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Propiedades del Suelo y Comunidades de  
Invertebrados como Indicadores del Estado del  
Suelo en Monocultivos de *Pinus radiata* y  
Bosque Nativo en Chile

**Tesis**

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En Cumplimiento Parcial De Los Requisitos  
Para Optar Al Grado De

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Por

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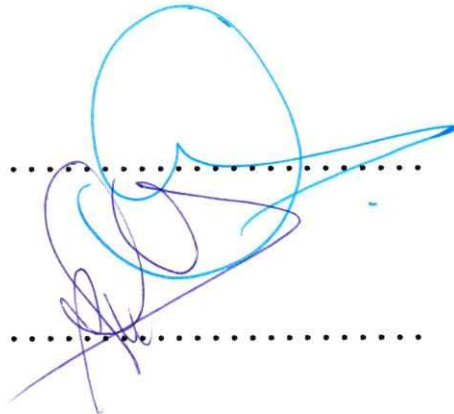
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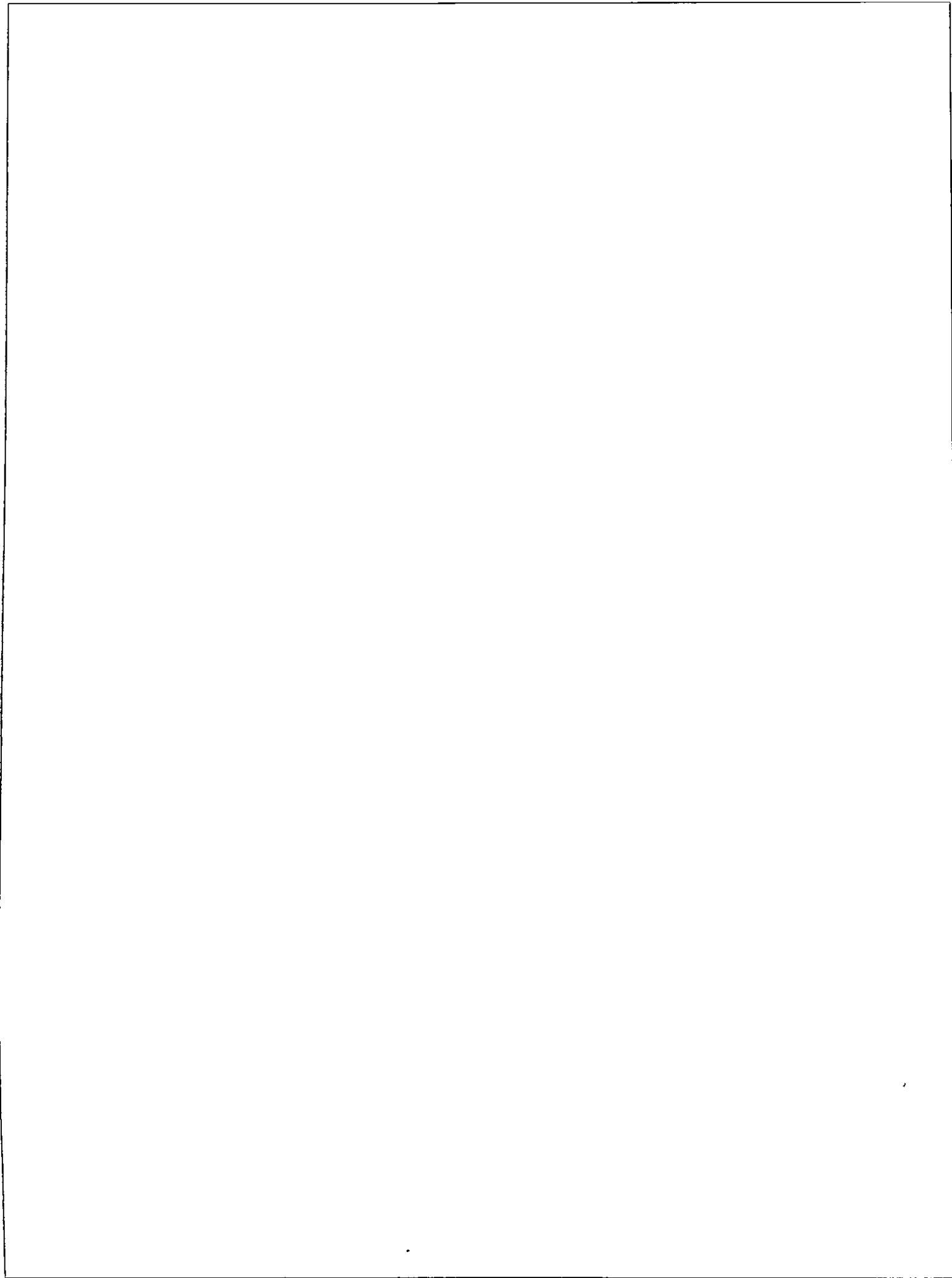
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## RESUMEN

El cambio de uso de suelo es uno de los principales factores del cambio global. En particular, las plantaciones forestales en forma de monocultivos han sido cuestionadas tanto por su real capacidad de amortiguar el cambio climático, así como por sus efectos sobre el suelo. Las plantaciones forestales hoy en día ocupan más de 3 millones de hectáreas del territorio centro-sur de Chile, sin embargo, sus efectos sobre el ecosistema edáfico y las comunidades de invertebrados que lo habitan no han sido estudiados. Los invertebrados edáficos tienen efectos sobre las propiedades químicas y físicas del suelo y, asimismo, las comunidades de plantas del ecosistema tienen efectos sobre la diversidad y abundancia de los invertebrados. Con el propósito de entender los posibles cambios en los ensamblajes edáficos asociados al remplazo del bosque nativo por monocultivos forestales, se compararon las biotas de suelos remanentes de bosque nativo Maulino con plantaciones forestales de *Pinus radiata* en la zona. Se realizaron colectas estacionales de invertebrados y se estimó la riqueza, abundancia y composición comunitaria en suelos de plantaciones y bosque nativo. Además, se realizaron análisis físicos y químicos de propiedades del suelo, tales como infiltración de agua, calidad química del suelo, pH, y contenido hídrico que son vitales para la biota. Tanto las propiedades físico-químicas como las comunidades de invertebrados resultaron significativamente diferentes entre suelos de bosque nativo y monocultivos, revelando una significativa pérdida de fertilidad del suelo y empobrecimiento de las comunidades de invertebrados que lo habitan. Las pérdidas de diversidad biológica y consiguiente disminución de procesos que desempeñan en el suelo, representan una amenaza para la salud de los suelos en el largo plazo, afectando negativamente condiciones del ecosistema del cual depende el bienestar humano.

## ABSTRACT

Land use change is one of the main drivers of global change. Despite the expansion of forest plantations worldwide, assuming a positive effect of their capacity to mitigate global warming and prevent soil erosion, questions have been raised about their real capacity to moderate climate change and their unknown effects on soils. Although forestry monocultures occupy more than 3 million hectares of land in south-central Chile, their ecological effects on soils and on soil biodiversity have not been assessed. Soil invertebrates are functionally relevant at the ecosystem scale because they modify soil chemical and physical properties that affect vegetation and at the same time, the plant community influences invertebrate diversity and abundance belowground. In this work, we compared soils of native Maulino forest remnants and pine monocultures on similar soils, with the aim of understanding changes in the structure and diversity of edaphic assemblages as a consequence of forest replacement by monocultures. We estimated differences in diversity, abundance, and community composition of the soil biota between native forests and pine monocultures, and analysed physical and chemical soil properties crucial for the biota, such as water content, water infiltration, nutrient status, and pH, which are also critical to plant-soil relationships. We found that both soil invertebrate communities and soil properties analysed differed significantly between native forest and monocultures sites, revealing a significant loss of soil fertility and a major reduction in taxonomic and functional diversity of soil invertebrates between forest and monoculture sites. Loss of biotic diversity above ground can have important consequences on key functions of soil organisms in the ecosystem. These changes occurring on a large scale may represent serious threats to soil ecosystem health, altering ecosystem properties that affect human wellbeing.

# INTRODUCTION

## Background

Anthropogenic land use change is considered one of the main drivers of global change in the 21<sup>st</sup> century (Sala et al. 2000, Pereira et al. 2010, Miranda et al. 2015). Since 1990, four million hectares of primary native forest have been lost globally, while at the same time forestry plantations -primarily monocultures of exotic species- have increased in area at an annual rate of 2%, accumulating 264 million hectares in 2010, an area expected to increase up to 300 million ha by 2020 (FAO 2010). Monocultures in forestry are often based on exotic species, which are planted globally, such as *Pinus radiata* and several species of *Eucalyptus*. Among the ecological consequences of replacing diverse native forest with forestry monocultures is the loss of biological richness above and belowground, leading to a general process of biotic homogenization (Chapin et al. 2000, Ibarra and Martin 2015, Mori et al. 2015). Because of biotic homogenization, community assemblages become dominated by few widespread species, while less common and often native species tend to disappear (Olden and Rooney 2006). This can be due to the replacement of rich native species assemblages by a few deliberately or accidentally introduced species, but also to the loss of rare groups, and the expansion of more generalist, widespread species (Mori et al. 2015), resulting in dominance by novel assemblages (*sensu* Hobbs et al. 2013).



Notwithstanding, there has been a spreading rhetoric –and misinformation- assuming a potential equivalence between tree plantations and forests (Espinosa et al. 2005, INFOR 2016), underestimating the ecological and biodiversity relevance of native forests. Even though the loss of soil ecological functions due to land cover change is hard to perceive visually, it has been proven to have strong negative effects on carbon storage, nutrient retention, and water provision in ecosystems (Bonan 2008, Chirino et al. 2010, Mori et al. 2015). Nevertheless, few studies have evaluated the direct effects of native forest replacement by exotic tree monocultures on soil invertebrate communities and associated soil properties, including soil physical structure and nutrient status, both of which could have negative consequences for productivity, tree regeneration patterns, the potential for restoration and even on the health of forestry plantations (Wright and Jones 2004).

