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

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Abstract

The management of industrial forestry plantations in temperate zones has generated a global debate over their capacity to maintain ecosystem services, including native biodiversity conservation, and how to transition toward more multifunctional management models within the forest industry. Although plantation forests are increasingly discussed as potential multifunctional systems, significant gaps remain in understanding the environmental and structural drivers that determine native biodiversity retention, underscoring the need for locally grounded empirical studies. This study evaluated native vascular plant diversity under *Pinus radiata* (Monterey pine or radiata pine) plantations at two sites in south-central Chile. Species diversity and tree regeneration was quantified using 120 understory plots (25 m² each) established in *P. radiata* plantations (>9 years) and reference native forests. All plantation plots were located within 500m of native forest. Stand structure was characterized in 24 structural plots (500 m² each), and microsite and soil properties were measured to assess their influence on understory plant composition. Plantations retained between 43 and 60% of the native richness recorded in reference forests, and showed similar understory microsite and soil chemical attributes. Stand structure was one of the main predictors of native richness underneath *P. radiata* canopy. Although nearby native forests maintained greater richness and regeneration, plantations with open and heterogeneous structures harbored high levels of diversity and favored the establishment of native species. These results reinforce the hypothesis that adjustments in management practices can improve the ecological compatibility of plantations. Furthermore, they highlight the potential of plantations within transitional silviculture frameworks to contribute to the restoration of ecological functions and to promote successional development trajectories toward native forest ecosystems.

Keywords: *Biodiversity retention, forest management, environmental factors, transitional forestry, silvicultural practices.*

1. Introduction

Forest plantations worldwide cover nearly 131 million hectares representing a major component of managed forests largely established and dedicated 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 widespread wood shortage resulting from natural forests degradation of accelerated industrialization and growing human populations (Bauhus et al., 2010; Diaci, 2006; Prado, 2015). This rapid expansion also reflects their high productivity, supported by intensive but relatively simple management regimes that enable predictable stand development and facilitate large-scale implementation (McEwan et al., 2020; Prado, 2015). Currently, despite representing less than 5% of the world's forest area (FAO, 2020), plantations supply nearly one-third of the global demand for industrial timber (Jürgensen et al., 2014; McEwan et al., 2020). Moreover, it is estimated that by 2040, approximately half of the global wood supply will come from plantations (Bauhus et al., 2010), particularly in regions where emerging economies predominate, such as Latin America, Africa, and parts of Asia (Carle & Homgren, 2008; Korhonen et al., 2021; Payn et al., 2015). Consequently, the establishment of forest plantations has been promoted as an efficient strategy to provide an alternative source of timber and to supply other increasingly valued ecosystem services, such as soil conservation and the regulation of hydrological processes (Bauhus et al., 2010; Prado, 2015, Cassiano et al. 2023). Several studies have also shown that plantations can reduce pressure on natural forests, by supplying wood from planted sources, thereby helping to mitigate degradation and deforestation processes (Pirard et al., 2016; Sedjo, 1999).

Despite these productive benefits, the massive expansion of the plantation model has also raised concerns due to its potential impacts on the provision of ecosystem services (Huettmann & Young, 2022; Salas et al., 2016). In several regions around the globe, local communities and environmental organizations have expressed apprehension about the model's effects on water access, land use, and the transformation of traditional landscapes (Cariola-Szuchman et al., 2018; Carte et al., 2021; Hughey et al., 2019). Large-scale forest plantations have been linked to a range of socio-environmental conflicts, mainly related to land tenure disputes and the limited distribution of economic opportunities they generate (Malkamäki et al., 2018). These issues, together with the uneven concentration of economic benefits, have intensified tensions surrounding the forestry sector, amid criticisms related to

biodiversity loss and ecosystem fragmentation (Cagnoni et al., 2023; Malkamäki et al., 2018).

In Chile, where more than 3 million hectares are covered by forest plantations, mainly *Pinus radiata* and *Eucalyptus spp*., these tensions have become particularly evident due to the sharp contrast between the sector's productive development and the environmental and social impacts perceived in local territories, especially in south-central Chile (Reyes & Nelson, 2014; Salas et al., 2016, Gerding 2025). The low structural diversity characteristic of monocultures, combined with the spatial uniformity resulting from even-aged stands, limits their capacity to provide ecosystem services compared with natural forests (Holt, 2012; Osuri et al., 2020). However, the magnitude of these impacts may differ according to the management practices applied, as certain silvicultural regimes can mitigate these effects and enhance specific ecosystem services (Amoroso et al., 2024; Tarasewicz & Jönsson, 2021).

