

# From soils to trees: Carbon stocks in high-graded, successional and old-growth forests in South American temperate rainforests

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## ABSTRACT

1. Forest ecosystems provide an essential service to humanity by storing carbon and helping to mitigate climate change. Temperate rainforests in South America can accumulate elevated levels of carbon both in aboveground biomass and in the soil. This varies depending on location, successional stage and conservation status.

2. In the Coastal Range of south-central Chile, evergreen hardwood-dominated forests include old-growth stands and disturbed forests in various successional stages. In the Llancahue Experimental Forest, we compared carbon stocks across four forest types: old-growth forests (OGF), high-graded forests (HGF), mixed secondary forests (MSF) and secondary forests dominated by *Nothofagus dombeyi* (NDSF). Using nine 400 m<sup>2</sup> plots per type of forest (total=36 plots), we sampled all trees with a diameter ≥5.0 cm, along with coarse woody debris, regeneration, herbaceous plants, shrubs, litter and soil. We estimated biomass using field samples and allometric equations. Carbon content was calculated using IPCC conversion factors.

3. OGF showed the highest carbon stock (507 Mg C/ha), followed by NDSF (442), MSF (365) and HGF (221). Carbon in trees and soils made up 82-91% of total stocks, with trees contributing more than soil in OGF and NDSF (~1.3 ratio), while soil was more significant in HGF and MSF (~0.8 ratio). We conclude that older, undisturbed forests store more carbon than younger or high-graded ones. However, the differences were smaller than expected.

4. Implications. This study adds important ecological information regarding the value of secondary and primary forests in carbon retention. Therefore, it also discusses the opportunities of managed or restored forests to contribute significantly to this objective, simultaneously allowing sustainable timber production.

[Keywords: ecological succession, ecological silviculture, evergreen forest, *Nothofagus dombeyi*, *Chusquea quila*]

## RESUMEN. Desde los bosques hasta el suelo: Reservas de carbono en bosques degradados, sucesionales y adultos en bosques templado lluviosos de Sudamérica

1. Los ecosistemas forestales prestan servicios esenciales a la humanidad al almacenar carbono y contribuir a mitigar el cambio climático. Los bosques templados lluviosos de Sudamérica pueden acumular altos niveles de carbono. Esto varía según ubicación, estado sucesional y nivel de conservación.

2. En la Cordillera de la Costa del centro-sur de Chile, los bosques siempreverdes dominados por especies latifoliadas incluyen bosques primarios y bosques perturbados en distintas etapas sucesionales. En el Bosque Experimental Llancahue comparamos las reservas de carbono en cuatro tipos de bosques: primarios (OGF), degradados (HGF), secundarios mixtos (MSF) y secundarios dominados por *Nothofagus dombeyi* (NDSF). Usando nueve parcelas de 400 m<sup>2</sup> cada una en cada tipo de bosque (total=36 parcelas) se registraron todos los árboles con diámetro ≥5.0 cm, la madera muerta gruesa, la regeneración, las plantas herbáceas, los arbustos, la hojarasca y el suelo. La biomasa se estimó mediante muestreos de campo y ecuaciones alométricas. El contenido de carbono se calculó usando factores de conversión del IPCC.

3. El OGF presentó la mayor reserva de carbono (507 Mg C/ha), seguido por el NDSF (442), el MSF (365) y el HGF (221). El carbono en árboles y suelos representó entre 82 y 91% del total, con una mayor contribución del compartimento arbóreo en OGF y NDSF (relación ~1.3). El suelo fue más relevante en HGF y MSF (relación ~0.8). Concluimos que los bosques más antiguos y no perturbados almacenan más carbono que los jóvenes o degradados. Sin embargo, las diferencias fueron menores a lo esperado.

4. Implicaciones. Este estudio adiciona información ecológica significativa sobre el valor de los bosques secundarios y primarios en cuanto a retención de carbono. Por lo tanto, también discute las oportunidades de bosques manejados o restaurados para contribuir a este objetivo, mientras que simultáneamente permiten una producción sustentable de madera.

[Palabras clave: sucesión ecológica, silvicultura ecológica, bosques siempreverdes, *Nothofagus dombeyi*, *Chusquea quila*]

## INTRODUCTION

Climate change is one of the major problems of the current world ecological crisis. Its origins and development are determined by continuous and increasing emissions of greenhouse gases to the atmosphere, being carbon dioxide (CO<sub>2</sub>) the main one. Main sources of carbon emissions are the excessive use of fossil fuels, land-use changes and forest degradation (Ordóñez and Masera 2001). These actions have contributed significantly to the increase in CO<sub>2</sub> concentrations in the atmosphere, with land degradation and land-use change responsible for almost 17% of carbon dioxide emissions (Santini et al. 2019). In this context, forest ecosystems are essential to mitigate climate change. Through the process of photosynthesis, they store about 60% of the available carbon in the atmosphere in the form of above- and belowground biomass (Le Quéré et al. 2013) and soil organic matter accumulated by an ecosystem over time (Guo and Gifford 2002). However, deforestation is annually releasing an average of around 5.2 Gt CO<sub>2</sub> (Friedlingstein et al. 2019), a quarter of all the released greenhouse gases. The release of carbon from deforestation or forest degradation affects the balance of the carbon cycle through the loss and acceleration of oxidation processes, which alters the availability of soil organic matter (Guo and Gifford 2002). Therefore, it is urgent to continue evaluating carbon losses and gains in diverse forest ecosystems throughout the world, especially considering the successional stages and conservation status of these ecosystems (Hernández-Moreno et al. 2020). While a variety of studies have quantified forest biomass in different ecosystems (e.g., to estimate its distribution in the topsoil, its nutrient availability or its carbon content [Pan et al. 2011; Mora et al. 2018]), this effort must expand to ecosystems worldwide to improve global estimates of the role of forests and forestry in climate change mitigation.

While temperate forests between 35 and 45 north or south latitude have the highest above-ground biomass carbon values in the world (Keith et al. 2009), temperate rainforests (DellaSala 2011; Veblen and Alaback 1996) constitute especially important ecosystems as a nature-based alternative to carbon storage due to their high structural complexity (sensu Ehbrecht et al. 2021), productivity and biomass (Donoso and Navarro 2025; Veblen and Alaback 1996). Chile has the largest area of temperate rainforests in the

Southern hemisphere, which occur between 37° S and 55° S (Veblen and Alaback 1996). Within these forests, the Evergreen Forest Type (EFT) represents 25% (3.5 million ha) of the total native forest area in the country, mainly from south-central Chile to northern Patagonia (37° S - 45° S) (CONAF 2021). They are dense multilayered and mixed forests from their mature to old-growth successional stages (Oyarzún et al. 2019; Donoso et al. 2018) and have a high forest structural complexity (sensu Ehbrecht et al. 2021). However, many of these forests have been severely disturbed by anthropic actions, especially timber harvesting through selective felling, fire and grazing (Vásquez-Grandón et al. 2018; González et al. 2015). Land clearing to develop agriculture and cattle raising has been historically a widespread practice in Chile (e.g., González et al. 2015) and elsewhere (e.g., Foster 1992), resulting in many areas revegetated with secondary forests (González et al. 2015). These secondary forests are dominant among native forests in the landscape of south-central Chile, while old-growth forests are scarce and have commonly been high-graded (Lara et al. 2016), especially at lower elevations (Donoso et al. 2014). In general, forest degradation through selective logging causes reductions in species richness (Clark and Covey 2012) and regeneration. In Chile, forest degradation continues especially through selective harvests to produce firewood (Reyes et al. 2018). Therefore, the challenge to sustain the provision of diverse ecosystem services of these valuable temperate rainforests includes the generation of greater knowledge of these services while at the same time developing appropriate conservation approaches.

