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Forest degradation modifies litter production, quality, and decomposition dynamics in Southern temperate forests

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Introduction: Anthropic disturbances are driving unprecedented changes in forest ecosystem functions and biogeochemical processes, hindering the forests' benefits to society. Litter decomposition is one of the most critical processes that regulate forests' carbon and nutrient cycling. However, how forest degradation affects litter decomposition and elemental dynamics requires further examination. The main objective of this study was to evaluate the effect of forest degradation on the production and decomposition of litter and C,N, and P dynamics in a temperate forest in south-central Chile.

Methods: Litter traps and litter bags were installed in three Long Term Research Forest Plots (LTER) representing different conservation states: mature, secondary, and degraded *Nothofagus* forests.

Results and Discussion: The total litter input varied between 3.5 to 1.1 Mg ha^{-1} $year^{-1}$ in the mature and degraded forests, respectively. We found the highest lignin and nutrient levels in the degraded forest and the lowest in the mature forest. In the mature forest, 44% of the initial litter was decomposed, while in the degraded forest it only reached 7%. Decomposing litter showed the lowest C:N and C:P ratios in the mature forest most of the year. The balance between inputs and outputs yielded a more substantial litter accumulation in the mature forests.

Conclusion: Our results strongly suggest that anthropogenic degradation altered litter quality and nutrient dynamics while decreasing litter production and decomposition.

KEYWORDS
carbon, nitrogen, phosphorous, forest disturbance, nutrient mineralization

1 Introduction

Loss and degradation of forests are driving unprecedented changes in biodiversity and ecosystem functioning (1). A critical soil process is litter decomposition, which, together with litterfall, represents one of the most important pathways for the flow of nutrients in forests and soil fertility (2). Litter nutrient dynamics are closely related to the litter decomposition rate, which directly determines the nutritional status of the ecosystem (3). For this reason, research on litter decomposition has become a relevant aspect of the study of forest functioning (4). However, the effect of anthropogenic disturbance on these processes in natural forests has been poorly studied (5).

Litter decomposition rates depend on the interaction of three major factors: climatic conditions, litter quality, and soil organisms (6). Climate has been considered the main factor on a global scale as it directly affects decomposition rates through temperature and humidity (7). On a smaller scale, decomposition rates are strongly influenced by litter quality. Higher litter quality (i.e., high N, P), high N:P ratio, and low lignin concentrations and C:N led to a higher decomposition rate and mineralization (8–10). Soil organisms, such as bacteria, fungi, and fauna, mediate litter decomposition by degrading complex compounds such as lignin and cellulose. However, their contribution to decomposition at a local scale depends on their composition and abundance, which vary with litter quality and microclimate (1, 11).

Forest degradation due to human activities, like logging, livestock grazing, and fire, can directly or indirectly alter the composition and structure of forests (12). For example, a decrease in tree basal area, an increase in canopy opening, a change in species composition, and loss of species have been documented in degraded forests (1). These can modify the environmental conditions and litter quality due to the changes in species composition and traits (13). Since litter decomposition and dynamics are related to humidity and temperature, they can be affected by forest management and disturbances (14). Despite its relevance, the effect of anthropogenic disturbance on these processes in natural forests has been poorly studied. Studies have demonstrated that changes in microclimatic conditions associated with canopy openness have led to an increase in soil temperature and changes in humidity (15). In particular, it has been shown that higher temperatures and lower soil moisture in tropical secondary forests can lead to slower decomposition compared to primary forests (16). Similarly, other studies in disturbed tropical forests have reported a decrease in litter decomposition due to reduced biological activity in these forests (1, 13). However, the responses of decomposition rates and nutrient dynamics have proven to be challenging to predict, as decomposition rates have been reported to increase, decrease, or even remain unchanged in different forest ecosystem types across the world (5, 14, 15).

The *Nothofagus* forests of South America, which occupy from 37° S to around 55°S in Chile and Argentina (17), are a relevant component of the Andean landscape as they grow in areas with large-scale disturbances and at high altitudes that other species are unable to colonize. The *Nothofagus* genus is an ecologically significant group severely threatened by human activities that are endangering many of its species (18). The *These* forests have been strongly degraded by selective logging of tree individuals (19) and cattle grazing (12). These processes currently affect large extents of *Nothofagus* forests (20, 21). The effect of forest degradation on litter dynamics of *Nothofagus* forests is poorly understood. It has been documented that the clearing of *Nothofagus* forests in the extreme south of Chile can cause a decrease in litter production and an increase in decomposition rates due to the rise of surface temperature (15), while other studies report inconsistent trends in decomposition rates (22). In addition, litter nutrient cycling in more septentrional *Nothofagus* forests has been rarely evaluated as most studies have focused on well-preserved evergreen rainforests or colder temperate forests further south (~38°- 52° LS) or compared different litter qualities (23).

Hence, this study aims to assess the dynamics of litter stoichiometry, production, decomposition, and mineralization of C, N, and P in *Nothofagus* forests displaying different conservation states. We hypothesize that degraded forests have a significantly lower input of C, N, and P by litterfall, lower litter decomposition rate, and mineralization than better-conserved forests.

2 Methods

2.1 Study area

The study area corresponded to the Ranchillo Alto estate, located in the Andes foothills, 33 km away from the town of Yungay, Ñuble Region (37°04' S and 71°39' W) (Figures 1A, B). It has a humid temperate Mediterranean climate with an average annual rainfall of 3000 mm, with rains concentrated between May and September in the autumn and winter seasons. The mean annual temperature is 13.5°C, with July being the coldest month with a mean annual temperature of 3°C, and January is the warmest month with a mean of 22.5°C. The area presents an extended season of low temperatures, frequent frosts, snowfall, and the presence of snow for 3 to 5 months. The soils have been described and correlated to the Yungay series Pachic Melanudands (Andisols), formed from thick recent volcanic ashes deposited over a glacio-fluvial material. These soils are very deep and well-drained, with high organic matter content, dominant pseudo-crystalline mineralogy, and a silty loam texture (24, 25).