Soil organisms perform a wide range of ecosystem processes that contribute to the health of ecosystems through the maintenance of nutrient cycling, water storage and primary productivity. Soil organisms are directly or indirectly involved in key soil processes such as decomposition of organic matter and maintenance of soil structure, and can serve as biotic filters through selectively feeding on leaves, roots or seeds (Heneghan et al. 1999). As aboveground trophic chains are sustained by primary production originated from autotrophs, the breaking down of belowground organic material performed by decomposers and detritivores provides the central input of nutrients and energy to the system. Therefore, as soil accumulates nutrients and energy through decomposition, communities in soil expand and becomes more complex.

The soil fauna consists in a diversity of invertebrate taxa widely ranging in sizes and ecological functions. From nematodes to worms, they all participate in the trophic chain and in the soil formation process, as decomposers of the detritus or mixing and structuring the

soil through bioturbation (Jouquet et al. 2006, Barot et al. 2007). Furthermore, previous works have reported positive interactions between soil invertebrates and soil microorganisms, whereby invertebrates activate microorganisms that are in a dormant state (Lavelle et al. 1997), and thus soil invertebrates not only enhance decomposition process by breaking down organic materials into smaller sizes, but also stimulate microbial activity.

On the other hand, plant cover and species composition in an ecosystem determine local environmental conditions such as light incidence, temperature, soil moisture, and substrate chemical quality by the production of litter and woody detritus (Bardgett and Wardle 2010). Furthermore, it has been reported that plant diversity is positively correlated with invertebrate diversity (Crisp et al. 1998, Siemann et al. 1998, De Deyn et al. 2003). In addition, plant specific physiological traits, such as litter production, tissue concentration of defensive compounds, or nutrient use efficiency, have great influence on the rate at which soil communities decompose organic matter (Aerts 1997, Cornelissen et al. 1999). Consequently, plant assemblage composition and soil communities are tightly related, through the quality and quantity of litter inputs available to soil communities.

## Research Problem

Pine monocultures are widely extended, particularly in New Zealand, Chile, Australia and Spain (Table 1). *Pinus radiata* silviculture is highly developed because it is a versatile, fast-growing, medium-density softwood, suitable for a wide range of end-uses, from soil erosion control to construction and energy production (Mead 2013). Besides its wide potential uses, tree plantations have been proposed as valuable carbon sinks, with a significant role in global warming mitigation (Espinosa et al. 2005). However, several threats

associated with pine silviculture have been documented, such as forest fires (Singh et al. 2010, Cruz et al. 2011), soil nutrient limitation, and water depletion (Turner and Lambert 1988, Chapela et al. 2001, Berthrong et al. 2009, Oyarzún et al. 2011, Hess and Austin 2017). In this light, the widespread notion of pine monocultures as sustainable ecosystems, and the assumed equivalence of natural and plantation forest processes and functions therefore must be revised.

**Table 1:** Estimated areas radiata pine monocultures around the world and the average annual change in area for the period 2008 and 2013 (from: Mead, 2013).

<b>Country</b>	<b>Estimated area (ha x 1000)</b>	<b>New area or loss (ha x 1000/yr)</b>
Australia	773 (2010)	1.5
<b>Chile</b>	<b>1478 (2009)</b>	<b>11.5</b>
Ecuador	20 (1990)	ND
New Zealand	1545 (2011)	-11
Italy	6 (2005)	0
Spain	287 (2006)	ND
South Africa	57 (2008)	-2
Argentina	5.5 (2011)	0
Other	35	ND
<b>Total</b>	<b>4207</b>	<b>-1</b>

\*ND= No data for the period.

In Chile, only half of the native forest cover estimated for the sixteenth century still remains (Lara et al. 2012), most of it confined to high elevations (above 600 m) in the Andean range or to the southernmost fjords and archipelagic territory of the country. Most deforestation was initially due to clearing of land for agricultural practices and timber harvest. The use of fire for forest clearing increased the extent of deforested land and since

'the mid 20<sup>th</sup> century, timber production became based on *P. radiata* and *Eucaliptus globulus* monocultures. The growth of monocultures has been exponential since 1974, presently reaching nearly 3 million hectares, particularly in the Coastal range of central Chile, where exotic forestry monocultures have replaced native forests to become the dominant land cover, by approximately 1999 (Miranda et al. 2015). Even though an increased water deficit has been reported in most of the areas covered by extensive plantations of these exotic tree species and that extensive monocultures now coincide with areas in the central Chilean lowlands and valleys that concentrate a high proportion of agricultural production and urban areas (Armesto et al. 1994, Villagrán et al. 2005), there has been little research on the effects of such massive land cover change and current management practices on soil functional status and fertility, which are ecosystem services valued by crop producers.

Given the lack of research on the ecological effects of extensive pine monoculture plantations on soil biota and its functions, the objective of this work was to assess some ecologically relevant soil properties in sites of pine monocultures and areas covered with native forest cover. We evaluated changes in soil invertebrate diversity and community composition in areas where native forests were replaced by *P. radiata* monocultures. We expected to find some key invertebrate groups that could be proposed as biological indicators of soil ecological status. Physical and chemical soil properties related to water and nutrient conservation were also measured, considering their functional relationship with the activity of soil organisms (Bardgett and Wardle 2010). Because of the importance of forests and particularly forest soils in mitigating climate change (Lal 2004), we also discuss the global context implications of the expanded practice of forestry monocultures in Chile.

## Working hypotheses

1. Due to the management practices currently in use by industrial pine forestry, such as clear cutting, removal of fallen branches and woody debris leftovers, we expected differences in soil structural properties, with greater soil compaction in plantation sites compared to unmanaged native forest sites. This would reduce water infiltration rates and diminish the water storage capacity of soils in plantations compared to native forest sites.
2. We expected soil nutrient status and water content to be lower in plantation sites due to greater uptake of nutrients and water by fast-growing pine monocultures (Turner & Lambert 1987). This forestry species could also be leading to a higher cation uptake and the replacement of exchangeable cations with  $H^+$  in soils, and therefore, to a subsequent acidification of soils under pine monocultures.
3. According to the increased soil compaction and soil perturbation (reduced water infiltration and nutrient limitation) in plantation sites, we expect that soil invertebrates will decline not only in abundance but also in taxonomic richness.
4. Because taxonomic richness has been positively related to ecosystem functions (Tilman et al. 2001, Naeem et al. 2012), we expect that significant reductions of invertebrate diversity will be related to changes in soil properties, measured in plantations with respect to native forests.

## MATERIALS AND METHODS

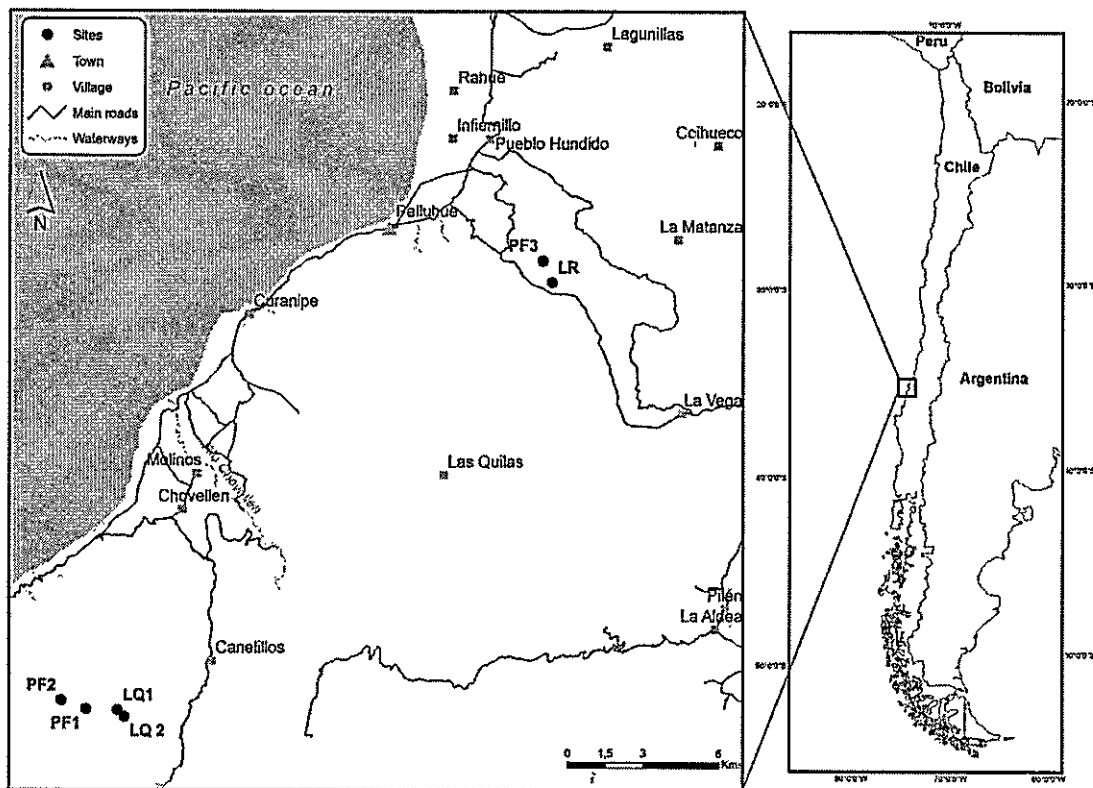
### Study area

The field study was carried out in the Coastal Range of El Maule region, Cauquenes province, in central Chile, where relative small native forest remnants are found in an area dominated by *P. radiata* monocultures. This area is under a Mediterranean-type climate, characterized by rainfall concentrated during winter, May to August, and hotter and drier summers, from September to April. Remnant native forests are a mixture of deciduous and evergreen species, with a canopy layer dominated by *Nothofagus glauca* (Nothofagaceae), *Persea lingue* (Lauraceae) and *Gevuina avellana* (Proteaceae), mixed with patches of *N. obliqua*, *N. alessandri* and *Aristotelea chilensis* (Elaeocarpaceae) (San Martín and Donoso 1995, Bustamante et al. 2005). In addition, several narrowly distributed, rare, and endangered species such as *N. alessandri*, *Pitavia punctata* (Rutaceae), and *Gomortega keule* (Gomortegaceae), all endemic to the Coastal Range of south-central Chile, can be found in some of the remnant forest patches in the area (San Martín 2003). Even though the main object of this study was to compare native forests with pine plantation, the native forest remaining has also been through a long history of degradation by logging and fire, which probably has led to the loss of some species in fragments of native forests as well.