Forest plantation management is commonly adjusted according to productive objectives, with management intensity increasing when higher timber profitability is desired, typically on higher-quality sites (Lieffers et al., 2023; Rubilar et al., 2018). This includes high establishment densities, multiple pruning, and successive thinnings within short rotations of less than 30 years, which typically conclude with extensive clear-cutting to restart the production cycle (Maclaren & Knowles, 2005). Although these strategies have proven effective, they have also been associated with reductions in functional diversity compared with non-intervened conditions (Chianucci et al., 2024). A clear example is the several areas planted with *P. radiata* in south-central Chile, where intensive management and the large area planted have led to pronounced fragmentation of natural landscapes, altering floristic composition and native species regeneration, promoting landscape homogenization, reducing the provision of ecosystem services, and lowering resilience to disturbances such as wildfires and also pest and diseases outbreaks (García et al., 2018; Paredes et al., 2022; Wang et al., 2022).

Given the impacts associated with intensive management, there is growing interest in developing new production models that integrate the provision of ecosystem services, including biodiversity conservation (Burger, 2009; Paquette & Messier, 2010). In response, several international certification standards have begun to promote more ecosystem-compatible management to improve environmental practices and reduce tensions with society (Howe et al., 2005; Thorning & Mark-Herbert, 2022). In this context, plantations can play a complementary conservation role due to their increasingly dominant presence in contemporary landscapes (Paquette & Messier, 2010; Silva et al., 2019). In Chile,

143 approximately 1.2 million hectares of plantations (~41%) are concentrated within less than
144 450 linear kilometers between 35° and 38° S, overlapping with areas of exceptionally high
145 plant diversity within a recognized biodiversity hotspot (Bannister et al., 2012; Vargas-Gaete
146 et al., 2020). This represents a significant opportunity to test innovative management and
147 silvicultural models in these landscapes, particularly considering the type of plantation model
148 that will be required in the future.

149 There is consensus regarding the potential of plantations to support biodiversity at
150 the landscape level (Pirard et al., 2016; Simões et al., 2024). Proximity to native forest
151 patches has been identified as a key variable, acting as a source of propagules for the
152 regeneration of native species and promoting their establishment and persistence in the
153 plantation understory (Chazdon et al., 2009; Vargas-Gaete et al., 2020). Likewise, landscape
154 heterogeneity, as occurs in "mosaic landscapes," can improve ecological connectivity and
155 facilitate the presence of species from different taxonomic groups (Schall et al., 2018). In
156 addition, management practices have been explored to modify plantation structure and
157 enhance their capacity to maintain biodiversity (McFadden & Dirzo, 2018). Establishing
158 uneven-aged or mixed-species plantations (Savilaakso et al., 2021; Sharma et al., 2016),
159 increasing rotation age (Coote et al., 2013; Pryde et al., 2015), and implementing differential
160 harvesting to maintain continuous canopy cover have been reported to improve micro-
161 environmental conditions for regeneration, thereby supporting native understory
162 development (Alday et al., 2017). Furthermore, reducing stand density has proven to be an
163 effective measure for increasing light availability and facilitating the establishment of native
164 species in the understory (Ali et al., 2019).

165 Despite these advances, important knowledge gaps remain in both the literature and
166 practice regarding the variability of ecological site and structural conditions that could
167 enhance biodiversity retention underneath plantation canopies (Wang et al., 2023). Because
168 the impact of plantations on biodiversity depends on management practices and local factors
169 such as climate, soil, and landscape structure, it is essential to study different geographic
170 contexts to identify common patterns (Smith et al., 2008).

171 Understanding how environmental factors and stand structure influence biodiversity
172 retention is key for explaining the variability observed among plantations. Biodiversity
173 underneath plantation canopies are determined by a combination of conditions operating at
174 multiple spatial and temporal scales. Site variables such as elevation, aspect, slope, and soil
175 fertility, together with microsite conditions including light availability and litter cover, influence
176 understory composition and regeneration (Carteron et al., 2020; Ma et al., 2018). However,

in plantation systems these effects are strongly modulated by stand structure and the silvicultural practices that determine it. Some studies have shown that canopy openness, stocking, and vertical heterogeneity regulate light penetration and resource competition, thereby influencing the richness and recruitment of native species (Forbes et al., 2019; Marshall et al., 2024; Wang et al., 2022). Likewise, plantation age determines when certain species can establish, as later stages of stand development often provide more favorable conditions for regeneration (Braun et al., 2017; Heinrichs et al., 2018). Therefore, integrating the combined influence of environmental conditions and stand attributes is fundamental to identify the factors that determine the capacity of *P. radiata* plantations to retain native biodiversity.

In this context, this study aims to characterize native plant biodiversity underneath *P. radiata* plantations in south-central Chile. We identify site, microsite and soil variables that enhance biodiversity retention in the understory and analyze the plantation structural attributes that promote the persistence of native tree species. Considering two sites dominated by *P. radiata* plantations, we hypothesized 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 compared with more homogeneous, closed-canopy plantations. Our aim is to understand how structural management in plantations influences plant biodiversity, providing a basis for developing better future plantation models that are multi-functional and compatible with conservation.

