Forest Ecology and Management 615 (2026) 123828

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Understory plant diversity in *Pinus radiata* plantations of Chile: The role of stand structural attributes

Natalia Gertner [a,b], Rodrigo Vargas-Gaete [a,b,c,*], Christian Salas-Eljatib [d], Andrés Fuentes-Ramírez [a,b,c], Juan Pedro Elissetche [b,e], Rafael Rubilar [b,f]

[a] Laboratorio de Ecosistemas y Bosques (EcoBos), Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de La Frontera, Casilla 54-D, Francisco Salazar 01145, Temuco 4811230, Chile
[b] Centro Nacional de Excelencia para la Industria de la Madera (CENAMAD), Pontificia Universidad Católica de Chile, Santiago, Chile
[c] Center for Biodiversity and Ecological Sustainability (C-BEST), Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de La Frontera, Temuco, Chile
[d] Laboratorio de Biometría y Modelación Forestal, Departamento de Gestión Forestal y su Medio Ambiente, Universidad de Chile, Santiago, Chile
[e] Departamento de Manejo de Bosques y Medio Ambiente, Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, 4030000, Chile
[f] Cooperativa de Productividad Forestal, Departamento de Silvicultura, Facultad de Ciencias Forestales, Universidad de Concepción, Concepción, 4030000, Chile

ARTICLE INFO

Keywords:
Plant biodiversity
Structural complexity
Plantation stands
Monterey pine
Environmental drivers
Transitional forestry
Ecosystem services

ABSTRACT

In temperate regions, industrial forestry plantations are increasingly evaluated for their potential to support multifunctional forest systems and sustain ecosystem services, including native plant biodiversity. However significant gaps remain in understanding the environmental and structural drivers of plant biodiversity within plantations, underscoring the need for locally grounded empirical studies. This study evaluated native vascular plant diversity beneath *Pinus radiata* plantations at two sites in south-central Chile. Species diversity and tree regeneration were quantified across 120 understory plots (25 m^2 each) established in *P. radiata* plantations stands (>9 years), using adjacent native forests as reference. Stand structure was characterized across 24 plots (500 m^2 each), while microsite and soil variables were measured to evaluate their influence on understory plant composition. Data were analyzed using multivariate ordination and generalized linear mixed models to examine relationships among stand structure, environmental variables, and understory vegetation. Stand structure in *P. radiata* plantations was a significant predictor of native plant species richness under the canopy. Although nearby native forests showed greater richness and regeneration, plantations sustained ~43–60% of the native species richness recorded in adjacent reference forests, particularly where canopy structure was more open and heterogeneous. These results indicate that management adjustments aimed at increasing structural complexity can improve the ecological compatibility of plantations. Furthermore, they highlight the potential of plantations within transitional silviculture to support ecosystem services and enhance ecological functionality.

1. Introduction

Forest plantations worldwide cover nearly 131 million hectares representing a major component of managed forests largely established for producing wood, fiber, and non-wood products (Bauhus et al., 2010; FAO, 2020). Since the first industrial trials in Europe in the 18th century, plantation forestry has expanded steadily. Its rapid spread during the 19th century was largely driven by wood shortages resulting from natural forests degradation, accelerated industrialization and growing human populations (Bauhus et al., 2010; Diaci, 2006; Prado, 2015). This rapid expansion reflects their high productivity, supported by intensive yet simple management that enable predictable stand development and large-scale implementation (McEwan et al., 2020; Prado, 2015). Currently, despite representing less than 5% of the global forest area (FAO, 2020), plantations supply nearly one-third of the industrial timber demand (Jürgensen et al., 2014; McEwan et al., 2020). By 2040, plantations are expected to supply about half of the global wood (Bauhus et al., 2010), particularly in emerging economies such as Latin America, Africa, and parts of Asia (Carle and Homgren, 2008; Korhonen et al., 2021; Payn et al., 2015). At the same time, their expansion has been promoted as an efficient strategy to provide timber while also contributing to certain ecosystem services, such as soil conservation and

* Corresponding author at: Laboratorio de Ecosistemas y Bosques (EcoBos), Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de La Frontera, Casilla 54-D, Francisco Salazar 01145, Temuco 4811230, Chile.
E-mail address: rodrigo.vargas@ufrontera.cl (R. Vargas-Gaete).

https://doi.org/10.1016/j.foreco.2026.123828
Received 24 December 2025; Received in revised form 17 April 2026; Accepted 20 April 2026

hydrological regulation (Bauhus et al., 2010; Prado, 2015; Cassiano et al., 2023). Plantations can also reduce pressure on natural forests, by supplying wood from planted sources, helping to mitigate degradation and deforestation processes (Pirard et al., 2016; Sedjo, 1999). However, the expansion of plantations has also raised concerns about trade-offs and negative impacts on other ecosystem services (Huettmann and Young, 2022; Salas et al., 2016). In several regions, communities and environmental organizations have highlighted impacts on water access, land use, and traditional landscapes (Cariola-Szuchman et al., 2018; Carte et al., 2021; Hughey et al., 2019). Large-scale plantations have been linked to socio-environmental conflicts, particularly over land tenure and uneven economic benefits (Malkamäki et al., 2018), intensifying tensions in the forestry sector alongside concerns about biodiversity loss and ecosystem fragmentation (Cagnoni et al., 2023; Malkamäki et al., 2018).

In Chile, where over 3 million hectares are covered by plantations, mainly *Pinus radiata* and *Eucalyptus spp*., these tensions are particularly evident, reflecting the contrast between the sector's productive growth and the local environmental and social impacts, especially in south-central regions (Reyes and Nelson, 2014; Salas et al., 2016, Gerding, 2025). The low structural diversity characteristic of even-aged monocultures, together with the homogenization of forest landscapes resulting from extensive and uniform management, limits their capacity to provide ecosystem services compared to natural forests (Holt, 2012; Osuri et al., 2020). However, the magnitude of these impacts may vary with stand structural conditions which are often shaped by silvicultural practices, as certain configurations can mitigate these effects and enhance specific ecosystem services (Amoroso et al., 2024; Tarasewicz and Jönsson, 2021).

Forest plantation management is often adjusted to maximize productivity typically involving high establishment densities, pruning, and thinning within short rotations that culminate in clear-cutting (Lieffers et al., 2023; Rubilar et al., 2018; Maclaren & Knowles, 2005). While effective for timber production, these conditions are associated with reduced functional diversity compared to less altered systems (Chianucci et al., 2024). In south-central Chile, extensive *P. radiata* plantations exemplify these patterns, with simplified and homogeneous stand conditions linked to landscape fragmentation, altered floristic composition, reduced native regeneration, and lower ecosystem service provision and resilience to disturbances such as wildfires and pest outbreaks (García et al., 2018; Uribe et al., 2020).

Despite these limitations, there is growing evidence that plantations can support biodiversity when favorable structural and landscape conditions are present (Pirard et al., 2016; Simões et al., 2024). Proximity to native forest patches has been identified as a key variable, acting as a source of propagules for the regeneration of native species and promoting their establishment and persistence in the plantation understory (Chazdon et al., 2009; Vargas-Gaete et al., 2020). Likewise, landscape heterogeneity can enhance connectivity and facilitate species presence (Schall et al., 2018). At the stand level, more diverse and heterogeneous structural conditions on plantations have been shown to support biodiversity by improving micro-environmental conditions for regeneration (McFadden and Dirzo, 2018; Wang et al., 2022). For example, lower stand density and increased canopy openness enhance light availability, facilitating the establishment and persistence of native understory species (Brockerhoff et al., 2008).

Silvicultural practices are known to shape stand structure and associated microsite conditions, which in turn can influence understory biodiversity. Practices such as establishing uneven aged or mixed species plantations (Savilaakso et al., 2021; Sharma et al., 2016), increasing rotation age (Coote et al., 2013; Pryde et al., 2015), and implementing harvesting approaches that maintain continuous canopy cover, have been shown to modify structural and microenvironmental conditions for regeneration, thereby supporting native understory development (Alday et al., 2017). In addition, reducing stand density has proven effective in increasing light availability and facilitating the establishment of native species in the understory (Ali et al., 2019).

Despite these advances, knowledge gaps remain regarding how variation in site and stand structural conditions interact to influence biodiversity beneath plantation canopies (Heinrichs et al., 2018; Kremer et al., 2022; Wang et al., 2021, 2023). Because these effects depend on local environmental context, including climate, soil, and landscape configuration, it is essential to examine different geographic settings to identify consistent patterns (Smith et al., 2008). Understanding how environmental factors and stand structure influence biodiversity is key to explaining variability among plantations and its underlying drivers. Biodiversity beneath plantation canopies are determined by a combination of conditions operating at multiple spatial and temporal scales. Site variables such as elevation, aspect, slope, and soil fertility, together with microsite conditions including light availability and litter cover, influence understory composition and regeneration (Carteron et al., 2020; Ma et al., 2018). In plantation systems these effects are strongly modulated by stand structure which regulates light penetration and resources availability. Attributes such as canopy openness, stocking, and vertical heterogeneity have been shown to influence the richness and recruitment of native species (Forbes et al., 2019; Heinrichs et al., 2018; Marshall et al., 2024; Wang et al., 2021). Plantation age also influences species establishment, as more developed stands tend to provide more favorable conditions for regeneration (Braun et al., 2017; Heinrichs et al., 2018). Integrating environmental conditions and stand attributes is therefore key to understanding the capacity of *P. radiata* plantations to support plant biodiversity.

