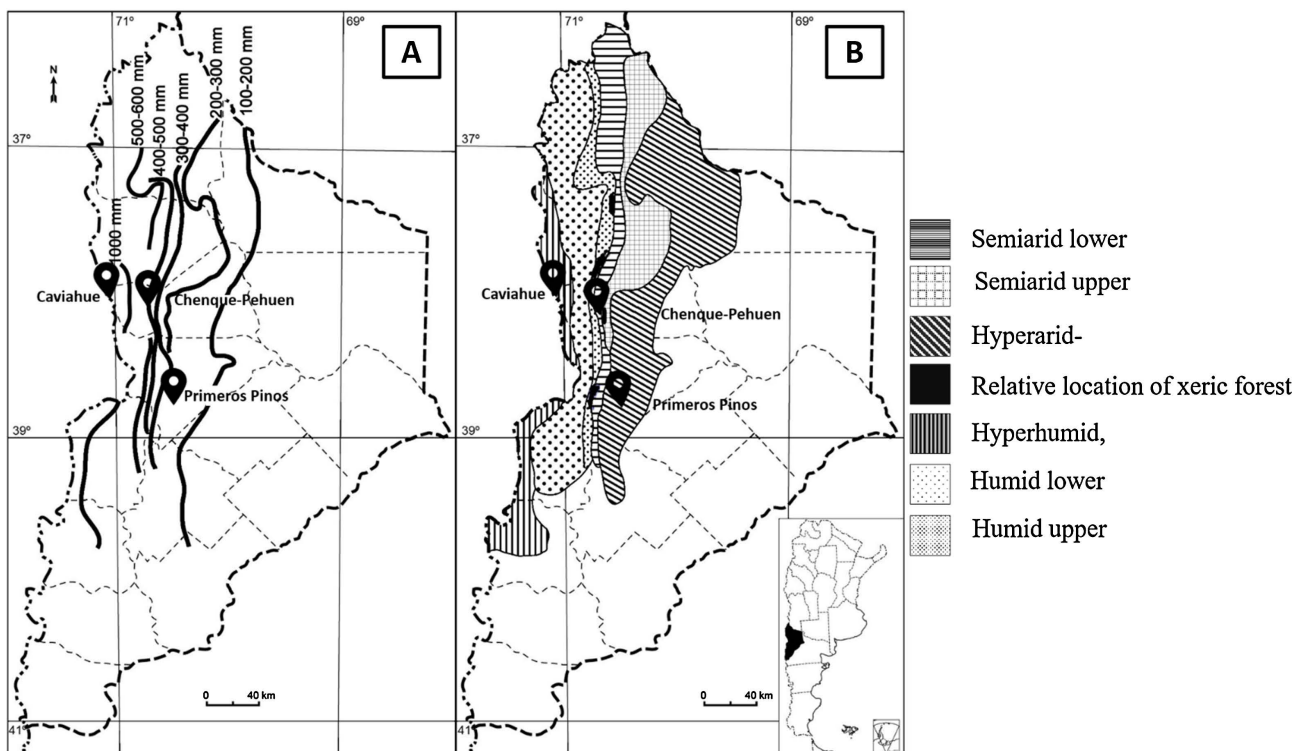

Figure 1. (A) Isohyets; (B) Bioclimatic condition.

Winters are cold, with temperatures dropping to −10˚C or lower. Annual precipitation varies, but is between 500 and 800 mm per year. Vegetation: *Nothofagus* trees (coihues and lengas) and the Patagonian pine (*A. araucana*) are found in this area. There are also a variety of shrubs and Andean grasslands. Primeros Pinos is located near the city of San Martín de Los Andes, province of Neuquén, at an altitude of about 1000 masl. The average annual temperature is around 8˚C. Winters are cold, with temperatures dropping to −5˚C. Annual precipitation varies but, is between 800 and 1000 mm per year. In this area, tree species such as the Patagonian pine (*A. araucana*), the Patagonian cypress (*Austrocedrus chilensis*), and lenga forests (*Nothofagus pumilio*) can be found. There is also a wide variety of shrubs and Andes plants. Villa Pehuenia: located in the province of Neuquén, near Lake Aluminé, at an altitude of around 1200 masl. It has a temperate mountain climate. The average annual temperature is around 10˚C. Winters are cold, with temperatures dropping to −5˚C or lower. Annual precipitation is usually around 700 mm. Vegetation includes the Patagonian pine (*A. araucana*), coihue forests (*Nothofagus dombeyi*), and lenga forests (*Nothofagus pumilio*). Pehuén forests (*A. araucana*), which are a native species of the region, can also be found.