2. Methods

2.1. Study area and sampling design

The study areas were selected within the intermediate depression landscape of south-central Chile, where landcover is dominated by *P. radiata* plantations that coexist with remnant fragments of native *Nothofagus*-dominated forests. Native forest fragments represent the last vestiges of the region's original vegetation (37–39° S; Roble–Raulí–Coigüe forest type; Fig. 1; Donoso, 1981; Otero, 2006) and are typically found between 200 and 800 m.a.s.l., on steep slopes (60–70%), 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 landscapes in which *P. radiata* forestry has expanded in Chile (Fuentealba et al., 2021; Lara et al., 2012; Luebert & Pliscoff, 2006).

The proximity between native forest patches and plantations allowed for comparisons of understory plant biodiversity under similar environmental conditions (Fig. 1A). The

selected sites included *P. radiata* stands between 10 and 30 years old, encompassing a range of management intensities from intensive regimes (≥ 2 pruning operations and at least one thinning) to extensive regimes (no pruning and only one thinning). 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).

To define potential sampling locations, vector layers of geomorphology, road networks, and urban areas were integrated with cartography of native vegetation and forest use (IDE, 2023); CONAF 2014, 2015). Site selection and spatial design were carried out in QGIS 3.30.2 using the Model Designer tool (QGIS Development Team, 2023). Following this procedure, and considering accessibility constraints, two study sites were defined: (1) Los Barros, in the Biobío Region (~5000 ha; 37°34′–37°37′ S), and (2) Rucamanque, in the 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 m² plot (20 × 25 m) for structural and soil sampling conditions, along with five 25 m² 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).

[Insert Fig.1 around here]

2.2. Data collection

In each structural plot (500 m²), all trees larger than 5 cm in diameter at breast height (DBH at 1.3 m) were measured for, noting species identity, measuring DBH with a metric diameter tape, total height using a Vertex hypsometer (Haglöf ®, Sweden). For each 25 m² subplot, the floristic composition of all vascular plants was recorded using the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1979), and tree regeneration (< 5 cm DBH) was quantified using 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 with a Nikon D5200 camera and an 8-mm Sigma lens to estimate incident radiation (Fournier & Hall, 2017).

To characterize soil chemical attributes, soil samples were collected at each 500 m² 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 estimated using the core method in a ~1 m³ pit, extracting undisturbed 100-cc cylinders for later determination of dry mass (Blake & Hartge, 1986).

2.3 Data analysis

Site, microsite, and soil variables were compiled for both study sites, contrasting native forest and plantation conditions. 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 & 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). Regeneration density (< 5 cm DBH) was calculated for each condition per height class (< 50, 51-200, > 200 cm). Significant differences among forest conditions within each height class were evaluated using post-hoc pairwise comparisons based on estimated marginal means, with $\alpha = 0.05$.

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 resulting first PCA represented a numerical value for stand structure of each plantation (Gewers et al., 2022). Values along the first PCA axis represented a structural gradient, with lower values indicating less intensive management and higher values reflecting more intensive silvicultural regimes. 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 to 3.0 suggest moderate and values >3.1 suggest high diversity (Magurran, 1988).

Floristic composition was evaluated using non-metric multidimensional scaling (NMDS; (function *metaMDS*, vegan package in R; Oksanen et al., 2015). The analysis was based on a dissimilarity matrix constructed from the relative abundances of species in each floristic subplot (n = 60), using the Bray–Curtis distance (Oksanen et al., 2015). To assess which site, microsite, soil, and stand structural variables were significantly associated with compositional patterns, we used the *envfit* function (with 999 permutations and $\alpha = 0.05$; Oksanen et al., 2015).

Finally, to assess the relationship between vascular plant species richness and the plantation structural gradient we fitted a generalized linear mixed model (GLMM) fitted with a Poisson distribution and a log link function, implemented with the *glmer* function (package *lme4*; Gilbert, 2024). In the model, species richness was treated as the response variable, the stand structural gradient and site as fixed predictor, and transect as random effects. Model validation included: (1) testing predictor significance using likelihood-ratio tests (drop1, test = "Chisq"; Dobson & Barnett, 2018), (2) evaluating model assumptions through simulated residuals (package DHARMa; Harting, 2022) and (3) assessing the influence of each transect on model coefficients using Cook's distance (package *influence.ME*; Nieuwenhuis et al., 2012).

3. Results

3.1. Site, microsite, and soil variables

The study sites showed some differences in their baseline environmental conditions. Los Barros presented 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).

