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Native Plant Diversity and Composition Across a *Pinus radiata* D. Don Plantation Landscape in South-Central Chile—The Impact of Plantation Age, Logging Roads and Alien Species

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Abstract: Alien tree plantations are expanding globally with potential negative effects for native biodiversity. We investigated plant species diversity and composition in a *Pinus radiata* landscape in south-central Chile, a biodiversity hotspot, by sampling understory vegetation in different plantation age classes, along forest roads and in natural forest remnants in order to find effective conservation measures for native biodiversity. Plantations, including different age classes and roadsides, maintained high native species richness at the landscape scale but supported a completely different community composition than natural forests. Thus, natural forest remnants must be conserved as plantations cannot replace them. Certain natural forest species occurred frequently in mature plantations and can represent starting points for retaining natural elements in plantations. Generalist native and alien species benefited from plantation management, mainly in young plantations and along roadsides. Stand maturation and a closed canopy, though, reduced alien species occurrences within plantations. Along roads, shade-tolerant aliens should be monitored and removed as they can potentially invade natural forests. Native species conservation in plantations requires a holistic approach of the full mosaic of land uses including the protection of remaining natural forests, alien species monitoring along roadsides and patches with continuous canopy cover to reduce pressure by alien species.

Keywords: forest management; forest roads; gamma-diversity; homogenization; age class; forest conservation; stand maturation; indicator species; extinction debt; *Nothofagus glauca*

1. Introduction

Human-induced conversion and degradation of natural habitats is one of the main global drivers of biodiversity loss [1,2]. Tree plantations of alien, fast growing species, are expanding globally [3] with overall negative effects on native biodiversity [4–6].

Mediterranean Chile is a biodiversity hotspot [7] but experienced major landscape changes in the past centuries. Since the colonization by Europeans in the 16th century, the productive and diverse coastal ranges were especially affected by deforestation [8–10]. While the lowlands of the coastal ranges were totally cleared for agricultural use, the hillsides often remained forested but were exploited for construction and firewood [11]. Subsequent soil impoverishment led to the abandonment of exploited sites that developed to shrubland and secondary forests. Thus, the coastal ranges were covered by a mosaic of different land use types, ranging from agricultural land to secondary native

forests, when the intensive expansion of forest plantations started around 1975 [12] favored by governmental subsidies [13]. Today, industrial plantations of the alien tree species *Pinus radiata* dominate the landscape while the natural forest is restricted to small isolated remnants. Even though the conversion rate of native forests into plantations decreased in the past decades, the plantation area is still growing [14] with the forestry sector being the second largest export industry in Chile [15].

Given this huge expansion of plantations, its impact on native biodiversity is crucial. There is growing evidence that, despite strong effects on community composition of different taxonomic groups compared to natural forest types [16], plantations can function as an alternative habitat for native birds [17], mammals [18] or arthropods [19] with positive effects for ecosystem services [20]. Thereby, a complex and diverse understory was often a strong predictor for species richness of higher trophic levels within plantations [16,20]. This underlines the importance of understanding how structure, richness and composition of the understory vegetation are affected across the management cycle in order to establish optimized management and conservation measures for native biodiversity.

The management cycle of pine plantations comprises a gradient in management intensity and environmental conditions from fresh clearcuts that are prepared for subsequent replanting to medium-aged plantations that are thinned and pruned—if designated for quality wood production (in contrast to pulp production)—to mature plantations that are not further managed up until the final harvest (i.e., a shifting habitat mosaic; [21]). Furthermore, plantations are highly fragmented by a dense logging road network that can function as dispersal corridors for alien species (e.g., [22–25]) that benefit from plantation management [26,27]. Unpaved roads can also attract many seed-dispersing mammals that use the linear corridors for defecation [28]. By this, they can contribute to long-distance dispersal of aliens [29], but also may connect isolated native plant populations and promote native plant species diversity [30]. By creating sharp edges, though, forest roads also increase the degree of fragmentation of plantations as well as the remaining natural forest remnants reducing native biodiversity [31]. To maintain native biodiversity, plant species either have to persist in phases of unsuitable conditions or mechanical disturbance in plantations or have to be able to re-colonize after local extirpation. Succession within plantations was often found to be positive for native species establishment and community restoration due to the promotion of natural habitat conditions with time [32–35]. Early phases, though, have been less studied even though they are considered to have the most severe effects on forest species that can determine further succession [36]. Young plantations as well as roadsides, however, may also offer environmental conditions and valuable habitats for native plant species adapted to disturbance and open canopies [9] that evolved with the long-term anthropogenic influence on the landscape [37]. Gomez et al. [38] for example detected many native and endemic plant species in a medium-aged pine plantation in Central Chile indicating a potential conservation value of plantation understories across the management cycle [39].

The conservation of native biodiversity is becoming an increasingly relevant issue for Chilean forest owners in order to obtain forest certification [40] or to promote ecosystem services [41], and requires the incorporation of alternative management strategies [36]. For establishing effective conservation measures and biodiversity oriented management strategies in intensively managed landscapes, urgent questions on the general effects of plantation landscapes, incorporating different age classes as well as the dense road network, on native and alien plant biodiversity, have to be answered as they determine the functioning of higher trophic levels. Here, we investigated plant species diversity and composition within a *Pinus radiata* landscape in south-central Chile by sampling understory vegetation in different plantation age classes, along roadsides and in natural forest remnants as a native reference. We specifically tested: (1) how plantations and the natural forest differ in regional plant species diversity considering different diversity measures; (2) how native and alien plant species richness and abundance change across the management cycle. We further investigated: (3) differences in community composition among age classes as well as the floristic distance to the natural forest and determined indicator species for plantations in comparison to the natural forest. Beta-diversity partitioning should further (4) reveal if differences in community composition among plantation age

classes and the natural forest are determined by richness differences indicating that plant assemblages in plantations are nested subsets of assemblages in the natural forests or by species turnover indicating that plantations are complementary to natural forests. This would suggest that plantations cannot be seen as a surrogate habitat for native diversity but that they may offer valuable habitats for non-forest specialists; (5) furthermore, forest roads are characterized by constant disturbance and different abiotic conditions compared to forest interiors. Thus, they can function as barrier or dispersal corridor for native and alien plants within the plantation landscape. By comparing community composition between forest and roadside habitats, we wanted to know how these artificial edges affect native and alien plant species in plantations and natural forests. We aim to provide relevant information for successful conservation measures for anthropogenic landscapes dominated by plantations.

2. Materials and Methods

2.1. Study Area

The study was conducted in a private forest in the north-western part of the administrative region Bío-Bío, south-central Chile, close to the town Quirihue in the Chilean coastal mountain range (Fundo “El Guanaco”; Figure 1). The study area comprised ca. 30 km². The climate is Mediterranean with an oceanic influence [9]. The mean annual precipitation is 625 mm; the mean annual temperature is 13.7 °C (years 2010 to 2016, weather station Coronel del Maule). The precipitation is seasonal and concentrated during the winter season [42]. The predominant soil type is a fertile, well-drained alfisol on igneous granite rock with a medium to fine texture and a high base saturation allowing a deep root development. The topography is hilly with slopes up to >50% that are susceptible to erosion [43].

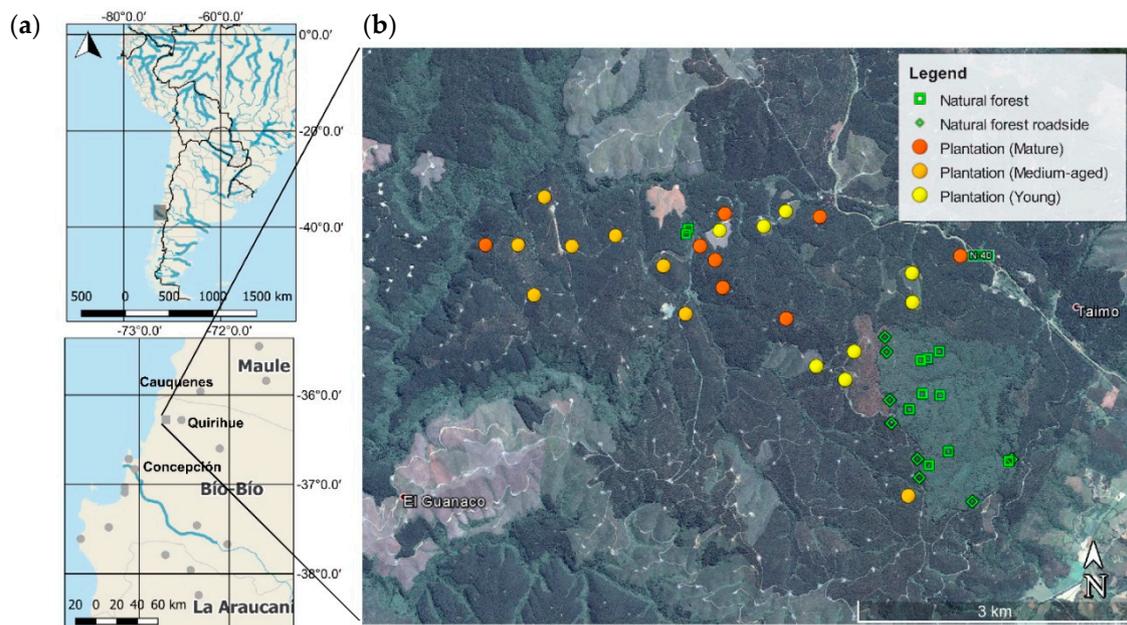


Figure 1. Location of the study area close to the town of Quirihue in the administrative region Bío-Bío, south-central Chile (a). The Google earth image © 2018 DigitalGlobe (from 1 January 2013) (b) shows the transect position across the study area in different plantation age classes (yellow to orange circles; $n = 8$ per age class) and in two natural forest remnants (green squares; $n = 11$). Roadside transects were located adjacent to the plantation interior transects with a minimum distance of 50 m ($n = 8$ per age class; not displayed), roadside transects adjacent to the natural forest were established within the large natural forest remnants (green diamonds, $n = 8$).

Pinus radiata plantations of different age classes dominate the landscape. In 2009 pine plantations comprised ca. 1.5 Million ha in Chile of which 44% were located in the Bío-Bío-region. The plantations

are managed in short rotation periods of 18 to 28 years. Site preparation before planting includes herbicide and fertilizer application and mechanical removal of weeds. Plantations for high quality wood production, as in the study area, are regularly pruned after initial establishment of ca. 1250 trees/ha starting at an age of five up to an age of ten. Two production thinnings are conducted in the first 15 years after establishment reducing the number of stems to 400 per ha. Afterwards, no more management operations occur until the final clearcut followed by site preparation and subsequent re-planting [44].

The potential natural vegetation in the study area is a deciduous forest of the endemic and as vulnerable listed *Nothofagus glauca* (= deciduous Maulino Forest; [45]) accompanied by evergreen tree species (e.g., *Aextoxicon punctatum*, *Gevuina avellana*), climbers (e.g., *Lapageria rosea*, *Lardizabala biternata*) and sclerophyllous elements (e.g., *Cryptocarya alba*, *Peumus boldus*, *Quillaja saponaria*). The natural vegetation is restricted to isolated remnants today [46], most of them with less than 100 ha in size [12]. Within the study area, though, beside small fragments, a natural forest remnant could be preserved, which represents the largest (ca. 200 ha) contiguous natural forest within the whole study area (personal communication, head of forest district) but is not officially protected (Figure 1).