The Llancahue Experimental Forest in the Central Depression of south-central Chile is a reserve at low elevations that maintains a mosaic of forests of the EFT in different successional stages and conservation status (Donoso et al. 2014). This site, where the climatic conditions are relatively homogeneous, provides an excellent opportunity to study the type and magnitude of a major ecosystem service—carbon storage—across a range of forest types, from heavily logged areas to diverse, complex and productive successional and old-growth temperate rainforests. Therefore, this study poses the following research question: ¿Are there significant differences in carbon stocks among the two types of secondary forests, old-growth forests and high-graded forests in the Llancahue Experimental Forest,

considering both above- and belowground components? Results reported here provide information on the capacity of different forests to store carbon and therefore better inform decision makers on the potential impacts of restoration, conservation or management actions to sustain this relevant service in these temperate rainforests.

## MATERIALS AND METHODS

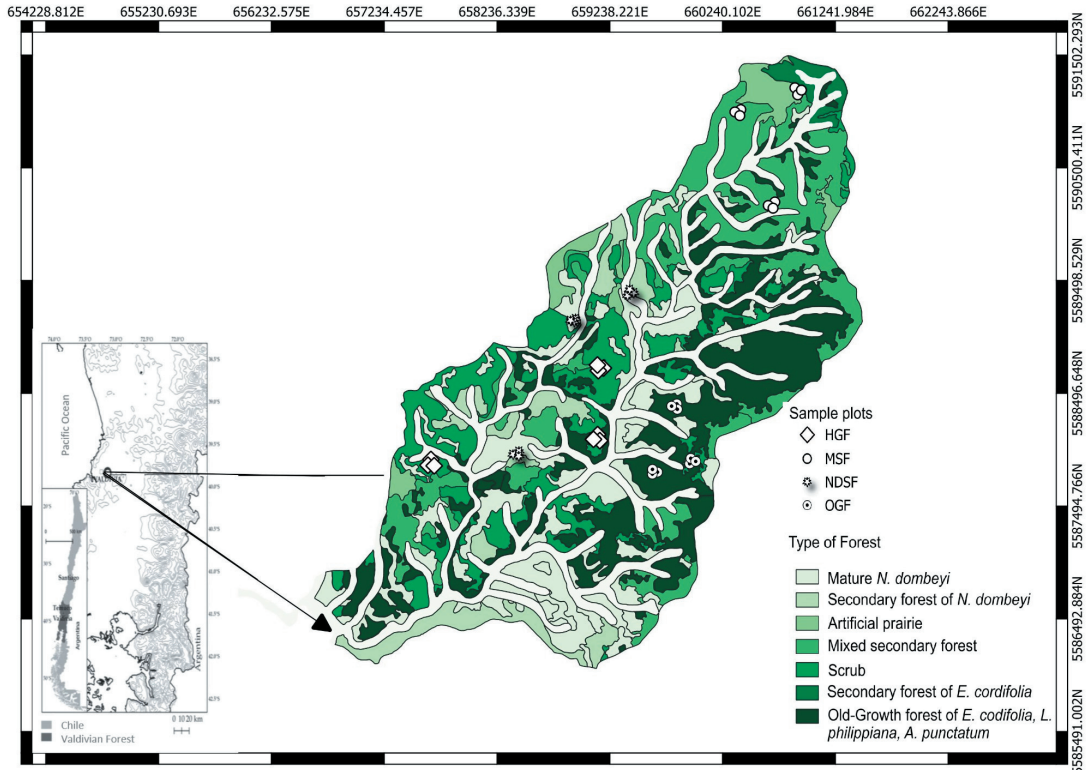
### Study area

We conducted this study in the Llancahue Experimental Forest in the Coastal Range near the city of Valdivia, located at 39°51'31.8" S and 73°08'12.9" (Figure 1). This forest covers 1270 ha between 50 and 400 m a.s.l. Most of this forest corresponds to the Evergreen Forest Type (EFT), which includes nearly 30 tree or arborescent species (Donoso et al. 2018). Average annual rainfall is 2300 mm and average annual temperature is 12.2 °C (Núñez et al. 2006). The terrain features moderate slopes (10-30%), and the soils, classified as Typic Paleudults (locally referred to as Correltúe and Los Ulmos soil series),

are moderately deep, clayey silt in texture, well-aerated, and have high infiltration rates (CIREN 2001).

### Experimental design

Four types of forests were the object of this study, including old-growth forests (OGF), two types of secondary forests (mixed secondary forest [MSF] and a secondary forest dominated by *Nothofagus dombeyi* Mirb. Oerst. [NDSF]) and high-graded forests with scattered trees and an understory dominated by the bamboo *Chusquea quila* Kunth (HGF) (Figure 2). In each forest type, we sampled nine 400 m<sup>2</sup> circular plots (radius 11.3 m) for a total of 36 plots (Figure 3). Within these plots, we measured nested subplots for trees, understory, regeneration, necromass and also collected soil samples. In the case of HGF, three high-graded forest stands were selected to establish the nine plots, with three plots in each stand following the same protocol. The three plots on each site were located at the vertices of an equilateral triangle, with a 50 m distance between the centers of the plots (Figure 3).



**Figure 1.** Geographical location of the Llancahue Experimental Forest and the sampling plots used in this study.

**Figura 1.** Ubicación geográfica del Bosque Experimental Llancahue y las parcelas de muestreo utilizadas en este estudio.



**Figure 2.** Representation (from left to right) of the mixed secondary forest (MSF), the *N. dombeyi* secondary forest (NDSF), the old-growth forest (OGF) and the high-graded forest (HGF).

**Figura 2.** Representación (de izquierda a derecha) del bosque mixto secundario (MSF), del bosque secundario de *N. dombeyi* (NDSF), del bosque adulto (OGF) y del bosque degradado (HGF).

#### *Biomass estimation of the tree pools*

Within each 400 m<sup>2</sup> plot, the diameter at breast height (DBH, cm) and total height (m) of all the trees  $\geq 5$  cm in DBH and  $>1.3$  m in total height of live and dead tree species were recorded with a diameter tape and the Vertex III laser instrument, respectively. With the information collected in the field, tree biomass (Mg/ha) was estimated with allometric functions for each species and in the case of species where no allometric function was available, functions were chosen for each of EFT (Milla et al. 2013), according to variables such as location (coastal range), diameter range, basal area range and main species composition that are provided for each function (Table 1). These estimates were scaled up to the hectare level (Mg/ha). To obtain the total biomass of standing dead trees, the total biomass functions of living trees were used, but a percentage was discounted depending on their state, following the proposal by Kauffman and Donato (2012). For recently dead trees with the presence of leaves and branches, the total calculated biomass was considered, for dead trees with the presence of branches, but without leaves, 78.5% of the calculated biomass was considered, and for dead trees without leaves or branches, only 23.4% of the biomass was considered.

