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Assessing the impact of plantation forestry on plant biodiversity A comparison of sites in Central Chile and Chilean Patagonia



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ABSTRACT

Effects of plantation forestry on biodiversity are controversially discussed in literature. While some authors stress positive effects, others tend to attribute a largely negative influence to plantations. One important factor steering the influence on biodiversity are management practices. A second important factor is the environmental matrix. Chile offers the option to analyse both factors jointly. The coastal range of central Chile has experienced rapid and widespread replacement of native Nothofagus spp. forests in favour of Pinus radiata plantations. Here, native forests remain limited to small patches surrounded by an environmental matrix of plantations. Management is rather intensive and not designed to maintain biodiversity. While in the coastal range of central Chile the transformation from native forests to non-native tree plantations has almost come to an end, spatial extension of P. contorta and P. ponderosa plantations has just recently begun in Chilean Patagonia. While the management is similar to central Chile, plantations rather exist as small patches surrounded by an environmental matrix of native plant formations (e.g. Nothofagus spp. forests and Nothofagus spp. scrublands). In the framework of this work, effects of the two diametric land usages on biodiversity are assessed and compared. Biodiversity is assessed at the α -, β - and γ -scale. At the α -scale, biodiversity impacts are inferred statistically, using one-way ANOVA and Tukey's PostHoc test. Biodiversity of plants at both sites is significantly reduced in plantations when compared to native forests or scrublands. Plantation forestry lowers α -biodiversity and does not provide additional habitats for specialists. At the β -scale, weak edge effects due to the presence of native forests are observed. In total, plantation forestry tends to promote plant invasions and impairs the survival of endemics. At the γ -scale, plant species communities where predominantly native and endemic in forests, predominantly introduced in plantations. Positive effects of the more native environmental matrix in Patagonia are not found to be stronger than in central Chile, therefore it is concluded that management imposes a much stronger influence. Results show, that the biodiversity impacts in

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Central Chile are transferable to Chilean Patagonia, where plantation forestry is increasingly established.

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1. Introduction

The relationship between biodiversity and plantation forestry has been controversially discussed in literature (Bremer and Farley, 2010; Brockerhoff et al., 2008; Stephens and Wagner, 2007; Kanowski et al., 2005). In many case studies, positive or at least neutral effects can be identified (Ferns et al., 1992; Allen et al., 1995; Chey et al., 1997; Murphy et al., 2008; Tomasevic and Estades, 2008). Other case studies pronounce negative effects (Friend, 1982; Freedman et al., 1996; Potton, 1994; Perley, 1994; Fomegas et al., 2004). Nonetheless, some tendencies are rather well established. There is strong agreement that an adequate management of plantations can help to maintain biodiversity. In contrast, unsustainable management can impair biodiversity (Cawsey and Freudenberger, 2008; Program and RIRDC, 2004; Taki et al., 2010). Furthermore, an important influence of the environmental matrix on biodiversity within highly managed landscapes like plantations is observed (Murphy and Lovett Doust, 2004; Baum et al., 2004; Tomasevic and Estades, 2008; Lin and Augspurger, 2008; Faria et al., 2009).

Chile is a well suited country to assess the influence of plantation forestry on biodiversity. Central Chile is considered a centre of biodiversity by various concepts (Brooks et al., 2006). At the same time, forestry with non-native tree species plantations is one of the strongest economic sectors of the country (Gwynne, 1996). Since the neoliberal turn of the Pinochet government, Chile has strongly subsidized plantation establishment in the central zone (most strongly in the VII. Región del Maule, VIII. Región del Biobío) (Clapp, 1995a,b, 2001). Thus, native forests of Nothofagus glauca (PHIL.) KRASSER, N. obliqua (MIRB.) OERST. and N. alessandrii ESPINOSA have been rigorously replaced by plantations (mainly of Pinus radiata D.Don and Eucalyptus globulus HABILL) (Smith-Ramirez, 2004), Since 1974, native forests have almost completely disappeared in the coastal range (Echeverria et al., 2006). Today, they cover only a few percent of their original habitats as small remnants. These remnants are surrounded by extensive plantations (Bustamante and Castor, 1998). Thus, the environmental matrix consists almost exclusively of non-native tree plantations. Plantations are managed in a rather unsustainable manner (Clapp, 1995a,b, 2001). Stands are mainly mono-specific and composed of cohorts of trees at the same age. No native trees are preserved within plantations. Harvesting is done by clear-cutting which is frequently followed by pesticide application. In the past, harvested sites were burned to avoid plant diseases. This practice has officially been abandoned, though, it is infrequently applied until today (Clapp, 1995a,b, 2001). Many Latin-American authors familiar with the situation expect negative influences on biodiversity e.g. Pauchard et al. (2006), Paritsis and Aizen (2008), Armesto et al. (1998) and Smith-Ramirez (2004) but see Estades and Temple (1999), Gomez et al. (2009) and Tomasevic and Estades (2008).

However, empirical evidence based on systematic comparisons of vegetation assessments for this assumption is not available.

A different image of land usage is found in Chilean Patagonia (XI. Región de Aysén). There, human-provoked fires between 1920 and 1960 cleared large areas of forests exposing soils to erosion and landslide risks (Langdon et al., 2010; Sanchez Jardon et al., 2010). In order to reduce erosion and landslide risks by exploiting the soil-stabilizing effect of tree ecosystems, thousands of hectares with fast growing non-native species, mainly *P. contorta* DOUGL. EX LOUD. and *P. ponderosa* DOUGL. EX P. ET C. LAWS. were planted for soil protection. However, in the 1970s plantation establishment continued, though, with productive purposes. Despite continued establishment, plantations cover less than one percent of the area (e.g. *N. antartica* (G. FORST.) OERST., *N. pumilio* (POEPP. AND ENDL.) KRASSER) (Langdon et al., 2010). While in central Chile, native formations are integrated into an environmental matrix of plantations, in Patagonia the situation is different. Plantations do not represent an environmental matrix but are themselves integrated into an environmental matrix of plantations are adopted from central Chile and plantations are operated by the same companies. Therefore plantation management – except that another *Pinus* species is planted – is largely comparable in Patagonia.

