Forest structure of three endemic species of the genus *Polylepis* (Rosaceae) in central Perú

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Abstract. *Polylepis* (Rosaceae) is the dominant tree genus in High-Andean forest ecosystems. These ecosystems are severely threatened, but little is known about their structure and functioning. We provide the first reports of the dasometric structure and spatial distribution of eight forests of *Polylepis canoi*, *P. flavipila* and *P. rodolfo-vasquezii* in the Central Peruvian Andes as fundamental information for management and conservation policies. We sampled all individuals ≥1 cm of diameter at ground level (DGL) in 20 plots of 10x10 m in each forest, and measured total height (TH) and DGL. Also, we mapped the spatial distribution of the individuals in two plots of 30x30 m (X and Y axes). We found differences in the dasometric structure between forests of the same species, which, in some cases, were associated with climate, soil or elevation variables. However, no well-defined pattern was found. The allometric relationships of the linear and non-linear models did not differ widely with respect to the R^2 nor to the Akaike (AIC) scores, indicating that the forests did not show a saturation of tree height with increasing diameter. In the *P. canoi* forests, individuals with diameters ≥10 cm were the most abundant. In contrast, the forests of *P. rodolfo-vasquezii* showed a predominance of individuals with diameters ≤10 cm, whereas *P. flavipila* presented an altered structure with no relationship between DGL and TH in one of the evaluated forests. The analysis of spatial distribution according to the Ripley's K function on a small scale revealed that *P. flavipila* and *P. canoi* presented random patterns, whereas *P. rodolfo-vasquezii* showed an aggregate pattern. Finally, our results showed that even forests of the same species have different dasometric structures, whereas spatial patterns differ only between species. So, caution must be taken when extrapolating information between species or forests during ecological studies and conservation actions.

[Keywords: High Andean forests, Ripley's K function, allometric models, *Polylepis*]

Resumen. Estructura forestal de tres especies endémicas del género *Polylepis* (Rosaceae) en la Región Central del Perú. El género *Polylepis* (Rosaceae) es el árbol dominante en los ecosistemas altoandinos. Estos ecosistemas están gravemente amenazados y poco se sabe sobre su estructura y funcionamiento. Proporcionamos los primeros reportes de la estructura dasométrica y la distribución espacial de ocho bosques de *Polylepis canoi*, *P. flavipila* y *P. rodolfo-vasquezii* en los Andes Centrales peruanos como información fundamental para el manejo y políticas de conservación. En cada bosque tomamos datos de todos los individuos ≥1 cm de diámetro a nivel del suelo (DNS) en 20 parcelas de 10x10 m y medimos la altura total (AT) y el DNS. Además, mapeamos la distribución espacial de los individuos en dos parcelas de 30x30 m (ejes X e Y). Encontramos diferencias en la estructura dasométrica entre bosques de la misma especie; en algunos casos, estas diferencias se asocian a variables de clima, de suelo o de elevación. Sin embargo, no se encontró un patrón definido. Las relaciones alométricas de los modelos lineales y no lineales no difieren respecto al R^2 ni a los valores de Akaike (AIC), lo que indica que los bosques no muestran una saturación de la altura con el incremento del diámetro. En los bosques de *P. canoi*, los individuos con diámetros ≥10 cm fueron los más abundantes; por el contrario, los bosques de *P. rodolfo-vasquezii* presentaron predominancia de individuos con diámetros ≤10 cm. *Polylepis flavipila* mostró una estructura alterada, sin relación entre DNS y AT en uno de los bosques evaluados. Los análisis de distribución espacial según la función K de Ripley a pequeña escala revelaron que *P. flavipila* y *P. canoi* poseen patrones aleatorios, mientras que *P. rodolfo-vasquezii* mostró un patrón agregado. Finalmente, nuestros resultados demuestran que incluso bosques de la misma especie tienen diferentes estructuras dasométricas, mientras que los patrones espaciales difieren sólo entre especies. Por ello, se debe tener cuidado al extrapolar información durante los estudios ecológicos y las acciones de conservación.

[Palabras clave: bosques altoandinos, función K de Ripley, modelos alométricos, *Polylepis*]

Introduction

Polylepis (Rosaceae) is the dominant tree genus in High-Andean forest ecosystems above 3500 m a. s. l. (lower down further south) from Venezuela to central Argentina (Zutta et al. 2012; Zutta and Rundel 2017). These forests provide environmental services in water regulation, mitigation of CO_2 emissions, soil protection and also provide habitats for endemic and threatened species (Fjeldså 2002; Fjeldså and Kessler 2006; Sevillano-Ríos and Rodewald 2017). Currently, about 35 *Polylepis* species are recognized (Boza et al. 2019; Kessler and Schmidt-Lebuhn 2006; Segovia-Salcedo et al. 2018), 22 of which (including seven endemic species) occur in Perú (Boza et al. in press; Mendoza and Cano 2012, 2011; Valenzuela and Villalba 2015).

It is well known that many *Polylepis* forests are currently facing substantial negative pressure due to human land use (Kessler 2002; Renison et al. 2006, 2004), including direct effects of timber extraction and indirect effects of grazing and associated grassland burning (Kessler 2002). This has rendered *Polylepis* forests one of the most threatened ecosystems in the world (IUCN 2018). Within the remaining forest patches, both historical climatic and microsite conditions as well as human impacts affect not only the spatial distribution at the landscape scale, but also the dasometric and spatial structure of the forest (Hensen et al. 2012; Hertel and Wesche 2008; Kessler et al. 2014) and, therefore, their ecosystem functions (Spies 1998; Sylvester et al. 2017).