The Copahue stratovolcano was full-filled in the late Cenozoic with 800 m deep ice bubble, and its glacial valley was up to 10 - 12 km long (González Díaz, 2005; Vigide et al., 2023). In the steppe, there is an irregular and thick cover of till. The modelling of the landscape began in the Pliocene, and later, in the Pleistocene, the climatic intervention changed the previous fluvial morphology for the glacial one. During the Pleistocene-Holocene (30 Ky), there was a glaciation, and in the Holocene, there was a post-glacial period, and the fluvial post-glacial cycle continues until today. In this area, there is a small field of rocky, extrusive sub-glacial bodies 8 - 10 m high, 4 - 6 m wide and 20 - 25 m long (drumlins), and many drift boulders in an irregular and thick cover of till (González Díaz, 2005). The area constitutes a relevant concentration of volcanic complexes developed during the last 5 My and forming a volcanic plateau of about 50 × 50 km (Tunstall & Folguera, 2005; Llano et al., 2023). Geomorphologically, the area belongs to the region with neo-tectonic evidence of an extensional failure, which means that the plio-quaternary sequences are found in failure (García Morábito & Folguera, 2005; Hurley et al., 2020). Superficial evidence of glaciers are grooves, furrows, and isolated moutonneés. The *Araucaria* forest in southern South America is found in the Mesozoic fossil record and on Tertiary rocks (Eocene, Oligocene, Miocene ages) (Rossetto-Harris et al., 2020).

The Patagonian climate is dominated by air masses from the Pacific Ocean, and the Andean Mountain determines the aridity on the oriental slope, making the area part of the Argentine Arid Diagonal (Martínez Carretero, 2013). Bioclimatically, the study area shows a marked west-east xericity gradient. In the Principal Cordillera, on the border with Chile, the >1000 mm isohyet runs, and 30 km to the east, in the steppe, the 300 - 400 mm and <200 mm isohyets (Figure 1(A)). The bioclimatic conditions of the study area were defined using the thermal-rainfall index (Martínez Carretero, 2004), and the different bioclimates were represented

on a bioclimatic map. The bioclimatic data for the area were obtained by averaging 20 years of temperature (maximum and minimum) and precipitation (in millimetres) records from 25 meteorological stations located in different locations in the northwest of the Neuquén province. Look at the thermal-rainfall index for some localities near the area (Table 1), the bioclimatic condition changes rapidly from a sub-humid place to another semi-arid (Figure 1(B)). The drumlins and drift boulder fields occur in the semi-arid sector.

Table 1. Bioclimatic conditions of the northwest localities of Neuquén province.

Locality	T° m + h (°C)	T° m + c (°C)	Rainfall (mm)	Pluviothermal Index	Bioclimate
Bajada del Agrio	21.3	5.3	84	19.74	Hyperarid
Bajada del añelo	21.7	5.6	110	25.03	Hyperarid
Barrancas	20.4	4.6	190	48.10	Semi-arid upper
Buta Co	21.1	5	164	39.03	Semi-arid upper
Buta Ranquil	20.4	4.7	139	35.27	Hyperarid
Churriaca	20.1	4.8	221	58.01	Semi-arid upper
Coihueco	20.8	5.2	176	43.39	Semi-arid upper
Colipilli	19.4	4.5	352	98.85	Semi-arid lower
Covunco Centro	10	4.7	120	30.14	Hyperarid
Ea. Tilhué	20.4	5.3	215	55.40	Semi-arid upper
El Cholar	19.5	5.4	618	176.02	Humid
El Palomar	18	4.5	724	238.35	Humid lower
Hualcupan	19.8	5.1	315	86.06	Semi-arid lower
Huantraicó	19.9	4.6	135	36.01	Semi-arid upper
Las Ovejas	18.4	4.9	520	165.32	Humid
Malal Ranquil	21	5.1	143	34.46	Hyperarid
Mallin del Toro	18.9	4.6	439	130.64	Subhumid
Mallin Quemado	20.3	4.5	177	45.17	Semi-arid upper
Ñorquin	19.4	5	577	164.22	Humid
Paso de las Bardas	21.3	5.2	143	33.52	Hyperarid
Pto. Ñirecó	19.1	4.5	379	110.00	Subhúmedo
Quili Malal	21.5	5.6	111	25.76	Hyperarid
Ranquil del Sur	19.4	4	205	56.89	Semiarid upper
Tilleria	22.2	5.9	123	26.85	Hyperarid
Varvarco	18.3	4.6	624	198.90	Humid