Nothofagus temperate forests are documented to be the result of large-scale natural disturbances, including volcanic eruptions, landslides, and floods, and on small-scale disturbances, such as windthrow (26, 27). When canopy gaps become large enough to foster seedling development, shade-intolerant species such as *Nothofagus alpina* (Poepp. & Endl.) Oerst. And *Nothofagus obliqua* (Mirb.) Oerst. Can recruit and establish secondary forests (28, 29).

The study plots are located at 1300-1400 m.a.s.l., with 10-20% predominant western-facing slopes. The dominating tree species corresponded to *Nothofagus* species, which formed nearly pure stands (Table 1). Due to different regimes in human disturbances, the three *Nothofagus* forests stands differed in terms of composition, structure, and conservation states i) mature forest of *N. dombeyi* (Mirb) Oerst., which represent a well-preserved forest form mainly by trees 10 to 20 m tall and with a majority diameter at breast height (DBH) between 16 to 52 cm, with individuals exceeding 100 cm DBH,

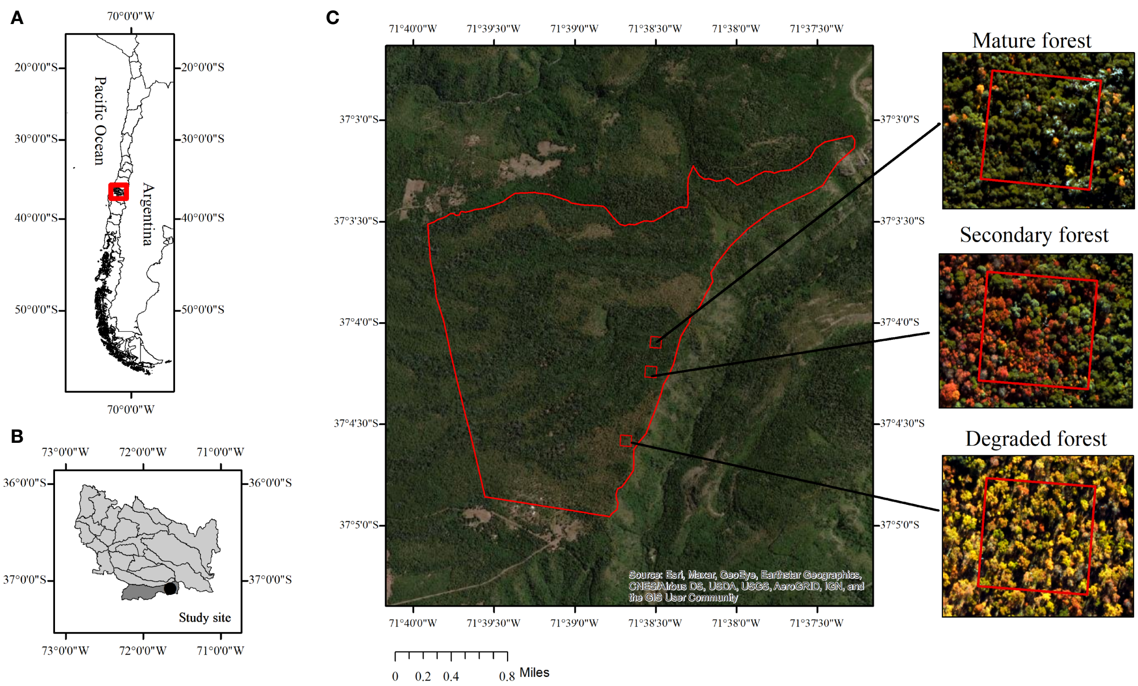

FIGURE 1
Map of Chile **(A)**. Location of the study area in central Chile **(B)** (black point). The red line shows the boundary of the Ranchillo Alto estate, and the red squares delineate the location of the Long-Term Research Forest (LTER) plots **(C)**. Image source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

and a composition of 97% perennial trees; ii) secondary forest of *N. alpina* originated from selective logging for firewood, charcoal, and timber since 1950, it has a composition of 48% evergreen and 52% deciduous trees; and iii) degraded forest dominated by *N. obliqua* altered by tree cutting, fire, cattle browsing, and grazing for approximately 65 years, which is composed of 100% deciduous trees (Figure 1C). Illegal intensive logging has occurred since the 1950s, affecting all *Nothofagus* forest stands, which can be verified by the presence of stumps across the area (Table 1). However, the degraded forest has experienced substantial felling of the largest and healthy tree individuals, yielding a largely coetaneous *N. obliqua* forest with a few smaller clusters of *N. dombeyi* trees. Forest regeneration in the degraded site has been further limited by fire and continuous and non-systemic grazing (21, 30). In 2015, a forest management plan began, gradually stalling illegal logging and regulating cattle grazing in the area.

2.2 Sampling design

Long-Term Ecological Research (LTER) plots of 100 x 100 m were established in each of the three forest stands. In each plot, we sampled litterfall and litter decomposition, for which sub-sampling plots were installed based on the GEM field manual (31) for intensive census plots, which are explained in detail below.

TABLE 1 Characteristics of the study forest stands in the LTER plots: mature, secondary, and degraded forests. Yungay, Chile.

