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Stand Characteristics, Leaf Traits and Growth of Threatened Conifer *Pilgerodendron uviferum* (Cupressaceae) in Southern Patagonia, Argentina

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Abstract: *Pilgerodendron uviferum* is an endemic Cupressaceae of Patagonia (Argentina) that is restricted to a small group of individual trees, growing in isolated populations (relicts) along its distribution. The main objective was to evaluate the habitat, forest structure, leaf traits, leaf nutrient reabsorption and growth of four relicts (area between 0.3 and 0.86 ha) in the Santa Cruz province (Argentina) to improve the available information for forest conservation purposes. Principal components analysis was conducted to determine the separation between relict populations based on their ecological characteristics (individual and habitat levels). We found contrasting environmental and forest structure conditions among the four studied relicts. For example, two relicts associated with *Nothofagus antarctica* showed higher values of *P. uviferum* tree density, DBH and dominant height at the stand level. Alongside that, these relicts presented a higher sapling density (1950–3167 ind ha^{-1}) and understory plant diversity compared to pure *P. uviferum* relicts growing near the ecotone with the steppe grassland. Specific leaf area, carbon and nutrient concentrations in *P. univerum* leaves varied depending on the relict conditions and tree age of the individuals. The mean nutrient resorption efficiency varied according to relicts and particular nutrients, ranging from 18.1% to 49.5% for Ca and P, respectively. The diameter growth of the dominant *P. univerum* trees ranged from 0.33 to 0.46 mm yr^{-1}, indicating that the species follows a stress-tolerant strategy. The information of this work may assist in the conservation of marginal *P. uviferum* forest communities spatially disconnected with continuous forests, growing in relicts.

Keywords: forest relict; forest dynamic; nutrient conservation; tree growth

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1. Introduction

Pilgerodendron uviferum (D. Don) Florin (Ciprés de las Guaitecas) is an endemic Cupressaceae of Argentinean Patagonia that is restricted to a small group of individual trees growing in isolated populations along its distribution [1]. Thus, the southernmost populations of *P. uviferum* in Argentina (Santa Cruz province) originally ranged over a large expanse but are now narrowly confined in isolated patches, also called forest relicts. According to Premoli et al. [2], these populations tend to be less genetically variable and therefore more affected by glacial activity than northern ones. This southernmost conifer species in the world is considered a long-lived species of slow growth that may live for more than 850 years, and grows in landscapes and on substrates shaped by glaciation, on acidic and poorly drained soils (e.g., wetlands, peats, bogs and moorlands), and wet sites [3].

The importance and uniqueness of these *P. uviferum* relict forests as refuges especially rely on valuable taxa, stable habitats and their high levels of endemicity [4]. Thus, relicts represent the extinction/diversification processes of a very high value for conservation biology, being the only surviving representatives of large groups that are mainly extinct [5]. Relict studies are needed to better understand regional extinctions and should be conserved as representatives of large and mainly extinct groups. Hence, relict tree species depend on distinct mechanisms promoting population persistence from complex ecological and evolutionary factors [6], where uncertainties raise within a regional climate in Patagonia that is now significantly hotter and drier than in the past [7]. However, there is a lack of forest relict studies in Argentinean Southern Patagonia. Vettese et al. [8] provided the first dendrochronological records of *Nothofagus antarctica* relicts in the Patagonian forest-steppe ecotone associated with documented changes in land use. Therefore, ecological studies of *P. uviferum* relicts and populations are an important task for the effective conservation of these forests and diversity.

Competition is a key factor driving forest dynamics and stand structure over time, mainly in marginal populations. The "slow seedling" hypothesis [9] proposes that because of slow growth rates caused by an inefficient transport system and low leaf photosynthetic capacity, gymnosperm seedlings are weak competitors with angiosperms in productive habitats. Thus, *P. uviferum* may be restricted to areas where the growth of angiosperms is reduced, e.g., on poorly drained and nutrient-poor soils. Some mechanisms of conifers that have been postulated to explain conifer persistence on unproductive sites are slow growth, longevity, reduced height, long-leaf life spans, and some morphological and biochemical adaptations [10,11]. However, in the *P. uviferum* relicts located in Southern Patagonia, there is practically no information about the main traits (e.g., leaf nutrient concentration, resorption, specific leaf area), physicochemical soil characteristics, and stand structure and dynamics (e.g., tree growth rate). While the nutrient concentration in plant tissues mainly depends on plant functional type and nutrient availability in soil, nutrient resorption, as an inherent physiological plant adaptation, is a key component of nutrient conservation strategies [12]. Efficient resorption becomes particularly important in poorly drained soils because most soils often have low levels of nutrients, and nutrient uptake by plants is limited [12]. Additionally, it influences many ecosystem processes, including carbon cycling and resource-use efficiency, and plant competition [13]. The objective of the present work was to evaluate the habitat, forest structure, leaf traits, leaf nutrient reabsorption and growth of the threatened conifer *P. uviferum* growing in four relicts in the Santa Cruz province (Argentina) to improve the available information for forest conservation purposes.

2. Materials and Methods

2.1. Characterization of the Study Area

The study was conducted in permanent plots established as part of the PEBANPA (Parcelas de Ecología y Biodiversidad de Ambientes Naturales en Patagonia Austral—Biodiversity and Ecological long-term plots in Southern Patagonia) network [14] located in Los Glaciares National Park (Figure 1). The sampled relicts were PU1 (50°05′23.2″ S; 73°13′33.8″ W) with an area of 0.86 ha and PU2 (50°05′50.5″ S; 73°13′19.7″ W) with an area of 0.3 ha, both associated with ñire (*Nothofagus antarctica*) and growing in Cipresales bay in the Upsala branch of Argentino Lake. The pure *P. uviferum* relict (PU3) (50°19′06.3″ S; 72° 49′12.3″W) of 0.5 ha is located in a wetland zone in the steppe dominated by *Festuca pallescens* and *Molinum spinosum* in Puerto Banderas in the Argentino Lake. Finally, the relict PU4 (50°32′52.0″ S; 72°56′46.9″ W) of 0.3 ha is associated with evergreen *N. betuloides* and *Drymis winterii* tree species in Puesto Camiseta in the Rico branch of Argentino Lake. Climate is characterized by short and cool summers, and long snowy winters. The mean annual precipitation (MAP) varies from 421 to 635 mm/yr, and the mean annual temperatures (MAT) fluctuates from 7.1 to 8.4 °C (Table 1).