2.2. Methods

Based on the analysis of ALOS-AvNYR satellite images with an accuracy of 5 meters, geomorphological units were identified at the geotope level. A geotope is a specific small area or geographical location that can be subdivided within the landscape, typically covering a few square metres. It is delimited by microtopography and the biotic components of vegetation and fauna, that influence its edaphic and microclimatic characteristics (Ordaz-Hernández et al., 2023). Each geotope is characterized by specific soil, climate, topography, and other factors that have led to a distinctive plant community. In total, three geotopes were defined: crest, slope of the rocky outcrop, and contact steppe. Within each geotope, 20 plots of 3×5 metres were randomly established. In each plot, all vascular plants were recorded, and the cover was estimated using the Braun-Blanquet scale (r = 1% - 10%; 1 = 10% - 20%; 2 = 21% - 40%; 3 = 41% - 60%; 4 = 61% - 80%; 5 ≥ 81%). The geosymphitosociological analysis of the vegetation was carried out according to the methodology of Martínez Carretero and Roig (1992). In addition, the height of characteristic species of the system such as *A. araucana* and the genus *Nothofagus*, was measured using the angle cross system and trigonometry. The herbarium materials were deposited at the Ruiz Leal Herbarium (MERL) of IADIZA. Plant nomenclature followed Zuloaga et al. (2008) and the Argentine Flora Database (IBODA). Each floristic type was named after the genus of the species with the highest average cover present, followed by the genus of the second most abundant species.

The data were entered into a matrix and analyzed using Principal Component Analysis (PCA) with Pearson's correlation for the matrix. In this study, abundance was assessed using an entropy statistic proposed by Shannon and Weaver (1949). We chose the Shannon-Weaver index because it takes into account species richness and the proportion of each species within a given community (Parchizadeh, 2020). The Shannon-Wiever index is calculated using the equation $H = - pi \cdot \ln pi$, where the quantity pi is the proportion of individuals. The Shannon-Wiever index is calculated using the equation $H = - pi \cdot \ln pi$, where the quantity pi is the proportion of individuals found in the ith species. The maximum diversity (Hmax) could be found in a situation where all species were equally abundant (Magurran, 2004; Chao et al., 2020). To evaluate the similarity between the different communities detected, the Jaccard index was used. Statistical analyses were performed using Infostat software version 2018 (Di Rienzo et al., 2015).

3. Results and Discussion

Five different communities were determined based on their floristic composition, average cover, and specific dominance (Table 2, Figure 2), classified physiognomically as: xeric *A. araucana* forest, mesic *A. araucana* forest, steppe, *Adesmia boronoides* shrubland, and *Chusquea couleou* shrubland. In Figure 2, it can be seen that with the PC 1 it is possible to differentiate the communities of xeric *A. araucana* forest, steppe of *M. spinosum*, and *Chusquea couleou* shrubland from the

Table 2. Floristic matrix of the *Araucaria araucana* forest. Specific cover in percentage.