This analysis aims to discuss the relative impact of two factors influencing plantations biodiversity in the two study regions. The relative impact of plantation management as one aspect of habitat quality is compared to the impact of the environmental matrix.

2. Study sites

2.1. Geography of central Chile

The VII. Región del Maule, VIII. Región del Biobío, which are part of Central Chile, belong to the temperate zone of the country extending from 35° to 37°S. It has a Mediterranean Csb climate (Koeppen–Geiger) with an annual mean temperature around 12 °C and an annual precipitation of around 1300 mm. The zone is morphologically determined by the coastal range,

a mountain range running from NNE to SSW. The central depression represents the interior of the country. Towards the east, the Andes represent a high mountain region.

The basement of the coastal range is made up of magmatic and metamorphic rocks of Palaeozoic age with younger (Quaternary and Tertiary) and volcanic material superimposed from the Andes. The two regions cover around 67 358 km² and are inhabited by 2.8 million inhabitants. The population density of around 41 persons per km² is among the highest of the country (Instituto Nacional de Estadisticas, 2002). Thus, the region represents a zone of intensive human activity and human modification of the natural environment has been profound in the past.

After the arrival of European colonists, vast parts of the formerly tree-covered zone have been opened by burning and agriculture was introduced. At that time, numerous European herbaceous species have successfully invaded the region (Holmgren et al., 2000). About the end of the 18th century, the first *Pinus* plantations were established in order to prevent erosion (Camus, 2003). Ever since, plantation establishment has intensified under the Pinochet government which strongly promoted forestry as part of the neoliberal economic strategy (Clapp, 1995a,b, 2001). Investments in forestry have been subsidized to 75% by the state (Ministerio De Agricultura, 1974). It has long been claimed that plantations are established exclusively on abandoned fields with the objective of erosion control.

However, recent studies based on remote sensing reveal that to a large extent, native *Nothofagus* forests have been cut down to establish plantations indeed. Deforestation was strongest between 1975 and 1990 (Echeverria et al., 2006). Today, almost the entire coastal range is covered with plantations of *P. radiata* and *E. globulus*. Only a few percent of the region remain forest covered (own data, unpublished).

2.2. Plant formations of central Chile

In central Chile, three types of plant formations were assessed. The deciduous Maulino forest is dominated by *N. glauca* and *N. alessandrii*. The forest represents the transition zone between sclerophyllous forests in the north and temperate rainforests in the south, thus typically sclerophyllous species like *Cryptocarya alba* (MOLINA) LOOSER or *Peumus boldus* MOLINA are frequently found in the understorey. The Maulino forest has one of the highest numbers of plant species among Chilean forests (Smith-Ramirez, 2004).

Pinus plantations are highly managed ecosystems that consist of a single tree species, usually with all individuals of the same age. The understorey below trees is sparsely vegetated and inhabited by only a few species and the same accounts for the herbaceous stratum. Plantations are harvested after 10 to 25 years by clear-cutting of the entire plantation.

A third plant formation is the scrublands of the central depression. They are usually made up of a single tree species, *A. caven*, whose geographical extension varies widely. After the Europeanization of the traditional Chilean agricultural system by Spanish and German settlers, the native sclerophyllous matorral declined. *A. caven* could successfully extend its area from its home region – the Gran Chaco region of South-America – and establish in the central depression. It is now considered the vegetational climax of the depression (Ovalle et al., 1996). *A. caven* is usually associated with some native shrubs (e.g. *Baccharis linearis* (RUIZ AND PAV.) PERS.) and European herbs like *Taraxacum spp., Haplopappus* spp. or *Rumex spp.* (Holmgren et al., 2000). These scrublands (called Espinales) are used as extensive agro-pastoral systems (Ovalle et al., 1996).

2.3. Geography of Chilean Patagonia

Chilean Patagonia is the south-western part of the continent, including the XI. and XII. administrative regions extending from 42° to 55°S. The study area is around Coyhaique (45°34S, 72°04W), the capital of XI. Región de Aysén. Climatic conditions range from continental trans-Andean Cfb climate (Koeppen–Geiger) with an average annual precipitation of 1205.9 mm and annual mean temperature of 8.2 °C at Coyhaique. Morphologically, the area is characterized by the Andes with rugged terrain up to 2600 m above sea level and glacial tectonics with open valleys and plain-form relief in the east, composed of silicic and intermediate rocks, as well as volcanic ashes. Andosolic soils are most frequent, while erosion became a common problem where forests have been cleared (Dube et al., 2009). Despite its larger size of 10 8494 km², the region is inhabited by only 103 000 persons and the population density is low (around 0.9 persons per km²). Nearly half of them live in Coyhaique (around 43 000) (Instituto Nacional de Estadisticas, 2002). Like in central Chile, 55% of the native forests in the open valleys have been cleared by fire clearance for the preparation of cattle and sheep rangelands since the arrival of settlers around 1900. As a consequence, introduced European herbs are naturalized meanwhile. Because of severe problems of erosion, *Pinus* plantations have been established in the national reserve Coyhaique since the 1960s. Recently, *P. contorta* and *P. ponderosa* have been planted commercially on large areas (Sanchez Jardon et al., 2010; Langdon et al., 2010).

2.4. Plant formations of Chilean Patagonia

The vegetation of Chilean Patagonia can be categorized into at least six main formations (Hildebrand Vogel et al., 1990; Gut et al., 2008; Schmithusen, 1956; Sanchez Jardon et al., 2010; Oberdorfer, 1960), three of which have been assessed herein: Native forests, *Pinus* plantations, and scrublands. Although *Pinus* plantations cover only a small amount of the Region, they are important with respect to biodiversity conservation. In central Chile, plantation establishment also began for erosion control purposes on small areas but has extended quickly to replace almost all formerly forested areas in the Coastal Range (Echeverria et al., 2006).