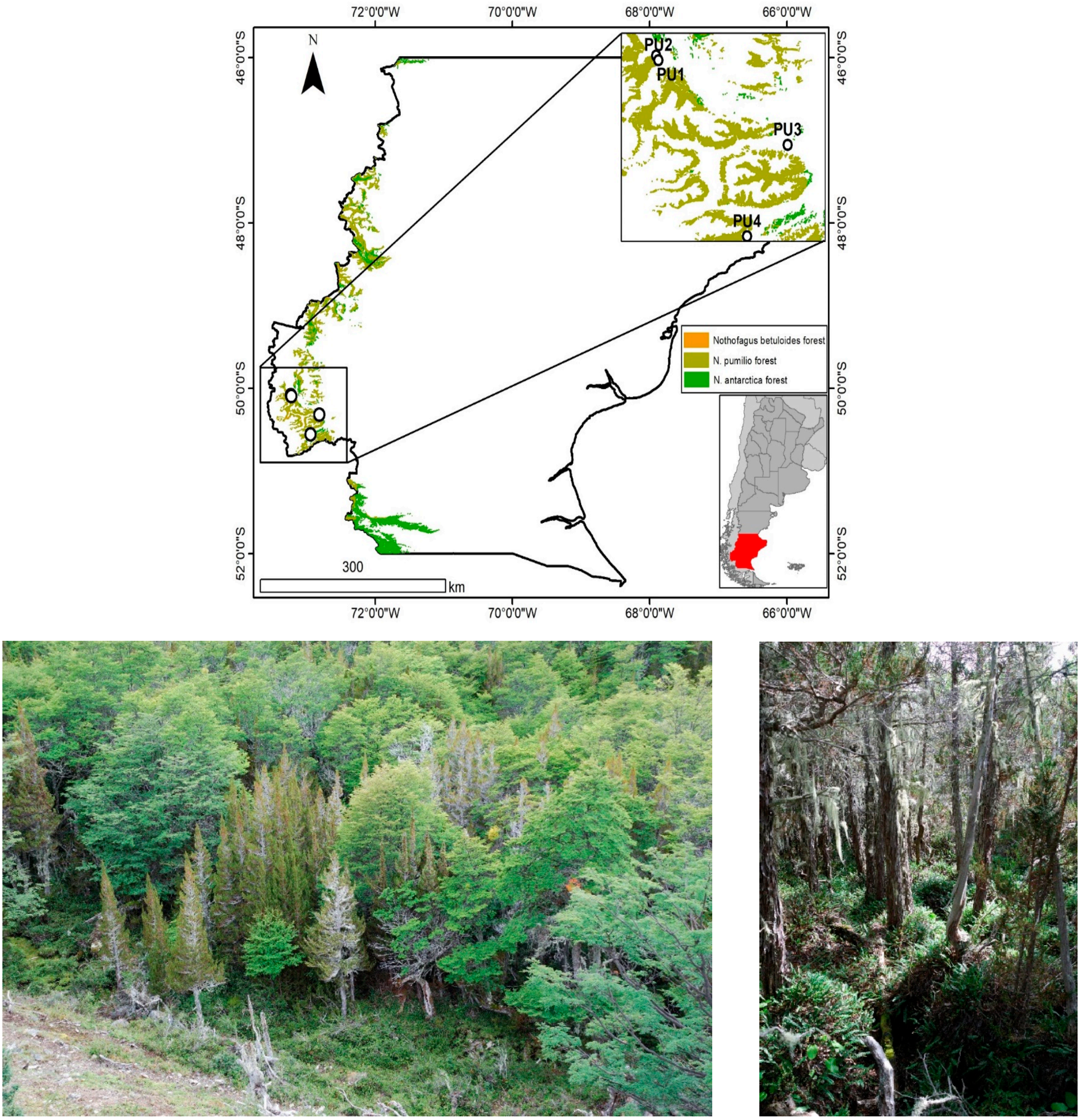

Figure 1. Location of *Pilgerodendrum univerum* relicts (P1–P4) in the Santa Cruz province (Argentina). Pictures show details of the sampled PU1 relict with an area of 0.86 ha associated with ñire (*Nothofagus antarctica*) at Cipresales bay in the Upsala branch of Argentino Lake.

Table 1. Mean (±standard deviation) forest structure and characteristics of *Pilgerodendrum univerum* relicts, Santa Cruz province, Southern Patagonia, Argentina. Different lower-case letters indicate significant ($p < 0.05$) differences among relicts.