Previous studies have shown that the structural and spatial heterogeneity of treeline habitats is related to elevation, latitude and topography (Bader and Ruijten 2008; Bunyan et al. 2015). *Polylepis subsericans* and *P. incana* evidence a relationship between the location of forests associated with topographic features which varies in relation to elevation (e.g., Coblentz and Keating 2008; Toivonen et al. 2018), whereas in other species such as *Polylepis flavipila*, *P. reticulata*, *P. incana* and *P. australis* the population structure and density have been characterized, demonstrating the importance of this information to know the current state of the forests and propose conservation actions (Camel and Castañeda 2018; Castro 2014; Cierjacks et al. 2008; Pacheco 2015; Renison et al. 2011). In disturbed forests, Kessler et al. (2014) found no saturation of tree height related to the increase of the diameter, since

cutting and extraction of firewood affected the largest trees, altering the dasometric and spatial structure of the forests. In contrast, forests that are of difficult access commonly have trees of greater diameter and height, but lower density per unit area (Anfodillo et al. 2012; Sylvester et al. 2017).

Besides the size structure, the spatial distribution of tress can also vary from aggregate to random or even regular patterns. These patterns vary according to functional traits such as growth shape, shade tolerance and seed dispersal, or external conditions such as presence of rock outcrops, slope and elevation (Du et al. 2017). Studies of *Polylepis flavipila*, *P. racemosa* and *P. subsericans* have shown that these species tend to have aggregate distributions associated with environmental variables such as humidity, soil depth and rock cover (Arizapana et al. 2016b; Hurtado 2014).

Finally, regeneration is also of crucial importance. In Ecuador, it has been found that *P. incana* shows more recruitment under the forest canopy due to less extreme climatic conditions and denser seed rain, whereas younger individuals in open habitats have higher growth rates due to higher light availability (Cierjacks et al. 2007; Morales 2017). In forests affected by cattle grazing, livestock does not affect the recruitment of seedlings or vegetative shoots in *P. pauta* forests, but the trampling of cattle leads to a significant increase in the abundance of seedlings for *P. incana* (Cierjacks et al. 2007).

In the present study, we focused on *Polylepis canoi*, *P. rodolfo-vasquezii* and *P. flavipila*, three poorly known species endemic to the central Peruvian Andes. Specifically, our aim was to compare the dasometric structure between forests of the same species and to characterize their spatial distribution, in order to understand the relative influences of environmental in determining forest structure.

Materials and Methods

Study sites

We studied eight relicts of *Polylepis* forests in the central Peruvian Andes at elevations ranging from 3698 to 4352 m a. s. l. (Table 1, Figure 1). Forests of *P. canoi* were studied at Nahuin (11°17′51′′ S - 75°30′6′′ W), Santa Rosa de Toldopampa (11°26′5′′ S - 74°53′57′′
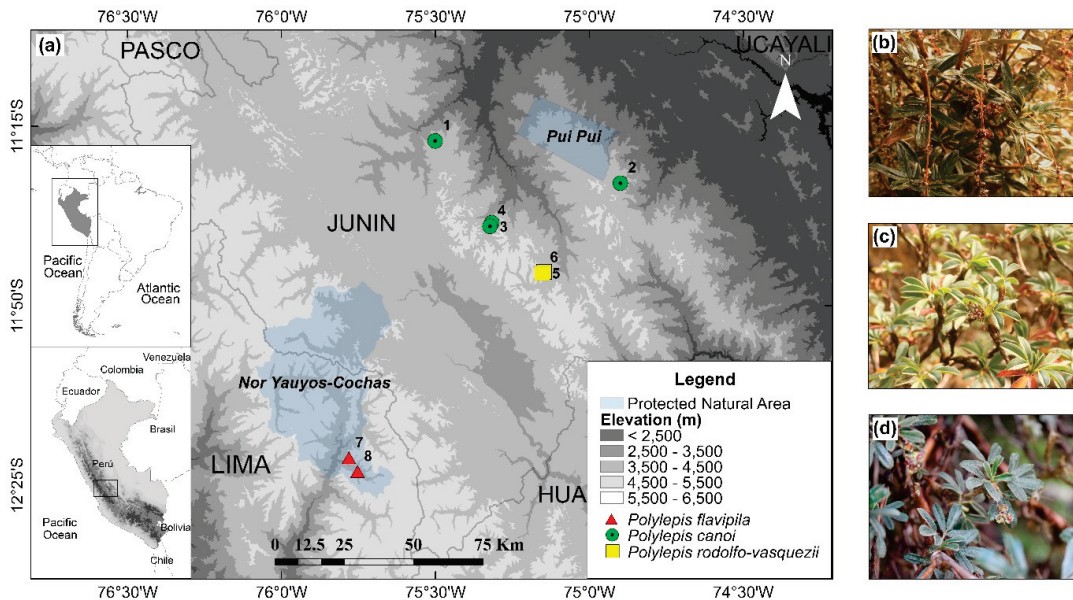
Figure 1. a) Map of the study area with the locations for the three endemic Peruvian species; b) *Polylepis canoi*; c) *P. rodolfo-vasquezii*; d) *P. flavipila*.

