UNIVERSIDAD DE CONCEPCIÓN
Dirección De Postgrado
Facultad De Ciencias Forestales
Programa de Magister en Ciencias Forestales

DINÁMICAS DE PRODUCCIÓN Y ROL DE LA MESOFAUNA EN LA DESCOMPOSICIÓN DE HOJARASCA EN BOSQUES TEMPLADOS CON DISTINTOS ESTADOS DE CONSERVACIÓN

Tesis para optar al grado de Magister en Ciencias Forestales

Fabiola Alejandra Leal Monsalvez

CONCEPCIÓN- CHILE

2022

Profesor Guía: Dr. Cristian Echeverría Leal
Depto. de Manejo de Bosques y Medio Ambiente,
Facultad de Ciencias Forestales
Universidad de Concepción

DINÁMICAS DE PRODUCCIÓN Y ROL DE LA MESOFAUNA EN LA DESCOMPOSICIÓN DE HOJARASCA EN BOSQUES TEMPLADOS CON DISTINTOS ESTADOS DE CONSERVACIÓN

Comisión Evaluadora:

Cristian Echeverría Leal (Profesor guía)
Ingeniero Forestal, PhD.

Daniel Aguilera Olivares (Profesor co-guía)
Licenciado en Biología,
Dr. En Ecología y Biología Evolutiva

Felipe Aburto Guerrero (Comisión evaluación)
Ingeniero Agrónomo, PhD.

Paula Gatica Saavedra (Comisión evaluación)
Bióloga, Dra. Ciencias Forestales

Director de Postgrado:
Dr. Regis Texeira
Ingeniero Químico, PhD.

Decano Facultad de Ciencias Forestales:
Dr. Manuel Sánchez O.
Ingeniero Forestal. Dr.

DEDICATORIA

“A Gastón Leal Martínez y Edith Garrido Valderrama”

AGRADECIMIENTOS

A mi profesor guía Cristian Echeverría por su confianza, comprensión y constante apoyo durante el desarrollo de mi tesis. También a mis profesores co-guías Felipe Aburto, Daniel Aguilera y Paula Gatica por su apoyo, comentarios y consejos brindados durante el desarrollo de este trabajo.

Al convenio entre ENEL y Universidad de Concepción N 73-J-21-ER2 y Foresta Nativa por brindar los recursos necesarios que hicieron posible el desarrollo de esta investigación y mi postgrado. Al igual, al Laboratorio de Investigación de Suelo, Agua y Bosques, al Laboratorio de Entomología Forestal y al Laboratorio de Tecnología de la Madera por brindar el apoyo y herramientas necesarias para la realización de este proyecto.

Al equipo de trabajo en terreno y al equipo de los distintos laboratorios quienes me acompañaron y asesoraron.

TABLA DE CONTENIDOS

ÍNDICE DE TABLAS

ÍNDICE DE FIGURAS

RESUMEN GENERAL

Las perturbaciones antrópicas están impulsando cambios sin precedentes en la biodiversidad y las funciones de los ecosistemas forestales. Los bosques templados de *Nothofagus* del centro-sur de Chile se encuentran fuertemente degradados, no obstante, se desconoce como esto afecta la descomposición de hojarasca y la dinámica de los nutrientes. El objetivo principal de este estudio fue evaluar la producción de hojarasca, su descomposición, las dinámicas del carbono (C), nitrógeno (N) y fósforo (P) y el rol de la mesofauna del suelo superficial en estos procesos. Se instalaron trampas de colecta de hojarasca y bolsas de descomposición con distinto tamaño de malla en parcelas de bosques de *Nothofagus* que representan cuatro estados de conservación: bosque maduro, bosque secundario, bosque degradado y sitio reforestado. Tanto la producción de hojarasca como su descomposición disminuyeron desde el bosque maduro al sitio reforestado; mientras que el efecto de la descomposición atribuido a la mesofauna aumentó en el bosque degradado, pero disminuyó en el sitio reforestado. Esta diferencia estuvo relacionada a los cambios en la composición de la mesofauna y su abundancia. Además, se encontró una mayor liberación de C, N y P en el tratamiento con mesofauna; sin embargo, su efecto sobre las relaciones estequiométricas fue variable entre los sitios de estudio. Se concluye que la degradación de los bosques afecta significativamente estos procesos biogeoquímicos, mientras que la mesofauna puede convertirse en un factor clave para la descomposición y liberación de nutrientes en bosques degradados.

GENERAL ABSTRACT

Anthropic disturbances are driving unprecedented changes in biodiversity and forest ecosystem functions. The temperate *Nothofagus* forests of central-southern Chile are highly degraded, however, it is unknown how this affects litter decomposition and nutrient dynamics. The main objective of this study was to evaluate the litter production, litter decomposition, the dynamics of carbon (C), nitrogen (N) and phosphorous (P) and the role of the surface soil mesofauna in these processes. Litter collection traps and decomposition bags with different mesh sizes were installed in *Nothofagus* forest plots representing four conservation states: mature forest, secondary forest, degraded forest and reforested site. Both litter production and decomposition decreased from the mature forest to the reforested site; while the effect of mesofauna increased in the degraded forest but decreased in the reforested site. This difference was related to changes in the composition of the mesofauna and its abundance. In addition, a higher release of C, N and P in the treatment with mesofauna were found; however, its effect on the stoichiometric relationships was variable along the study sites. We conclude that forest degradation significantly affects these biogeochemical processes, while mesofauna can become a key factor for decomposition and nutrient release in degraded forests.

I.INTRODUCCIÓN GENERAL

Las actividades humanas han ocasionado la pérdida y degradación de los ecosistemas naturales, afectando a gran parte de los bosques del mundo (Hansen et al., 2013). Esto ha traído consigo un declive sin precedentes en la biodiversidad y con ello, cambios impredecibles el funcionamiento de los ecosistemas (Paudel et al., 2015). La descomposición de la hojarasca es un proceso clave para el flujo de masa y energía debido a que devuelve los nutrientes al suelo (Song et al., 2008), lo que permite el ciclaje y la recirculación de los elementos (Bohara et al., 2019). En muchos bosques la caída de hojarasca y su descomposición representan la fuente principal de algunos nutrientes limitantes como el nitrógeno, por lo cual, estos procesos pueden determinar la productividad y crecimiento de las plantas (Krishna and Mohan, 2017). Sin embargo, la perturbación de los bosques puede alterar los factores que influencian la descomposición de la hojarasca, entre ellos, las condiciones micro climáticas, la calidad de la hojarasca y los organismos del suelo. A pesar de su importancia, pocos estudios han evaluado el efecto de la degradación forestal sobre la descomposición de hojarasca y la dinámica de los nutrientes (Paudel et al., 2015).

Estudios a escala global han demostrado que el clima es el factor dominante que determina la descomposición de la hojarasca por medio de la temperatura y humedad (Aerts, 1997). Se ha demostrado que los climas más cálidos y húmedos favorecen el proceso de descomposición, mientras que climas fríos y secos retardan este proceso. Del mismo modo, la calidad de la hojarasca puede afectar las tasas de descomposición y liberación de nutrientes (Cornwell et al., 2008). En este sentido, se ha comprobado que altas concentraciones de N y P pueden acelerar el proceso de descomposición, mientras que las altas concentraciones de lignina y altas relaciones C:N y C:P pueden disminuir las tasas de este proceso (Bakker et al., 2011, Prescott, 2010). A escala mundial estos factores explican alrededor del 65% de la variación en las tasas de descomposición (García-Palacios et al., 2013), al mismo tiempo que afectan la presencia y actividad de los organismos descomponedores. Entre los organismos descomponedores se encuentran las bacterias y hongos, los cuales se encargan de degradar los compuestos de la materia orgánica. Por otro lado, la fauna del suelo también se considera un factor importante porque puede consumir y triturar grandes cantidades de hojarasca, lo cual estimula la actividad de los microorganismos del suelo (Frouz, 2018). Sin embargo, la contribución de la fauna del suelo depende de diferentes factores a escala local como la composición, abundancia y actividad de estos organismos, lo cual ha sido menos estudiado.

Se ha demostrado que la fauna del suelo puede incrementar la mineralización del carbono y distintos nutrientes como el nitrógeno, fósforo y potasio desde la hojarasca en descomposición (Moreno et al., 2022, Yang and Li, 2020). Aunque su efecto directo sobre la mineralización de nutrientes es bajo, pueden ejercer un mayor efecto indirecto mediante el consumo de biomasa microbiana, lo que permite la liberación de los nutrientes inmovilizados por esta (Crowther et al., 2012). A pesar de que se reconoce la importancia de algunos grupos de fauna en la descomposición de la hojarasca, la evidencia empírica del papel de la diversidad faunística en este proceso sigue siendo escasa (Frouz, 2018). Algunos estudios han encontrado que una mayor abundancia y diversidad de fauna se correlaciona con una mayor descomposición, aunque también se han reportado efectos neutrales (Hättenschwiler et al., 2005). Se reconoce que la presencia de especies clave como las hormigas, termitas y lombrices tienen un fuerte impacto en la descomposición (McGlynn and Poirson, 2012). Al igual, la mesofauna se considera como un componente relevante dado que incluye grupos de fauna abundantes y diversos como Acari y Collembola. Sin embargo, las comunidades de fauna del suelo y su actividad varían entre los distintos biomas (González and Seastedt, 2001), por lo cual su efecto sobre el proceso de descomposición también es variable.

Investigaciones previas han demostrado que el efecto de excluir la fauna del suelo reduce las tasas de descomposición en un 35% a escala mundial (Zhang et al., 2015), aunque este efecto depende de la región climática (García-Palacios et al., 2013). Por ejemplo, un estudio en bosques tropicales húmedos encontró un efecto de la fauna del suelo de hasta un 66% sobre las tasas de descomposición (González & Seastedt, 2001), mientras que este efecto disminuye en regiones donde las condiciones climáticas restringen la actividad de la biota, como son las regiones frías y con baja humedad. En este sentido, un metaanálisis reciente mostró que en los bosques templados de China la fauna mejoró las tasas de descomposición en un 28% (Zan et al., 2022). Sin embargo, la mayoría de estos estudios se han realizado en bosques del hemisferio norte, mientras que los bosques templados del hemisferio sur han sido menos estudiados. Además, los estudios se han centrado en bosques naturales no perturbados, por lo que el proceso de descomposición y el papel de la fauna del suelo han sido escasamente evaluados en bosques alterados por perturbaciones humanas.

La degradación forestal genera cambios en la estructura de los bosques. Por una parte, la tala crea aberturas en el dosel que aumentan la radiación solar que llega al suelo, lo que conduce a un aumento de su temperatura y una disminución de su humedad, generando cambios en el microclima (Paudel et al., 2015). Estos factores pueden alterar la presencia y actividad de la fauna del suelo, produciendo cambios en su efecto sobre la descomposición de la hojarasca y la dinámica de los nutrientes (García-Palacios et al., 2013; Moreno et al., 2022). Se ha documentado que la tala de los bosques reduce la importancia de los invertebrados en la descomposición debido a la disminución de la abundancia de especies clave para este proceso (Ewers et al., 2015), lo que ha llevado a reducir las tasas de descomposición en bosques tropicales perturbados (Stone et al., 2020). Sin embargo, la respuesta de este proceso es difícil de predecir, ya que se ha informado que las tasas de descomposición pueden aumentar, disminuir o incluso mantenerse en distintos tipos de bosque a nivel mundial (Cowan and Anderson, 2019, Yeong et al., 2016).

Los bosques de *Nothofagus* de América del Sur, que ocupan desde los 37°S hasta alrededor de los 55°S en Chile y Argentina (Veblen et al., 1996), han sido fuertemente degradados y destruidos por la acción antrópica, principalmente por presiones como la tala selectiva de individuos arbóreos (Armesto et al., 2010) y el pastoreo de ganado (Zamorano-Elgueta et al., 2014). Estos procesos afectan grandes extensiones de bosques de *Nothofagus* (Alfaro et al., 2018) y sus efectos en la dinámica de la hojarasca son poco conocidos. Se ha documentado que la tala de estos bosques puede provocar un aumento en las tasas de descomposición (Peri et al., 2008, Bahamonde et al., 2012); sin embargo, el ciclo de nutrientes en los bosques de *Nothofagus* ha sido escasamente evaluado, mientras que se desconoce el efecto que tiene la mesofauna sobre la descomposición y dinámica de los nutrientes en estos ecosistemas.

Debido a lo anteriormente planteado, este estudio busca evaluar la dinámica de producción de hojarasca, sus tasas de descomposición y el efecto de la mesofauna en la descomposición y mineralización de C, N y P en bosques de *Nothofagus* con diferentes estados de conservación.

HIPÓTESIS GENERALES

1. Sitios deforestados y bosques degradados presentan una menor tasa de descomposición de hojarasca y liberación de nutrientes en comparación a bosques mejor conservados, debido a las condiciones abióticas adversas y la menor calidad de la hojarasca

2. La riqueza, abundancia, diversidad y biomasa de la mesofauna disminuye en bosques con menor estado de conservación, disminuyendo su contribución relativa en las tasas de descomposición y mineralización de nutrientes

OBJETIVO GENERAL

Evaluar las dinámicas de producción de hojarasca, las tasas de descomposición y liberación de C, N y P y el rol de la mesofauna en estos procesos en bosques de *Nothofagus* con distintos estados de conservación

OBJETIVOS ESPECÍFICOS

1. Caracterizar las dinámicas de producción y descomposición de hojarasca y liberación de C, N y P
2. Relacionar la calidad de la hojarasca y condiciones del sitio con las tasas de descomposición y liberación de C, N y P
3. Determinar la contribución de la mesofauna en las tasas de descomposición de hojarasca y liberación de C, N y P

II. Forest degradation alters litter production, stoichiometry, and decomposition dynamics in Southern Temperate Forests

Abstract

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 regulating forest ecosystems' carbon and nutrient cycling. However, it is unclear how degradation affects litter decomposition and, as a result, carbon and nutrient cycling dynamics. The main objective of this study was to evaluate the effect of forest degradation on the production and decomposition of litter and C:N:P stoichiometry dynamics in a temperate forest in south-central Chile. Litter traps and litter bags were installed in three Long Term Research Forest Plots (LTER) representing different conservation states of *Nothofagus* sp.: mature, secondary, and degraded forest. The production, decomposition of litter, and C, N, and P concentrations were evaluated monthly for one year. 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 (lowest C:N and C:P ratios) in the degraded forest and the lowest in the mature forest. The average remanent litter mass reached 56% in the mature forest, while it was only 93% in the degraded forest, despite having a similar level of aromaticity and recalcitrance. Decomposing litter showed the lowest C:N and C:P ratios in the mature forest during most of the year. Despite their more substantial decomposition and nutrient release, the balance between inputs and outputs yielded a more significant accumulation of litter in the mature forests. Our results strongly suggest that anthropic degradation (i.e., logging and livestock grazing) and derived changes in forest composition and structure have significantly altered litter quality, production, decomposition, and derived nutrient dynamics. Further research should be focused on assessing how changes in litter dynamics affect natural forest regeneration, soil biogeochemical functioning, and composition, structure, and activity of soil fauna.

Keywords: carbon, nitrogen, phosphorous, soil, forest degradation, nutrient mineralization.

1. Introduction

Loss and degradation of forests are driving unprecedented changes in biodiversity and ecosystem functioning (Paudel et al., 2015). 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 (Berg and McClaugherty, 2014). Litter nutrient dynamics are closely related to the litter decomposition rate, which directly determines the nutritional status of the ecosystem (Bohara et al., 2019b). For this reason, research on litter decomposition has become a relevant aspect in the study of forest functioning (Zhao et al., 2006). However, there is limited knowledge about this process in disturbed forests (Cowan and Anderson, 2019).

Litter decomposition rates depend on the interaction of three major factors: climatic conditions, litter quality, and soil organisms (Lavelle et al., 1993). Climate has been considered the main factor on a global scale as it directly affects decomposition rates through temperature and humidity (Aerts, 1997). On a smaller scale, decomposition rates are strongly influenced by litter quality. High litter quality (i.e., high N, P) and low lignin concentrations and C:N and N:P ratios led to a higher decomposition rate and mineralization (Aubert et al., 2010, Prescott, 2010, Sanchez, 2001). 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 (Paudel et al., 2015, García-Palacios et al., 2013).

Forest degradation due to human activities, like logging, livestock grazing, and fire, can directly or indirectly alter the composition and structure of forests (Zamorano-

Elgueta et al., 2014). For example, a decrease in the basal area of trees, an increase in canopy opening, and loss of species in degraded forests have been documented (Paudel et al., 2015). These can modify the forest litter quality and change the environmental conditions (Stone et al., 2020). Since litter decomposition and dynamics are related to humidity and temperature, they can be affected by forest management and disturbances (Blanco et al., 2011). 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 (Bahamonde et al., 2012). In particular, it has been shown that high temperatures and low soil moisture in tropical secondary forests can lead to slower decomposition compared to primary forests (Ostertag et al., 2008). However, the responses of decomposition rates and nutrient dynamics are difficult to predict, as decomposition rates have been reported to increase, decrease, or even remain unchanged in different forest ecosystem types arround the world (Blanco et al., 2011, Bahamonde et al., 2012, Cowan and Anderson, 2019).

The *Nothofagus* forests of South America, which occupy from 37°S to about 55°S in Chile and Argentina (Veblen, 1995), 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. In addition, *Nothofagus* species are an ecologically significant group that is in decline due to anthropogenic threats, which has led to many species being threatened with extinction (Baldwin et al., 2018). The *Nothofagus* forests have been strongly degraded and destroyed by anthropic action, mainly through pressure such as selective logging of tree individuals (Armesto et al., 2010) and cattle grazing (Zamorano-Elgueta et al., 2014). These processes are currently affecting large extents of *Nothofagus* forests (Altamirano and Lara, 2010, Alfaro et al., 2018), and their effects on litter dynamics are poorly understood. It has been documented that the clearing of *Nothofagus* forests can cause a decrease in the production of litter and an increase in the rates of decomposition (Peri et al., 2008, Bahamonde et al., 2012). However, nutrient cycling in *Nothofagus* forests has been poorly evaluated, and studies are mainly focused on well-preserved forest systems (37°- 52° LS) or comparing different litter qualities (Lusk et al., 2001).

This study seeks to evaluate the dynamics of litter stoichiometry, production and decomposition, and mineralization of C, N, and P in *Nothofagus* forests in 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 site

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) (Figure 1A and 1B). 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 the warmest month with a mean of 22.5°C. The area presents an extended season of low temperatures, frequent frosts, 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 (CIREN, 1999, Crovo et al., 2021a).

Nothofagus temperate forests is documented to be the result of large-scale natural disturbances such as volcanic eruptions, landslides, and floods; and on a small-scale natural disturbances, such as falling trees due to wind (Pollmann and Veblen, 2004, Veblen et al., 1996). When canopy gaps become large enough to foster seedling development, the shade-intolerant species such as *Nothofagus alpina* (Poepp. & Endl.) Oerst. and *Nothofagus obliqua* (Mirb.) Oerst. can recruit and establish secondary forests (Pollmann, 2002, Donoso et al., 1993).

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, 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 logs 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 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 (Alfaro et al., 2018, Atenas-Navarrete et al., 2021). In 2015, a forest management plan began to be applied, gradually stopping illegal logging and regulating cattle grazing in the area.