Climate	Relict PU1	Relict PU2	Relict PU3	Relict PU4
MAT (°C)	8.3 ± 0.83	8.2 ± 0.74	8.4 ± 0.91	7.1 ± 0.65
MAP (mm/yr)	633 ± 58.8	635 ± 63.4	421 ± 39.9	469 ± 51.3

Table 1. *Cont.*

Climate	Relict PU1	Relict PU2	Relict PU3	Relict PU4
Variables at the stand level				
Total stand density (trees/ha)	10,553 ± 3612 a	12,833 ± 1069 a	325 ± 54 c	1533 ± 238 b
Total stand basal area (m^2/ha)	50.1 ± 17.4 a	68.2 ± 11.7 a	0.51 ± 0.06 b	44.0 ± 14.4 ab
Stand canopy cover (%)	65.9 ± 25.6 a	87.3 ± 8.7 a	3.8 ± 0.2 c	31.3 ± 21.1 b
Variables of *Pilgerodendrum uviferum*				
Stand density (trees/ha)	8667 ± 3150 a	10,900 ± 656 a	325 ± 54 b	433 ± 62 b
Age (years)	124 ± 18 a	115 ± 15 a	106 ± 11 b	82 ± 9 b
DBH (cm)	5.7 ± 2.1 a	4.5 ± 2.9 a	3.5 ± 2.8 ab	2.9 ± 1.5 b
Dominant height (m)	6.2 ± 0.9 a	6.6 ± 0.5 a	3.5 ± 0.2 b	3.7 ± 0.3 b
Female trees (%)	37.2 ± 3.82 c	19.3 ± 2.18 d	69.2 ± 1.86 b	80.1 ± 2.13 a
Seedling density (individuals/ha)	3773 ± 802 b	1300 ± 212 c	6125 ± 754 a	1900 ± 125 c
Sapling density (individuals/ha)	3167 ± 1214 a	1950 ± 314 a	520 ± 85 b	400 ± 54 b
Variables of understory				
Plant diversity (N°)	50 ± 7 a	58 ± 4 a	42 ± 9 ab	36 ± 6 b
Vegetation cover (%)	165 ± 21 b	189 ± 12 ab	142 ± 15 b	202 ± 15 a

2.2. Environmental and Stand Characteristics

In each relict, three circular plots of 500 m^2 were randomly located in each stand to characterize the forest structure (tree density, basal area, dominant height, canopy cover, DBH, percentage of female trees), and seedling (<1.0 cm diameter at breast height, DBH and <1.3 m height) and sapling (<1.0 cm DBH and >1.3 m height) densities. To evaluate the understory, we used the point-intercept method [15] with 50 intercept points (e.g., every 1 m) along transects at each relict. At each point, we recorded vascular plants (dicots, monocots and ferns) to determine vascular understory species richness and forest floor cover.

Ten bulked soil sample cores in each of the four study areas, 0–30 cm in depth, were taken at random for soil analysis. The soil samples were air-dried and ground to pass a 2 mm sieve. The pH was determined with an electronic meter immersed in a 1:5 mixture of soil and water. The percentage clay, silt and sand were determined using a Malvern Mastersizer 2600 laser particle size analyzer (Malvern Instruments Ltd., Worsestershire, UK). Soil organic carbon (SOC) analysis was carried out by using the traditional wet digestion method, soil nitrogen (SN) concentration was obtained with the semi-micro Kjeldahl method, and available soil phosphorus (SP) was analyzed by the Truog P method [16]. Major cations (Mg, K, Ca) were measured using standard analytical techniques with an atomic absorption spectrophotometer.

2.3. Leaf Traits, Leaf Nutrient Reabsorption and Tree Diameter Growth

Samples of green and senescent leaves were randomly collected from 10 mature trees and also from 10 saplings at each relict, then dried in a forced draft oven at 65 °C to constant weight, and ground in a mill containing a 1 mm stainless-steel screen for nutrient analyses. Nitrogen (N) content was determined using the semi-micro Kjeldahl technique (Sparks 1996). Phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S) concentrations were determined with a plasma emission spectrometer (Shimadzu ICPS-1000 III, Kyoto, Japan) following the methodology proposed by Johnson and Ulrich (1959). Organic carbon (C) content was quantified with a LECO CR-12 elemental analyzer [17]. Nutrient resorption efficiency was calculated based on the nutrient concentration in green leaves minus the nutrient concentration in senescent leaves divided by the nutrient concentration in green leaves, and then multiplied by 100. The leaf area and dry weight values of individual leaves were used in the calculation of the specific leaf area (SLA), which was determined using a one-image analysis software (DT-Scan, Delta-T Ltd., Cambridge, UK).

Finally, dendrochronological samplings were conducted to identify differences in tree growth among relicts, measuring 5 dominant trees at each relic and 2 cores by tree using increment borers. For analysis, we used the mean of these two core samples. The samples were processed according to conventional techniques used in dendrochronology [18]. Tree growth rings were dated under a binocular magnifier, and the ring widths were measured with an accuracy of 0.001 mm using a Velmex machine (Velmex, INC, Bloomfield, NY, USA).

2.4. Statistical Analyses

Forest structure, leaf traits, leaf nutrient reabsorption and diameter growth variables were analyzed with a one- and two-way analysis of variance (ANOVA), using relicts as the main factor. Significant differences were compared with the Tukey test with a significance level of $p < 0.05$. Principal component analysis (PCA) was used to analyze the relationships among climatic (MAP and MAT), soil physical–chemical characteristics, vegetation variables (forest and understory), specific leaf area, leaf nutrients concentrations and nutrient resorption. Pearson correlation coefficients were determined between climatic and soil characteristics, forest structure and understory vegetation, and leaf traits and nutrient resorption for the stands of *P. uviferum* forests. Finally, simple linear regressions were performed using the variables with the highest correlation values obtained from PCA (coefficient > 0.90).

