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Leaf Litterfall and Decomposition of *Polylepis reticulata* in the Treeline of the Ecuadorian Andes

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*Leaf litterfall contributes significantly to carbon fluxes in forests. A crucial open question for the sustainability of mountain forests is how climate change will affect this and other carbon fluxes (*eg *photosynthesis and respiration). Leaf litterfall and decomposition of* Polylepis reticulata*, an endemic species of the Andes, were analyzed during a period of 1 year at 6 experimental plots located in the Andean* páramo *between 3700 and 3900 m above sea level in Cajas National Park, Ecuador. Litterfall was collected in each plot using 5 randomly distributed traps. Every trap had a 40-cm diameter (0.125 m^2) and was suspended 0.8 to 1.0 m above the ground. The decomposition rate of the leaf litter was analyzed using litter bags. Eighteen bags with approximately 20 g of dry litter were placed in the litter layer in each experimental plot and collected 30, 60, 90, 150, 210, 300, and 365 days after they were installed. The mean annual litterfall recorded was 3.77 Mg ha^{-1}, representing 51% of the leaf biomass present in the canopy, so the leaf life span of* P. reticulata *in Cajas National Park is 1.98 years. Litterfall occurred all year, with no significant seasonal pattern. The mean decomposition rate (*k*) obtained for this study period was 0.38 $year^{-1}$. This study contributes to the information gap on litterfall and decomposition in natural forests located at the highest elevations in the world.*

Keywords: Polylepis reticulata*; litterfall; decomposition; Ecuadorian Andean highlands; Cajas National Park.*

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Introduction

Polylepis reticulata, an endemic threatened tree species of the Central Andes (Goldstein et al 1994; Romoleroux et al 2008), is distributed throughout Ecuador and in some remote areas in northern and central Peru (Mendoza and Cano 2011; Zutta et al 2012). Growing at elevations between 2850 and 4300 m above sea level (masl) (Romoleroux and Pitman 2004), this woody angiosperm forms one of the world's highest treelines (Goldstein et al 1994; Toivonen 2014) and is vulnerable to extinction according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Romoleroux and Pitman 2004). Presently, the *Polylepis* forests of the Andean highlands represent one of South America's most endangered forest ecosystems (Hensen et al 2011), primarily because of continued defragmentation and anthropogenic activity (Hensen 2002; Kessler 2002).

Highland mountain areas are more sensitive to variations in climate conditions and are expected to experience stronger temperature fluctuations in the future than other parts of the planet (Beniston 2003). Treelines have therefore been proposed as potential indicators of the response of ecosystems to climate change (Kimball and Weihrauch 2000). Regional climate models project changes in temperature and precipitation patterns, which would affect ecosystem processes such as net primary production (NPP) and respiration (Melillo et al 1993; Cao and Woodward 1998). Neither the intensity of these changes nor their direction (increase or decrease) is understood (Nemani et al 2003; Zhao and Running 2010). However, some phenological changes have already been observed (Walther et al 2002; Cleland et al 2007). Leaf life span, leaf litterfall, and decomposition rates are showing changes in different ecosystems across the globe (Zhang et al 2008; Chave et al 2010).

Litterfall and decomposition rates are influenced by factors such as latitude, elevation, rainfall, seasonal changes, vegetation density, and species composition (Williams-Linera and Tolome 1996; Lin et al 2004). During the coming decades, litterfall and decomposition are expected to experience profound changes in high mountain forests (eg because of climate change), which will in turn affect carbon fluxes and stocks in these sensitive forest ecosystems. The consequences of these carbon cycle changes may be significant in terms of the