2.2. Data Sampling

We recorded vascular plant species in plantation forests of different age classes (eight plantation stands per age class), in two natural forest remnants and along forest roadsides adjacent to the plantations and the natural forest (Figure 1). For *Pinus radiata* plantations, three different age classes were considered: (1) young plantations < 5 years of age (PY) before pruning starts with heights of *P. radiata* mainly < 5 m; (2) medium-aged plantations > 5 and <10 years of age (PM) affected by thinning and pruning; (3) old to mature plantations > 10 years of age (PO) where management had already ceased (Figure 2). For each plantation age class eight 2 by 50 m transects were established in forest interiors and along roadsides. Roadside and interior transects of plantations were established as pairs with a minimum distance of 50 m between both habitats (Table A1 in Appendix A). Additionally, as a native reference, nine transects were randomly placed within the large natural forest remnant and two additional transects within a small ca. 4 ha remnant (Nat). A closed canopy characterized both remnants. Eight road transects were established adjacent to the large natural forest remnant in order to assess the effect of forest roads within the natural forest (Figures 1 and 2). Mean distance between forest interiors and road transects was higher compared to plantations (Table A1).

For roadsides, the distance of each transect to the forest edge and the road width (both measured from the transect center) did not differ between forest types (Table A1). Roads were additionally assigned to different use categories based on a subjective evaluation of the frequency of vehicle traffic from 1 (main road) to 5 (no traffic during observation period). Traffic was significantly lower at natural forest roads compared to roads in medium-aged and mature plantations with young plantations having intermediate values (Table A1). Note, however, that this observation of traffic during the observation period only represents a short-term situation during the survey period and can markedly differ from long-term traffic intensity that depends on season and on the current focus of harvesting. Plantation age classes did not differ in their minimum distance to natural forest remnants scattered across the landscape (Table A1).

Each transect was divided into five 2 × 10 m subplots on which vegetation surveys were conducted. On each subplot, we recorded the cover of the tree (woody species > 5 m), shrub (woody species > 0.5 m and < 5 m) and herb layer (herbaceous species and woody species ≤ 0.5 m) directly in percent as well as the cover of all vascular plants within these layers using the scale of Braun-Blanquet [47]. Surveys were conducted in spring 2012 (November) and summer 2013 (February) to account for differing phenology. For species occurring in spring and summer, the higher cover value was used. For the current study, we concentrated on all vascular plants occurring in the shrub and herb layer. We distinguished between native and alien species according to Zuloaga et al. [48].

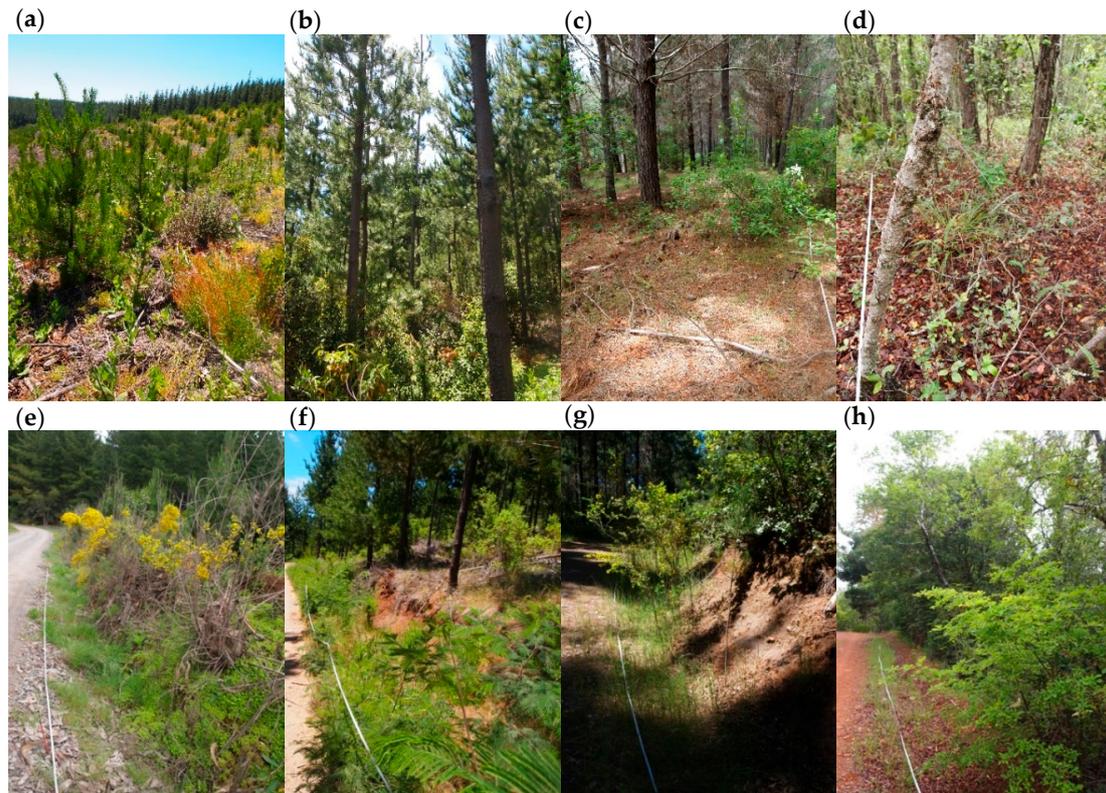


Figure 2. Example transects in forest interiors (a–d) and along roadsides (e–h). Transects were established in and adjacent to young plantations (a,e), in and adjacent to medium-aged plantations (b,f), in and adjacent to old to mature plantations (c,g) and in and adjacent to natural forests (d,h).

We measured light intensity as the indirect site factor obtained from five hemispheric photographs per transect (1 per subplot). Photographs were taken at 2 m height in February when trees were fully foliated using a Solariscope (Behling SOL300, Wedemark, Germany) which provides values for direct site factor, indirect site factor, total site factor, and openness by directly analyzing hemispherical photographs. We took soil samples from the upper 5 cm of the mineral soil pooling five samples (1 per subplot) per transect. Soil samples were analysed for pH and the carbon to nitrogen ratio. Litter layer thickness was also determined (five measurements per transect). All roads were unpaved but stabilized using gravel (except for one road along a young plantation). Roadside transects started with 0.5 m distance from the roadside edge. Plots were located at elevations between 370 and 550 m above sea level.

2.3. Data Analysis

To compare regional native plant species diversity of plantations and the natural forest, we used the species accumulation curves framework by Chao et al. [49] which provides estimators for inter- and extrapolation of different Hill numbers and uses a bootstrapping method for constructing confidence intervals (function iNEXT; R package iNEXT, version 2.0.12). Hill numbers are diversity indices that incorporate frequency of occurrence and species richness. Hill numbers with $q < 1$ disproportionately favor single occurring species, with $q = 1$ species are weighted proportionally to their frequency in the samples, while all orders >1 disproportionately favor common species. With the Hill numbers $q = 0$ (species richness), 1 (Shannon diversity) and 2 (Simpson diversity) we could consider infrequent and frequent species within one framework. We estimated diversity for forest interiors and roadsides separately incorporating all age classes as well as for both habitats combined based on species occurrences within transects. Even though the approach allows for comparing unequal sample sizes, an extrapolation is only robust up to the doubled minimum sample size [49]. In our study, natural forest transects represented the minimum with $n = 11$ interior transects and $n = 8$ roadside transects. Sample sizes for comparing

diversity between plantations and the natural forest were therefore set to not exceeding the doubled minimum sample size. Diversity is significantly different, if the 95% confidence intervals do not overlap.

To detect differences among age classes and between age classes and the natural forest for environmental variables, cover of vegetation layers as well as native and alien transect-based species richness and cover values, we used linear mixed effect models with forest type as fixed and subplot nested in transect as random effect (lme function; R package nlme, version 3.1-137).

Differences in species composition between plantation age classes and the natural forest as well as between forest interiors and roadsides were investigated using non-metric multidimensional scaling (NMDS; metaMDS function with Bray-Curtis distance and $k = 2$ dimensions; R package vegan, version 2.5-2) for the total species pool and for native species only based on plant species occurrences at transect level. Due to the rareness of alien species in the natural forest, they were not considered separately. We further calculated two dissimilarity indices between plantation age classes and the natural forest for native species: The Jaccard dissimilarity and the Morisita–Horn dissimilarity. Dissimilarity indices were calculated pairwise by contrasting each natural forest interior transect with interior transects of each plantation age class. We used the presence/absence-based Jaccard dissimilarity to reveal the potential effect of local colonization or extirpation of species on floristic dissimilarity between plantations and the natural forest in course of stand maturation within plantations. We conducted diversity partitioning according to Baselga [50] in order to quantify real species turnover (species replacement component) vs. dissimilarity caused by species richness differences between transects (nestedness component; function beta.pair of the betapart package). For also integrating effects of species abundances on dissimilarity, we additionally calculated the abundance-based Morisita–Horn Index [51] that is not influenced by differences in species richness between transects (function vegdist of the vegan package, version 2.5-2). The same two indices were calculated for alien and native species comparing forest interior and roadside transects within each plantation age class and within the natural forest (only native species).

We identified indicator species among native and alien plants for plantation interiors, plantation roadsides, the natural forest and natural forest roadsides using an indicator species analysis (ISA) according to Dufrene and Legendre [52]. A second ISA was conducted to find indicator species for each plantation age class (interior and roadside) without considering the natural forest. The ISA calculates an indicator value (IV) for each species per habitat type as the proportional abundance of a species within a group relative to the abundance in all groups multiplied by the proportional frequency of this species in each group. The calculated IV ranges between 0 (no indication) and 1 (perfect indication) with a perfect indicator being exclusively present in a certain habitat with a high abundance and frequency. The significance of each indicator value was tested by Monte Carlo simulation using 1000 iterations [53]. We used the function indval of the R package labdsv, version 1.8-0 for indicator species analyses. Indicator species were further characterized regarding life cycle (short-lived; perennial; woody), growth form (herbs, grasses, shrubs, trees, ferns, climbers; [48]) and association to natural forests based on literature records. Species listed as characteristic or frequent in natural forest communities (including sclerophyllous, evergreen and deciduous forests; [54]) were classified as forest species (cat 1), species characteristic both in forest and in open vegetation types (including the Chilean Matorral and herbaceous communities; [54]) were regarded as intermediate (cat 2); species only characteristic in open vegetation types were classified as light-demanding open site species (cat 3; see [55]).

For analyses, the software R3.5.0 was used. If not stated otherwise statistical significance is $p < 0.05$. Plant species names follow the nomenclature of Zuloaga et al. [48].