3. Results

3.1. Forest Structure Characteristics

When analyzing the forest structure of relict forests, PU1 and PU2 stands presented more total tree density, basal area and canopy cover compared to the PU3 and PU4 stands (Table 1). When only *P. univerum* variables were analyzed, PU1 and PU2 stands showed higher tree density, DBH and dominant tree height than the PU3 and PU4 stands (Table 1). *P. univerum* dominant tree age ranged from 82 years in PU4 to 124 years in PU1. The highest proportion of female trees occurred in PU4. When forest regeneration variables were analyzed, while the PU1 and PU2 stands had the highest sapling density (1950–3167 individuals/ha), the PU3 stand showed the highest seedling density, with a mean value of 6125 individuals/ha (Table 1). Plant diversity of the understory layer varied from 36 (PU4) to 58 (PU2) species, and the vegetation cover ranged from 142% (PU3) to 202% (PU4) (Table 1). The dominant and most representative plant species in PU1, PU2 and PU4 were *Blechnum penna-marina* (fern), *Ranunculus biternatus*, *Veronica serpyllifolia*, *Empetrum rubrum*, *Maytenus magellanica* and *Gaultheria mucronata*, associated with *Escallonia rubra*, *Ranunculus uniflorus*, *Adenocaulen chilense*, *Berberis microphylla*, *Valeriana lapathifolia* and *Chloraea magellanica*. For PU4 located in a wetland zone in the steppe, the dominant and most representative plant species were grasses and graminoids such as *Carex auri*, *C. barrosii*, *Deschampsia flexuosa*, *Dactylis glomerata*, *Eleocharis albibracteata*, *Festuca pallescens*, *Poa Alopecurus*, *P. pratensis*, associated with *Chiliotrichium diffusum*, *Gunnera magellanica*, *Acaena ovalifolia*, *Aster vahlii*, *Anagallis alternifolia* and *Euphrasia antarctica*.

PU1 and PU2 relicts presented a silty–loam soil texture, while soils in PU3 had a loam texture and PU4 a sandy–clay loam texture (Table 2). The pH values were moderately acidic, decreasing from 6.5 in PU2 to 4.9 in PU4 relicts. SOC and SN contents were lower and SP higher in PU4 compared to the other relicts. Additionally, while soil K and Mg contents were higher in PU3, soil Ca was higher in PU1 and PU2 (Table 2).

Table 2. Mean (±standard deviation) soil properties of the sampled *Pilgerodendrum univerum* relicts, Santa Cruz province, Southern Patagonia, Argentina. Different lower-case letters indicate significant ($p < 0.05$) differences among relicts.

Relict	Clay (%)	Silt (%)	Sand (%)	pH	Organic Carbon (%)	N (%)	P (ppm)	K (cmol Kg^{-1})	Mg (cmol Kg^{-1})	Ca (cmol Kg^{-1})
PU1	20.1	47.8	32.1	5.6 ± 0.6 ab	10.2 ± 1.4 a	1.89 ± 0.1 ab	10.1 ± 1.1 b	0.2 ± 0.03 c	4.0 ± 0.4 c	134.2 ± 14.4 a
PU2	18.1	31.2	50.7	6.5 ± 0.7 a	10.5 ± 1.8 a	1.85 ± 0.2 ab	7.2 ± 0.8 c	0.2 ± 0.04 c	4.8 ± 0.6 c	144.1 ± 15.2 a
PU3	20.4	38.5	41.1	6.0 ± 0.5 a	10.4 ± 1.1 a	2.10 ± 0.3 a	6.0 ± 0.7 c	1.3 ± 0.12 a	20.1 ± 1.8 a	88.8 ± 9.1 b
PU4	26.2	10.0	63.8	4.9 ± 0.4 b	9.1 ± 0.9 a	1.68 ± 0.2 b	34.3 ± 2.8 a	0.9 ± 0.1 b	6.8 ± 0.8 b	96.3 ± 10.3 b

3.2. The Leaf Traits, Leaf Nutrient Reabsorption and Tree Diameter Growth of Pilgerodendrum univerum

The specific leaf area (SLA) of *P. univerum* was significantly lower in PU3 (Table 3). There was a tendency for SLA to decrease in the leaves of saplings compared with leaves from mature trees. The carbon and nutrient concentrations of leaves varied ($p < 0.05$) depending on relict characteristics and tree age (Table 3). The carbon concentration in tissues ranged from 44.9% (sapling leaves in PU4) to 49.4% (mature tree leaves in PU3). There was tendency for a higher nutrient concentration in the leaves of sapling compared to leaves from mature trees, except Ca, which showed the opposite tendency. N, P, K, Mg and S were more concentrated ($p < 0.05$) in the leaves at PU4, while Ca was more concentrated in PU3. Finally, the total nutrient concentration graded according to the relics (PU4 > PU1 > PU2 > PU3).

Table 3. Mean (standard deviation) specific leaf area (SLA, m^2/g), and carbon and nutrient concentrations (data expressed as a % of dry matter) of green leaves of *Pilgerodendrum univerum* mature trees and saplings grown in relicts in the Santa Cruz province (Argentina). Different lower-case letters for mature trees and upper-case letters for saplings indicate significant ($p < 0.05$) differences among relicts.

Stand		SLA	C	N	P	K	Mg	S	Ca
PU1	Mature tree	0.032 ± 0.002 ab	46.5 ± 5.4 a	0.92 ± 0.11 a	0.09 ± 0.01 a	0.47 ± 0.06 a	0.04 ± 0.007 b	0.13 ± 0.02 a	1.94 ± 0.2 b
	Sapling	0.030 ± 0.001 AB	45.6 ± 4.8 A	1.02 ± 0.09 A	0.17 ± 0.02 A	0.58 ± 0.05 A	0.10 ± 0.011 A	0.19 ± 0.03 A	1.85 ± 0.5 B
PU2	Mature tree	0.034 ± 0.003 a	48.5 ± 6.2 a	0.83 ± 0.08 ab	0.08 ± 0.01 ab	0.49 ± 0.07 a	0.08 ± 0.009 a	0.14 ± 0.02 a	1.73 ± 0.3 bc
	Sapling	0.033 ± 0.001 A	45.2 ± 3.4 A	0.88 ± 0.07 AB	0.12 ± 0.02 AB	0.53 ± 0.03 AB	0.11 ± 0.024 A	0.18 ± 0.04 A	1.68 ± 0.2 C
PU3	Mature tree	0.029 ± 0.002 b	49.4 ± 7.1 a	0.75 ± 0.05 b	0.06 ± 0.005 b	0.24 ± 0.04 b	0.07 ± 0.009 ab	0.07 ± 0.01 b	2.86 ± 0.4 a
	Sapling	0.028 ± 0.001 B	47.7 ± 4.4 A	0.79 ± 0.09 B	0.09 ± 0.009 B	0.38 ± 0.01 B	0.04 ± 0.008 B	0.11 ± 0.03 B	2.04 ± 0.1 A
PU4	Mature tree	0.035 ± 0.003 a	46.9 ± 3.7 a	0.95 ± 0.07 a	0.11 ± 0.05 a	0.48 ± 0.06 a	0.10 ± 0.04 a	0.16 ± 0.02 a	1.58 ± 0.3 c
	Sapling	0.033 ± 0.002 A	44.9 ± 2.9 A	1.14 ± 0.12 A	0.19 ± 0.04 A	0.66 ± 0.05 A	0.12 ± 0.03 A	0.25 ± 0.04 A	1.37 ± 0.2 D