### Sites selection

Native forest sites used for comparison with plantations were selected in two protected areas of the Maule Region: 1) Los Ruiles National Reserve (35°35'57"S; 72°21'06"W) and 2) Los Queules National Reserve (35°59'19"S; 72°41'15"W). The former

is a relatively small remnant patch of secondary and riparian forest (45 ha), while the second is a larger fragment of continuous broad-leaved, evergreen native forest (600 ha). Three sampling sites were selected considering a distance of at least 50 m from the edge of each forest patch (Magura 2002), predominantly in areas with gentle slopes ( $<30^\circ$ ), two in Los Queules and one in Los Ruiles natural reserve. In addition, we selected three sampling sites of *P. radiata* plantations with an age of 10-15 years old, an average stem diameter at breast height of  $26.34 \pm 3.27$  cm, with presence of an established understorey, and which were relatively close to each native forest site ( $<5$  km), with the aim of avoiding large differences in weather conditions, soil type, or topography (Fig. 1). Selecting paired sites in this way (stratified sampling) helped to control for unknown environmental variations (Green 1979). Fieldwork was conducted in two contrasting seasons of the year characterized by different moisture availability and biological activity in this Mediterranean-climate region (i.e. the wet period of Autumn-Winter 2016, and the drier period of Spring-Summer 2017).



**Figure 1:** Study sites in Cauquenes province, El Maule region. Black dots are native forest sites (LQ1: Los Queules 1, LQ2: Los Queules 2, LR: Los Ruiles) and pine monoculture sites (PF1: Pine Plantation 1, PF2: Pine Plantation 2, PF3: Pine Plantation 3).

## Sampling

In each forest and plantation sites, we setup a 30 m transect starting at a random point with a north-south direction. At 0, 15 and 30 m from the start of the transect, we rolled two dice to determine the number of steps away from the transect where sampling plots would be established. We setup three plots of 10×10 m, and within each plot, all canopy and understory woody plant species were identified, and their relative cover was visually estimated, defining five categories of cover (i.e. 0-10%, 11-20%, 21-50%, 51-75%, 76-100%, van der Maarel 2007). Subsequently, we proceeded to randomly select three points within each 10×10 m plot



from where soil cores were extracted (10 cm diameter, 15 cm long) to collect invertebrate assemblages. In the same sampling points, we estimated water infiltration, using the formula: Infiltration ( $\text{cmh}^{-1}$ ) =  $Q/A \times T$ , where “Q” is the quantity of water ( $250 \text{ cm}^3$ ), “A” the area ( $78.5 \text{ cm}^2$ ), and “T” the time (h) (Franzluebbbers 2002). We also extracted soil samples for assessing nutrient status by extraction of total carbon and nitrogen using dry combustion (Carlo-Erba Elemental Analysis), pH (measured with ExStik pH Meter Extech PH100), and water content by the gravimetric method.

### Soil invertebrate extraction and identification

Soil cores from each site were stored at low temperature (c.  $5^\circ \text{C}$ ) in a closed plastic bag prior to transportation to the laboratory. Soil samples were immediately placed and maintained in Berlese funnels for three consecutive days to extract invertebrates (Basset et al. 2003) and on the third day, all the soil remaining in the funnel was manually examined under a  $3\times$  magnifying scope for any remaining individuals. Identification of soil invertebrates was made at the taxonomic level of order for most groups, but for those better known, such as Coleoptera, identifications were possible at the family level with several identification keys (Martínez and Casanueva 1995, Borkent and Wirth 1997, Rusek 1998, Covarrubias and Contreras 2004, Jerez and Moroni 2006, Milcu et al. 2006, Thyssen 2009, Eisenhauer et al. 2011, Cabrera 2014, Covarrubias 2017), and with the help of an entomologist expert from the Department of Entomology of the Metropolitan University of Education Science (UMCE, for its initials in Spanish), Santiago de Chile.

## Data analysis

Because of the rapid turnover of invertebrate populations through the year, and the contrasting weather conditions between Spring-Summer and Autumn-Winter sampling periods, we assumed the three sites sampled for invertebrates in each season as independent samples, therefore we considered a total of  $N=6$  independent samples per site, three in Spring-Summer and three in Autumn-Winter. Differences in understory vascular plant cover, soil properties (pH, total carbon and nitrogen, gravimetric water content and water infiltration), and invertebrate assemblages (taxonomic diversity and abundance) among sites representing different forest ecosystems, were tested with one-way ANOVA ( $N=6$ ), and because we found differences in soil properties between sampling sites, they were compared with nested ANOVAs ( $N=3$ ) to account for differences among sites within each ecosystem type.

Invertebrate diversity under pine monoculture and native forest sites was estimated using Shannon's diversity index, using the number of individuals of each order for the calculation ( $H = -\sum(p_i \cdot \ln(p_i))$ ), where "H" is the diversity index and "p" is the proportion of species *i* relative to the total number of species, and then compared using one-way ANOVA. To assess the relationship between understory plant diversity and soil invertebrate diversity, we used Fisher's Alpha diversity index (Fisher et al. 1943); the diversity of plants and invertebrates were correlated using the Pearson's product-moment correlation test (Rodgers and Nicewander 1988). Additionally, we made correlations between soil properties and invertebrate diversity to assess for possible factors that could account for changes in invertebrate composition. All data were normalized when necessary.

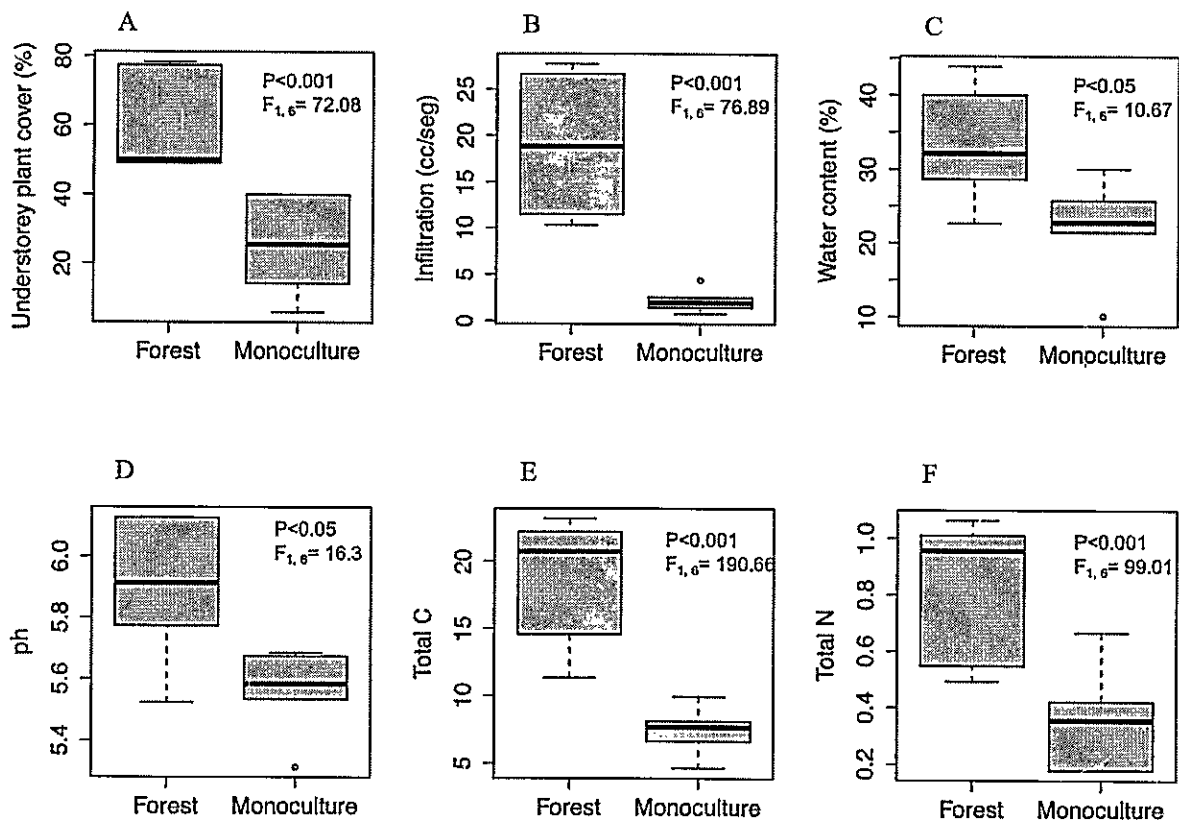
We computed sample-based rarefaction curves with 95% confidence intervals (Colwell et al. 2004) to compare differences in invertebrate's order richness among samples from native forests and pine monocultures. Rarefaction compares the total number of individuals counted with repeated random sampling to the total number of species found in soil samples (Colwell and Coddington 1994). We also computed the total species richness estimator Chao (Colwell et al. 2004).