Native forests are dominated by *N. pumilio*, associated with around ten main understorey species, e.g. *Osmorhiza chilensis* HOOK. ET ARN. Along the transition zone to the temperate evergreen forests the ratio of *Nothofagus dombeyi* MIRB increases. In humid areas, the understorey is dominated by the bamboo *Chusquea coleou* E. DESVAUX EX GAY while other areas contain mainly hemicryptophytes. Native forests can mainly be found on steep slopes and in higher altitudes or less accessible areas. Where land-use intensity is low, the *N. antarctica* forests begin to regenerate. These forests hold a high structural diversity and high species richness. Similar to central Chile, forest plantations are mono-specific and coeval cohorts. In contrast to central Chile, *P. contorta* and *P. ponderosa* are most frequent, sporadically, *Pseudotsuga menziesii* (MIRB) FRANCO and *P. sylvestris* L. are planted. *P. contorta* and *P. ponderosa* invasions can be observed around Coyhaique, despite the fact that most plantations are younger than 30 years (Langdon et al., 2010). In the open valleys the plantations are found between the border area to native forests in higher altitudes and scrublands in the valley floor.

These scrublands mainly consist of *N. antarctica* and *Berberis microphylla* G. FORST with varying coverage. Further native shrubs are found there, e.g. *B. darwinii* HOOKER or *Embothrium coccineum* J.R. ET G. FORSTER. European herbs compete with native species and partly species from the steppe in this transition zone. Among other factors, the understorey is strongly dependent on land-use and grazing intensity, as well as the local microclimate. The abundance of the scrublands is limited in the east by aridness. It should be noted that while forests and plantations are composed of the same genders in central Chile and Chilean Patagonia, scrublands differ. While the main tree species in central Chile is *A. caven*, scrublands are made up of *Nothofagus spp.* trees in Patagonia. Despite this floristic dissimilarity, scrublands can be compared w.r.t. the fact that they represent degraded succession stages of *Nothofagus spp.* ecosystems at both sites.

3. Theoretical considerations

Within this section, some theoretical considerations regarding biodiversity effects and impacts on the plant community composition as induced by the aforementioned situations will be discussed.

3.1. Biodiversity effects of plantation forestry

The international debate on biodiversity within plantations has been summarized before, here, the regional results are to be outlined. Simberloff et al. (2010) point out that invasive conifers of the southern hemisphere generally threaten native biodiversity. Effects are induced by biotic and abiotic pathways. The formation of dense thickets alters abiotic conditions, for instance, light availability (due to shadening and coverage of the ground with conifer needles), nutrient availability, soil acidification and competition for growing space. Biotically, propagule pressure and allelopathy and mass effects due to their sheer size may threaten native diversity. Management practices, such as clearfelling, pesticide application and fire clearing induces further environmental factors. More complex, the presence of the conifers also alters community patterns (e.g. herbivory) which have a potentially significant effect.

In total, Conget and Núñez-Ávila (2008) and Clapp (1995a,b, 2001) assume largely negative impacts of Chilean tree plantations to native biodiversity. This influence is attributed mainly to management practices (clearfelling, pesticide application, fire clearing, monocultural management, destruction of micro-habitat diversity) which, furthermore, imposes the risk of invasions with native plants. Hence, in our study, we expects negative biodiversity impacts and plant invasions as much within the native forest (in proximity to plantations) as within the plantations themselves.

3.2. Effects of habitat fragmentation

Plantation forestry frequently leads to habitat fragmentation of pristine ecosystems. Fahrig (2003) reviews the evidence for biodiversity impacts of habitat fragmentation. She points out that the influence of habitat loss on biodiversity is much stronger than the influence of habitat fragmentation. Nonetheless, habitat fragmentation can have additional negative impacts on biodiversity and is expected to be especially severe where both processes co-occur. Fischer and Lindenmayer (2007) point out that biodiversity impacts due to habitat fragmentation are caused by habitat isolation, loss and degradation, but also by alterations in community patterns. They impact negatively on numerous taxa including vascular plants.

Krauss et al. (2010) show that habitat fragmentation induced by agriculture in Europe has immediate and long term effects on plant vascular diversity. While immediate effects may not be as severe as frequently expected, a long term decline in habitat connectivity and quality may lead to an extinction debt. Plant vascular diversity was more strongly influenced by past landscape conditions indicating that diversity impacts are time-lagged but severe.

Echeverria et al. (2006) analyse the forest fragmentation of central Chilean native forests. Classifying three landsat images (1975, 1990, 2000) and using standard landscape metrics as offered by FRAGSTATS (McGarigal et al., 2002) they show that native forests not only disappear in favour of plantation forestry, but get fragmented also. For instance, the largest patch of native forest decreases from 6.91% in 1975 to 0.16% in 2000. The number of patches per hectare (i.e. patch density) rose from 0.93 in 1975 to 1.36 in 2000. Consequently, the core habitat decreases significantly, from over 21,000 ha in 1975 to only 839 in 2000. Hence, native forest patches become increasingly isolated from one another.

The situation is different in Chilean Patagonia, where Bizama et al. (2011) have studied forest fragmentation (between 1900 and 1998). Firstly, the drivers of forest loss and fragmentation – until now – is not predominantly the forest industry, but fire clearance by agricultural and pastoral settlers. The largest patch of native forest in 1998 is still 53.8% and patch density is at 4.3. Hence, forests in Chilean patagonia are far less fragmented than in Central Chile. Their patches are significantly larger and thus, the core habitat is larger. Since habitat loss and habitat fragmentation are more pronounced in central Chile than in Chilean Patagonia, biodiversity impacts resulting from these processes are expected to be more severe in the first study site. Effects of habitat loss are expected to become obvious at the landscape level (where continuously missing forests should lead to lower species richness), effects of fragmentation at the plot level (where remain species within the understory are fewer).

3.3. Expected community composition

As previously discussed, the strongly altered configuration of the setting of biotic and abiotic factors within plantations alter biodiversity with a tendency to negative impacts. As to our conviction, the number and complexity of these phenomena regarding its impacts *on community composition* are hard to judge a priori. CSR-Theory would predict that species composition is dominated by stress- and competition-strategists, the first ones present due to their ability to survive management practices better than other species, the second present due to their ability to survive competition for environmental factors (Grime, 2006). We expect the community composition to be composed by a smaller number of species (than within native forest), which are tolerant to the discussed harsh environmental pressures. Such species are favoured the release of less stress tolerant competitors.