The mean nutrient resorption efficiency varied according to the relict site (Figure 2). Also, the nutrient resorption efficiency showed a different magnitude response depending on a particular nutrient. For example, the maximum value of the mean nutrient resorption efficiency was obtained for P (grand mean of 49.5%) and the minimum for Ca (18.1%) with intermediate values of 32.1% for Mg, 29.8% for S, 47.2% for N and 43.3% for K.

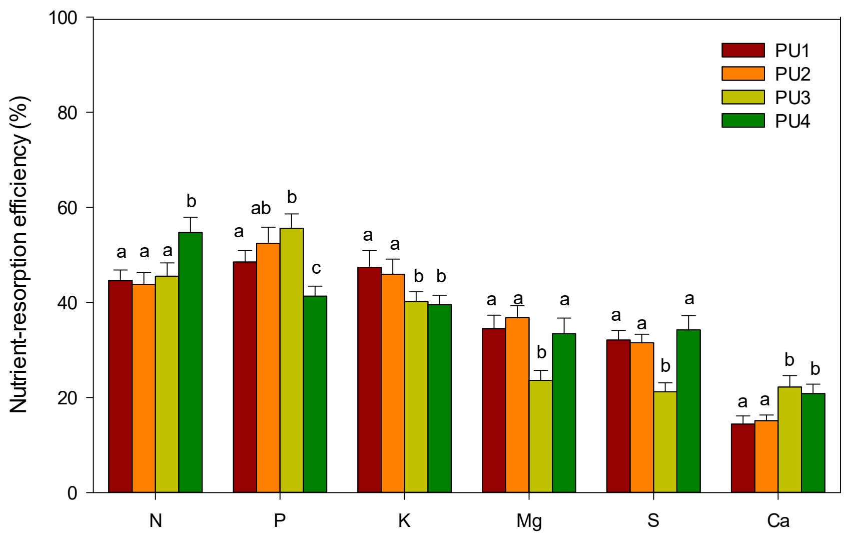

Figure 2. Nutrient resorption efficiency of dominant *Pilgerodendrum univerum* trees growing in the relicts (P1–P4) of the Santa Cruz province (Argentina) and standard deviation values. Different lower-case letters indicate significant ($p < 0.05$) differences among relicts for each nutrient.

The mean DBH growth of dominant *P. univerum* trees ranged from 0.33 to 0.46 mm/yr, growing in PU3 and PU1, respectively (Table 4). While the maximum DBH growth was recorded in PU1 with a value of 1.25 mm/yr, the minimum DBH growth of 0.08 mm/yr occurred in PU3.

Table 4. Mean, maximum and minimum (±standard deviation) diameter at the breast-height (1.30 m, DBH) growth of dominant *Pilgerodendrum univerum* trees growing in relicts, Santa Cruz province, Southern Patagonia, Argentina. Different lower-case letters indicate significant (p < 0.05) differences among relicts.

Relict	Mean DBH Growth (mm/yr)	Maximum DBH Growth (mm/yr)	Minimum DBH Growth (mm/yr)
PU1	0.46 ± 0.05 a	1.25 ± 0.13 a	0.18 ± 0.04 a
PU2	0.39 ± 0.04 ab	0.85 ± 0.09 b	0.15 ± 0.03 ab
PU3	0.33 ± 0.02 b	0.46 ± 0.04 d	0.08 ± 0.01 b
PU4	0.35 ± 0.03 b	0.67 ± 0.05 c	0.11 ± 0.02 b

Principal component analysis (Figure 3) determined that the four *P. uviferum* relicts were grouped based on climate, soil characteristics, forest structure, understory and leaf traits. PCA determined that the first two axes explained >90% of the total variance (60–69% and 25–32% for axis 1 and axis 2, respectively). Climate and edaphic variables split PU1–PU2, PU3 and PU4, which were explained by the higher MAP values, soil clay content, and SN and SP contents (Figure 3A). A similar pattern was observed for leaf traits and leaf nutrient reabsorption according to axes 1 and 2 (Figure 3C), defined by the differences in specific leaf area, C and N contents in leaves, and N and K resorption values. However, PCA based on forest structure and understory variables determined a clear separation among the four relics of *P. uviferum* (Figure 3B). This gradient was strongly correlated with the higher values of female trees, dominant height, stand density, seedling density and understory plant cover.