This study aims to characterize native plant biodiversity beneath *P. radiata* plantations in south-central Chile. We evaluate how site, microsite and soil conditions together with stand structural attributes of plantations can influence plant biodiversity and regeneration of native tree species. We hypothesize that the capacity of plantations to support native plant diversity varies with stand structure, being higher in stands with lower stocking and greater canopy openness than in more homogeneous, closed-canopy plantations. Our goal is to identify the structural conditions that favor biodiversity, providing a basis for the development of more multifunctional plantation systems compatible with conservation.

2. Methods

2.1. Study area and sampling design

The study area was defined within the intermediate depression of south-central Chile, focusing on landscapes where land cover is dominated by *P. radiata* plantations that coexist with fragments of native *Nothofagus*-dominated forests (Fig. 1). Native forest fragments represent the last vestiges of the region's original vegetation (37–39° S; Roble (*Nothofagus obliqua*) –Raulí (*N. alpina*) – Coigüe (*N. dombeyi*); Ro-Ra-Co forest type; Fig. 1; Donoso, 1981; Otero, 2006) and are typically found between 200 and 800 m.a.s.l., on steep slopes (>30%), and on soils of volcanic origin, ranging from old red clays to recent Andisols derived from recent volcanic ash (Schlatter and Gerding, 2024). These edaphic and topographic conditions are representative of the intermediate depression landscapes in which *P. radiata* forestry has expanded in Chile (Fig. 1; Fuentealba et al., 2021; Lara et al., 2012; Luebert and Pliscoff, 2006)

The proximity between native forest patches and plantations allowed for comparisons of understory plant biodiversity under similar environmental conditions (Fig. 1b). The selected sites included *P. radiata* stands between 9 and 37 years old, representing a range of structural conditions associated with different silvicultural histories. These included stands with multiple pruning and thinning operations, as well as stands with minimal intervention. Each plantation stand was located adjacent to, or within 500 m of *Nothofagus* native forests characterized by secondary or mature structure, dense to semi-dense canopies, and tree heights greater than 8 m (CONAF, 2014).

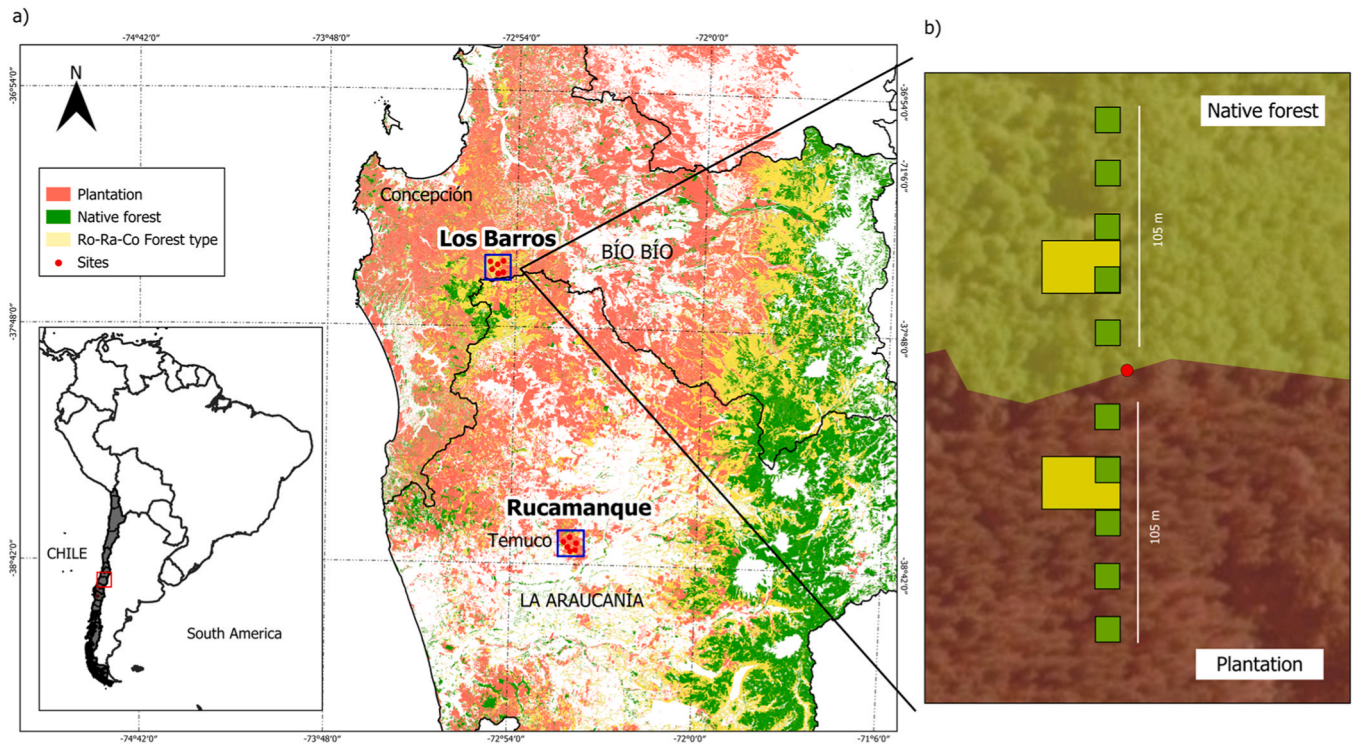

Fig. 1. A) Map of the study area. Blue squares indicate study sites and the red dots sampling points. B) Schematic representation of the transects established at each sampling point. Green squares correspond to the 5 × 5 m vegetation plots, and yellow rectangles correspond to the 20 × 25 m structural plots. Ro-Ra-Co forest type correspond to secondary *Nothofagus spp.* dominated forests.

Sampling locations were defined by integrating cartography of native vegetation and forest use within a GIS framework (CONAF, 2014, 2015; IDE, 2023; QGIS Development Team, 2023), applying criteria of accessibility, adjacency to native forest patches, and spatial configuration. Following this procedure, two study sites were defined: (1) Los Barros, in the Biobío Region (~5000 ha; 37°34′–37°37′ S), and (2) Rucamanque, in La Araucanía Region (~2500 ha; 38°36′–38°39′ S; Fig. 1). At each site, six sampling points were selected (twelve in total), where two 105 m line transects were established: one oriented towards the native forest and the other towards the plantation (Fig. 1b).

Each transect included one 500 m^2 plot (20 × 25 m) for structural and soil sampling conditions, along with five 25 m^2 subplots (5 × 5 m) placed every 20 m to record floristic, regeneration and microsite variables (Fig. 1b). In total, twenty-four stand structural plots were established (12 in plantations and 12 in native forests), along with 120 subplots (60 per condition).

2.2. Data collection

Field data were collected between November 2023 and February 2024 across multiple field campaigns, covering the main growing season. In each structural plot (500 m^2), all trees larger than 5 cm in diameter at breast height (DBH at 1.3 m) were measured recording species identity, DBH with a metric diameter tape, and total height with a Vertex hypsometer (Haglöf ®, Sweden). For each 25 m^2 subplot, the floristic composition of all vascular plants was recorded following the Braun–Blanquet cover–abundance scale (Braun-Blanquet, 1979), and tree regeneration (< 5 cm DBH) was quantified by height classes (< 50 cm; 50–200 cm; > 200 cm). To characterize microsite conditions, the percentage cover of mineral soil, litter, and coarse woody debris was visually estimated (Mueller-Dombois et al., 2008). Additionally, hemispherical photographs were taken at 80 cm above ground level under diffuse light conditions (i.e., overcast sky or low sun angle) following standard protocols using a Nikon D5200 camera fitted with a 8-mm Sigma lens to estimate incident radiation (Fournier and Hall, 2017).

To characterize soil chemical attributes, soil samples were collected at each 500 m^2 plots (six per site). At each sampling unit, twelve cores were taken with a soil auger at 0–20, 21–40, and 41–100 cm depth. Subsamples were then composited by depth for subsequent chemical analyses (~700 g; SAG, 2010). Bulk density was determined using the core method, by collecting undisturbed 100 cc soil samples from a ~1 m^3 pit for subsequent dry mass determination (Blake and Hartge, 1986).

2.3. Data analysis

Site, microsite, and soil variables were compiled for both study sites, contrasting native forest and plantation conditions in relation to understory biodiversity patterns. To characterize stand structure, we calculated key stand attributes for each sampling unit, including stocking, basal area, diameter of the mean basal area tree (QMD), volume, and top height. For the latter, we applied the methodology proposed by García (1998), which estimates top height using the tallest trees in the plot and incorporates an area-based adjustment in the number of trees considered. Stand volume was estimated using species-specific allometric models based on diameter and height, prioritizing locally calibrated equations when available (Salas, 2002). Native forest age was estimated from stand structure variables following Ro–Ra–Co growth references (Donoso, 1993; Salas and García, 2006). Incident radiation was estimated from hemispherical photographs using the Gap Light Analyzer software, which calculates canopy openness and light transmission based on gap fraction analysis (Fraser et al., 1999; Moretti et al., 2019). Soil samples were air-dried and sieved (<2 mm) for chemical analyses. Soil pH was measured in a 1:2.5 soil–water suspension; total carbon and nitrogen were determined using the Dumas-TCD method (SERCON IRMS); and available nutrients were analyzed following standard procedures for Chilean soils (Sadzawka et al., 2006). Values were averaged across depths for each plot. All statistical analyses

were conducted in R (R Core Team, 2025).