Characteristics	Mature forest	Secondary forest	Degraded forest
Conservation status	Well preserved	Altered	Degraded
Composition[1]	*N. dombeyi* (97%) and *N. obliqua* (3%)	*N. dombeyi* (48%) and *N. alpina* (52%)	*N. obliqua* (100%)
Density (tree/ha)	572	610	136
Basal area (m^2/ha)	58.6	55.7	25.8
Tree stumps (N/ha)	26	84	18
Openness canopy (%)	10%	11%	52%
Leaf Area Index[2]	3.2 (0.06)	0.9 (0.02)	0.5 (0.04)
Soil temperature[2] (°C)	6.9 (0.3)	7.1 (0.2)	9.9 (0.4)
Soil moisture[2] (%)	22.9 (6.5)	21.9 (2.5)	15.8 (0.9)

[1]In parentheses is the percentage of dominance of each species
[2]In parentheses is the standard deviation.

2.3 Sampling of litter biomass

Twenty-five 20x20 m subplots were delimited in each LTER plot (Supplementary Figure 1). In each subsampling plot, a 1x1 m litter collection trap was placed in April 2018 (75 total traps). The collection was carried out monthly from December 2018 until December 2019. The collection of samples during July 2019 was suspended due to adverse climatic conditions that impeded fieldwork (i.e., snowfall). The biomass collected in each trap was stored in hermetic bags. The content was transferred to paper bags and placed on a convection stove at 65°C for 48 to 72 hours until a constant weight was reached. Subsequently, the dry weight of each sample was determined.

2.4 Sampling of litter decomposition bags

Sixteen 25x25 m subplots were established in each LTER plot. Twelve correlatively numbered decomposition bags were placed at the center of each subplot (576 total bags) (32). Recently fallen litter was collected directly from the forest floor in each LTER plot during April and May 2018. The litter was dried at 65°C to constant weight, and a homogeneous sample was generated per plot. An aliquot of approximately 10 ± 1 g was removed and placed in 20x20 cm 1 mm mesh bags. The bags were installed in November 2018 between the litter layer and the mineral soil, simulating natural litter decomposition processes. The litter bag collection started in December 2018, after which a bag of each subplot was collected monthly for a year. Each bag was independently stored in airtight bags until delivery to the laboratory, where the material was dried at 65°C until constant weight. Posteriorly, the decomposition rate (k) was determined with the exponential model described by Olson (33) using Eq. (1).

$$\boldsymbol{k} = \frac{-\ln(x_1/x_0)}{t} \quad (1)$$

Where X_0 are initial and X_1 final litter weight in a time t (33).

2.5 Remaining Litter stock

The remaining litter stock was calculated by subtracting the total annual decomposed litter to the annual input due to litterfall. The decomposed annual litter was calculated by multiplying the percentage of decomposed litter at the end of the study year by the annual input of litter. The remaining litter stock should approximate the total amount of litter remaining on the forest floor in each forest plot after a year.

2.6 Carbon, nutrient, and litter quality analysis

The carbon and nutrient content of the fallen litter and litter of decomposition bags was determined. An aliquot of the sampled material from each bag was taken at each sampling date and combined into a composite sample for each plot. These were pre-grounded in a chipper to 2mm and then pulverized in an 8000M Mixer/Mill® steel pearl mill from SPEX SamplePrep. Posteriorly 2.00 ± 0.1 mg of each sample in tin capsules were weighed in a Sartorius model ME36S microbalance (Sartorius AG, Germany). The total C and nitrogen (N) contents were determined by the Dumas-TCD dry combustion method (SERCON® Limited, UK). Total phosphorus (P) was determined by the calcination method for plant tissue described by Sadzawka et al. (34). With these results, we calculated C:N, C:P, and N:P on a mass basis for litterfall and decomposing litter. The lignin concentration was determined following the methodology used by Mendonça et al. (35). For this, extractables were removed with ethanol/toluene; then hydrolysis was carried out with 72% H_2SO_4 in a water bath at 30°C for 1 hour. The acid was then diluted to 3% with water, and the mixture was autoclaved for one hour at 121°C. The residual material was cooled and filtered, and the solids dried to constant weight at 105°C and determined as insoluble lignin. Soluble lignin was determined by measuring the absorbance of the solution at 205 nm (35).

Fourier-transform infrared (FTIR) band indices were calculated as a complementary measure to characterize litter quality. Index I (Eq. 2) have been used to indicate differences in the degree of decomposition. In this study, we used it to show the degree of aromaticity of the litter material (i.e., aromatic versus aliphatic bonds). Similarly, Index II (Eq. 3) was used as a proxy for organic matter recalcitrance (36). These indices are based on the intensities of the FTIR bands representing various functional groups, which are detailed below:

$$Index\ \ I = \frac{Aromatic\ \ functional\ \ groups\ \ area\ \ (bands\ \ 1650 + 920)}{Aliphatic\ \ functional\ \ groups\ \ area\ \ (bands\ \ 2924 + 2850 + 1470)} \quad (2)$$

$$Index\ \ II = \frac{C - functional\ \ groups\ \ area\ \ (bands\ \ 2924 + 2850 + 1650 + 1470 + 920)}{O - functional\ \ groups\ \ area\ \ (bands\ \ 3400 + 1080)} \quad (3)$$

According to Veum et al. (37), Index I is the ratio of aromatic C=C (bands 1650 and 920) to aliphatic and CH (bands 2924, 2850, and 1470) functional groups; this index has been shown to increase with the degree of soil organic matter decomposition. Index II represents relative recalcitrance as the ratio between C (bands 2924, 2850, 1650,1470 and 920) and O (bands 3400 and 1080) functional groups, which is higher in more recalcitrant organic matter (37). For this analysis, original litter samples used for the litter bags were ground in a chipper at 2 mm, milled, and analyzed in an FT-IR Spectrometer (Thermo Scientific, Nicole iS5) with attenuated total reflectance (ATR) and automatic baseline correction. Spectra were obtained in triplicates, each based on the mean of 64 scans at 4000–400 cm^{-1} with a resolution of 4 cm^{-1}. Based on the spectrum's prominent peaks and shoulders, seven bands representing organic functional groups were identified, and the indices I and II were calculated. Peaks were selected, and absorbance intensity was measured after background removal using Essential FTIR (v3.50.205).