The results of Pearson's correlation coefficient showed a negative and significant correlation between female tree percentage and vegetation cover (r = −0.98; p < 0.05), and SLA and soil N (r = − 0.96; p < 0.05). In contrast, height had a positive correlation with density and MAP (r = 0.97 and 0.98, respectively; p < 0.05). Also, the soil clay content had a positive correlation with N resorption (r = 0.98; p < 0.05), and the MAP was positively correlated with K resorption (r = 0.96; p < 0.05). The dominant height of *P. univerum* trees was positively correlated with total stand density and MAP (Figure 4A,C). On the other hand, the percentage of *P. univerum* female trees showed a negative correlation with understorey vegetation cover (Figure 4B), and SLA was negatively correlated soil nitrogen content (Figure 4D). In addition, N and K resorption showed a positive correlation with soil clay content (Figure 4E) and MAP (Figure 4F), respectively.

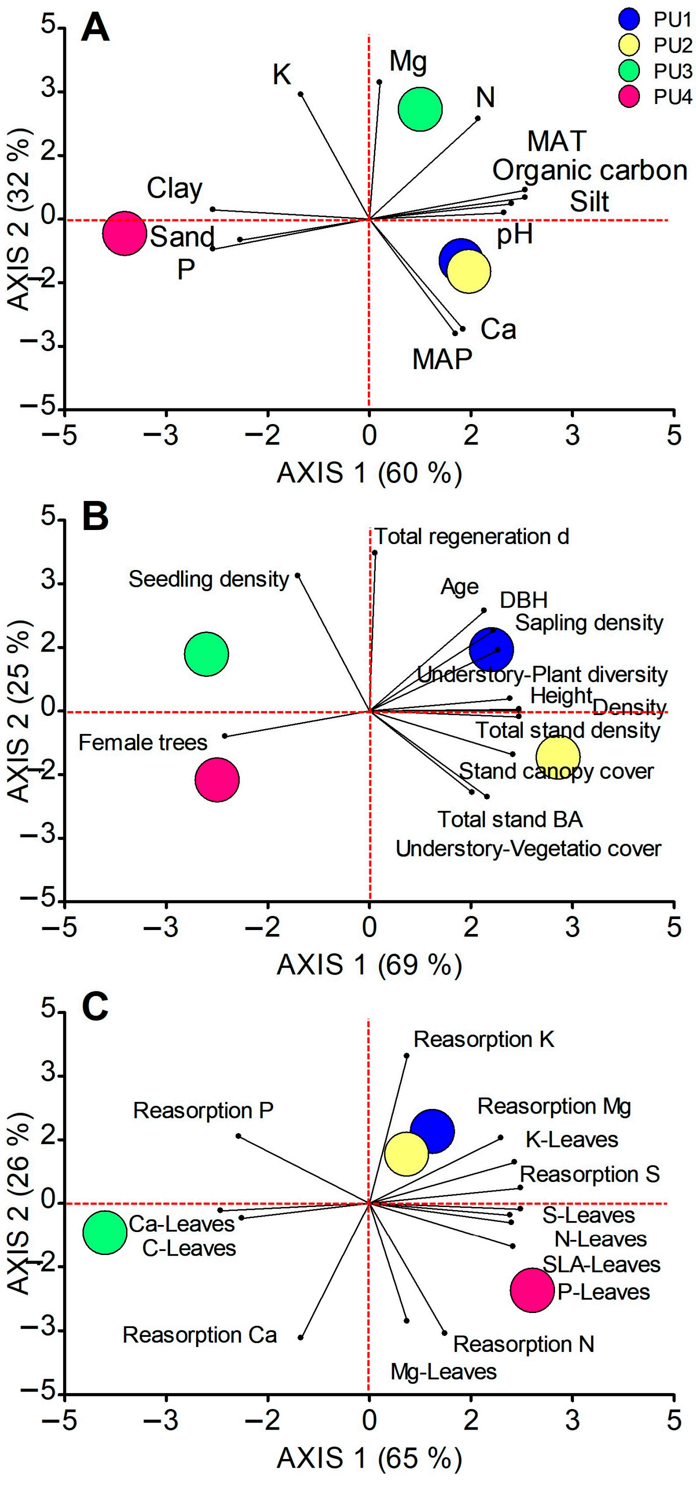

Figure 3. Principal components analysis including (**A**) soil physical–chemical characteristics and climate, (**B**) stand structure, and (**C**) leaf traits and leaf nutrient reabsorption for the four *P. univerum* relicts areas (PU1 and PU2 both associated with *Nothofagus antarctica* and growing in Cipresales bay, Upzala branch of Argentino Lake; PU3 pure *P. uviferum* relict located in a wetland zone in the steppe in Puerto Banderas, Argentino Lake; PU4 associated with evergreen *N. betuloides* and *Drymis winterii* in Puesto Camiseta, Rico branch of Argentino Lake).