Simonetti et al. (2007) show that influences on herbivory and microclimate have an impact on seedling growth of native species. Reductions in insect herbivory, as a consequence of forest fragmentation, leads to an increased seedling growth of several native species. Although results relate to forest patches the same should hold true for plantations: influences on colonization, survival and establishment of native species in human-modified landscapes are complex and must be studied on a case-wise basis.

Guerrero and Bustamante (2007) evaluate in field an laboratory investigations, whether the native tree species *C. alba* can regenerate below *P. radiata* canopies. They conclude that this is possible so that *C. alba* can potentially survive in plantation dominated landscapes. Estades et al. (2012) discuss that *Gomortega keule*, a monotypic family of southern Chile, is threatened in plantation understories.

Several findings regarding invasive species have been published. García et al. (2014) analyse the role of different environmental factors favouring the spread of the invasive plant species *T. monspessulana* in Chile. They show that the presences of the plant is higher in plantations. Results are confirmed for other plantation types by Pauchard et al. (2008a). Pauchard and Alaback (2004) show that invasive species spreading and establishment is facilitated by roads. If this holds true, one should expect plantations to be more strongly colonized by invasive species, since plantation management creates artificial roads and road-like pathways. These findings are supported by Bustamante and Castor (1998) who show that *P. radiata* plantations understories are characterized strongly by introduced species.

To sum up this rationale, Estades et al. (2012) expect the plant community of plantations to be 1. more homogenous, 2. dominated by introduced species.

4. Methods

4.1. Vegetation assessments

In 2011 and 2012, field studies in both regions, central Chile and Chilean Patagonia, were realized. The objective of these field studies was to assess biodiversity conditions among a gradient of intensity of usage ranging from extensively used *Nothofagus spp.* forest, moderately used scrublands to intensively used *Pinus spp.* plantations. Then a similar gradient was assessed in Chilean Patagonia in order to compare biodiversity conditions within this differently structured landscape. As the maps in Fig. 1 reveal, sampling is more concentrated in Chilean Patagonia than in central Chile. That is due to the fact that plantations cover a large proportion of the coastal range of central Chile, and thus, native forest patches included within plantations are strongly dispersed over the entire coastal range. In contrast, plantations in Chilean Patagonia are strongly concentrated around Coyhaique. A total of 66 vegetation sites are dealt with in this study, among them 15 *Nothofagus* forests, 15 *Pinus* plantations and 15 scrublands in central Chile and seven plots of each type in Chilean Patagonia. The species number, abundance and minimum areal distribution were assessed according to the method of Braun Blanquet (1964). In order to be able to analyse β -diversity, coupled samples (e.g. a plantations site in immediate vicinity to a native forests site) were assessed. A total of ten coupled samples was assessed, five at each study site. Vegetation strata were identified and exhaustive sampling was carried through in all strata.

The size of the patches studied varied substantially and differed between both study sites. This is due to the fact that in Central Chile, native forests appear as small patches, surrounded by large plantations and in Chilean Patagonia, the situation is inversed. Sampling was designed to cover these distances as follows. It was assured, that regardless of the study site and



Fig. 1. Maps of the two study regions and locations of biodiversity assessments.

plant formation, the respective patch had a minimum size of one ha.¹ Within such patches, the minimum areal according to Braun Blanquet (1964) was determined and sampled. Thus, the size of the patches is larger than 1 ha, and at least the size of the minimum areal. The exact size of each patch was not recorded, though since this would have meant measuring huge areas of plantations in Central Chile and huge forests in Chilean Patagonia. For the plantation samples coupled with native forest, the closest source of species (from another plant formation) is the respective forest, which is directly adjacent to the plantation. The coupled samples were not sampled within the ecotone between both sites, but in the centre of the patches. For the remainder of the vegetation assessments, the distance to the nearest source of species was larger. In order to analyse data statistically, abundance values were transformed into relative abundances according to Pellissier et al. (2004): A species with a Braun-Blanquet abundance value of e.g. 2 has a cover between 25% and 50%. Its cover is averaged to r_i , where $r_i = (0.25 + 0.5)/2 = 0.375$. Other Braun-Blanquet abundance values were transformed accordingly. Species with a value of + were given $r_i = 0.025$ and species with r were given $r_i = 0.00625$. Then, the relative abundance of a species is calculated as $p_i = r_i / \Sigma r_i$.

4.2. Biodiversity indices

Within this report, the number of observed species *N* is taken as a first indicator of biodiversity. Furthermore, Lande et al. (2000) suggest that the Simpson index should always be considered in biodiversity analyses. The Simpson index, in the form recommended by Lande (1996), is computed as:

$$SD^{\alpha} = 1 - \Sigma p_i^2, \quad SD^{\alpha} \in [0, 1)$$
⁽¹⁾

where p_i again is the relative abundance (Simpson, 1949). The higher the index, the more diverse is the community. As Smith and Wilson (1996) point out, an important requirement for any evenness index should be its independence on *N*. Since SD^{α} fails this criterion, and several others, Smith and Wilson (1996) recommend to use an evenness index called E_{VAR}^{α} instead, which is defined as:

$$E_{VAR}^{\alpha} = 1 - \frac{2}{\pi} \arctan\left[\frac{1}{N} \sum_{i=1}^{N} \left(\ln(p_i) - \mu_{\ln}\right)^2\right], \quad E_{VAR}^{\alpha} \in [0, 1]$$
(2)

where:

$$\mu_{ln} = \frac{1}{N} \sum_{i=1}^{N} \ln(p_i).$$
(3)

¹ Note that although this is a rather small minimum size, applying a larger minimum size for forest remnants is difficult in Central Chile where most patches are even smaller than 1 ha.



Fig. 2. Boxplots of the biodiversity data of Central Chile. Left: Species richness *N*, Centre: Simpson Diversity *SD*^α, Right: Smith–Wilson Evenness *E*^α_{VAR}. FOR: forest, SCL: scrubland, PLT: plantation.