Figura 1. a) Mapa del área de estudio con las ubicaciones de las tres especies endémicas peruanas; b) *Polylepis canoi*; c) *P. rodolfo-vasquezii*; d) *P. flavipila.*

Table 1. Evaluated forests. Abbreviations: A.M.T.: annual mean temperature (°C); A.P.: annual precipitation (mm/year). Climatic data taken from CHELSA (Karger et al. 2017). Disturbance events: a=forest or grassland burning; b=livestock grazing; c=firewood extraction; d=peat moss extraction; e=agriculture; f=presence of roads; g=presence of the hemiparasite *Tristerix chodatianus.*

Tabla 1. Bosques evaluados. Abreviaturas: T.M.A.: temperatura media anual (° C); P.A.: precipitación anual (mm / año). Datos climáticos tomados de CHELSA (Karger et al. 2017). Eventos de perturbación: a=quema de bosques o pastizales; b=pastoreo de ganado; c=extracción de leña; d=extracción de turba; e=agricultura; f=presencia de caminos; g=presencia del hemiparásito *Tristerix chodatianus.*

Species	Region	Locality	Elevation (m a. s. l.)	A.M.T.	A.P.	Disturbance events
P. canoi	Junín	Tasta	3896±22.1	7.17±0.07	1834±0.36	a, b, d
		Nahuin	3698±56.3	8.28±0.48	1493±48.00	b, c
		Jucha	3931±25.0	6.9±0.94	1328±40.70	a, b, d, e
		Llantaco	3771±75.6	7.1±0.89	1242±60.40	a, b, d, e
P. rodolfo-vasquezii		Paucho	4254±34.6	5.3±0.00	1266±0.44	a, b, c, e, f
		Quilcaycocha	4352±30.7	5.1±0.00	1254±0.41	a, b, c, e, f
P. avipila	Lima	Shaitura	4218±101	5.5±0.71	667±41.90	a, b, c, e, g
		Chaqsii-Chaqsii	4010±59.6	6.4±0.25	530±8.61	a, b, c, e, f, g

W) and Curimarca (11°33′49′′ S - 75°19′1′′ W). These forests presented on average the highest levels of annual mean precipitation (1474 mm/year) and annual mean temperature (7.3 °C). The areas are characterized by open and shrubby vegetation composed by *Buddleja*, *Gynoxys*, *Miconia* and scattered *Polylepis* stands surrounded by Puna pasture. Signs of human activities where evident all over the area, as burning forest or grassland, livestock, extraction of peat moss and agriculture (Table 1). The species *P. rodolfo-vasquezii* was studied at the community of Pomamanta (11°43′36′′ S - 75°9′9′′ W), where annual mean precipitation is 1260 mm/year and annual mean temperature 5.3 °C. The area is characterized by having many rock outcrops and grasslands. Finally, *P. flavipila* was evaluated at the Nor Yauyos-Cochas Landscape Reserve in the district of Laraos (12°19′38′′ S - 75°46′48′′ W), where there are low levels of annual mean precipitation (598 mm/year) and annual mean temperature (5.9 °C). The area is characterized by abundant grassland with shrubby plants such as *Escallonia*, *Baccharis* and *Senecio* (Trinidad and Cano 2016). These forests are

affected by the presence of roads, livestock, extraction of firewood and the hemiparasite *Tristerix chodatianus* (Camel et al. 2019).

Field sampling

Fieldwork was carried out between July 2016 and June 2017. At each forest stand, we established 20 plots of 10x10 m selected by random sampling. When plots fell in areas of difficult access, they were relocated to the nearest accessible place. Plot elevation and UTM coordinates were recorded for the extraction of climatic data annual mean temperature (A.M.T.) and annual precipitation (A.P.) from the CHELSA database (Karger et al. 2017). Soil samples were collected from each plot, mixed into two groups of ten to form two samples by locality and the following parameters were analyzed: pH, organic matter, total nitrogen, available phosphorus, available potassium and cation exchange capacity.

In each plot, we measured tree diameter at ground level (DGL) and total height (TH) of all individuals that had a diameter ≥1 cm at ground level. However, in order to obtain the DGL and TH averages that were comparable with literature values, only individuals ≥10 cm of DGL were considered (Kessler et al. 2014; Sylvester et al. 2017). To estimate tree height, we used a 3 m topographic survey line segmented every 50 cm (Kessler et al. 2014). In addition, to evaluate the spatial distribution of the individuals, we established two plots of 30x30 m in each forest, in which all individuals ≥1 cm of DGL were spatially located with metric tapes (X and Y axis) (Du et al. 2017).

Statistical analyses

We used mixed effects models and Tukey's *post hoc* tests to compare diameter at ground level DGL and TH between localities of the same species. To account for the possible lack of independence between plots within localities, we included the plots as a random factor. A Gaussian error distribution with identity link function was used to fit the TH model of *P. rodolfo-vasquezii* to meet the normality assumption as tested by Shapiro-Wilk test. Since the distribution of DGL of *P. canoi*, *P. rodolfo-vasquezii* and *P. flavipila* and TH of *P. canoi* and *P. flavipila* was positively skewed, we fitted the generalized linear mixed models (GLMM) with Gamma family and "log" link.