Tree regeneration density (< 5 cm DBH) was calculated per plot and summarized by forest condition (i.e., plantation or native forest) and height class. Significant differences among forest conditions within each height class were evaluated using post-hoc pairwise comparisons of estimated marginal means with Tukey adjustment ($\alpha = 0.05$).

To synthesize structural variables associated with silvicultural management in plantations, we generated a structural gradient using Principal Component Analysis (PCA; *prcomp* function in R, R Core Team, 2025), integrating stand diameter, top height, stocking, and basal area for each plot. Prior to analyses, all variables were standardized (mean = 0, standard deviation = 1) to avoid scaling effects. The first principal component (PC1) summarize the structural variation among plantations, providing a numerical index for each stand (see Table S1 for loadings and explained variance; Gewers et al., 2022). This axis defined a structural gradient, with lower values indicating simpler stand structures and higher values reflecting more complex and heterogeneous conditions.

As indicators of species diversity, we estimated native and exotic species richness, tree species richness, and total vascular plant richness, along with the Shannon index (H′), which combines species richness and evenness. H' ranges from 0 (a single species) to > 4 in highly diverse communities; where < 1.5 values indicate low diversity, 1.6–3.0 suggest moderate and values > 3.1 suggest high diversity (Magurran, 1988). To analyze the understory floristic similarity between plantations and native forests (used as reference), we applied Sørensen dissimilarity (β-diversity) based on presence–absence data, partitioning it into turnover and nestedness, which reflects species replacement and species loss or gain, respectively (betapart package in R; Baselga and Orme, 2012). Significant differences between turnover and nestedness components were evaluated across paired transects using Wilcoxon tests ($\alpha = 0.05$; R Core Team, 2025).

Floristic composition was evaluated using non-metric multidimensional scaling (NMDS; metaMDS function, vegan package in R), based on Bray–Curtis dissimilarity of species relative abundances (n = 60; Oksanen et al., 2015). Associations between site, microsite, soil, and stand structural variables and floristic composition were assessed using the envfit function (999 permutations, $\alpha = 0.05$; Oksanen et al., 2015).

Finally, we modelled the relationship between vascular plant species richness and the plantation structural gradient by fitting a Poisson mixed-effects model having the transects nested within sites. We did so to account for the discrete nature of the response variable and hierarchical structure of the data. The model was fitted by maximum likelihood using the lme4 package implemented in R (Gilbert, 2024). Model assessment included: (a) testing predictor significance using likelihood-ratio tests, (b) evaluating model assumptions through simulated residuals (DHARMa; Harting, 2022), and (c) assessing the influence of each transect on model coefficients using Cook's distance (influence.ME; Nieuwenhuis et al., 2012).

3. Results

3.1. Site, microsite, and soil variables

Baseline environmental conditions at both sites are presented in Table 1. Los Barros showed higher altitude and soils with lower nitrogen, carbon, and potassium levels compared with Rucamanque. Soil pH and electrical conductivity (EC) were similar across forest conditions, remaining slightly acidic. Plantations at both sites showed greater canopy openness and higher incident radiation than native forests, whereas the remaining microsite variables were comparable between native forest and plantation (Table 1).

3.2. Stand attributes and tree regeneration

P. radiata plantations differed structurally between sites: while stands at Los Barros were relatively uniform in age and density, those at Rucamanque exhibited greater heterogeneity (Table 2). In contrast native forests at Rucamanque reflected a more mature condition than at Los Barros, with higher mean diameters and top heights (Fig. 2; Table 2).

Table 1
Environmental variables of the two study sites. Mean values of site variables, microsite and soil attributes are presented for each forest condition (NF = native forest, PL = plantation). The coefficient of variation (CV%) is shown in parentheses. For aspect the mode is presented.

	Los Barros		Rucamanque	
Site variables	**NF (n = 6)**	**PL (n = 6)**	**NF (n = 6)**	**PL (n = 6)**
Elevation (m.a.s.l.)	801.1 (4)	826.2 (7)	510.0 (30)	425.4 (21)
Slope (°)	10.0 (60)	8.4 (60)	10.2 (11)	13.8 (72)
Aspect	SO	NO	SO	SO
Microsite variables	**NF (n = 30)**	**PL (n = 30)**	**NF (n = 30)**	**PL (n = 30)**
Woody debris (%)	20.0 (70)	27.5 (70)	10.2 (92)	30.0 (53)
Mineral soil (%)	2.0 (121)	2.0 (43)	3.0 (82)	2.0 (142)
Leaf litter (%)	90.0 (24)	95.0 (6)	80.0 (10)	95.0 (19)
Canopy open (%)	10.8 (58)	18.4 (50)	12.6 (49)	16.3 (51)
Total radiation transmission (mol/m^2/d)	18.3 (40)	21.9 (38)	17.1 (33)	19.0 (39)
Soil attributes	**NF (n = 6)**	**PL (n = 6)**	**NF (n = 6)**	**PL (n = 6)**
pH (H2O)	4.5 (6)	4.6 (8)	4.8 (8)	4.9 (10)
EC (dS/m)	0.06 (39)	0.06 (35)	0.1 (86)	0.09 (67)
N (%)	0.1 (40)	0.1 (61)	0.4 (98)	0.6 (63)
C (%)	3.2 (31)	3.6 (49)	5.9 (85)	8.0 (44)
P (mg/Kg)	3.0 (38)	3.3 (28)	2.3 (28)	2.2 (29)
K (mg/Kg)	54.0 (54)	50.0 (35)	155.0 (72)	110.0 (71)
BD (g/cm3)	0.8 (18)	0.7 (16)	0.6 (34)	0.6 (28)

Native tree regeneration was generally more abundant in native forests than in plantations at both study sites (Fig. 2). At Los Barros, native forests presented high density of seedlings (0–50 cm height), exceeding 5000 individuals per hectare. This height class was also the most represented in plantations, though with substantially lower densities. At Rucamanque, overall regeneration was less dense; however, plantations contained a greater proportion of individuals in more advanced height classes (Fig. 2). At both sites, *N. obliqua* dominated the early stages of regeneration in native forests, while *Eucryphia cordifolia*, *Persea lingue*, and *Gevuina avellana* were more frequent in taller height classes. In plantations, *Aristotelia chilensis* was the most abundant regenerating species (See Table S2).

3.3. Plant biodiversity within plantations

Plant biodiversity within plantations was lower than in native forests, with native species richness corresponding to 43–60% of values observed under reference conditions (median values; Table 2). Despite this difference, Shannon diversity remained relatively high across all conditions, indicating that plantations supported diverse understory communities (Table 2). Within plantations, vascular plant richness varied along the structural gradient, with lower richness observed in denser stands characterized by higher stocking. In contrast, higher values along the gradient, associated with more open structures and greater incident radiation, were linked to greater native species richness, as represented by the native species richness isolines (Fig. 3). Plant communities in plantations differed compositionally from those in native forests, primarily through species turnover rather than nestedness (see Fig. S1). Consistently multivariate analysis also showed a clear differentiation in the floristic composition of plantations according to the study site (Fig. 3). Overall, floristic composition within plantations

Table 2
Structural attributes and floristic richness and diversity. Median values for each variable are shown for native forest (NF) and *P. radiata* plantation (PL) in both study sites. For structural attributes minimum and maximum values are shown in parentheses; for floristic richness and diversity the coefficient of variation (CV%) is reported.* Ages for native forest (NF) were inferred from stand structural attributes, based on published growth information for this forest type (Donoso, 1993; Salas and García, 2006).

	Los Barros		Rucamanque	
Structural attributes	**NF (n = 6)**	**PL (n = 6)**	**NF (n = 6)**	**PL (n = 6)**
Age (years)	~ 55 (40–70)*	17.5 (16–20)	~80 (60–100)*	21.5 (9–37)
Stocking (trees/ha)	1650 (1160–3240)	820 (460–3540)	660 (200–940)	590 (360–900)
Basal area (m^2/ha)	41.5 (28.6–63.6)	49.5 (38.7–86)	30 (22.3–73.7)	41 (24.5–75.3)
QMD (cm)	16.5 (14.3–23.4)	27.7 (17.6–32.7)	24.1 (18–65.1)	33.2 (24.3–37.8)
Top height (m)	20.7 (17.2–25.1)	24.7 (21.7–27.5)	22 (18.5–32)	23 (16.7–30.2)
Volume (m^3)	317 (168.3–532.7)	340.6 (283.8–511.4)	241.8 (145.6–711.7)	265.6 (107–596.9)
Floristic richness and diversity	**NF (n = 30)**	**PL (n = 30)**	**NF (n = 30)**	**PL (n = 30)**
Native richness	10.6 (32)	4.6 (54)	8.9 (41)	5.4 (44)
Exotic richness	0.1 (305)	1 (0)	0	1 (19)
Trees richness	5.1 (36)	2.5 (53)	3.2 (48)	2.6 (42)
Total richness	10.7 (32)	5.6 (44)	8.9 (41)	6.4 (38)
Shannon diversity	4.1	3.5	3.5	3.3