On of the main advantages of E_{VAR}^{α} is, that it is not dependent on *N*. For the β aspect of biodiversity Lennon et al. (2001) adapt the Sørensen similarity index in order to correct biases of this index. The Lennon index is computed as:

$$LD^{\beta} = 1 - (a/a + \min(b, c)), \quad LD^{\beta} \in [0, 1].$$
(4)

A Lennon index of $LD^{\beta} = 0.0$ states that the number of shared species a is maximal. This means that all species that occur in the less diverse site are also present in the more diverse site. A Lennon index of $LD^{\beta} = 1$ states that there are no shared species. Thus, SD^{β} has to be inverted to $1 - SD^{\beta}$ to be comparable to LD^{β} .

At the γ -scale, total numbers of species were counted after distinguishing the occurring plants. Secondly, species were categorized according to their origin. They were assigned into the categories 'endemic', 'native' and 'introduced'. Note that the γ -scale is of particular importance in Central Chile, where less than 4% of near natural forests remain due to plantation establishment. Here, it is particularly important that plantations do host a high number of species. If they do not, biodiversity at the γ -scale will decline harshly.

4.3. Statistical treatment

In order to derive meaningful conclusions, data for α -diversity (namely species richness *N*, Simpson diversity SD^{α} and Smith–Wilson evenness E_{VAR}^{α}) were described with descriptive statistics (Boxplots) and with inferential statistics, all results were produced using the statistical package R (R Development Core Team, 2008). Regarding inferential statistics, the following approach was chosen. Differences in terms of α -diversity between the different habitat types (native forest, scrubland and plantation) were tested using a one-way ANOVA. One-way ANOVA basically tests whether the variances between factor groups is significantly larger than variances within factor groups. ANOVA requires data to be Gaussian-distributed and homoscedastic. Gaussianness was tested using the Shapiro–Wilk test and homoscedasticity using Bartlett's test, which has been shown particularly suited to test for the homoscedasticity of Gaussian-distributed data. ANOVA merely shows whether between-group or within-group variances are stronger. However, it does not show the significances of differences between individual groups (between forests and plantations, forests and scrublands, scrublands and plantations). In order to do so, Tukey's post-hoc test has been applied, which tests the significances between different groups. All tests were performed using a significance level of $\alpha = 0.0001$.

5. Results

5.1. Central Chile

At the α scale, the mean species richness in *Pinus* plantations is 8.8 (cf. Table 1 and Fig. 2), with a minimum of only 4 species. In general, younger plantations with a more open canopy host more species than older plantations do. Within the *Nothofagus* forests, the mean species richness is 31.3 and thus significantly higher. Within the *Acacia* scrublands, a mean species richness of 15.2 is found. As Table 1 reveals, the same ranking as for species richness is found for the Simpson diversity index. Remarkably, even the most diverse *Pinus* plantation yields a lower species richness and Simpson index than the least diverse *Nothofagus* forest.

Gaussianness and homoscedasticity could be assumed for each of the plant formations to be tested, hence, one-way ANOVA with Tukey's Post-hoc test was applied. Statistical results are summarized in Fig. 2 and Table 4. As the table reveals, differences in terms of species richness *N* were highly significant (results of one-way ANOVA). This is due to highly significant differences of *N* between forest and plantations, and forests and scrublands (results of Tukey's Post-hoc test). The species richness of *N* is higher for forests than for other plant formations. Furthermore, differences in terms of Simpson diversity

Table 1

Comparison of α biodiversity: species richness N, Simpson diversity SD^{α} , Simpson evenness SE^{α} and evenness E_{VAR}^{α} . Data are Mean, Standard Error, (Min.–Max.)

Study region	Ecosystem	$N \in [0, \infty]$	$SD^{\alpha} \in [0, 1)$	$E_{VAR}^{\alpha} \in (0, 1]$
Central Chile	Forests	31.3,1.89,(21–49)	.87,.00,(.80–.92)	.35,.02,(.24–.54)
Central Chile	Scrublands	15.2,1.14,(9–20)	.75,.02,(.55–.84)	.29,.01,(.21–.43)
Central Chile	Plantations	8.8,,55,(4–19)	.41,.05,(.05–.76)	.27,.04,(.15–.70)
Chil. Patagonia	Forests	16.2,1.46,(11–23)	.82,.02,(.71–.87)	.44,.03,(.28–.54)
Chil. Patagonia	Scrublands	15.8,1.21,(12–19)	.85,.02,(.72–.89)	.44,.05,(.30–.70)
Chil. Patagonia	Plantations	7.8,1.22,(4–14)	.42,.05,(.25–.65)	.31,.03,(.22–.39)

Table 2

Comparison of indices for β similarity of *Nothofagus* forests and *Pinus plantations*. Sørensen index S^{β} , Lennon index L^{β} , difference in species richness ΔN and values required for computing indices (a, b and c, see text).

Study regions	Ecosys. A	Ecosys. B	а	b	С	ΔN	$1 - S_{\beta}$	L_{β}
Central Chile	Forest	Plant.	5	19	31	12	.83	.79
Central Chile	Forest	Plant.	8	0	27	27	.63	.00
Central Chile	Forest	Plant.	7	9	28	19	.73	.56
Central Chile	Forest	Plant.	13	6	22	16	.52	.32
Central Chile	Forest	Plant.	7	2	36	34	.73	.22
						Ø=	.69	.38
Chil. Patagonia	Forest	Plant.	1	3	19	16	.92	.75
Chil. Patagonia	Forest	Plant.	3	4	22	18	.81	.57
Chil. Patagonia	Forest	Plant.	3	7	15	8	.79	.70
Chil. Patagonia	Forest	Plant.	2	8	14	6	.85	.80
Chil. Patagonia	Forest	Plant.	2	4	21	17	.86	.67
						Ø=	.84	.70

 SD^{α} were highly significant (results of one-way ANOVA), since forests and scrublands show significantly higher SD^{α} values than plantations do (results of Tukey's Post-hoc test). Other tests performed did not produce significant results (cf. Table 4).