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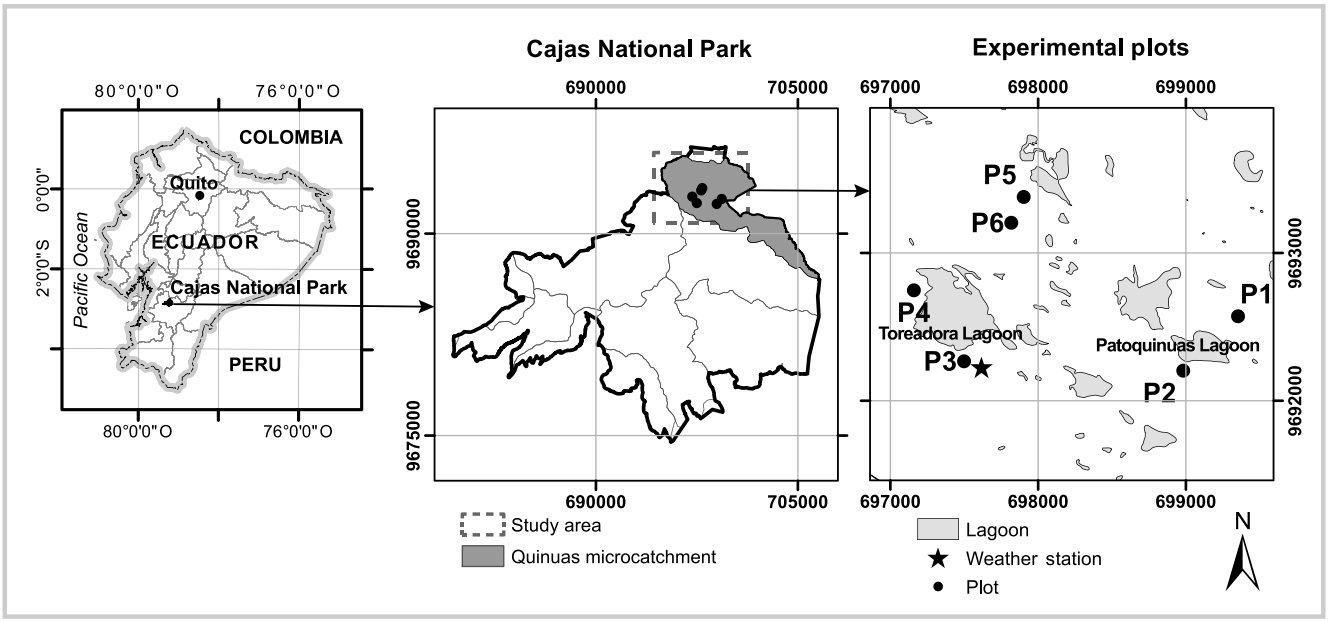
FIGURE 1 Location of the study area in the context of Ecuador and the PNC. (Map by Juan Pinos)



damage to some ecosystems, because more carbon is expected to feed water bodies. The economic costs of removing this carbon excess, say, from water in the scope of treatment processes (Feyen and Vázquez 2011) will also increase. In Ecuador, it is important to anticipate these changes and their social implications in a watershed such as Cajas National Park (PNC), which is the main source of water for the city of Cuenca, the country's third-largest city.

Previous forest studies have focused on distribution and taxonomy, hydrology, and biogeochemistry in Ecuadorian mountain ecosystems (Sklenář and Jørgensen 1999; Célleri and Feyen 2009; Homeier et al 2012), but litterfall and decomposition studies are lacking. The current study helps to address this gap by providing an analysis of leaf litterfall and decomposition rates at 6 patches of *Polylepis reticulata* located in the PNC, a representative region of southern Ecuadorian mountain *páramo* conditions.

This work was carried out as part of a multidisciplinary comprehensive study of *Polylepis reticulata* forest ecosystems that seeks to understand the structure, biomass, production, content, and circulation of bioelements in catchments of the Ecuadorian Central Andes. These studies are being developed in the context of a heuristic assessment of Ecuadorian Andean ecosystems conditions that is being implemented by the University of Cuenca, Ecuador, with the main objective of generating appropriate knowledge on the basis of which suitable management policies could be established. So far, a review of the literature suggests that this is the first study of litterfall and perhaps the second study on litter decomposition of *Polylepis reticulata* that has been implemented in the whole South American Andean region.

Methodology

Study area

The current study was conducted in the Quinuas River microcatchment within the PNC, 1 of Ecuador's 50 protected areas, located in the southern part of the country (Figure 1). The park spans 28,500 ha and hosts about 3800 water bodies, of which 150 are lakes larger than 2 ha. It is characterized by its unique geology, ecology, and geomorphology. Its position near the equator, high elevation (about 4500 masl at its highest point), and climate categorize the area as being Andean *páramo,* with a high daily thermal amplitude, high ultraviolet radiation, decreased oxygen concentration, and low atmospheric pressure (Bucheli 2008). Climatic conditions and the isolating effects of the mountains result in high rates of endemism (Bucheli 2008), which has led to the recognition of the Cajas area as a biodiversity hotspot (Myers et al 2000) and its designation as a national park to protect it from increasing anthropogenic pressure.

The current study was carried out from April 2014 to June 2015. Six 10×10 m^2 experimental plots were selected near the center of different forest patches to avoid any edge effect, which may affect the appropriate estimation of litterfall and decomposition rates (Sizer et al 2000). Sample plots were located at similar elevations (within the interval of 3735–3930 masl), but their slope and orientation varied significantly. As Table 1 illustrates, most plots were located on steep slopes characteristic of the study zone. Plots 4 and 6, however, were chosen in almost entirely flat areas to cover all topographic conditions.

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TABLE 1 Topographic characteristics of the study plots.