3. Results

3.1. Native Plant Diversity in Plantations Compared to the Natural Forest

In total, we sampled 176 plant species, 58 were alien and 118 native species with 46 being endemic to Chile (see Tables A2 and A3 for all recorded species in forest interior and roadside transects).

Three sampled species (*Citronella mucronata*, *Nothofagus glauca*, *Podocarpus salignus*) are mentioned in the list of threatened plants of central and south Chile and are classified as vulnerable (*C. mucronata* as potentially vulnerable) due to deforestation [45]. While *C. mucronata* and *P. salignus* were almost exclusively recorded in natural forest transects, *N. glauca* also occurred in young and mature plantations, in the latter even with a higher cover value compared to the natural forest (Table A2). All alien species occurred within the plantation landscape, with 36 alien species occurring exclusively in plantations or at adjacent roadsides. 22 alien species were also associated with natural forest roadsides. *Pinus radiata* was the only alien plant species to occur within natural forest interiors (on three transects). 70 native species occurred in both habitat types; 27 native species were exclusively recorded within or adjacent to plantations, 21 native species were only associated with the natural forest. This is reflected in no significant differences in native plant species richness ($q = 0$) between plantations and the natural forest when forest interiors, roadsides and all age classes were included (Figure 3a). Particularly forest interiors showed equal native diversity across Hill numbers (Figure 3b), whereas roadsides adjacent to the natural forest harbored significantly more native species than plantation roadsides (Figure 3c). This determined a significantly higher Shannon ($q = 1$) and Simpson diversity ($q = 2$) of the natural forest compared to plantations (Figure 3a). This significant difference can also be explained by a steeper decline of native diversity in plantations compared to the natural forest with increasing Hill numbers, indicating that infrequent species contribute to the diversity in plantations.

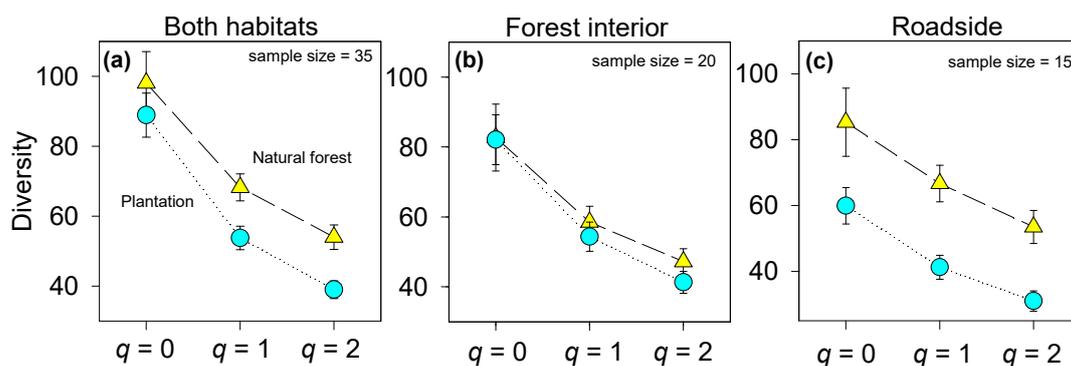


Figure 3. Regional native plant species diversity comparing plantations (cyan) and the natural forest (yellow). Diversity was quantified for Hill numbers $q = 0, 1$, and 2 , which increasingly weight occurrence frequency of species, using sample-size based rarefaction and extrapolation to factor out differences in sample size. Sample size was chosen below the doubled minimum sample size of transects sampled within the natural forest. Diversity was estimated for (a) forest interiors and roadsides combined (both habitats) as well as for (b) forest interiors and (c) roadsides separately. * indicate significant differences between forest types.

3.2. Differences in Environmental Conditions and Plant Species Richness among Age Classes

When distinguishing into age classes, young plantations with almost no tree layer differed from older plantations regarding light availability (higher) and litter layer thickness (lower; Table 1). Due to the fast growth of *Pinus radiata*, the tree layer cover was almost similar in medium-aged and mature plantations but significantly lower compared to the natural forest. Litter layer thickness was significantly highest in the natural forest. In general, plantation interiors were characterized by lower shrub layer abundance than the natural forest, whereas young to medium-aged plantations had a higher herb layer cover. Along roadsides, plantation age classes were very similar in vegetation structure but showed a light gradient from young to mature plantations. Roadsides adjacent to the natural forest showed similar light conditions than roadsides of mature plantations, but had a higher litter layer thickness because of a higher tree and shrub layer cover. The herb layer abundance was significantly lower compared to plantation roadsides (Table 1). Soil variables were not different among forest types.

Table 1. Vegetation structure and environmental characteristics of the different plantation age classes in comparison to the natural forest. Given are transect-based mean values (with standard deviation in parenthesis) of vegetation layer cover and measured environmental variables. Different letters indicate significant differences among age classes and the natural forest respectively based on linear mixed model results.

	Forest Interior				Roadside			
	PY	PM	PO	Nat	PY	PM	PO	Nat
Structure								
Cover tree layer (%)	2.9 (8.1) a	57.6 (15.1) b	61.3 (12.1) b	78.6 (7.6) c	- a	12.6 (12.6) ab	28.6 (19.9) b	48.6 (20.8) c
Cover shrub layer (%)	22.9 (18.4) a	19.3 (19.7) a	31.3 (11.2) a	59.1 (16.8) b	10.2 (16.2) a	21.2 (19.8) a	25.8 (14.8) a	46.8 (10.0) b
Cover herb layer (%)	32.3 (11.1) ab	39.5 (19.4) a	17.6 (12.8) b	21.1 (10.4) b	44.1 (13.9) a	47.3 (25.8) a	36.7 (14.4) a	14.7 (8.4) b
Environment								
Light (%)	84.6 (11.5) a	16.9 (7.3) b	12.7 (5.7) b	8.9 (3.9) b	82.3 (10.1) a	50.9 (9.4) b	29.9 (14.9) c	27.6 (18.6) c
Litter (cm)	0.2 (0.2) a	2.4 (1.0) b	3.6 (0.5) b	6.3 (2.5) d	0.3 (0.4) a	0.3 (0.3) a	1.1 (0.6) a	2.5 (1.4) b
pH	5.3 (0.2)	5.4 (0.1)	5.2 (0.2)	5.2 (0.3)	5.3 (0.1)	5.2 (0.2)	5.2 (0.1)	5.4 (0.3)
C/N	23.1 (9.5)	22.6 (3.2)	27.1 (8.5)	24.3 (2.8)	16.0 (5.4)	13.7 (3.8)	14.6 (4.2)	15.3 (4.6)

Despite a large difference in light availability, young plantation interiors had similar native species richness than natural forests, whereas medium-aged to mature plantations had less species than the natural reference (Figure 4). Native species cover, though, was lower in plantations than in the natural forest across age classes. In accordance with regional diversity, plantation roadsides were poorer in native species than natural forest roadsides across the management cycle.

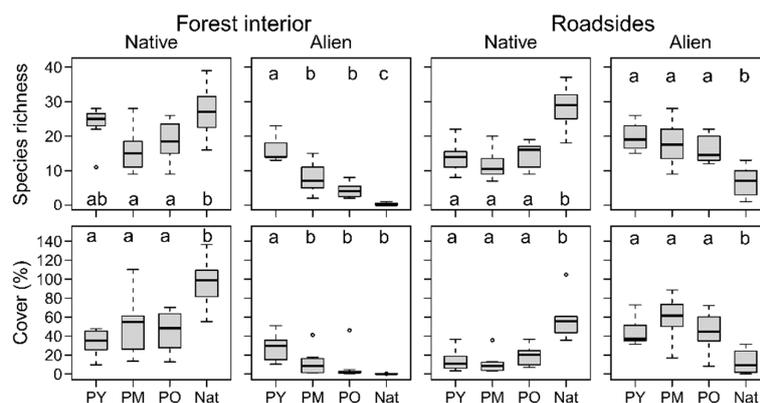


Figure 4. Mean transect-based species richness and cover values (shrub and herb layer values were summed up) of native and alien species in forest interiors and roadsides of the different plantation age classes and of the natural forest (PY = young plantation, PM = medium-aged plantation, PO = old to mature plantation, Nat = Natural forest). For plantation age classes and roadsides $n = 8$ transects per forest type were considered. For natural forest interiors, $n = 11$ transects were sampled. Different letters indicate significant differences among plantation age classes and the natural forest respectively based on linear mixed model results.

Alien species richness and abundance was highest in young plantations and decreased with stand maturation in forest interiors. Along roadsides though, alien species richness and abundance remained constant and was significantly higher compared to the natural forest across the management cycle (Figure 4).

3.3. Species Composition of Forest Types and Habitats

NMDS-ordinations show a clear difference in species composition between the natural forest and plantation age classes for forest interiors and roadsides considering all species (Figure 5a) as well as native species only (Figure 5b). There was no overlap between natural forest and plantation interiors, even though mature plantations showed the lowest distance to the natural forest. This is verified by the calculated dissimilarity indices that were significantly lower between the natural forest and mature plantations than between the natural forest and younger plantation age classes (Figure 6). Nevertheless, Jaccard dissimilarity was determined by species replacement underlining the almost complete difference in species composition. For natural forests, transects sampled in the small remnant did not differ from transects sampled in the large remnant.

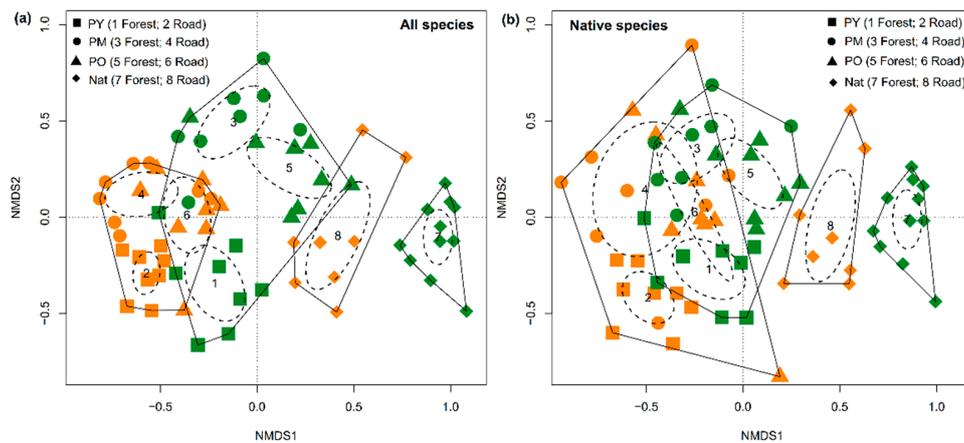


Figure 5. Two-dimensional NMDS ordination of species composition based on species cover values in forest interior (green symbols) and roadside transects (orange symbols). Ordination was conducted with all species recorded ((a); stress value = 0.181) and with native species only ((b); stress value = 0.201). Polygons (solid lines) frame the two forest types (plantation vs. natural forest (Nat)) separately for interiors and roadsides. The ellipses (dashed line) indicate the standard error around the centroids of the natural forest transects (Nat) and each plantation age class (PY = young plantation, PM = medium-aged plantation, PO = old to mature plantation) separately for interiors and roadsides.