At the β scale, five *Pinus* plantations in direct vicinity to *Nothofagus* forests were sampled. As Table 2 reveals, LD^{β} diversity indices tend to be rather low, the lowest value is 0.0 – a case where all species found in the *Pinus* plantation were also found in the *Nothofagus* forest. The average LD^{β} is 0.38 and the average $1-SD^{\beta}$ is 0.69. This indicates that the number of shared species tends to be high and close to the number of species in the less diverse community (the plantations). Plantations are frequently inhabited by introduced shrubs in the understorey which tend to enter forests in the vicinity of plantations. Vice versa, certain native species from forests – like *Aristotelia chilensis* (MOLINA) STUNTZ, *Persea lingue* NEES, *C. alba* or *P. boldus* – are also found within plantations, albeit much less frequent.

At the γ scale, 159 plant species in total were found, among them, 65 were native (41%), 40 endemic (25%) and 54 introduced species (34%) (cf. Table 3). Results are visualized in Fig. 4. In *Nothofagus* forests, 124 of these species were found of which 54 were native (44%). 34 species were endemits (27%) and 36 were introduced species (29%). In contrast to that, 53 species were found in plantations of *P. radiata*. Among them, 22 were native (42%). Altogether, 9 endemits were found within plantations (17%) and 22 introduced species (42%). In *A. caven* scrublands, 59 species were found, 16 of them being native (27%), 9 endemic (15%) and 34 introduced (58%).²

5.2. Chilean Patagonia

At the α scale, the mean species richness in *Pinus* plantations is 7.8 (cf. Table 1 and Fig. 3), with a minimum of 4 species under a monospecific *P. contorta* plantation on the north face of mount Cinchao and a maximum of 14 under *P. sylvestris* on the north face of mount Mackkay, both north of Coyhaique. Young plantations with an open canopy, again show a higher species richness. Within the sampled *Nothofagus* forests, the mean species richness *N* is 16.2 species. The scrublands assessed have an average species richness of 15.8. However, for the Simpson diversity index and evenness E_{VAR}^{α} (cf. Table 1), scrublands yield higher values than forests do. Again, the most diverse *Pinus* plantation yields a lower Simpson index than the least diverse *Nothofagus* forest. Concerning species richness, the most diverse plantation hosted only slightly more taxa (3 species) than the least diverse forest (see Fig. 3).

Gaussianness and homoscedasticity could be assumed for each of the plant formations to be tested, hence, one-way ANOVA with Tukey's Post-hoc test was applied. Statistical results are summarized in Fig. 3 and Table 4. The differences in terms of species richness *N* were highly significant according to the results of one-way ANOVA. Results of Tukey's Post-hoc test show that this is due to significant differences between forests and plantations and scrublands and plantations.

² Note that endemic species are counted separately from native species, i.e. endemic species – which are native as well – are not added to the number of native species. Thus, the gradient of intensity of use does hold for the overall number of species but not for native, endemic and introduced species since scrublands have lower percentages of native and endemic and higher percentages of introduced species.



Fig. 3. Boxplots of the biodiversity data of Chilean Patagonia. Left: Species richness *N*, Centre: Simpson Diversity *SD*^α, Right: Smith–Wilson Evenness *E*^α_{VAR}. FOR: forest, SCL: scrubland, PLT: plantation. (Axis scaling according to Fig. 2).



Fig. 4. Species composition at the *γ*-scale of Central Chile. Percentages of endemic, native and introduced species in a: all systems, b: forests, c: scrublands, d: plantations.

Differences in terms of Simpson diversity SD^{α} were also significant (results of one-way ANOVA), again, due to significant differences between forests and plantations and scrublands and plantations (results of Tukey's Post-hoc test). Other tests performed did not produce significant results (cf. Table 4).

Table 3

comparison of figures for y diversity in central enficiencian ratagonia (fi.u., no data)	Com	parison o	of figures	for γ of	diversity in	Central	Chile and	Chilean	Patagonia	(n.d.: no	data)
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Study region	Ecosystem	Num of plots	Overall species	Native species	Endemic species	Introduced species
Central Chile	All systems	45	159(100%)	65(41%)	40(25%)	54(34%)
Central Chile	Forests	15	124(100%)	54(44%)	34(27%)	36(29%)
Central Chile	Scrublands	15	59(100%)	16(27%)	9(15%)	34(58%)
Central Chile	Plantations	15	53(100%)	22(42%)	9(17%)	22(42%)
Chil. Patagonia	All systems	21	70(100%)	39(57%)	2(3%)	29(40%)
Chil. Patagonia	Forests	7	46(100%)	30(65%)	2(4%)	14(30%)
Chil. Patagonia	Scrublands	7	33(100%)	17(52%)	2(6%)	14(42%)
Chil. Patagonia	Plantations	7	27(100%)	14(52%)	0(0%)	13(48%)

Table 4

Results of the statistical treatment at the α -scale for Central Chile and Chilean Patagonia. ANOVA and Tukey's post hoc tests results.

Study site	α-value	ANOVA-	Values	5			Tukey's PLT-	Test FOR	Tukey's SCL-	Test FOR	Tukey's SCL-	Test PLT
		р	F- Val.	Mean Sq (Res.)	Sum Sq (Res.)	Df (Res.)	р	diff	р	diff	р	diff
Central Chile	Species Rich.	≤2e−16 ^{***}	101.3	2638 (26)	5277 (1094)	2 (42)	.000***	-26.13	.000***	-17.00	4.29e-5	9.133
Central Chile	Simps. Div.	1.53e-9	34.2	.687 (.0201)	1.375 (.844)	2 (42)	.000	413	.092	111	.000	.302
Central Chile	SmWil. Even.	.364	1.035	.012 (.012)	.025 (.508)	2 (42)	.979	007	.385	053	.496	045
Patagonia	Species Rich.	.000***	12.96	154.71 (11.94)	309.4 (214.9)	2(18)	.000****	-8.142	1.000	.000	.000	8.142
Patagonia Patagonia	Simps. Div. SmWil.	4.3e-7^{***} .05	36.89 2.878	.377 (.010) .029 (.010)	.754 (.184) .005 (.186)	2 (18) 2 (18)	. 000 *** .078	399 126	.9947 .801	.005 —.034	. 000 .238	.404 .090
	Even.											