Plot ID	Latitude	Longitude	Elevation (m)	Slope (°)	Aspect (°)
1	2°46′48″S	79°12′24″W	3811	20	105
2	2°47′00″S	79°12′36″W	3841	25	30
3	2°46′58″S	79°13′24″W	3930	25	340
4	2°46′42″S	79°13′35″W	3890	0	110
5	2°46′21″S	79°13′11″W	3833	30	45
6	2°46′27″S	79°13′13″W	3735	3	85

Climate

Climate data for the period October 2012 to April 2015 were available from a weather station located in the central part of the study area. During this period, annual mean precipitation was 876 mm, annual mean reference crop potential evapotranspiration (ET_0) was estimated as 715 mm, and annual mean temperature was 5.44°C. The maximum recorded temperature was 17.2°C, while the minimum temperature was about −2.4°C. The average daily thermal amplitude was around 8.5°C (Figure 2). Because of the position of the sampling plots near to the equator, solar radiation is steady throughout the year. Hence, the annual solar radiation was about 4300 $MJ \cdot m^{-2}$, a relatively low value because of the frequent presence of clouds in the area.

Litterfall

Five 40-cm-diameter conical traps were placed randomly (but avoiding canopy gaps) in each plot. Each trap covered a surface area of about 0.125 m^2, with 2-mm mesh spacing, and was located 0.8 to 1.0 m above ground level. Litterfall was collected at intervals of 15 to 30 days over the course of 1 year. Litterfall samples collected after 30 days did not show any sign of decomposition. Samples were processed in the laboratory, where leaves were dried at a temperature of 85°C over 24 hours or until a constant weight was obtained. In addition to litterfall, leaf turnover rate was calculated with leaf biomass present in the canopy in relation to leaf fall value.

Litter decomposition

The litter bag technique was used to estimate the decomposition rate (Bärlocher 2005). Bags (225 cm^2, with 2-mm mesh spacing) were filled with approximately 20 g of litter collected previously from the forest floor and dried in the laboratory as described earlier. The density of the initial litter placed in the bags was estimated using subsamples of the collected material. A total of 18 bags per plot were placed in the litter layer and covered with local litter and moss to reproduce natural conditions. The bags were placed in each plot on different dates between April and June 2014.

Randomly selected bags were collected 30, 60, 90, 150, 210, 300, and 365 days after they were installed. Three bags were removed 30, 60, 90, and 150 days after the installation date, when variation in leaf mass was greater. Two bags were removed at 210, 300, and 365 days after installation. The contents of the bags were dried in the laboratory at 85°C using a dry air oven for 24 hours or until a constant weight was achieved.

The litter decomposition rate (k) expressed per year was estimated using Olson's model (1963), which assumes a negative logarithmic function:

$$k = -\frac{\ln\left(\frac{m_1}{m_0}\right)}{t} \quad (1)$$

where m_0 is the initial weight (g m^{-2}) and m_1 is the final weight (g m^{-2}) at a given time interval t (Table 2).

Statistical analyses

Differences in litterfall between plots were tested using a one-way analysis of variance (ANOVA). All variables (topographic and structural) were grouped into 2 groups (higher and lower than the mean). Multiple linear

FIGURE 2 Daily thermal amplitude measured at a 2-m height from December 2012 to April 2015 at Toreadora Weather Station in the PNC.

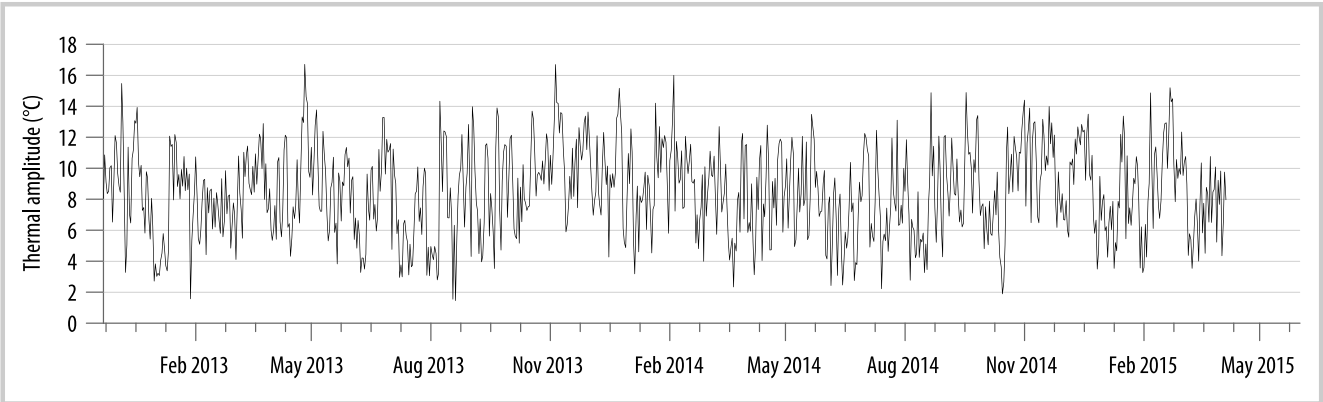

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TABLE 2 Structural variables, leaf litterfall, and decomposition rates at the 6 experimental plots.[a)]