[Insert Table 1 around here]

3.2. Stand attributes, tree regeneration, and vascular plant diversity

The structure of native forests at Rucamanque reflected a more mature condition than at Los Barros, with higher mean diameters and top heights (Fig. 2). *P. radiata* plantations also

differed structurally between sites: while stands at Los Barros were relatively uniform in age and density, those at Rucamanque exhibited greater heterogeneity (Table 2). Although total richness and diversity were higher in native forests, plantations retained between 43% and 60% of their native species richness, and Shannon index values indicated high diversity across all conditions (Table 2). Native species also dominated over exotics in the understory of both forests and plantations.

[Insert Table 2 around here]

Native tree regeneration was generally more abundant in native forests than in plantations at both study sites (Fig. 2). At Los Barros, native forests had a high density of seedlings in the 0–50 cm height class, exceeding 5,000 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. 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 (Appendix 1).

[Insert Fig.2 around here]

3.3 Plant biodiversity retention within plantations

Multivariate analysis showed a clear differentiation in the floristic composition of plantations according to the study site (Fig. 3). In general, plantations with lower management intensity, characterized by higher stocking, showed lower vascular plant richness. In contrast, plantations with more open stand structures and higher levels of incident radiation were associated with greater native species richness. Variables such as soil bulk density, incident radiation, slope, and soil pH were also significantly correlated with variation in floristic composition, indicating that stand structure, microsite and soil attributes relate to biodiversity retention under plantation canopies.

[Insert Fig.3 around here]

This was consistent with the GLMM results (Fig. 4), which showed a positive and significant effect of the structural gradient on native species richness ($\beta = 0.153$, $p = 0.034$), equivalent to an estimated 16.6% increase in richness per unit increase along the gradient (Fig. 4). The site had no detectable effect ($p = 0.81$), indicating consistency across locations. The

random-effect variance (SD = 0.222) reflected transect-level heterogeneity and residual diagnostics confirmed an adequate model fit.

[Insert Fig.4 around here]

4. Discussion

4.1. Environmental attributes and their influence on plant diversity under plantations

The capacity of ecosystems to sustain biodiversity depends primarily on the interaction among environmental variables, proximity to propagule sources, and the functional traits of species (Kimmins, 2004; Lázaro-Lobo & Ervin, 2020). This study evaluated the presence of native vascular species beneath the canopies of exotic *P. radiata* plantations located near or adjacent to patches of temperate forests dominated by *Nothofagus* in southern Chile.

In general, despite differences in altitudinal gradients and soil attributes between the two study sites, native species presence, regeneration and diversity under plantations appear to be more strongly influenced by variables associated with stand structure, microsite heterogeneity, and land use history. Similarly, previous studies have shown that in conifer plantations, modifications on canopy structure largely determine understory richness, provided elements for soils to maintain the minimum conditions necessary for native plant establishment (Ali et al., 2019; Ferris et al., 2000). Although Los Barros exhibits poorer soils and higher altitude, this site showed greater floristic richness and more abundant tree regeneration in native forests. In contrast, Rucamanque, with more fertile soils, had a more stable floristic composition but lower regeneration density. This pattern indicate that land-use history and stand structure exert a stronger influence on native vegetation responses. Thus, the differences observed between sites reflect how topographic gradients and historical management can modulate local diversity in ways that are not necessarily aligned with site quality (Kelly & Ray, 2023; Lara et al., 2012; Peña et al., 2016)

Microsite variables and soil chemical attributes were largely similar between native forests and plantations. 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, conversion to *P. radiata* plantations has not substantially modified microsite conditions or soil chemical properties, resulting in an understory environmentally similar to that of the adjacent reference 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 to 37 years old, they likely fall within an intermediate age range in which soil chemical properties do not differ markedly from those of the adjacent native forest.

One of the main trends observed when contrasting native forests and plantations was canopy openness, which was consistently higher in plantations, a pattern aligned with the effects of silvicultural management (i.e., thinning and pruning) on vertical structure and light availability. This increased in radiation input creates more heterogeneous conditions, expanding the range of available niches and facilitating the establishment of both native and exotic herbaceous and shrub species (Granados-Peláez et al., 2018; Z. Wang et al., 2022). This pattern was reflected in the high vascular plant diversity recorded underneath *P. radiata* canopies (Shannon H' > 3). The combination of microsite conditions that remain similar to those of native forests, such as litter, woody debris, and soil structure, together with greater canopy openness in plantations, helps to explain their ability to 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 that by around 15 years of age, plantations retained approximately half of the native richness of adjacent reference forests.