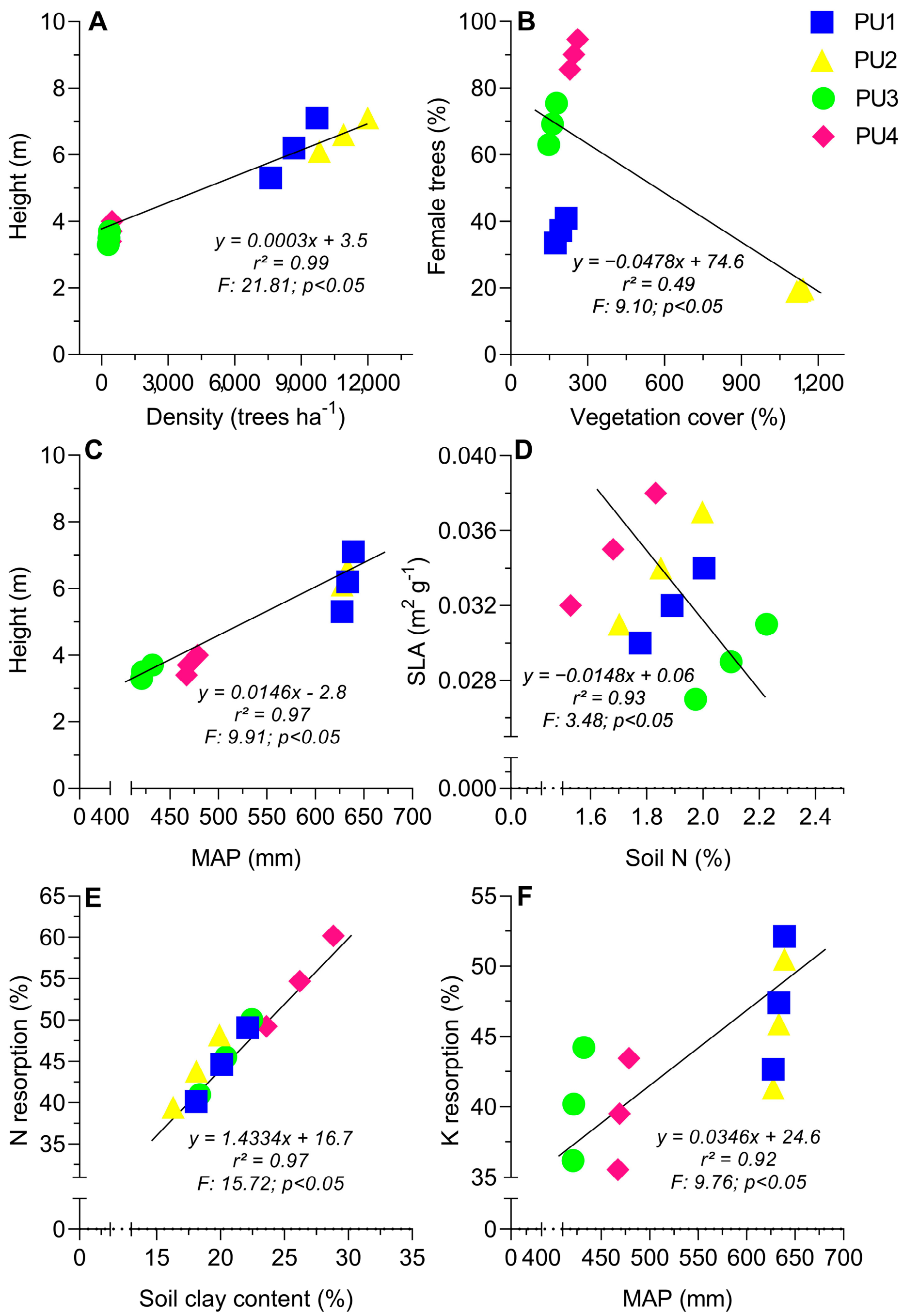

Figure 4. Relationships among soil physical–chemical characteristics, climate, stand structure, leaf traits and leaf nutrient reabsorption (d.f. = 13) for the four *P. univerum* relict areas of Santa Cruz (Patagonia, Argentina). (**A**) Dominant height of dominant *P. univerum* trees and total stand density, (**B**) percentage of *P. univerum* female trees and understorey vegetation cover, (**C**) dominant height of dominant *P. univerum* trees and the mean annual precipitation (MAP), (**D**) specific leaf area (SLA) and soil nitrogen content, (**E**) N resorption and soil clay content, (**F**) K resorption and MAP. Lines show linear regression, where r^2 = adjusted parameter and p = probability.

4. Discussion

We found contrasting environmental and forest structure conditions between the four studied relicts of *P. univerum* in Southern Patagonia. For example, PU1 and PU2, both associated with *N. antarctica*, showed more tree density, basal area and crown canopy cover, and higher tree density, DBH and dominant height of *P. univerum* trees, where the highest sapling density (1950–3167 individuals/ha) and plant understory diversity compared with pure *P. uviferum* growing near the steppe (PU3) and stands were associated with evergreen *N. betuloides* and *Drymis winterii* trees (PU4). This is consistent with Rovere et al. [1] who reported great variation in the forest structure and vegetation of eight *Pilgerodendron* known populations in Argentina, based on information about the physical characteristics of the habitats, vegetation composition and disturbance types. These differences were confirmed by principal component analysis (PCA), where the four relicts were grouped based on climate, soil characteristics, forest structure, understory, leaf traits and leaf nutrient reabsorption. For example, climate and edaphic variables together with leaf traits variables showed a clear separation between PU1–PU2, PU3 and PU4 relicts, while by using forest structure and understory variables we determined a clear separation between all *P. uviferum* relicts. Furthermore, in the present study we found that *P. uviferum* is restricted to a small group of individual trees growing in isolated populations with areas between 0.3 and 0.86 ha. It has been hypothesized that the establishment pulses of *P. uviferum* occurred in open sites with waterlogged soils and when enough seed is available [19]. Also, it has been proposed that in the absence of disturbances, as the soil drainage improves, the establishment of *P. uviferum* will gradually decline and it may be replaced by more shade-tolerant angiosperm species following the "slow seedling" hypothesis [20]. For the small size of the studied relict, *P. uviferum* in Southern Patagonia are restricted to those areas where the growth of angiosperm trees (*N. antarctica* in PU1 and PU2, and *N. betuloides* and *Drymis winterii* in PU4) is reduced in these poorly drained and nutrient-poor soils. This was confirmed by the higher number of *P. uviferum* seedlings (range from 1300 to 6125 individuals/ha) and saplings (400–3167 individuals/ha) in the evaluated relicts. However, according to Bannister et al. [3], when considering the regeneration assessments, it is evident that there is abundant and continuous recruitment of individuals, which, owing to their slow growth, simply take a very long time to reach the 5 cm threshold for forest inventories. Therefore, the incorporation of seedlings and saplings into tree population dynamics studies appears to be important in *P. uviferum* forests, because seedlings need many decades to reach the minimum DBH. Thus, estimations from the present study could indicate that there is no lack of recruitment of individuals. The dominant height of *P. univerum* trees were positively correlated with tree density and MAP (Figure 4A,C). Soil texture- and temperature-related variables contributed the most to *N. antarctica* forest productivity in southern Patagonia [21]. In addition, tree populations that are characterised by a particularly low degree of variation could be considered conservation priorities. According to Allnutt et al. [22], the *P. univerum* population with least variation, between 16 populations for this species, was the pure relict PU3. This is particularly vulnerable because of its very small size and extreme isolation. Therefore, this particular relict should be accorded as a high priority for conservation action in the future.