Plot	Density (trees·ha^{-1})	Dbh ± SE (cm)	Basal area (m^2·ha^{-1})	LAI	SLW (g·m^{-2})	LB (Mg·ha^{-1})	Leaf litterfall (Mg·ha^{-1})	*k* (year^{-1})
1	8800	6.62 ± 0.34	61.11	3.29	163	5.36	4.16	0.40
2	1300	14.49 ± 2.35	28.20	2.60	177	4.60	3.39	0.37
3	2000	13.46 ± 1.80	38.10	3.51	195	6.84	4.65	0.33
4	1700	22.33 ± 1.93	74.55	3.30	226	7.46	3.45	0.33
5	3100	15.75 ± 0.96	67.13	6.17	173	10.67	4.17	0.44
6	7250	9.36 ± 0.38	54.12	4.90	202	9.90	2.78	0.40

[a)]SE, standard error; Dbh, diameter at breast height; LAI, leaf area index; SLW, specific leaf weight; LB, leaf biomass; *k*, decomposition rate.

regression was applied to explore the relationships between structural and topographic variables. Analysis of covariance (ANCOVA) was used to analyze differences in decomposition rates. All analyses were performed after normalizing the variables (using the statistical software SPSS v. 18).

Results

Litterfall

The average annual leaf litterfall recorded was 3.77 Mg·ha^{-1}. Litterfall occurred year-round (Figure 3) at a steady rate. Because of the constant climate conditions

FIGURE 3 Mean daily leaf litterfall measured in g·m^{-2}·day^{-1} (± SD) for the 6 forest plots of *Polylepis reticulata,* April 2014–June 2015. The litter traps were installed between April and June 2014. The initial points of the different plots vary according to the installation date.