#### *Biomass estimation of coarse woody material (CWM)*

A subplot 25 m<sup>2</sup> in size (5 m x 5 m) was measured in quadrant I in the northeast direction of each plot (Figure 3). In these plots, the diameter and length of all coarse woody material (CWM) was recorded, which

was defined as all logs and dead branches with diameters  $\geq 7.5$  cm. The CWM was classified according to its degree of decomposition according to Schlegel and Donoso (2008). CWM with a low level of decomposition was considered that which still retained its bark, and its hardness was considerable, and was given a basic density (g/cm<sup>3</sup>) of 0.51. CWM with a high level of decomposition was considered that which had a high level of decomposition but still maintained the original shape of the log or branch and was given a basic density (g/cm<sup>3</sup>) of 0.25. For each log or branch we measured the diameter at both ends. With the data collected, the volume for each piece found within the plot was determined, using the Smalian method (Burkhardt et al. 2018) (Equation 1).

$$V=L\left(\frac{\pi(D_1/2)^2+\pi(D_2/2)^2}{2}\right)$$

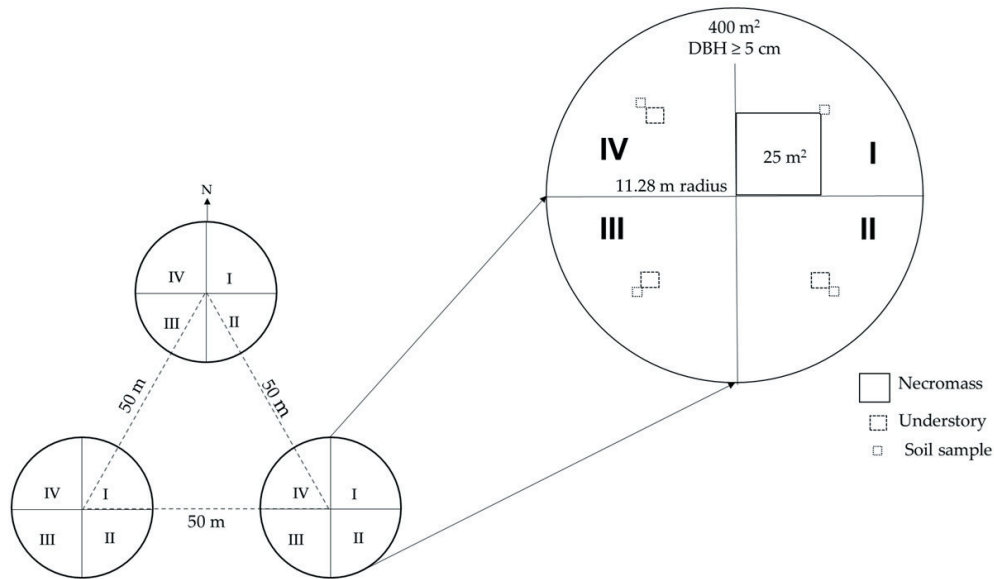
Equation 1

where L=length of the trunk (m) and  $D_1$  and  $D_2$ =minimum and maximum diameter (cm), respectively.

Subsequently, the final volume of each decomposition class of the CWM was weighted by the respective density (kg/m<sup>3</sup>) of each decomposition category (sensu Schlegel and Donoso 2008).

#### *Biomass estimation in understory and fine woody material (FWM: diameters $\leq 7.5$ cm)*

Understory biomass was estimated for tree regeneration (individuals with DBH  $<5$  cm),



**Figure 3.** Design of each sampling plot, including subplots for the measurement of different carbon compartments in the forests.

**Figura 3.** Diseño de cada parcela de muestreo, incluyendo subparcelas para la medición de diferentes compartimentos de carbono en los bosques.

**Table 1.** Allometric equations used to estimate forest biomass in the four sampled forests (Milla et al. 2013). The allometric equation was chosen according to the stand structural characteristics (density, diameter range and basal area) and location of the forests sampled.

**Tabla 1.** Ecuaciones alométricas utilizadas para estimar la biomasa forestal en los cuatro bosques muestreados (Milla et al. 2013). Las ecuaciones alométricas se seleccionaron en función de las características estructurales del rodal (densidad, rango dimétrico y área basal) y la ubicación de los bosques muestreados.

| Type of forest/ Species                          | Allometric equations                    | R <sup>2</sup> (%) | Sxy  |
|--|---|--------------------|------|
| <i>Laureliopsis philippiana</i> (Looser) Schodde | PSA=EXP(-0.88067+2.00017 * ln DBH)      | 96                 | s/i  |
| <i>Saxegothaea conspicua</i> Lindl.              | PSA=EXP(-0.2277+1.77378 * ln DBH)       | 99                 | s/i  |
| <i>Drimys winteri</i> J.R. Forst. and G. Forst.  | PSA=-5.73651+EXP(3.25257+0.07943 * DBH) | 97                 | s/i  |
| <i>Eucryphia cordifolia</i> Cav.                 | PSA=EXP(-1.45875+2.23536 * ln DBH)      | 99                 | s/i  |
| <i>Gevuina avellana</i> Molina                   | PSA=EXP(-1.84774+2.23221 * ln DBH)      | 97                 | s/i  |
| <i>Nothofagus dombeyi</i> (Mirb.) Oerst          | PSA=-577.329+EXP(6.11716+0.02752 * DBH) | 99                 | s/i  |
| <i>Weinmannia trichosperma</i> Cav.              | PSA=-170.119+EXP(5.23563+0.03876 * DBH) | 97                 | s/i  |
| HGF  | Ln TDW=-1.835+2.291 * ln DBH            | 98                 | 0.27 |
| MSF  | Ln TDW=-1.624+2.235 * ln DBH            | 96                 | 0.28 |
| NDSF   | TDW=EXP(2.5502+0.1207 * DBH)            | 93                 | s/i  |
| NDSF   | TDW=0.0839 * DBH <sup>2.4567</sup>      | 94                 | s/i  |
| OGF  | ln TDW=-2.041+2.340 * ln DBH            | 99                 | 0.23 |

TDW=tree dry weight (kg/tree). ln=natural logarithm. DBH=diameter at breast height (cm). R<sup>2</sup>=coefficient of determination. Sxy=standard error.

TDW=peso seco del árbol (kg/árbol). ln=logaritmo natural. DBH=diámetro a la altura del pecho (cm).

R<sup>2</sup>=coeficiente de determinación. Sxy=error estándar.

shrubs, herbaceous plants, vines and ferns, recording them in three 1 m<sup>2</sup> subplots (Figure 3), where species and total height were noted for tree species and percent cover for non-tree

species. Subsequently, all plant material from each plot was collected and placed in plastic bags, along with FWM (diameters ≤7.5 cm), litterfall (Oi+Oe) and humus (Oa), and sent

to the Forest Nutrition and Soil Laboratory (NSF) at the Universidad Austral de Chile for classification, weighing and oven-drying at 60 °C until a constant weight was reached.

Based on this information, the moisture content per sample was determined:

$$\text{Moisture content \%} = \frac{\text{wet weight (g)} - \text{dry weight (g)}}{\text{dry weight (g)}} * 100$$

Equation 2

Subsequently, Equation 3 was used to determine the proportion of wet weight that corresponds to biomass.

$$\text{Biomass} = \frac{\text{total wet weight of the material (g)}}{1 + (\text{moisture content (\%)} / 100)}$$

Equation 3

Once a constant weight was achieved and the biomass of the FWM (diameters  $\leq 7.5$  cm), litterfall (Oi+Oe) and humus (Oa) was determined, a 10 g subsample from each subplot was taken and sent to the laboratory to analytically determine the percentage of carbon present in each component. Subsequently, the values were extrapolated to one hectare and expressed in Mg C/ha.