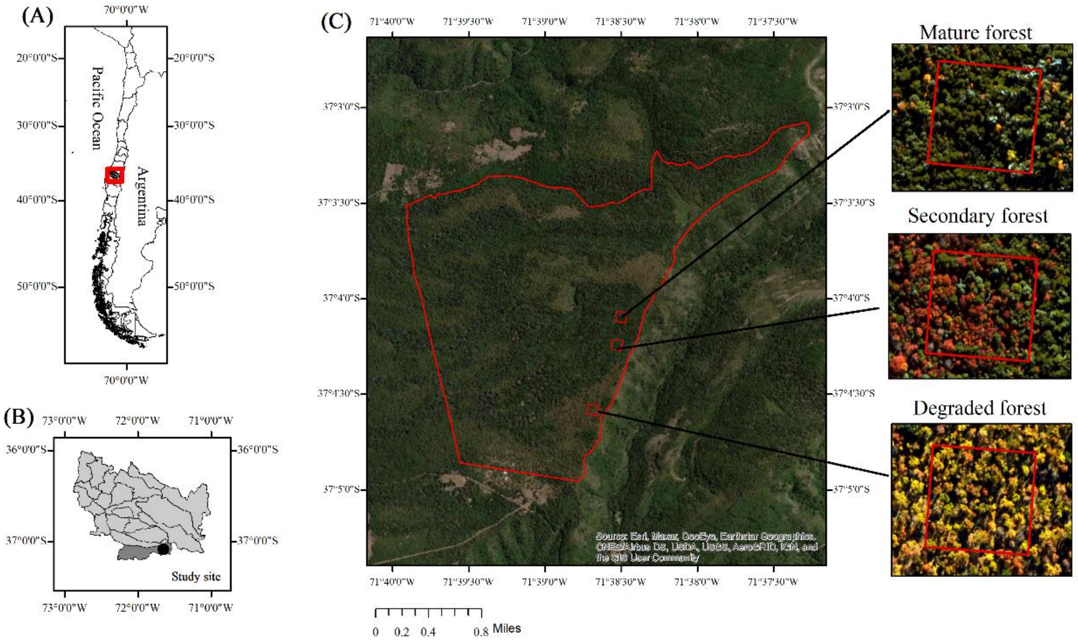

Figure 1. Map of Chile (A). Location of the study area in central Chile (B) (black point). Boundary of Ranchillo Alto estate and location of the three Long-Term Research Forest (LTER) plots (C). Image source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the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

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

Characteristics	Mature forest	Secondary forest	Degraded forest
Conservation status	Well preserved	Altered	Degraded
Composition [a]	*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 (m²/ha)	58.6	55.7	25.8
Tree stumps (N/ha)	26	84	18

Openness canopy (%)	10%	11%	52%
Leaf Area Index [b]	3.2 (0.06)	0.9 (0.02)	0.5 (0.04)
Soil temperature [b] (°C)	6.9 (0.3)	7.1 (0.2)	9.9 (0.4)
Soil moisture [b] (%)	22.9 (6.5)	21.9 (2.5)	15.8 (0.9)

[a] In parentheses is the percentage of dominance of each species

[b] In parentheses is the standard error.

2.2 Sampling design

Long-Term Ecological Research (LTER) plots of 100x100 m were established in each one of the three forests stands. In each plot, we sampled litterfall and litter decomposition, for which sub-sampling plots were established based on the GEM field manual (Marthews et al., 2014) for intensive census plots, which are explained in detail below.

2.2.1 Sampling of litter biomass

Twenty-five 10x10 m sub-sampling plots were established. 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 of 2019 was suspended due to adverse climatic conditions that impeded fieldwork (i.e., snowfall). In order to determine the dry weight, samples were individually transferred to paper bags and placed on a convection stove at 65°C for 48 to 72 hours until a constant weight was reached.

2.2.2 Sampling of litter decomposition analyses

Sixteen 25x25 m subplots were established (Figure 2). Twelve correlatively numbered decomposition bags were placed at the center of each subplot (576 total bags) (following Chadwick et al., 1998). For these bags, recently fallen litter was collected directly from the forest floor during April and May 2018 and dry weight was determined as above. After mixing, a homogeneous sample was generated from which an aliquot of approximately 10 ±1 g was extracted and placed in 1 mm mesh bags of 20x20 cm. These 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 dry weight was determined. Posteriorly, the decomposition rate (*k*) was determined with the exponential model described by Olson:

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

Where x_0 and x_1 are litter weight at times t_0 and t, respectively (Olson, 1963).

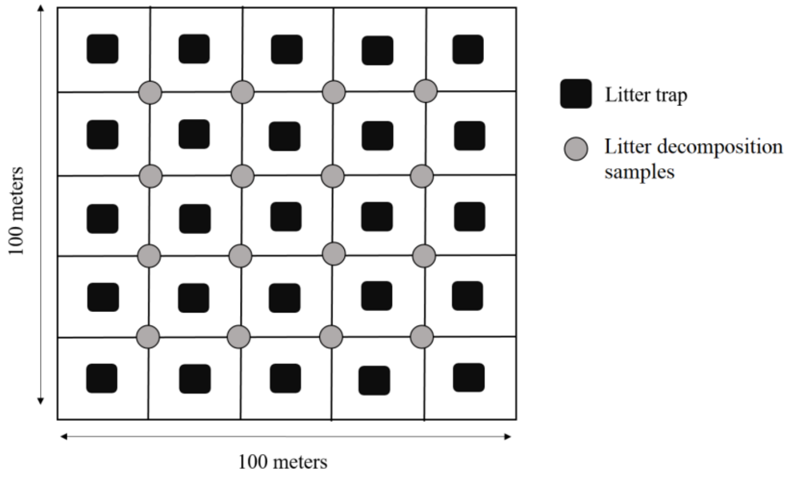

Figure 2. Distribution of sub-plots for litter fall and decomposition samples within 1 ha plot.

2.3 Stock remaining

The remaining litter stock was calculated using the difference between the annual input due to litterfall and the total annual decomposed litter. This indicated the total amount of litter remaining on the forest floor in each forest plot after a year.

2.4 Carbon and nutrient analyses

The carbon and nutritional content of the litterfall and the litter from the decomposition bags were 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 N contents were determined by the Dumas-TCD dry combustion method (SERCON® Limited, UK). Total P was determined by the calcination method for plant tissue described by Sadzawka et al. (2007) (Sadzawka et al., 2007). 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. (2008). 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 (Mendonça et al., 2008).

As a complementary measure to characterize litter quality, Fourier-transform infrared (FTIR) band indices were calculated (Equation 2). Index I has been used to indicate differences in degree of decomposition, but in this study, we used it as an indicator of the degree of aromaticity of the litter material (i.e., aromatic versus aliphatic bonds). Similarly, Index II was used as a proxy for organic matter recalcitrance (Margenot et al., 2015). These indices are based on the intensities of the FTIR bands representing various functional groups, which are detailed below:

$$\boldsymbol{Index\ I = \frac{1650 + 920}{2924 + 2850 + 1470}}$$

$$\boldsymbol{Index\ II = \frac{2924 + 2850 + 1650 + 1470 + 920}{3400 + 1080}}$$

Index I is the ratio of aromatic C=C to aliphatic and CH 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 and O functional groups, which is higher in more recalcitrant organic matter (Veum et al., 2014). 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).

2.5 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 (Kassambara, 2021) and “CAR” R (Fox and Weisberg, 2019) 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.

Decomposition rate (k) was transformed to 1/k, which fulfilled the assumption of normality and homogeneity of variances. An ANOVA was performed to evaluate differences in the k value between forest types. Because significant effects of forest type 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 (Team, 2013). Means and standard deviation 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, which was the lowest in the secondary forest (Table 2). The Index I was lower in the litter of the mature and degraded forests, and higher in secondary forest, indicating higher aromaticity of litter in secondary forest. On the other hand, the Index II was higher in the mature and degraded forests, suggesting greater 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).

Table 2. The initial concentration of litter C, N, P, lignin, Index I and II among mature, secondary, and degraded *Nothofagus* forests LTER plots. Different letters indicate significant differences ($p < 0.05$).

Forest type	C (%)	N (%)	P (%)	Lignin (%)	Index I	Index II

Mature forest	48.79^{a}	0.85^{a}	0.031^{a}	42.57^{a}	0.59^{a}	1.88^{a}
Secondary forest	49.12^{a}	0.93^{b}	0.034^{b}	40.72^{b}	0.86^{b}	0.98^{b}
Degraded forest	45.63^{b}	0.98^{c}	0.037^{c}	45.37^{c}	0.54^{a}	1.79^{a}

The annual litterfall ranged from 1.2 Mg ha^{-1} year^{-1} in the degraded forest to 3.7 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.

Table 3. Mean annual litterfall (Mg ha^{-1} year^{-1}) and C, N and P (kg ha^{-1}) among mature, secondary, and degraded *Nothofagus* forests LTER plots from December 2018 to December 2019. Different letters indicate significant differences ($p < 0.05$).

Forest type	Biomass (Mg ha^{-1} year^{-1})	C (kg ha^{-1})	N (kg ha^{-1})	P (kg ha^{-1})
Mature forest	3.781^{a}	1739.74^{a}	26.21^{a}	0.97^{a}
Secondary forest	2.767^{b}	1146.87^{b}	19.06^{b}	0.67^{b}
Degraded forest	1.222^{c}	528.07^{c}	10.33^{c}	0.37^{c}

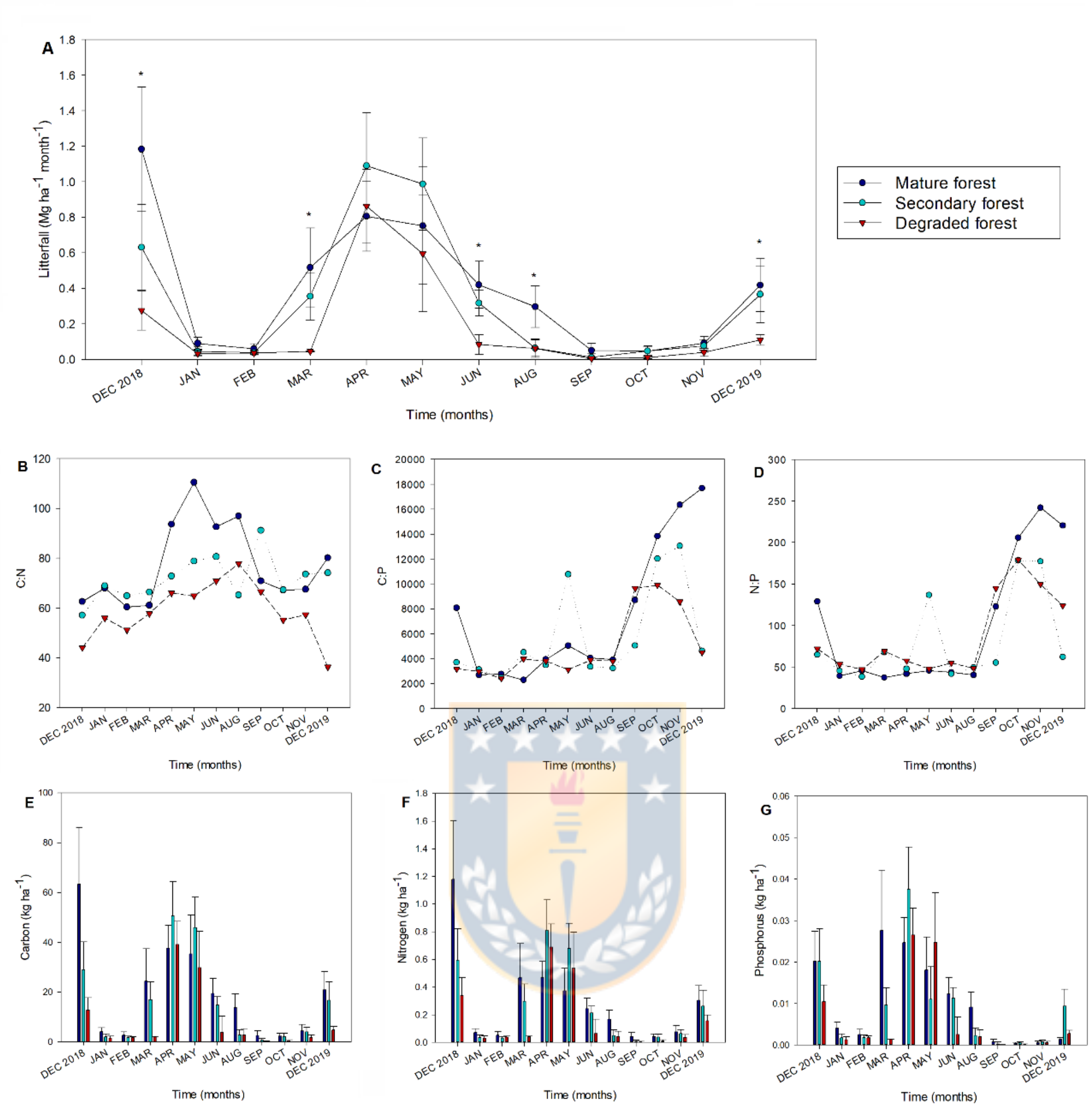

Figure 3. Litter biomass (A), molar C:N (B), C:P (C) and N:P (D) stoichiometric ratios, and Carbon (E), Nitrogen (F) and Phosphorous (G) of litterfall from December 2018 to December 2019 in mature (dark blue), secondary (light blue), and degraded (red) *Nothofagus* forests LTER plots. For A significant differences within each month are shown with an asterisk.

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 3B). 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 (Figure 3C, 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 monthly amounts of C, N, and P contributed by litter varied throughout the year and between forest plots (Figure 3E, F and G respectively). Annually the total amount of C in the litter varied 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 2). 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 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 3). 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 rate of decomposition was also observed in September (spring).

Table 4. Mean decomposition rate and remaining mass (%) after 390 days of decomposition in mature, secondary, and degraded *Nothofagus* forests LTER plots. Different letters indicate significant differences ($p < 0.05$).

Forest type	Decomposition rate	Remaining mass (%)
Mature forest	0.00149^{a}	56.62^{a}
Secondary forest	0.00112^{b}	65.40^{b}
Degraded forest	0.00018^{c}	93.23^{c}

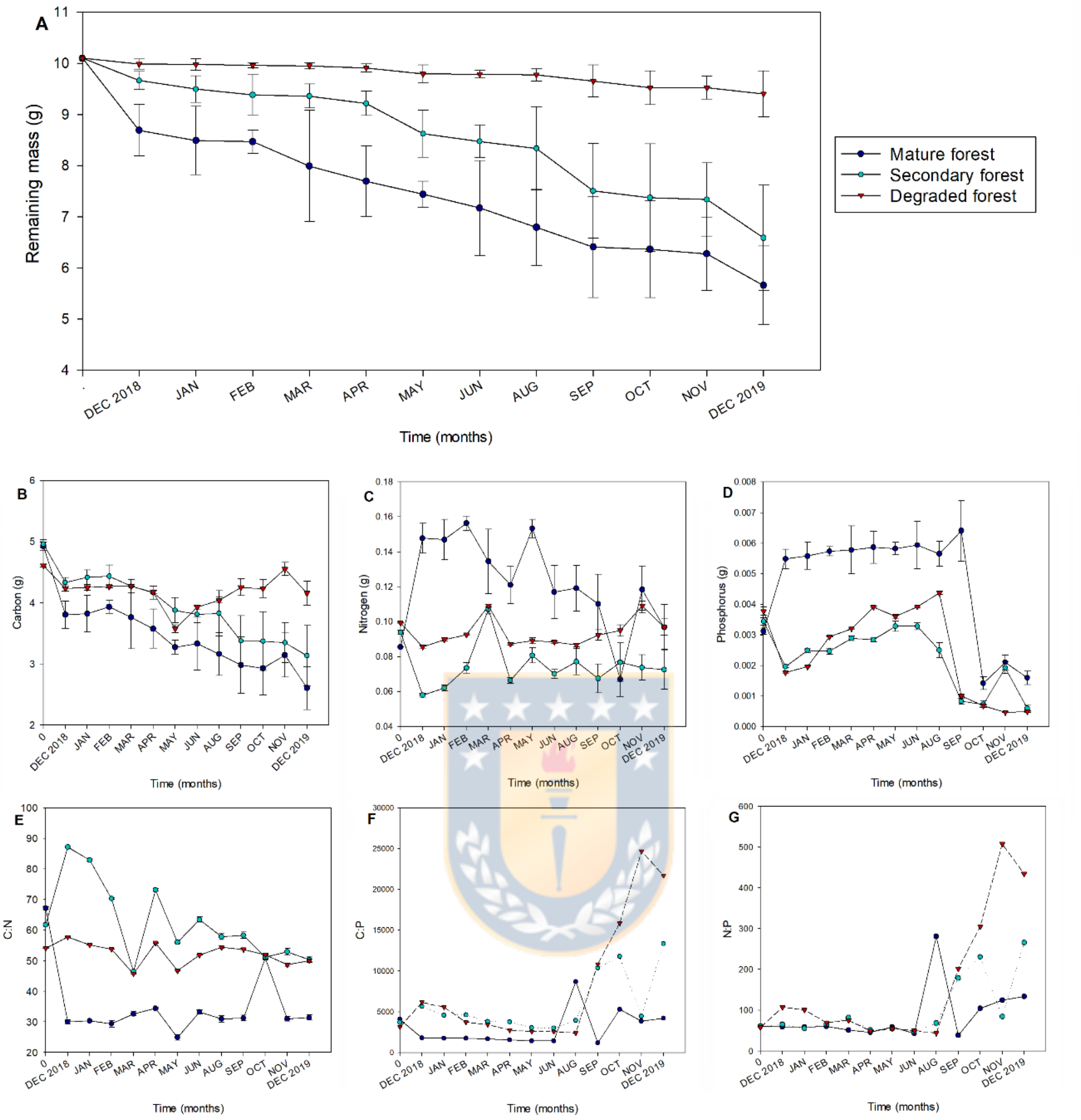

Figure 4. Remaining litter biomass (A), mass of Carbon (B), Nitrogen (C) and Phosphorus (D), and molar C:N (E), C:P (F) and N:P (G) stoichiometric ratios during litter decomposition from December 2018 to December 2019 in mature (dark blue), secondary (light blue), and degraded (red) *Nothofagus* forests LTER plots.

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 increase from May to November (Figure 4B). N presented an initial net accumulation in mature forest, which decreased towards the end of the year (Figure 4C). The secondary forest showed a slight decrease in N content. In contrast, in the degraded forest, the 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 4D). On the other hand, litter P in the secondary and degraded forests dropped during the first month and then gradually increased until the spring when it fell significantly.

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 4E). 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 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 (Figure 4F and 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, 1.81 Mg ha^{-1} in secondary forest, and 1.14 Mg ha^{-1} in the degraded forest (Table 5).

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

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. 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 high nutrient content did not result in high litter decomposition rates, probably due to its high lignin concentration and adverse abiotic and biotic conditions for decomposition to proceed (e.g., high temperature, low humidity, low mesofauna, and microbial population and activity) (Paudel et al., 2015, Stone et al., 2020).

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 the *Nothofagus* forests of central and southern Chile (Staelens et al., 2011, Caldentey et al., 2001), but it was slightly lower than that observed in temperate forests in other regions (4.7 to 6.0 Mg ha^{-1} yr^{-1}) (Zhang et al., 2014). In the case of the degraded forest, it presented values of litterfall similar to those reported for managed *Nothofagus* forests (Caldentey et al., 2001). The litterfall in the degraded forest was lower than the values found in mature and secondary forests, possibly due to its lower basal area, larger canopy opening, and smaller LAI (Thakur et al., 2019, Saarsalmi et al., 2007). This lower litter production decreases carbon and nutrient inputs to the soil, limiting plant growth on the degraded sites (Garcia-Oliva et al., 2014, Vesterdal et al., 1995, Jandl et al., 2007).

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 (McGroddy et al., 2004). 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 (Macinnis-Ng and Schwendenmann, 2015), which contributes to internal recycling and conservative use of this nutrient (Spohn et al., 2021). On the other hand, the N:P and C:P ratios increased from spring to summer, suggesting a preferential relocation of phosphorus, which was especially relevant for the mature forest that presented the highest ratios. This contrasts with Caldentey et al. (2001), 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 forest, a perennial species that has a longer leaf life span and a low N and P concentration. This suggests higher recycling and more conservative nutrient use strategies in the mature forest (Yan et al., 2006, Spohn et al., 2021).

The nutrient mass contributed by litterfall strongly depended on the quantity of litter produced, whereby it was higher in autumn for N and P in all forest plots. 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 (Staelens et al., 2011). This difference could be due to the lower density of trees in the present study compared to that obtained by Staelens et al. (2011), 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 (Pérez et al., 1998). 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 (Perakis and Hedin, 2002). 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 C, N, and P in the litter in the degraded forest (Table 2) suggest this site has a better quality of litter than the secondary and mature forests. The latter result is consistent with previous studies in tropical forests that have shown an increase in litter quality along disturbance gradients (Bakker et al., 2011). This is explained by the recruitment of fast-growing species with economical litter traits, which lead to rapid rates of decomposition (Kazakou et al., 2006). However, the higher nutrient concentration did not yield higher decomposition rates. Secondly, the results of indices I and II indicate an equal level of aromaticity and recalcitrance of the litter of the mature and degraded forests. Thus, the decomposition rates are likely controlled by other factors. Our result suggests that high concentrations of lignin in the litter of degraded forest, together with the adverse environmental conditions, could lead to low decomposition rates (Rahman et al., 2013). Recent studies have shown a deceleration of litter decomposition and lignin degradation in cleared forests, which could explain the lower decomposition in the degraded forest (Wu et al., 2022).