To assess differences and similarities in the composition of invertebrates from each site and between forests and monocultures, we computed a Bray-Curtis cluster dendrogram using beta diversity indices (performed with Vegan package in R (Oksanen et al. 2007)). Finally, to integrate both abiotic and biotic information for forests and monocultures, we computed a non-metric multidimensional scaling (NMDS) and the statistics analysis of similarities (ANOSIM) with Chao distance. All statistics were performed in R v.3.2.0 (R Core Team 2015) for all the analyses.

## RESULTS

### Soil properties

Understorey plant cover, water infiltration rates, water content, pH, and total C and N differed significantly between soils from different forest sites, and between forests and monocultures (Appendix 1). Soils under pine monocultures were more acid, less permeable (characterized by significantly lower infiltration rates) and almost two times drier for the same time of the year than under native forest. Understorey plant cover percentage differed between pine plantations and native forest, with significantly lower cover in pine monocultures, 25% versus 50% in native forests (Fig. 2 A). Water infiltration and soil moisture were both also significantly lower in monoculture sites, infiltration rate in monocultures being almost ten times lower of the rate found in native forest sites; while soil moisture was almost 10% lower in monoculture sites than in native forest sites (Fig. 2 B and C, respectively). Soil pH was lower and less variable under monoculture sites, while under native forest was higher and with a larger variance (Fig. 2 D). Finally, soils under pine monoculture sites had both less than a half total carbon and nitrogen than soils under native forest (Fig. 2 E and F, respectively). Additionally, Tukey's test on nested ANOVA showed that seasonal variation within each ecosystem type was less important in the soil properties than the difference between native and plantation ecosystems (Appendix 2).

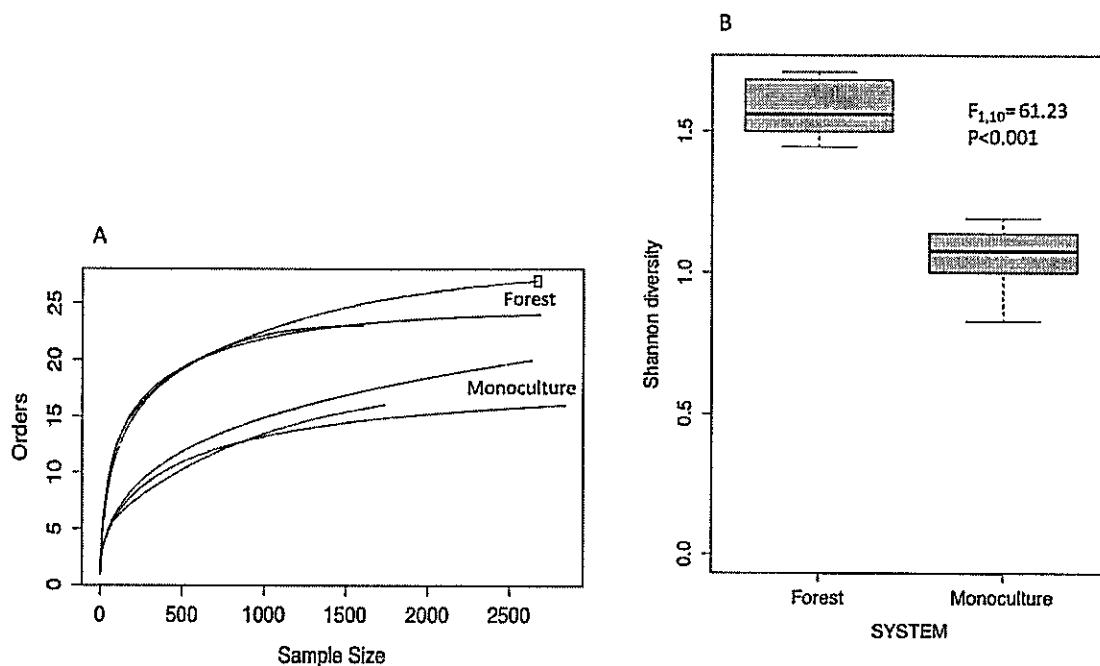


**Figure 2:** Box plot comparison of soil properties between native forest and pine plantations. A) Infiltration rate (cm/h), B) water content (%), C) pH, D) total carbon, E) total carbon, F) total nitrogen. Grey boxes represent the distance between the 1<sup>st</sup> and the 3<sup>d</sup> quartile, the thick black lines are the medians and the vertical dashed lines are the minimum and maximum values, in each case (N=3). P values refer to nested ANOVAS.

### Soil invertebrate diversity and abundances

We found a total of 27 orders of soil invertebrates in all samples, all of them were present in native forest, while 22 orders were found in pine monocultures. The five orders found only in native forest sites were Opilions, Neuroptera, Trichoptera, Onychophora and Anoplura. Rarefaction curves showed that accumulation of invertebrate orders collected from soil samples reached a *plateau* in both forests and monocultures (Fig. 3A), implying that the

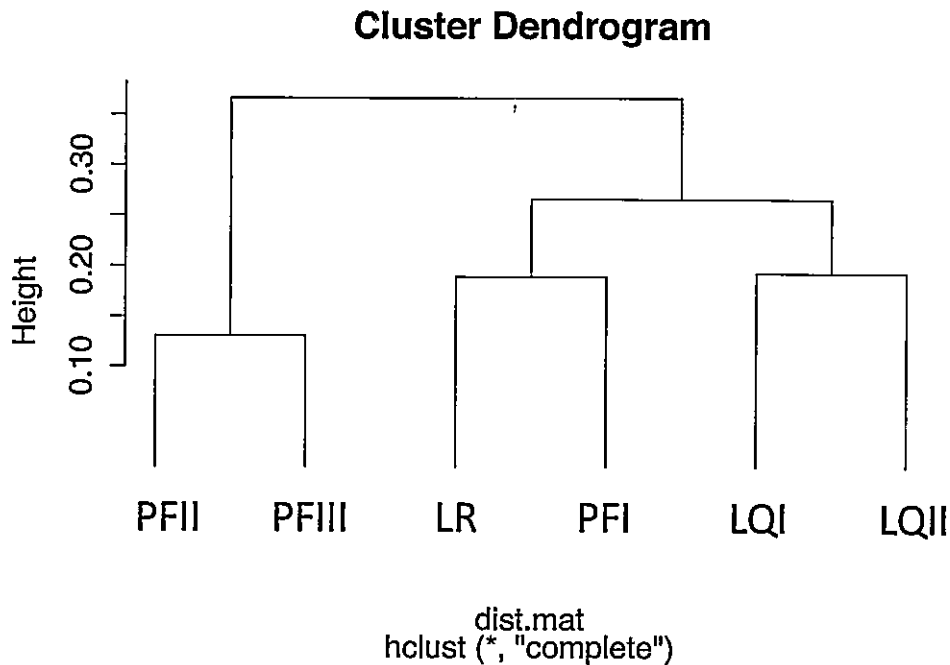
sampling effort was likely sufficient to characterize the soil fauna. Estimation of the total number of orders present in soil samples was performed using the index Chao1, which showed lower overall values in monocultures than in forest sites ( $22 \pm 2.580$  and  $27 \pm 0.735$  orders, respectively).



**Figure 3:** A) Rarefaction analysis of the total number of invertebrate orders as a function of the total number of individuals captured in the soil cores from three native forest sites and three pine monoculture sites: B) Alpha diversity index in native forest sites and pine monoculture sites,  $F_{1,10}=61.23$ ,  $P<0.001$ ,  $N=6$ .

Similarly, Shannon diversity index for invertebrate orders was significantly lower in pine monoculture sites ( $F_{1,10}=61.23$ ,  $P<0.001$ ). A beta diversity cluster dendrogram showed two different community clusters, one grouping sites of native forest and another combining two of the three pine monoculture sites; the third pine monoculture site was more similar to Los Ruiles native forest than to the other two monoculture sites (Fig. 4). Alpha diversity did

not change significantly between winter and summer seasons in each system, instead the largest difference was recorded between plantation and forest systems in each season (Appendix 3).



**Figure 4:** Bray-Curtis cluster dendrogram of differences in composition of soil invertebrate communities present in three pine monoculture sites (PFI, PFII and PFIII) and three native forest sites (LR, LQI and LQII).