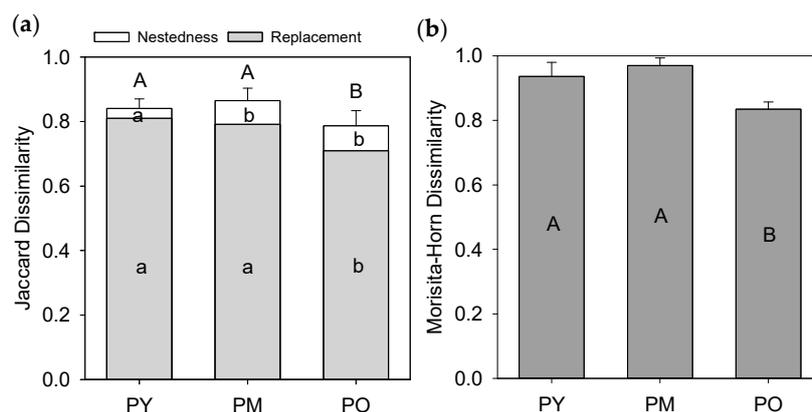


Figure 6. Mean pair-wise dissimilarity between natural forest transects and transects of young plantations (PY), medium-aged plantations (PM) and old to mature plantations (PO) in forest interiors. (a): Presence/absence-based Jaccard dissimilarity partitioned into the replacement and nestedness component according to Baselga [50]; (b): the abundance-based Morisita-Horn Index. Different lowercase letters indicate significant differences in replacement and nestedness component among forest types. Different uppercase letters indicate significant differences for the overall dissimilarity indices between forest types.

For roadsides, native species dissimilarity between plantations and the natural forest remained similar across age classes and was determined by species replacement (Figure A1). Plantation and natural forest roadsides showed no overlap in the ordination space (Figure 5a,b).

Alien species as part of the total species pool largely homogenized species composition at roadsides and reduced the overlap with plantation interiors compared to the ordination of native species only. In plantation interiors, alien species slightly increased the distance among age classes (Figure 5a,b). In general, plantation roadsides and interiors showed an overlap in native species composition in contrast to the natural forest.

3.4. Dissimilarity between Forest Interiors and Roadsides

Mean pairwise Jaccard dissimilarity of native species between road and forest interior transects was lowest for young plantations with a significant difference to mature plantations. In addition, the nestedness component was significantly higher and the replacement component significantly lower compared to mature plantations and the natural forest. Thus, turnover of native species between habitats increased with stand maturation within plantations due to increasing differences in environmental conditions between habitats. Abundance based Morisita–Horn dissimilarity showed no difference among forest types (Figure 7).

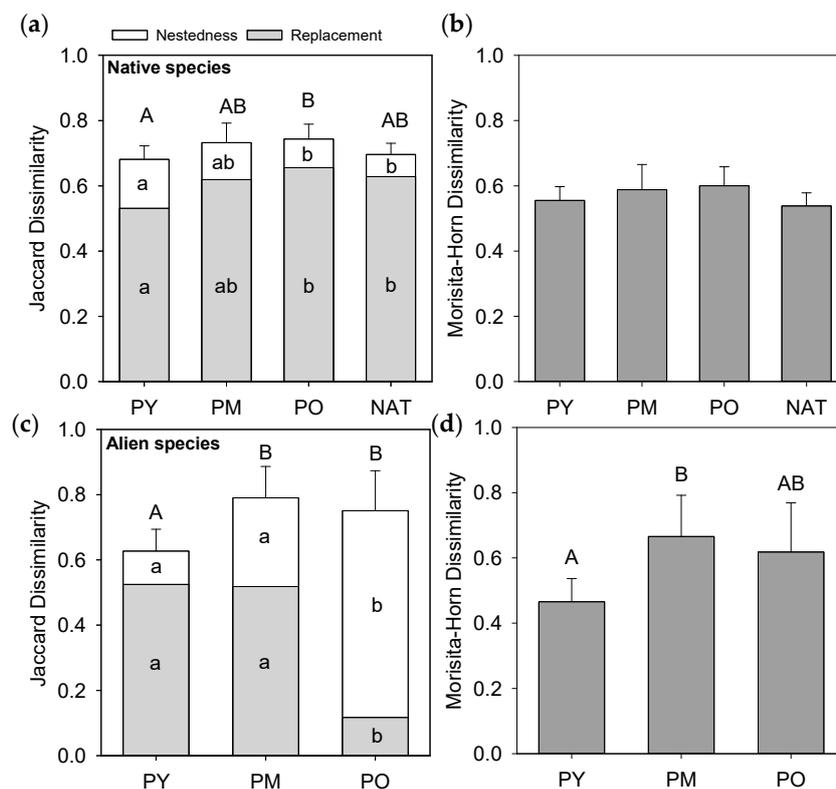


Figure 7. Mean pair-wise dissimilarity for native and alien species between roadside and interior transects within plantation age classes (PY = Young plantation, PM = medium-aged plantations, PO = old to mature plantations) and the natural forest (native species only). (a,c): Presence/absence-based Jaccard dissimilarity partitioned into the replacement and nestedness component according to Baselga [50] for native (a) and alien (c) species; (b,d): The abundance-based Morisita–Horn Index for native (b) and alien (d) species. Different lowercase letters indicate significant differences in replacement and nestedness component among forest types. Different uppercase letters indicate significant differences for the overall dissimilarity indices between forest types. As *Pinus radiata* was the only alien species in natural forest transects, alien species dissimilarity between forest and road transects was not considered for the natural forest.

Jaccard and Morisita–Horn dissimilarity of alien species was lowest comparing road and forest transects of young plantations and increased with stand maturation. A higher dissimilarity in older age classes was mainly driven by an increasing nestedness component. Thus, with decreasing alien species richness in course of stand maturation, alien species present in plantation interiors became a small subset of alien species occurring along roads (Figure 7).

3.5. Determination of Indicator Species for Forest Interiors and Roadsides

71 of the 176 species could be identified as indicators either for natural forests or plantations or for distinct plantation age classes (Table 2). 27 species were indicative for natural forest interiors, all being native (14 species) or endemic (13 species), perennial or woody species. Indicators included all growth forms and were mainly typical forest species. Among characteristic species of open vegetation types, *Gaultheria insana* had a high indicator value within natural forests, indicating former disturbances or management practices. Only four species were identified as indicators for plantation interiors (*Galium hypocarpium*, *Piptochaetium panicoides*, *Muehlenbeckia hastulata* and *Dioscorea bridgesii*), all of them being native. The low number of native indicators underlines the fact that native diversity in plantations depended on infrequent species. No alien species was a pure indicator of plantation interiors as alien diversity in interiors was largely a subset of alien diversity at roadsides. The native tree species *Nothofagus obliqua*, *Cryptocarya alba* and *Gevuina avellana* were indicative of natural forest roads accompanied by the endemic and perennial herbs *Solenomelus pedunculatus*, *Alstroemeria ligtu* and *Oxalis arenaria*. 16 plant species were indicators of plantation roadsides with 15 of them being alien. *Gamochaeta coarctata* was the only native indicator species for plantation roads in ISA 1. The majority of indicators of plantation roadsides were short-lived herbs or graminoids characteristic of open vegetation types.

Table 2. Indicator species of forest interiors and roadsides in plantations and the natural forest. We conducted two indicator species analysis (ISA).

	Cluster	ISA1		ISA2		Origin	LC	GF	Forest	
		Pl. vs. Nat		Pl Age Classes						
		IV	p	IV	p					
Natural forest interior										
<i>Ugni molinae</i>	Nat (I)→PO (I)	0.840	0.001	→	0.454	0.007	N	w	s	1
<i>Gaultheria insana</i>	Nat (I)	0.770	0.001				N	w	s	3
<i>Relchela panicoides</i>	Nat (I)→PO (I)	0.768	0.001	→	0.403	0.009	N	p	g	1
<i>Lapageria rosea</i>	Nat (I)	0.658	0.001				E	p	cl	1
<i>Lomatia hirsuta</i>	Nat (I)	0.614	0.001				N	w	t	1
<i>Uncinia phleoides</i>	Nat (I)	0.611	0.001				N	p	g	1
<i>Aextoxicon punctatum</i>	Nat (I)	0.546	0.001				N	w	t	1
<i>Lithraea caustica</i>	Nat (I)	0.535	0.001				E	w	t	2
<i>Bomarea salsilla</i>	Nat (I)	0.512	0.009				E	p	h	1
<i>Galium cotinoides</i>	Nat (I)	0.485	0.001				E	p	h	nd
<i>Azara integrifolia</i>	Nat (I)→PO (I)	0.478	0.006	→	0.679	0.001	E	w	t	1
<i>Ribes punctatum</i>	Nat (I)→PM (I)	0.463	0.009	→	0.313	0.021	N	w	s	1
<i>Sophora macrocarpa</i>	Nat (I)	0.434	0.003				E	w	t	1
<i>Citronella mucronata</i>	Nat (I)	0.408	0.002				E	w	t	1
<i>Colletia hystrix</i>	Nat (I)	0.399	0.005				N	w	s	1
<i>Nothofagus glauca</i>	Nat (I)→PO (I)	0.354	0.024	→	0.309	0.038	E	w	t	1
<i>Podanthus ovatifolius</i>	Nat (I)	0.337	0.044				E	w	s	3
<i>Vicia nigricans</i>	Nat (I)	0.305	0.013				N	p	h	1
<i>Olsynium scirpoideum</i>	Nat (I)	0.290	0.025				E	p	h	3
<i>Cynanchum pachyphyllum</i>	Nat (I)	0.288	0.016				N	p	h	1
<i>Blechnum hastatum</i>	Nat (I)	0.286	0.010				N	p	f	1
<i>Senna stipulacea</i>	Nat (I)	0.273	0.007				E	w	s	1
<i>Gilliesia montana</i>	Nat (I)	0.231	0.022				E	p	h	nd
<i>Elytropus chilensis</i>	Nat (I)	0.182	0.031				N	p	cl	1
<i>Synammia feuillei</i>	Nat (I)	0.182	0.037				N	p	f	1
<i>Sanicula crassicaulis</i>	Nat (I)	0.182	0.040				N	p	h	1
<i>Viola portalesia</i>	Nat (I)	0.182	0.035				E	w	s	1
<i>Nothofagus obliqua</i>	Nat (R)	0.730	0.001				N	w	t	1
<i>Cryptocarya alba</i>	Nat (R)	0.571	0.001				E	w	t	2

Table 2. Cont.