The remaining mass agrees with previous studies in temperate *Nothofagus* forests, except for the degraded forest, which presented a 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 (Caldentey et al., 2001, Bahamonde et al., 2012). 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 (Lal, 2005, Blanco et al., 2011). Research in degraded tropical forests exhibits a reduction in decomposition rates as the intensity of disturbances increases (Stone et al., 2020). An earlier study conducted on the same study plots showed that bacterial and fungal soil communities differed at the genus level between forest types (Atenas-Navarrete et al., 2021). Likewise, the authors reported a change in the structure of the microbial community in the most degraded forests, which could affect the litter decomposition. Furthermore, other authors have reported a reduction in microbial activity after logging (Zhang and Zak, 1995). 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 (Wang et al., 2018, Rahman et al., 2013), reduced faunal activity can also explain the low decomposition rates found in the degraded forest (Stone et al., 2020). We also observed a noticeable reduction in understory coverage and composition which could also explain a reduction in litter decomposition driven by a decrease of mesofauna activity (Li et al., 2021). 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. (2011), 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 (Manzoni et al., 2010, Heuck and Spohn, 2016). The accumulation of N at the beginning of decomposition may be due to microbial immobilization under low N availability (Kiser et al., 2013). 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 (Crovo et al., 2021b).

C:P and N:P values indicated a period of initial immobilization and high mineralization towards the end of the study year. This initial accumulation may be due to external sources, for example, the precipitation and fall of new litter from the canopy (Lanuza et al., 2019) or livestock grazing (Crovo et al., 2021b). 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 (Pandey et al., 2007). This could explain the increase in N:P and C:P ratios at the beginning of the spring (September) when conditions are more favorable for plants, microbial, soil fauna growth and dispersal, and nutrient mineralization (Gautam et al., 2016).

As the decomposition progresses, there was a decreasing trend of the C:N and C:P relationships until reaching values close to 37 - 51 and 700 – 900 (Moore et al., 2006). 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 (Moore et al., 2011). In addition, due to the low decomposition rates found, a more extended study period may be necessary to observe a convergence towards lower C:P ratios (Rustad, 1994, Liu et al., 2016).

The difference in nutrient dynamics during litter decomposition between forest conservation states may be due to the difference in the litter quality (Parton et al., 2007, Cowan and Anderson, 2019). 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 (Gautam et al., 2016). (Gautam et al., 2016). 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 (Osono and Takeda, 2004). 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. The litter decomposition rate was much higher in the mature forest than in the other forest types. After balancing inputs and outputs, the mature forest presents the highest accumulation of litter on the forest floor. However, due to its higher decomposition rate, there could be 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 the forest's production and functions (Garcia-Oliva et al., 2014, Bravo-Oviedo et al., 2017, Bohara et al., 2019b).

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

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. High decomposition in mature *Nothofagus* forests indicates faster nutrient cycling, especially compared to degraded forests. Furthermore, nutrient reabsorption in mature forests suggests a more efficient internal cycle despite the lower litter quality. On the contrary, low litterfall and low decomposition in degraded forests indicate an altered functioning of these processes, which can affect the provision of ecosystem services such as C 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 affect more strongly decomposition rates in these forests, such as microclimatic conditions or soil organisms, which warrant further evaluation.

The 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 to organic soil horizons. A more in-depth evaluation of microclimatic conditions and soil microbial and fauna communities is needed to elucidate the factors affecting nutrient decomposition and release rates.

Acknowledgments

We thank the collaboration project N 73-J-21-ER2 between ENEL-Universidad de Concepción and Foresta Nativa, which supported the financing of this study, and the Facultad de Ciencias Forestales of the Universidad de Concepción for allowing us to carry out this study in the Ranchillo Alto National Protected Property. We also thank all the students and colleagues who helped us in the fieldwork and processing of the samples. Special mention to Dr. Regis Teixeira and Claudia Vidal from the Centro de Biotecnología of the Universidad de Concepción for their support in determining lignin and FTIR analyses.

References

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos, 439-449.

Alfaro, M., Dube, F., & Zagal, E. (2018). Soil quality indicators in an Andisol under different tree covers in disturbed *Nothofagus* forests. Chilean journal of agricultural research, 78(1), 106-116.

Altamirano, A., & Lara, A. (2010). Deforestación en ecosistemas templados de la precordillera andina del centro-sur de Chile. Bosque (Valdivia), 31(1), 53-64.

Armesto, J. J., Manuschevich, D., Mora, A., Smith-Ramirez, C., Rozzi, R., Abarzúa, A. M., & Marquet, P. A. (2010). From the Holocene to the Anthropocene: A historical framework for land cover change in southwestern South America in the past 15,000 years. Land Use Policy, 27(2), 148-160.

Atenas-Navarrete, A., Aburto, F., González-Rocha, G., Guzmán, C. M., Schmidt, R., Scow, K., & Lara, E. Á. (2021). Anthropogenic Disturbances Alter Surface Soil Biogeochemical Pools and Microbial Diversity in Andean Temperate Forests. Available at SSRN 4030349.

Aubert, M., Margerie, P., Trap, J., & Bureau, F. (2010). Aboveground–belowground relationships in temperate forests: plant litter composes and microbiota orchestrates. Forest Ecology and Management, 259(3), 563-572.

Bahamonde, H. A., Peri, P. L., Alvarez, R., Barneix, A., Moretto, A., & Pastur, G. M. (2012). Litter decomposition and nutrients dynamics in *Nothofagus antarctica* forests under silvopastoral use in Southern Patagonia. Agroforestry Systems, 84(3), 345-360.

Bakker, M. A., Carreño-Rocabado, G., & Poorter, L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. Functional Ecology, 25(3), 473-483. doi:https://doi.org/10.1111/j.1365-2435.2010.01802.x

Baldwin, H., Barstow, M., & Rivers, M. (2018). The red list of *Nothofagus*. BGCI, Richmond, UK.

Berg, B., & McClaugherty, C. (2014). Plant litter: Decomposition, humus formation, carbon sequestration.

Blanco, J. A., Imbert, J. B., & Castillo, F. J. (2011). Thinning affects Pinus sylvestris needle decomposition rates and chemistry differently depending on site conditions. Biogeochemistry, 106(3), 397-414.

Bohara, M., Yadav, R. K. P., Dong, W., Cao, J., & Hu, C. (2019). Nutrient and isotopic dynamics of litter decomposition from different land uses in naturally restoring Taihang Mountain, North China. Sustainability (Switzerland), 11(6). doi:10.3390/su11061752

Bravo-Oviedo, A., Ruiz-Peinado, R., Onrubia, R., & del Río, M. (2017). Thinning alters the early-decomposition rate and nutrient immobilization-release pattern of foliar litter in Mediterranean oak-pine mixed stands. Forest Ecology and Management, 391, 309-320.

Caldentey, J., Ibarra, M., & Hernández, J. (2001). Litter fluxes and decomposition in *Nothofagus* pumilio stands in the region of Magallanes, Chile. Forest Ecology and Management, 148(1-3), 145-157.

Chadwick, D. R., Ineson, P., Woods, C., & Piearce, T. G. (1998). Decomposition of Pinus sylvestris litter in litter bags: influence of underlying native litter layer. Soil Biology and Biochemistry, 30(1), 47-55.

CIREN. (1999). Estudio agrológico VIII región: CIREN Santiago, Chile. Centro de información de Recursos Naturales, CIREN N°121.

Cowan, O. S., & Anderson, P. M. L. (2019). Litter decomposition variation across a degradation gradient and two seasons in a critically endangered vegetation type within the Fynbos biome, South Africa. South African Journal of Botany, 121, 200-209. doi:https://doi.org/10.1016/j.sajb.2018.11.002

Crovo, O., Aburto, F., Albornoz, M. F., & Southard, R. (2021). Soil type modulates the response of C, N, P stocks and stoichiometry after native forest substitution by exotic plantations. Catena, 197, 104997.

Crovo, O., Aburto, F., da Costa-Reidel, C., Montecino, F., & Rodríguez, R. (2021). Effects of livestock grazing on soil health and recovery of a degraded Andean Araucaria forest. Land Degradation & Development, 32(17), 4907-4919.

Donoso, P., Donoso, C., & Sandoval, V. (1993). Proposición de zonas de crecimiento de renovales de roble (*Nothofagus obliqua*) y raulí (*Nothofagus alpina*) en su rango de distribución natural. Bosque(2), 37-55%V 14. doi:10.4206/bosque.1993.v14n2-06

Fox, J., & Weisberg, S. (2019). An {R} Companion to Applied Regression. An R companion to applied regression, 3rd ed: Sage Publications. Retrieved from https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Garcia-Oliva, F., Covaleda, S., Gallardo, J. F., Prat, C., Velazquez-Duran, R., & Etchevers, J. D. (2014). Firewood extraction affects carbon pools and nutrients in remnant fragments of temperate forests at the Mexican Transvolcanic Belt. Bosque, 35(3), 311-324. doi:10.4067/s0717-92002014000300006

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology letters, 16(8), 1045-1053.

Gautam, M. K., Lee, K.-S., Song, B.-Y., Lee, D., & Bong, Y.-S. (2016). Early-stage changes in natural 13C and 15N abundance and nutrient dynamics during different litter decomposition. Journal of Plant Research, 129(3), 463-476. doi:10.1007/s10265-016-0798-z

Heuck, C., & Spohn, M. (2016). Carbon, nitrogen and phosphorus net mineralization in organic horizons of temperate forests: stoichiometry and relations to organic matter quality. Biogeochemistry, 131(1), 229-242.

Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., . . . Naeem, S. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs, 75(1), 3-35.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., . . . Byrne, K. A. (2007). How strongly can forest management influence soil carbon sequestration? Geoderma, 137(3-4), 253-268.

Kassambara, A. (2021). Rstatix: Pipe-Friendly Framework for Basic Statistical Tests; R Package Version 0.7. 0. 2021. In.

Kazakou, E., Vile, D., Shipley, B., Gallet, C., & Garnier, E. (2006). Co-variations in litter decomposition, leaf traits and plant growth in species from a Mediterranean old-field succession. Functional Ecology, 20(1), 21-30. doi: https://doi.org/10.1111/j.1365-2435.2006.01080.x

Kiser, L. C., Fox, T. R., & Carlson, C. A. (2013). Foliage and litter chemistry, decomposition, and nutrient release in Pinus taeda. Forests, 4(3), 595-612.

Lal, R. (2005). Forest soils and carbon sequestration. Forest Ecology and Management, 220(1), 242-258. doi:https://doi.org/10.1016/j.foreco.2005.08.015

Lanuza, O., Casanoves, F., Delgado, D., & Van den Meersche, K. (2019). Leaf litter stoichiometry affects decomposition rates and nutrient dynamics in tropical forests under restoration in Costa Rica. Restoration Ecology, 27(3), 549-558. doi:10.1111/rec.12893

Lavelle, P., Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. Biotropica, 130-150.

Li, R., Guan, X., Han, J., Zhang, Y., Zhang, W., Wang, J., . . . Wang, S. (2021). Litter decomposition was retarded by understory removal but was unaffected by thinning in a Chinese fir [Cunninghamia lanceolata (Lamb.) Hook] plantation. Applied Soil Ecology, 163, 103968.

Liu, D., Keiblinger, K. M., Leitner, S., Mentler, A., & Zechmeister-Boltenstern, S. (2016). Is there a convergence of deciduous leaf litter stoichiometry, biochemistry and microbial population during decay? Geoderma, 272, 93-100. doi:https://doi.org/10.1016/j.geoderma.2016.03.005

Lusk, C. H., Donoso, C., Jiménez, M., Moya, C., Oyarce, G., Reinoso, R., . . . Matus, F. (2001). Descomposición de hojarasca de Pinus radiata y tres especies arbóreas nativas. Revista chilena de historia natural, 74(3), 705-710.

Macinnis-Ng, C., & Schwendenmann, L. (2015). Litterfall, carbon and nitrogen cycling in a southern hemisphere conifer forest dominated by kauri (Agathis australis) during drought. Plant Ecology, 216(2), 247-262.

Manzoni, S., Trofymow, J. A., Jackson, R. B., & Porporato, A. (2010). Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. Ecological monographs, 80(1), 89-106.

Margenot, A. J., Calderón, F. J., Bowles, T. M., Parikh, S. J., & Jackson, L. E. (2015). Soil organic matter functional group composition in relation to organic carbon, nitrogen, and phosphorus fractions in organically managed tomato fields. Soil Science Society of America Journal, 79(3), 772-782.

Marthews, T., T, R., Oliveras, I., R, U., S, M., D, M., . . . R, C. (2014). Measuring Tropical Forest Carbon Allocation and Cycling v3.0.

McGroddy, M. E., Daufresne, T., & Hedin, L. O. (2004). Scaling of C: N: P stoichiometry in forests worldwide: Implications of terrestrial redfield-type ratios. Ecology, 85(9), 2390-2401.

Mendonça, R. T., Jara, J. F., González, V., Elissetche, J. P., & Freer, J. (2008). Evaluation of the white-rot fungi Ganoderma australe and Ceriporiopsis subvermispora in biotechnological applications. Journal of Industrial Microbiology and Biotechnology, 35(11), 1323.

Moore, T. R., Trofymow, J., Prescott, C. E., & Titus, B. (2011). Nature and nurture in the dynamics of C, N and P during litter decomposition in Canadian forests. Plant and Soil, 339(1), 163-175.

Moore, T. R., Trofymow, J. A., Prescott, C. E., Fyles, J., & Titus, B. D. (2006). Patterns of Carbon, Nitrogen and Phosphorus Dynamics in Decomposing Foliar Litter in Canadian Forests. Ecosystems, 9(1), 46-62. doi:10.1007/s10021-004-0026-x

Olson, J. S. (1963). Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. Ecology, 44(2), 322-331. doi:10.2307/1932179

Osono, T., & Takeda, H. (2004). Accumulation and release of nitrogen and phosphorus in relation to lignin decomposition in leaf litter of 14 tree species. Ecological Research, 19(6), 593-602.

Ostertag, R., Marín-Spiotta, E., Silver, W. L., & Schulten, J. (2008). Litterfall and decomposition in relation to soil carbon pools along a secondary forest chronosequence in Puerto Rico. Ecosystems, 11(5), 701-714.

Pandey, R., Sharma, G., Tripathi, S., & Singh, A. (2007). Litterfall, litter decomposition and nutrient dynamics in a subtropical natural oak forest and managed plantation in northeastern India. Forest Ecology and Management, 240(1-3), 96-104.

Parrott, L. (2010). Measuring ecological complexity. Ecological Indicators, 10(6), 1069-1076.

Parton, W., Silver, W. L., Burke, I. C., Grassens, L., Harmon, M. E., Currie, W. S., . . . Hart, S. C. (2007). Global-scale similarities in nitrogen release patterns during long-term decomposition. Science, 315(5810), 361-364.

Paudel, E., Dossa, G. G., de Blécourt, M., Beckschäfer, P., Xu, J., & Harrison, R. D. (2015). Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. Ecosphere, 6(12), 1-20.

Perakis, S. S., & Hedin, L. O. (2002). Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. Nature, 415(6870), 416-419.

Pérez, C. A., Hedin, L. O., & Armesto, J. J. (1998). Nitrogen mineralization in two unpolluted old-growth forests of contrasting biodiversity and dynamics. Ecosystems, 1(4), 361-373.

Peri, P., Bahamonde, H., Monelos, L., & Pastur, G. M. (2008). Producción de hojarasca en bosques primarios y bajo manejo silvopastoril de *Nothofagus antarctica* en la provincia de Santa Cruz, Argentina. Segunda reunión sobre *Nothofagus* en la Patagonia, EcoNothofagus, 149-155.

Pollmann, W. (2002). Effects of natural disturbance and selective logging on *Nothofagus* forests in south-central Chile. Journal of Biogeography, 29(7), 955-970.

Pollmann, W., & Veblen, T. T. (2004). *Nothofagus* regeneration dynamics in south-central Chile: a test of a general model. Ecological Monographs, 74(4), 615-634.

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry, 101(1-3), 133-149.

Rahman, M. M., Tsukamoto, J., Rahman, M. M., Yoneyama, A., & Mostafa, K. M. (2013). Lignin and its effects on litter decomposition in forest ecosystems. Chemistry and Ecology, 29(6), 540-553.

Rustad, L. E. (1994). Element dynamics along a decay continuum in a red spruce ecosystem in Maine, USA. Ecology, 75(4), 867-879.

Saarsalmi, A., Starr, M., Hokkanen, T., Ukonmaanaho, L., Kukkola, M., Nöjd, P., & Sievänen, R. (2007). Predicting annual canopy litterfall production for Norway spruce (Picea abies (L.) Karst.) stands. Forest Ecology and Management, 242(2-3), 578-586.

Sadzawka, A., Carrasco, M., Demanet, R., Flores, H., Grez, R., Mora, M., & Neaman, A. (2007). Métodos de análisis de tejidos vegetales. Serie Actas INIA, 40, 140.

Sanchez, F. G. (2001). Loblolly pine needle decomposition and nutrient dynamics as affected by irrigation, fertilization, and substrate quality. Forest Ecology and Management, 152(1-3), 85-96.

Spohn, M., Aburto, F., Ehlers, T. A., Farwig, N., Frings, P. J., Hartmann, H., . . . Oelmann, Y. (2021). Terrestrial ecosystems buffer inputs through storage and recycling of elements. Biogeochemistry, 156(3), 351-373. doi:10.1007/s10533-021-00848-x

Staelens, J., Ameloot, N., Almonacid, L., Padilla, E., Boeckx, P., Huygens, D., . . . Godoy, R. (2011). Litterfall, litter decomposition and nitrogen mineralization in old-growth evergreen and secondar y deciduous *Nothofagus* forests in south-central Chile. Revista chilena de historia natural, 84(1), 125-141.

Stone, M. J., Shoo, L., Stork, N. E., Sheldon, F., & Catterall, C. P. (2020). Recovery of decomposition rates and decomposer invertebrates during rain forest restoration on disused pasture. Biotropica, 52(2), 230-241.

Team, R. C. (2013). R: A language and environment for statistical computing.

Thakur, T. K., Swamy, S., Bijalwan, A., & Dobriyal, M. J. (2019). Assessment of biomass and net primary productivity of a dry tropical forest using geospatial technology. Journal of Forestry Research, 30(1), 157-170.

Veblen, T. T. (1995). The ecology of the conifers of southern South America. Ecology of the southern conifers, 120-155.

Veblen, T. T., Donoso, C., Kitzberger, T., & Rebertus, A. J. (1996). Ecology of southern Chilean and Argentinean *Nothofagus* forests. The ecology and biogeography of *Nothofagus* forests, 10, 93-353.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R. F., & Jackson, R. B. (2012). Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecological monographs, 82(2), 205-220.

Vesterdal, L., Dalsgaard, M., Felby, C., Raulund-Rasmussen, K., & Jørgensen, B. B. (1995). Effects of thinning and soil properties on accumulation of carbon, nitrogen and phosphorus in the forest floor of Norway spruce stands. Forest Ecology and Management, 77(1), 1-10. doi:https://doi.org/10.1016/0378-1127(95)03579-Y

Veum, K. S., Goyne, K. W., Kremer, R. J., Miles, R. J., & Sudduth, K. A. (2014). Biological indicators of soil quality and soil organic matter characteristics in an agricultural management continuum. Biogeochemistry, 117(1), 81-99.

Wang, L., Zhang, J., He, R., Chen, Y., Yang, L., Zheng, H., . . . Liu, Y. (2018). Impacts of soil fauna on lignin and cellulose degradation in litter decomposition across an alpine forest-tundra ecotone. European Journal of Soil Biology, 87, 53-60.

Wu, A., Yin, R., Xu, Z., Zhang, L., You, C., Liu, Y., . . . Tan, B. (2022). Forest gaps slow lignin and cellulose degradation of fir (Abies faxoniana) twig litter in an alpine forest. Geoderma, 424, 116010. doi:https://doi.org/10.1016/j.geoderma.2022.116010

Yan, E.-R., Wang, X.-H., & Huang, J.-J. (2006). Shifts in plant nutrient use strategies under secondary forest succession. Plant and Soil, 289(1), 187-197.

Zamorano-Elgueta, C., Cayuela, L., Rey-Benayas, J. M., Donoso, P. J., Geneletti, D., & Hobbs, R. J. (2014). The differential influences of human-induced disturbances on tree regeneration community: a landscape approach. Ecosphere, 5(7), 1-17.