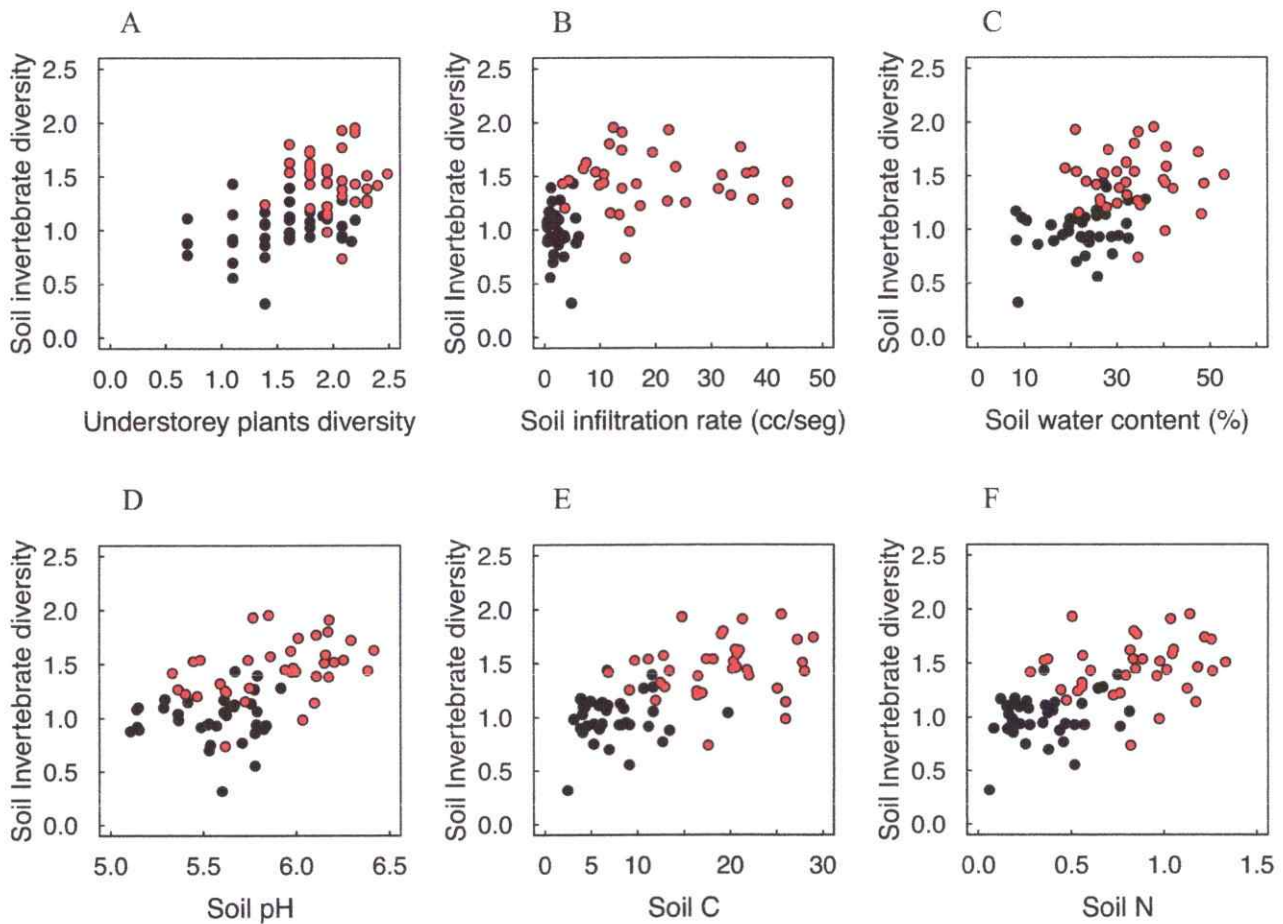
### Biotic and abiotic controls on soil invertebrate communities

In our samples, the diversity of understorey plants was positively correlated with invertebrate community diversity in each site (Fig. 5A), indicating the dependence of soil invertebrate diversity belowground on above-ground plant diversity. Moreover, when the understorey plant diversity in pine monocultures was higher than 2.0, invertebrate species

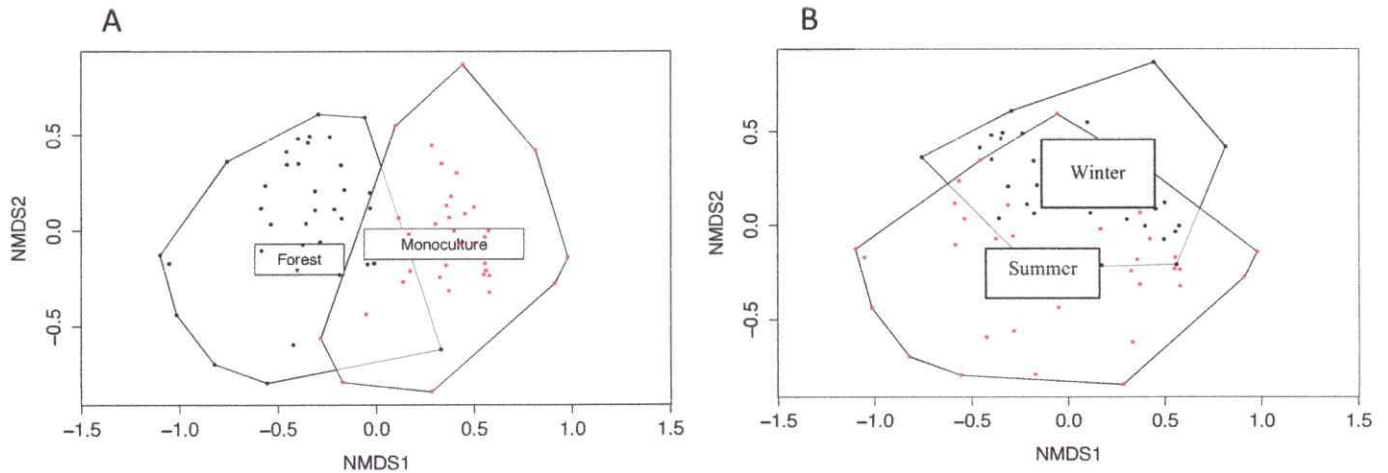
richness does not reach a diversity value of 1.5, but in native forests, invertebrate diversity goes up to 2.0 for the same values of understorey plant diversity. Even though this correlation only considers the presence and absence of different plant species (and not their abundance), understorey plant cover was also significantly lower in monoculture plots than in native forests (30% and 50%, respectively, Appendix 4). Moreover, soil invertebrate taxonomic diversity (at the order level) was highly correlated with measured soil properties (Fig. 5B, C, D and F), and plots from each ecosystem type were highly and distinctively grouped in both sides of the correlation (black dots and red dots in Fig. 5). This result supports a possible functional relationship between invertebrate assemblages and soil properties, as soils of pine monocultures tend to be more acid and compacted, with less nutrients, with lower moisture content for the same dates, and a with lower invertebrate diversity than native forest types.

Non-metric multidimensional scaling (NMDS) ordination showed that when differentiating plots sampled in native forest (black dots Fig. 6A) from those sampled in monocultures (red dots), the separation in soil properties between monoculture and native forest plots was much larger than the differentiation between summer and winter samples (Fig. 6B). We also calculated ANOSIM statistic to test these differences in invertebrate communities, which were much higher for the comparison of pine monocultures and native forest ( $R=0.421$ ,  $P<0.001$ ) than between seasons (i.e. winter versus summer,  $R=0.111$ ,  $P<0.05$ ). Furthermore, when soil properties were represented in the ordination, pH, infiltration rates and understorey plant cover were the main factors differentiating between soil invertebrate communities (Appendix 5). The same graph also reveals that the invertebrate groups that accounted for the main differences between soil communities, were Onychophora, Opilionida, Diplopoda, Scorpiones, Diptera and Nematoda.





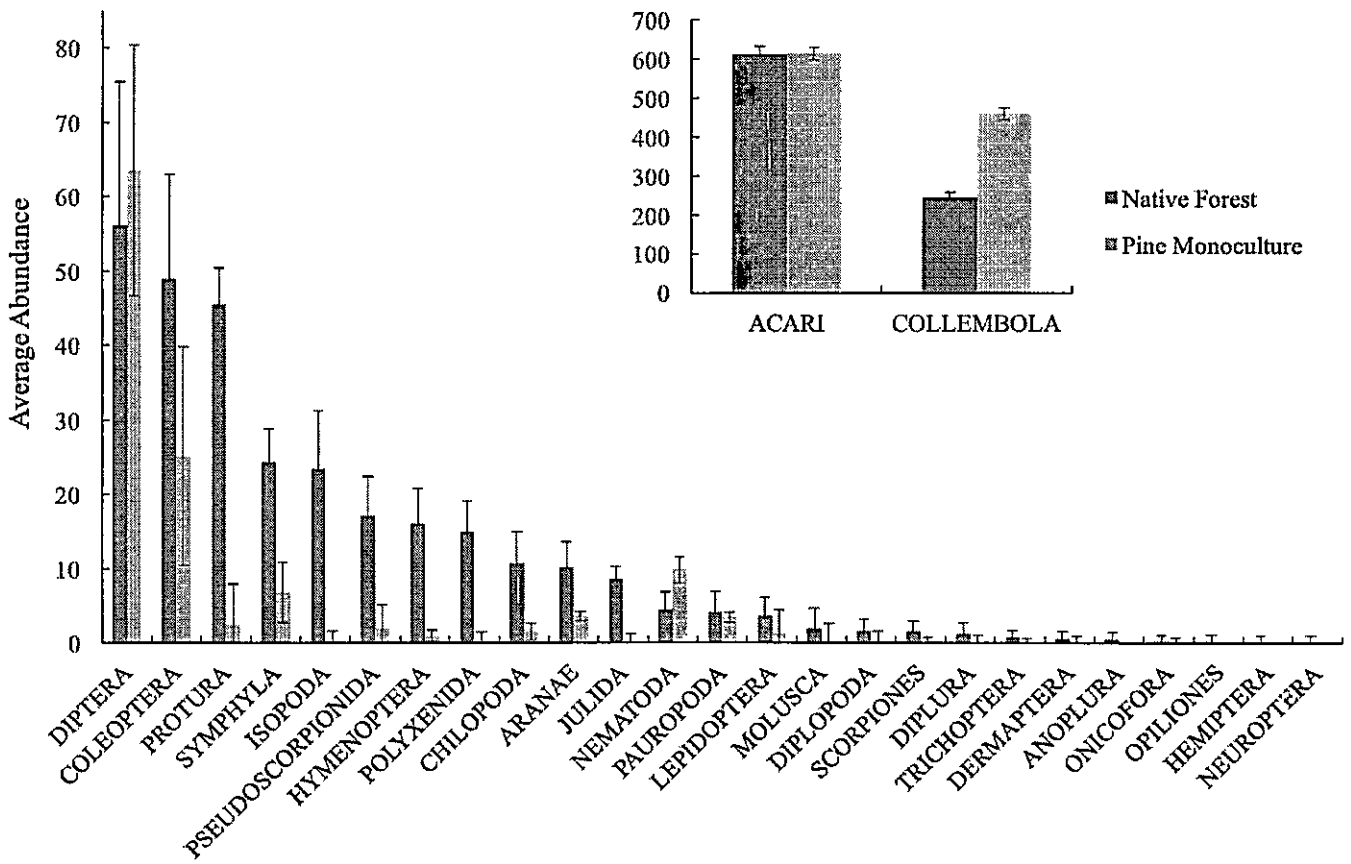
**Figure 5:** Correlation plots between soil invertebrate community alpha diversity index and A) understorey vascular plant alpha diversity, Pearson's product-moment correlation = 0.46,  $t = 4.3883$ ,  $df = 70$ ,  $P < 0.001$ ; B) soil infiltration rate (cc/seg.), Pearson's product-moment correlation = 0.42,  $t = 3.8627$ ,  $df = 70$ ,  $P < 0.001$ ; C) soil water content (%), Pearson's product-moment correlation = 0.28,  $t = 2.4646$ ,  $df = 70$ ,  $P < 0.001$ ; D) soil pH, Pearson's product-moment correlation = 0.53,  $t = 5.1579$ ,  $df = 70$ ,  $P < 0.001$ ; E) total soil carbon, Pearson's product-moment correlation = 0.39,  $t = 3.3169$ ,  $df = 70$ ,  $P < 0.001$ ; and F) total soil nitrogen, Pearson's product-moment correlation = 0.35,  $t = 2.9712$ ,  $df = 70$ ,  $P < 0.001$ . Red dots are measurements made in pine monoculture plots and black dots are native forest plots ( $N=72$ ).