Also, we used F and LSD tests at a confidence interval of 95% to compare the means of soil parameters, climate variables (A.M.T. and A.P.) and elevation of the forests. To assess the relation between DGL and TH, we used a linear model: f(Y)=a+bx and the non-linear models: Logistic f(Y)=a/(1+b*exp(-c*X)), Gompertz f(Y)= a*exp(-b*exp(-c*X)) and Schumacher f(Y)=exp(a+b(1/X)), with Y representing TH and X representing DGL (Grothendieck 2013; Kahm and Kschischo 2012). The coefficient of determination and the Akaike information criterion (AIC) were used for model selection. Finally, we applied Ripley's K function (r) to analyze the spatial patterns of *Polylepis* trees. For univariate point patterns, a simulation envelope of L(r) was developed through Monte Carlo simulations based on a homogenous Poisson process. For this purpose we used the nlme and spatstat packages in R (Baddeley et al. 2018; Pinheiro and Bates 2018) while the spatial visualization of the basal area was done using the gridExtra, cowplot and ggplot2 packages (Auguie and Antonov 2017; Wickham and Chang 2016; Wilke 2017).

Results

Dasometric structure and allometry

Stem density in the eight studied forests varied from 595 stems/ha (Tasta) to 2735 stems/ha (Quilcaycocha) (Table 2). All forests showed a typical decline in frequency of individuals with increasing stem diameter at sizes >10 cm, but with marked differences in the lower size classes (Table 2). Thus, whereas most forests had few individuals <10 cm DGL, the two forests of *P. rodolfo-vasquezii* had the highest frequencies in this class. In accordance with this, the forests of this species had the lowest mean stem diameters, whereas the forests of *P. canoi* had the highest values (Table 2). Also, *P. canoi* showed differences of diametric classes among its populations, ranging from 595 stems/ha at Tasta to 1070 stems/ha at Llantaco (Table 2).

The forests of *P. canoi* showed significant heterogeneity of TH and DGL between localities, with the highest DGL at Tasta and the highest TH at Tasta and Nahuin (Figure 2, Table 3). The two forests of *P. rodolfo-vasquezii* presented similar patterns in DGL, but not in TH. In contrast, these dasometric variables were different in the two *P. flavipila* forests,

Table 2. Localities and evaluated species, area of the forests, density of trees per hectare, percentage of individuals according to diameter classes, and vegetation cover in plots of 10x10 m.

Tabla 2. Localidades y especies evaluadas, área de los bosques, densidad de árboles por hectárea, porcentaje de individuos según las clases de diámetro y cobertura vegetal en parcelas de 10x10 m.

Tree species	Locality	Forest area (ha)	Density (stems/ha)	Stems ≥1–≤9.9	Stems ≥10–≤19.9	Stems ≥20–≤29.9	Stems ≥30–≤39.9	Stems ≥40
						DGL (cm)		
P. canoi	Tasta	5612	595	-	5.88%	15.12%	26.89%	52.11%
	Nahuin	28421	800	10.00%	32.50%	25.00%	23.12%	9.38%
	Jucha	5895	885	28.82%	54.24%	15.82%	0.56%	0.56%
	Llantaco	10919	1070	31.31%	62.15%	6.07%	0.47%	-
P. rodolfo-vasquezii	Paucho	14952	2635	77.60%	18.22%	4.18%	-	-
	Quilcaycocha	3039	2735	83.73%	11.88%	4.39%	-	-
P. avipila	Shaitura	189835	960	50.52%	31.25%	10.94%	7.29%	-
	Chaqsii-Chaqsii	44225	1135	33.04%	63.44%	2.64%	0.88%	-

Table 3. DGL and TH of three *Polylepis* species at eight localities. Different letters are significantly different at *P*≤0.05 with Tukey's test after GLMM.

Tabla 3. DNS y AT de tres especies de *Polylepis* en ocho localidades. Las diferentes letras son significativamente diferentes a *P*≤0.05 con la prueba de Tukey después del análisis GLMM.