#### Soil sampling

Five soil samples were collected (Figure 3) using 100 cm<sup>3</sup> cylinders to determine bulk density through the volumetric cylinder method described by MacDicken (1997). This method consists of inserting the cylinder into the soil to a depth of 30 cm without compressing it, emptying the contents into a bag, recording the wet weight and then oven-drying the sample at 105 °C until reaching a constant weight, which corresponds to the dry weight. Bulk density (BD) was calculated according to Equation 4:

$$\text{BD} \left( \frac{\text{g}}{\text{cm}^3} \right) = \frac{(\text{Dry weight} - \text{Bag weight})}{(\text{Cylinder Volume } 100 \text{ cm}^3)}$$

Equation 4

To determine % of carbon, another five soil samples were collected (next to the site where the material for bulk density determination was extracted). These samples considered the soil profile down to 30 cm. Each sample was taken with a small shovel and mixed until the colour was uniform. This material was then sieved through a 5 mm mesh, and a random

subsample of 100 g was taken and sent to the laboratory to determine the % of carbon using the sodium dichromate oxidation technique (Walkley and Black, 1934).

#### Carbon density in live wood, necromass and in the soil

Once the biomass was determined, the carbon stored in each component was estimated: for the carbon in living biomass (tree layer), the values obtained by Gayoso and Guerra (2005) for temperate rainforests (49.6 $\pm$ 0.93%) were used. In the case of litterfall (Oi+Oe), humus (Oa) and *C. quila*, the value experimentally obtained in the laboratory for each type of sample was used. For necromass (CWM and FWM) and understory vegetation, the general carbon conversion factor (0.5) proposed by the IPCC (IPCC 2006) was applied. In the case of soil, Equation 5 was applied, using the bulk density obtained in Equation 4 and the data obtained in the laboratory.

$$\text{Mg} \frac{\text{C}}{\text{ha}} = \frac{\text{carbon content \%}}{\text{C}} * \text{BD} \frac{\text{g}}{\text{cm}^3} * \frac{\text{sampling}}{\text{soil depth}}$$

Equation 5

The surface area assumed for extrapolation to a hectare was  $\sim 3.33$  cm<sup>2</sup> per cylinder, which corresponds to the horizontal area covered by the cylinder. Since five samples were taken per plot, the actual total area was 16.65 cm<sup>2</sup>, and this value was used as the extrapolation factor to 1 ha.

#### Analyses

First, we characterized each forest according to some structural variables: density (trees/ha), basal area (m<sup>2</sup>/ha) and quadratic mean diameter (cm), and the importance value (IV) of the species, with the IV calculated from relative tree density and relative basal area for each species. The data obtained in the field was grouped for analysis by stratum and type of forest to evaluate carbon content. We used a generalized linear model (GLM), under the scheme of nested plots with repeated measures, where the type of forest was used as a fix effect and the strata (trees, understory, forest floor and soil) as random effects, using the R software (R Development Core Team 2011) and the lme4 package (Bates and Maechler 2009). Since the sphericity in the data was not met, a correction was made using the Greenhouse-Greisser test. For the cases where differences were detected, the

Bonferroni test ( $\alpha=0.05$ ) was used to compare the means among the four forest ecosystems and strata.

## RESULTS

### General description of the forests

Tree density was significantly higher in MSF and lower in HGF compared to the other three forests, which had no significant differences

between them (Table 2). Basal area was highest in the OGF, but did not significantly differ with the two secondary forests; the HGF had significantly lower values of basal area. Regarding the quadratic mean diameter, the OGF exhibits larger values compared to the NDSF and MSF, which is consistent with the fact that these forests are in a more advanced successional stage. Both the HGF and the OGF were dominated by shade-tolerant species in

**Table 2.** Summary of stand variables of the four forests evaluated in the Llancahue Experimental Forest.

**Tabla 2.** Resumen de las variables de rodal de los cuatro bosques evaluados en el Bosque Experimental Llancahue.

| Variable                        | Forest type |            |           |           |
|---------------------------------|-------------|------------|-----------|-----------|
|                                 | HGF         | MSF        | NDSF      | OGF       |
| Tree density (trees/ha)         | 428±36c     | 4644±1578a | 1375±583b | 1275±272b |
| Basal area (m <sup>2</sup> /ha) | 27.9±18b    | 60.0±30a   | 69.3±11a  | 80.8±25a  |
| Quadratic stand diameter (cm)   | 26.6±8      | 11.1±4.6   | 23.4±4.8  | 30.1±6.4  |

HGF=high-graded forests with scattered trees and an understory dominated by the bamboo *Chusquea quila*. MSF=mixed secondary forest. NDSF=secondary forest dominated by *Nothofagus dombeyi*. OGF=old-growth forests. Different letters in each row illustrate significant differences among forest types for a given variable ( $P<0.05$ ). HGF=bosques degradados con árboles dispersos y un sotobosque dominado por el bambú *Chusquea quila*. MSF=bosque secundario mixto. NDSF=bosque secundario dominado por *Nothofagus dombeyi*. OGF=bosques adultos primarios. Las letras diferentes en cada fila indican diferencias significativas entre los tipos de bosque para una variable dada ( $P<0.05$ ).

**Table 3.** Importance value for each tree species for each forest evaluated in the Llancahue Experimental Forest.

**Tabla 3.** Valor de importancia de cada especie arbórea para cada bosque evaluado en el Bosque Experimental Llancahue.

| Species  | Shade tolerance | HGF  | MSF  | NDSF | OGF  |
|--|-----------------|------|------|------|------|
| <i>Aextoxicon punctatum</i> Ruiz and Pav.            | Tolerant        | 12.2 | 0.4  | 3.3  | 19.4 |
| <i>Amomyrtus luma</i> (Molina) D. Legrand and Kausel | Tolerant        | 2.3  | 5.9  | 1.7  | 2.0  |
| <i>Amomyrtus meli</i> (Phil.) D. Legrand and Kausel  | Tolerant        | -    | 17.2 | 0.7  | 3.9  |
| <i>Caldcluvia paniculata</i> Cav. (D. Don)           | Tolerant        | -    | -    | 2.0  | -    |
| <i>Laureliopsis philippiana</i> (Looser) Schodde     | Tolerant        | 47.8 | 3.6  | 3    | 36.3 |
| <i>Lomatia dentata</i> (Ruiz and Pav.) R. Br         | Tolerant        | -    | 2.5  | 0.6  | 2.4  |
| <i>Myrceugenia ovata</i> (Phil.) L.E. Navas          | Tolerant        | -    | 3.9  | 1.2  | 0.6  |
| <i>Myrceugenia planipes</i> (Hook. and Arn.) O. Berg | Tolerant        | 2.9  | 2.5  | -    | 6.8  |
| <i>Persea lingue</i> (Ruiz and Pav.) Nees            | Tolerant        | -    | 3.7  | 2.5  | -    |
| <i>Saxegothaea conspicua</i> Lindl.                  | Tolerant        | -    | 1.3  | 0.7  | -    |
| <i>Dasyphyllum diacanthoides</i> (Less.) Cabrera     | Midtolerant     | -    | 4.7  | -    | 1.3  |
| <i>Drimys winteri</i> J.R. Forst. and G. Forst.      | Midtolerant     | -    | 3.4  | 5.3  | 2.3  |
| <i>Eucryphia cordifolia</i> Cav.                     | Midtolerant     | 3.3  | 15.6 | 22.6 | 17.1 |
| <i>Gevuina avellana</i> Molina                       | Midtolerant     | 5.8  | 9.2  | 4.3  | 4.3  |
| <i>Laurelia sempervirens</i> (Ruiz and Pav.) Tul.    | Midtolerant     | -    | 0.6  | 3.5  | 1.9  |
| <i>Podocarpus salignus</i> D. Don                    | Midtolerant     | -    | 1.17 | 4.1  | -    |
| <i>Tepualia stipularis</i> (Hook. and Arn.) Griseb.  | Midtolerant     | -    | -    | 1.2  | -    |
| <i>Lomatia ferruginea</i> (Cav.) R. Br               | Midtolerant     | -    | 4.8  | 1.7  | 0.7  |
| <i>Embothrium coccineum</i> J.R. Forst. and G. Forst | Intolerant      | -    | 3.9  | -    | -    |
| <i>Gaultheria mucronata</i> (L.f.) Hook. and Arn     | Intolerant      | -    | 0.5  | -    | -    |
| <i>Lomatia hirsuta</i> Diels ex J.F. Macbr           | Intolerant      | -    | 4.0  | 2.5  | -    |
| <i>Nothofagus dombeyi</i> (Mirb.) Oerst              | Intolerant      | 23.4 | -    | 33.8 | -    |
| <i>Ovidia pillopillo</i> (Gay) Meisn                 | Intolerant      | -    | 4.6  | -    | -    |
| <i>Raukaua laetevirens</i> (Gay) Frodin              | Intolerant      | -    | -    | 2.2  | -    |
| <i>Rhaphithamnus spinosus</i> (Juss.) Moldenke       | Intolerant      | 2.3  | 2.8  | 2.3  | 1.6  |
| <i>Weinmannia trichosperma</i> Cav.                  | Intolerant      | -    | 4.0  | 0.8  | 1.0  |