2.7 Data analysis

Litterfall mass was compared between forest stands and through time by a non-parametric Kruskal-Wallis test, as normality was not met according to Shapiro-Wilk tests. If the Kruskal-Wallis test indicated at least one significant difference between groups, Wilcoxon signed-rank tests were used. The same approach was used to compare the mass of C, N, and P, for which the “RSTATIX” R (38) and the “CAR” R (39) packages were used. Indices I and II and initial concentrations of C, N, and P were compared using Welch’s T-tests because the data met the normality assumptions but not homoscedasticity.

The decomposition rate (k) was transformed to 1/k, fulfilling the normality and homogeneity assumption. An ANOVA was performed to identify significant differences in the *k-mean* values between forest types. Because significant effects of forest stands were found, a Tukey’s test was carried out. The remaining litter mass was compared with a Kruskal-Wallis test because the homogeneity assumption was met, but not normality. If this indicated at least one significant difference between groups, Wilcoxon rank-sum *post hoc* tests were performed, a non-parametric alternative to two-sample t-tests. All the statistical and graphic analyses were executed in R version 3.2.1 (40). Averages and standard error were reported in all the analyses, and $p< 0.05$ were considered significant.

3 Results

The initial concentration of N and P in the litter differed between forest stands, from lowest to highest: mature forest, secondary forest, and degraded forest. At the same time, the degraded forest had a significantly lower concentration of C and the highest concentration of lignin. Lignin was the lowest in the secondary forest (Table 2). The Index I was lower in the litter of both the mature and degraded forests, and highest in the secondary forest, indicating greater aromaticity of litter in the secondary forest. On the other hand, the Index II was higher in the mature and degraded forests, suggesting greater potential recalcitrance of the material compared to the litter of the secondary forest, which is consistent with its lowest lignin and total C contents (Table 2).

The annual litterfall ranged from 1.2 Mg ha$-^1$ year$-^1$ in the degraded forest to 3.8 Mg ha$-^1$ year$-^1$ in the mature forest (Table 3). Mature and secondary forests had a significantly higher litterfall than the degraded forest ($p< 0.05$). The three forest plots followed the same pattern of litterfall across the year, increasing during the autumn (Figure 2A) and with a minimum during the summer and spring months.

The C:N ratio of litterfall varied throughout the year and between forest plots, from lowest to highest: degraded forest, secondary forest, and mature forest (between March and August) (Figure 2B). The litterfall C:P and N:P ratios followed a similar tendency for all forest plots over time, with a considerable increase in spring between September and December (Figures 2C, D). The mature forest showed a sharper increment in C:P and N:P in spring than the other forest types; however, litterfall production during this period abruptly declined.

The amounts of litter C, N, and P inputs varied throughout the year and between forest plots (Figure 2E–G respectively). Annually, the total amount of C in the litter went between 528.1 and 1739.7 kg ha$-^1$ year$-^1$ for degraded and mature forests, respectively. Similarly, the quantity of N ranged from 10.3 kg ha$-^1$ year$-^1$ in the degraded forest to 26.2 in mature forest, and P from 0.37 kg ha$-^1$ year$-^1$ in the degraded forest to 0.97 in the mature forest (Table 3). The mean annual amount of C, N, and P contributed by the mature forest was significantly higher than the other forest stands ($p< 0.05$).

After one year, the remaining litter mass was 56% for the mature forest, 65% for the secondary forest, and 93% for the degraded forest. The decomposition constant (k) was significantly higher in the mature forest, followed by the secondary, which was also considerably higher than k in the degraded forest ($p< 0.05$). In the same way, the mass of remaining litter differed substantially between the forest conservation states (Table 4). Regarding temporal variation, the highest decomposition rates were observed in the first month after installation and in the last month, both corresponding to December, and varied significantly between forest plots (Figure 3A). In the case of secondary forest, a high decomposition rate was also observed in September (spring).

Decomposing litter total C decreased significantly over time in all forest plots, but this trend was more consistent in the mature and secondary forests. In the degraded forest, total litter C tended to

TABLE 2 The initial concentration of litter C, N, P, lignin and Index I and II in mature, secondary, and degraded *Nothofagus* forests LTER plots.

Forest type	C (%)	N (%)	P (%)	Lignin (%)	Index I	Index II
Mature forest	48.8 ± 0.5^a	0.85 ± 0.00^a	0.031 ± 0.0^a	42.6 ± 0.9^a	0.59 ± 0.04^a	1.88 ± 0.31^a
Secondary forest	49.1 ± 0.4^a	0.93 ± 0.01^b	0.034 ± 0.0^b	40.7 ± 0.9^b	0.86 ± 0.05^b	0.98 ± 0.05^b
Degraded forest	45.6 ± 0.1^b	0.98 ± 0.00^c	0.037 ± 0.0^c	45.4 ± 0.5^c	0.54 ± 0.08^a	1.79 ± 0.38^a

Different letters indicate significant differences ($p< 0.05$).

TABLE 3 Mean annual litterfall (Mg ha$-^1$ year$-^1$) and C, N and P (kg ha$-^1$) in mature, secondary, and degraded *Nothofagus* forests LTER plots from December 2018 to December 2019.

Forest type	Biomass (Mg ha$-^1$ year$-^1$)	C (kg ha$-^1$)	N (kg ha$-^1$)	P (kg ha$-^1$)
Mature forest	3.78 ± 0.32^a	1739.7 ± 153.8^a	26.2 ± 2.3^a	0.97 ± 0.08^a
Secondary forest	2.77 ± 0.28^b	1146.9 ± 130.9^b	19.1 ± 2.2^b	0.67 ± 0.07^b
Degraded forest	1.22 ± 0.17^c	528.1 ± 76.1^c	10.3 ± 1.5^c	0.37 ± 0.06^c

Different letters indicate significant differences ($p<0.05$).