| Species	Variable	Locality	Estimate	SE	t value	Pr(>|z|)	Tukey
P. canoi	DGL	Tasta	40.8	±2.26	12.03	<2e-16	a
		Nahuin	24.7	±1.36	5.65	1.58E-08	b
		Jucha	15.9	±0.88	49.69	<2e-16	c
		Llantaco	14.5	±0.81	-1.15	0.251	c
	TH	Tasta	8.1	±0.23	6.89	1.71E-11	a
		Nahuin	8.1	±0.21	7.11	3.73E-12	a
		Jucha	6.1	±0.17	64.51	<2e-16	c
		Llantaco	6.8	±0.18	2.78	0.005	b
P. rodolfo-vasquezii	DGL	Paucho	14.9	±0.62	63.85	<2e-16	a
		Quilcaycocha	16.4	±0.71	1.66	0.096	a
	TH	Paucho	5.7	±0.13	43.35	<2e-16	a
		Quilcaycocha	4.2	±0.14	-7.79	3.01E-08	b
P. flavipila	DGL	Shaitura	16.2	±0.92	2.34	0.019	a
		Chaqssi	13.5	±0.72	46.74	<2e-16	b
	TH	Shaitura	5	±0.44	4.06	4.99E-05	a
		Chaqssi	3	±0.28	12.03	<2e-16	b
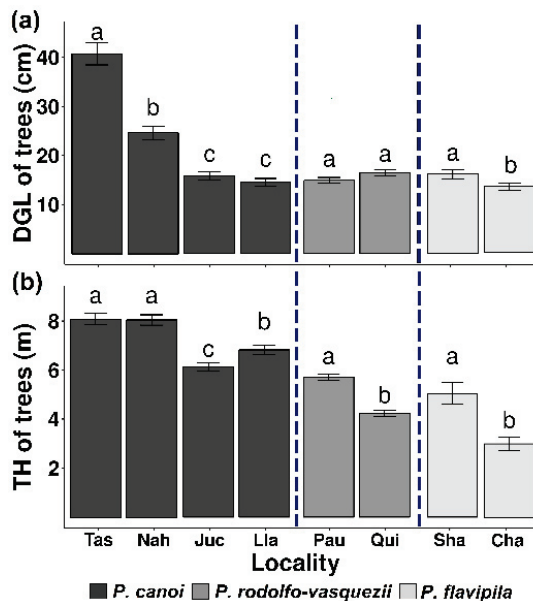
Figure 2. Comparisons of the forest structure between localities of the same species. (a) DGL of trees. (b) TH of trees. Different letters are significantly different at *P* ≤ 0.05 as per Tukey's test after GLMM. Error bars represent the 95% confidence intervals. Localities abbreviations: Pau=Paucho; Qui=Quilcaycocha; Cha=Chaqsii-Chaqsii; Sha=Shaitura; Lla=Llantaco; Juc=Jucha; Tas=Tasta; Nah=Nahuin.

Figura 2. Comparaciones de la estructura forestal entre localidades de la misma especie. (a) DNS de los árboles. (b) AT de árboles. Diferentes letras son significativamente diferentes a *P* ≤ 0.05 según la prueba de Tukey después del análisis GLMM. Las barras de error representan los intervalos de confianza al 95%. Abreviaturas de las localidades: Pau=Paucho; Qui=Quilcaycocha; Cha=Chaqsii-Chaqsii; Sha=Shaitura; Lla=Llantaco; Juc=Jucha; Tas=Tasta; Nah=Nahuin.

Table 4. Statistical analysis of the Logistic, Gompertz, Schumacher and linear mathematical models.

Tabla 4. Análisis estadístico de los modelos matemáticos Logísticos, Gompertz, Schumacher y lineal.

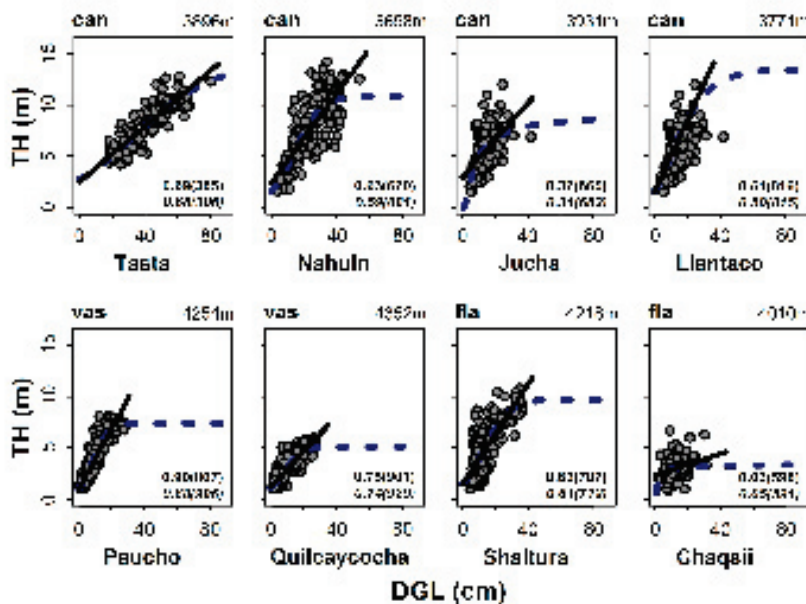| Species	Locality	Formula	Parameter	SE	t-value	R^2	AIC
P. canoi	Tasta	Logistic	a=14.19	1.91	7.44	0.69	385
			b=4.21	0.5	8.4		
			c=0.04	0.01	4.78		
		Linear	a=2.50	0.37	6.77	0.68	386
			b=0.14	0.01	15.9		
	Nahuin	Logistic	a=10.93	0.51	21.61	0.63	670
			b=5.98	1.47	4.08		
			c=0.13	0.02	6.22		
		Linear	a=2.42	0.37	6.48	0.59	681
			b=0.22	0.01	15.33		
	Jucha	Schumacher	a=2.23	0.05	41.27	0.37	665
			b=-6.41	0.7	-9.12		
		Linear	a=2.98	0.31	9.7	0.31	682
			b=0.18	0.02	9		
	Llantaco	Gompertz	a=13.48	2.57	5.23	0.51	816
			b=0.77	0.08	10.06		
			c=0.08	0.02	3.58		
		Linear	a=1.56	0.32	4.85	0.5	815
			b=0.35	0.02	14.68		
P. rodolfo-vasquezii	Paucho	Logistic	a= 7.40	0.14	53.92	0.9	867
			b=6.27	0.2	31.01		
			c=0.21	0.01	30.77		
		Linear	a=0.92	0.04	22.12	0.88	996
			b=0.30	0.01	62.12		
	Quilcaycocha	Logistic	a= 5.15	0.17	30.54	0.75	901
			b=3.56	0.14	24.88		
			c=0.17	0.01	14.58		
		Linear	a=1.18	0.04	32.41	0.74	929
			b=0.17	0.01	39.56		
P. flavipila	Shaitura	Logistic	a=9.76	0.69	14.09	0.63	707
			b=5.38	0.7	7.72		
			c=0.13	0.02	6.89		
		Linear	a=1.45	0.21	6.82	0.61	712
			b=0.24	0.01	17.57		
	Chaqsii-Chaqssi	Schumacher	a=1.22	0.06	22.11	0.03	598
			b=-1.48	0.56	-2.65		
		Linear	a=2.32	0.17	13.28	0.05	591
			b=0.05	0.01	3.79		