Physiognomy Geomorphological unit Community	Forest-xeric-Rocky material, drummlins *Araucaria araucana*	Scrubland Sandy soils *Chusquea culeou*	Scrubland Local foothills of rocky outcrops *Adesmia boronioides*	Steppe Steppary sandy soils *Mulinum spinosum*	Forest-mesic-Local foothills with intense superficial runoff *Araucaria araucana*
Festuco-*Araucarietum typicum* Gandullo (2003)					
Araucaria araucana 16 m (A.a.)	90	30	.	3	30
Araucaria araucana 3 m	17	45	.	3	3
Belloetosum chilensis Gandullo (2003)					
Mulinum leptacanthum	45	.	30	.	.
Sysirinchium arenarium var. *arenarium*	30	3	.	3	.
Nothofago-Berberidion Esk. 69					
Festuca scabriuscula (F.sc.)	17	.	.	3	.
Adesmietun boroniodis Roig 94					
Adesmia boronioides (A.b.)	3	3	90	17	.
Mulinum spinosum (M.sp.)	17	30	30	67	.
Nassauvietosum aculeatae Gandullo (2003)					
Grindelia prunelloides	17	.	.	17	.
Euphorbia collina (E.col.)	3	3	.	30	.
Sisyrinchium graminifolium (S.gr.)	3	3	17	30	.
Berberidio-*Nothofagetalia antarcticae* Esk. 69					
Nothofagetea pumilionis antarcticae Oberd. 60					
Baccharis magellanica (B.ma.)	30	3	.	30	.
Acaena pinnatifida (A.pi.)	3	17	.	30	.
Nothofagus antarctica 1 m (N.a.r.)		.		.	80
Nothofagus antarctica 3 m (N.a.)	3	.	.	3	60
Nothofagus pumilio 25 m (N.p.)	.		.	.	30
Nothofagus pumilio 0.5 m		3	.	.	3

Species proper of the xeric forest: *Senecio polyphyllus, Carex* sp. *boelckeiana, Chevreulia diemii, Nassauvia latifolia, Senecio leuco-phyton, Berberis* af. *darwinii, Draba australis, Berberis* af. *heterophylla, Galium* af. *comberi, Cardamine hirsuta, Astragalus pata-gonicus, Relbunium chaetophorum, Senecio filaginoides* var. *filaginoides, Hordeum halophyllum, Loasa* af. *acanthifolia, Zephy-rantes* sp. (cover < 2.5%). Species proper of the steppe: *Adesmia corymbosa, Euphorbia latifolia, Senna kurtzii, Adesmia adrianii, Juncus leuserii, Astragalus* af. *neoburkartianus, Gnaphalium andicola, Anarthrophyllum strigulipetalum, Lathyrus multiceps,*