Zhang, H., Yuan, W., Dong, W., & Liu, S. (2014). Seasonal patterns of litterfall in forest ecosystem worldwide. Ecological Complexity, 20, 240-247.

Zhang, Q., & Zak, J. C. (1995). Effects of gap size on litter decomposition and microbial activity in a subtropical forest. Ecology, 76(7), 2196-2204.

Zhao, G.-F., Cai, Y.-B., Luo, Y.-Y., Li, M.-H., & Yu, M.-J. (2006). Nutrient dynamics in litter decomposition in an evergreen broad-leaved forest in East China. Acta Ecologica Sinica, 26(10), 3286-3295.

III. Forest degradation alters litter production, decomposition dynamics and soil mesofauna community in southern Temperate Forests

Abstract

Biodiversity loss due to human disturbance in forests is driving changes in ecosystem functioning. Litter decomposition is one of the critical processes that regulate the carbon and nutrient cycle. The temperate *Nothofagus* forests of central-southern Chile are heavily degraded; however, it is unclear how this affects soil fauna and its effect on litter decomposition and nutrient cycling. The main objective of this study was to evaluate the role of soil mesofauna in the decomposition and release of nutrients in forests in different conservation states. Decomposition bags with mesh size 0.1 and 2 mm were installed in long-term research forest plots representing four conservation states: mature, secondary and degraded forest, and a reforested site. Litter decomposition and concentrations of C, N and P were evaluated monthly for one year, and the richness, abundance and diversity of the mesofauna were evaluated five times a year. We found that the contribution of mesofauna to decomposition was 20% higher in degraded forest compared to mature and secondary forest but was lower in the reforested prairie. This difference was related to changes in the composition of the fauna and its abundance. In addition, the mesofauna was associated with a higher release of C (9%), N (9%) and P (22%), but its effect on the C:N:P stoichiometry was variable between sites. We conclude that the mesofauna is a relevant factor in the litter decomposition in the degraded forest, and in the release of nutrients in all the sites. However, the loss of key orders can reduce their effect on these processes.

1. Introduction

The relationship between forest degradation, biodiversity and ecosystem functioning remains controversial (Cowan & Anderson 2019). Yet it is becoming increasingly urgent to assess due to the increasing loss and degradation of forests (Hansen et al., 2013). Litterfall represents a crucial pathway for the return of nutrients to the soil, and contributes a large part of the nutrients necessary for plant growth (Krishna & Mohan 2017). Before nutrients can be assimilated by plants, decomposition of organic matter and nutrient mineralization must occur. Hence, litter decomposition is recognized as an essential biogeochemical process for the carbon and nutrient cycling (Bohara et al., 2019). Forest degradation can alter the factors that influence litter production as well as decomposition processes controlled by microorganisms and fauna. However, the effect of forest degradation on this process and on the soil fauna has still been poorly studied (Paudel et al., 2015).

Litter decomposition is mainly controlled by climate, litter quality and decomposers (Krishna & Mohan 2017; Lavelle et al., 1993). Previous studies have shown that climate influences decomposition on a global and regional scale through precipitation and temperature (Aerts, 1997). Likewise, litter quality can determine rates of decomposition and nutrient release on a regional scale (Cornwell et al., 2008), however, the contribution of these factors depends on decomposition time and ranges of climate and litter traits considered (Canessa et al., 2021). It has been shown that high nutrient concentrations, particularly N and P, and low lignin concentrations and low C:N ratios can lead to higher decomposition rates (Yang & Chen 2009, Bakker et al., 2011). These factors affect the presence and activity of soil fauna, which in turn influence the overall decomposition rates and mineralization of nutrients at a local scale (Wall, et al., 2008). It is globally recognized that climate and litter quality explain about 65% of the variation in decomposition rates (García-Palacios et al., 2013). However, the contribution of soil fauna on litter decomposition depends on different factors at a local scale, such as composition, abundance and activity of organisms, which has been considerably less studied (González & Seastedt, 2001).

Although litter decomposition is recognized as a predominantly microbial process, soil fauna plays a key role by consuming and breaking up large amounts of litter, which stimulates the activity of decomposing microorganisms (Frouz 2018). On the other hand, mesofauna can exert a selective pressure depending on their feeding habits; for example, the fauna that feeds on fungal and bacterial hyphae can change the biomass, composition and competitive interactions between these groups, allowing the release of the immobilized nutrients and encourage their mineralization (Kaneko et al., 1998, Crowther et al., 2012). Experiments both in the field and in microcosm have found that the presence of macro and mesofauna can increase the mineralization of nitrogen, phosphorus and potassium (González & Seastedt 2001, Yang & Li 2020, Moreno et al., 2022), improving primary productivity (Huhta et al., 1991). However, the evidence is still contradictory, and more research is needed to elucidate the effects of fauna on the nutrient dynamics of decomposing litter (Frouz, 2018).

In particular, soil mesofauna is considered as an important component on litter decomposition because it includes groups of abundant and diverse soil organisms (Frouz, 2018). Although the importance of some particular groups of mesofauna in litter decomposition is recognized, empirical evidence of the role of faunal diversity on this process remains scarce (Gessner et al., 2010). A few studies have found that greater fauna abundance and diversity correlate with greater decomposition (Handa et al., 2014; Stone et al., 2020), although neutral effects have also been reported (Hättenschwiler et al., 2005). It is recognized that the presence of key species such as ants, termites and earthworms have a strong impact on decomposition (McGlynn & Poirson, 2012, Dechaine et al., 2005). Soil faunal communities and their effect on this process can vary between forest types, the litter quality and climatic region (García-Palacios et al., 2013). A study in humid tropical forests found that soil fauna can represent up to 66% of total forest decomposition (González & Seastedt, 2001), while this effect may be less in temperate ecosystems, where weather patterns seasonal conditions restrict the activity of the biota (Heneghan et al., 1999). A recent meta-analysis in Chinese temperate forests found a 28% reduction in decomposition when soil fauna was excluded (Zan et al., 2022). At a global level, by experiments with fauna exclusion, a 35% reduction in decomposition rates has been reported (Zhang et al., 2015). However, most of these studies have been carried out in forests of the northern hemisphere, while temperate forests of the southern hemisphere have been less studied. The latter is relevant because these forests have a lower input of nutrients by atmospheric deposition, for which the main source of nutrients such as N comes from the decomposition of organic matter and mineralization of elements (Pérez et al., 2003). Particularly, litter decomposition studies in Chile have focused on evaluating the effects of climate and litter traits (Canessa et al., 2021, Bahamonde et al., 2012, Vivanco & Austin 2019), while very few studies have evaluated the role of soil fauna and diversity on the decomposition process (Marín et al., 2021) In addition, studies have focused on undisturbed natural forests, so the decomposition process and the role of soil fauna have been poorly evaluated in forests altered by human disturbances (Paudel et al., 2015).

Forest degradation can alter above-ground vegetation and litter fauna community (Stone et al., 2020). Changes in forest structure due to logging or clearing create canopy openings exposing the forest floor to direct solar radiation, increasing temperature and decreasing soil moisture (Paudel et al., 2015). In addition, alteration in species composition can change the forest litter quality. These factors can alter the presence and activity of soil fauna, affecting litter decomposition and nutrient dynamics (García-Palacios et al., 2013, Moreno et al., 2022). Forest disturbance by logging has been documented to reduce the importance of fauna in decomposition, due to decreased abundance of key species (Ewers et al., 2015). The latter led to reduced decomposition rates in disturbed tropical forests (Stone et al., 2020). However, the response of this process is difficult to predict, as decomposition rates have been reported to increase, decrease, or even not change in different forest ecosystem types across the world (Bahamonde et al., 2012, Cowan & Anderson 2019, Yeong et al., 2016)

The *Nothofagus* forests of South America extend from 37°S to around 55°S in Chile and Argentina (Pollmann and Veblen, 2004) represent the largest extension of temperate forests in the southern hemisphere. They have been strongly degraded by human action due to practices such as selective logging and cattle grazing (Altamirano & Lara 2010, Alfaro et al., 2018, Zamorano-Elgueta et al., 2014, Atenas-Navarrete et al., 2021). Nutrient cycling in disturbed *Nothofagus* forests has been poorly evaluated, while the effect of fauna on litter decomposition and nutrient release remains largely unknown (Lusk et al., 2001). Studies in central-southern Chile found that the composition and diversity of detritivores fauna vary widely among different types of vegetation cover (Martinez & Casanueva, 1993) and are very sensitive to changes and disturbances in their habitat (Cifuentes-Croquevielle et al., 2020). However, changes in the composition and diversity of litter fauna in *Nothofagus* forests with different degrees of disturbance have not been evaluated.

This study seeks to i) evaluate the dynamics of litter production, ii) quantify the role of the mesofauna in the decomposition and mineralization of C, N, and P iii) identify the main groups of organisms that participate in litter decomposition in *Nothofagus* forests in different conservation states. We hypothesize that litter production is low in degraded sites, likewise, richness of orders, abundance, and diversity of mesofauna decreases in forests with low conservation status, decreasing their relative contribution to decomposition rates and nutrient mineralization.

2. Methods

2.1 Study site

This study was performed in Ranchillo Alto National Protected Land, located in the Andean foothills, 33 km from the town of Yungay, Ñuble Region (37°04' S and 71°39' W) (Figure 1A). The area has a humid temperate Mediterranean climate with an average annual rainfall of 3,000 mm, concentrated in the autumn and winter seasons (May to September). The average annual temperature is 13.5°C, with an average temperature of 3°C in the coldest month (July), and an average temperature of

22.5°C in the warmest month (January). There is a prolonged season of low temperatures, frequent frosts and the presence of snow for 3 to 5 months. The study plots are located at 1300-1400 m a.s.l., oriented towards the west and with a predominant slope of 10-20%. The soils are characterized by being very deep, well drained and with a silty loam texture. They are associated with the Yungay Pachic melanudands (Andisols) series, formed from recent volcanic ash deposited on glacio-fluvial material (CIREN 1999).

The vegetation is composed of temperate forests of *Nothofagus* species, which formed almost pure stands. The development of pure stands of *Nothofagus* is the result of large-scale natural disturbances, such as volcanic eruptions, landslides, and floods; and on a small scale, such as trees falling by the wind (Pollmann & Veblen 2004, Veblen et al., 1996). When canopy gaps become large enough, shade-intolerant species such as *Nothofagus alpina* (Poepp. & Endl.) and *Nothofagus obliqua* (Mirb.) can recruit and establish secondary forests (Pollmann 2002, Donoso et al., 1993).

Due to human disturbance, the study *Nothofagus* forests differed in terms of composition and structure, based on which different conservation states were determined: mature forest of *Nothofagus dombeyi* (Mirb) Oerst., represented a well-preserved forest dominated by trees from 10 to 20 m tall and with a majority DBH between 16 to 52 cm, with individuals that exceeded 100 cm diameter at breast height (DBH); secondary forest of *Nothofagus alpina* (Poepp. & Endl.) Oerst., disturbed by logging for firewood, charcoal and timber at least since 1950. Degraded forest is dominated by *Nothofagus obliqua* (Mirb.) Oerst., altered by logging, browsing, and cattle grazing for approximately 65 years; and a highly degraded site where forest was cleared for firewood use and cattle grazing, which was recently (2 years) reforested with *N. obliqua*, *N. alpina* and *N. dombeyi* (Figure 1C). Illegal intensive logging occurred since the 1950s and affected the entire forested area, which can be verified by the presence of cut tree stumps (Table 1). Currently, the most altered sites corresponded to the reforested site, and in lesser degree to the *N. obliqua* forest, since both were degraded by continuous and non-systemic grazing (Alfaro, et al. 2018). Since 2015, a management plan began to be applied that stopped illegal logging and regulated cattle grazing in the area.

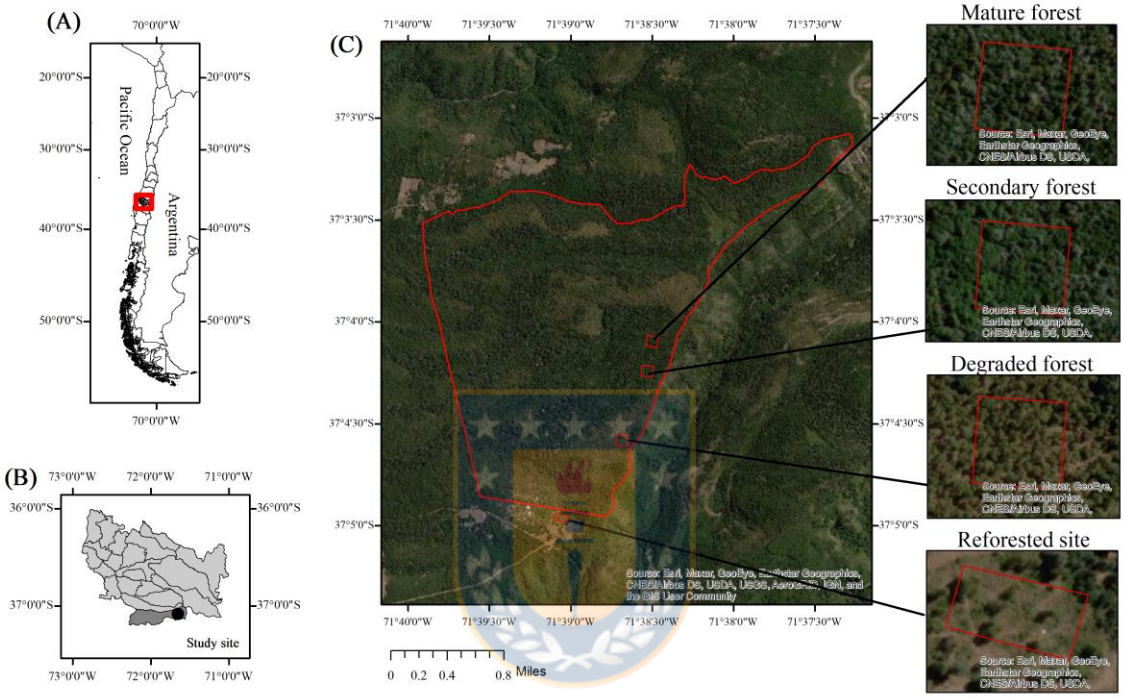

Figure 1. Map of Chile (A). Location of the study area in central Chile (B) (black point). Boundary of Ranchillo Alto estate and location of Long-Term Research Forest (LTER) plots (C). Image source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, and the GIS User Community.

Table 1. Characteristics of study forest: mature forest, secondary forest, and degraded *Nothofagus* forest and a reforested site. Yungay, Chile.

Characteristics	Mature forest	Secondary forest	Degraded forest	Reforested site

Conservation status	Well preserved	Altered	Degraded	Degraded
Composition [a]	*N. dombeyi* (97%) *N. obliqua* (3%)	*N. dombeyi* (48%) *N. alpina* (52%)	*N. obliqua* (100%)	*N. dombeyi* (61%) *N. obliqua* (39%)
Density (tree/ha)	572	610	136	43
Basal area (m^2/ha)	58.6	55.7	25.8	4.4
Tree stumps (N/ha)	26	84	18	75
Openness canopy (%)	7%	10%	53%	83%
Leaf Area Index [b]	3.5 (0.5)	3.8 (0.5)	1.4 (0.4)	0.5 (0.6)
Leaf functional trait	97% evergreen 3% deciduous	48% evergreen 52% deciduous	100% deciduous	61% evergreen 39% deciduous

[a] In parentheses is the percentage of dominance of each species

[b] In parentheses is the standard error.

2.2 Sampling design

Long-Term Ecological Research (LTER) plots of 100 x 100 m were established in each study condition. In each plot, we sampled litter fall and litter decomposition for 1 year, for which sub-sampling plots were established based on the GEM field manual (Marthews et al., 2014) for intensive census plots, which are explained in detail below.

2.2.1 Sampling of litter biomass

Twenty-five 10x10 m subsampling plots were established, in each one a 1x1 m litter collection trap was placed at the beginning of March 2021. The collection was carried out monthly from April 2021 to March 2022. The collection of samples during July was suspended because the presence of snow prevented the collection of litter. The biomass collected in each trap was stored in hermetic bags until arrival to the laboratory. The content was transferred to paper bags and placed on a convection stove at 65°C for 48 hours or until a constant weight was reached. Subsequently, the dry weight of each sample was determined.

2.2.2 Sampling of litter decomposition analyses

Sixteen 25x25 m subplots were established, of which eight were randomly selected for the installation of decomposition bags. Twelve 0.1 mm fine mesh bags and twelve 2.0 mm coarse mesh bags were installed in the center of each subplot. These mesh sizes were used to restrict and allow mesofauna access to decomposition bags, respectively (Bradford, et al. 2002). Each bag measured 20x20 cm and were filled with 10 ± 1 g of litter, which was collected from the mature, secondary and degraded forest floor during February 2021 and dried at 65°C to constant weight. Subsequently, the litter from each study site was homogenized and placed in decomposition bags. For the reforested site, a mixture of litter from the three forests mentioned above was used.

These bags were installed in early March 2021 between the litter layer and the mineral soil. Bag collection began a month after installation. A 0.1 mm mesh bag and a 2.0 mm mesh bag were collected monthly from each subplot for a year. Each bag was stored independently in hermetic bags until arrival at the laboratory, the leaves were cleaned of soil debris and dried at 65°C to constant weight.

Subsequently, dry weight was evaluated, and the decomposition rate was determined with the exponential model described by Olson:

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

Where X_0 are initial and X_1 final litter weight in a time t (Olson 1963).

2.2.3 Mesofauna sampling

Soil fauna sampling was performed five times a year, covering the seasons of fall, winter, spring, and summer. The contents of the bags of both mesh sizes were placed in Berlese-Tullgren extractors for 48 hours to remove the litter mesofauna. All extracted mesofauna were stored in 70% v/v alcohol, identified at order level and counted with a stereoscopic microscope (OLYMPUS SZ40). Mites were excluded from the analysis due to their small size (<0.1 mm) and because they were present in equal abundance in both mesh sizes. After the mesofauna extraction, the remaining litter was cleaned and dried at 65°C until constant weight, then the mass loss was determined.

Order richness, mesofauna abundance and diversity were evaluated using the Shannon–Wiener and and inverse Simpson diversity indices in R version 3.2.1 (Team 2013), for which the packages vegan v2.6-2 (Jari Oksanen et al., 2022) and BiodiversityR (Kindt and Coe, 2005) were used. In addition, the effect of fauna on litter mass loss was calculated by:

$$\boldsymbol{L_{fauna}} = \frac{\boldsymbol{L_{2.0}} - \boldsymbol{L_{0.1}}}{\boldsymbol{L_{2.0}}}$$

Where $L_{2.0}$ corresponds to the mass loss of 2.0 mm mesh bags, and $L_{0.1}$ to the mass loss of 0.1 mm mesh bags (Wang et al., 2015).

2.3 Nutritional analysis

The content of C, N and P of the decomposing litter was determined on each sampling date. For this, a composite sample was obtained with the litter from the decomposition bags for each study site, and for each mesh type. To evaluate C and N, the litter was pre-ground 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). Then, the C and N content were determined by the Dumas-TCD dry combustion method with a GSL solid sample preparation module (20-20 IRMS-GSL, SERCON® Limited, UK). Total P was determined by the calcination method for plant tissue (Sadzawka, et al. 2007). With these results, we calculated C: N, C: P, and N: P, on a mass basis.

The initial lignin concentration was determined following the methodology used by Mendonça et al. (2008). 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 with water to 3% and the mixture was autoclaved for 1 h at 121°C. The residual material was cooled and filtered, 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 (Mendonça, et al. 2008).

2.4 Monitoring of soil environmental parameters

We compared microclimatic soil conditions at the four study sites throughout the year. For this, a meteorological station was installed at the center of each plot, which was associated with Soil Moisture and Temperature Sensors (CS655, CAMPBELL SCIENTIFIC, INC.) to measure the temperature and volumetric water content in the soil at a depth of 30 cm. In each plot the data was recorded in triplicate daily every 15 minutes. These data were analyzed on a monthly level.

2.5 Data analysis

All the statistical analyses were executed in R version 3.2.1 (Team, 2013). To compare the initial concentrations of C, N, P, lignin and C/N and N/P ratios, Welch's T tests were performed to compare unequal variance samples, since the data met the normality assumptions but not homoscedasticity. The annual litterfall met the normality and homoscedasticity requirements according to the Shapiro-Wilks test and the Levene test, for which an ANOVA was applied. Because significant differences were found between groups, a Tukey test was performed. Means and standard error were reported in all the analyses.