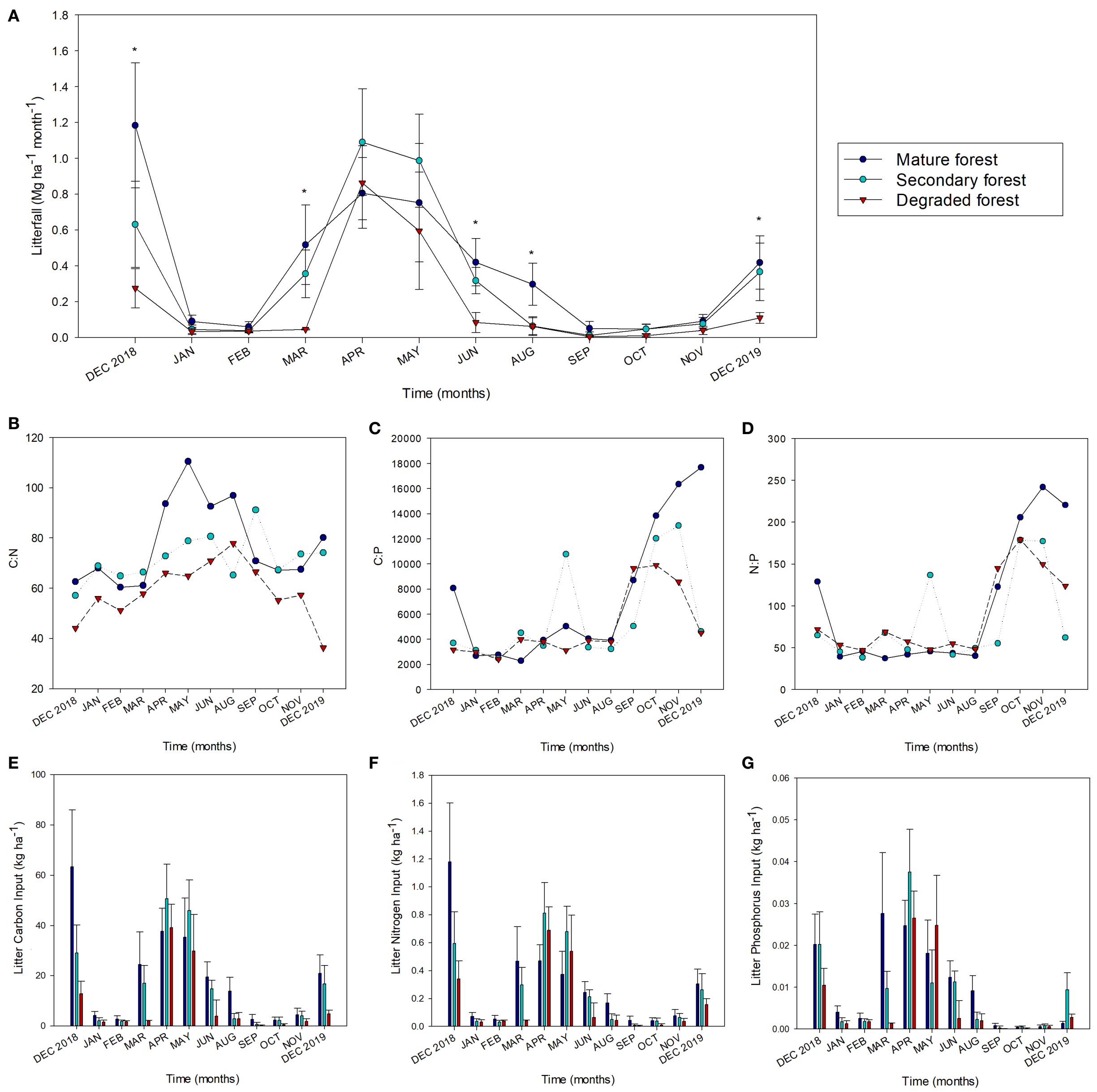

FIGURE 2
Litter biomass **(A)**, molar C:N **(B)**, C:P **(C)** and N:P **(D)** stoichiometric ratios, and Carbthe **(E)**, Nitrogen **(F)** and Phosphorous **(G)** average inputs from December 2018 to December 2019 in mature (dark blue), secondary (light blue), and degraded (red) *Nothofagus* forests LTER plots. For **(A, E, F, G)** the error bars represent the standard deviation. For A significant differences within each month are shown with an asterisk.

increase from May to November (Figure 3B). N presented an initial net accumulation in mature forest, which decreased towards the end of the year (Figure 3C). The secondary forest showed a slight decrease in N content. In contrast, in the degraded foresmount amount of N remained relatively constant between the beginning and the end of the study period. P increased substantially in the mature forest after the first month and stayed steady until the spring, when it dropped significantly until the end of the experiment (Figure 3D). On the contrary, litter P in the secondary and degraded forests dropped during the first month and then gradually increased until the spring when it fell significantly.

TABLE 4 Mean decomposition rate and remaining mass (%) after 390 days of decomposition in mature, secondary, and degraded *Nothofagus* forests LTER plots.

Forest type	Decomposition rate	Remaining mass (%)
Mature forest	0.00149 ± 0.00008[a]	56.62 ± 1.9[a]
Secondary forest	0.00112 ± 0.00010[b]	65.40 ± 2.6[b]
Degraded forest	0.00018 ± 0.00003[c]	93.23 ± 1.1[c]

Different letters indicate significant differences ($p< 0.05$).