4.2. Influence of stand structure and forest management on understory composition and regeneration in 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) appear to create conditions that favor the retention 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 understory microsites. At Los Barros, where plantations consisted of stands of similar age (17–20 years), stocking and canopy cover reflected the applied silvicultural interventions, showing that thinning and pruning may modify stand structure in predictable ways that, in this case, increased light availability and facilitated the establishment of native species. At Rucamanque, by contrast, the greater age heterogeneity (10–37 years) indicate that plantation structure reflects a combined influence of

management and environmental factors. Importantly, more productive sites tend to receive more intensive management because they can support higher commercial yields (Sedjo, 1999; Zhao et al., 2016). However, this same productivity, characterized by better site conditions and soils and more vigorous growth, can also enhance biodiversity retention, provided that remnant native forest patches remain 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 consistent presence of native regeneration, especially *Aristotelia chilensis* and *Nothofagus obliqua* underneath plantation canopies, demonstrates that these systems can function as refuges for certain species when nearby propagule sources and sufficient light conditions are available. This result is consistent with studies showing that exotic plantations can sustain native plant communities when seed dispersal is not limited (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 & 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).

Together, these results show that, even under traditional productive management regimes, plantations can develop structures that are functionally similar to systems transitioning toward mixed forests, where spatial and light heterogeneity enables the coexistence of native and exotic species. Thus, stand-level management decisions, particularly those related to density and canopy openness, have direct implications for the ability of *P. radiata* plantations to support and maintain native species underneath their canopies across the landscape.

4.3 Biodiversity retention patterns in plantations

The results of both the NMDS ordination and the GLMM analyses highlight that stand structure is a key determinant of floristic diversity under *P. radiata* plantations. Plantations with lower management intensity, characterized by high stockings of smaller *P. radiata* individuals providing consequently low light availability conditions, showed lower under canopy native species richness; contrastingly, while more open structures with taller and larger trees support higher under canopy species richness. These patterns reflect the cumulative effects of silvicultural practices, particularly thinning and pruning, on light availability, spatial heterogeneity, and resource competition, all of which are critical factors for understory species establishment (Odland et al., 2021; Xu et al., 2020).Thus even production-oriented management can indirectly create conditions that facilitate the colonization of native species.

The observed structural gradient synthesizes the variation resulting from management decisions: initial spacing, frequency and intensity of thinning and pruning determine canopy openness and the accumulation of coarse woody debris. Previous studies in temperate systems have shown that such practices increase environmental heterogeneity, promote the development of microhabitats, and facilitate propagule arrival (Brockerhoff et al., 2008; Wang et al., 2022). Similarly, in this study, native species richness responded along the structural gradient, with an increase of about 17% for each unit of the defined management gradient.

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, indicating that the mechanisms of biodiversity retention linked to stand structure may operate broadly being not strictly dependent on local contexts. The fact that relatively simple structural modifications can enhance biodiversity retention highlights an important opportunity for conservation and restoration in plantation-dominated landscapes. This potential becomes even more relevant in a context of increasing societal and market demand to integrate ecosystem services, nature's contributions to people (NCP), and environmentally responsible management

practices within the forestry sector (Ellis et al., 2019; Salas et al., 2016; Sheppard et al., 2020).

4.4 Towards plantation management for conservation and biodiversity retention

The results of this study provide empirical evidence that supports current research trends recognizing forest plantations as environments with potential for native biodiversity retention (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, plantations can function as secondary habitat for native vegetation. However, this capacity is strongly linked to stand structure and to the cumulative effects of management practices. 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 conserving a substantial fraction of native forest biodiversity without requiring full conversion to natural forest. Consequently, even modest adjustments in silvicultural practices can translate into meaningful ecological benefits for the conservation of native vegetation.

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 advocates a gradual shift from traditional management models toward more diverse and resilient forest systems. This approach seeks to integrate continuity among different forest types, improve productive efficiency, reduce environmental impacts, and simultaneously enhance the ecological and public value of forests through greater conservation capacity and the provision of 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.

The incorporation of transitional silviculture principles in Chile would represent a paradigm shift: moving from viewing plantations solely as timber production systems to considering them as multifunctional spaces capable of simultaneously contributing to conservation. This

change is not only conceptual but also operational, as it requires integrating biodiversity criteria into regional forest planning, including the strategic selection of sites for targeted thinning, the retention of native companion species, and the conservation of structural habitat elements (Bekris et al., 2021; Hartley, 2002). The adoption of these practices could strengthen the ecological and social resilience of forested landscapes in southern Chile, aligning with global objectives for the sustainable management of temperate forests (Naciones Unidas, 2015).

Although plantations can contribute to maintaining part of the native flora across the landscape, our study reaffirms that native forests, even when persisting as small patches or fragments, remain the main centers of biodiversity and the most important sources of natural regeneration. Moreover, although plantations retain a significant fraction of native species richness, the floristic composition they support is not identical to that of native forests: some species are less frequent or absent, while others occur exclusively in plantations. Therefore, management strategies should be oriented toward complementarity, prioritizing the active protection and connectivity of native forest remnants while adjusting silvicultural practices in plantations to maximize their ecological compatibility and their role as corridors and secondary habitats.