A generalized linear model (GLM) was used to detect differences in the decomposition rate, remaining mass and C, N and P remaining between study sites, time and mesofauna treatment. Likewise, a GLM was used to compare the richness, abundance and diversity of mesofauna between the same factors mentioned above. All GLM used the DescTools package (Signorell et al., 2022) and “glm” function with a Gaussian error distribution. We also compared the fit between models by Akaike Information Criterion (AIC) and were checked for homoscedasticity and normality of residuals.

The variation between the study sites in the composition of the mesofauna for each sampling date was visualized with a non-metric multidimensional scaling (NMDS). Each date had between 14 to 16 orders of mesofauna and 8 sites corresponding to the samples of each forest. This was run using "metaMDS" of vegan, with Bray-Curtis distances between sites. To test whether the composition of the mesofauna differed significantly between sites, an analysis of similarity (ANOSIM) with 9999 permutations was used, using the function "anosim" in vegan package. In addition, an analysis of indicator species was carried out to identify the orders that were significantly associated with each site. For this, we used the indicspecies package (Cáceres and Legendre, 2009) and the "multipatt" function.

3. Results

Soil temperature at 30 cm depth was higher in the degraded forest and the reforested site from late spring and throughout the summer. However, in the coldest winter months (July and August) the mature and secondary forest had higher temperatures. The soil water content was higher in the reforested site during almost the whole study year (Figure 2).

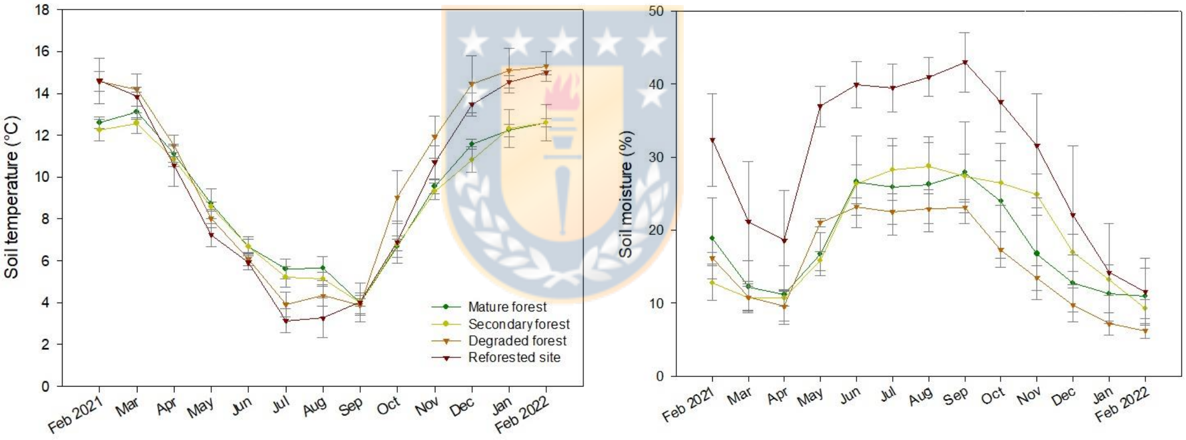

Figure 2. Soil temperature (°C) and soil moisture (%) at 30 cm deep in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile between February 2021 to February 2022.

Initial litter nutrient concentrations varied between forest types and were higher for N and P in the degraded forest and reforested site, respectively. The highest lignin concentrations were found in the reforested site. On the other hand, the C/N ratios were higher in the mature and secondary forest, while the N/P ratios were higher in the degraded forest. On the other hand, the lignin/N ratio was higher in the reforested site and mature forest, and lower in the degraded forest (Table 2). This index reflects a greater availability of N in the litter of degraded forest, and therefore, a higher quality of this material.

Table 2. Initial content of C, N, P, lignin and C:N, N:P and Lignin:N ratios in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile. Different letters indicate significant differences ($p<0.05$).

Forest type	C (%)	N (%)	P (%)	Lignin (%)	C:N	N:P	Lignin:N
Mature forest	50.70^{a}	1.04^{a}	0.053^{a}	42.61^{a}	56.4^{a}	43.4^{a}	40.6^{a}
Secondary forest	48.18^{b}	1.06^{b}	0.059^{b}	41.10^{b}	53.2^{b}	39.5^{b}	38.9^{b}
Degraded forest	49.20^{ab}	1.33^{c}	0.057^{c}	45.40^{c}	43.2^{c}	51.9^{c}	34.2^{c}
Reforested site	46.04^{c}	1.09^{d}	0.063^{d}	45.60^{c}	49.3^{d}	38.1^{b}	41.9^{d}

The mean annual litterfall was higher in the mature and secondary forest, where a litterfall of 4.6 and 4.1 Mg ha^{-1} year^{-1}, respectively, was found. The litterfall in the degraded forest was half of these values, reaching 2.0 Mg ha^{-1} year^{-1}, while the reforested site had a mean annual of 0.2 Mg ha^{-1} year^{-1} (Table 3).

Table 3. Mean annual litterfall (Mg ha^{-1} year^{-1}) and standard error (SE) in mature, secondary, and degraded *Nothofagus* forests and a reforested site from March 2021 to February 2022 in central Chile (n=25). Different letters indicate significant differences ($p<0.05$).

Forest type	Biomass (Mg ha^{-1} year^{-1})	SE
Mature forest	4.584^{a}	0.572
Secondary forest	4.138^{a}	0.531
Degraded forest	2.035^{b}	0.415
Reforested site	0.189^{c}	0.054

All forests followed a similar litterfall pattern, which had an increase in autumn and a second increase in winter, with a minimum litterfall during spring. However, the reforested site had only a slight increase in litterfall in autumn and maintained a low and constant fall for the rest of the year (Figure 3).

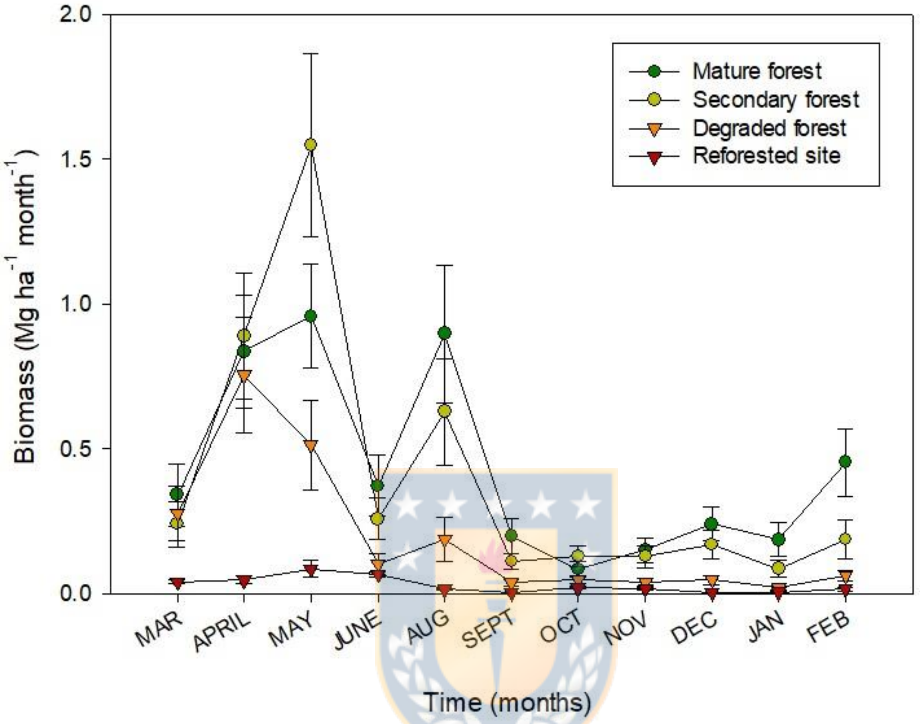

Figure 3. Litter biomass (Mg ha^{-1} month^{-1}) in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile.

Decomposition time, forest type, and mesofauna treatment all had significant effects on the remaining mass of decomposing litter (p <0 .001) (Table 4). After one year, the decomposition rate (k) was higher in the treatment with inclusion of mesofauna for all forest types. Likewise, the remaining litter mass was significantly lower when the mesofauna was included.

Decomposition rates varied between forest types according to the mesofauna exclusion treatment. In the absence of mesofauna, the decomposition rates were higher in the mature and secondary forest, intermediate in the degraded forest and lower in the reforested site. However, including mesofauna, the decomposition rates of the degraded forest equaled those of the mature and secondary forest. The same happened with the remaining mass (Table 5).

The effect of the mesofauna was greater in the degraded forest, where litter decomposition increased by 28.5%, while in the mature and secondary forest it had a similar effect, increasing decomposition by 8.7%. This effect was lowest at the reforested site, where decomposition only increased by 3.9% (Table 5).

Table 4. GLM results in relation to factors decomposition time, forest type and mesofauna treatment on the remaining mass. Significance levels: *** $p<0.001$

Factor	df	F	p
Decomposition time	1	3948.4	<0.001 ***
Forest type	3	195.28	<0.001 ***
Mesofauna treatment	1	255.72	<0.001 ***

Table 5. Mean decomposition rate (k) and remaining mass (%) after 360 days of decomposition in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile. Lowercase letters indicate significant differences between treatments with and without mesofauna within each forest, while capital letters indicate differences between forest types ($p<0.05$)

Forest type	Decomposition rate (k)		Remaining mass (%)		Mesofauna effect (%)
	Without mesofauna	With mesofauna	Without mesofauna	With mesofauna	
Mature forest	0.0014^{aA}	0.0016^{bA}	60.24^{aA}	55.44^{bA}	8.66
Secondary forest	0.0013^{aA}	0.0016^{bA}	61.67^{aA}	56.76^{bA}	8.65
Degraded forest	0.0010^{aB}	0.0017^{bA}	70.91^{aB}	55.19^{bA}	28.48

Reforested site	0.0008^{aC}	0.0009^{bB}	74.31^{aB}	71.52^{bB}	3.90

The effect of mesofauna on litter decomposition varied between forest conditions and over time. During early winter (month 4) a decrease in the effect of mesofauna on decomposition was observed; however, during subsequent months the remaining mass was significantly lower in the presence of mesofauna for mature, secondary and degraded forest. The effect of mesofauna remained relatively constant over time in mature and secondary forest; nevertheless, in degraded forest this effect increased since early spring. In the reforested site the effect of the mesofauna was less clear, and differences were found only in some months (Figure 4).

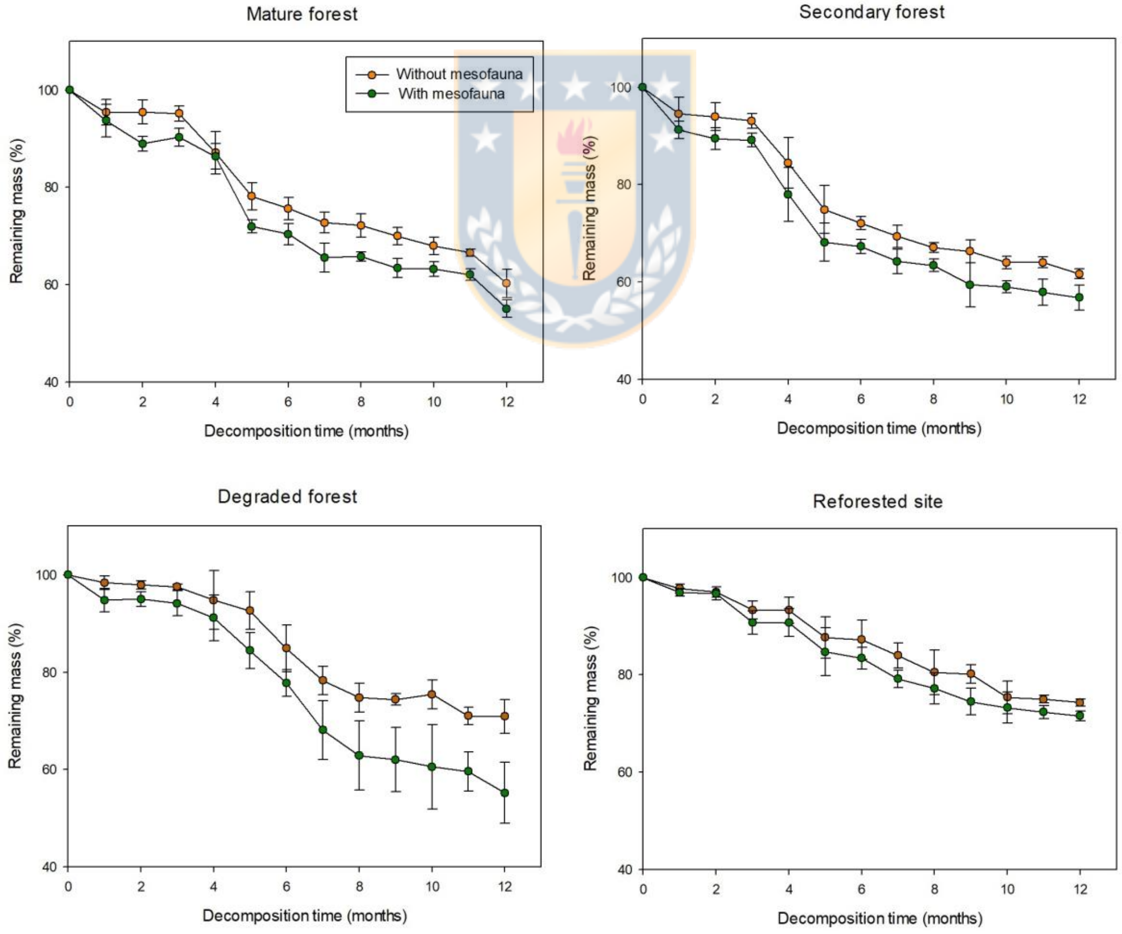

Figure 4. Remaining litter mass (%) without and with mesofauna in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile. The orange circles represent the mean of the treatment without mesofauna, and the green circles the treatment with mesofauna.

The mass of C remaining in the decomposition bags showed a consistent decrease over time, and similarly to the remaining mass, and it was lower in the treatment with inclusion of mesofauna for all forest conditions (Figure 5). On the other hand, the mass of N and P remaining also showed a decrease in the treatment with mesofauna, although they followed less clear release and immobilization dynamics over time (Supplementary material).

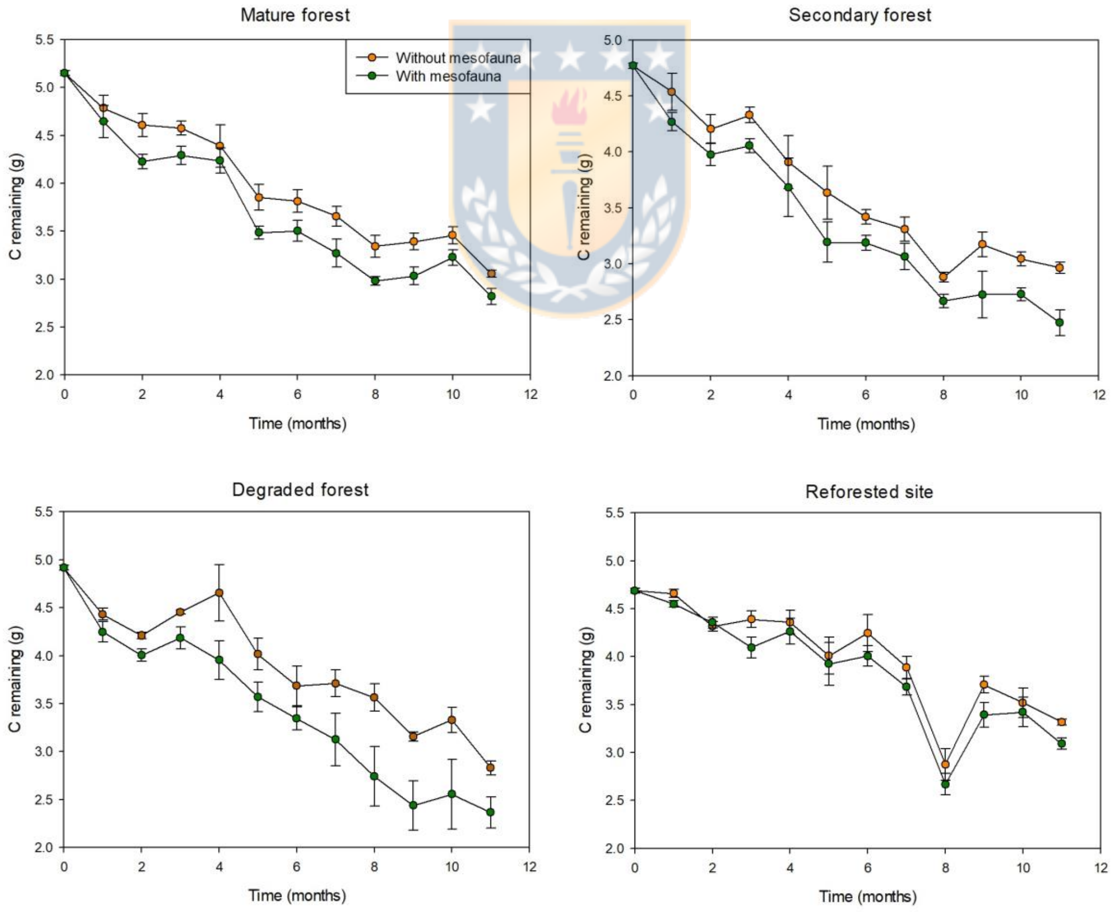

Figure 5. Remaining carbon mass (g) in the decomposition bags without and with mesofauna in mature, secondary, and degraded *Nothofagus* forests and a reforested site.

The C:N ratio of the decomposing litter varied according to the forest type and the mesofauna treatment. The mature forest presented lower C:N ratios throughout the year in the presence of mesofauna; however, the secondary forest showed an increase in the C:N ratio when the mesofauna was included. The degraded forest and the reforested site did not show a clear difference between the mesofauna treatments. All forest types showed a decrease in the C:N ratio towards the end of the study year, although they showed variable increases throughout the year (Figure 6).

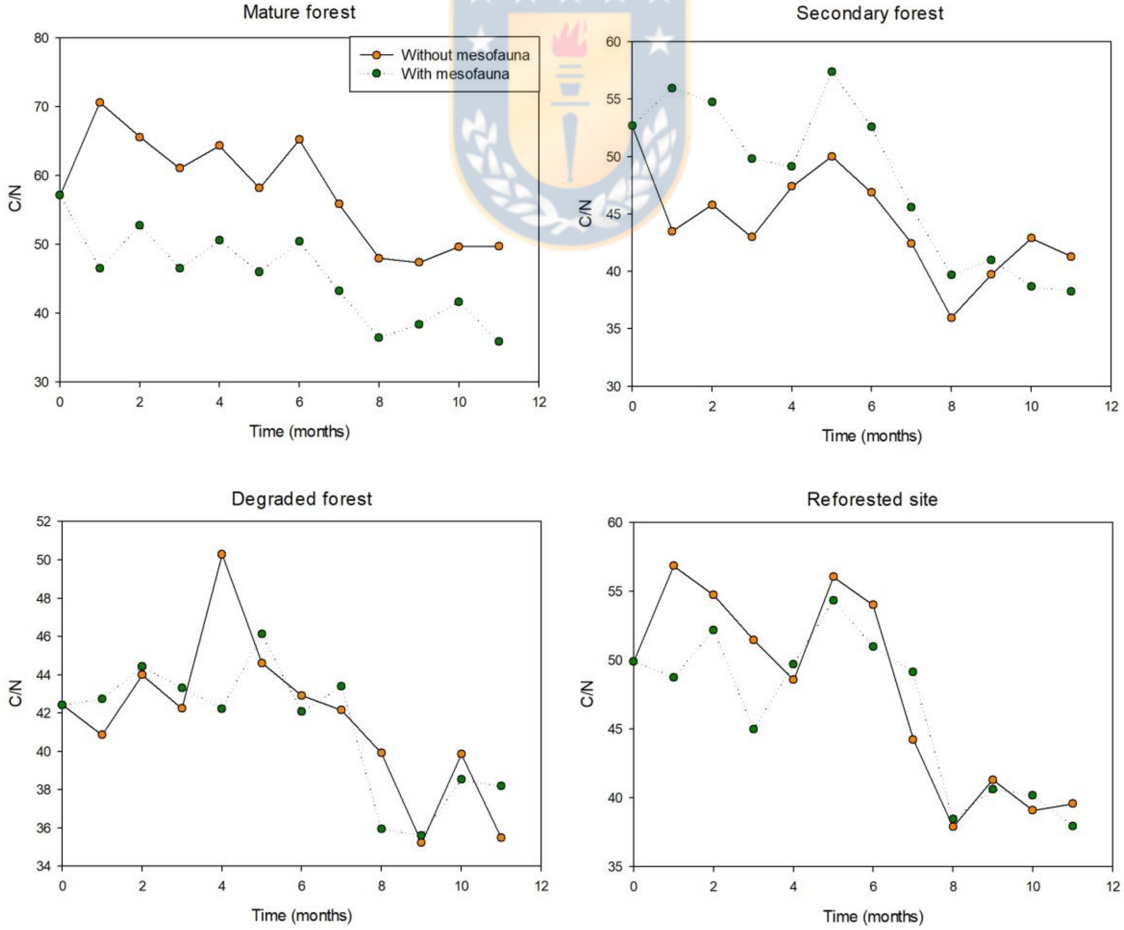

Figure 6. C:N ratio of the decomposing litter in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile.