Polygala hickeniana, Calandrinia colchaguensis, Stipa chrysophylla (cover < 2.5%). <u>Common species xeric forest-steppe</u>: *Poa* af. *holciformis, Perezia pygmaea, Schyzachirium paniculatum, Galium richardianum, Geranium sessiliflorum, Calandrina graminifolia, Erigeron imbricatus, Perezia* af. *pilifera, Erodium cicutarium, Acaena sericea, Viola vulcanica, Ranunculus peduncularis, Gaultheria pumila, Stipa speciosa, Bromus tectorum, Fabiana imbricata, Nassauvia hillii, Junellia thymifolia, Bredemeyera colletioides* (cover 2.5%). <u>Accompaniment species</u>. <u>Forest xeric</u>: *Berberis empetrifolia* (B.em.) (45), *Nassauvia aculeata* var. *aculeata, Poa* af. *dusenii, Rumex acetocella, Senecio subumbellatus, Senecio* af. *spathulata* (S.sp.) (27.5), *Chlorea magellanica* (C.ma.), *Ephedra frustillata* (E.fr.), *Nothofagus antarctica* 3m (N.a.), *Chloraea alpina* (Ch.al.), *Festuca pallescens* (F.pa.), *Calceolaria mendocina* (C.me.), *Senecio bracteolatus* (S.br.), Discaria nana, *Cerastium arvense* (C.ar.), *Chiliotricum rosmarinifolium, Cajophora coronata* (17.5), *Chusquea culeou* (Ch.c.), *Oreomyrrhis chilensis* (O.ch.), *Vicia nigricans* (V.n.), *Luzula chilensis* (L.ch.), *Nardophyllum obtusifolium, Chuquiraga oppositifolia* (Ch.op.), *Taraxacum gilliesii, Trifolium repens, Bredemeyera colletioides, Maihuenia poeppigii* (M.po.), *Colletia spinosisima, Ribes magellanicum, Relbunium richardianum, Baccharis serratodentata, Baccharis patagónica, Escallonia serrata, Arenaria serpens* (A.se.), *Berberis* af. *chillanensis, Lithodraba mendocinensis, Fragaria chiloensis, Pernettya mucronata, Taraxacum officinale, Quinchamaliun chilense* (2.5). <u>Scrubland (sandy soils)</u>: *Chusquea culeou* (Ch.c.) (90), *Oreomyrrhis chilensis* (O.ch.) (45), *Vicia nigricans* (V.n.), Calceolaria mendocina (C.me.), Chloraea alpina (Ch.al.), Cerastium arvense (C.ar.) (27.5), *Rumex acetocella, Arenaria serpens* (A.se.), *Luzula chilensis* (L.ch.), *Ranunculus pedicularis* (R.pe.) (17.5), Berberis af. *chillanensis, Lithodraba mendocinensis, Fragaria chiloensis, Pernettya mucronata, Taraxacum officinale, Poa* af. *dusenii, Taraxacum gilliesii, Festuca pallescens* (F.pa.), *Discaria nana, Relbunium richardianum, Baccharis serratodentata, Escallonia serrata, Senecio subumbellatus, Senecio* af. *spathulata* (S.sp.), *Arjona patagonica* (A.pa.), *Calandrinia affinis, Quinchamaliun chilense* (2.5). <u>Scrubland (rocky outcrops)</u>: *Berberis empetrifolia* (27.5), *Chusquea culeou* (Ch.c.), *Happlopapus paucidentatus* (H.p.), *Nardophyllum obtusifolium, Chloraea alpina* (Ch.al.), *Festuca pallescens* (F.pa.), *Senecio bracteolatus* (S.br.), *Rumex acetocella, Cerastium arvense* (C.ar.), *Maihuenia poeppigii* (M.po.), *Chiliotricum rosmarinifolium, Cajophora coronata* (17.5). <u>Steppe</u>: *Berberis empetrifolia* (45), Poa af. *dusenii, Calceolaria mendocina, Chloraea alpina, Cerastium arvense, Senecio subumbellatus* (27.5), *Nassauvia aculeata* var. *aculeata, Chuquiraga oppositifolia* (Ch.op.), *Taraxacum gilliesii, Senecio* af. *spathulata* (S.sp.), Arenaria serpens (A.se.), *Trifolium repens, Ephedra frustillata, Festuca pallescens, Senecio bracteolatus, Chloraea magellanica, Rumex acetocella , Maihuenia poeppigii* (17.5), *Chusquea culeou* (Ch.c.), *Luzula chilensis* (L.ch.), *Nardophyllum obtusifolium, Bredemeyera colletioides, Ranunculus pedicularis* (R.pe.), *Arjona patagónica* (A.pa.), *Calandrinia affinis, Colletia spinosisima, Ribes magellanicum, Relbunium richardianum, Baccharis serratodentata, Baccharis patagonica, Escallonia serrata, Discaria nana* (2.5).

communities of mesic *A. araucana* forest and *Adesmia boronoides* shrubland. The first three communities presented the highest values of species richness. This heterogeneity reflects the complexity of forest landscapes in the region, and suggests the existence of different ecological conditions and successional processes in each of them, consistent with previous research highlighting the structural and floristic variability of forests in mountainous environments (Lawes et al., 2004; Cabrera et al., 2019).

In particular, a clear differentiation was observed between both the xeric and the mesic *A. araucana* forests, consistent with the results of other studies that have highlighted physiognomic and structural differences between different forest types in the region (Lawes et al., 2004; Martínez Pastur et al., 2024). This structural and floristic differentiation may be influenced by a number of environmental factors, including water availability, soil texture, solar exposure, and the geomorphological history of the area (Gandullo, 2003; Sanguinetti & Kitzberger, 2009).