The C:N on the decomposing litter was lower for the mature forest, intermediate for the degraded forest, and higher for the secondary forest (Figure 3E). There was a substantial decrease in the C:N ratio in the mature forest after the first month. Conversely, C: N ratios in the secondary forest increase abruptly after the first month and then gradually decrease until the end of the experiment (except

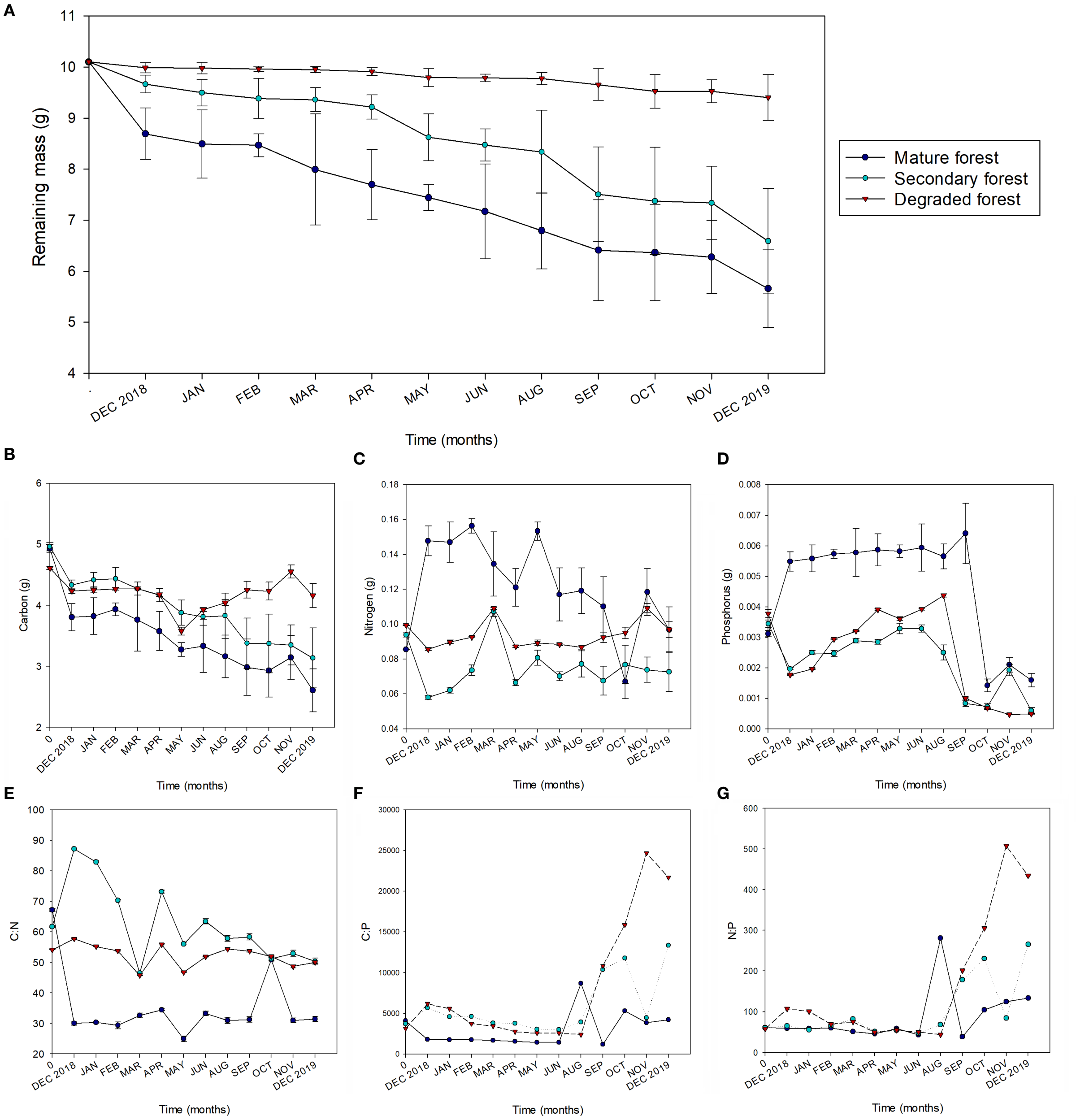

FIGURE 3
Remaining litter biomass **(A)**, mass of Carbon **(B)**, Nitrogen **(C)** and Phosphorus **(D)**, and molathe:N **(E)**, C:P **(F)** and N:P **(G)** stoichiometric ratios during litter decomposition from December 2018 to December 2019 in mature (dark blue), secondary (light blue), and degraded (red) *Nothofagus* forests LTER plots. For **(A–D)** the error bars represent the standard deviation.

for a substantial drop observed in March). Meanwhile, the values of the degraded forest were relatively constant between the start and the end of the experiment. The C:P and N:P ratios followed a similar trend over the evaluated period, with a differential increment in spring and summer among forest plots (Figures 3F, G).

Finally, the total balance between all inputs of litter and decomposition outputs indicates that the remnant stock of litter is 2.14 Mg ha^{-1} in mature forest, which represents 56.6% of litter inputs; 1.81 Mg ha^{-1} in secondary forest, equivalent to 65.3% of litter inputs; and 1.14 Mg ha^{-1} in the degraded forest, equivalent to 93.4% of litter inputs (Table 5).

4 Discussion

Our results support the hypothesis that a degraded forest has a lower nutrient input due to a lower litterfall and decomposition rate. However, contrary to our expectations, the chemical quality of the litter (i.e., nutrient stoichiometry) did not help explain this behavior. Nutrient contents were higher in the degraded forest than in the mature and secondary forest. Although this higher nutrient content did not lead to higher litter decomposition rates, probably due to its higher lignin concentration and the adverse abiotic conditions for decomposition to proceed, especially lower soil moisture (1, 13).