**** p < 0.0001.

At the β scale, the Lennon indices (cf. Table 2) yield results different from those in central Chile. The indices are rather high with the lowest value yielded being 0.57. The average LD^{β} value is 0.70 and the average $1-SD^{\beta}$ is 0.80. That means that the number of shared species is low in comparison to the number of species in the less diverse community. It should be kept in mind though that species richness of *Pinus* plantations is lower in Chilean Patagonia than in central Chile. This is due to the fact that less native species are found in plantations there. Furthermore, the understorey of plantations is less populated by introduced shrub species. On the other hand, less introduced species from plantations have been observed to enter forests.

At the γ scale, 70 plant species were found in total. Among them, 39 were native (57%), two endemic (3%) and 29 were introduced species (40%) (cf. Table 3). Results are visualized in Fig. 5. *Nothofagus* forests inherit 46 species in total, among which 30 are native (65%), two endemic (4%) and 14 are introduced (30%). Of the 27 species found in *Pinus* plantations, 14 are native (52%) and 13 introduced species (42%), no endemic occurred. The species composition in the herbaceous stratum of plantations is dominated by European herbs, mainly from the genus *Poa*, *Trifolium* and *Taraxacum*. In scrublands, 33 species are found in total, 17 of which are native (52%), both endemics occurred (6%) and 14 plant species were introduced (42%). Although some endemic species exist in Chilean Patagonia, the vast majority of native species also appears in Argentinean Patagonia and is thus not recorded as endemic in Chilean vegetation databases. Consequently, the gradient does hold for overall and native species but not for introduced species.

6. Discussion

This study has compared biodiversity impacts of plantation forestry in Central Chile and Chilean Patagonia. It has related its results to 1. habitat quality (management practices) and 2. edge effects. Results show that at the α and γ -scale, biodiversity impacts of plantation forestry are comparable at both study sites.

At first, the discussion compares the two study sites to each other. The total number of species found at both study sites reflects the intensity of anthropogenic disturbance. Nevertheless, the total numbers of species found in forests are lower in Chilean Patagonia than in central Chile. It has to be kept in mind, though, that Chilean Patagonia is not a biodiversity hotspot in the sense of Myers et al. (2000), thus, a lower α diversity can be expected there. In Chilean Patagonia, scrublands are more similar to forests than in Central Chile, as shown in the statistical analysis (results of Tukey's Post-hoc tests in Table 3). It has to be kept in mind that the *Nothofagus* scrublands are the result of degradation of *Nothofagus* forests in Patagonia. In contrast, *A. caven* scrublands are a succession following degradation. Accordingly, they have few features in common with



Fig. 5. Species composition at the *γ*-scale of Chilean Patagonia. Percentages of endemic, native and introduced species in a: all systems, b: forests, c: scrublands, d: plantations.

forests. At the γ scale, plantations in both regions host a higher percentage of introduced and a lower percentage of native species.

Both regions show different patterns of β diversity. While Lennon indices are rather low in central Chile, they are higher in Chilean Patagonia. The main reason explaining the higher Lennon indices in Chilean Patagonia is the higher habitat diversity there. In central Chile, forest plantations cover the major part of the coastal range and build an environmental matrix forest remnants are immersed into. Thus, the floristic connection between forests and plantations is naturally high. In Chilean Patagonia, other habitats like prairies and steppes are present and the higher relief energy promotes micro-habitat diversity. Plantations are not only connected to forests but to other habitats as well and floristic connection between forests and plantations is lower.

Another reason is that the understorey of plantations in Chilean Patagonia is less dominated by introduced shrubs. Some of these shrubs like *T. monspessulana* have a fire induced dispersal mechanism, suggesting that their expansion has been be promoted by recent anthropogenic fires due to plantation management in central Chile (Pauchard et al., 2008b). The seeds of others like *A. dealbata* are dispersed with gravel during road construction which explains their vast distribution in south-central Chilean plantations (Fuentes Ramirez et al., 2011). At the γ scale, absolute figures should not be compared directly since sampling effort was different (15 assessments in central Chile, seven in Chilean Patagonia). However, relative figures of native and introduced species are similar. Plantations are much less diverse than less intensely used ecosystems. They host less native species and tend to promote introduced species.

Secondly, the discussion relates the findings of this study to the findings of other authors for central Chile. Few work exists to clarify the relationship between biodiversity and plantation forestry on the basis of systematic comparison. Thus, it is difficult to relate the findings of this report to results of other authors. Estades and Temple (1999) and Vergara and Simonetti (2004) provide data on bird diversity. Many bird species are less frequent within plantations than within native forests. However, eight bird species are more frequent within the managed habitat. Saavedra and Simonetti (2005) find

mammal diversity decreased alarmingly within plantations. Barbosa and Marquet (2002) show that fragmentation caused by plantation forestry may reduce beetle diversity. Smith-Ramirez (2004) points out the general threats to the biodiversity hotspot.

Next, our findings are related to the findings of other authors for chilean Patagonia. Our findings confirm the results of Paritsis and Aizen (2008) for Argentina who find the diversity of plants, beetles and birds significantly reduced in plantations. Corley et al. (2012) confirm these findings for plants and beetles, however, the diversity of ants is much less affected. Comparing the two study regions, it can be stated that despite the differences in land use, the spatial context into which plantations are integrated and floristic differences, biodiversity conditions are remarkably similar at the α and γ scale. In Patagonia, human impact has traditionally been low. Plantation forestry only covers around 0.5% of the area. Given these facts, for Patagonia it is a reasonable assumption to expect a lower impact of plantation forestry on biodiversity due to neighbourhood and matrix effects. However, the conditions found during the field campaign do not confirm this assumption for the α and γ scales.

Third, the discussion relates the results to results from other countries. Many authors from other parts of the world confirm the findings on the relationship between *P. radiata* plantation forestry and biodiversity. Ogden et al. (1997) show negative impacts on biodiversity in New Zealand, Gill and Williams (1996) in Australia, Atauri et al. (2004) in Spain and Senbeta and Teketay (2001) in Ethiopia. However, as the authors point out, the impact on biodiversity strongly depends on plantation management. In summary, the study is consistent with related work for Chile and studies from other countries.