	Cluster	ISA1		ISA2		Origin	LC	GF	Forest	
		Pl. vs. Nat		Pl Age Classes						
		IV	p	IV	p					
Natural forest interior										
<i>Solenomelus pedunculatus</i>	Nat (R)	0.490	0.002			E	p	h	2	
<i>Gevuina avellana</i>	Nat (R)	0.418	0.008			N	w	t	1	
<i>Alstroemeria ligtu</i>	Nat (R)	0.340	0.016			E	p	h	2	
<i>Oxalis arenaria</i>	Nat (R)	0.258	0.028			E	p	h	nd	
<i>Tristerix corymbosus</i>	Nat (R)	0.206	0.036			N	w	s	2	
Plantation interior										
<i>Lactuca serriola</i>	PY (I)				0.779	0.001	A	s	h	3
<i>Geranium robertianum</i>	PY (I)				0.612	0.001	A	s	h	2
<i>Galium hypocarpium</i>	P (I)→PY (I)	0.472	0.035	→	0.559	0.001	N	p	h	1
<i>Pinus radiata</i>	PY (I)				0.538	0.008	A	w	t	nd
<i>Calandrinia compressa</i>	PY (I)				0.500	0.003	E	s	h	3
<i>Gnaphalium cheiranthifolium</i>	PY (I)				0.438	0.016	N	p	h	3
<i>Geranium core-core</i>	PY (I)				0.427	0.005	N	p	h	3
<i>Lardizabala biternata</i>	PY (I)				0.363	0.035	E	w	cl	1
<i>Galium aparine</i>	PY (I)				0.360	0.040	A	s	h	3
<i>Cirsium vulgare</i>	PY (I)				0.356	0.025	A	s	h	3
<i>Sonchus oleraceus</i>	PY (I)				0.285	0.047	A	s	h	3
<i>Piptochaetium panicoides</i>	P (I)→PM (I)	0.695	0.001	→	0.537	0.001	N	p	g	nd
<i>Muehlenbeckia hastulata</i>	P (I)→PM (I)	0.687	0.001	→	0.450	0.011	N	w	s	2
<i>Quillaja saponaria</i>	PO (I)				0.496	0.001	E	w	t	2
<i>Dioscorea bridgesii</i>	P (I)→PO (I)	0.439	0.007	→	0.438	0.003	E	p	cl	nd
Plantation Road										
<i>Hypochaeris radicata</i>	P (R)	0.737	0.001				A	p	h	3
<i>Sanguisorba minor</i>	P (R)	0.670	0.001				A	p	h	3
<i>Vulpia bromoides</i>	P (R)	0.546	0.005				A	s	g	3
<i>Aira caryophyllea</i>	P (R)	0.346	0.029				A	s	g	3
<i>Rosa rubiginosa</i>	P (R)	0.288	0.037				A	w	s	3
<i>Rumex acetosella</i>	P (R)→PY (I)	0.405	0.045	→	0.397	0.044	A	p	h	3
<i>Plantago lanceolata</i>	P (R)→PY (R)	0.931	0.001	→	0.560	0.002	A	p	h	2
<i>Linum usitatissimum</i>	P (R)→PY (R)	0.409	0.017	→	0.492	0.011	A	s	h	3
<i>Logfia gallica</i>	P (R)→PY (R)	0.291	0.027	→	0.474	0.005	A	s	h	3
<i>Erodium cicutarium</i>	PY (R)				0.459	0.002	A	s	h	3
<i>Oxalis micrantha</i>	PY (R)				0.409	0.048	N	s	h	3
<i>Gamochoeta coarctata</i>	P (R)→PY (R)	0.341	0.036	→	0.399	0.001	N	s	h	3
<i>Senecio sylvaticus</i>	PY (R)				0.352	0.030	A	s	h	3
<i>Acacia dealbata</i>	P (R)→PM (R)	0.282	0.029	→	0.572	0.001	A	w	s	3
<i>Bromus hordeaceus</i>	P (R)→PM (R)	0.326	0.007	→	0.489	0.001	A	s	g	3
<i>Holcus lanatus</i>	PM (R)				0.450	0.005	A	s	g	3
<i>Hypericum perforatum</i>	P (R)→PM (R)	0.704	0.001	→	0.427	0.003	A	p	h	3
<i>Margyricarpus pinnatus</i>	PM (R)				0.389	0.021	N	w	s	nd
<i>Agrostis capillaris</i>	P (R)→PM (R)	0.668	0.001	→	0.369	0.011	A	p	g	3
<i>Daucus carota</i>	PM (R)				0.326	0.037	A	s	h	3
<i>Trifolium arvense</i>	P (R)→PM (R)	0.222	0.036	→	0.279	0.029	A	s	h	3
<i>Genista monspessulana</i>	P (R)→PO (R)	0.744	0.001	→	0.464	0.022	A	w	s	2

ISA1 compared forest (P (I), Nat (I)) and road transects (P (R), Nat (R)) of plantations (including all age classes) and the natural forest (Pl vs. Nat). ISA2 contrasted forest (PY (I), PM (I), PO (I)) and road transects (PY (R), PM (R), PO (R)) of different plantation age classes only (Pl age classes). Arrows indicate species that were identified as indicators in both ISA. Given is also the origin of species (N = Native, E = Endemic, A = Alien), the life cycle (LC: s = short-lived, p = perennial, w = woody), the growth form (GF: cl = climber, f = fern, g = graminoid, h = herb, s = shrub, t = tree) and the forest association (Forest: 1 = typical in natural forest communities, 2 = in natural forests and open vegetation types, 3 = in open vegetation types, nd = not defined). Alien species are highlighted in bold.

When contrasting only the plantation age classes in a second indicator species analysis (ISA2), five species that have been identified as natural forest indicators in ISA1 showed high indicator values for medium-aged (*Ribes punctatum*) or mature plantations (*Ugni molinae*, *Relchela panicoides*, *Azara integrifolia* and *Nothofagus glauca*) in ISA2. Among tree species, *Quillaja saponaria* also occurred frequently in mature plantations. All mentioned species are typical forest species of the study area. Most indicators were, however, determined for the young age class with six alien and five native, predominantly herbaceous, species. Five alien indicator species of plantation roadsides showed no preference for an age class and occurred across the whole management cycle. Most indicators

though were associated with young or medium-aged plantation roads with *Gamochoaeta coarctata*, *Oxalis micrantha* (both young plantation roadsides) and *Margyricarpus pinnatus* (medium-aged plantation roadsides) representing the only native indicator species. The alien *Genista monspessulana* was the only indicator species of mature plantation roadsides. This shrub species is characteristic of disturbed areas [56] but has also naturalized in deciduous and sclerophyllous forest communities (category 2 of forest association; Table 2; [54]).

4. Discussion

4.1. Effects of the Plantation Management Cycle on Native Plant Diversity

Pine plantations maintained relatively high native species richness not significantly different from (mature) natural forests and associated roadsides when regional diversity was considered. This result was, however, only detected when infrequent species were taken into account (Hill number $q = 0$). With increasing Hill numbers, native plant species diversity was significantly higher in the natural forest compared to plantations. This result in combination with significantly lower cover values of native species in plantations compared to the natural forest indicates infrequent occurrences and small population sizes of native plant species in plantations that may be prone to local extinction [57]. Some native species found within plantations may represent relict species (e.g., *Lapageria rosea*, *Sophora macrocarpa*, *Persea lingue*, *Raukahu valdiviensis*; Table A1) of the former natural forest that was replaced by plantations. Some tree species thereby benefit from the ability for vegetative propagation [38]. These species and native species richness in general may describe a local extinction debt waiting to be paid [58–61] that will presumably lead to a diversity decline with increasing rotation periods as shown by Frank [62]. A first indication of this debt starting to be paid may be seen in the low mean native species richness of medium-aged plantations that was below numbers of the young and old age classes (even though not significant). With the plantation expansion having started before 1975 within the study area [12], mature plantations presumably are in their second rotation while medium-aged plantations are already in their third. Herbicide application after harvesting, as seen in newly established young plantations may have already decreased typical forest species in medium-aged plantations (e.g., *Cryptocarya alba*, *Nothofagus glauca*, *Lithraea caustica*, *Azara integrifolia*; Table A2). To counteract a further decrease in native diversity, the maintenance of natural forests as seed sources within a plantation landscape [63,64] as well as the retention and propagation of native tree species within plantations instead of a complete removal of residual understory vegetation in course of site preparation can be important options to maintain and increase native biodiversity [36,62,65].

Despite this, a variety of native species seems to be adapted to anthropogenic disturbances and may have colonized plantation interiors in course of the management cycle. The more favorable light conditions within, mainly young, plantations compared to the natural forest and a thinner litter layer have promoted species of open forest or herbaceous communities that were missing or less abundant in the natural forest transects (e.g., *Pasithea caerulea*, *Conanthera bifolia*, *Escallonia pulverulenta*, *Teucrium bicolor*; Table A2; [9,46,54]). Thereby, the different environmental conditions across the plantation cycle support different species as also indicated by different indicator species across the management cycle. This promotes regional diversity of plantations. Transect-based species richness was particularly high for young plantation interiors caused by remnants of the previous mature plantations accompanied by a high number of short-lived, ruderal native species (e.g., *Calandrinia compressa*, *Oxalis micrantha*, *Gamochoaeta coarctata*). *C. compressa* was even identified as an indicator species for young plantations, while the other mentioned species were more frequent at adjacent roadsides. With increasing plantation age, though, transect based native species richness as well as the number of indicator species decreased, showing that plantations are highly variable in species richness, cover and composition across the management cycle. With increasing rotations, the variability may further increase when late-successional species either decrease or disappear completely due to active removal or missing regeneration [62,66]. In addition, distinct compositional

differences to the natural forest remained with stand ageing and were determined by species replacement. Thus, plant communities in natural forests cannot be replaced by those in the understories of forest plantations [16]. They are highly complementary with plantations mainly offering habitat for ruderal species as well as early successional species [62,65]. Certain natural forest species though (e.g., *Ugni molinae*, *Nothofagus glauca*, *Quillaja saponaria*) were maintained in mature plantations. The frequent occurrences of these species can represent important starting conditions for retaining native elements across further rotations.

4.2. The Effect of Forest Roads on Native Plant Diversity in Plantations and Natural Forests

Forest roads function differently for native species in plantations and natural forests. Despite floristic dissimilarities between plantation interiors and roadsides within age classes, NMDS ordination showed a strong overlap between interiors and roadsides across age classes (Figure 5b) indicating a similar species composition between habitats and a dominance of generalist species. *Aristotelia chilensis* can be mentioned as an example here as this tree species occurred frequently in interior and roadside transects of plantations (Tables A2 and A3; [62,67]). Natural forest interiors and roadsides, though, did not overlap in species composition indicating a higher specialization of species within natural forests as well as more distinct differences in environmental conditions among habitat types. Natural forest interiors promoted, rather, shade-tolerant species, whereas adjacent roadsides offered sites for a successful germination and establishment of both shade-tolerant as well as more light-demanding species [68]. This accounts for characteristic tree and shrub species of the natural forest (e.g., *Cryptocarya alba*, *Gevuina avellana*, *Nothofagus obliqua*; [69,70]) as well as for several geophytic species including orchids (*Gavilea venosa*, *Chloraea lamellata*, Table A3). Roadsides thereby adopt the function of canopy gaps [71,72] and promote regional diversity. This supports other studies which even detected a positive effect of roads on protected species [73] and underlines the potential role of forest roads to diminish dispersal limitations for native plant species [30]. The high native species diversity of natural forest roads and its impact on regional diversity (see Figure 3) also indicates that a complete assessment of the effect of plantations replacing the natural forest on native biodiversity requires the incorporation of different successional stages in both forest types.