TABLE 5 Litter inputs, decomposition outputs, and remaining stock (Mg ha^{-1}) between December 2018 and December 2019 in mature, secondary, and degraded *Nothofagus* forests LTER plots.

Forest type	Inputs (Mg ha^{-1})	Outputs (Mg ha^{-1})	Stock remaining (Mg ha^{-1})
Mature forest	3.78	1.64	2.14
Secondary forest	2.77	0.96	1.81
Degraded forest	1.22	0.08	1.14

4.1 Litter production and C:N:P stoichiometry

The annual litterfall in forest types was within the observed range (1.0 to 5.8 Mg ha^{-1} yr^{-1}) for *Nothofagus* forests of central and southern Chile (22, 41), but it was slightly lower than the range observed in temperate forests in other regions (4.7 to 6.0 Mg ha^{-1} yr^{-1}) (42). In the case of the degraded forest, it presented values of litterfall similar to those reported for managed *Nothofagus* forests (41). Litterfall in the degraded forest was lower than in mature and secondary forests, which coincides with its low basal area, high canopy opening, and low LAI (43, 44). This reduced litter production can decrease carbon and nutrient inputs to the soil, limiting plant growth and regeneration on degraded sites (45–47).

Litter C:N, C:P, and N:P ratios were high in all forest plots compared to those reported for leaf litter from other temperate forests on a global scale (48). As expected, the stoichiometric relations varied over the year. An increment was observed in the C:N ratio from autumn to winter, coinciding with the season of higher litterfall. The lower N concentration during these months may reflect preferential reabsorption of this element by vegetation (49), which contributes to internal recycling and conservative use of this nutrient (50, 51). On the other hand, the N:P and C:P ratios increased from spring to summer, suggesting a preferential relocation of phosphorus, which was particularly high in the mature forest. This contrasts with Caldentey et al. (41), who found a decrease in the concentration of P in the litter in autumn and winter. The difference between forest types may be due to the dominance of *N. dombeyi* in mature forests, a perennial species that has a longer leaf life span and a low N and P concentration. The observed temporal trends suggest higher recycling and more conservative nutrient use strategies in the mature forest (51, 52).

The litter C, N, and P inputs strongly depended on the quantity of litter produced, being higher in autumn for N and P in all forest plots (Figures 2E, F, G). The annual amount of nutrients provided by the litter was lower than that indicated by other studies in temperate forests of central-southern Chile, which report values between 44 to 69 kg ha^{-1} year^{-1} for N and 2.6 to 3.6 kg ha^{-1} year^{-1} for P (22). This difference could be due to the lower density of trees in the present study compared to that obtained by Staelens et al. (22), lower N and P soil availability (P-fixing andosol and low atmospheric N inputs), and the difference in species composition. It has been documented that temperate ecosystems tend to have low levels of N and P due to the low atmospheric and weathering inputs and hydrologic losses of dissolved organic P and N, all of which result in low nutrient concentrations in soils (53). Likewise, low N mass in the degraded forest may be due to episodic N losses associated with fires and removal from logging, grazing, and other local disturbances (54). The total C, N, and P mass contributed by the mature forest confirm that litter in these well-preserved forests is a more substantial C and nutrient reservoir. The greater availability and active internal cycling of these elements in mature forests sustain forest productivity and regeneration, supporting other critical ecosystem processes.

4.2 Litter decomposition and nutrient dynamics

The initial concentrations of N, and P in the degraded forest litter (Table 2) suggest that this site has a better nutritional quality than the secondary and mature forests. This may be due to the fact that the degraded forest is mostly composed of deciduous species composition, which has been shown to have a higher nutrient content compared to the litter of perennial species (55). The latter result is also consistent with previous studies in tropical forests that have shown an increase in litter quality along disturbance gradients (56). This is explained by the recruitment of fast-growing species with economic litter traits, which could lead to rapid decomposition rates (57). However, the higher nutrient concentration in the degraded forest did not yield higher decomposition rates. In fact, we found that litter from mature and secondary forest composed of a mix of deciduous and evergreen species decomposed faster than deciduous litter from degraded forest. In addition, the FTIR-derived indices I and II suggest similar aromaticity and recalcitrance levels between the litter of the mature and degraded forests. Thus, the decomposition rates are likely controlled by factors different than nutrient concentration. Our results suggest that high lignin concentrations in degraded forest litter, together with environmental factors (i.e., higher soil temperature and limited surface moisture) could lead to reduced decomposition rates, as other authors have suggested (58). Recent studies have also shown a deceleration of litter decomposition and lignin degradation in cleared forests with heightened direct solar radiation (59).

Moreover, the reduced decomposition in the degraded forest could also be due to the lower litter diversity compared to the mature and secondary forests (60), which had a greater mix of species. Synergistic effects on decomposition have been documented when litter species of different quality are mixed, which could accelerate the rate of decomposition in these forests (61). Some mechanisms that explain this effect are the interaction between the microbiomes associated with each litter type, the complementary effects of soil fauna and decomposing organisms, and the improvement in microclimatic conditions during decomposition (60), mechanisms that could be absent in the degraded forest.

The remaining mass agrees with previous studies in temperate *Nothofagus* forests, except for the degraded forest, which displayed a much larger remaining mass of 93%. This result differs from earlier studies in *Nothofagus* forests, which found increased decomposition rates in disturbed forests associated with higher temperature and humidity (15, 41). In our study, the degraded forest had a higher temperature but lower soil moisture, which could affect the decomposition process. However, our results are consistent with studies that also report a reduction in litter decomposition after clear-cutting or thinning, associated with a decrease in soil moisture and its biological activity (14, 62). Similarly, a reduction in decomposition rates has been observed in degraded tropical forests exhibits as the intensity of disturbances increases (13).