terms of their IV (Table 3), although the latter having much greater stocks (Table 3 and Table 4). The species that had the highest IV (Table 3) were also the ones that stored the most carbon in the OGF, the NDSF and the HGF; but in the case of MSF, *Dasyphyllum diacanthoides* was the second species with the highest contribution in carbon due to the presence of large trees

(>40 cm in DBH), despite not being among the species with the highest IV.

Total carbon stocks

The OGF accumulated the greatest amounts of total carbon, with 506.8 Mg C/ha, followed by the NDSF with 442.3 Mg C/ha and the MSF

**Table 4.** Stored carbon (Mg C/ha) in each forest studied in the Llancahue Experimental Forest. The mean and standard deviation values are presented for the subtotal corresponding to each forest component.

**Tabla 4.** Carbono almacenado (Mg C/ha) en cada bosque estudiado en el Bosque Experimental Llancahue. Se presentan los valores de media y desviación estándar para el subtotal correspondiente a cada componente forestal.

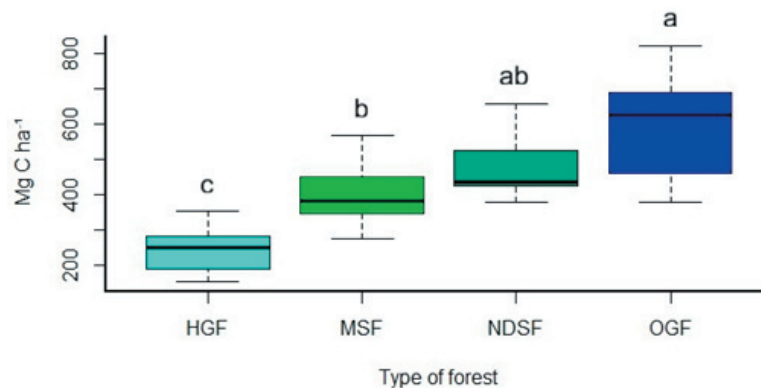
| Forest component | Type                | HGF         | MSF           | NDSF          | OGF          |
|------------------|---------------------|-------------|---------------|---------------|--------------|
| Trees            | Alive               | 80.5c       | 142.8bc       | 203.7ab       | 264.1a       |
|                  | Dead                | 10.9        | 3.5           | 4.3           | 1.6          |
|                  | Subtotal            | 91.42±57.3c | 146.28±73.8bc | 207.90±37.6ab | 265.68±98.5a |
| Understory       | Shrubs              | 0.00c       | 2.80a         | 0.52bc        | 1.73ab       |
|                  | Herbs               | 0.03        | 0.1           | 0.03          | 0.40         |
|                  | Regen.              | 0           | 0.29          | 0.35          | 0.14         |
|                  | <i>Chusquea</i> sp. | 12.00a      | 0.22b         | 0.56b         | 0.21b        |
|                  | Subtotal            | 12.0±5.5a   | 3.4±2.4b      | 1.5±1.1b      | 2.5±1.2b     |
| Forest floor     | CWM (low decomp.)   | 0.46        | 12.98         | 41.9          | 18.07        |
|                  | CWM (high decomp.)  | 0           | 17.82         | 9.73          | 7.12         |
|                  | LWM                 | 7.56        | 8.71          | 8.27          | 5.36         |
|                  | Litterfall (Oi+Oe)  | 2.15c       | 10.61 a       | 10.59 a       | 6.97b        |
|                  | Humus (Oa)          | 2.03c       | 3.16bc        | 6.88 a        | 3.86b        |
|                  | Subtotal            | 12.2±3.3b   | 53.3±42.7ab   | 77.4±68a      | 41.4±44ab    |
| Soil             | 0-30 cm             | 105.4±17c   | 161.6±18.6b   | 155.6±43.2b   | 197.3±50.6a  |
| Total            |                     | 221.1±99c   | 364.6±92.4b   | 442.3±80.3ab  | 506.8±128a   |

CWM=coarse woody material (diameter ≥7.6cm). LWM=fine woody debris (diameter ≤7.5 cm).

\*Means that do not share the same letter are significantly different (P<0.05).

CWM=material leñoso grueso (diámetro ≥7.6 cm). LWM=material muerto fino (diámetro ≤7.5 cm).

\*Las medias que no comparten la misma letra son significativamente diferentes (P<0.05).



**Figure 4.** Boxplots for the total carbon (Mg C/ha) for each sampled forest in the evergreen forests in the Llancahue experimental forest. The horizontal line inside the box represents the median (Q2), indicating the central value of the data distribution. The box represents the interquartile range (IQR=Q3-Q1), which contains the middle 50% of observation. Different letters illustrate significant differences among forest types (P<0.05).

**Figura 4.** Carbono total (Mg C/ha) para cada bosque muestreado en los bosques siempreverdes del bosque experimental de Llancahue. Letras diferentes indican diferencias significativas entre tipos de bosque (P<0.05). La línea horizontal dentro de la caja representa la mediana (Q2), indicando el valor central de la distribución de los datos. La caja representa el rango intercuartil (IQR=Q3-Q1), que contiene el 50% de las observaciones del centro.

with 364.5 Mg C/ha (Table 4). As expected, the HGF had the least carbon, with 221.05 Mg C/ha (Figure 4). The OGF had a significantly greater carbon stock than the MSF and the HGF, and the MSF also differed significantly from the HGF. The Greenhouse-Greisser test indicated that there were significant differences in the carbon stocks of different components in the forests (i.e., trees, understory, forest floor and soil), as well as in the interaction of the forests and these components ( $F=7.638$ ;  $P<0.05$ ). Carbon stocks exhibited a significant component for forest development stage interaction. Carbon stored in tree biomass and soil increased consistently with forest development, reaching maximum values in old-growth forests. In contrast, understory carbon declined with advancing development stage, with higher values in early and intermediate forests and markedly lower values in old-growth stands. Carbon stocks in the forest floor varied less among development stages. These contrasting responses among components indicate that the effect of forest development on carbon storage differs among ecosystem components (Table 4).