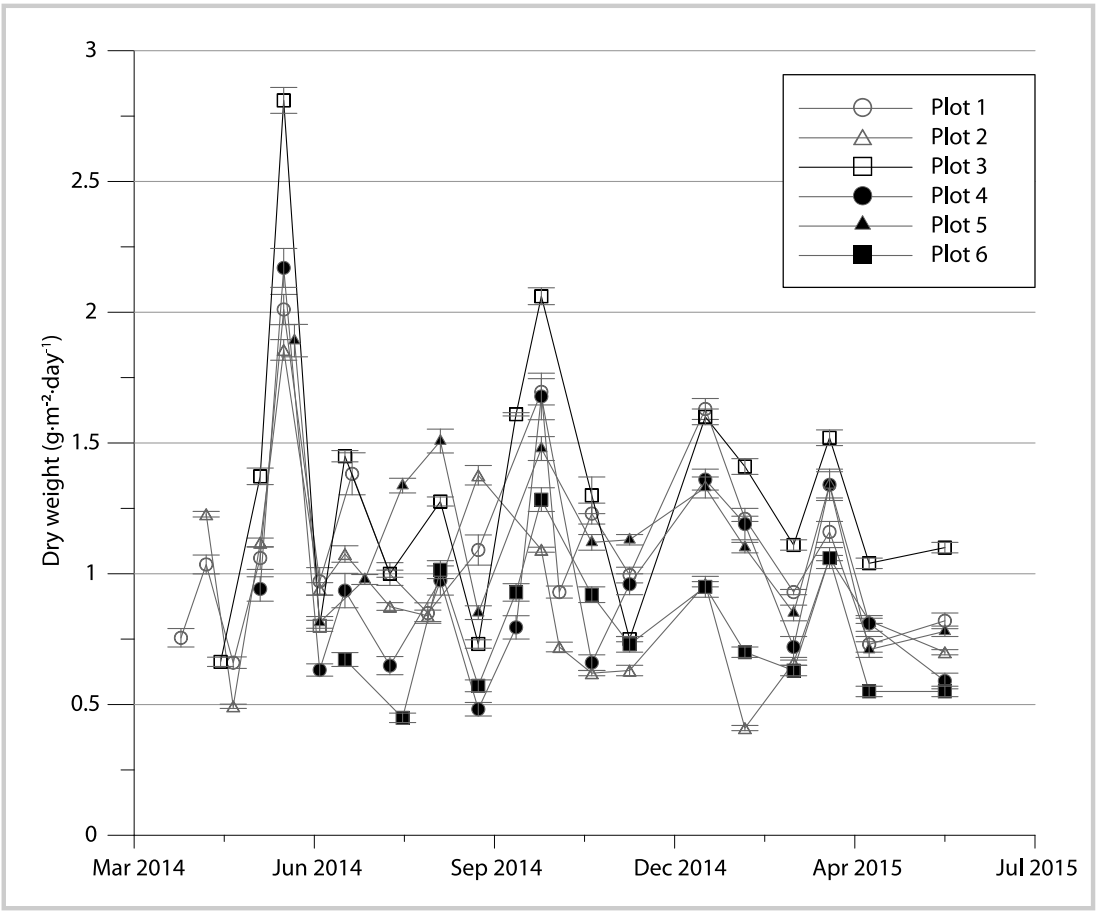

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TABLE 3 Results of the ANOVA for structural and topographic variables.

Variables[a)]	Grouping condition	Significance level ε [b)]	Result
Plots	Litterfall at each plot	0.034 (96.6)	Not significant
Structural variables			
Density (trees·ha^{-1})	>4500 <4500	0.099 (90)	Significant
Dbh (cm)	>15 <15	0.666 (33.4)	Significant
Basal area (m^2·ha^{-1})	>50 <50	0.233 (76.7)	Significant
Leaf area index (m^2·m^{-2})	>3.50 <3.50	0.004 (99.6)	Not significant
Specific leaf weight (g·m^{-2})	>190 <190	0.165 (83.5)	Significant
Leaf biomass (g·m^{-2})	>700 <700	0.543 (45.7)	Significant
Topographic variables			
Elevation (masl)	>3840 <3840	0.639 (36.1)	Significant
Slope (°)	>20 <20	0.024 (97.6)	Not significant
Aspect (°)	North South	0.543 (45.7)	Significant

[a)]All variables were grouped in 2 classes (higher and lower than the mean).
[b)]The significance level ε is indicated with the confidence level (as a percentage) in parentheses.

present in the study site throughout the year, litterfall did not show seasonality, although some variation was recorded. Maximum monthly litterfall took place in the months of May and October 2014, while the lowest leaf litter value was observed in April 2014, with values ranging between 2.12 g·m^{-2}·day^{-1} (end of May) and 0.60 g·m^{-2}·day^{-1} (April). On average, 51% of the leaf biomass in the canopy, estimated as 7.47 Mg·ha^{-1}, falls every year as leaf litter, resulting in a turnover rate of 1.98 years.

The ANOVA showed that litterfall is significantly related to all structural variables except leaf area index (Table 3). The differences in specific leaf weight in the different plots can explain this result. Among the topographic variables, altitude and aspect significantly affected the litterfall values, but slope did not.

Structural variables explain 37.8% of litterfall variance according to multiple linear regression analysis; topographic variables explain 34% of litterfall variance. The 2 sets of data together did not increase the explained variance because of the elevated correlation (r between 0.90 and 0.99) between both sets of parameters, because structural variables depend strongly on the topographical traits of the plots.

Litter decomposition

Figure 4 shows that leaf litter decomposition in all plots followed a logarithmic decomposition model as a function of the elapsed time since installation of the litter bags. The decomposition rate did not vary significantly as a function of the sampling plots ($\varepsilon = 0.017$), which accentuates the conclusions regarding the shape of the decomposition model. The leaves in the litter bags lost 30% of their original dry weight after about 1 year (from the installation date), with a decomposition rate of 0.38 year^{-1}.

Discussion

Litterfall

Treelines are established at higher elevations in the tropics compared to other latitudes. Studies on litterfall in forests above 3400 masl are rare, and forests at this elevation are concentrated near the equator in the Andes,