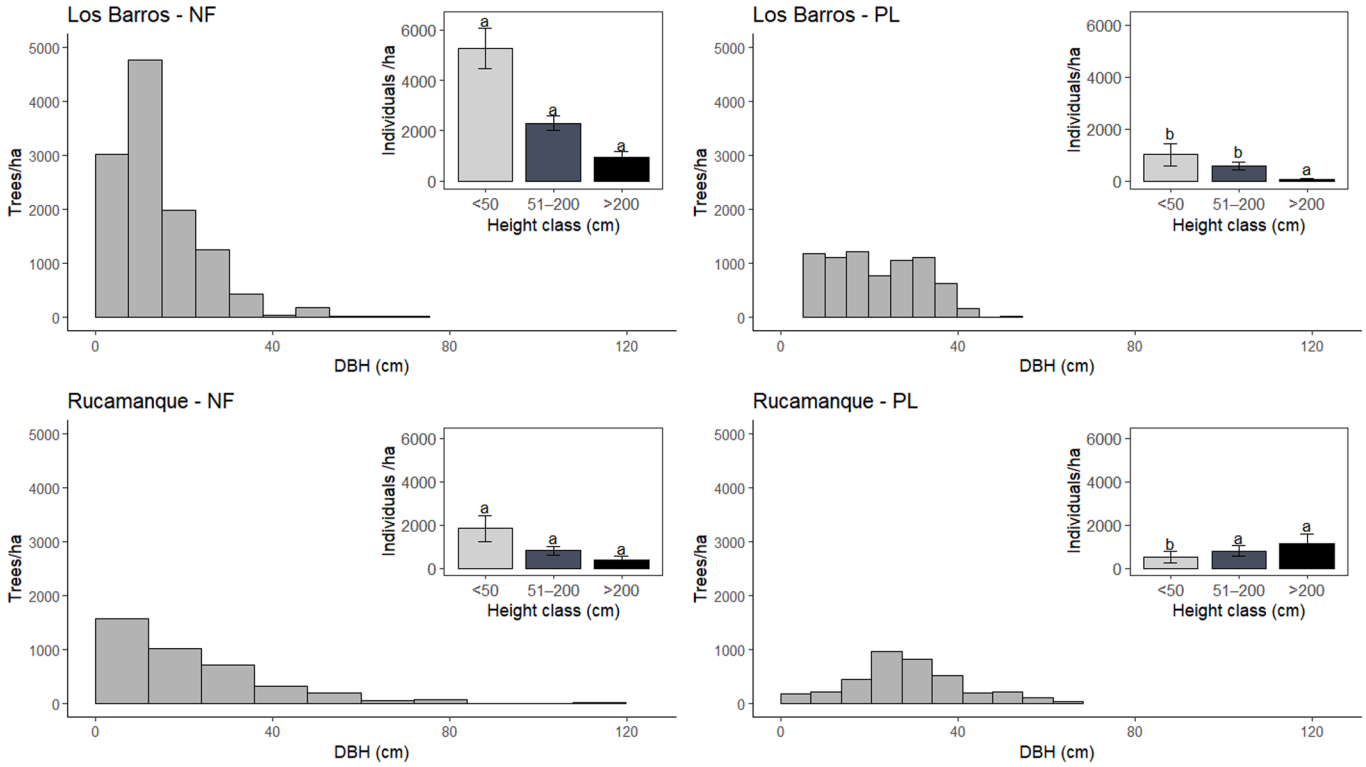

Fig. 2. Distribution of trees per hectare across diameter at breast height (DBH) classes in native forests (NF) and plantations (PL) at both study sites: Los Barros and Rucamanque. The inset panels show the density of native regeneration (individuals/ha) across height classes for each forest cover type. Bars indicate standard errors, and letters above denote significant differences between forest conditions within the same height class ($p < 0.05$).

was significantly associated with stand structure and environmental variables, including soil bulk density, incident radiation, slope, and soil pH (Fig. 3).

In line with these patterns the GLMM results (Fig. 4), showed a positive and significant effect of the structural gradient on native species richness ($\beta = 0.163$, $p = 0.0015$), equivalent to an estimated 17.7% increase in richness per unit increase along the gradient (Fig. 4). Variation in richness was primarily associated with local-scale differences within sites, with little to no variation among sites. Model details are provided in Table S3.

4. Discussion

4.1. Environmental attributes and native vascular plants under plantations

The capacity of forest ecosystems to sustain vascular plant diversity depends on interactions among light availability, soil properties, propagule inputs from surrounding vegetation, and species-specific regeneration strategies (Grubb, 1977; Brockerhoff et al., 2008; Lázaro-Lobo and Ervin, 2020). In this study, we evaluated native plant diversity and tree regeneration beneath the canopies of exotic *P. radiata* plantations located adjacent to temperate *Nothofagus* forests in southern Chile.

Despite differences in altitude and soil attributes between study sites, contrasting patterns of native species regeneration and diversity were

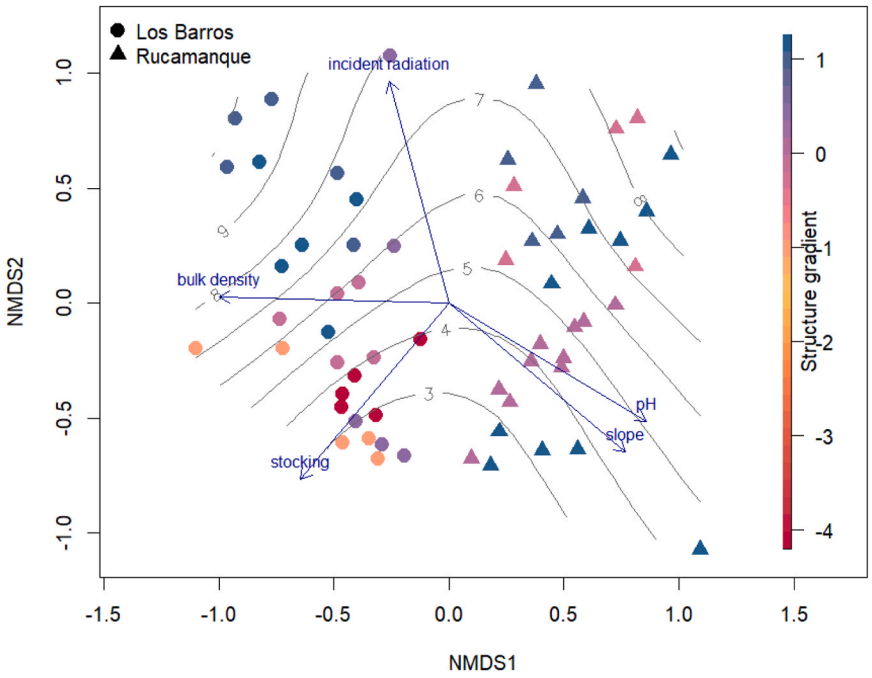

Fig. 3. NMDS ordination based on the floristic composition of 60 plots established in the understory of *P. radiata* plantations at Los Barros and Rucamanque (Bray–Curtis distance, stress = 0.19). Arrows indicate variables significantly correlated with the ordination (95% confidence), including incident radiation ($r^2 = 0.24$, $p = 0.001$), bulk density ($r^2 = 0.28$, $p = 0.001$), stocking ($r^2 = 0.15$, $p = 0.004$), pH ($r^2 = 0.31$, $p = 0.001$), and slope ($r^2 = 0.24$, $p = 0.001$). Isolines represent native species richness (ordisurf, vegan; Oksanen et al., 2015). The stand structural gradient is represented by the color scale, ranging from simpler to more complex structural conditions (red to blue; $r^2 = 0.1604$, $p = 0.006$).

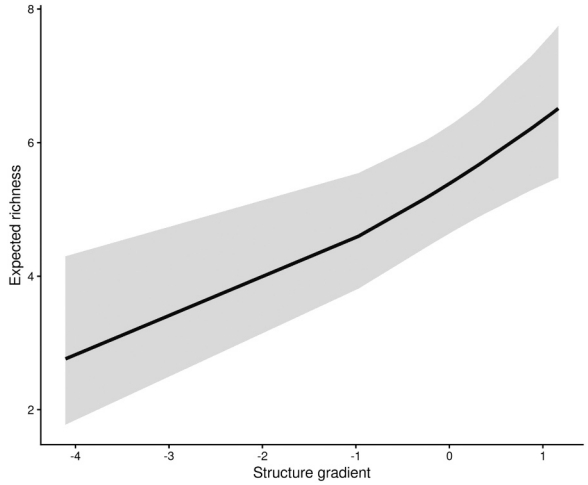

Fig. 4. Relationship between the expected richness of native vascular plant species and the structural gradient of *P. radiata* plantations across both study sites, fitted using a generalized linear mixed model (GLMM, Poisson family). Lines represent the model fit, and shaded areas indicate 95% confidence intervals.

observed. Los Barros, characterized by higher elevation and comparatively poorer soils, exhibited greater floristic richness and more abundant tree regeneration in native forests than Rucamanque. In contrast, the latter, with more fertile soils, exhibited more similar plant diversity between plantations and native forest conditions. These patterns suggest that factors beyond overall site quality are influencing understorey vegetation. Accordingly, differences in plantation understory composition between sites appear to be driven by topographic and structural attributes, potentially including legacy effects of past use and management, rather than overall site quality (Kelly and Ray, 2023; Kremer et al., 2022).

Microsite variables and soil chemical attributes were largely similar between native forests and plantations in both study sites. Coarse woody debris, mineral soil exposure, litter cover, as well as soil pH, nutrient levels, and bulk density, showed comparable values across both forest cover types. This suggests that, in this case, *P. radiata* plantations have not substantially modified microsite conditions or soil chemical properties, resulting in an understory environment relatively similar to that of the adjacent *Nothofagus* forest. The observed similarity may be related to plantation age. Some studies indicate that soil changes tend to be most pronounced in very young stands (< 10 years) or in overmature stands (> 40 years), where nutrient declines typically occur (Jeong et al., 2017; Yin et al., 2021). Given that the plantations evaluated here range from ~10–37 years old, they likely fall within an intermediate age range in which soil chemical properties do not differ markedly from those of nearby native forests.