Figure 3. Diameter at Ground Level (DGL) and Total Height (TH) relationships for three *Polylepis* species at eight locations in Perú. Numbers are R^2 values followed by AIC values in parentheses, for non-linear models (upper numbers, dashed lines) and linear models (lower numbers, solid lines). Abbreviations of the Species: can=*P. canoi*; vas=*P. rodolfo-vasquezii*; fla=*P. flavipila.*

Figura 3. Relaciones entre el diámetro al nivel del suelo (DNS) y la Altura Total (AT) de tres especies de *Polylepis* en ocho localidades del Perú. Los números son valores R^2 seguidos de valores AIC entre paréntesis, para modelos no lineales (números superiores, líneas discontinuas) y modelos lineales (números inferiores, líneas continuas). Abreviaturas de las especies: can=*P. canoi*; vas=*P. rodolfo-vasquezii*; fla=*P. flavipila.*

with TH being higher at Shaitura (Figure 2, Table 3).

Considering the relationship of TH to DGL (Figure 3) in the four forests of *P. canoi*, the non-linear models performed worse than the linear models, showing that there was no saturation of tree height with increasing diameter. According to the extrapolation of the allometric models, *P. canoi* can grow up to an approximate average height of 14 m (Table 4). The same pattern was observed in the forests of *P. flavipila* and *P. rodolfo-vasquezii*. Although the Chaqsii-Chaqsii forest of *P. flavipila* showed a low coefficient of determination when compared to Shaitura, this was due to the loss of altimetric classes in the forest (Figure 3). On the other hand, well-distributed stretches of young and mature trees in the *P. rodolfo-vasquezii* forests led to high coefficients of determination (0.75 and 0.90). According to the adjusted parameters of the nonlinear equation, the species would grow up to an approximate average height of 7.4 m under the environmental conditions of Paucho and Quilcaycocha (Table 4).

Environmental variables

For *P. canoi* forests, no patterns were observed in the soil parameters associated with the

dasometric characteristics, even though the Tasta locality presented the highest values of annual precipitation (Figure 4), which coincided with the highest averages of DGL and TH (Figure 2). On the other hand, the *P. rodolfo-vasquezii* forests showed significant differences in elevation and precipitation, but not for the soil variables (Figure 4). Finally, in *P. flavipila* forests, Shaitura had the highest values of elevation, precipitation, organic matter and total nitrogen (Figure 4). These variables coincided with the highest averages of DGL and TH, with respect to the Chaqsii-Chaqsii forest (Figure 2).

Spatial distribution patterns

According to the univariate analyses of Ripley's K function, the *P. rodolfo-vasquezii* forests showed an aggregated pattern due to the high presence of young trees with diameters between 1-10 cm (Figure 5e, f). Conversely, the other two species showed random spatial distribution patterns. *P. flavipila* showed a tendency towards aggregation up to a distance of 1.5 m, but at greater distances the curve remained within the confidence limits with tendencies towards random distribution at the Chaqsii-Chaqsii locality (Figure 5h). This phenomenon was due to the presence of multi-
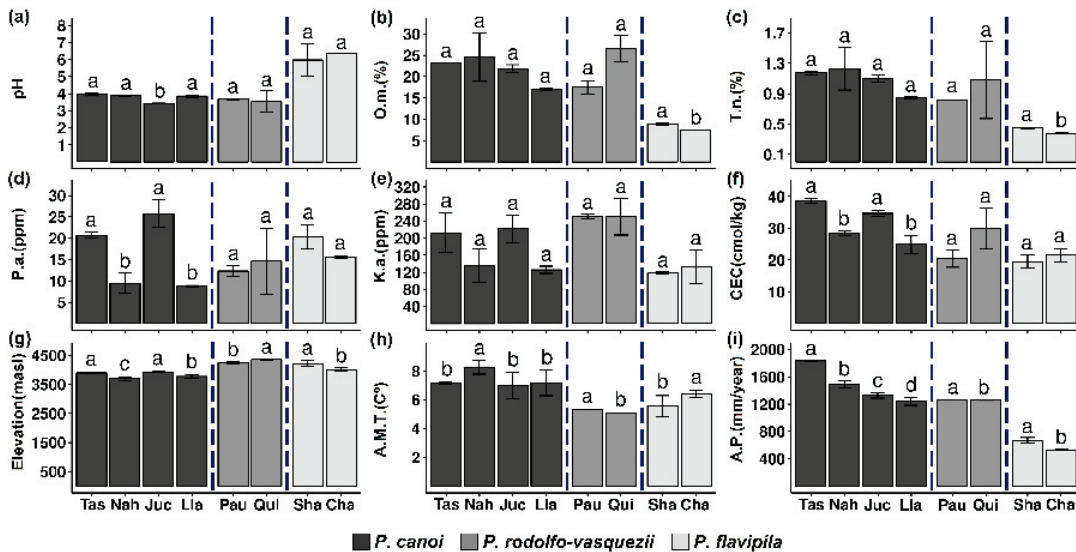