In the mesic forest, *Nothofagus antarctica* dominates with a height of 25 - 30 meters and 70% - 80% vegetation cover. It occupies slopes between 20 - 25 degrees with south and east exposures. This floristic composition pattern is consistent with previous studies documenting the association of *A. araucana* with *Nothofagus* species in areas of higher humidity (Martínez Carretero, 2009). Additionally, the presence of mollic and lithic soils with sandy-loam textures and in part with

volcanic ash accumulation in this forest suggests a complex geomorphological history, possibly related to the Middle Miocene and Pliocene volcanic events (Pesce, 1989; Mundo et al., 2012). *Araucaria araucana* reaches 16 meters in height and 40% - 50% coverage, accompanied by species such as *Osmorhiza chilensis* (Apiaceae), *Discaria nana* (Rhamnaceae), *Gaultheria mucronata* (Ericaceae), *Empetrum rubrum* (Ericaceae), and *Chiliotrichum rosmarinifolium* (Asteraceae), among others. Bioclimatically, it extends into subhumid and humid zones, belonging to Nothofagetea Pumilionis Antártidae Oberdorfer 1960. According to Sanguinetti & Kitsberger (2009), Echeverria et al. (2004), and Gallia et al. (2021), the seeds of *A. araucana* in this forest have between 2% and 100% germination.

In contrast, the xeric forest was characterized by the exclusive presence of *A. araucana*, together with herbaceous and shrub species adapted to drought conditions and rocky soils. This restricted distribution of *A. araucana* in xeric environments has been previously documented by Martínez Carretero (2009), who suggested that rocky outcrops serve as refugia for this species under adverse climatic conditions. In the xeric forest, *A. araucana* is the only tree, with 80% - 100% vegetation cover. Many species typical of rocky environments are present, such as *Happlopapus paucidentatus* (Asteraceae), *Maihuenia poepigii* (Cactaceae), *Bredemeyera colletioides* (Polygalaceae), *Senecio polyphyllus* (Asteraceae), *Nassauvia hillii* (Poaceae), *Junellia thymifolia* (Verbenaceae), and *Chevreulia diemii* (Asteraceae). Taxonomically, the soils are Haploxerolls entic. Bioclimatically, it extends over semi-arid and arid zones, belonging to Festuco-Araucarietum typicum Gandullo, 2003. This forest appears on rocky as patch-like in the landscape. The xeric forest in Argentina constitutes the eastern distribution limit of this species. Rocky sites act as persistence niches, where vegetative regeneration plays a relevant role (Bond and Midgley, 2001; Carvallo et al., 2019), and where favorable microsites are required for post-dispersal establishment (Duplancic, 2015). According to Izquierdo (2009), and Donoso et al. (2024), the *A. araucana* seeds achieve only 12% - 13% germination in this forest.

The steppe appears as a shrubland of *Mulinum spinosum* (Apiaceae) with *Baccharis magellanica* (Asteraceae), *Stipa chrysophylla*, and *Festuca scabriuscula* (Poaceae) as dominant species. Many herbaceous species such as *Bromus tectorum* (Poaceae), *Euphorbia collina* (Euphorbiaceae), *Chloraea magellanica*, Ch. alpina (Orchidaceae), *Astragalus af. neoburkartianus* (Fabaceae), *Sisyrinchium graminifolium* (Iridaceae), and *Ranunculus peduncularis* (Ranunculaceae), among others, are accompanying species. The soils are between 60 and 80 cm deep, well-drained, sometimes with volcanic ash, and show signs of frost during the year. Floristically, the steppe belongs to Molinio-Arrhenatheretea Tüxen 1937.

Floristic analysis and principal component analysis (**Figure 2**) show that the three studied units—xeric forest, steppe, and mesic forest—are distinct. The community of *Adesmia boronioides* (Fabaceae) on sandy slopes of drumlins marks the contact between the xeric forest and the steppe.