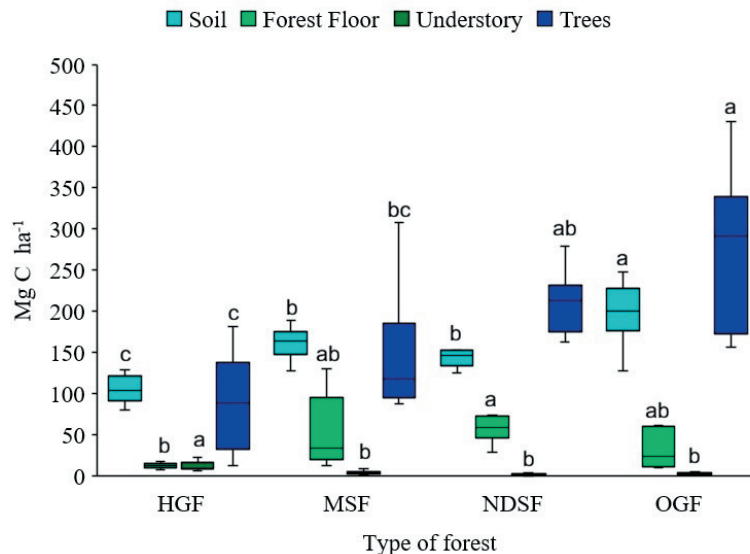
#### Carbon stocks in trees

Carbon stocks in the tree pools showed significant differences ( $F=10.347$ ;  $P<0.001$ )

among the sampled forests (Table 4), with the OGF having the highest carbon values (265.7 Mg C/ha). The NDSF and MSF had 207.9 and 146.3 Mg C/ha, respectively. The HGF had the lowest values (91.4 Mg C/ha), of which only 11.7% corresponds to the contribution of carbon from standing dead trees (Table 4). The tree layer was the component with the highest contribution of aboveground carbon (>70%). However, in the case of carbon, the tree and soil components are the ones that contribute the most carbon to the stock for all the forests evaluated (Figure 5). The tree species that made a greater contribution to the carbon stocks in each forest were *Laureliopsis philippiana* (118.9 Mg C/ha), *Eucryphia cordifolia* (62.1 Mg C/ha) and *Aextoxicon punctatum* (58.2 Mg C/ha) in the OGF; *N. dombeyi* (145.5 Mg C/ha) and *E. cordifolia* (39.9 Mg C/ha) in the NDSF; *E. cordifolia* (27.4 Mg C/ha), *D. diacanthoides* (19.1 Mg C/ha) and *Gevuina avellana* (18.4 Mg C/ha) in the MSF, and *L. philippiana* (52.9 Mg C/ha) and *N. dombeyi* (26.4 Mg C/ha) in the HGF (Figure 6).

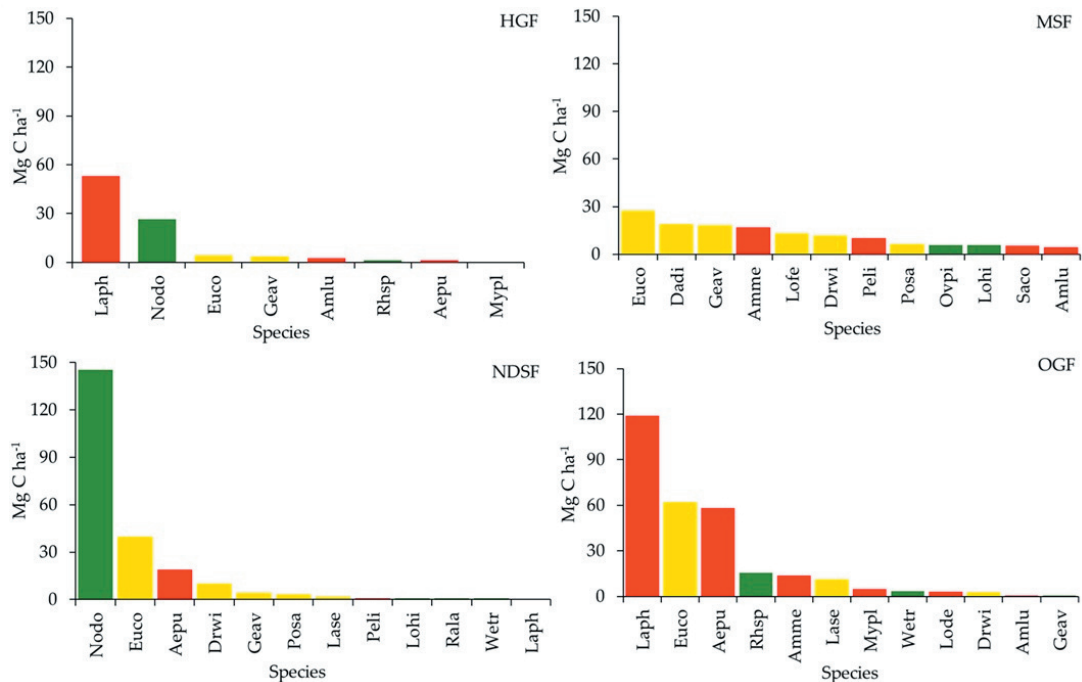
#### Carbon stocks in the understory

The HGF had significantly higher carbon stocks in the understory layer than the other three forest ecosystems, which was explained



**Figure 5.** Boxplot for carbon stocks by aboveground and belowground biomass components (trees, understory, forest floor and soil) for the four sampled forests in Llancahue Experimental Forest. The horizontal line inside the box represents the median (Q2), indicating the central value of the data distribution. The box represents the interquartile range (IQR=Q3-Q1), which contains the middle 50% observations.

**Figura 5.** Reservas de carbono de acuerdo a los componentes de biomasa aérea y subterránea (árboles, sotobosque, piso forestal y suelo) para los cuatro tipos de bosques muestreados en el Bosque Experimental Llancahue. La línea horizontal dentro de la caja representa la mediana (Q2), indicando el valor central de la distribución de los datos. La caja representa el rango intercuartil ((IQR=Q3-Q1), que contiene el 50% de las observaciones del centro.



**Figure 6.** Carbon contribution of the species with the highest importance value for each type of forest (HGF=forest dominated by *Chusquea quila*. MSF=mixed secondary forest. NDSF=secondary forest dominated by *Nothofagus dombeyi*. OGF=old-growth forest) in the Llancahue Experimental Forest. Species acronyms: Aepu (*Aextoxicon punctatum*), Amlu (*Amomyrtus luma*), Amme (*Amomyrtus meli*), Capa (*Caldcluvia paniculata*), Dadi (*Dasyphyllum diacanthoides*), Drwi (*Drimys winteri*), Emco (*Embothrium coccineum*), Euco (*Eucryphia cordifolia*), Gamu (*Gaultheria mucronata*), Geav (*Gevuina avellana*), Laph (*Laureliopsis philippiana*), Lase (*Laurelia sempervirens*), Lode (*Lomatia dentata*), Lofe (*Lomatia ferruginea*), Lohi (*Lomatia hirsuta*), Myov (*Myrceugenia ovata*), Nodo (*Nothofagus dombeyi*), Ovpi (*Ovidia pillopillo*), Peli (*Persea lingue*), Posa (*Podocarpus salignus*), Rala (*Raukaura laetevirens*), Rhsp (*Rhaphithamnus spinosus*), Saco (*Saxegothea conspicua*), Test (*Tepualia stipularis*) and Wetr (*Weinmannia trichosperma*). Shade tolerance: tolerant (red); mid-tolerant (yellow); intolerant (green).