4.3. Alien Species within the Plantation Landscape

Alien species were mainly associated with plantations. Stand ageing, though, clearly reduced alien species richness and abundance in plantation interiors, confirming results by Frank [62] from the IX. region of Chile. This fact may be integrated in concepts that aim to suppress alien species invasion for example by increasing rotation length or by maintaining a continuous canopy in places. It also reflects the dominance of shade-intolerant, often short-lived, species within the Chilean alien flora that benefit from disturbances early after harvesting with open soil conditions and high light availability (see Table 2; [56]). This accounts for a variety of alien species that were determined as indicator species for young plantations or associated roadsides (e.g., *Vulpia bromoides*, *Galium aparine*, *Sonchus oleraceus*). With increasing plantation age, light availability decreased and litter layer thickness increased providing less suitable colonization sites within forests and leading to local extirpation of alien species. At roadsides, stand ageing had no effect on alien species richness as disturbance remained high due to constant wood transportation traffic. Roadsides, therefore, can act as propagule sources for alien plants across stand ages and enable a fast recolonization of young plantation interiors after the final harvest besides a potential recolonization from the soil seed bank [62]. Roads also ensure a constant propagule supply of alien species that are partially shade-tolerant and potentially able to invade the natural forest particularly after disturbances [65]. Relevant species are for example *Agrostis capillaris*, *Rubus ulmifolius* or *Genista monspessulana* that frequently occurred in mature plantations and at forest roads across the management cycle. *R. ulmifolius* and *G. monspessulana* are two prominent invasive alien species in central Chile, which show a high plasticity in their invaded range allowing an adaptation to novel environments such as light limited understories [63,74]. *G. monspessulana* was the only indicator

species at mature plantation roadsides and also occurred at roadsides of the natural forest underlining the invasion potential in the long-term, as seen within natural forest fragments of different sizes in central Chile [75]. During the present observation, though, alien species were still almost absent from the large natural forest as well as from the smaller fragment.

Alien species richness was also low along natural forest roadsides, presumably due to the lower traffic here compared to plantations. Furthermore, the concurrent high diversity and abundance of native species hints towards an interaction between native and alien species as stated by the biotic resistance hypothesis, which assumes that high local native richness provides low niche vacancy for aliens [76]. In the study area, high native and low alien species numbers along natural forest roads also reflect available seed sources in the vicinity that are decisive for native species diversity along roads in south-central Chile [63]. The continuous construction of new logging roads (personal observation) within the plantation landscape though, will further increase the pressure by alien species as it facilitates their spread across the landscape. It will also lead to an overall homogenization of community composition at roadsides as demonstrated by ordination results [77] and contributes to an overall landscape homogenization caused by the large-scale plantation management [62].

5. Conclusions

Our results show that industrial pine plantations composed of different age classes and forest roads partially maintained high native species richness at the landscape scale but supported a completely different community composition than natural forests. Even though certain natural forest species characterized mature plantations, infrequent occurrences of late successional species may represent an extinction debt. With the further loss of natural forests, some native species may therefore go locally extinct with increasing rotations, particularly regarding the practice of understory removal after final harvest.

Plantations, however, promoted generalist native species as well as alien species. Although there was a clear reduction in alien species diversity with plantation age, partially shade-tolerant alien species were maintained within old plantations and can further spread into forests starting from roadsides that maintained high alien species richness throughout the management cycle.

If forest owners aim to integrate the conservation of native species diversity into plantation management, our results give evidence for the following conservation measures: (1) Conservation and propagation of natural forest remnants: The last remaining natural forest remnants have to be protected from exploitation and conversion as they largely complement regional native species diversity. Our study shows that larger forest remnants still exist beyond protected areas within private forests, and that even these unprotected forests are still resistant to alien species invasion [27]. But even small fragments were not significantly different in species composition and are therefore highly valuable within the landscape. Within mature plantations, frequently occurring native tree species (e.g., *Azara integrifolia*, *Quillaja saponaria*, *Nothofagus glauca*) should be retained and promoted as natural forest islands within plantations. This would increase connectivity of native patches, stand structure as well as stand heterogeneity with potential positive effects for native biodiversity [36,65]. In clearcuts and young plantations, residual native tree species from previous mature stages should not be actively removed; (2) Alternative forest management options for alien species reduction in the vicinity of natural forests: As alien species decreased with plantation age, a continuous cover of pines in densities of around 400 trees/ha [78] as a buffer zone around natural forests might reduce the propagule pressure of alien species. This, however, would require management options that allow for a continuous cover [79]. Such alternative management options can further facilitate a regeneration of natural forest understories [78]. In Mediterranean Europe *Pinus radiata* plantations have a rotation period of approximately 40 years and were found to converge in understory community composition with time when compared to natural forest understories [35]. A tendency towards a decreasing floristic dissimilarity to the natural forest from young to mature plantations was also verified by this study, there was, however, no overlap in community composition; (3) Monitoring and active removal of

potential forest invaders along roads: Particularly in the vicinity to natural forest remnants, potential forest invaders that are able to survive in light-limited forest interiors (e.g., *Genista monspessulana*, *Rubus ulmifolius*) should be monitored and removed. This removal may further increase the competitive ability of native tree species.

With these measures promoting heterogeneity beyond plantation age classes, native species conservation in landscapes dominated by forestry plantations is possible but requires a holistic approach of the full mosaic of land uses.

We presented results for a plantation landscape containing large and small natural forests as seed source for native species. With natural forest remnants of different sizes and qualities scattered across Mediterranean Chile [75,80], we consider our results valid across many anthropogenic plantation landscapes. Nonetheless, in order to understand the overall effect of large-scale industrial plantations on native biodiversity more studies in differently composed landscapes are necessary including a comparison with the whole range of successional stages not only in plantations but also within natural forests.

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Appendix A

Table A1. Landscape variables of roadside and forest interior transects. For roadsides the distance to the forest edge and the road width were determined (measured from the transect center). Roads were assigned to different use categories based on a subjective evaluation of the frequency of vehicle traffic from 1 (main road) to 5 (no traffic during observation period). For forest interior transects, the distance to the nearest road was determined (minimum distance was 50 m). For both habitat types the minimum distance to natural forest remnants based on aerial photographs was determined. Given are mean values per transects with standard deviation in parenthesis. Different lower case letters indicate significant differences among forest types.

	Roadsides				Forest Interiors			
	PY	PM	PO	Nat	PY	PM	PO	Nat
Distance to forest edge (m)	1.1 (1.5)	3.9 (2.0)	3.1 (2.1)	1.0 (0.5)	-	-	-	-
Road width (m)	5.3 (1.0)	4.9 (0.6)	5.5 (0.6)	4.9 (0.7)	-	-	-	-
Mean road use category (1–5)	2.8 (1.5) ab	2.1 (0.6) ab	1.9 (0.8) a	3.3 (0.7) b	-	-	-	-
Distance to road (m)	-	-	-	-	55.3 (8.6) a	67.6 (11.9) a	79.8 (18.8) a	290.1 (142.9) b
Distance to natural forest (m)	425.1 (237.1)	509.9 (350.4)	558.8 (405.4)	-	418.8 (261.6)	534.0 (351.6)	566.5 (387.9)	-

Table A2. Species recorded in forest interior transects of the natural forest (Nat), old to mature pine plantation (PO), medium-aged pine plantations (PM) and young pine plantations (PY). Given are occurrence frequency values (F) representing the percentage occurrence in transects and the mean cover values (mCv) in % (cover values of + are < 0.05%). Alien and native origin according to Zuloaga et al. [48]. * marks endemic species. Species are ordered based on their decreasing frequency from the natural forest to young plantations.

	Nat		PO		PM		PY	
	F (%)	mCv (%)	F (%)	mCv (%)	F (%)	mCv (%)	F (%)	mCv (%)
	n = 11		n = 8		n = 8		n = 8	
Alien species								
<i>Pinus radiata</i>	27	0.1	100	0.5	38	0.5	100	13.9
<i>Rubus ulmifolius</i>			88	4.6	88	5.0	75	0.2
<i>Genista monspessulana</i>			63	1.0	38	2.5	38	0.1
<i>Agrostis capillaris</i>			38	0.7	75	2.9	88	2.2
<i>Rumex acetosella</i>			38	0.2	38	0.1	88	1.3
<i>Hypochaeris radicata</i>			25	+	50	0.1	50	0.2
<i>Plantago lanceolata</i>			25	+	13	+	38	0.4
<i>Sanguisorba minor</i>			25	+	13	+	38	0.5
<i>Hypericum perforatum</i>			13	+	50	0.3	13	0.1
<i>Rosa rubiginosa</i>			13	0.1			13	+
<i>Lactuca serriola</i>					38	+	100	2.4
<i>Euphorbia peplus</i>					38	0.1	50	0.1
<i>Verbascum virgatum</i>					38	0.1	38	0.1
<i>Briza minor</i>					25	+	88	0.9
<i>Anagallis arvensis</i>					25	+	75	0.7
<i>Cirsium vulgare</i>					25	+	75	0.3
<i>Senecio sylvaticus</i>					25	+	63	0.3
<i>Sonchus oleraceus</i>					25	+	63	0.2
<i>Daucus carota</i>					25	+		
<i>Trifolium dubium</i>					25	0.1		
<i>Aira caryophylla</i>					13	+	50	0.4
<i>Arrhenaterum elatius</i> ssp. <i>bulbosus</i>					13	+		
<i>Bromus hordeaceus</i>					13	+		
<i>Holcus lanatus</i>					13	+		
<i>Juncus</i> cf. <i>effusus</i>					13	0.1		
<i>Logfia gallica</i>					13	+		
<i>Poa pratensis</i>					13	+		
<i>Trifolium arvense</i>					13	+		
<i>Geranium robertianum</i>							63	0.7
<i>Vulpia bromoides</i>							63	0.7
<i>Carduus pycnocephalus</i>							38	0.1
<i>Galium aparine</i>							38	0.6
<i>Anthoxanthum odoratum</i>							25	0.5
<i>Avena fatua</i>							25	0.1
<i>Erodium cicutarium</i>							25	0.1
<i>Mentha pulegium</i>							25	+
<i>Silybum marianum</i>							25	0.2
<i>Taraxacum officinale</i>							25	0.1
<i>Cerastium fontanum</i> ssp. <i>vulgare</i>							13	+
<i>Cynosurus echinatus</i>							13	+
<i>Euphorbia lathyris</i>							13	+
<i>Gastridium phleoides</i>							13	+
<i>Linum usitatissimum</i>							13	+
<i>Medicago lupulina</i>							13	0.1
<i>Medicago polymorpha</i>							13	+
<i>Sonchus asper</i>							13	+
<i>Vicia hirsuta</i>							13	0.1
Total species number	1		10		27		38	
Native species								
<i>Cryptocarya alba</i> *	100	3.9	50	2.2	38	1.5	63	4.1
<i>Ugni molinae</i>	100	23.4	50	3.0			13	+
<i>Gaultheria insana</i>	100	25.1	25	2.9				
<i>Azara integrifolia</i> *	91	3.0	75	1.4			63	0.1
<i>Lithraea caustica</i> *	91	5.6	50	0.9	13	0.4	50	0.6
<i>Relchela panicoides</i>	91	1.6	50	0.4	13	+	13	+
<i>Nothofagus glauca</i> *	91	1.9	38	4.7			13	0.9

Table A2. Cont.