Diversity and similarity analyses revealed interesting patterns in the structure
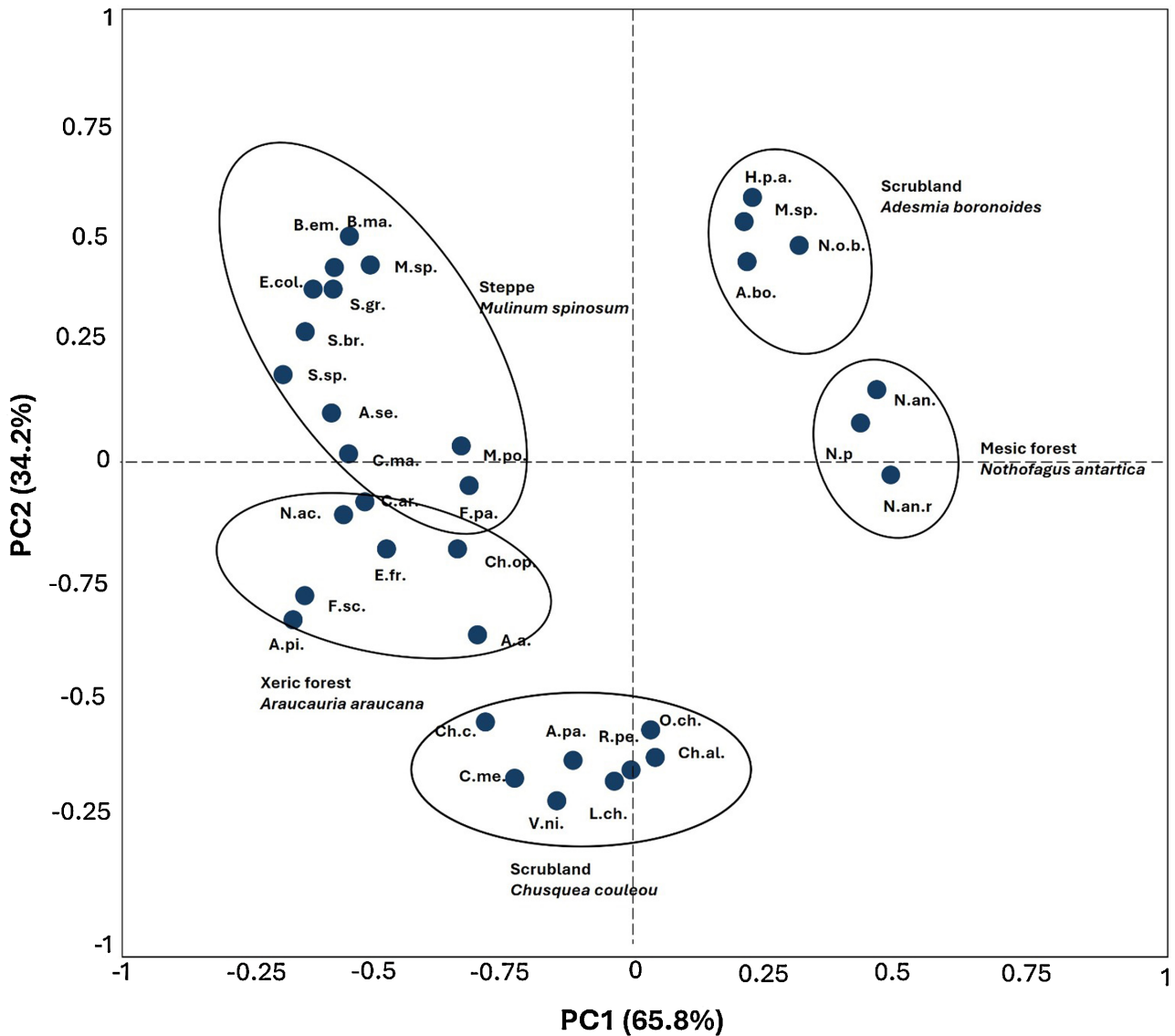
Figure 2. Ordination of communities related to the *A. araucana* forest. Abbreviations as in Table 1.