One of the main differences between native forests and plantations was canopy openness, which was consistently higher in plantations, reflecting the effects of silvicultural practices (i.e., thinning and pruning) on vertical structure and light availability. This increase in radiation input creates more heterogeneous conditions, expanding the range of available niches that may facilitate the establishment of both native and exotic herbaceous and shrub species (Granados-Peláez et al., 2018; Wang et al., 2021). This mechanism is consistent with the high vascular plant diversity recorded underneath *P. radiata* canopies (Shannon H' > 3). This pattern helps explain why plantations sustain between 43% and 60% of the native species richness found in adjacent reference forests. Comparable results have been reported by Heinrichs et al. (2018), who found that native species richness in *P. radiata* plantations did not differ significantly from that observed in nearby native forests, and by Becerra and Simonetti (2020), who documented similar levels of native species richness in *P. radiata* plantations.

4.2. Stand structure and management effects on native tree regeneration within plantations

Although the silvicultural practices applied in the evaluated plantations were not designed for conservation or restoration objectives, shifts in stands structural attributes (i.e., lower density and larger DBH and top heights) created conditions that support the presence and regeneration of native species. Differences observed between sites illustrate how distinct management regimes can shape the structural development of *P. radiata* stands and, consequently, the availability of different understory microsites. At Los Barros, plantations of similar age (16–20 years) reflected silvicultural interventions, with thinning and pruning modifying stand structure, increasing light availability, and promoting native species establishment. At Rucamanque, by contrast, the greater age heterogeneity (9–37 years) of the plantation stands reflects a combined influence of management and environmental factors. In general, more productive sites receive more intensive management because they can support higher commercial yields (Sedjo, 1999; Zhao et al., 2016). At the same time, high site productivity may enhance native plant biodiversity when remnant native forest patches are available as propagule sources. This pattern aligns with observations from *Pinus* spp. plantations in temperate regions of Argentina, New Zealand, and Spain, where management intensity has been reported to promote understory diversity (Marshall et al., 2023; Onaindia et al., 2013; Trentini et al., 2020).

The recurrent presence of native tree regeneration, particularly *Aristotelia chilensis* and *N. obliqua*, indicates that plantations can function as refuges when propagule sources and sufficient light are available, a pattern consistent with studies showing that plantations sustain native communities where seed dispersal is not limiting (García et al., 2016; Pritchard et al., 2024).

The predominance of small seedlings (< 50 cm) within plantations at Los Barros indicates an early stage of colonization, where recruitment is active. In contrast, the higher proportion of individuals in advanced height classes under the plantation canopy at Rucamanque suggests a more mature regeneration trajectory, likely initiated during periods when the canopy was more open and light availability was greater. This pattern coincides with observations from southern Chile, where initial regeneration tends to occur during opportunity windows created by thinning, whether through management or natural treefall, prior to full canopy closure (Kremer and Bauhus, 2025). Over time, depletion of the seed bank and increasing resource competition limit additional recruitment, favoring the persistence of early cohorts. These patterns depend on historical land use, which determines the available seed bank (Navarro-González et al., 2013) and are further influenced by canopy structure, as less dense stands offer higher water availability and more favorable conditions for the establishment of new seedlings (Granados-Peláez et al., 2018).

4.3. Plant diversity patterns in P. radiata stands

The results of both the NMDS ordination and the GLMM analyses highlight that plantation stand structure is a key determinant of floristic diversity beneath *P. radiata* canopies. Plantations characterized by high stockings of smaller *P. radiata* individuals and consequently lower light availability, showed lower understorey native species richness. In contrast, more open structures with taller and larger trees supported higher understorey species richness. These patterns reflect variation in light availability, heterogeneity, and resource competition, which drive understory species establishment (Odland et al., 2021; Xu et al., 2020).

The observed structural gradient captures variation in stand attributes among the plantation stands, reflecting differences in structural complexity through canopy openness, density, and tree size. Previous studies in temperate forests have shown that structurally complex conditions increase environmental heterogeneity, promoting the development of microhabitats that facilitate propagule arrival (Brockerhoff et al., 2008; Wang et al., 2021). Consistently, in this study, native species richness increased along the structural gradient, with an estimated rate of 17.7% per unit.

Compositional differences between sites reflect the modulating role of the landscape context. In Rucamanque, the continuity of surrounding native forest enhances propagule arrival and the persistence of species typical of those forests within plantation understories. In contrast, Los Barros, located in a more fragmented landscape, showed a higher proportion of opportunistic or disturbance-tolerant species, including exotics, a pattern also described by García et al. (2016) and Heinrichs et al. (2018) in similar *P. radiata* contexts.

Despite these differences, the positive relationship between stand structure and native species richness was consistent across both sites, suggesting that variation is largely associated with local-scale differences. The fact that relatively simple structural modifications can enhance biodiversity conservation highlights an important opportunity for management and restoration in plantation-dominated landscapes.

4.4. Towards structural drivers of plant biodiversity in plantation stands

This study provide empirical evidence that supports current research trends recognizing forest plantations as environments with potential for native biodiversity conservation (Horák et al., 2019; Simões et al., 2024). In particular, the ability of *P. radiata* plantations to maintain up to 60% of the species richness of adjacent native forests demonstrates that, in landscapes with nearby propagule sources (< 500 m), plantations can function as secondary habitat for native vegetation. However, this capacity is strongly linked to stand structure and microsite conditions. In this regard, interventions aimed at increasing heterogeneity, such as progressive thinning, selective pruning, or the creation of controlled canopy openings, can improve habitat quality and promote native species regeneration (Marshall et al., 2023; Zhao et al., 2016). When plantations reach a more open and structurally diverse condition, they are capable of supporting a substantial fraction of native plant diversity without requiring full conversion to natural forest. Consequently, even modest silvicultural adjustments that modify stand structure can translate into meaningful ecological benefits.

Taken together, these findings align with the principles of transitional silviculture, which proposes that forest plantations can be gradually transformed toward structures, compositions, and functional attributes more similar to those of natural forests, without fully abandoning productive objectives (Jones et al., 2023; Pritchard et al., 2024). Transitional silviculture promotes a shift from traditional management toward more diverse and resilient forest systems, integrating continuity among forest types while improving productivity, reducing environmental impacts, and enhancing ecological and societal value through ecosystem functions. (Jones et al., 2023). Although it has been developed mainly in New Zealand, our results suggest that its principles are applicable to the context of south-central Chile. In fragmented landscapes where native forest remnants are scarce and dispersed, *P. radiata* plantations could play a key role as ecological bridges, enhancing connectivity and facilitating the establishment of native species, thereby contributing to increased landscape functionality.

Incorporating transitional silviculture in Chile would shift plantations from timber-focused systems to multifunctional landscapes contributing to conservation. This requires integrating biodiversity criteria into forest planning, including targeted thinning, retention of native species, and conservation of natural structural elements (Bekris et al., 2021; Hartley, 2002). These practices could enhance the ecological and social resilience of forested landscapes in southern Chile, aligning with global sustainability goals (United Nations, 2015).

Although plantations can contribute to maintaining part of the native flora across the landscape, native forests, even as small patches or fragments, are key to sustaining biodiversity and serve as the main sources of natural regeneration. Understory floristic composition in plantations differs from native forests, reflecting species turnover, with

some species absent and others unique to plantations. Therefore, management strategies should be oriented toward complementarity, prioritizing the active protection and connectivity of native forest remnants while adjusting silvicultural practices in plantation stands to maximize their ecological compatibility and their role as corridors and secondary habitats (Estades et al., 2012; McFadden and Dirzo, 2018).

Finally, our results highlight key questions about the mechanisms regulating biodiversity beneath plantations, particularly how stand structure interacts with ecological filters such as seed bank depletion or edaphic changes that may limit long-term recruitment (Berthrong et al., 2009). It is also necessary to assess species persistence after canopy opening and their successional roles in transitions toward reference forests (Onaindia et al., 2013). Addressing these questions will help refine management strategies and inform the broader debate on plantation conversion in temperate landscapes.

5. Conclusion

Understanding how forest plantations can contribute to biodiversity conservation is essential in landscapes where native forest cover has declined. *P. radiata* plantations in south-central Chile can sustain a significant fraction of the local native flora, supporting ~43–60% of the species richness recorded in adjacent reference native forests. Although microsite variables such as light availability and soil attributes, including pH and nutrients, explained part of the floristic variation within plantations, stand level structural characteristics, which can be shaped by management, showed stronger association with understorey biodiversity. This pattern should be interpreted cautiously, as it reflects structural conditions rather than a direct effect of management intensity. In general, plantations with more open and heterogeneous stand structures supported higher levels of native species richness, likely driven by increased light availability and structural heterogeneity influencing understory communities. In contrast, adjacent native forests consistently maintained higher species richness, diversity, and tree regeneration, underscoring the need to explicitly integrate native forest conservation within forest management models. Our results show that plantations can play a complementary role in maintaining native flora at the landscape level. Overall, this study provides empirical evidence that contributes to the ongoing debate on the conservation value and conversion potential of plantations, demonstrating that stand-level management decisions can meaningfully influence understory biodiversity. These findings identify specific structural attributes that can be integrated into silvicultural planning to enhance biodiversity retention in plantation-dominated landscapes.