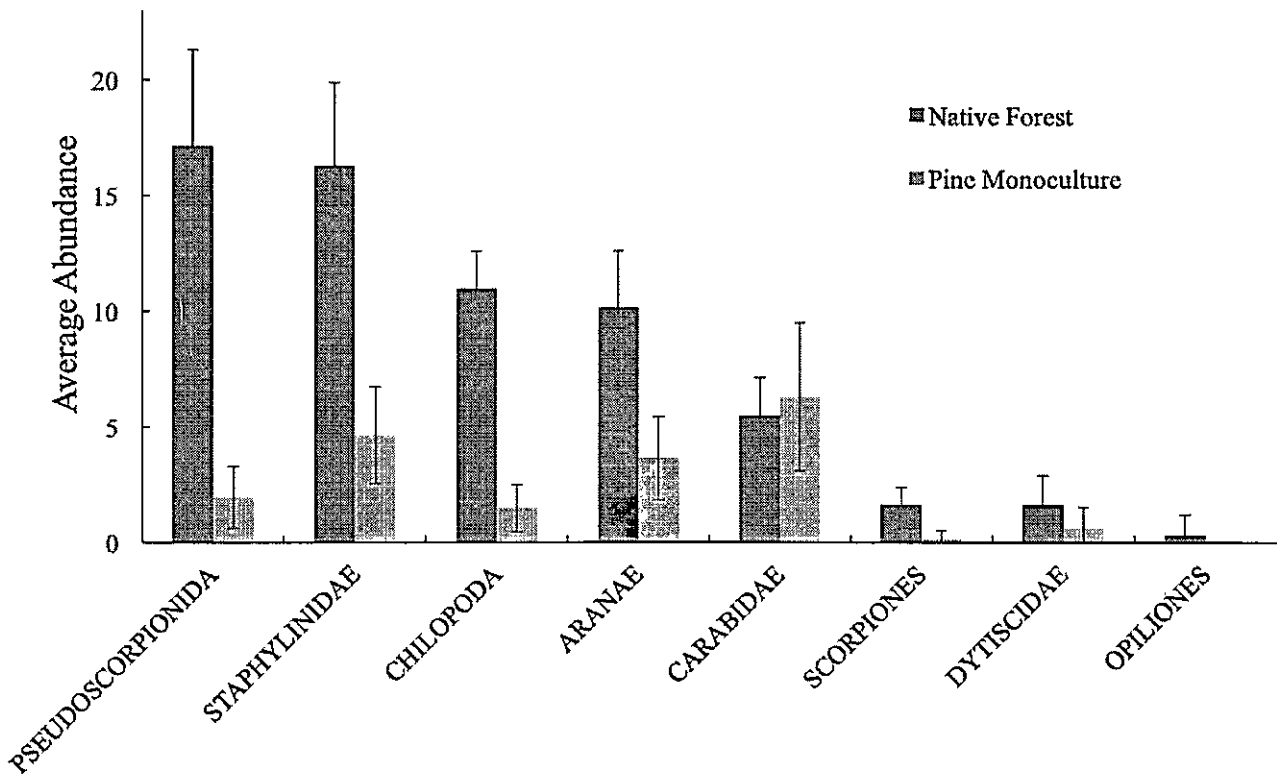
**Figure 6:** NMDS ordination of invertebrate assemblages A) red points are pine monoculture plots and black points are native forest plots, B) red points are plots sampled on summer and black points are plots sampled on winter. Stress = 0.196

### Differences between invertebrate communities

We found remarkable differences in edaphic community composition between forests and plantations, even though the overall number of individuals was similar across sites. Rare groups (those with less than five individuals average) from native forests (i.e. Anoplura, Neuropteran, Onychophora, Trichoptera and Opiliones) were completely absent from pine monocultures. On the other hand, groups of Collembola, Diptera and Nematoda were more abundant in soils of pine monoculture than in native forest (Fig. 7). Number of top predators (i.e. Chilopoda, Aranae, Scorpiones, Pseudoscorpionida and Staphylinidae) were significantly less abundant in pine monoculture than in forest sites (Fig.8).



**Figure 7:** Average abundance of invertebrate orders in native forest sites (black bars) and pine monoculture sites (grey bars). Vertical lines indicate standard error. Orders of invertebrates are organized according to their decreasing abundance in native forest. Inset shows the abundance of the two most abundant orders (Acari and Collembola). N=6 for all comparisons.



**Figure 8:** Average abundance of soil predators in native forest sites (black bars) and pine monoculture sites (grey bars). Vertical lines indicate standard error. Taxa are organized according to decreasing abundance in native forest sites. N=6 for all comparisons.

## DISCUSSION

Remarkable and consistent differences in soil properties were found between native forests and plantation ecosystems, which were related to strong differences in underground invertebrate community assemblages. With respect to soil status and the characteristics of the biota, these differences clearly differentiated two ecological systems: native forest and pine monoculture. In our study, native forest soils were less compacted, less acidic, maintained higher water contents independent of the season of the year, and were richer in nutrients than soils from the forestry monocultures sampled. These differences were manifested despite the similar general climate and soil types where both ecosystems developed. Differences in soil structure and above-ground plant communities accounted for the contrasting invertebrate assemblages, diversity and composition of each system, with pine monoculture invertebrate communities being significantly less diverse than those from native forest. According to our analysis this lower invertebrate diversity was highly correlated with soil properties that might be promoting this diversity loss. Although it is difficult to disentangle causal relationships with respect to the observed changes in community composition and changes in soil properties, current management of plantations (shallow cutting and burning of the residual biomass after harvest) and differences in tree canopy composition (*P. radiata* monoculture) can be proposed as the main factors that differentiated ecologically between these ecosystems and native forests, producing changes

in the diversity and composition of soil communities and ecological processes that sustain them.

### Soil properties, ecosystem processes, and functional links with invertebrate communities

Soil properties measured in this study represented environmental proxies of soil structure and ecosystem functions that are relevant to the maintenance of long-term productivity (Bardgett and Wardle 2010). We measured water infiltration rate as an indicator of soil compaction and aeration, and water content as the capacity of soils to retain water in a highly seasonal Mediterranean-type climate where water supply is contrastingly different between fall-winter and spring-summer (Armesto et al. 1995). In this regard, results from this study confirm recent assessments of the indirect effects of forestry monoculture plantations on water resources in Chile (Huber et al. 2008, Oyarzún et al. 2011, Oyarzun and Herve-Fernandez 2015). These studies documented that massive monoculture plantations had less water retention, affecting its availability for human use and, at the same time, caused greater nutrient loss in sediments via stream water due to runoff, compared to areas dominated by native vegetation. The relation to water supply is a crucial management aspect of forestry in south-central Chile, because water provision is one of the most valued ecosystem services that forests provide to local communities, and it is also strongly sensitive to land use and climate change (Bonan 2008). These results are consistent with studies suggesting that tree monoculture plantations are a major driver of widespread hydrologic crisis across large extensions of south-central Chile, where a drying trend is causing a descent of the water table during the austral summer (Oyarzún and Huber 1999, Huber and Trecaman

2002, Huber and Trecaman 2003, Huber et al. 2008), and our results further confirms this trend.

Previous studies have reported soil acidification and nutrient depletion under pine plantations (Brand et al. 1986, Turner and Lambert 1988, Alfredsson et al. 1998, Berthrong et al. 2009, Chirino et al. 2010); however, studies have not tested these effects in a broader context in Chile despite the rapid expansion of tree monocultures. The decrease in soil pH under monocultures has been attributed to the redistribution of mineral exchangeable cations from soil to fast-growing tree biomass; then, cations tend to be depleted in soil exchange sites and replaced by  $H^+$ , thereby turning soils increasingly acid (Berthrong et al. 2009). Considering that forest soils tend to be more acidic than other ecosystems due to increased production of carbonic acid from higher rates of autotrophic respiration (Richter and Markewitz 1995), the greater acidification of pine monocultures soils may also be a consequence of rapid cation uptake by the fast-growing pine species (Berthrong et al. 2009). Furthermore, soil acidification is reported to have a detrimental effect on soil fertility (Berthrong et al. 2009), and also to modify soil faunal communities (Loranger et al. 2001, Augusto et al. 2002) because of differences in pH preferences among invertebrate communities (Hyvönen and Persson 1990, Van Straalen and Verhoef 1997, Van Straalen 1998). For example, Collembolans have been observed to increase with soil acidity, which in turn can be explained by physiological adaptations to acid soils (Loranger et al. 2001). Accordingly, in this work we found that unlike most other invertebrate orders recorded, groups such as Collembolans and Nematodes were almost twice more abundant in pine monocultures. A possible explanation of this trend is that, as in pine monoculture sites we found less predators, maybe these populations are not being controlled by their natural predators and therefore are more abundant than in native forests sites.