Finally, the results of our study raise key questions regarding the mechanisms that regulate biodiversity retention under plantations. A remaining challenge is to understand how stand structural attributes interact with other ecological filters, such as seed bank depletion or edaphic changes associated with successive rotations, that may limit long-term native recruitment (Berthrong et al., 2009). It is also necessary to assess the persistence of native species following canopy opening and to characterize their successional potential, considering that some may act as facilitators in transitions toward reference forests (Onaindia et al., 2013). Addressing these questions will help refine management strategies and contribute to the global debate on plantation conversion in temperate landscapes, a central issue in contemporary ecological restoration and in the promotion of multifunctional plantations.

5. Conclusions

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, retaining ~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 are directly linked to management, had a stronger influence on biodiversity retention. In particular, plantations with more open and heterogeneous stand structures supported higher levels of native species richness. Native forests, however, consistently maintained higher species richness, diversity, and tree regeneration, underscoring the need to integrate active conservation strategies into 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.

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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.

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Figures and tables

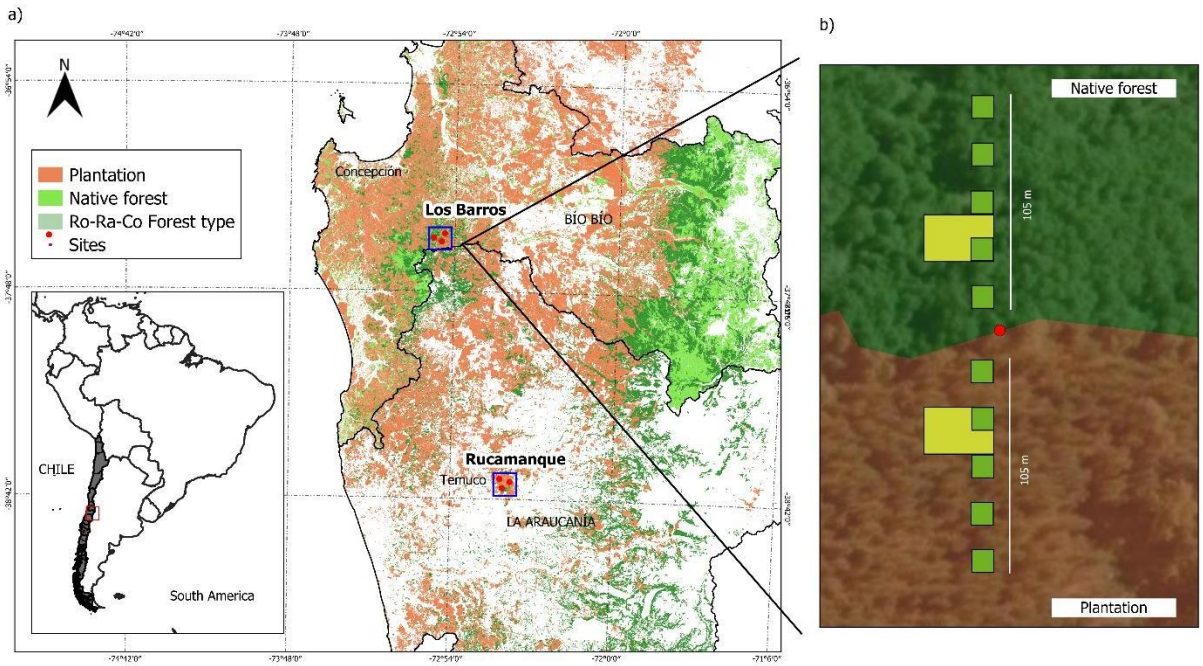

Fig. 1. A) Map of the study area. Blue squares indicate the study sites. B) Schematic representation of the transects established at each sampling point. Green squares correspond to the 5 × 5 m vegetation plots, and yellow rectangles correspond to the 20 × 25 m structural plots. Ro-Ra-Co forest type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