CRediT authorship contribution statement

Juan Pedro Elissetche: Writing – review & editing. **Andrés Fuentes-Ramírez:** Writing – review & editing, Visualization. **Rafael Rubilar:** Writing – review & editing. **Christian Salas-Eljatib:** Writing – review & editing, Formal analysis, Data curation. **Rodrigo Vargas-Gaete:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Natalia Gertner:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation.

Disclosure of Generative AI assistance

Generative AI tools were used only for English-language editing and text clarification. No AI contributed to the study design, data analysis, or interpretation, and the authors take full responsibility for the content.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We acknowledge the financial support of the Centro ANID Basal CENAMAD (FB210015) and the Dirección de Investigación of Universidad de La Frontera. We thank Javiera Córdova, Antonia Briones, and Bernardita Díaz Mons (EcoBos, UFRO) for their valuable assistance during field data collection. We also thank Esteban Sepúlveda for support with plant identification. We are also grateful to two anonymous reviewers whose comments substantially improved the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123828.

Data availability

Data will be made available on request.

References

Alday, J.G., Etxeberria, E., Ametzaga, I., 2017. Conversion of *Pinus radiata* plantations to native forest after harvest operations: a north Iberian Peninsula case study. Eur. J. For. Res. 136 (5), 801–810. https://doi.org/10.1007/s10342-017-1071-2.

Ali, A., Dai, D., Akhtar, K., Teng, M., Yan, Z., Urbina-Cardona, J.N., Müllerová, J., Zhou, Z., 2019. Response of understory vegetation, tree regeneration, and soil quality to manipulated stand density in a *Pinus massoniana* plantation. Glob. Ecol. Conserv. https://doi.org/10.1016/j.gecco.2019.e00775.

Amoroso, M.M., Chillo, V., Enríquez, A., 2024. Sustainable timber production in afforestations: trade-offs and synergies in the provision of multiple ecosystem services in northwest Patagonia. For. Ecol. Manag. 574, 122345. https://doi.org/10.1016/j.foreco.2024.122345.

Baselga, A., Orme, C.D.L., 2012. betapart: an R package for the study of beta diversity. Methods Ecol. Evol. 3, 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x.

Bauhus, J., van der Meer, P., Kanninen, M., 2010. Ecosystem goods and services from plantation forests. Routledge. ⟨https://books.google.es/books?hl=en&lr=&id=sRPyipMfZ8sC&oi=fnd&pg=PR1&dq=Bauhus+goods+servicees+plantatios&ots=nd7jie2clX&sig=RREPSAyrmGk6bco6JO-O0gAm7a8⟩.

Becerra, P.I., Simonetti, J.A., 2020. Diversidad de plantas nativas y exóticas en fragmentos de bosque y plantaciones forestales en un paisaje costero de Chile central. Bosque 41 (2), 125–136. https://doi.org/10.4067/S0717-92002020000200125.

Bekris, Y., Prevéy, J., Brodie, L.C., Harrington, C., 2021. Effects of variable-density thinning on non-native understory plants in coniferous forests of the Pacific Northwest. For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2021.119699.

Berthrong, S., Jobbágy, E., Jackson, R.B., 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. Ecol. Appl. a Publ. Ecol. Soc. Am. 19 (8), 2228–2241. https://doi.org/10.1890/08-1730.1.

Blake, G.R., Hartge, K.H., 1986. Bulk Density. En Methods of Soil Analysis. John Wiley & Sons, Ltd, pp. 363–375. https://doi.org/10.2136/sssabookser5.1.2ed.c13.

Braun, A.Ch, Troeger, D., Garcia, R., Aguayo, M., Barra, R., Vogt, J., 2017. Assessing the impact of plantation forestry on plant biodiversity. Glob. Ecol. Conserv. 10, 159–172. https://doi.org/10.1016/j.gecco.2017.03.006.

Braun-Blanquet, J., 1979. Fitosociología: bases para el estudio de las comunidades vegetales. H. Blume Ediciones.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17 (5), 925–951. https://doi.org/10.1007/s10531-008-9380-x.

Cagnoni, L.B., Weidlich, E.W.A., Guillemot, J., Morselo, C., Weih, M., Adler, A., Brancalion, P.H.S., 2023. Stakeholders' perspectives of species diversity in tree plantations: a global review. Curr. For. Rep. 9 (4), 251–262. https://doi.org/10.1007/s40725-023-00194-1.

Cariola-Szuchman, L., Izquierdo, A.E., & Hilgert, N.I. (2018). Social perception of tree plantations in the Atlantic forest of Argentina: The role of management scale. https://doi.org/10.15451/ec2018-10-7.14-1-38.

Carle, J., Homgren, P., 2008. Wood from planted forests a global outlook 2005-2030. For. Prod. J. 58 (12), 6–18.

Carte, L., Hofflinger, Á., Polk, M.H., 2021. Expanding exotic forest plantations and declining rural populations in la araucanía, Chile. Article 3. Land 10 (3). https://doi.org/10.3390/land10030283.

Carteron, A., Parasquive, V., Blanchard, F., Guilbeault-Mayers, X., Turner, B., Vellend, M., Laliberté, E., 2020. Soil abiotic and biotic properties constrain the establishment of a dominant temperate tree into boreal forests. J. Ecol. 108, 931–944. https://doi.org/10.1111/1365-2745.13326.