Studies of exotic plantations in central Chile have documented similar trends in entomofaunal diversity when comparing between pine monoculture and remnants of native forest (Estades and Escobar 2005, Briones and Jerez 2007, Cerda et al. 2015, Fierro et al 2017). Although these authors have highlighted the importance of maintaining understorey plant cover for the conservation of invertebrate communities (Grez et al. 2003), in this study we document that understorey plant species richness and cover were both significantly lower in every monoculture plot than in rainforest plots, presumably due to the high plantation tree densities, strong shading, and management practices, such as shallow cutting and short replacement rate (less than 15 years). The limited understorey plant cover, and the minimal canopy tree diversity of monocultures compared to remnant native forests, are likely to greatly influence soil properties and edaphic communities by enhancing differences among microsites. The reduced habitat heterogeneity and lower litter diversity, characteristic in monocultures, offer less possibilities for shelter and nourishment to a broad diversity of soil invertebrates, possibly leading to a rapid biotic homogenization process, where less common groups ("rare" taxa, see Fig. 7) present in native forests sites, such as Trichoptera, Anoplura, Hemiptera, Neuroptera and Onycophora, disappeared completely in pine monoculture sites, while the most common groups (i.e., Acari, Collembola and Diptera) become more abundant in plantations than in native forest. This replacement of rare species by common ones is a known feature of the global process of biotic homogenization (Ibarra and Martin 2015, Mori et al. 2015).

Soil invertebrates are at the top of the trophic chains in soil, and therefore their abundance reflects the integration of a range of underground biological processes occurring in soils (Doubé and Schmidt 1997). In this work, top predators (i.e. Aranae, Chilopoda, Scorpiones, Pseudoscorpionida and Staphilinidae) were at least twice more abundant in soils



from native forests than in pine monoculture sites. This high abundance of top predators is likely to be an indicator of higher ecosystem productivity in native forests, as energy constraints determine the presence and abundance of top predators, with more productive ecosystems sustaining longer trophic chains than less productive ecosystems (Borer et al. 2003, Arim et al. 2006). Moreover, total soil carbon and nitrogen contents, which are often used as indicators of overall soil fertility (Berthrong et al. 2009), were both significantly lower in pine monoculture sites, supporting the hypothesis that pine monocultures are generally less productive than native forests, a condition that could be intensified by greater nutrient uptake by the fast-growing canopy of *P. radiata*. Even though further analysis is needed to assess the specific linkages between the different invertebrate groups found in soil and their functional roles in the ecosystem, we propose that invertebrate communities are suitable indicators of ecosystem health status because of their prominent place in the community of soil organisms and their function in promoting soil fertility and environmental heterogeneity (Doubt and Schmidt 1997).

### Invertebrate communities as ecosystem indicators

Seasonal changes were less important in terms of both soil properties and community composition than differences between native forest and pine monoculture stands, reinforcing the idea that monoculture plantations are functionally different from floristically diverse native forests. NMDS ordination suggested that differences in soil invertebrate communities could be explained at least partly by contrasting soil properties such as soil nutrient content and water infiltration rates, thus revealing a functional linkage between soil biodiversity and ecosystem processes. Regarding soil invertebrate community composition, one of the native

forest sites (Los Ruiles) resulted more similar to a pine monoculture site (Plantation 1), in contrast to our expectations and trends of the other sites. This result may be related to the small area of the native forest remnant in Los Ruiles (<40 ha), and the fact that the site is surrounded by pine monocultures (Fig. 1), therefore having strong edge effect. In addition, this remnant was probably affected by repeated disturbance in the past including fire, logging, and more recently invasion by exotic plant species. On this subject, if we postulate a continuum of stages from a “healthy forest ecosystem” to a highly degraded forest ecosystem, the threshold for a regime shift (Folke et al. 2004) will be dependent on the taxonomic and functional diversity preserved not only in the conservation single area, but in productive areas as well. In this regard, we propose that a main task to ensure more healthy ecosystem processes on productive areas requires to improve the understanding of the functional interactions that characterize healthy ecosystems, in this case the maintenance of underground soil processes and their connections with the aboveground ecosystem, represented by canopy and understorey plant cover and litter chemical inputs.

The present work contributes to disentangle the question about what makes a forest a forest (Chazdon et al. 2016), or what makes a native forest different from a tree plantation. We argue here that the answer goes beyond tree cover, pointing to a complex system defined by vertical layering, above and below ground linkages, and functional biodiversity components, all of which are products of species identities, biogeochemical process, ecosystem functions and land cover history (Pickett and Cadenasso 2002, Aslam et al. 2015, Chazdon et al. 2016). The challenge hereafter for plantations must be about how to make a productive area more sustainable by preserving biotic diversity and ecosystem processes, and therefore we propose soil health as a critical aspect to focus on, and we suggest that

underground invertebrate communities are a suitable tool to measure such health, providing a critical ecosystem health indicator.

### Tree monocultures as carbon sinks and biodiversity reservoirs

The timber industry has long been considered as a contributor to the mitigation of climate change, under the argument that increasing cover of fast-growing trees should enhance carbon capture. In fact, tree cover is generally quantified as an indicator of the capacity of vegetation on land to act as carbon sink for the mitigation of climate warming (Naudts et al. 2016). At the same line, some tree monocultures are often treated as biodiversity reservoirs (Estades et al. 2005), supporting the idea of a functional replacement from native forests to tree monocultures, as habitat for many species (Espinosa et al. 2005). Nevertheless, this statement has two important caveats: first, that many monocultures are placed on sites that were previously forested, and native forests can store much more carbon and for longer times than tree plantations, distributed in epiphytes, understory plants, litter and soil (Bonan 2008), and also to provide more habitat possibilities for animal communities (e.g., fallen logs and standing dead trees, Lindenmayer and Franklin 2002, Lindenmayer et al. 2012). In this work, we tested the idea of pine monocultures as an underground reservoir for soil invertebrates, compared with native forest communities, and we found that neither the invertebrate diversity, nor soil properties were similar between these two ecosystem types. On the other hand, the conversion of broadleaved forests to coniferous plantations has implications for the albedo and tree evapotranspiration, which could have impacts on increasing atmospheric warming (Naudts et al. 2016). Even further, Naudts et al. (2016) reported increased carbon emissions from forestry plantations in Europe after 50 years of

forest management, questioning the role of plantations as a carbon sink, as often argued. In this regard, we propose that the replacement of floristically diverse forests by plantations, although cover could remain the same, does not mean the replacement of one system by an analogous one, because many hardly visible ecological functions, such as those provided underground by soil processes, might be significantly changed.

## CONCLUSION

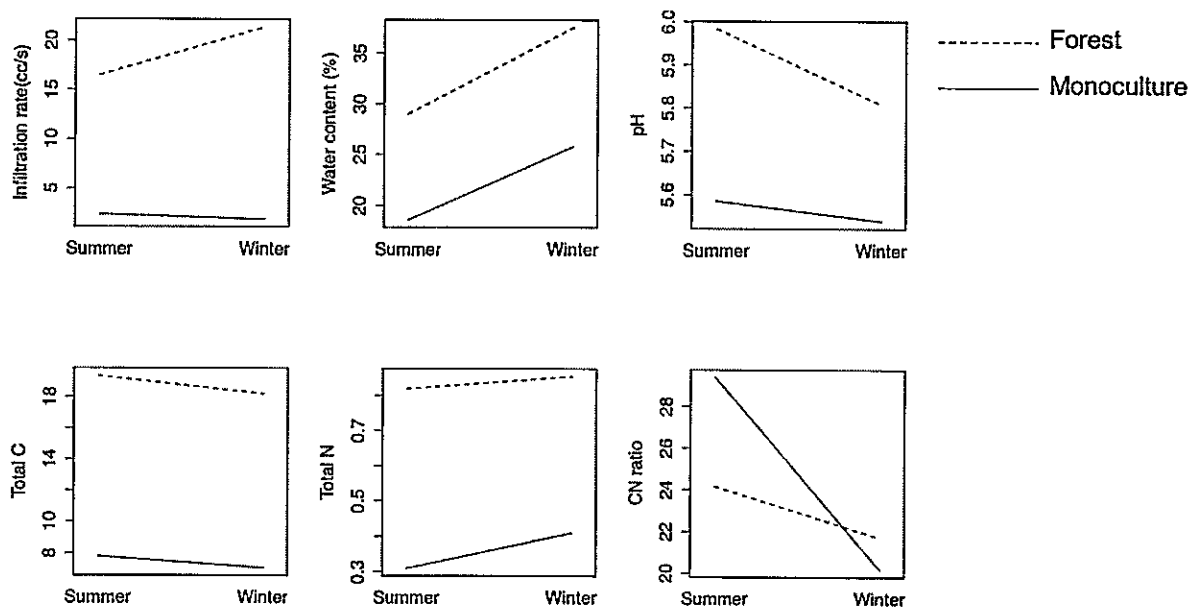
This study supports previous evidence that there is considerable loss of plant and animal diversity in monocultures, documenting the loss of belowground biodiversity in the case of soil invertebrates, which are less conspicuous than other animal species. Conclusive results about the status of biological communities and soil properties under *P. radiata* monocultures indicate significant impoverishment of soil communities in the lapse that plantations have been in place (often less than 40 years) and, equally concerning, changes in critical ecosystem processes that involve salient ecosystem features, such as nutrient cycling, soil structure and water storage. This issue should alert government agencies about public policies that promote monoculture expansion, especially considering that economic development must never set aside ecological consequences, as these policies ultimately affect both, ecosystem health and human welfare, particularly in the long-term, affecting inter-generational values.