	Nat		PO		PM		PY	
	F (%)	mCv (%)	F (%)	mCv (%)	F (%)	mCv (%)	F (%)	mCv (%)
	n = 11		n = 8		n = 8		n = 8	
Native species								
<i>Lomatia hirsuta</i>	91	1.9	25	0.1	13	0.1		
<i>Bomarea salsilla</i> *	82	1.6	50	0.2	13	+	50	0.1
<i>Lapageria rosea</i> *	82	4.1	13	0.1	13	0.5	38	0.1
<i>Podanthus ovatifolius</i> *	82	1.9	13	+			50	0.5
<i>Piptochaetium panicoides</i>	73	0.6	88	7.0	100	26.5	100	5.8
<i>Uncinia phleoides</i>	73	1.2	13	+	25	0.4		
<i>Dioscorea bridgesii</i> *	64	0.1	100	0.7	88	0.2	63	0.3
<i>Peumus boldus</i> *	64	3.8	63	1.0	75	1.6	63	0.9
<i>Ribes punctatum</i>	64	0.6	25	+	63	0.1	25	+
<i>Galium cotinoides</i> *	64	0.3			13	+		
<i>Aristolelia chilensis</i>	55	0.4	88	11.7	100	11.0	88	1.4
<i>Gevuina avellana</i>	55	5.0	13	0.1	13	+	25	0.1
<i>Vicia nigricans</i>	55	0.3			13	0.4	25	+
<i>Persea lingue</i>	55	0.3			13	1.3	13	0.4
<i>Aextoxicon punctatum</i>	55	1.1						
<i>Escallonia pulverulenta</i> *	45	0.5	63	3.8	88	0.7	63	0.7
<i>Colletia hystrix</i>	45	0.4	25	+	13	+	13	+
<i>Sophora macrocarpa</i> *	45	0.5	13	+				
<i>Citronella mucronata</i> *	45	0.4						
<i>Teucrium bicolor</i> *	36	+	50	0.1	50	0.1	63	0.9
<i>Quillaja saponaria</i> *	36	0.6	50	1.7				
<i>Cynanchum pachyphyllum</i>	36	0.1	13	+				
<i>Blechnum hastatum</i>	36	0.3			13	0.1		
<i>Gilliesia montana</i> *	36	0.1						
<i>Olsynium scirpoideum</i> *	36	0.1						
<i>Solenomelus pedunculatus</i> *	27	0.2	38	0.2	13	+	25	+
<i>Tristagma bivalve</i> *	27	+	38	0.1	13	+	25	+
<i>Luma apiculata</i>	27	0.2	25	0.1	25	0.2	50	0.1
<i>Gochmatia foliolosa</i> *	27	0.1	25	0.9	13	0.1	13	+
<i>Oxalis arenaria</i> *	27	+	13	+				
<i>Alstroemeria ligtu</i> *	27	+					13	0.2
<i>Gavilea venosa</i> *	27	+						
<i>Podocarpus salignus</i> *	27	0.1						
<i>Senna stipulacea</i> *	27	0.2						
<i>Pasithea coerulea</i>	18	+	63	0.2	13	0.5	50	0.1
<i>Lardizabala biternata</i> *	18	+	13	+			50	1.0
<i>Carex setifolia</i>	18	+	13	+				
<i>Lomatia dentata</i>	18	0.3			13	0.1	13	0.1
<i>Proustia pyrifolia</i> *	18	0.1			13	+		
<i>Baccharis racemosa</i>	18	+			13	+		
<i>Dioscorea humifusa</i> *	18	1.1						
<i>Viola portalesia</i> *	18	0.1						
<i>Adiantum chilense</i>	18	+						
<i>Elytropus chilensis</i>	18	0.2						
<i>Synammia feuillei</i>	18	+						
<i>Sanicula crassicaulis</i>	18	+						
<i>Galium hypocarpium</i>	9	+	88	0.2	88	0.2	100	1.4
<i>Baccharis rhomboidalis</i>	9	+	38	0.1	13	1.1	38	0.1
<i>Nassella laevissima</i>	9	+	13	+	38	0.1	63	1.3
<i>Margyricarpus pinnatus</i>	9	+			13	+	13	+
<i>Myoschilos oblongum</i>	9	+			13	0.1		
<i>Schinus polygama</i>	9	0.1			13	0.4		
<i>Chiropetulum tricuspidatum</i>	9	0.1					25	+
<i>Dioscorea auriculata</i> *	9	+					13	+
<i>Maytenus boaria</i>	9	+					13	+
<i>Chusquea quila</i> *	9	0.3						
<i>Greigia sphacelata</i> *	9	+						
<i>Laurelia sempervirens</i> *	9	0.3						
<i>Libertia sessiliflora</i> *	9	+						
<i>Boquila trifoliolata</i>	9	0.2						
<i>Calceolaria corymbosa</i>	9	0.1						
<i>Cardamine vulgaris</i>	9	+						
<i>Oxalis perdicaria</i>	9	+						
<i>Rhaphithamnus spinosus</i>	9	+						

Table A2. Cont.

	Nat		PO		PM		PY	
	F (%)	mCv (%)						
	n = 11		n = 8		n = 8		n = 8	
Native species								
<i>Senecio cymosus</i>	9	0.1						
<i>Tristerix corymbosus</i>	9	+						
<i>Muehlenbeckia hastulata</i>			75	0.3	100	2.1	88	1.2
<i>Danthonia chilensis</i> var. <i>aureofulva</i>			50	0.1	25	0.2	63	0.8
<i>Stachys gilliesii</i>			50	0.1			63	0.1
<i>Gamochaeta coarctata</i>			38	0.2	38	0.1	100	0.3
<i>Lathyrus magellanicus</i>			38	0.1	25	+	25	0.1
<i>Conanthera bifolia</i> *			38	0.1			25	0.1
<i>Piptochaetium montevidense</i>			25	+			13	+
<i>Alstroemeria revoluta</i> *			25	+				
<i>Acaena argentea</i>			13	+	50	0.5	75	1.5
<i>Lepechinia chamaedryoides</i> *			13	+	38	+		
<i>Cissus striata</i>			13	+	38	0.1		
<i>Chascolytrum subaristatum</i>			13	+	25	0.1	13	0.1
<i>Oxalis micrantha</i>			13	+	13	+	88	2.7
<i>Geranium core-core</i>			13	+	13	+	75	0.1
<i>Glandularia laciniata</i>			13	+	13	+	13	+
<i>Adesmia spec.</i>			13	0.4			13	0.1
<i>Chloraea lamellata</i> *			13	+				
<i>Raukava valdiviensis</i> *			13	+				
<i>Gnaphalium cheiranthifolium</i>					25	0.1	75	0.6
<i>Hypericum caespitosum</i> *					25	+	25	3.6
<i>Calceolaria dentata</i>					13	+	13	0.5
<i>Eryngium paniculatum</i>					13	0.1	13	+
<i>Lobelia tupa</i> *					13	0.1		
<i>Berberis bidentata</i> cf.					13	+		
<i>Bromus berterioanus</i>					13	+		
<i>Carex phalaroides</i>					13	+		
<i>Mutisia spinosa</i>					13	0.1		
<i>Sisyrinchium graminifolium</i>					13	+		
<i>Calandrinia compressa</i> *							50	0.1
<i>Oenothera stricta</i>							25	+
<i>Solanum crispum</i>							25	+
<i>Calceolaria purpurea</i> *							13	+
<i>Adenocaulon chilense</i>							13	+
<i>Cicendia quadrangularis</i>							13	+
<i>Juncus bufonius</i>							13	+
<i>Nothofagus obliqua</i>							13	0.4
<i>Soliva sessilis</i>							13	0.1
<i>Stellaria debilis</i>							13	+
Total species numbers	73		53		55		62	

Table A3. Species recorded at roadside transects of the natural forest (Nat), old to mature pine plantations (PO), medium-aged pine plantations (PM) and young pine plantations (PY). Given are occurrence frequency values (F) representing the percentage occurrence in transects and the mean cover values (mCv) in % (cover values of + are < 0.05%). Alien and native origin according to Zuloaga et al. [48]. * marks endemic species. Species are ordered based on their decreasing frequency from the natural forest to young plantations.

	Nat		PO		PM		PY	
	F (%)	mCv (%)						
	n = 8		n = 8		n = 8		n = 8	
Alien species								
<i>Pinus radiata</i>	100	3.5	100	0.6	88	2.4	88	8.0
<i>Agrostis capillaris</i>	88	7.0	100	20.9	100	24.8	88	15.8
<i>Genista monspessulana</i>	50	0.3	100	10.6	100	7.4	75	1.3
<i>Rumex acetosella</i>	38	+	100	0.3	88	0.7	88	0.3
<i>Hypochaeris radicata</i>	38	+	88	0.7	88	1.0	88	0.6
<i>Lactuca serriola</i>	38	0.1	63	0.1	38	0.1	100	0.5

Table A3. Cont.