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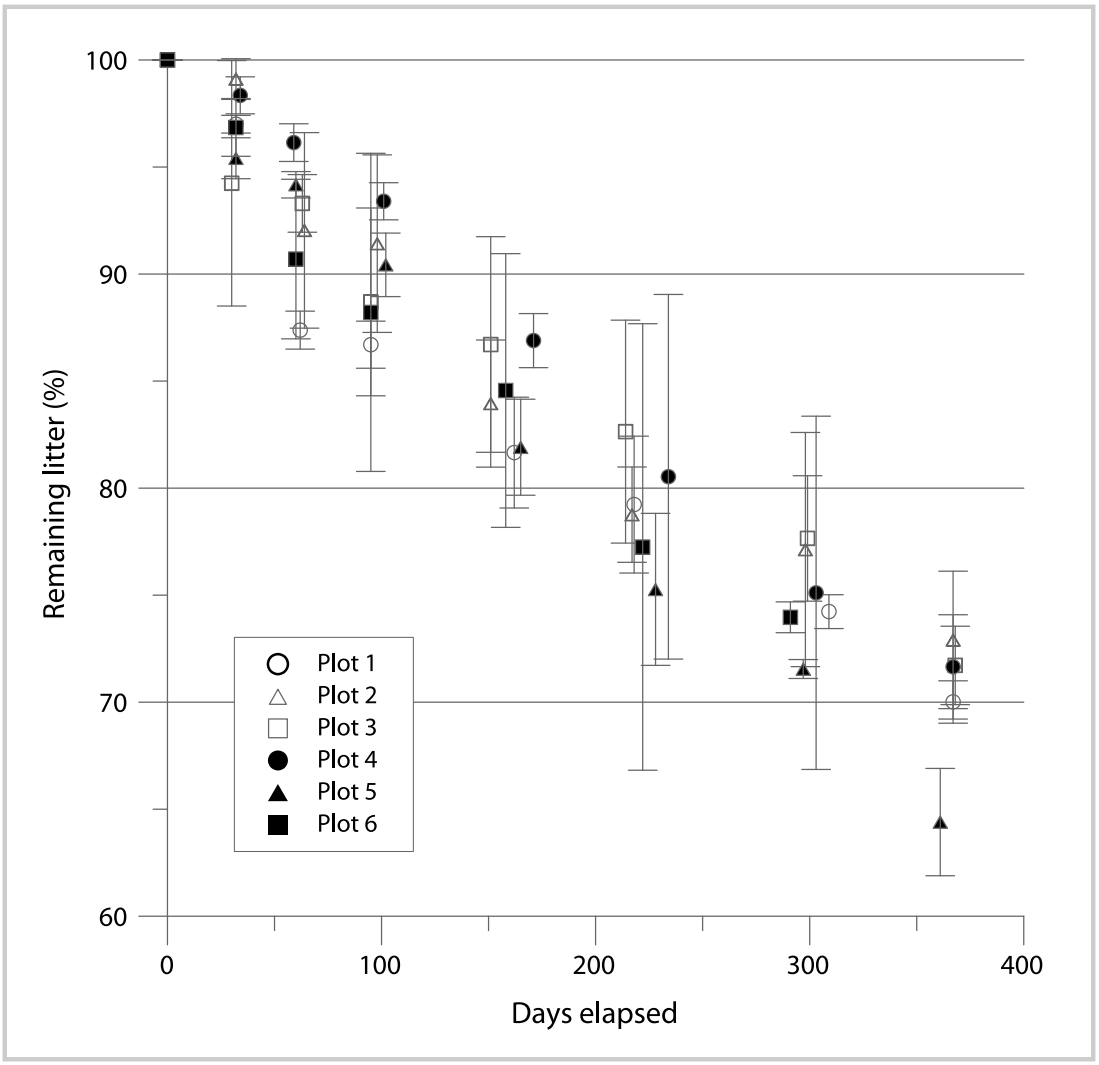
FIGURE 4 Litter decomposition (± SD) at the 6 experimental plots as a function of the elapsed days. The lack of the last point in plot 6 is because the corresponding bags were lost.



Southeast Asia (Indonesia, Malaysia, and Papua New Guinea), and East Africa. High-elevation treelines are also located in the Himalaya.

This study contributes to the knowledge regarding ecological processes like leaf litterfall and decomposition in forests dominated by *Polylepis reticulata,* which is one of the few species adapted to elevations above 3700 masl. The study was carried out between 3700 and 3900 masl and is one of the first studies of leaf litterfall in high Andean forests. Leaf litterfall depends directly on the leaf biomass present in the canopy, leaf life span, and associated turnover rate. Both litterfall and turnover rate are crucial to understanding the carbon fluxes in the forest and to monitoring how these fluxes respond to climate change.

It is not clear how litter production changes with elevation. Moser et al (2007) found that leaf area index and stand leaf biomass decrease along an elevational transect between 1050 and 3060 masl in tropical montane forests in southern Ecuador. Many authors have found that litterfall decreases with elevation at sites around the world (Heaney and Proctor 1989, Costa Rica; Veneklaas 1991, Colombia; Garkoti and Singh 1995, Central Himalaya; Kitayama and Aiba 2002, Borneo; Röderstein et al 2005, Ecuador; Girardin et al 2014, Peru; Moretto and Martínez 2014, Argentina; Zhou et al 2014, Eastern Asia). In contrast, Rana et al (1989) did not find any reduction in litterfall along an elevational gradient in the Central Himalaya. After processing data from 28 old-growth tropical forests, Clark et al (2001) concluded that litterfall does not change systematically with elevation. However, the 28 forests analyzed in this study were all located below 2500 masl. Röderstein et al (2005), despite finding variations in leaf litterfall with increasing elevation,

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carried out an analysis of 18 tropical mountain forests and found no significant statistical relationship between elevation and leaf litterfall.