Figure 4. Edaphological and climatic variables of the *Polylepis* forests in central Perú. (a) Soil pH; (b) Organic matter percentage=O.m. (%); (c) Total nitrogen percentage=T.n. (%); (d) Phosphorus availability=P.a. (ppm); (e) Potassium availability=K.a. (ppm); (f) Cation exchange capacity=CEC (cmol/kg); (g) Elevation (m a. s. l.); (h) Annual mean temperature=A.M.T. (°C); (i) Annual precipitation=A.P. (mm/year).

Figura 4. Variables edafológicas y climáticas de los bosques de *Polylepis* en el centro del Perú. (a) pH del suelo; (b) Porcentaje de materia orgánica=M.o. (%); (c) Porcentaje total de nitrógeno=N.t. (%); (d) Disponibilidad de fósforo=D.p. (ppm); (e) Disponibilidad de potasio=D.k. (ppm); (f) Capacidad de intercambio catiónico=CIC (cmol/kg); (g) Elevación (m s. n. m.); (h) Temperatura media anual=T.M.A. (°C); (i) Precipitación anual=P.A. (mm/año).
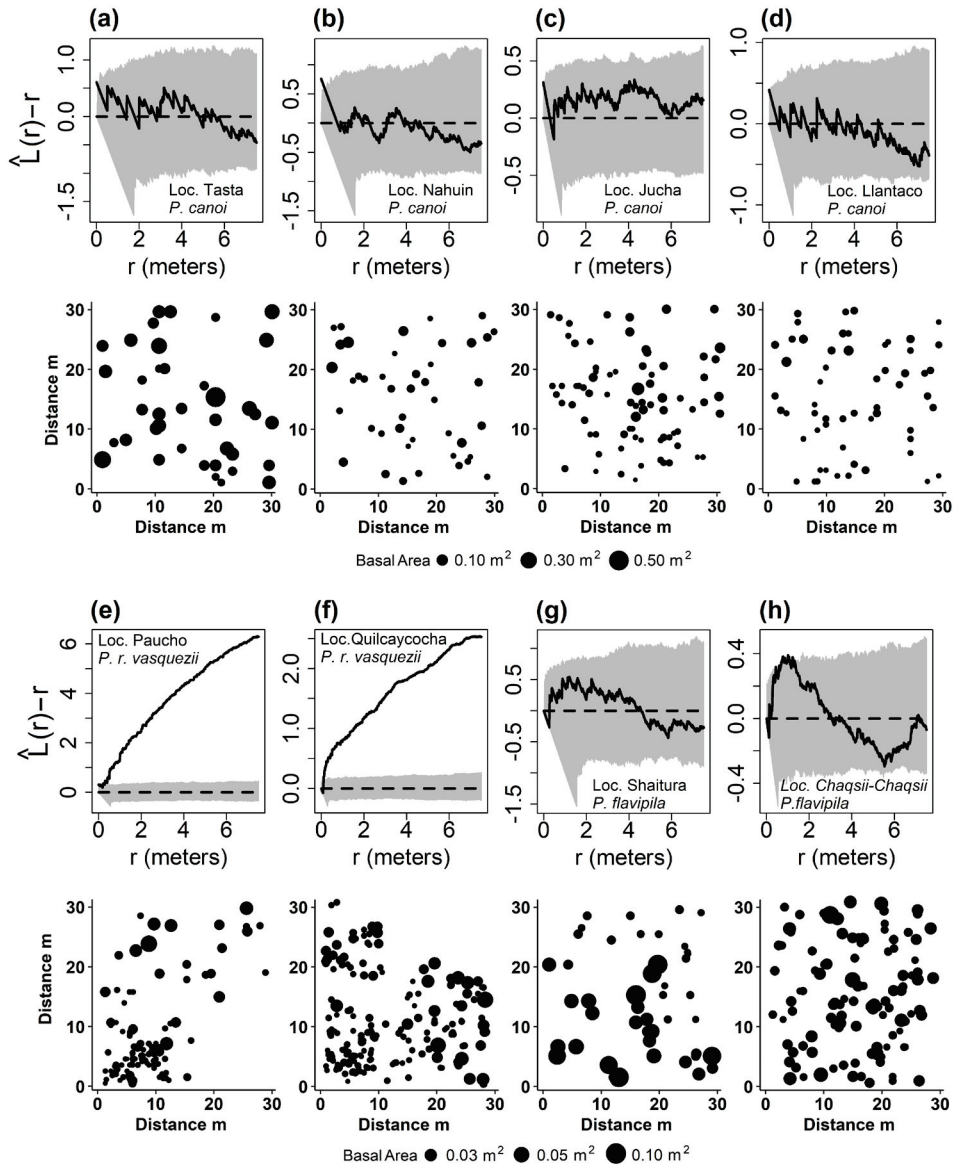
Figure 5. Spatial patterns according to the univariate Ripley's K function (r) and spatial distribution of the trees basal area in 30x30 m plots. *Polylepis canoi* and *P. flavipila* presented random spatial patterns, whereas *P. rodolfo-vasquezii* had an aggregate distribution.