**Figura 6.** Contribución de carbono de las especies con mayor valor de importancia para cada tipo de bosque (HGF=bosque dominado por *Chusquea quila*. MSF=bosque secundario mixto. NDSF=bosque secundario dominado por *Nothofagus dombeyi*. OGF=bosque adulto) en el Bosque Experimental Llancahue. Acrónimos de especies: Aepu (*Aextoxicon punctatum*), Amlu (*Amomyrtus luma*), Amme (*Amomyrtus meli*), Capa (*Caldcluvia paniculata*), Dadi (*Dasyphyllum diacanthoides*), Drwi (*Drimys winteri*), Emco (*Embothrium coccineum*), Euco (*Eucryphia cordifolia*), Gamu (*Gaultheria mucronata*), Geav (*Gevuina avellana*), Laph (*Laureliopsis philippiana*), Lase (*Laurelia sempervirens*), Lode (*Lomatia dentata*), Lofe (*Lomatia ferruginea*), Lohi (*Lomatia hirsuta*), Myov (*Myrceugenia ovata*), Nodo (*Nothofagus dombeyi*), Ovpi (*Ovidia pillopillo*), Peli (*Persea lingue*), Posa (*Podocarpus salignus*), Rala (*Raukaura laetevirens*), Rhsp (*Rhaphithamnus spinosus*), Saco (*Saxegothea conspicua*), Test (*Tepualia stipularis*), Wetr (*Weinmannia trichosperma*). Tolerancia a la sombra: tolerante (rojo); semitolerante (amarillo); intolerante (verde).

by the high cover (near 100%) of *C. quila* (Table 4). The MSF ranked second in carbon stocks in this layer, with 82.1% in the shrub component concentrated in the species *Rhamnus diffusus* and *Gaultheria mucronata*. In the OGF, *Nertera granadensis* was the herbaceous plant with the highest carbon reserves in this understory layer. In the NDSF, the vine *Luzuriaga radicans* and the herbaceous *Nertera granadensis* contributed 35.6% to the carbon stock of the shrub layer.

#### Carbon stocks in the forest floor

No significant differences were observed between the forests for coarse woody material

(CWM), although the secondary forests had greater carbon stocks in this component (Table 4). In the secondary forests, low decomposition CWM contributed more carbon in NDSF, while high decomposition CWM did in the MSF. In the case of the OGF, there was an accumulation of 25.1 Mg C/ha, of which ~72% corresponds to low decomposition CWM, with HGF being the forest with less material accumulated (0.46 Mg C/ha), all corresponding to low decomposition CWM material. In the case of the FWM (diameters  $\leq 7.5$  cm), no significant differences were observed among the forests, although the secondary forests accumulated lightly greater stocks (Table 4). The secondary forests (MSF and NDSF) had similar values (10

Mg C/ha), statistically different from the other two forests ( $P < 0.05$ ) in this component. They were followed by OGF (6.97 Mg C/ha) and HGF (2.15 Mg C/ha) (Table 4). The humus (Oa) was significantly higher in NDSF compared to the other three forests, and significantly higher in OGF compared to HGF, with MSF but did not differ between NDSF, OGF and HGF, with NDSF being the one that accumulated the most carbon in this component, followed by OGF, MSF and HGF (Table 4).

#### Soil carbon stocks

Differences in this component were like those observed for the tree layer. The OGF was significantly greater and almost doubled the carbon stocks (197 Mg/ha) in the soil layer, compared to the values estimated for HGF (197 Mg/ha). However there were no significant differences with MSF and NDSF, where these two secondary forests had similar values (Table 4). The two secondary forests did not differ in carbon stocks in this compartment, but both had significantly greater stocks than the HGF.

## DISCUSSION

### *Aboveground carbon stocks in old-growth, successional and high-graded temperate forests*

The vast region of the temperate biome (Olson et al. 2001) is home to a great variety of forest types, where especially climate determines differences in tree diversity, growth and productivity and, therefore, of carbon stocks (Lal and Lorenz 2012). Within temperate forests, particularly temperate rainforest (which occur in regions with mild temperatures, high rainfall and often coastal influences [DellaSala et al. 2011]), are the most carbon-dense forests, with the *Eucalyptus* forests of southern Australia (1302 Mg/ha of aboveground live and dead carbon) and the conifer forests of US Pacific Northwest (762 Mg/ha of aboveground live and dead carbon) ranking first (Keith et al. 2009). For the temperate rainforests of the Southern hemisphere (excluding those dominated by *Eucalyptus* sp.), the highest values are reported for old-growth forests in the Chilean Andes (Table 5). Successional forests in this region have lower carbon density values (Table 5),

**Table 5.** Carbon stocks in different temperate forest ecosystems of the Southern Hemisphere.

**Tabla 5.** Reservas de carbono en diferentes ecosistemas de bosques templados del hemisferio sur.

| Type of forest           | Country or region | Tree | Understory | Dead wood | Soil (Mg/ha) (0-30 cm) | Roots | Total | Reference             |
|--------------------------|-------------------|------|------------|-----------|------------------------|-------|-------|-----------------------|
| Secondary-Patagonia      | Argentina         | 122  | ND*        | 70        | 111                    | 36    | 339   | Loguercio et al. 2024 |
| Secondary                | New Zealand       | 137  | ND         | 13        | 33                     | ND    | ND    | Davis et al. 2003     |
| Secondary-Coastal        | Chile             | 161  | 1.2        | 51        | 149                    | 44    | 405   | Gayoso 2001           |
| Secondary-Andes          | Chile             | 313  | 9.7        | 31        | ND                     | 88    | 441   | Gayoso 2001           |
| Secondary-Coastal (NDSF) | Chile             | 208  | 1.5        | 77        | 156                    | ND    | 442   | This study            |
| Secondary-Coastal (MSF)  | Chile             | 146  | 3.4        | 53        | 162                    | ND    | 365   | This study            |
| Secondary-Coastal        | Chile             | 140  | 0.5        | 14        | ND                     | 39    | 193   | Gayoso 2001           |
| Mature                   | New Zealand       | 123  | ND         | 11        | 33                     | ND    | ND    | Davis et al. 2003     |
| Old growth               | New Zealand       | 213  | ND         | ND        | 55.0                   | ND    | 344   | Hart et al. 2003      |
| Old growth-Coastal       | Chile             | 282  | 2.8        | 60        | ND                     | 80    | 424   | Gayoso 2001           |
| Old Growth-Andean        | Chile             | 243  | 9.7        | 32        | 144                    | ND    | 428   | Gayoso 2001           |
| Old growth-Andean        | Chile             | 484  | ND         | 38        | ND                     | ND    | 522   | Pilquinao et al. 2011 |
| Old growth-Coastal       | Chile             | 359  | ND         | 12        | ND                     | ND    | 370   | Pilquinao et al. 2011 |
| Old-growth-Coastal       | Chile             | 266  | 2.5        | 41        | 197                    | ND    | 507   | This study            |
| High-graded (HGF)        | Chile             | 91   | 12         | 12        | 105                    | ND    | 221   | This study            |

\*ND=non determined

which is consistent with findings elsewhere (Nyirambangutse et al. 2017; Gayoso and Guerra 2005; Brown and Lugo 1990). While we did not find reports of carbon stocks in high-graded forests, like the HGF evaluated in the present study, these had stock values comparable to many secondary forests (Table 5).