The C:P ratio showed an initial increase in all forest types, followed by a decrease towards the end of the study year. In all forest types, the C:P ratio was higher with the presence of mesofauna, although the values approached those of the treatment without mesofauna towards the end of the year (Figure 7). On the other hand, the N:P ratio had a similar dynamic to the C:P, with an initial increase followed by a decrease over time. In the mature forest, this ratio was always higher for the treatment with mesofauna, while the other forests showed a similar pattern until early spring, after which the N:P ratio was equal between the treatment with and without mesofauna (Figure 8).

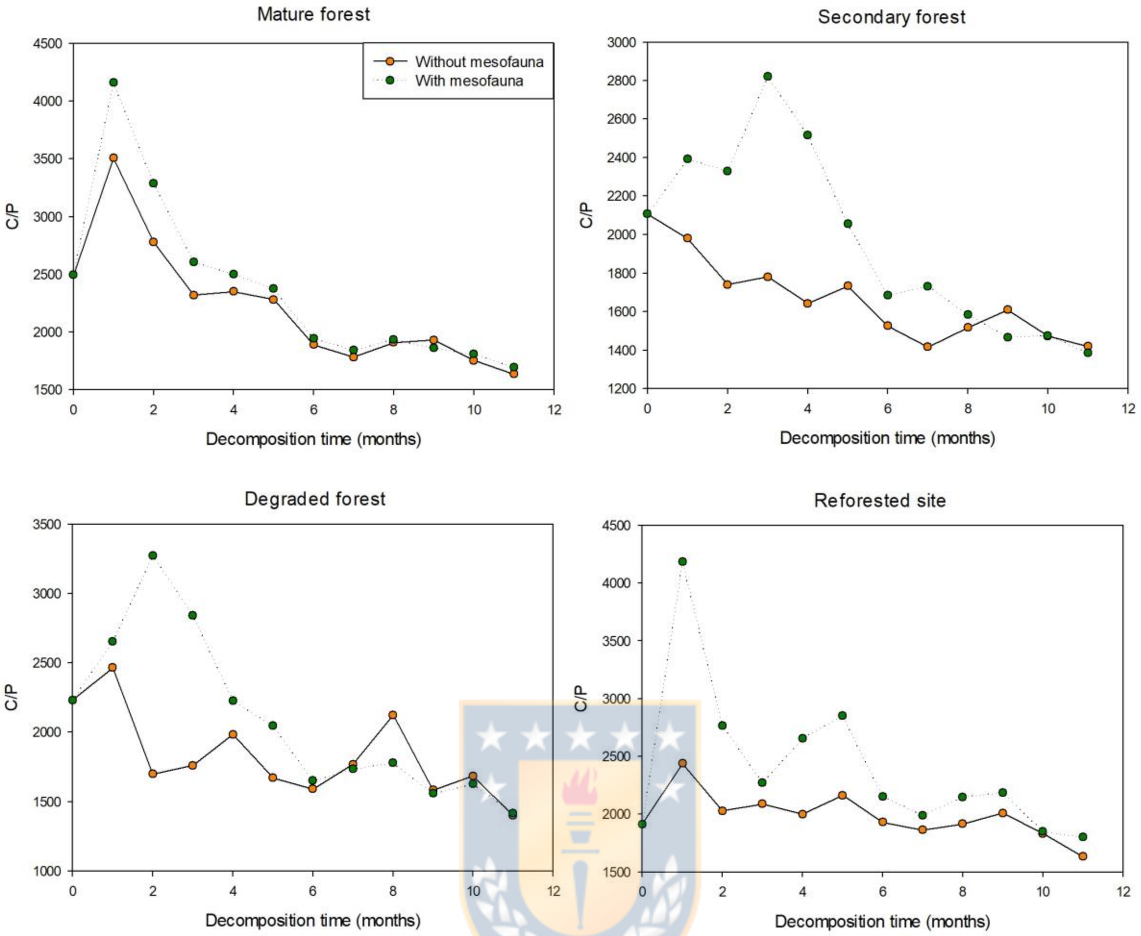

Figure 7. C:P ratio of the decomposing litter in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile.

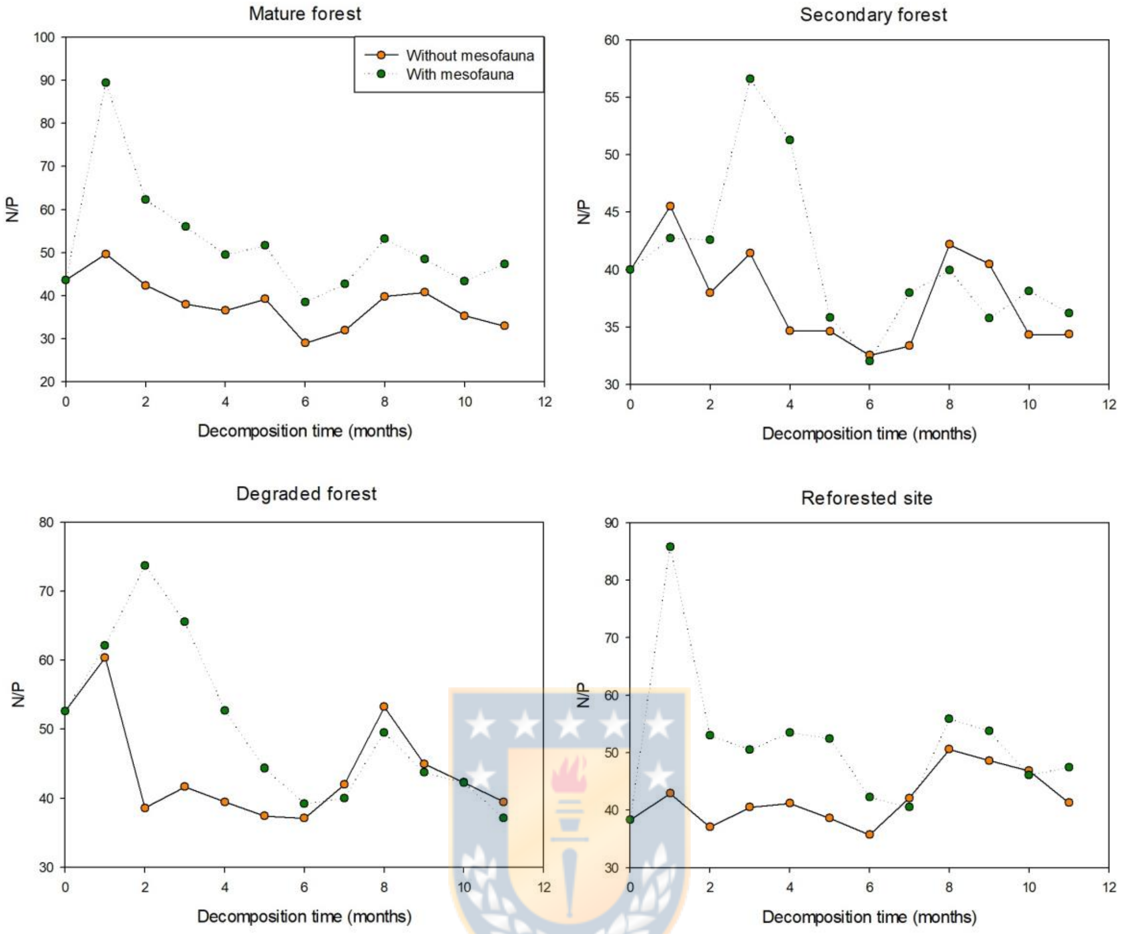

Figure 8. N:P ratio of the decomposing litter in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile.

In all months, both the richness and the abundance of mesofauna were lower in the exclusion treatment in contrast to the mesofauna inclusion treatment. Order richness in the treatment with mesofauna was similar among all forest types, with slight variations between months. Almost every month showed a higher richness for the mature, secondary and degraded forest, and a lower richness in the reforested site, except in winter (July) (Figure 9). Mesofauna abundance varied between months, being higher between winter and spring (July and November), and decreased towards January in summer. Abundance remained higher among mature, secondary, and degraded forests, varying by month, and was lower at the reforested site during the last three months (Figure 10). The Shannon diversity index only showed significant differences in September (spring), where it was lower in secondary forest, and in January (summer), where it was higher in mature and secondary forest, and lower in degraded forest and reforested site. The Simpson diversity index showed a lower dominance of species in the degraded forest and reforested site in November, while in January these results were reversed, finding a lower dominance in the mature and secondary forest.

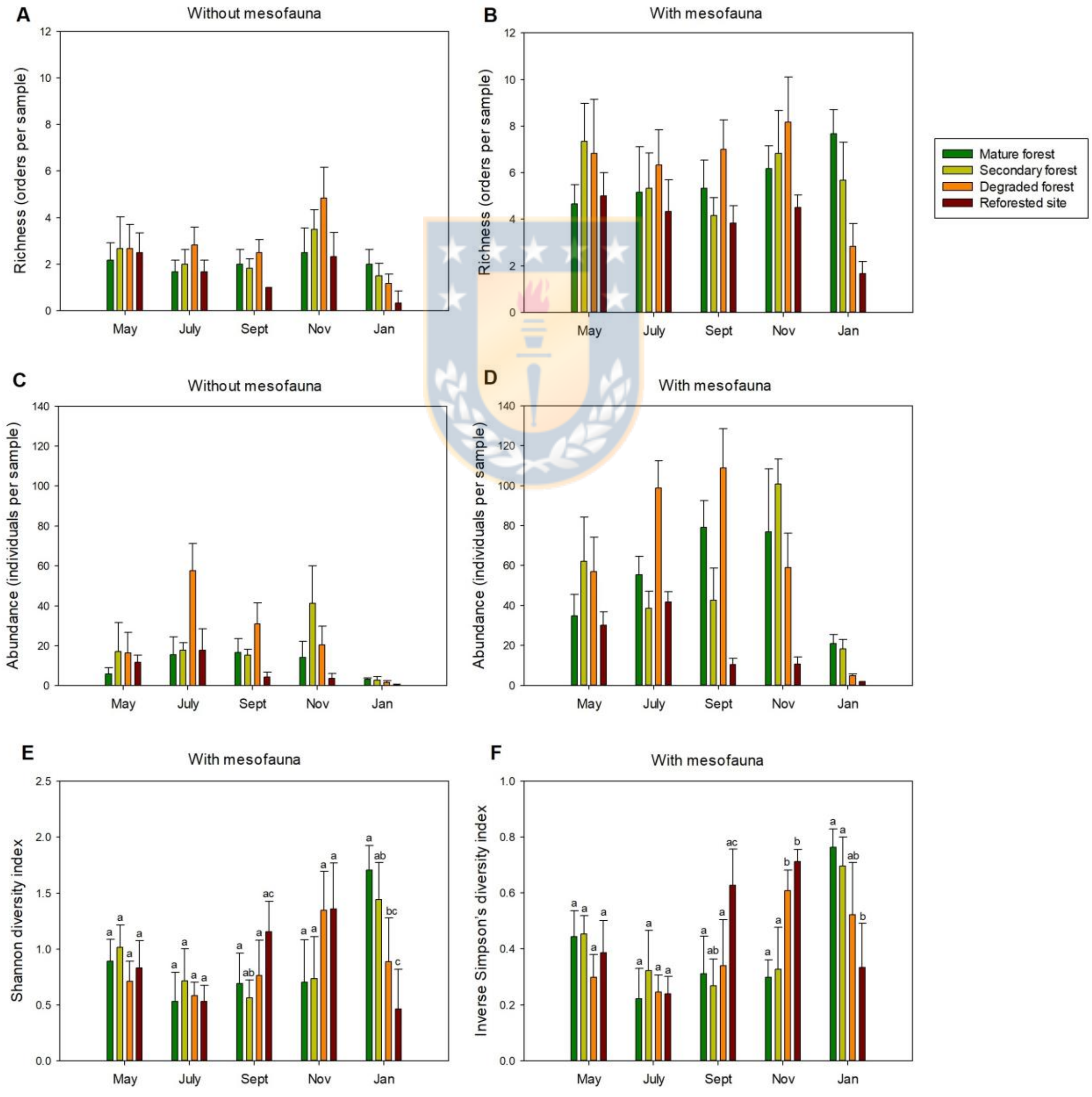

Figure 9. Mesofauna richness with A) exclusion and B) without exclusion of mesofauna; Abundance with C) exclusion and D) without exclusion of mesofauna; E) Shannon diversity index and F) Inverse Simpson's diversity index without exclusion of mesofauna throughout the year.

The NMDS ordinations show the pattern of similarities between sites according to the composition of the mesofauna. They revealed a clear separation between sites for all months, except for July where there is less differentiation. Despite this, ANOSIM indicated significant differences in the composition of mesofauna between sites for all months ($p<0.01$). In particular, September and January showed a differentiation between all sites, while in the other months the mature, secondary and degraded forest showed greater similarity. The reforested site showed a clear differentiation with all forest types in the last three months, while in May and July its composition was similar to that of the degraded forest (Figure 12).

The Indicator Species Analysis provided the list of orders that drive the differences in the communities between the study sites (Figure 13). Significant differences were found in the orders between the sites over time ($p<0.05$), and there were also significant differences in the composition of the communities of each site between months. Between autumn and spring, all sites had a higher relative abundance of Collembola, except the reforested site, which had a higher abundance of orders such as Hymenoptera, Pseudoscorpionida, Isopoda and Psocoptera. In summer the relative abundance of Collembola decreased, then other groups such as Lepidoptera, Psocoptera, Myriapoda, Hemiptera and Anareae increased in abundance. Forest types differed in relative abundance of Coleoptera, Myriapoda, Diptera, Anareae, Isopoda, and Pseudoescorpionida over the months.

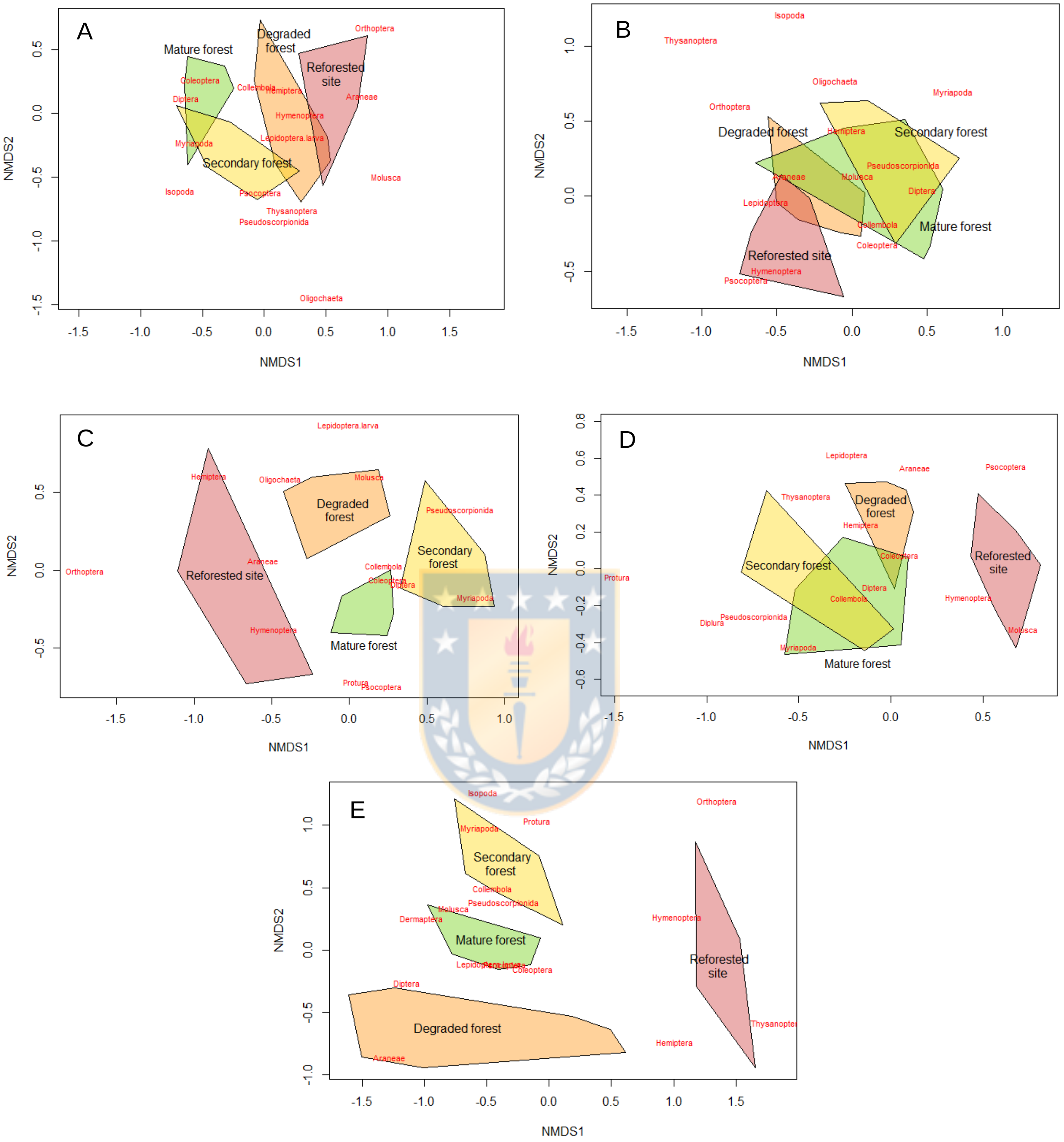

Figure 12. Non-metric multidimensional scaling of mesofauna orders (NMDS) in May (A), July (B), September (C), November (D) and January (E). Polygons represent the union between sampling plots of each forest (green=mature forest, yellow=secondary forest, orange=degraded forest, red=reforested site)

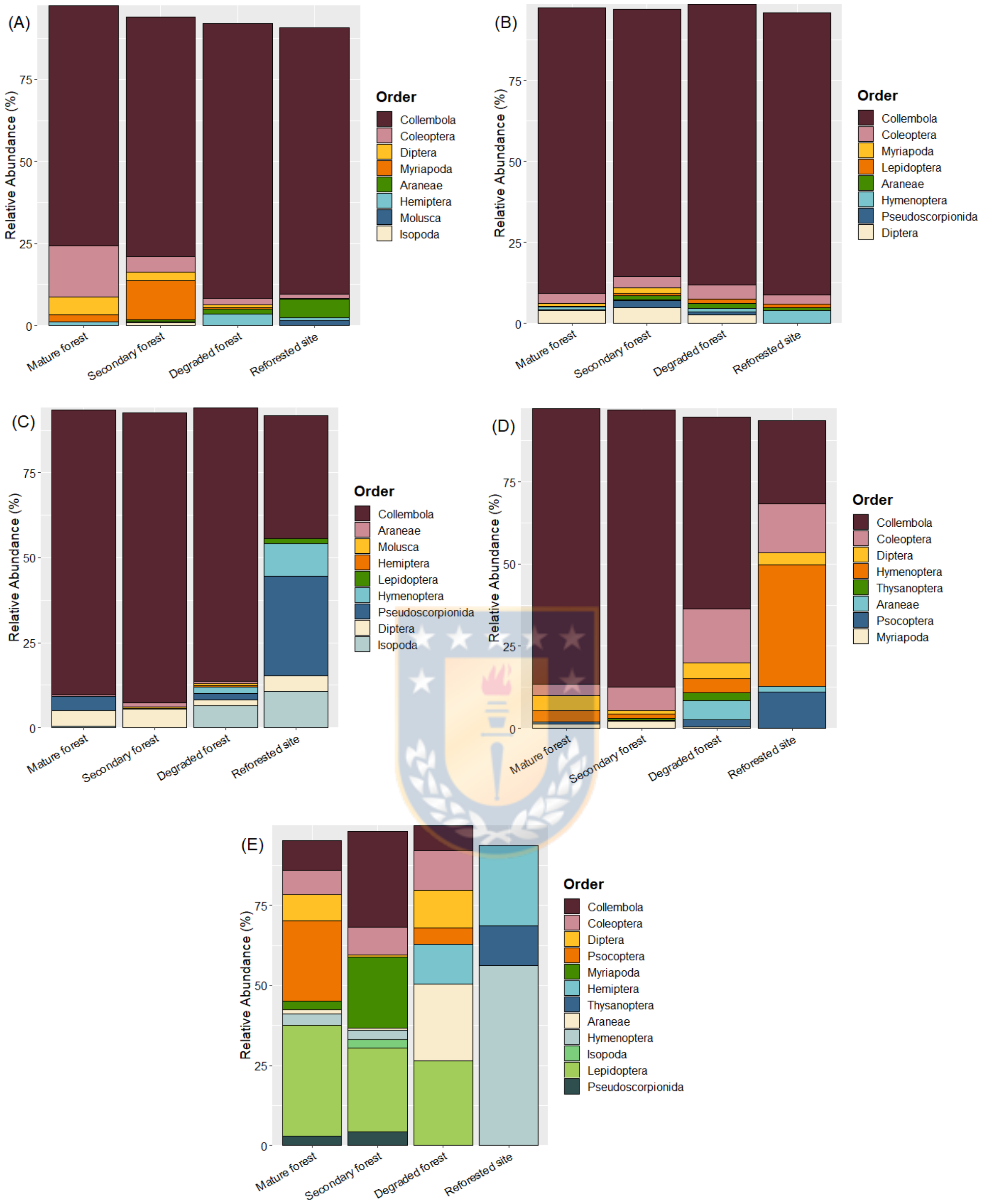

Figure 13. Relative abundance (%) of mesofauna in May (A), July (B), September (C), November (D) and January (E) in mature, secondary, and degraded *Nothofagus* forests and a reforested site in central Chile.