Specific leaf area (SLA) and nutrient concentrations in *P. univerum* leaves varied depending on relict site conditions and the aging of individuals. Particularly, the SLA and most nutrient concentrations (except Ca) of *P. univerum* leaves was significantly lower in the stand growing near the steppe (PU3) compared with other relicts. The marginal site of PU3 is located near the steppe in a windy environment with a higher evapotranspiration rate which can reduce tree growth, nutrient uptake and tissue nutrient concentration. These changes are consistent with Lambers et al. [23] who reported that plants have greater C concentrations of "least expensive" (in terms of ATP required for biosynthesis) structural carbohydrates and lignin compounds when growth conditions become less favorable compared with a higher concentration of 'most expensive' lipid and protein compounds characteristic of fast-growing species. This may influence the low SLA values found in PU3. Low-SLA plants invest more dry matter per leaf and often have low relative growth rates and net rates of photosynthesis. Thus, for *P. univerum* with the lowest SLA and growing in a harsh site conditions or nutrient deficient soils, where it is important to maintain leaf function when conditions are unfavorable for leaf production [24]. This was confirmed with the negative correlation between SLA and soil nitrogen content (Figure 4D). The differences that we found in SLA between relicts is consistent with Huxman et al. [25], who reported that even within plant ecosystems, there can be considerable SLA variation among species, reflecting the local-scale spectra of leaf investment strategies. The lower nutrient concentration found in PU3 is consistent with Frangi et al. [26] who reported that nutrient (K, Mg, N and P) concentrations and stocks of mature *Nothofagus pumilio* stands in Tierra del Fuego (Argentina) decreased with elevation (worst site conditions) by reducing the rates of nutrient uptake and tree growth requirements. According to Peri et al. [27,28], almost all nutrient concentrations in *N. antarctica* leaves decreased as the age increased in less-favorable site-quality conditions. In contrast, Ca concentration showed a different response and increased in tree leaves growing in PU3. This may be due to trees with lower growth rates and nutrient uptake taking more Ca at the expense of other nutrients by changing allocation to structural tissues.

Resorption is a strategy of plants to conserve nutrients, and it is essential for modeling nutrient cycling. The mean nutrient resorption efficiency varied according to the relict site and on a particular nutrient, ranging from 18.1% and 49.5% for Ca and P, respectively. According to Pérez et al. [29], *P. uviferum* and *Fitzroya cupressoides*, one of the dominant tree species in a conifer forest in southern Chile (42°3′ S), showed high N resorption values and one of the lowest proficiency values (<0.50%), indicating high nutrient use efficiency (NUE) compared with species in a mixed broad-leaved forest. This is consistent with the general view that conifer-dominated forests are more N-use-efficient than angiosperm-dominated forests [30]. In addition, N and K resorption showed a positive correlation with soil clay content (Figure 4E) and MAP (Figure 4F), respectively. Vergutz et al. [31], in a global resorption efficiency study and regarding climate, indicated that the same growth form growing in different climates can show different resorption efficiencies and that the climate characteristic with the greatest influence on nutrient resorption is the mean annual temperature. Although nutrient resorption has been predicted to be higher in plants growing in wetter soils prone to leaching, no correlation between soil moisture and nutrient retention was found in a *Austrocedrus chilensis* tree [32]. Furthermore, the mean DBH growth of dominant *P. univerum* trees ranged from 0.33 to 0.46 mm/yr. This is consistent with Bannister et al. [3] who reported that the annual diameter increment at the root collar of *P. uviferum* seedlings was extremely slow (<1 mm/yr) and significantly higher in disturbed than in undisturbed forests. The extremely slow diameter and shoot growth of trees in undisturbed forests is indicative of a species with a stress-tolerant strategy. In this context, longevity (>880 years), extremely slow growth capacity, tolerance to shade and stress, decay resistance and the capacity to develop adventitious roots (e.g., facilitation of the supply of oxygen in waterlogged soils) may be the primary mechanisms that lead to the persistence of *P. uviferum* at these unproductive sites [33]. This is consistent with Esse et al. [34] who reported that *P. uviferum* forest communities can persist over time due to the high water table that limits the competitive effect from other tree species less tolerant to a high soil water table and organic matter.

5. Conclusions

The objective of the present work was to evaluate the habitat, forest structure, leaf traits, leaf nutrient reabsorption and growth of the threatened conifer *P. uviferum* growing in four relicts in Santa Cruz province (Argentina) to improve the available information for the conservation of these endemic forests. We found that *P. uviferum* associated with *N. antarctica* showed a higher tree density, DBH and dominant height, sapling density and plant understory diversity compared with pure *P. uviferum* growing near the steppe and stands associated with evergreen *N. betuloides* and *Drymis winterii* trees. The SLA and most nutrient concentrations (except Ca) of *P. univerum* leaves were significantly lower in the stand growing near the steppe compared with other relicts. The mean nutrient resorption efficiency varied according to the relict site and on a particular nutrient, ranging from 18.1% and 49.5% for Ca and P, respectively. The mean DBH growth of dominant *P. univerum* trees ranged from 0.33 to 0.46 mm/yr. Therefore, the information of this work may assist the conservation of marginal *P. uviferum* forests spatially disconnected with continuous forests. Also, the evaluated relicts might provide indicators of the potential characteristics that enable some taxa to survive regional or lineage extinctions.

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