An earlier study conducted on the same study plots showed that bacterial and fungal soil communities differed at the genus level between forest types (30). Likewise, these authors reported a change in the structure of the microbial community in the most degraded forests, which could affect litter decomposition. Furthermore, other authors have reported reduced microbial activity after logging (63). The harsher conditions for microbes may have also reduced the activity of soil mesofauna. Due to the importance of these organisms for the decomposition of organic matter, particularly in the degradation of lignin (58, 64), reduced faunal activity can also explain the low decomposition rates found in the degraded forest (13). We also observed a noticeable reduction in understory coverage and plant composition, which could explain a reduction in litter decomposition driven by a decrease in mesofauna activity (65). However, this is an aspect that needs to be further studied.

The accumulation of N in all forest types, followed by short nutrient release periods, coincides with Staelens et al. (22), who reported the same trends for other deciduous species. The initial immobilization has been reported in different parts of the world for temperate and boreal climates (66, 67). The accumulation of N at the beginning of decomposition cycle may be due to microbial immobilization under low N availability (68). This explains the high accumulation of N and the lower C:N ratio in mature forests, which presented the lowest initial content of this element. Despite the higher litter quality (higher N content) in the degraded forest, it tended to accumulate more N than in the secondary forest. This N enrichment could result from external inputs from grazing livestock in the degraded forest area (69).

C:P and N:P values indicated a period of initial immobilization and high mineralization towards the end of this study. This initial accumulation may be due to external sources, for example, the precipitation and fall of new litter from the canopy (70) and also livestock grazing (69). The content of P decreased drastically starting in spring, which suggests more substantial mineralization of this element and reabsorption after the rainy season. Seasonal patterns in humidity and temperature that control microbial communities can influence changes in stoichiometry (71). During the spring (September) the conditions are more favorable for plant growth, microbial and soil fauna dispersion, which stimulates the mineralization of elements, especially P (72). This could explain the increase in N:P and C:P ratios in the remaining litter.

As the decomposition progressed, there was a decreasing trend in the C:N and C:P ratios until reaching values close to 37 - 51 and 700 - 900 (73). In our study, the C:N ratio decreased with decomposition, reaching values close to those indicated; however, the C:P ratio increased towards the end of the period, reaching values much higher than those reported by these authors. This may be due to high initial C:P values, which have led to high ratios during decomposition (74). In addition, due to the low decomposition rates found, a more extended study period may be necessary to observe a convergence toward lower C:P ratios (75, 76).

The difference in nutrient dynamics during litter decomposition between forest conservation states may be due to the difference in litter quality (5, 77). Different authors have found an initial immobilization of N and P in low-quality litter and a more significant release of these elements during the decomposition of high-quality litter (72). In our study, we found a greater initial immobilization of N and P in the mature forest, which presented the lowest concentrations of these nutrients. However, despite the higher quality of the litter in the degraded forest, it did not show a greater nutrient release. On the other hand, it has been reported that high concentrations of lignin in the litter can increase the initial immobilization of N and P due to the formation of recalcitrant substances (78). We found a high concentration of lignin in all forest stands but the lowest in the secondary forest, which coincidentally presented the lowest initial immobilization.

4.3 Remaining litter stock

The annual litter production was three times higher in the mature forest and two times higher in the secondary than in the degraded forest. After balancing inputs and outputs by decomposition, the mature forest presents the highest accumulation of litter on the forest floor. Due to its higher decomposition rate, we could also expect a higher carbon influx into the mineral horizon and nutrient influx through mineralization. Previous studies have found less litterfall and nutrient influx in degraded Mediterranean, Temperate, and Tropical forests, along with a depletion of ecosystem carbon stocks and reduced soil nutrient availability. Both factors decrease the recycling of nutrients and limit forest productivity, soil functionality, and the provision of ecosystem services (3, 47, 79, 80).

The differences in litterfall, decomposition, and dynamics of C, N, and P showed that forest degradation in these sites altered litter production, litter quality, and the dynamics of C, N, and P mineralization. Hampering these critical biogeochemical processes limit soil fertility and thus the regenerative capacity, productivity, and ecological complexity of these forests, making them less resilient to ever-increasing biotic and abiotic disturbances driven by global change (81).

5 Conclusions

Litter dynamics and nutrient cycling of *Nothofagus* forests vary according to their conservation state. Forest degradation by human disturbances results in different amounts of litterfall, decomposition rates, and contrasting C, N, and P dynamics. Higher decomposition in mature *Nothofagus* forests indicates faster nutrient cycling than in the degraded forest. Furthermore, nutrient reabsorption in mature forests suggests a more efficient internal cycle despite their lower litter quality. On the contrary, low litterfall and low decomposition in degraded forests indicate an altered ecological functioning, which can reduce the availability and release of nutrients limiting ecosystem productivity and regeneration, as well as hindering the provision of key benefits such as carbon sequestration and nutrient cycling. These findings support the importance of preserving mature forests to maintain biogeochemical processes and, thus, the productivity and sustainability of terrestrial ecosystems. On the other hand, despite the recognized importance of litter quality for litter decomposition, we found that other factors may be co-limiting decomposition rates in degraded forests, such as changes in microclimatic conditions, which may also hinder decomposers activity. Highly dynamic C:N:P stoichiometry of litterfall and litter emphasizes the need for long-term monitoring of these parameters to fully understand the multi-elemental cycling during decomposition and transformation of litter into organic soil horizons.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

FL wrote the original manuscript draft and performed the data curation and statistical analysis under the guidance of FA. FA contributed to the conception and design of the study methodology and funding acquisition. NA collected samples, performed analysis and organized the database, wrote sections of the manuscript, and implemented the methodology. CE contributed to the funding acquisition. PG provided additional data and database organization. All authors contributed to the manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsoil.2023.1111694/full#supplementary-material

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