## APPENDIX

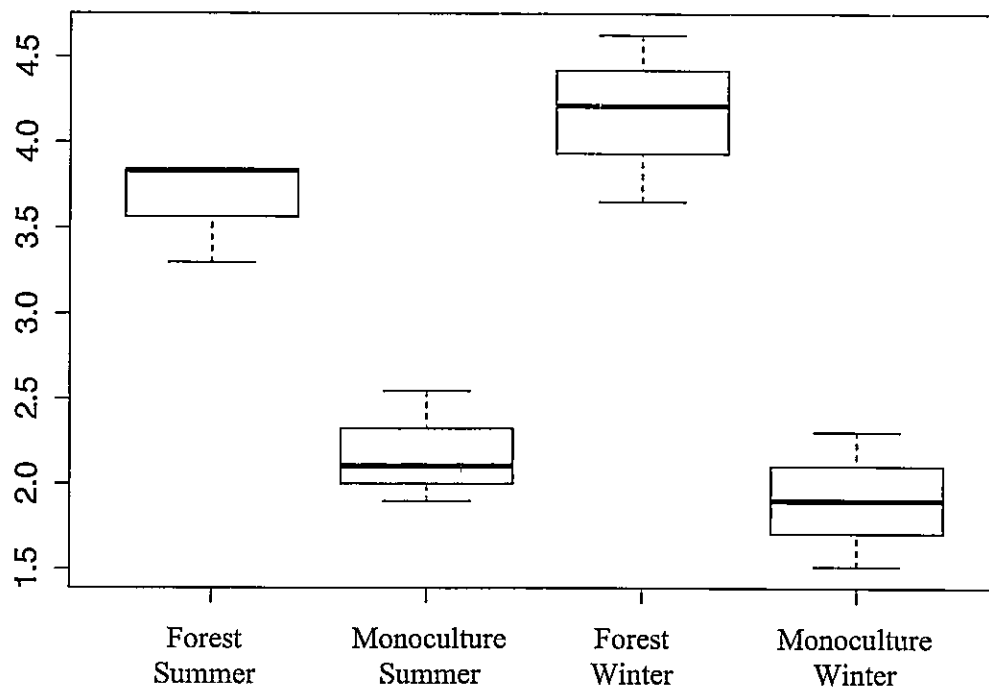
1. **Table 2:** Nested ANOVAs for differences between site properties and ecosystems. In the analysis, Sites are nested in System.

Site property			P	$\eta^2$
Understorey plant cover	Site(System)	$F_{4,6}=9.4$	<0.001	0.862
	System	$F_{1,6}=72.08$	<0.001	0.923
Infiltration	Site(System)	$F_{4,6}=4.74$	<0.05	0.760
	System	$F_{1,6}=76.89$	<0.001	0.928
Water content	Site(System)	$F_{4,6}=2.24$	0.181	0.599
	System	$F_{1,6}=10.67$	<0.05	0.640
pH	Site(System)	$F_{4,6}=3.28$	0.094	0.686
	System	$F_{1,6}=16.3$	<0.05	0.731
C	Site(System)	$F_{4,6}=14.17$	<0.05	0.904
	System	$F_{1,6}=190.66$	<0.001	0.969
N	Site(System)	$F_{4,6}=15.69$	<0.05	0.913
	System	$F_{1,6}=99.01$	<0.001	0.943

2. Tukey's test for nested Anova of seasonal variation (Spring-Summer and Autumn-Winter) of soil properties (Infiltration rate (cc/s), Water content (%), pH, Total C, Total N and C/N ratio), between remnant native Forest (dashed line) and tree Monoculture (continuous line).

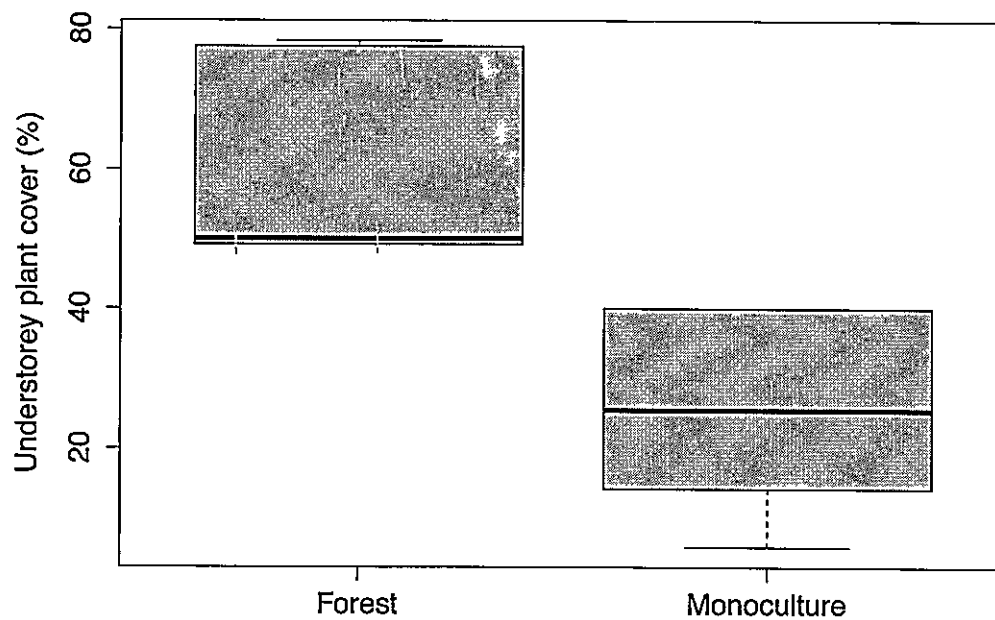


3. Seasonal variation in invertebrate diversity. Boxes represent the distance between the 1<sup>st</sup> and the 3<sup>d</sup> quartile, the black line is the median and the vertical dashed lines are the minimum and maximum values, on each case (N=6).

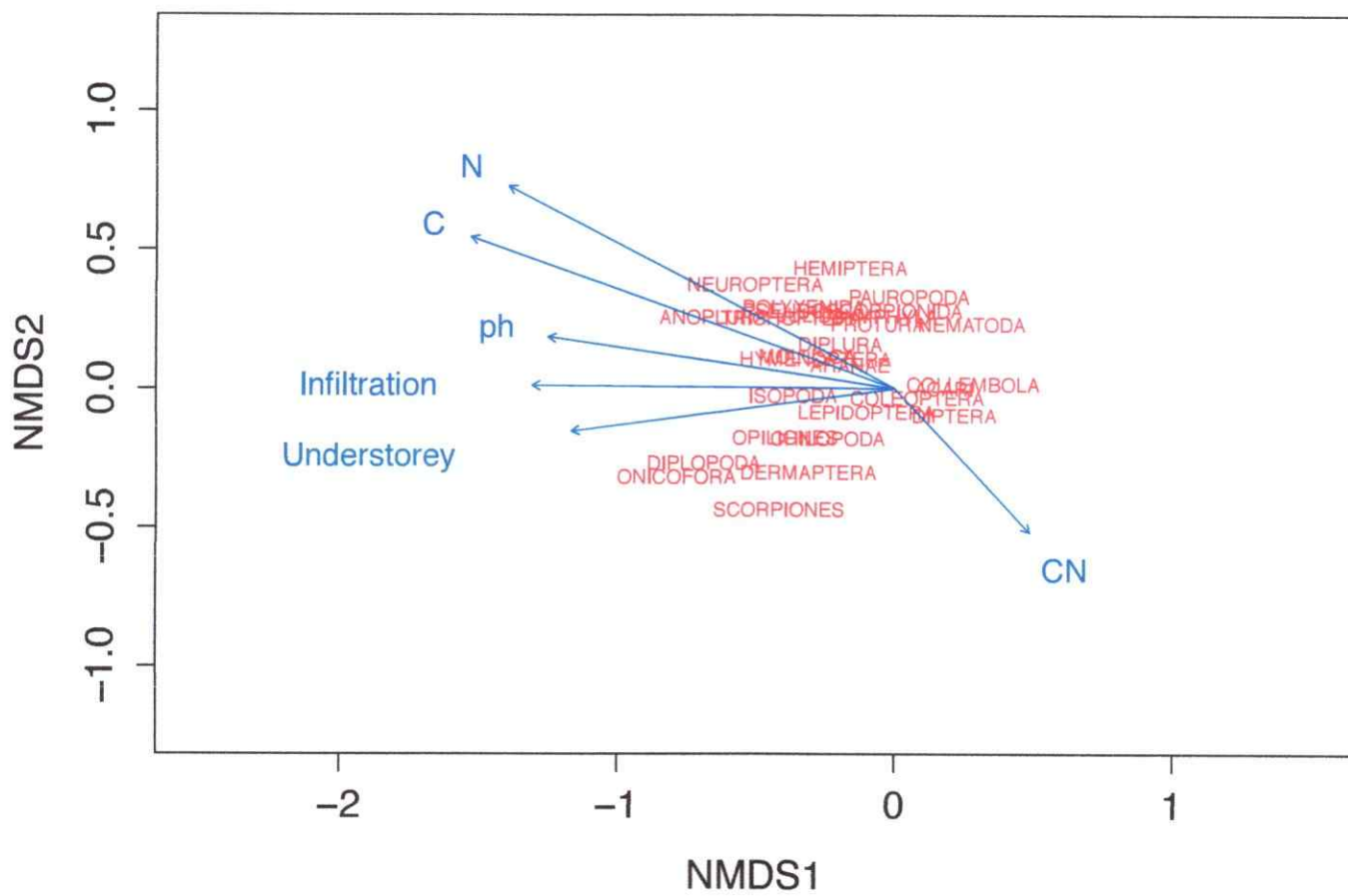




4. Understorey plant cover (%) between native forest and pine monoculture. Boxes represent the distance between the 1<sup>st</sup> and the 3<sup>d</sup> quartile, the black line is the median and the vertical dashed lines are the minimum and maximum values, on each case (N=6).



5. NMDS ordination of soil invertebrate orders sampled (in red letters) and soil abiotic properties (blue vectors).



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