In this study, trees accumulated the greatest carbon in the OGF and the NDSF, but most carbon stocks in the MSF and the HGF were in the soil, although their absolute values were lower than in NDSF and OGF. The high relative proportion of soil carbon in the secondary forest with lower biomass (MSF) and in the HGF reflects that these forests have established or are the result of harvesting in sites that were covered by forests that accumulated abundant carbon in this compartment.

The third most important component in terms of carbon stocks was the forest floor. Values were especially high in NDSF due to CWD in low decomposition state. Carbon stocks in the forest floor are dependent on inputs (Davis et al. 2003), and inputs of dead biomass have been high in NDSF. This forest had the highest carbon in standing dead trees, and in CWM with low levels of decomposition, reflecting a recent rapid process of dead wood dynamics. From a perspective of forest dynamics (Oliver and Larson 1996), this suggests that the understory reinitiation stage (as NDSF; González et al. 2015) is in an active process of competition-driven tree mortality of relatively larger trees with more biomass compared to the stem exclusion stage (MSF; González et al. 2015), which ranked second in C on forest soil. The OGF and the HGF had the least amounts of C in the forest floor; the former, especially because of low relative values of CWM of low decomposition; the latter, for overall low numbers in all measured variables in the forest floor. The forest floor, added to dead trees, provide a good representation of the dynamics of dead biomass. Also, in the organic layer (Oa sub-horizon), the NDSF had the greatest carbon stocks. Carbon stored in the litter depends directly on the production rate of each type of plant community as well as on mineralization and decomposition rates, and time (Arnaldos et al. 2004). In NDSF, *N. dombeyi*, the dominant species, has leaves with slow decomposition rates (Pérez et al. 1991), which explains these values that nearly doubled those in the OGF, the MSF and HGF.

The remaining aboveground compartments had minor contributions to carbon stocks. The understory contributed only 0.5 to 5% of the carbon stocks in these forests, even in the case of high cover of *C. quila* in the HGF (see also González and Donoso 1999) or of *C. culeou* in other forest ecosystems (Veblen et al. 1979). Shrubs and herbaceous species in early developmental stages always have a relatively greater (though still minor) importance, as observed in the MSF in this study (see also Pausas and Paula 2012). Fine woody material (FWM or LWM), although not very significant in terms of climate change mitigation, is highlighted for its importance as a combustible material, contributing to fire risk. In the case of HGF and MSF, ladder fuels are present, meaning there is vegetal material connecting the understory to the tree canopy, which plays a fundamental role in forest fire dynamics. Their presence significantly increases the risk of a surface fire climbing into the canopy, generating much more intense and difficult-to-control crown fires (Flores-Garnica et al. 2018).

#### *Soil carbon stocks in old-growth, successional and high-graded temperate forests*

Carbon stored in the soil was higher in the OGF, followed by the MSF, NDSF and HGF, the two latter being within the range of values (111 and 151 Mg C/ha) reported by Rojas et al. (2020) for soils under native forests in the region. The OGF and the MSF accumulated more carbon than forests reported by Gayoso and Guerra (2005) for similar old-growth forests (181 Mg C/ha). The *Nothofagus*-dominated NDSF had less carbon in this compartment (156 Mg C/ha) compared to the data reported for Andisols under the deciduous *Nothofagus obliqua* forests in south-central Chile (230 and 260 Mg C/ha) (Thiers 2004). Gayoso and Guerra (2005) evaluated the availability of carbon in evergreen forests in three development stages, a mixed forest (200 Mg C/ha), a secondary (199 Mg C/ha), and an old-growth forest (184 Mg C/ha), and values were within the range of those obtained in the evergreen forests evaluated in the present study.

Suárez et al. (2016) report that forest soils down to 30 cm depth typically contain 20-300 Mg C/ha, depending on forest type, climate and soil characteristics. Temperate rainforests tend to store the highest carbon levels among temperate forests due to soil

moisture supporting continuous organic matter decomposition (Keith 2014). Soil carbon in the HGF was 53% lower compared to the OGF, consistent with Martínez et al. (2008), who reported that soil carbon stocks decline by ~50% as ecosystem degradation advances, as observed in the HGF.

#### Management implications

While the HGF is not a desired state (Vásquez-Grandón et al. 2018), especially since *C. quila* prevents the reorganization of the forest ecosystem (González et al. 2015; González and Donoso 1999), the control of the understory to promote tree regeneration would not mean an important loss in carbon; in the case of this study, it is concentrated in the soil. On the contrary, this control would be key to the restoration of these ecosystems. However, the maintenance of residual trees in these types of forests would play an important role in providing seeds or other propagules for regeneration, in retaining carbon, and would also contribute to developing more diverse and structurally complex forests (*sensu* Adams et al. 2021).

Likewise, variations were observed between tree species in the four stages of development, as expressed in the relative importance value of the species. Gayoso (2001) reported that the species that make up the evergreen forest accumulate between 42.7% and 46.6% of its total biomass. In the case of the secondary forests, in the NDSF *N. dombeyi* and *E. cordifolia*, both long-lived pioneers, were dominant and the species that accumulated more carbon, while in the MSF also *E. cordifolia* plus *G. avellana* (relatively short-lived pioneer) and *D. diacanthoides* (mid-tolerant) were the species that accumulated more carbon. In the OGF *E. cordifolia* maintains a high importance, jointly with *L. philippiana*, *A. punctatum*, both late-successional shade-tolerant species (Figure 6) reflecting the increasing importance of shade-tolerant species with the advance of succession.

Perspectives for forest management of these forests are promising in terms of carbon stocks, especially if the principles of ecological silviculture (Palik et al. 2020), mostly the development of diverse and complex forests, are followed, which has been proposed for the forest type studied here (Donoso and Soto 2024). These types of practices have been conducted in these forests through variable-density thinnings (Donoso et al. 2020) and

irregular shelterwood (Donoso et al. 2024). As these forests grow more rapidly with forest management and many trees achieve greater sizes, an increasing proportion of the harvests in either intermediate or regeneration cuts could be destined to timber (especially in timber-sized secondary forests and mature forests) and carbon stocks would likely continue to increase. Similarly, especially for some private landowners the management of the old-growth forests, through uneven-aged silvicultural systems, could also be a continued means to the provision of high-quality timber while maintaining high carbon stocks and structurally complex forests. These climate-smart forestry solutions seem promising for well-conserved forests. In the case of high-graded forests, these have near half of the carbon found in old-growth forests and have a great potential for rehabilitation either through natural or artificial regeneration (Vásquez-Grandón et al. 2018).

#### CONCLUSIONS

Old-growth forests (OGF) had greater total carbon values in the tree and soil pools, which jointly explain between 82 and 91% of the total carbon (without the root component) in the forest ecosystems in the studied hardwood-dominated evergreen temperate rainforests at mid-elevations in the coastal range. However, the tree component has a greater contribution in mature and old-growth forests, while the soil component has a greater contribution in the young and high-graded forests. The greater values in the mature secondary forest compared to the young secondary forest occur because of the different stage of forest dynamics of these forests (understory reinitiation vs. stem exclusion), but also because of the dominance of *N. dombeyi* in the former, which is the fastest growing tree species in this region. These forests have lower C values than some temperate rainforests, but higher than most other forests in the temperate biome. These results illustrate that more complex forests (i.e., multilayered dense forests with tall trees) are fundamental to increase carbon stocks in these ecosystems.

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AVAILABILITY OF DATA AND MATERIALS. The data sets generated and/or analysed during the current study are not publicly available as they are part of doctoral research but could be made available upon request from the

corresponding author and used to generate insights for public use.

CONFLICT OF INTERESTS. The authors declare that they have no competing interests.

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