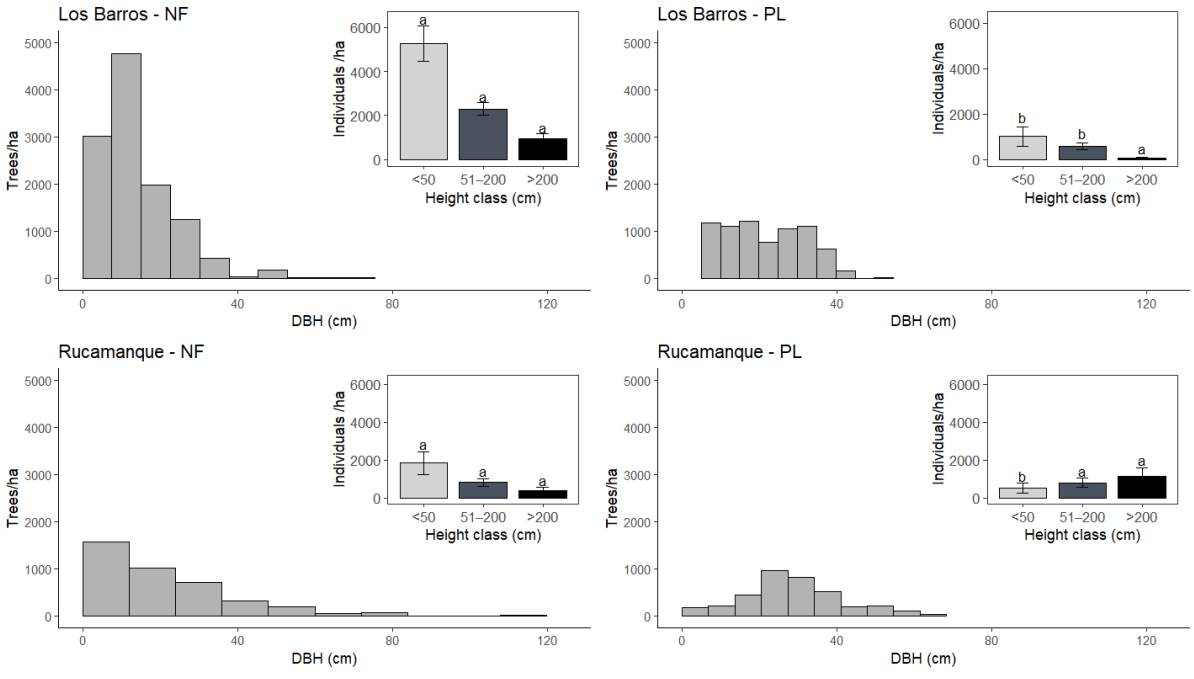

Fig. 2. Distribution of trees per hectare across diameter at breast height (DBH) classes in native forests (NF) and plantations (PL) at both study sites: Los Barros and Rucamanque. The inset panels show the density of native regeneration (individuals/ha) across height classes for each forest cover type.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

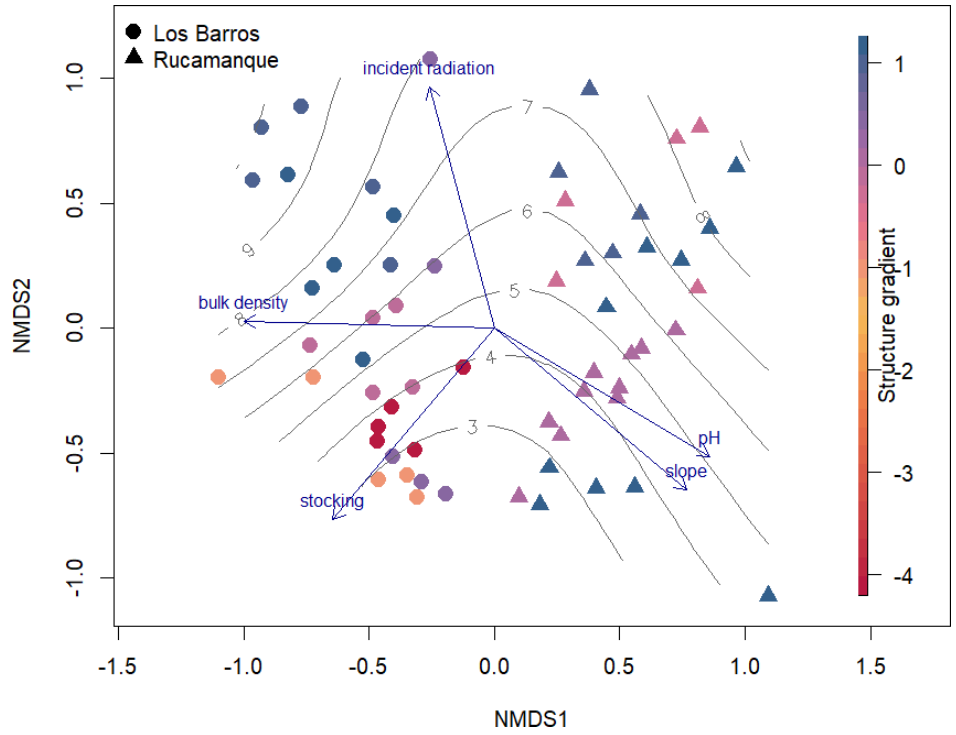

Fig. 3. NMDS ordination based on the floristic composition of 60 plots established in the understory of *P. radiata* plantations at Los Barros and Rucamanque (Bray-Curtis distance, stress = 0.19). Arrows indicate variables significantly correlated with the ordination (95% confidence), including incident 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 per plot (ordisurf, vegan; Oksanen et al., 2015). The stand structural gradient is shown in the color scale (red = lower management intensity, blue = higher management intensity) ($r^2 = 0.1604$, $p = 0.006$).