Chave et al (2010) published a database of 81 forest sites across tropical South America, of which the mean leaf fall is about 5.74 $Mg \cdot ha^{-1} \cdot year^{-1}$. Takeda (1996) gave a range of litterfall for tropical forests of 5 to 15 $Mg \cdot ha^{-1} \cdot year^{-1}$. These values are clearly higher than the annual leaf litterfall value reported herein (3.77 $Mg \cdot ha^{-1} \cdot year^{-1}$). The value reported in this study is similar to the value reported by Velez et al (1998) of 3.9 $Mg \cdot ha^{-1} \cdot year^{-1}$ for a *Polylepis quadrijuga* forest in a Colombian *páramo* at 3200 masl. Veneklaas (1991) obtained a total litterfall value of about 4.31 $Mg \cdot ha^{-1} \cdot year^{-1}$ for tropical mountain rain forests at 3370 masl in Colombia, where leaves represented about 65% of the total litterfall. Garkoti and Singh (1995) reported a leaf litterfall value of 1.67 $Mg \cdot ha^{-1} \cdot year^{-1}$ for a Himalayan forest located at 3300 masl. In a tropical upper mountain forest in Costa Rica situated at 2900 masl, Köhler et al (2008) found that leaf litterfall depends on the age of the forests, where forests 10–15 years old had an average litterfall value of 7.87 $Mg \cdot ha^{-1} \cdot year^{-1}$, 40-year-old forests had a value of 12.59 $Mg \cdot ha^{-1} \cdot year^{-1}$, and old growth forests had a value of 7.20 $Mg \cdot ha^{-1} \cdot year^{-1}$. In an Andean forest in Colombia located at 2400 masl, Ramírez-Correa et al (2007) obtained a value of 7.87 $Mg \cdot ha^{-1} \cdot year^{-1}$ (leaves represented 69% of the total litterfall). More similar to the conditions reported herein, Homeier et al (2012) reported a leaf litter value of 3.46 $Mg \cdot ha^{-1} \cdot year^{-1}$ for a tropical humid forest located at 2000 masl in the Andes of southern Ecuador. Also in southern Ecuador, Röderstein et al (2005) found a gradient of leaf litter in tropical montane forest from 8.62, to 4.33, and to 2.63 $Mg \cdot ha^{-1} \cdot year^{-1}$ at 1890, 2380, and 3060 masl, respectively. In this context, the values obtained in this study are comparable to those reported for mountain tropical forests and are slightly lower than most values reported for lower-elevation forests, suggesting a gradient in elevation; this contrasts with the opinion of Rana et al (1989) and Clark et al (2001), who did not find any relationship between litterfall and elevation. However, the current study did not explore this issue, particularly because these forests are located at higher elevations. Low temperature linked to high elevation can limit forest production (Bader et al 2007) and can explain the lower litterfall values derived from the current study.

Although some variation could be seen, litterfall was not seasonal because of the constant climatic conditions present in the study site throughout the year. Maximum monthly litterfall took place in the months of May and October 2014, whereas the lowest leaf litter value was observed in April 2014. The maximum leaf litter value was approximately 4 times greater than the minimum and occurred during a period of higher precipitation, which suggests that litterfall is strongly influenced by wind and rain.

Decomposition

Several studies have shown that litter decomposition rates decrease with elevation regardless of litter type and litter quality (Kitayama and Aiba 2002; Illig et al 2008; Salinas et al 2011; Moretto and Martínez 2014; Zhou et al 2014; Berger et al 2015). Many authors have concluded that decomposition rates vary as a function of temperature, moisture, and quality of litterfall material, as indicated by nutrient concentration and lignin content in the structural tissues (eg Garkoti and Singh 1995). Temperature is considered the overriding environmental factor affecting litter decomposition, although moisture limitation is also recognized as an important factor in many tropical and temperate regions (Salinas et al 2011). The nature of litter chemistry likely has a major influence on the decomposition rate (Zhou et al 2014). In the presence of extremely high or low temperatures, decomposition is inhibited (Witkamp 1966; Arguello 1991). According to Olson (1963), low temperatures in high mountain areas tend to retard biological activity, resulting in low rates of decomposition.

It is well known that soil moisture has a crucial effect on soil microbial activity and thus on the decomposition rates of organic matter. In this study, temperature was one of the main regulators controlling the litter decomposition rates (mean temperature throughout the year was around 5°C). This is the result of climate conditions linked to elevation. In the PNC, soils are constantly wet or even saturated as a consequence of the higher precipitation compared to evapotranspiration and the lack of seasonality because of the proximity to the equator. Moisture, which was not monitored in this study, is not a limiting factor in the study area.