of the studied plant communities. Considering the Shannon-Weaver diversity index, the following values were obtained: xeric *A. araucana* forest: 3.9; *Ch. culeou* (Poaceae): 3.06; *A. boronioides*: 2.23; *M. spinosum*: 3.75; mesic *A. araucana* forest: 1.30, showing that the xeric forest had the highest floristic richness, which can be attributed to the adaptation of the present species to extreme aridity and solar exposure (Kruger et al., 1997; Bhatta et al., 2021). When the Jaccard similarity coefficient was calculated, the highest similarity was found between the xeric forest and the *M. spinosum* shrubland (0.58) in the steppe, and the lowest value was found between both types of *Araucaria* forest (0.03). The low similarity between the two types of *A. araucana* forests suggests a marked differentiation in species composition between these environments, possibly due to differences in water and nutrient availability (Izquierdo, 2009; Hiltner et al., 2016). This pattern of genetic differentiation among *A. araucana* populations in different types of forests in the

longitudinal border of distribution, with reduced allelic richnesss and increased genetic differentiation, suggests lasting isolation and local adaptations to environmental conditions (Templeton et al., 2021; Gallo et al., 2004; Marchelli & Gallo, 2004; Fuentes et al., 2021; Nin et al., 2023). The *Araucaria* forest located in contact with the steppe shows minor genetic allozymic diversity due to the unidirectionality of winds toward the east during the pollination (Bekessy et al., 2002). This genetic differentiation follows the precipitation gradient with plants tolerant of drought in the arid border. In this way, *Araucaria* populations in both Andean slopes are adapted to a regime of precipitation of each region. The xeric forest (**Figure 3**) shows the higher interpopulation variation (121.18%) (Bekessy et al., 2002), possibly due to isolation for vulcanism or glaciation, and having multiple refuges for migration. Rafii & Dodd (1998), and Nin et al. (2023) found differences in the proportional composition of foliar epicuticular wax alkanes, indicating a clear adaptation to xeric conditions. Additionally, the geographical distribution of *A. araucana* in the region could be influenced by historical events such as glaciation and volcanic activity. The presence of glacial refugia and adaptation to specific climatic conditions could explain the observed genetic diversity in different populations (Stefenon et al., 2019; Premoli et al., 2000).

Figure 3. Typic xeric forest of *A. araucana* on rocky outcrops in arid environment.

In addition, we hypothesize that *A. araucana* expanded in the post-glacial period from the Nahuelbuta cordillera in Chile, where there is no evidence of periglacial activity, which might have acted as a small refuge for many plant species. Areas surrounding the Nahuelbuta hill would have been the less affected by drought and peri-glacier processes, conserving the pre-glacier soils and plant cover (Sepúlveda-Espinoza et al., 2022). Current high concentration of species and endemism suggest the Nahuelbuta area as glacial refuge, particularly elements of warmer forest as *Fitzroya* (Cupressaceae) and *Araucaria* (Premoli et al., 2000,

Villagrán & Armesto 2005; Fuentes et al., 2021), at the current this area is considered one of the best conserved (Drake et al., 2009; Fuentes et al., 2021; Mardones & Scherson, 2023). Many authors have mentioned the xeric forest in ecotone with the steppe (Peña & Gandullo, 2000; Gandullo, 2003; Moreno-Gonzalez et al., 2021; Echeverria et al., 2022). However, considering the geomorphological and floristical analysis, we conclude that there is no ecotone between both xeric forest and steppe, with the xeric forest being a vegetation unit independent of the mesic *Araucaria* forest and the *Mulinum-Festuca* steppe.

4. Conclusion

This study has provided a detailed insight into the diversity and structure of *A. araucana* forests in the studied region. We have identified five distinct plant communities, each with unique characteristics regarding floristic composition and environmental conditions. The differentiation between xeric and humid *A. araucana* forests highlights the significant influence of factors such as water availability and solar exposure on species distribution and composition. Additionally, the low similarity between the two types of *A. araucana* forests suggests marked genetic and ecological differentiation, possibly related to local adaptations to specific environmental conditions. The xeric forest shows bioclimatic, geomorphologic, floristic, and genetic identity, and its persistence depends principally on agamic regeneration and follows a slow process of genetic typing, constituting a particular *Araucaria* forest that requires its proper conservative and restoration activities.

These results have important implications for the conservation and management of *A. araucana* forests. Understanding the diversity and structure of these ecosystems is crucial for developing effective conservation strategies that take into account local variability and the specific needs of each plant community. Furthermore, we emphasize the importance of continuing research on the ecology and dynamics of these forests, especially in the context of climate change and anthropogenic pressure.

Funding

Acknowledgements

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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