4. Discussion

Our results support the hypothesis that the most degraded sites (i.e., degraded forest and the reforested site), have less litterfall and slower decomposition. However, the richness, abundance and diversity of mesofauna in the degraded forest equaled that of the mature and secondary forest during almost all the sampling months, while only the recently reforested prairie plot showed a decrease in richness and abundance. The composition of mesofauna was different among all study LTER plots but remained similar for the three forested conditions. Contrary to expectations, the contribution of the mesofauna to litter decomposition was greater in the degraded forest plot and lowest in the reforested plot. C and P concentrations decreased in presence of mesofauna across conditions while the dynamics of N was less clear. Below we provide a more detailed discussion of our main findings.

4.1. Litter production

Annual litterfall was slightly lower than the range reported for temperate broadleaf forests on a global scale (4.7 to 6.0 Mg ha-1 yr-1) (Zhang et al., 2014), but remained within the range observed in previous studies in *Nothofagus* forests (Staelens et al., 2011). Mature and secondary forest showed similar annual litter biomass and fall patterns, despite the fact that mature forest is predominantly evergreen, while secondary forest was 52% deciduous. This difference may explain the higher peak fall of litter during the fall for the secondary forest. In contrast, the mature forest had two similar peaks of litterfall in autumn and winter, the latter possibly due to windfall. The degraded forest was mostly deciduous, so it also had a higher litterfall in autumn, yet its annual litter biomass was half in relation to mature and secondary forest, possibly due to its lower density of trees and greater canopy opening (Hirabuki, 1991). On the other hand, the reforested site presented the lowest litterfall throughout the study year, which coincides with its low density of trees and a canopy opening of 83%. It should be noted that despite the fact that it was reforested two years ago, the individuals have not yet reached a height or development sufficient to close their canopy. The lower litterfall in the degraded forest and reforested site decreases the input of nutrients and carbon that enter the soil, which can affect soil organisms and limit plant growth (Krishna and Mohan, 2017). Previous studies in forests disturbed by anthropic action have shown a decrease in litterfall (Staelens et al., 2011, Oraon et al., 2018), which coincides with the results obtained in our study.

4.2 Mesofauna effect on litter decomposition and nutrient dynamics

Previous studies in temperate forests have found that the effect of mesofauna on litter decomposition is approximately 28%, although there are also studies that did not find a significant effect on decomposition rates for these ecosystems (Heneghan et al., 1999). In our study, the effect of the mesofauna varied according to the forest conservation state, from 8.7% in the mature and secondary forest to 28.5% in the degraded forest and was the lowest in the newly reforested site with 3.9%. Despite the high amount of litterfall in mature and secondary forest, which represents habitat and food source for fauna (Sayer et al., 2010), the lower contribution of the fauna to the litter decomposition may be due to the low quality of the material for its consumption (García-Palacios et al., 2013), particularly the high C:N ratios. In contrast, the degraded forest showed a higher litter quality, especially a higher concentration of N, lower C:N and Lignin:N ratios, which could improve its decomposition by the mesofauna (Handa et al., 2014).

The difference in the effect of the mesofauna between sites may also be due to differences in the microclimate, especially in the reforested site (prairie), which had a reduced number of trees and thus a lower canopy cover. This could lead to increased direct solar radiation, which has been reported to inhibit the activity of soil biota (fauna and microorganisms) (Zhang and Zak, 1995), and is also associated with reduced decomposition rates (Yeong et al., 2016, Bravo-Oviedo et al., 2017). Although the reforested site maintains a higher soil water content throughout the year, this factor does not seem to have improved decomposition rates. Likewise, the quality of the initial litter had intermediate values in relation to the other sites, therefore, it follows that a limiting factor on this process may be the soil biota, in particular, the lack of key decomposers and the low abundance of mesofauna found. This agrees with the results of Stone et al. (2020), who found a decrease in the abundance of macro and mesodecomposers, and with it, lower rates of decomposition in degraded pastures.

The degraded forest maintained a higher soil temperature during the warm season than that of the mature and secondary forest, and like that of the reforested site, despite its greater tree cover. But in contrast to the reforested site, soil water content was lower throughout the year. Despite these adverse conditions, the degraded forest had a similar richness and abundance of mesofauna, and even higher in some months than the mature and secondary forest. We note that this may be due to the presence of a dense understory composed of *Chusquea quila*, a fast-growing bamboo species that colonize open forests (Fajardo and de Graaf, 2004). Because understory vegetation provides shelter, food, shade, and microhabitat for soil mesofauna (Taki et al., 2010), this could influence its presence and enhance the effect of mesofauna on decomposition (Li et al., 2021).

The effect of the mesofauna was not continuous over time but had variations between months. In particular, its contribution decreased at the beginning of the cold season between autumn and winter (fourth month) in all forest condition (Figure 4), which may be related to a decrease in the mesofauna activity due to restrictive weather conditions, especially low temperatures (Wall et al., 2008). The greatest decreases in the remaining mass occur in the autumn for all types of forest, despite the fact that the contribution of the mesofauna was not significant during that period. This may be due to increased activity of soil microorganisms, especially decomposing fungi (Voříšková and Baldrian 2013) which requires further study.
On the other hand, in the degraded forest a high drop in remnant mass was maintained throughout the winter until early spring (fourth to eighth month), where

there was an increased effect of mesofauna on decomposition rates. This could be due to a greater activity of individuals of Collembola, Coleoptera and Lepidoptera, that were found to be significantly associated with this forest condition.

Previous studies have found that differences in the effect of mesofauna on decomposition rates between forests are related to the difference in composition, richness, abundance, and diversity of soil fauna (González and Seastedt, 2000). In our study, the abundance of mesofauna was lower in the reforested site, which presented the lowest values of mass loss and mesofauna effect. Particularly, we noticed a decrease in the abundance of key decomposers, such as Collembola, Coleoptera, Diptera and Lepidoptera larvae (Figure 13). This is consistent with previous studies that found a decrease in the abundance of key functional groups in logged forests (Ewers et al., 2015), which was associated with less litter decomposition. Secondly, the degraded forest presented a greater abundance of mesofauna between winter and spring and presented a greater effect of the mesofauna on decomposition. However, it should be noted that the abundance in spring did not differ from the mature forest, so the difference in the mesofauna effect cannot be explained only by the difference in abundance. Another factor that may explain this is the presence of orders such as Coleoptera, Diptera and Lepidoptera, which were strongly associated with this forest since early spring. These orders are composed of detritivorous organisms in their larval phase, which can consume and break large amounts of litter. For this reason they have been considered as a key functional group for the decomposition and cycling of nutrients (Frouz, 2018).

No consistent relationships were found with order richness, thus suggesting that the presence of key groups, such as detritivores, may be generating differences in litter decomposition more than the number of orders (Moreno et al., 2022, Heemsbergen et al., 2004). Finally, different studies have reported a direct relationship between soil fauna diversity and decomposition rates (Handa et al., 2014, González et al., 2014). However, the indices evaluated in this study did not show a pattern consistent with litter decomposition.

Mesofauna decrease the mass of C remaining in the litter at all study sites (except in the reforested site). This is consistent with other studies conducted in temperate forests, which have found a significant loss of C and N in litter in the presence of microbes and mesofauna (García-Palacios et al., 2016). Likewise, the mass of N and P remaining remained lower for the treatment with mesofauna during almost the entire sampling year (Supplementary Material), although these relationships in the secondary forest and reforested site were less clear for N. Despite the latter, a clear effect of the treatment with mesofauna was found on the mass of P remaining in the reforested site, despite its low decomposition. A widely accepted mechanism that explains this is related to the consumption of microorganisms by the fauna, which allows the release of nutrients immobilized by them, leading to greater efficiency in the mineralization of nutrients (Frouz, 2018).

The C:N ratio was lower when the mesofauna was present in the mature forest, which coincides with previous studies in tropical forests (González and Seastedt, 2001). However, an opposite behavior was observed in the secondary forest. These differences may be due to the different feeding habits of the mesofauna, which may impact the release of N (Moreno et al., 2022). It is possible that the mesofauna present in the secondary forest consumes litter with higher N content, which could increase the C:N ratio of this material. Associated with this forest, a greater abundance of Myriapoda was found, an order that was absent or in low abundance in the other plots. A previous study conducted in Canadian forests found that the presence and activity of Myriapoda significantly increased the mineralization and release of N (Cárcamo et al., 2000), so this may be a key group that affected the C:N ratio.

The dynamics in the C:P and N:P ratio were similar for all forest types over time, with an increment in these ratios under the presence of mesofauna. This may be due to a higher consumption and release of P by the activity of these organisms (Moore et al., 2006). The difference in the C:P and N:P ratio with and without mesofauna decreased over time, which may be due to the incorporation of P from exogenous sources for both the bags with and without mesofauna. Previous studies have found that the effect of soil fauna on P release is influenced by local-scale climate and initial litter quality (Peng et al., 2019). However, despite the fact that the quality of the initial litter in our study was different, and the microenvironmental conditions of the soil also varied between some sites, the dynamics of P in the presence of fauna remained relatively similar between sites.

Finally, a significant differentiation was observed in the composition of the mesofauna communities between sites, in addition, the NMDS results showed a clear seasonal dynamic in the communities throughout the year. The difference between sites may be related to the quantity and quality of the litter, which affects the structure of the microhabitat and the availability of resources (Hättenschwiler et al., 2005). Mature, secondary and degraded forest were associated with a higher abundance of detritivorous mesofauna, especially Collembola, Myriapoda, Coleoptera, Diptera and Lepidoptera larvae. In contrast, the reforested site was found to be mostly associated with groups of predatory mesofauna such as Araneae and Pseudoscorpionida, and other generalist groups such as Hymenoptera, Hemiptera and Thysanoptera. This is consistent with previous studies, which have reported a change in the composition of the fauna towards more generalist groups, and a lower abundance in forests disturbed by logging or canopy removal (Zhao et al., 2011, Martínez-Falcón et al., 2015, Richardson et al., 2010).

5. Conclusions

The effect of mesofauna on litter decomposition of *Nothofagus* forests varies according to the state of conservation of these sites. The mesofauna had a greater effect on decomposition in the degraded forest plot, allowing decomposition values close to those of mature and secondary forest. This proves that the mesofauna can be a key factor in the recovery of the decomposition process in degraded *Nothofagus* forests.

Mesofauna effect on P mineralization did not seem to be affected by the forest condition, since it showed a similar effect in all forest conditions and in the reforested site. This highlights the important role of the mesofauna in the release of P in the degraded forest and the reforested site. Secondly, its effect on N dynamics differed between forest types, possibly due to the difference in its community composition.

The abundance and composition of the mesofauna differed markedly in the reforested site (prairie) compared to the other forest types. A loss of key orders that drive decomposition processes was evidenced at this site, which slowed down this process. Nevertheless, to better understand the effect of mesofauna diversity on decomposition, a more detailed identification of species may be necessary, along with a separation of other factors that affect decomposition rates such as litter quality and climate.

Finally, in this study we identified key mesofauna orders affecting decomposition and nutrient release processes in *Nothofagus* forests, however a more complete understanding of the ecology of these groups may increase our understanding of nutrient cycling functioning in these ecosystems. Many of these species that represent key organisms for soil processes remain little explored.

Acknowledgments

We thank the collaboration project N 73-J-21-ER2 between ENEL-Universidad de Concepción and Foresta Nativa, which supported the financing of this study, and the Facultad de Ciencias Forestales of the Universidad de Concepción for allowing us to carry out this study in the Ranchillo Alto National Protected Property. We also thank all the students and colleagues who helped us in the fieldwork and processing of the samples. Special mention to Dr. Regis Teixeira and Claudia Vidal from the

Centro de Biotecnología of the Universidad de Concepción for their support in determining lignin.

References

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos, 439-449.

Alfaro, M., Dube, F., & Zagal, E. (2018). Soil quality indicators in an Andisol under different tree covers in disturbed *Nothofagus* forests. Chilean journal of agricultural research, 78(1), 106-116.

Altamirano, A., & Lara, A. (2010). Deforestación en ecosistemas templados de la precordillera andina del centro-sur de Chile. Bosque (Valdivia), 31(1), 53-64.

Atenas-Navarrete, A., Aburto, F., González-Rocha, G., Guzmán, C. M., Schmidt, R., Scow, K., & Lara, E. Á. (2021). Anthropogenic Disturbances Alter Surface Soil Biogeochemical Pools and Microbial Diversity in Andean Temperate Forests. Available at SSRN 4030349.

Bahamonde, H. A., Peri, P. L., Alvarez, R., Barneix, A., Moretto, A., & Pastur, G. M. (2012). Litter decomposition and nutrients dynamics in *Nothofagus antarctica* forests under silvopastoral use in Southern Patagonia. Agroforestry Systems, 84(3), 345-360.

Bakker, M. A., Carreño-Rocabado, G., & Poorter, L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. Functional Ecology, 25(3), 473-483. https://doi.org/https://doi.org/10.1111/j.1365-2435.2010.01802.x

Bohara, M., Yadav, R. K. P., Dong, W., Cao, J., & Hu, C. (2019). Nutrient and isotopic dynamics of litter decomposition from different land uses in naturally restoring Taihang Mountain, North China. Sustainability, 11(6), 1752.

Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H., & Newington, J. E. (2002). Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos, 99(2), 317-323.

Bravo-Oviedo, A., Ruiz-Peinado, R., Onrubia, R., & del Río, M. (2017). Thinning alters the early-decomposition rate and nutrient immobilization-release pattern of foliar litter in Mediterranean oak-pine mixed stands. Forest Ecology and Management, 391, 309-320.

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. Ecology, 90(12), 3566-3574.

Canessa, R., van den Brink, L., Saldaña, A., Rios, R. S., Hättenschwiler, S., Mueller, C. W., Prater, I., Tielbörger, K., & Bader, M. Y. (2021). Relative effects of climate and litter traits on decomposition change with time, climate and trait variability. Journal of Ecology, 109(1), 447-458.

Cárcamo, H., Abe, T., Prescott, C., Holl, F., & Chanway, C. (2000). Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. Canadian Journal of Forest Research, 30(5), 817-826.

Cifuentes-Croquevielle, C., Stanton, D. E., & Armesto, J. J. (2020). Soil invertebrate diversity loss and functional changes in temperate forest soils replaced by exotic pine plantations. Scientific Reports, 10(1), 1-11.

CIREN. (1999). Estudio agrológico VIII región: CIREN Santiago, Chile. Centro de información de Recursos Naturales, CIREN N°121.

Cornwell, W. K., Cornelissen, J. H., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., & Pérez-Harguindeguy, N. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters, 11(10), 1065-1071.

Cowan, O. S., & Anderson, P. M. L. (2019, 2019/03/01/). Litter decomposition variation across a degradation gradient and two seasons in a critically endangered vegetation type within the Fynbos biome, South Africa. South African Journal of Botany, 121, 200-209. https://doi.org/https://doi.org/10.1016/j.sajb.2018.11.002

Crowther, T. W., Boddy, L., & T Jones, H. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. The ISME Journal, 6(11), 1992-2001.

Dechaine, J., Ruan, H., Sanchez-de Leon, Y., & Zou, X. (2005). Correlation between earthworms and plant litter decomposition in a tropical wet forest of Puerto Rico. Pedobiologia, 49(6), 601-607.

Donoso, P., Donoso, C., & Sandoval, V. (1993, 1993-12-31). Proposición de zonas de crecimiento de renovales de roble (*Nothofagus obliqua*) y raulí (*Nothofagus alpina*) en su rango de distribución natural. Bosque(2), 37-55%V 14. https://doi.org/10.4206/bosque.1993.v14n2-06

Ewers, R., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T. R., Bakhtiar, E. Y., Chey, V. K., Chung, A. Y. C., Davies, R. G., Edwards, D. P., Eggleton, P., Fayle, T. M., Hardwick, S. R., Homathevi, R., Kitching, R. L., Khoo, M. S., Luke, S. H., March, J. J., Nilus, R., Pfeifer, M., Rao, S. V., Sharp, A. C., Snaddon, J. L., Stork, N. E., Struebig, M. J., Wearn, O. R., Yusah, K. M., & Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest [Article]. Nature

Communications, 6, Article 6836. https://doi.org/10.1038/ncomms7836

Ewers, R. M., Boyle, M. J., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T. R., Bakhtiar, E. Y., Chey, V. K., & Chung, A. Y. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest. Nature Communications, 6(1), 1-7.

Fajardo, A., & de Graaf, R. (2004). Tree dynamics in canopy gaps in old-growth forests of *Nothofagus pumilio* in Southern Chile. Plant Ecology, 173(1), 95-105.

Frouz, J. (2018). Effects of soil macro-and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma, 332, 161-172.

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology letters, 16(8), 1045-1053.

García-Palacios, P., McKie, B. G., Handa, I. T., Frainer, A., & Hättenschwiler, S. (2016). The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. Functional Ecology, 30(5), 819-829.

Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. Trends in Ecology & Evolution, 25(6), 372-380.

González, G., Lodge, D. J., Richardson, B. A., & Richardson, M. J. (2014). A canopy trimming experiment in Puerto Rico: The response of litter decomposition and nutrient release to canopy opening and debris deposition in a subtropical wet forest. Forest Ecology and Management, 332, 32-46.

González, G., & Seastedt, T. (2000). Comparison of the abundance and composition of litter fauna in tropical and subalpine forests. Pedobiologia, 44(5), 545-555.

González, G., & Seastedt, T. R. (2001). Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology, 82(4), 955-964.

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M. O., Jabiol, J., & Makkonen, M. (2014). Consequences of biodiversity loss for litter decomposition across biomes. Nature, 509(7499), 218-221.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., & Loveland, T. R. (2013). High-resolution global maps of 21st-century forest cover change. Science, 342(6160), 850-853.

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst., 36, 191-218.

Heemsbergen, D., Berg, M., Loreau, M., Van Hal, J., Faber, J., & Verhoef, H. (2004). Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science, 306(5698), 1019-1020.

Heneghan, L., Coleman, D. C., Zou, X., Crossley Jr, D., & Haines, B. (1999). Soil microarthropod contributions to decomposition dynamics: tropical–temperate comparisons of a single substrate. Ecology, 80(6), 1873-1882.