The average k value calculated in this study (0.38 ± 0.02 y^{-1}) is lower than the values reported in previous studies: For example, the value is below the range of 0.5 $year^{-1}$ for Mediterranean forests to 2 $year^{-1}$ for tropical forests published by Álvarez (2001). Kitayama and Aiba (2002) reported k values of 0.87 $year^{-1}$ (site on sedimentary rock) and 0.44 $year^{-1}$ (site on ultrabasic rock) for tropical mountain rain forests in Borneo situated at 3100 masl. Rave-Oviedo et al (2013) found k values of 1.74 and 1.76 $year^{-1}$ for Andean forests in Colombia at elevations of 1800 to 2100 masl, values that are higher than the ones presented herein because of the higher average temperature (21.5°C) and the carbon-to-nitrogen (C/N) relationship that was found in their study. Salinas et al (2011) carried out a decomposition study along an elevational gradient in Peruvian forests; the respective k values ranged from 0.37 to 1.58 $year^{-1}$ across species. At the highest elevation (3025 masl), the mean k value was 0.426 $year^{-1}$. It is believed that this higher k value, in comparison to the result presented herein, is a result of the higher temperature and precipitation in their study zone (11°C and 1706 mm $year^{-1}$, respectively).

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The lower values found in the present study can be explained by the specific weather conditions of the PNC with higher elevation and therefore lower temperatures that reduce the k values. Nevertheless, lower decomposition rates have been found in the scope of studies such as that of Zhang et al (2008), which built a global database (considering data from 110 sites) of litter decomposition rates, resulting in 293 k values ranging from 0.006 to 4.993 year^{-1}.

The litter mass remaining in our bags after 1 year of decomposition was around 70%. A period of 1.82 years is needed to decompose half of the initial litter mass ($t_{50\%}$). Berger et al (2015) found similar decomposition rates in the Austrian Alps: a remaining weight of 65.3% (beech forest) and 64.6% (pine forest) after a period of 1 year and a loss of 54% (beech) and 50% (pine) after a period of 2 years. However, Mayor and Henkel (2006) noted faster decomposition rates for a tropical forest in Guyana, where only 35% of the litter remained after 1 year.

In the dry and cold conditions of the Chimborazo *páramo* (4000–4200 masl, 3.5°C, and 700 mm year^{-1}), Duchicela (2011) found a lower decomposition rate (0.22 year^{-1}) for *Polylepis reticulata*. The lower temperature and precipitation conditions compared to those found in the current study area can explain this lower k value. In the same study, the author analyzed the decomposition rate of 2 *Polylepis* species, *Polylepis pauta* (0.43 year^{-1}) and *Polylepis incana* (0.73 year^{-1}), for a site in the Inga *páramo* located at an elevation similar to that of the current study site (with precipitation of 1600 mm year^{-1} and an annual mean temperature of 5°C).

The chemical composition of leaves is also an important factor for understanding the decomposition process (Witkamp 1966). Sclerophyllous leaves always have lower decomposition rates than malacophyllous ones because of the higher content of cellulose and lignin. Specific leaf weight can be regarded as a sclerophyllous index (Garkoti and Singh 1995; Moro and Domingo 1996). *Polylepis* has sclerophyllous leaves (Fernández et al 2001); in this study, *Polylepis reticulata* has a specific leaf weight of 189 g·m^{-2}, which is relatively high. The high cellulose and lignin content contribute to reducing the rate of litter decomposition because of the difficulty of breaking down the carbon bonds (Fioretto et al 2005). This litter is not only resistant to physical factors but also supports smaller populations of decomposer microbes (Singh et al 1990).

Conclusions

In these Andean treeline forests, environmental conditions associated with high elevation drive litterfall and decomposition dynamics. As a consequence of the leaf life span of 1.98 years, a significant part of the carbon uptake in photosynthesis is allocated to renewing almost half of the canopy annually, which can contribute to explaining the low growth rate of these forests. How climate change will affect the litterfall and decomposition rates is still an open question, one that is crucial for understanding the sustainability of these mountain forests.

Global climate change is likely to increase decomposition rates where long-term warming occurs in the absence of moisture constraints. Suitable temperatures may accelerate litter decomposition by enhancing the metabolic activity of litter microbes. The response of the litter cycle to changes in temperature will affect rates of mineralization, nutrient supply, and hence the carbon cycle, especially in these mountain ecosystems.

This study contributes to the information gap on litterfall and decomposition in natural forests living at the highest elevations in the world. However, changes in litterfall and decomposition rates over elevational gradients have not been considered in this paper. Further studies about the variations in litterfall and decomposition along gradients are needed to better understand these processes. Further studies are also needed to clarify photosynthesis and respiration rates and to understand the factors limiting the growth of these forests (carbon uptake or meristematic activity).

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