Figure 5. Patrones espaciales por la función K de Ripley univariado (r) y distribución espacial del área basal de árboles en parcelas de 30x30 m. *Polylepis canoi* y *P. flavipila* presentan patrones espaciales aleatorios, mientras *P. rodolfo-vasquezii* presenta una distribución agregada.

stemmed trees with several basal ramifications (Figure 5h).

DISCUSSION

Comparing the forest structure of eight forest stands of three endemic *Polylepis* species in central Perú, we found differences in the dasometric structure of forests of the same species, but not in their patterns of spatial distribution. We also found that there was no

saturation of the height with the increasing diameter of the trees for all localities.

The *Polylepis canoi* forests of the Tasta and Nahuin localities were characterized by much taller and thicker trees compared to the two other localities. It could be argued that at these localities the trees experience less severe growth conditions, with relatively higher temperatures and precipitation levels (Castro 2014; Mendoza 2005).

The forests of *P. canoi* were characterized by presenting a tall and dense structure limiting the amount of light in the forest understory and inhibiting the development of young seedlings (Morales et al. 2017), unlike a forest of *P. besseri* in which the absence of regeneration is due to a high degree of human impact (Martínez and Villarte 2009). Although the degree of anthropic impact in each forest was not measured, we recorded the presence of some human activities such as the presence of cattle, extraction of peat moss (*Sphagnum magellanicum*) and forest fires, which were accentuated in the Jucha and Llantaco localities (Orellana-Mendoza et al. 2016), according to our observations in the field.

The populations of *P. rodolfo-vasquezii* studied here had a greater presence of natural regeneration, which explains the dominance of the diametric categories between 1 cm and 10 cm (Table 2) and, in contrast, a very low density of mature trees, which could be an indicator of selective felling (Fernández et al. 2001). Similar patterns have been found in the closely related species *P. pepei* as a response to increasingly stressful environmental conditions at high elevations related to low temperatures, low precipitation and high radiation levels (Hertel and Wesche 2008). This could be the case of *P. rodolfo-vasquezii*, which registers low temperatures and is located at high elevations; however, the evidence of livestock and fires particularly in these forests would better explain this pattern (Table 1) (Cierjacks et al. 2007). Soil variables would not explain these patterns for the forests evaluated.

The dasometric characteristics of the *P. flavipila* forests were significantly different between sites. In the Shaitura forest we found trees with greater height and diameter as well as high concentrations of organic matter, total nitrogen and precipitation, suggesting that tree height was influenced by soil fertility and water availability. In addition, this locality is located at higher elevations than the Chaqsii-Chaqsii forest, which is otherwise fragmented by a road accentuating the effects of human impacts. On up to 48% of the tree individuals we also recorded the presence of the hemiparasite *Tristerix chodatianus* which affects the tops of the tallest trees, increasing the mortality rate of trees (Arizapana 2018; Camel et al.2019). Together, these factors may explain the loss of altimetric categories and consequently the low correlation between DGL and TH for this particular forest.

The allometric analysis of the relationship of DGL and TH showed that there was no saturation of tree height with increasing diameter. This suggests that all the forests evaluated were composed of young trees. Older trees which reach a growth saturation point were inexistent probably due to human activities of cutting, firewood extraction and fires, which alters the dasometric and spatial structure of the forests (Kessler et al. 2014).

Focusing on the spatial distribution of *Polylepis* individuals at a small spatial scale, we found both random and aggregated patterns. *Polylepis rodolfo-vasquezii* presented an aggregated distribution with small trees more clustered than the larger trees (Cierjacks et al. 2007; Hertel and Wesche 2008). On the other hand, the forests of *P. flavipila* and *P. canoi* presented a random distribution, presumably related to tolerance to shade, intraspecific competition and seed dispersal. At Chaqsii-Chaqsii, *P. flavipila* showed an aggregate pattern at distances of 1.5 m as a result of trees with basal branching (Camel and Castañeda 2018). In previous studies at somewhat larger spatial scales, *P. racemosa* and *P. subsericans* were found to have aggregated spatial distributions associated to soil moisture and depth, in addition to rock cover (Hurtado 2014). At even larger scales, a study of geostatistics in *P. flavipila* forests showed a loss of the spatial dependence of basal area in an entire forest as a result of the heterogeneity of the habitat and anthropic effects such as overgrazing and logging (Castañeda et al. 2017). It is thus evident that the spatial structure of the *Polylepis* forests is not only influenced by the heterogeneity of the Andean topography, local micro-climatic variations, anthropogenic disturbances, diseases, phenology and ecological adaptations of the different species (Du et al. 2017; Hurtado 2014; Sylvester et al. 2017), but also that such relationships are scale-dependent.

CONSERVATION IMPLICATIONS

The three *Polylepis* species we studied are red-listed (Mendoza and León 2006; Valenzuela and Villalba 2015). For the first time, we provide forest and species specific data on tree density, dasometric and spatial patterns which may be used as reference values for reforestation programs which aim at reconstructing forests with a semi-natural structure as here reported.

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