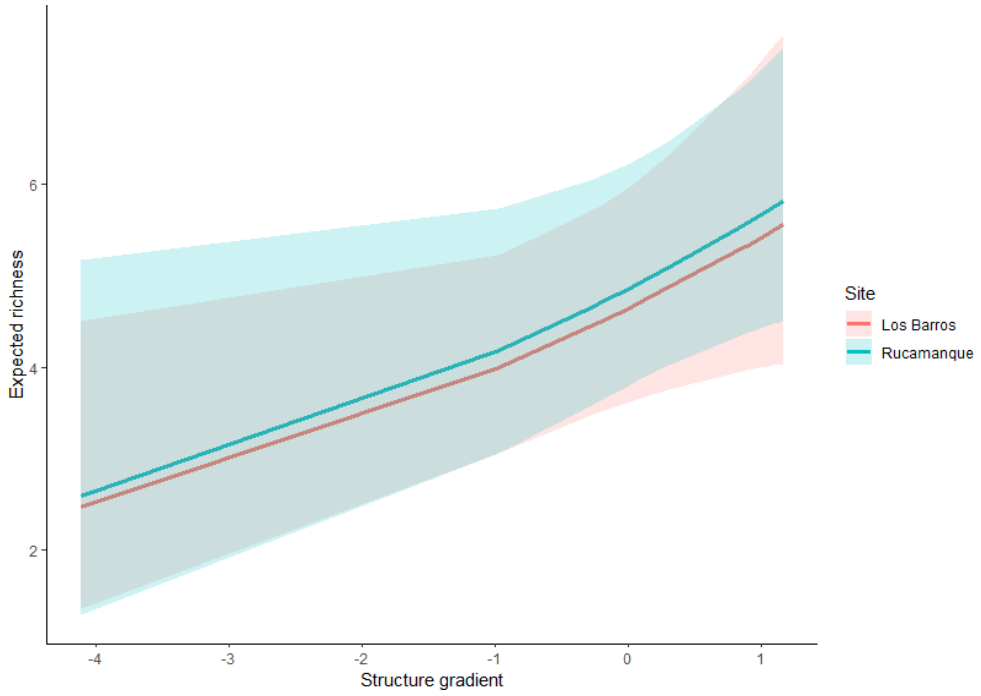

Fig. 4. Relationship between the expected richness of native vascular plant species and the structural gradient of *P. radiata* plantations at Los Barros and Rucamanque, fitted using a generalized linear

mixed model (GLMM, Poisson family). Lines represent the model fit, and shaded areas indicate 95% confidence intervals.

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 (7)
BD (g/cm3)	0.8 (18)	0.7 (16)	0.6 (34)	0.6 (28)

Table 2. Stand 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 stand attributes minimum and maximum is shown in parentheses and the coefficient of variation (CV%) for floristic richness and diversity.* Native forest (NF) ages were inferred from stand structural attributes, based on growth information for this forest type (Donoso 1993; Salas and García 2006).

	Los Barros		Rucamanque	
Stand 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 (m²/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

953 ## Appendix

954 1. Tree regeneration per hectare by height class in native forest (NF) and *P. radiata* plantations (PL) at
955 both study sites. The coefficient of variation (CV%) is shown in parentheses.

Height (cm)	**< 50**		**51 – 200**		**> 200**	
Condition (n = 30)	**NF**	**PL**	**NF**	**PL**	**NF**	**PL**
			Los Barros			
Nothofagus obliqua	1436 (173)	480 (366)	215 (173)	309 (194)	62 (624)	22 (591)
Persea lingue	613 (149)	13 (547)	213 (149)	13 (547)	106 (195)	0
Podocarpus salignus	560 (199)	13 (547)	93 (216)	0	240 (375)	0
Gevuina avellana	437 (99)	27 (380)	462 (169)	0	225 (186)	13 (547)
Pinus radiata	0	320 (296)	13 (547)	160 (224)	0	80 (547)
Others (27)	2221	307	1311	158	327	5
Total	**5267**	**1160**	**2307**	**640**	**960**	**120**
			Rucamanque			
Nothofagus obliqua	1493 (202)	0	0	0	0	0
Eucryphia cordifolia	62 (462)	0	250 (202)	13 (548)	75 (316)	27 (390)
Dasyphyllum diacanthoides	13 (556)	0	50 (443)	0	113 (316)	0
Aristotelia chilensis	13 (556)	194 (376)	103 (557)	327 (151)	13 (557)	909 (230)
Persea lingue	188 (565)	188 (566)	66 (276)	188 (315)	0	63 (330)
Others (16)	84	138	344	272	201	161
Total	**1853**	**520**	**813**	**800**	**186**	**1160**

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