Cassiano, C.C., Moreira, R.M. e, Ferraz, S.F. de B., 2023. Fast-growing forest management to regulate the balance between wood production and water supply. Sci. Agric. 80, e20210148. https://doi.org/10.1590/1678-992X-2021-0148.
Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S. E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. J. Soc. Conserv. Biol. 23 (6), 1406–1417. https://doi.org/10.1111/j.1523-1739.2009.01338.x.
Chianucci, F., Napoleone, F., Ricotta, C., Ferrara, C., Fusaro, L., Balducci, L., Trentanovi, G., Bradley, O., Kovacs, B., Mina, M., Cerabolini, B.E.L., Vandekerkhove, K., De Smedt, P., Lens, L., Hertzog, L., Verheyen, K., Hofmeister, J., Hošek, J., Matula, R., Burrascano, S., 2024. Silvicultural regime shapes understory functional structure in European forests. J. Appl. Ecol. 61 (10), 2350–2364. https://doi.org/10.1111/1365-2664.14740.
CONAF. (2014, 2015). Sistema de Informacion Territorial—CONAF 2020. ⟨https://sit.conaf.cl/⟩.
Coote, L., Dietzsch, A.C., Wilson, M.W., Graham, C., Fuller, L., Walsh, A., Irwin, S., Kelly, D., Mitchell, F., Kelly, T., O'Halloran, J., 2013. Testing indicators of biodiversity for plantation forests. Ecol. Indic. 32, 107–115. https://doi.org/10.1016/J.ECOLIND.2013.03.020.
Diaci, J. (Ed.), 2006. Nature-Based Forestry in Central Europe: Alternatives to Industrial Forestry and Strict Preservation. Biotechnical Faculty, University of Ljubljana. ⟨https://www.prosilva.org/fileadmin/prosilva/4_News_Information/03_Articles_Presentations/04_books/diaci_nature_based_forestry-2_0.pdf#page=11⟩.
Donoso, C. (1981). Tipos forestales de los bosques nativos. Proyecto CONAF/PNUD/FAO. ⟨https://es.scribd.com/document/633186176/Tipos-Forestales-de-los-Bosques-Nativos-DONOSO-1981⟩.
Donoso, C., 1993. Bosques templados de Chile y Argentina: variación, estructura y dinámica. Editor. Univ.
Estades, C., Grez, A.A., Simonetti, J., 2012. Biodiversity in Monterrey Pine Plantations. Proceeding of Biodiversity Conservation in Agroforestry Landscapes: Challenges and Opportunities. Editorial Universitaria, Santiago, Chile, pp. 77–98.
FAO, 2020. Global Forest Resources Assessment 2020. FAO. https://doi.org/10.4060/ca8753en.
Forbes, A.S., Norton, D.A., Carswell, F.E., 2019. Opportunities and limitations of exotic *Pinus radiata* as a facilitative nurse for New Zealand indigenous forest restoration. New Z. J. For. Sci. 49. https://doi.org/10.33494/nzjfs492019x45x.
Fournier, R.A., Hall, R.J. (Eds.), 2017. Hemispherical Photography in Forest Science: Theory, Methods, Applications, 28. Springer Netherlands. https://doi.org/10.1007/978-94-024-1098-3.
Fraser, G., Canham, C., & Lertzman, K. (1999). Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation.
Fuentealba, A., Duran, L., Morales, N.S., 2021. The impact of forest science in Chile: history, contribution, and challenges. Can. J. For. Res. 51 (6), 753–765. https://doi.org/10.1139/cjfr-2020-0471.
García, O., 1998. Estimating top height with variable plot sizes. Can. J. For. Res. 28, 1509–1517.
García, R.A., Franzese, J., Policelli, N., Sasal, Y., Zenni, R.D., Nuñez, M.A., Taylor, K., Pauchard, A., 2018. Non-native Pines Are Homogenizing the Ecosystems of South America. In: Rozzi, En.R., May Jr., R.H., Chapin III, F.S., Massardo, F., Gavin, M.C., Klaver, I.J., Pauchard, A., Nuñez, M.A., Simberloff, D. (Eds.), From Biocultural Homogenization to Biocultural Conservation. Springer International Publishing, pp. 245–263. https://doi.org/10.1007/978-3-319-99513-7_15.
García, V., Simonetti, J., Becerra, P., 2016. Lluvia de semillas, depredación de semillas y germinación de especies nativas en plantaciones de *Pinus radiata* en Chile centro-sur: efecto de la distancia a bosque nativo y presencia de sotobosque. Bosque 37 (2), 359–367. https://doi.org/10.4067/S0717-92002016000200014.
Gerding, V., 2025. Ciencia y plantaciones forestales en Chile, ¿algún desencuentro? Bosque 46, 121–127. https://doi.org/10.4067/s0717-92002025000200121.
Gewers, F.L., Ferreira, G.R., Arruda, H.F.D., Silva, F.N., Comin, C.H., Amancio, D.R., Costa, L.D.F., 2022. Principal component analysis: a natural approach to data exploration. ACM Comput. Surv. 54 (4), 1–34. https://doi.org/10.1145/3447755.
Gilbert, J.B., 2024. Modeling item-level heterogeneous treatment effects: a tutorial with the glmer function from the lme4 package in R. Behav. Res. Methods 56 (5), 5055–5067. https://doi.org/10.3758/s13428-023-02245-8.
Granados-Peláez, C., Santibáñez-Andrade, G., Guerra-Martínez, F., Serrano-Giné, D., García-Romero, A., 2018. Evaluation of multi-causal dynamics of variability composition of patch edges in temperate forest. For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2018.07.027.
Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.
Harting, F. (2022). DHARMa: Diagnóstico residual para modelos de regresión jerárquica (multinivel/mixta) [Software]. ⟨https://cran.r-project.org/web/packages/DHARMa/index.html⟩.
Hartley, M., 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manag. 155, 81–95. https://doi.org/10.1016/S0378-1127(01)00549-7.
Heinrichs, S., Pauchard, A., Schall, P., 2018. Native plant diversity and composition across a *Pinus radiata* d.don plantation landscape in South-Central Chile—the impact of plantation age, logging roads and alien species. Forests 9 (9). https://doi.org/10.3390/f9090567.
Holt, T.V., 2012. Trade-offs between tree cover, carbon storage and floristic biodiversity in reforesting landscapes. Landsc. Ecol. ⟨https://www.academia.edu/86374620/Trade_offs_between_tree_cover_carbon_storage_and_floristic_biodiversity_in_reforesting_landscapes⟩.
Horák, J., Brestovanská, T., Mladenović, S., Kout, J., Bogusch, P., Halda, J.P., Zasadil, P., 2019. Green desert?: Biodiversity patterns in forest plantations. For. Ecol. Manag. 433, 343–348. https://doi.org/10.1016/j.foreco.2018.11.019.
Huettmann, F., Young, B.D., 2022. The So-called Modern 'Sustainable Forestry' Destroys Wilderness, Old-Growth Forest Landscapes and Ecological Services Worldwide: A Short First-Hand Review and Global Narrative on the Use of 'Growth-and-Yield' as a Destructive and Even Impossible Goal. In: Kumar, En.M., Dhyani, S., Kalra, N. (Eds.), Forest Dynamics and Conservation: Science, Innovations and Policies. Springer Nature, pp. 53–82. https://doi.org/10.1007/978-981-19-0071-6_3.
Hughey, K.F.D., Kerr, G.N., Cullen, R., 2019. Public Perceptions of New Zealand Environment. EOS Ecology, Christchurch.
IDE. (2023). Infarestructura de datos geoespaciales Chile. IDE Chile. ⟨https://www.ide.cl/⟩.
Jeong, J., Bolan, N., Harper, R., Kim, C., 2017. Distribution of carbon and nitrogen in forest floor components in *Pinus radiata* plantations of different ages in South Australia. Aust. For. 80, 104–199. https://doi.org/10.1080/00049158.2017.1321465.
Jones, A.G., Cridge, A., Fraser, S., Holt, L., Klinger, S.P., McGregor, K.F., Paul, T.S.H., Payn, T., Scott, M., Yao, R.T., Dickinson, Y., 2023. Transitional forestry in New Zealand: re-evaluating the design and management of forest systems through the lens of forest purpose. Biol. Rev. 98. https://doi.org/10.1111/brv.12941.
Jürgensen, C., Kollert, W., Lebedys, A., 2014. Assessment of industrial roundwood production from planted forests. (FAO Planted Forests and Trees Working Paper Series). ⟨https://openknowledge.fao.org/server/api/core/bitstreams/2de6f55e-9170-4703-8028-74809aeb2045/content⟩.
Kelly, J.F., Ray, J., 2023. Regional impacts of agricultural land use history on forest vegetation and soils: comparing primary and post-agricultural forests in Northern New Jersey. For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2023.121427.
Korhonen, J., Nepal, P., Prestemon, J.P., Cubbage, F.W., 2021. Projecting global and regional outlooks for planted forests under the shared socio-economic pathways. New For. 52 (2), 197–216. https://doi.org/10.1007/s11056-020-09789-z.
Kremer, K.N., Bauhus, J., 2025. Restoring native forests from *Pinus radiata* plantations: natural regeneration of native tree species in response to different harvesting treatments in central Chile. Restor. Ecol. 33 (1), e14309. https://doi.org/10.1111/rec.14309.
Kremer, K., Promis, Á., Bauhus, J., 2022. Natural advance regeneration of native tree species in *Pinus radiata* plantations of south-central chile suggests potential for a passive restoration approach. Ecosystems 25, 1096–1116. https://doi.org/10.1007/s10021-021-00704-x.
Lara, A., Solari, M.E., Prieto, M.D.R., Peña, M.P., 2012. Reconstrucción de la cobertura de la vegetación y uso del suelo hacia 1550 y sus cambios a 2007 en la ecorregión de los bosques valdivianos lluviosos de Chile (35o—43o 30′ S). Bosque 33 (1), 13–23. https://doi.org/10.4067/S0717-92002012000100002.
Lázaro-Lobo, A., Ervin, G., 2020. Native and exotic plant species respond differently to ecosystem characteristics at both local and landscape scales. Biol. Invasions 1, 143–156.
Lieffers, V.J., Pinno, B.D., Johnson, A., Hossain, K.L., Gooding, T., 2023. Intensive management increases flexibility in managing wood supply. Can. J. For. Res. 53 (7), 544–555. https://doi.org/10.1139/cjfr-2022-0317.
Luebert, F., Pliscoff, P., 2006. Sinopsis bioclimática y vegetacional de Chile. Editor. Univ.
Ma, S., Verheyen, K., Props, R., Wasof, S., Vanhellemont, M., Boeckx, P., Boon, N., Frenne, P., 2018. Plant and soil microbe responses to light, warming and nitrogen addition in a temperate forest. Funct. Ecol. 32, 1293–1303. https://doi.org/10.1111/1365-2435.13061.
Maclaren, J., & Knowles, R. (2005). Silviculture of Radiata pine (Vol. 5). [Christchurch, N.Z.]: New Zealand Institute of Forestry Inc., [2005]. ⟨https://natlib.govt.nz/records/21984108⟩.
Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Springer Netherlands. https://doi.org/10.1007/978-94-015-7358-0.
Malkamäki, A., D'Amato, D., Hogarth, N.J., Kanninen, M., Pirard, R., Toppinen, A., Zhou, W., 2018. A systematic review of the socio-economic impacts of large-scale tree plantations, worldwide. Glob. Environ. Change 53, 90–103. https://doi.org/10.1016/j.gloenvcha.2018.09.001.
Marshall, G.R., Manley, B., Wyse, S.V., 2024. Vegetation patterns in mature plantations of *Pinus radiata* and *Pseudotsuga menziesii*: Implications for forest transitions. For. Ecol. Manag. 572, 122264. https://doi.org/10.1016/j.foreco.2024.122264.
Marshall, G.R., Wyse, S.V., Manley, B.R., Forbes, A.S., 2023. International use of exotic plantations for native forest restoration and implications for Aotearoa New Zealand. N. Z. J. Ecol. 47 (1), 1–12.
McEwan, A., Marchi, E., Spinelli, R., Brink, M., 2020. Past, present and future of industrial plantation forestry and implication on future timber harvesting technology. J. For. Res. 31 (2), 339–351. https://doi.org/10.1007/s11676-019-01019-3.
McFadden, T.N., Dirzo, R., 2018. Opening the silvicultural toolbox: a new framework for conserving biodiversity in Chilean timber plantations. For. Ecol. Manag. 425, 75–84. https://doi.org/10.1016/j.foreco.2018.05.028.
Moretti, A.P., Olguin, F.Y., Pinazo, M.A., Gortari, F., Bahima, J.V., Graciano, C., 2019. Supervivencia y crecimiento de un árbol nativo maderable bajo diferentes coberturas de dosel en el Bosque Atlántico, Misiones, Argentina. Ecol. ía Austral 29 (1). https://doi.org/10.25260/EA.19.29.1.0.779.
Mueller-Dombois, D., Bridges, K., Daehler, C., 2008. Biodiversity Assessment of Tropical Island Ecosystems: PABITRA Manual for Interactive Ecology and Management. Bishop Museum Press. ⟨https://www.nhbs.com/biodiversity-assessment-of-tropical-island-ecosystems-book⟩.
Navarro-González, I., Pérez-Luque, A.J., Bonet, F., Zamora, R., 2013. The weight of the past: Land-use legacies and recolonization of pine plantations by oak trees. In:

Ecological applications: a publication of the Ecological Society of America, 23, pp. 1267–1276. https://doi.org/10.1890/12-0459.1.
Nieuwenhuis, R., Grotenhuis, M., Pelzer, B., 2012. Influence.ME: tools for detecting influential data in mixed effects models. R. J. 4, 38–47. https://doi.org/10.32614/RJ-2012-011.
Odland, M., Goodwin, M., Smithers, B.V., Hurteau, M., North, M., 2021. Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. For. Ecol. Manag. 495. https://doi.org/10.1016/j.foreco.2021.119361.
Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P., O'Hara, B., Simpson, G., Solymos, P., Stevens, H., & Wagner, H. (2015). Vegan: Community Ecology Package. R Package Version 2.2-1, 2, 1-2.
Onaindia, M., Fernández de Manuel, B., Madariaga, I., Rodríguez-Loinaz, G., 2013. Co-benefits and trade-offs between biodiversity, carbon storage and water flow regulation. For. Ecol. Manag. 289, 1–9. https://doi.org/10.1016/j.foreco.2012.10.010.
Osuri, A.M., Gopal, A., Raman, T.R.S., DeFries, R., Cook-Patton, S.C., Naeem, S., 2020. Greater stability of carbon capture in species-rich natural forests compared to species-poor plantations. Environ. Res. Lett. 15 (3), 034011. https://doi.org/10.1088/1748-9326/ab5f75.
Otero, L., 2006. La huella del fuego. Historia de los bosques nativos. Poblamiento y cambios en el paisaje del sur de Chile. Pehuen. ⟨https://tienda.pehuen.cl/products/la-huella-del-fuego⟩.
Payn, T., Carnus, J.-M., Freer-Smith, P., Kimberley, M., Kollert, W., Liu, S., Orazio, C., Rodriguez, L., Silva, L.N., Wingfield, M.J., 2015. Changes in planted forests and future global implications. For. Ecol. Manag. 352, 57–67. https://doi.org/10.1016/j.foreco.2015.06.021.
Pirard, R., Secco, L., Warman, R., 2016. Do timber plantations contribute to forest conservation. Environ. Sci. Policy 57, 122–130. https://doi.org/10.1016/J.ENVSCI.2015.12.010.
Prado, J.A. (2015). Plantaciones Forestales, más allá de los árboles. Colegio de Ingenieros Forestales. ⟨https://issuu.com/ediarte/docs/libroplantforestales/39⟩.
Pritchard, A.S.E., Larcombe, M.J., Steel, J.B., Lord, J.M., 2024. Plant diversity under native and exotic forests: implications for transitional forestry in Aotearoa New Zealand. For. Ecol. Manag. 572, 122314. https://doi.org/10.1016/j.foreco.2024.122314.
Pryde, E.C., Holland, G., Watson, S., Turton, S., Nimmo, D., 2015. Conservation of tropical forest tree species in a native timber plantation landscape. For. Ecol. Manag. 339, 96–104. https://doi.org/10.1016/J.FORECO.2014.11.028.
QGIS Development Team, 2023. QGIS Geographic Information System (Versión 3.30.2) [Software]. Open Source Geospatial Foundation. ⟨https://qgis.org/⟩.
R Core Team. (2025). R: The R Project for Statistical Computing. ⟨https://www.r-project.org/⟩.
R. Vargas-Gaete P. Arroyo D. Penneckamp Sotobosque de plantaciones: Breve guía de plantas que crecen bajo plantaciones de Pinus radiata en el centro-sur de Chile.
Reyes, R., Nelson, H., 2014. A tale of two forests: why forests and forest conflicts are both growing in Chile. Int. For. Rev. 16 (4), 379–388.
Rubilar, R.A., Lee Allen, H., Fox, T.R., Cook, R.L., Albaugh, T.J., Campoe, O.C., 2018. Advances in silviculture of intensively managed plantations. Curr. For. Rep. 4 (1), 23–34. https://doi.org/10.1007/s40725-018-0072-9.
Sadzawka, A., Carrasco, M., Grez, R., Mora, M., Flores, H., Reaman, A., 2006. Métodos de análisis recomendados para los suelos de Chile. Revisión 2006, Instituto de Investigaciones Agropecuarias. ed, Serie Actas INIA Nº 34. Santiago, Chile,.
SAG. (2010). Protocolo toma muestras suelo. ⟨https://www.sag.gob.cl/sites/default/files/Protocolo%20toma%20muestras%20suelo.pdf⟩.
Salas, C., 2002. Ajuste y validación de ecuaciones de volumen para un relicto del bosque de Roble-Laurel-Lingue. Bosque 23 (2), 81–92. https://doi.org/10.4067/S0717-92002002000200009.
Salas, C., Donoso, P.J., Vargas, R., Arriagada, C.A., Pedraza, R., Soto, D.P., 2016. The Forest Sector in Chile: an overview and current challenges. J. For. 114 (5), 562–571. https://doi.org/10.5849/jof.14-062.
Salas, C., García, O., 2006. Modelling height development of mature Nothofagus obliqua. For. Ecol. Manag. 229 (1-3), 1–6. https://doi.org/10.1016/j.foreco.2006.04.015.
Savilaakso, S., Johansson, A., Häkkilä, M., Uusitalo, A., Sandgren, T., Mönkkönen, M., Puttonen, P., 2021. What are the effects of even-aged and uneven-aged forest management on boreal forest biodiversity in Fennoscandia and European Russia? A systematic review. Environ. Evid. 10, 1–38. https://doi.org/10.1186/s13750-020-00215-7.
Schall, P., Gossner, M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J.C., Overmann, J., Renner, S., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. J. Appl. Ecol. 55, 267–278. https://doi.org/10.1111/1365-2664.12950.
Schlatter, J., Gerding, V., 2024. Nutrición forestal. Ediciones Universidad Austral de Chile.
Sedjo, R.A., 1999. The potential of high-yield plantation forestry for meeting timber needs. New For. 17 (1), 339–360. https://doi.org/10.1023/A:1006563420947.
Sharma, A., Bohn, K.K., Jose, S., Dwivedi, P., 2016. Even-aged vs. uneven-aged silviculture: implications for multifunctional management of southern pine ecosystems. Forests 7 (4). https://doi.org/10.3390/f7040086.
Simões, L.H., Guillemot, J., Ronquim, C.C., Weidlich, E.W.A., Muys, B., Fuza, M.S., Lima, R.A., Brancalion, P., 2024. Green deserts, but not always: a global synthesis of native woody species regeneration under tropical tree monocultures. Glob. Change Biol. 30. https://doi.org/10.1111/gcb.17269.
Smith, G.F., Gittings, T., Wilson, M.W., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D., Mitchell, F., Kelly, T., Iremonger, S., McKee, A., Giller, P., 2008. Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodivers. Conserv. 17, 991–1015. https://doi.org/10.1007/s10531-007-9274-3.
Tarasewicz, N.A., Jönsson, A.M., 2021. An ecosystem model based composite indicator, representing sustainability aspects for comparison of forest management strategies. Ecol. Indic. 133, 108456. https://doi.org/10.1016/j.ecolind.2021.108456.
Trentini, C., Campanello, P.I., Villagra, M., Ferreras, J., Hartmann, M., 2020. Thinning partially mitigates the impact of atlantic forest replacement by pine monocultures on the soil microbiome. Front. Microbiol. 11. https://doi.org/10.3389/fmicb.2020.01491.
United Nations, 2015. Transforming our world: the 2030 Agenda for Sustainable Development.
Uribe, S.V., Estades, C.F., Radeloff, V.C., 2020. Pine plantations and five decades of land use change in central Chile. PLOS ONE 15, e0230193. https://doi.org/10.1371/journal.pone.0230193.
Wang, T., Dong, L., Liu, Z., 2023. Climate strengthens the positive effects of stand structure on understory plant diversity in chinese temperate forests. Forests. https://doi.org/10.3390/f14112138.
Wang, Z., Jiang, L., Gao, J., Qing, S., Pan, C., Wu, Y., Yang, H., Wang, D., 2022. The influence of microhabitat factors on the regeneration and species composition of understory woody plants in *Pinus tabuliformis* plantations on the Loess Plateau. For. Ecol. Manag. https://doi.org/10.1016/j.foreco.2022.120080.
Wang, C., Zhang, W., Li, X., Wu, J., 2021. A global meta-analysis of the impacts of tree plantations on biodiversity. Glob. Ecol. Biogeogr. 31 (3), 576–587. https://doi.org/10.1111/geb.13440.
Xu, X., Wang, X., Hu, Y., Wang, P., Saeed, S., Sun, Y., 2020. Short-term effects of thinning on the development and communities of understory vegetation of Chinese fir plantations in Southeastern China. PeerJ 8. https://doi.org/10.7717/peerj.8536.
Yin, X., Zhao, L., Fang, Q., Ding, G., 2021. Differences in soil physicochemical properties in different-aged *Pinus massoniana* plantations in Southwest China. Forests. https://doi.org/10.3390/f12080987.
Zhao, D., Kane, M.B., Teskey, R., Fox, T., Albaugh, T., Allen, H.L., Rubilar, R., 2016. Maximum response of loblolly pine plantations to silvicultural management in the southern United States. For. Ecol. Manag. 375, 105–111. https://doi.org/10.1016/j.foreco.2016.05.035.