	Nat		PO		PM		PY	
	F (%)	mCv (%)						
	n = 8		n = 8		n = 8		n = 8	
Alien species								
<i>Briza minor</i>	38	0.1	50	0.1	75	0.2	88	2.9
<i>Avena fatua</i>	38	0.1	38	0.1	38	0.1	50	0.2
<i>Plantago lanceolata</i>	25	+	100	0.6	100	2.5	100	4.6
<i>Senecio sylvaticus</i>	25	+	63	0.1	25	+	75	0.4
<i>Anagallis arvensis</i>	25	+	25	0.1	25	+	50	0.7
<i>Acacia dealbata</i>	25	0.6	13	2.1	75	8.1	13	0.4
<i>Cirsium vulgare</i>	25	+	13	+			63	0.3
<i>Taraxacum officinale</i>	25	+					13	+
<i>Sanguisorba minor</i>	13	+	100	1.2	75	1.4	63	0.8
<i>Hypericum perforatum</i>	13	+	75	0.2	100	0.8	100	0.4
<i>Lotus pedunculatus</i>	13	0.1	38	0.1	38	+	13	+
<i>Eucalyptus globulus</i>	13	0.1	25	+			25	+
<i>Briza maxima</i>	13	0.1	13	0.2	25	+	25	0.1
<i>Sherardia arvensis</i>	13	+	13	+	13	+	13	+
<i>Crepis capillaris</i>	13	+					13	+
<i>Galega officinalis</i>	13	0.4					13	+
<i>Rubus ulmifolius</i>			75	5.9	50	4.2	50	0.7
<i>Rosa rubiginosa</i>			63	0.2	25	0.5	13	+
<i>Vulpia bromoides</i>			50	0.1	75	1.9	63	2.9
<i>Aira caryophylla</i>			38	0.2	50	0.3	75	0.2
<i>Mentha pulegium</i>			38	+	25	0.1		
<i>Bromus hordeaceus</i>			25	0.1	63	0.9	13	0.1
<i>Linum usitatissimum</i>			25	+	38	0.1	63	0.5
<i>Sonchus oleraceus</i>			25	+	13	+	50	0.1
<i>Logfia gallica</i>			25	+	13	+	50	0.6
<i>Cynosurus echinatus</i>			25	0.1	13	+	25	+
<i>Trifolium arvense</i>			13	0.1	50	0.2	13	+
<i>Holcus lanatus</i>			13	+	50	0.3		
<i>Verbascum virgatum</i>			13	+	38	0.1	50	0.1
<i>Euphorbia peplus</i>			13	0.1	25	0.1	25	+
<i>Geranium robertianum</i>			13	+	13	+		
<i>Vicia hirsuta</i>			13	+	13	+		
<i>Anthoxanthum odoratum</i>			13	+			50	0.5
<i>Carduus pycnocephalus</i>			13	+			38	+
<i>Medicago lupulina</i>			13	+				
<i>Daucus carota</i>					38	0.3		
<i>Chamaemelum mixtum</i>					25	+	13	+
<i>Tolpis barbata</i>					25	+		
<i>Arrhenatherum elatius</i> ssp. <i>bulbosus</i>					25	0.2		
<i>Dactylis glomerata</i>					25	0.8		
<i>Gastridium phleoides</i>					13	+	13	+
<i>Erodium cicutarium</i>							63	0.3
<i>Silybum marianum</i>							25	0.4
<i>Cerastium fontanum</i> ssp. <i>vulgare</i>							13	+
<i>Galium aparine</i>							13	+
<i>Sonchus asper</i>							13	+
<i>Barbarea verna</i> cf.							13	0.1
Total species numbers	22		38		39		44	
Native species								
<i>Piptochaetium panicoides</i>	100	1.0	75	3.4	100	2.6	100	4.2
<i>Ugni molinae</i>	100	3.4	38	0.3				
<i>Bomarea salsilla</i> *	100	0.8	25	+	13	+	25	+
<i>Cryptocarya alba</i> *	100	8.6	13	+	13	+	25	0.1
<i>Aristotelia chilensis</i>	88	5.7	100	7.7	75	4.0	63	0.3
<i>Gaultheria insana</i>	88	6.4	25	0.5	25	+		
<i>Azara integrifolia</i> *	88	2.2	13	+			13	+
<i>Gevuina avellana</i>	88	4.6						
<i>Galium hypocarpium</i>	75	0.3	88	0.3	38	0.1	100	0.3
<i>Solenomelus pedunculatus</i> *	75	0.6	50	0.1	13	+	13	+
<i>Peumus boldus</i> *	75	4.1	38	1.0			13	+
<i>Ribes punctatum</i>	75	0.2			25	0.1		
<i>Lapageria rosea</i> *	75	0.8			13	0.1		

Table A3. Cont.

	Nat		PO		PM		PY	
	F (%)	mCv (%)						
	n = 8		n = 8		n = 8		n = 8	
Native species								
<i>Nothofagus obliqua</i>	75	4.7						
<i>Gamochaeta coarctata</i>	63	0.2	75	0.2	63	0.1	100	0.6
<i>Podanthus ovatifolius</i> *	63	2.4					25	0.4
<i>Danthonia chilensis</i> var. <i>aureofulva</i>	50	+	50	0.1	50	0.2	88	0.5
<i>Teucrium bicolor</i> *	50	0.1	50	0.2	25	+	63	0.1
<i>Baccharis rhomboidalis</i>	50	0.3	13	+	13	0.1	25	0.1
<i>Alstroemeria ligtu</i> *	50	0.3	13	+			25	0.1
<i>Lithraea caustica</i> *	50	3.3	13	0.1			13	+
<i>Lardizabala biternata</i> *	50	0.2	13	0.4				
<i>Lomatia hirsuta</i>	50	0.9	13	+				
<i>Dioscorea bridgesii</i> *	38	0.1	75	0.3	63	0.1	13	+
<i>Lathyrus magellanicus</i>	38	+	25	+			25	+
<i>Oxalis arenaria</i> *	38	0.1	13	+				
<i>Gochmatia foliolosa</i> *	38	0.2			13	0.1		
<i>Colletia hystrix</i>	38	+			13	+		
<i>Quillaja saponaria</i> *	38	0.9					13	+
<i>Olsynium scirpoideum</i> *	38	+						
<i>Mutisia spinosa</i>	38	+						
<i>Oxalis micrantha</i>	25	+	63	0.1	13	+	75	3.5
<i>Tristagma bivalve</i> *	25	+	50	+			13	+
<i>Escallonia pulverulenta</i> *	25	0.6	38	2.7	88	1.5		
<i>Oxalis perdicaria</i>	25	+	38	+			13	+
<i>Gnaphalium cheiranthifolium</i>	25	+	25	+	13	+	88	0.4
<i>Nassella laevisissima</i>	25	0.1	25	+	13	+	63	1.9
<i>Pasithaea coerulea</i>	25	0.1	25	0.1				
<i>Alstroemeria revoluta</i> *	25	+	13	+	25	+		
<i>Luma apiculata</i>	25	0.1	13	0.8	13	0.1	13	+
<i>Relchela panicoides</i>	25	0.1	13	+	13	+		
<i>Adiantum chilense</i>	25	0.2	13	0.1	13	+		
<i>Nothofagus glauca</i> *	25	1.1	13	+			13	0.1
<i>Proustia pyrifolia</i> *	25	+						
<i>Sophora macrocarpa</i> *	25	+						
<i>Gavilea venosa</i> *	25	0.1						
<i>Gilliesia montana</i> *	25	0.1						
<i>Galium cotinoides</i> *	25	0.1						
<i>Blechnum hastatum</i>	25	0.1						
<i>Lomatia dentata</i>	25	0.1						
<i>Boquila trifoliolata</i>	25	0.1						
<i>Vicia nigricans</i>	25	0.1						
<i>Uncinia phleoides</i>	25	0.1						
<i>Tristerix corymbosus</i>	25	0.2						
<i>Muehlenbeckia hastulata</i>	13	+	63	0.2	63	0.7	25	0.1
<i>Acaena argentea</i>	13	+	63	0.2	50	0.1	38	0.5
<i>Stachys gilliesii</i>	13	0.1	38	0.1			25	+
<i>Geranium core-core</i>	13	+	13	+			25	+
<i>Citronella mucronata</i> *	13	+	13	+				
<i>Oenothera stricta</i>	13	+			38	0.1	13	+
<i>Conanthera bifolia</i> *	13	+			25	+	13	+
<i>Cissus striata</i>	13	+			13	+	13	+
<i>Schinus polygama</i>	13	+			13	+		
<i>Chloraea lamellata</i> *	13	+						
<i>Calandrinia compressa</i> *	13	+						
<i>Libertia sessiliflora</i> *	13	+						
<i>Chusquea quila</i> *	13	+						
<i>Podocarpus salignus</i> *	13	0.1						
<i>Dioscorea humifusa</i> *	13	1.3						
<i>Cynanchum pachyphyllum</i>	13	+						
<i>Chiropetalum tricuspdatum</i>	13	+						
<i>Calceolaria corymbosa</i>	13	+						
<i>Soliva sessilis</i>	13	+						
<i>Myoschilos oblongum</i>	13	0.1						
<i>Rhaphithamnus spinosus</i>	13	0.1						
<i>Persea lingue</i>	13	0.1						
<i>Carex setifolia</i>	13	0.1						

Table A3. Cont.

	Nat		PO		PM		PY	
	F (%)	mCv (%)						
	n = 8		n = 8		n = 8		n = 8	
Native species								
<i>Baccharis racemosa</i>			25	0.1	25	+	25	+
<i>Sisyrinchium graminifolium</i>			25	+				
<i>Glandularia laciniata</i>			13	+	13	+	13	+
<i>Hypericum caespitosum</i> *			13	+			13	+
<i>Embothrium coccineum</i>			13	+				
<i>Maytenus boaria</i>			13	+				
<i>Bromus lithobius</i>			13	+				
<i>Eryngium paniculatum</i>			13	0.1				
<i>Margyricarpus pinnatus</i>					50	0.1		
<i>Chascolytrum subaristatum</i>					38	0.1	38	0.1
<i>Adesmia spec.</i>					38	0.1	25	0.1
<i>Lobelia tupa</i> *					13	0.4	13	+
<i>Piptochaetium montevidense</i>					13	+	13	0.1
<i>Stachys ochroleuca</i> *					13	+		
<i>Hypochaeris scorzonerae</i> cf. *					13	+		
<i>Bromus berteroaanus</i>					13	+		
<i>Calceolaria dentata</i>							25	+
<i>Baccharis linearis</i> *							13	0.1
<i>Carex phalaroides</i>							13	+
<i>Conyza bonariensis</i>							13	+
<i>Solanum crispum</i>							13	+
<i>Collomia biflora</i>							13	+
Total species numbers	77		46		40		45	

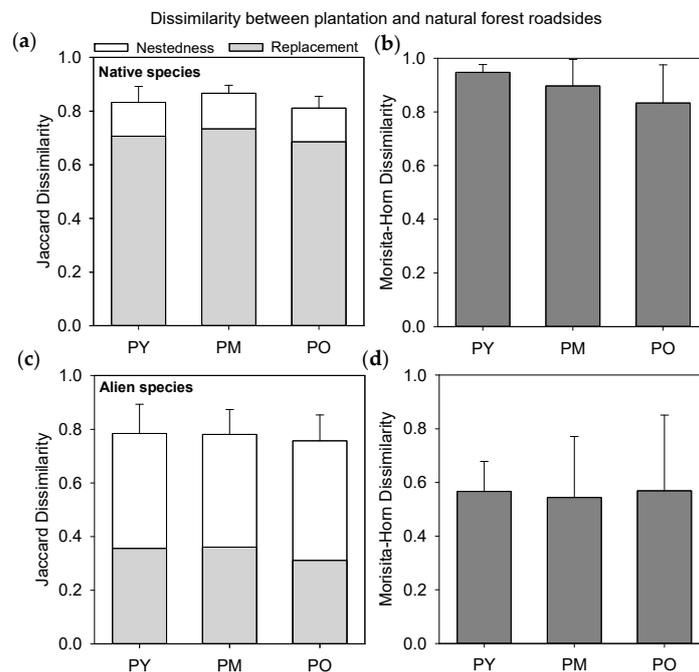


Figure A1. Mean pair-wise dissimilarity for native and alien species between transects of natural forest roadsides and roadside transects of young plantations (PY), medium-aged plantations (PM) and old to mature plantations (PO). (a,c): Presence/absence-based Jaccard dissimilarity partitioned into the replacement and nestedness component according to Baselga [50] for native (a) and alien (c) species; (b,d): The abundance-based Morisita–Horn Index for native (b) and alien (d) species. There were no significant differences among plantations age classes.

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