Heneghan, L., Coleman, D. C., Zou, X., Crossley Jr., D. A., & Haines, B. L. (1999). Soil microarthropod contributions to decomposition dynamics: Tropical-

Temperate comparisons of a single substrate. Ecology, 80(}6), 1873-1882. https://doi.org/10.1890/0012-9658(1999)080[1873:Smctdd]2.0.Co;2

Hirabuki, Y. (1991). Heterogeneous dispersal of tree litterfall corresponding with patchy canopy structure in a temperate mixed forest. Vegetatio, 94(1), 69-79.

Huhta, V., Haimi, J., & Setälä, H. (1991). Role of the fauna in soil processes: techniques using simulated forest floor. Agriculture, Ecosystems & Environment, 34(1-4), 223-229.

Jari Oksanen, G. L. S., F. Guillaume Blanchet, Roeland Kindt,, Pierre Legendre, P. R. M., R.B. O'Hara, Peter Solymos, M., Henry H. Stevens, E. S., Helene Wagner, Matt Barbour, Michael, Bedward, B. B., Daniel Borcard, Gustavo Carvalho, Michael, Chirico, M. D. C., Sebastien Durand, Heloisa Beatriz, Antoniazi Evangelista, R. F., Michael Friendly, Brendan, Furneaux, G. H., Mark O. Hill, Leo Lahti, Dan McGlinn,, Marie-Helene Ouellette, E. R. C., Tyler Smith, Adrian, & Stier, C. J. F. T. B. a. J. W. (2022). vegan: Community Ecology Package. R package version 2.6-2. https://CRAN.R-project.org/package=vegan

Kaneko, N., McLean, M. A., & Parkinson, D. (1998). Do mites and Collembola affect pine litter fungal biomass and microbial respiration? Applied Soil Ecology, 9(1-3), 209-213.

Kindt, R., & Coe, R. (2005). Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF). {http://www.worldagroforestry.org/output/tree-diversity-analysis

Krishna, M., & Mohan, M. (2017). Litter decomposition in forest ecosystems: a review. Energy, Ecology and Environment, 2(4), 236-249.

Krishna, M. P., & Mohan, M. (2017). Litter decomposition in forest ecosystems: a review [Review]. Energy, Ecology and Environment, 2(4), 236-249. https://doi.org/10.1007/s40974-017-0064-9

Lavelle, P., Blanchart, E., Martin, A., Martin, S., & Spain, A. (1993). A hierarchical model for decomposition in terrestrial ecosystems: application to soils of the humid tropics. Biotropica, 130-150.

Li, R., Guan, X., Han, J., Zhang, Y., Zhang, W., Wang, J., Huang, Y., Xu, M., Chen, L., & Wang, S. (2021). Litter decomposition was retarded by understory removal but was unaffected by thinning in a Chinese fir [Cunninghamia lanceolata (Lamb.) Hook] plantation. Applied Soil Ecology, 163, 103968.

Lusk, C. H., Donoso, C., Jiménez, M., Moya, C., Oyarce, G., Reinoso, R., Saldaña, A., Villegas, P., & Matus, F. (2001). Descomposición de hojarasca de Pinus radiata y tres especies arbóreas nativas. Revista chilena de historia natural, 74(3), 705-710.

Marín, C., Rubio, J., & Godoy, R. (2021). Chilean blind spots in soil biodiversity and ecosystem function research. bioRxiv.

Marthews, T., T, R., Oliveras, I., R, U., S, M., D, M., Y, M., Phillips, O., Huaraca Huasco, W., Ruiz-Jaen, M., C, G., Butt, N., & R, C. (2014). Measuring Tropical Forest Carbon Allocation and Cycling v3.0.

Martínez-Falcón, A. P., Moreno, C. E., & Pavón, N. P. (2015). Litter fauna communities and litter decomposition in a selectively logged and an unmanaged pine-oak forest in Mexico. Bosque, 36(1), 81-93.

Martinez, R. I., & Casanueva, M. E. (1993). Ácaros Oribátidos del alto Bío-Bío, Chile:

diversidad y abundancia relativa (Acari: Oribatida). Gayana Zoología (Chile), 57, 7-19.

McGlynn, T. P., & Poirson, E. K. (2012). Ants accelerate litter decomposition in a Costa Rican lowland tropical rain forest. Journal of Tropical Ecology, 28(5), 437-443.

Mendonça, R. T., Jara, J. F., González, V., Elissetche, J. P., & Freer, J. (2008). Evaluation of the white-rot fungi Ganoderma australe and Ceriporiopsis subvermispora in biotechnological applications. Journal of Industrial Microbiology and Biotechnology, 35(11), 1323.

Moore, T. R., Trofymow, J. A., Prescott, C. E., Fyles, J., & Titus, B. D. (2006, 2006/02/01). Patterns of Carbon, Nitrogen and Phosphorus Dynamics in Decomposing Foliar Litter in Canadian Forests. Ecosystems, 9(1), 46-62. https://doi.org/10.1007/s10021-004-0026-x

Moreno, I. I., Barberena-Arias, M. F., González, G., Lodge, D. J., & Cantrell, S. A. (2022). Canopy opening increases leaf-shredding arthropods and nutrient mineralization but not mass loss in wet tropical forest. Ecosphere, 13(6), e4084. https://doi.org/https://doi.org/10.1002/ecs2.4084

Olson, J. S. (1963). Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. Ecology, 44(2), 322-331. https://doi.org/10.2307/1932179

Oraon, P., Singh, L., & Jhariya, M. K. (2018). Forest floor biomass, litterfall and physico-chemical properties of soil along the anthropogenic disturbance regimes in tropics of Chhattisgarh, India. Journal of Forest and Environmental Science, 34(5), 359-375.

Paudel, E., Dossa, G. G., de Blécourt, M., Beckschäfer, P., Xu, J., & Harrison, R. D. (2015). Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. Ecosphere, 6(12), 1-20.

Peng, Y., Yang, W., Yue, K., Tan, B., & Wu, F. (2019, 2019/06/01). Impacts of soil fauna on nitrogen and phosphorus release during litter decomposition were differently controlled by plant species and ecosystem type. Journal of Forestry Research, 30(3), 921-930. https://doi.org/10.1007/s11676-018-0664-z

Pérez, C. A., Armesto, J. J., Torrealba, C., & Carmona, M. R. (2003). Litterfall dynamics and nitrogen use efficiency in two evergreen temperate rainforests of southern Chile. Austral Ecology, 28(6), 591-600.

Pollmann, W. (2002). Effects of natural disturbance and selective logging on *Nothofagus* forests in south-central Chile. Journal of Biogeography, 29(7), 955-970.

Pollmann, W., & Veblen, T. T. (2004). *Nothofagus* regeneration dynamics in south-central Chile: a test of a general model. Ecological Monographs, 74(4), 615-634.

Richardson, B. A., Richardson, M. J., González, G., Shiels, A. B., & Srivastava, D. S. (2010). A canopy trimming experiment in Puerto Rico: the response of litter invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. Ecosystems, 13(2), 286-301.

Sadzawka, A., Carrasco, M., Demanet, R., Flores, H., Grez, R., Mora, M., & Neaman, A. (2007). Métodos de análisis de tejidos vegetales. Serie Actas INIA, 40, 140.

Sayer, E. J., Sutcliffe, L. M., Ross, R. I., & Tanner, E. V. (2010). Arthropod abundance and diversity in a lowland tropical forest floor in Panama: the role of habitat space vs. nutrient concentrations. Biotropica, 42(2), 194-200.

Signorell, A., Aho, K., Alfons, A., Anderegg, N., Aragon, T., Arppe, A., Baddeley, A., Barton, K., Bolker, B., & Borchers, H. W. (2022). DescTools: Tools for descriptive statistics. R package version 0.99, 49, 17. https://cran.r-project.org/package=DescTools

Staelens, J., Ameloot, N., Almonacid, L., Padilla, E., Boeckx, P., Huygens, D., Verheyen, K., Oyarzun, C., & Godoy, R. (2011). Litterfall, litter decomposition and nitrogen mineralization in old-growth evergreen and secondar y deciduous *Nothofagus* forests in south-central Chile. Revista chilena de historia natural, 84(1), 125-141.

Stone, M. J., Shoo, L., Stork, N. E., Sheldon, F., & Catterall, C. P. (2020). Recovery of decomposition rates and decomposer invertebrates during rain forest restoration on disused pasture. Biotropica, 52(2), 230-241.

Taki, H., Inoue, T., Tanaka, H., Makihara, H., Sueyoshi, M., Isono, M., & Okabe, K. (2010). Responses of community structure, diversity, and abundance of understory plants and insect assemblages to thinning in plantations. Forest Ecology and Management, 259(3), 607-613.

Team, R. C. (2013). R: A language and environment for statistical computing.

Veblen, T. T., Donoso, C., Kitzberger, T., & Rebertus, A. J. (1996). Ecology of southern Chilean and Argentinean *Nothofagus* forests. The ecology and biogeography of *Nothofagus* forests, 10, 93-353.

Vivanco, L., & Austin, A. T. (2019, 2019/06/01/). The importance of macro- and micro-nutrients over climate for leaf litter decomposition and nutrient release in Patagonian temperate forests. Forest Ecology and Management, 441, 144-154. https://doi.org/https://doi.org/10.1016/j.foreco.2019.03.019

Voříšková, J., & Baldrian, P. (2013). Fungal community on decomposing leaf litter undergoes rapid successional changes. The ISME Journal, 7(3), 477-486.

Wall, D. H., Bradford, M. A., ST. JOHN, M. G., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. E., Dangerfield, J. M., Parton, W. J., Rusek, J., & Voigt, W. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Global Change Biology, 14(11), 2661-2677.

Wang, Z., Yin, X., & Li, X. (2015). Soil mesofauna effects on litter decomposition in the coniferous forest of the Changbai Mountains, China. Applied Soil Ecology, 92, 64-71.

Yang, X., & Chen, J. (2009). Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China [Article]. Soil Biology and Biochemistry, 41(5), 910-918. https://doi.org/10.1016/j.soilbio.2008.12.028

Yang, X., & Li, T. (2020). Effects of terrestrial isopods on soil nutrients during litter decomposition. Geoderma, 376, 114546.

Yeong, K. L., Reynolds, G., & Hill, J. K. (2016). Leaf litter decomposition rates in degraded and fragmented tropical rain forests of Borneo. Biotropica, 48(4), 443-452.

Zamorano-Elgueta, C., Cayuela, L., Rey-Benayas, J. M., Donoso, P. J., Geneletti, D., & Hobbs, R. J. (2014). The differential influences of human-induced disturbances on tree regeneration community: a landscape approach.

Ecosphere, 5(7), 1-17.

Zan, P., Mao, Z., & Sun, T. (2022). Effects of soil fauna on litter decomposition in Chinese forests: a meta-analysis. PeerJ, 10, e12747.

Zhang, H., Yuan, W., Dong, W., & Liu, S. (2014). Seasonal patterns of litterfall in forest ecosystem worldwide. Ecological Complexity, 20, 240-247.

Zhang, Q., & Zak, J. C. (1995). Effects of gap size on litter decomposition and microbial activity in a subtropical forest. Ecology, 76(7), 2196-2204.

Zhang, W., Yuan, S., Hu, N., Lou, Y., & Wang, S. (2015). Predicting soil fauna effect on plant litter decomposition by using boosted regression trees. Soil Biology and Biochemistry, 82, 81-86.

Zhao, J., Wang, X., Shao, Y., Xu, G., & Fu, S. (2011). Effects of vegetation removal on soil properties and decomposer organisms. Soil Biology and Biochemistry, 43(5), 954-960.

IV. DISCUSIÓN Y CONCLUSIONES GENERALES

Este estudio permitió evidenciar que la degradación de los bosques afecta significativa y negativamente la producción de hojarasca, su descomposición y dinámica del C, N y P. Por una parte, el bosque maduro de *Nothofagus* mostró un ciclo interno de nutrientes más eficiente, lo cual se evidenció en las altas relaciones C:N y C:P de la hojarasca caída en los meses de mayor producción. Por otro lado, a pesar de la menor calidad de su hojarasca, es decir, menores concentraciones de N y P en comparación con el bosque secundario y degradado, el bosque maduro presentó las mayores tasas de descomposición y liberación de nutrientes. Al contrario, el bosque degradado tuvo las menores tasas de descomposición de hojarasca a pesar de su mejor calidad, por lo cual, inferimos que otros factores pueden estar limitando las tasas de descomposición de estos bosques como son las condiciones micro climáticas y los organismos del suelo.

Adicionalmente, este estudio demostró que la composición de la comunidad de mesofauna y su abundancia, junto con su efecto sobre las tasas de descomposición de hojarasca, también se ven afectadas por el nivel de degradación de los bosques. En este sentido, encontramos que las comunidades de mesofauna fueron similares en el bosque maduro, secundario y degradado, aunque estas difirieron significativamente según las estaciones del año. El bosque degradado presentó los mayores valores de abundancia total, mientras que el sitio reforestado mostró una menor abundancia total y de órdenes de mesofauna detritívora, lo cual se asoció con tasas de descomposición más bajas. Al igual, encontramos que la mesofauna tuvo una mayor importancia para la descomposición en el bosque degradado, lo cual condujo a valores de descomposición iguales a los del bosque maduro y secundario cuando la mesofauna estaba presente. Por otro lado, la mesofauna tuvo un efecto significativo sobre la liberación de C, N y P en todos los tipos de bosque y el sitio reforestado, lo cual destaca su importancia para liberación de nutrientes inmovilizados por los microorganismos.

Los hallazgos expuestos demuestran que la perturbación humana de los bosques producto de la tala y ganadería afectan tanto a la producción de hojarasca y su descomposición, como a la comunidad de mesofauna del suelo y su rol sobre la descomposición y liberación de los nutrientes. Obstaculizar estos procesos biogeoquímicos puede limitar la fertilidad del suelo y, por lo tanto, la capacidad regenerativa, la productividad y la complejidad de estos bosques, haciéndolos menos resistentes a las perturbaciones bióticas y abióticas impulsadas por el cambio global. Sin embargo, la mesofauna demostró ser un factor clave en la recuperación del proceso de descomposición en bosques degradados de *Nothofagus* y en la liberación de los nutrientes en todos los sitios de estudio, lo cual, puede ayudar a la recuperación de estos ecosistemas degradados.

V. REFERENCIAS GENERALES

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos, 439-449.

Alfaro, M., Dube, F., & Zagal, E. (2018). Soil quality indicators in an Andisol under different tree covers in disturbed *Nothofagus* forests. Chilean journal of agricultural research, 78(1), 106-116.

Armesto, J. J., Manuschevich, D., Mora, A., Smith-Ramirez, C., Rozzi, R., Abarzúa, A. M., & Marquet, P. A. (2010). From the Holocene to the Anthropocene: A historical framework for land cover change in southwestern South America in the past 15,000 years. Land Use Policy, 27(2), 148-160.

Bahamonde, H. A., Peri, P. L., Alvarez, R., Barneix, A., Moretto, A., & Pastur, G. M. (2012). Litter decomposition and nutrients dynamics in *Nothofagus antarctica* forests under silvopastoral use in Southern Patagonia. Agroforestry Systems, 84(3), 345-360.

Bakker, M. A., Carreño-Rocabado, G., & Poorter, L. (2011). Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. Functional Ecology, 25(3), 473-483. https://doi.org/https://doi.org/10.1111/j.1365-2435.2010.01802.x

Bohara, M., Yadav, R. K. P., Dong, W., Cao, J., & Hu, C. (2019). Nutrient and isotopic dynamics of litter decomposition from different land uses in naturally restoring Taihang Mountain, North China. Sustainability, 11(6), 1752.

Cornwell, W. K., Cornelissen, J. H., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., & Pérez-Harguindeguy, N. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology letters, 11(10), 1065-1071.

Cowan, O. S., & Anderson, P. M. L. (2019, 2019/03/01/). Litter decomposition variation across a degradation gradient and two seasons in a critically endangered vegetation type within the Fynbos biome, South Africa. South African Journal of Botany, 121, 200-209. https://doi.org/https://doi.org/10.1016/j.sajb.2018.11.002

Crowther, T. W., Boddy, L., & T Jones, H. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. The ISME Journal, 6(11), 1992-2001.

Ewers, R. M., Boyle, M. J. W., Gleave, R. A., Plowman, N. S., Benedick, S., Bernard, H., Bishop, T. R., Bakhtiar, E. Y., Chey, V. K., Chung, A. Y. C., Davies, R. G., Edwards, D. P., Eggleton, P., Fayle, T. M., Hardwick, S. R., Homathevi, R., Kitching, R. L., Khoo, M. S., Luke, S. H., March, J. J., Nilus, R., Pfeifer, M., Rao, S. V., Sharp, A. C., Snaddon, J. L., Stork, N. E., Struebig, M. J., Wearn, O. R., Yusah, K. M., & Turner, E. C. (2015). Logging cuts the functional importance of invertebrates in tropical rainforest [Article]. Nature Communications, 6, Article 6836. https://doi.org/10.1038/ncomms7836

Frouz, J. (2018). Effects of soil macro-and mesofauna on litter decomposition and soil organic matter stabilization. Geoderma, 332, 161-172.

García-Palacios, P., Maestre, F. T., Kattge, J., & Wall, D. H. (2013). Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology letters, 16(8), 1045-1053.

González, G., & Seastedt, T. R. (2001). Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology, 82(4), 955-964.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., & Loveland, T. R. (2013). High-resolution global maps of 21st-century forest cover change. Science, 342(6160), 850-853.

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst., 36, 191-218.

Krishna, M. P., & Mohan, M. (2017). Litter decomposition in forest ecosystems: a review [Review]. Energy, Ecology and Environment, 2(4), 236-249. https://doi.org/10.1007/s40974-017-0064-9

McGlynn, T. P., & Poirson, E. K. (2012). Ants accelerate litter decomposition in a Costa Rican lowland tropical rain forest. Journal of Tropical Ecology, 28(5), 437-443.

Moreno, I. I., Barberena-Arias, M. F., González, G., Lodge, D. J., & Cantrell, S. A. (2022). Canopy opening increases leaf-shredding arthropods and nutrient mineralization but not mass loss in wet tropical forest. Ecosphere, 13(6), e4084. https://doi.org/https://doi.org/10.1002/ecs2.4084

Paudel, E., Dossa, G. G., de Blécourt, M., Beckschäfer, P., Xu, J., & Harrison, R. D. (2015). Quantifying the factors affecting leaf litter decomposition across a tropical forest disturbance gradient. Ecosphere, 6(12), 1-20.

Peri, P., Bahamonde, H., Monelos, L., & Pastur, G. M. (2008). Producción de hojarasca en bosques primarios y bajo manejo silvopastoril de *Nothofagus antarctica* en la provincia de Santa Cruz, Argentina. Segunda reunión sobre *Nothofagus* en la Patagonia, EcoNothofagus, 149-155.

Prescott, C. E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry, 101(1-3), 133-149.

Song, B., Yin, X., Zhang, Y., & Dong, W. (2008). Dynamics and relationships of Ca, Mg, Fe in litter, soil fauna and soil in Pinus koraiensis-broadleaf mixed forest. Chinese Geographical Science, 18(3), 284-290.

Veblen, T. T., Donoso, C., Kitzberger, T., & Rebertus, A. J. (1996). Ecology of southern Chilean and Argentinean *Nothofagus* forests. The ecology and biogeography of *Nothofagus* forests, 10, 93-353.

Yang, X., & Li, T. (2020). Effects of terrestrial isopods on soil nutrients during litter decomposition. Geoderma, 376, 114546.

Yeong, K. L., Reynolds, G., & Hill, J. K. (2016). Leaf litter decomposition rates in degraded and fragmented tropical rain forests of Borneo [Article]. Biotropica, 48(4), 443-452. https://doi.org/10.1111/btp.12319

Zamorano-Elgueta, C., Cayuela, L., Rey-Benayas, J. M., Donoso, P. J., Geneletti, D., & Hobbs, R. J. (2014). The differential influences of human-induced disturbances on tree regeneration community: a landscape approach. Ecosphere, 5(7), 1-17.

Zan, P., Mao, Z., & Sun, T. (2022). Effects of soil fauna on litter decomposition in Chinese forests: a meta-analysis. PeerJ, 10, e12747.

Zhang, W., Yuan, S., Hu, N., Lou, Y., & Wang, S. (2015). Predicting soil fauna effect on plant litter decomposition by using boosted regression trees. Soil Biology and Biochemistry, 82, 81-86.