In literature, there is some discussion whether *P. radiata* plantations may serve as an alternative habitat for native species. Brockerhoff et al. (2005) clearly identify *P. radiata* plantations in New Zealand as an alternative habitat for beetles, a finding confirmed by Berndt et al. (2008) for Australia. However, Pawson et al. (2009) point out that plantations in New Zealand mostly increase the abundance of exotic beetle species. Results presented herein show that many species were never found within plantations and furthermore, those that were typical for the understorey of plantations (e.g. *T. monspessulana* or *R. ulmifolius*) are also present in other disturbed habitats and in forests. Furthermore, *Pinus* plantations tend to promote invasions of non-native species (Gill and Williams, 1996; Ogden et al., 1997; Bustamante and Simonetti, 2005; Williams and Wardle, 2005; Brockerhoff et al., 2003). The latter finding is confirmed by the results of this study. In total, the findings of these study doubt the hypothesis that plantations may serve as alternative habitats, at least, for most endemic and native species. For this reason, results on α and γ diversity were comparable for both study sites. As expected by Conget and Núñez-Ávila (2008) and Clapp (1995a,b, 2001) the effects of plantation forestry to native biodiversity are severe and negative, obviously. Plantations reduce biodiversity and induce biological homogenization.

However, at the β scale, differences are observed. Plantations in Chilean Patagonia clearly show a higher β diversity compared to native forests. This difference represents a matrix effect. Plantations benefit from habitat diversity in Chilean Patagonia. Results confirm the findings of Baum et al. (2004), and Faria et al. (2009) that diversity can be increased by maintaining a mosaic of natural ecosystems within plantations that can be used as stepping stones for species. However, if plantation patches are too large, biodiversity cannot benefit from the matrix (Tomasevic and Estades, 2008; Lin and Augspurger, 2008; Murphy and Lovett Doust, 2004). The preoccupation of Echeverria et al. (2006) and Bizama et al. (2011) about biodiversity impacts due to habitat fragmentation, can be confirmed obviously, although the data presented herein do not disentangle adverse effects on biodiversity statistically. Furthermore, as pointed out by Estades et al. (2012), Pauchard et al. (2008a), García et al. (2014) and other studies, plantation forestry itself (and the establishment and management processes required for it) not only homogenize communities, but also lead to a dominance of 2. dominated by introduced species.

On the basis of these findings, there is evidence to attest a beneficial effect of the more native environmental matrix on plantations biodiversity. Plantations integrated into a diverse environmental matrix benefit at the β scale. In central Chile, where the ecotone between forest and plantations is relatively small in comparison to the size of the plantations, such benefits are not observed.

Nonetheless, these findings stress the importance of habitat quality. The more natural environmental matrix in Chilean Patagonia does not seem to bring significant improvements at the α and γ scale when compared to central Chile, where plantations form the environmental matrix. Assuming an important contribution of the environmental matrix to plant biodiversity, one should expect the impact on α diversity to be less in Chilean Patagonia. Instead, *Pinus* plantations are even less diverse in Chilean Patagonia. The fact that plantations are monospecific cohorts, that no native species are preserved within plantations and the harvesting by clear-cutting impose harsh selection factors to species and reduce micro-habitat diversity. This assumption is underpinned by the higher diversity in younger plantations. There, the habitat is more diverse and selection factors are less severe. Hence, more species are competitive in younger plantations. On the basis of existing literature discussing the importance of appropriate management for biodiversity conditions, management practices in Chile have to be considered the strongest influencing factors on biodiversity at the α and γ scales.

It is a valid assumption to consider management practices as the most decisive factor of habitat quality which steers biodiversity conditions (since at least at the mesoscale, other environmental factors are comparable between forests and plantations). Habitat quality, according to our results, is the most important factor for the ability of plants to survive within an ecosystem (and thus for the biodiversity of the ecosystem). Habitat quality determines the influence of ecological parameters directly effective at the site. The environmental matrix itself has an indirect influence on habitat quality since it may provide an inventory of possible candidate species to ecosystems in its vicinity. The successful survival of these candidates within the ecosystem is then controlled by habitat quality.

7. Conclusions

The study conducted represents a case study on the relationship between biodiversity and plantation forestry in a country that strongly promotes commercial plantation forestry and where biodiversity conservation is neglected (Clapp, 2001, 1995a,b; Asmüssen and Simonetti, 2007). In both study regions, a strong negative impact of plantation forestry on plant biodiversity is observed. The species richness is reduced and so is the number of native species—and endemic species in central Chile. For most of these species, *Pinus* plantations do not serve as an alternative habitat, many species may be threatened by extinction. No habitat specialists were found, which would occur exclusively within plantations. These findings stress the importance of native forest remnants in central Chile which continuously disappear. In Chilean Patagonia, these results show the importance of developing an adequate conservation strategy.

Appropriate biodiversity conservation strategies need to be developed and industrial plantation companies need to be more strongly regularized as towards biodiversity conservation in order to prevent a biodiversity severe biodiversity impacts in Patagonia.

References

Allen, R., Platt, K., Wiser, S., 1995. Biodiversity in New Zealand plantations. New Zealand For. 39 (4), 26–29.

Armesto, J., Rozzi, R., Smith Ramirez, C., Arroyo, M., 1998. Conservation targets in South American temperate forests. Science 282 (5392), 1271–1272.

Asmüssen, M., Simonetti, J., 2007. Can a developing country like Chile invest in biodiversity conservation? Environ. Conserv. 34 (03), 183-185.

Atauri, J., de Pablo, C., de Agar, P., Schmitz, M., Pineda, F., 2004. Effects of management on understory diversity in the forest ecosystems of northern Spain. Environ. Manag. 34 (6), 819-828.

Barbosa, O., Marquet, P., 2002. Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. Oecologia 132 (2), 296–306. Baum, K.A., Haynes, K.J., Dillemuth, F.P., Cronin, J.T., 2004. The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85 (10),

2671–2676. Berndt, L.A., Brockerhoff, E.G., Jactel, H., 2008. Relevance of exotic pine plantations as a surrogate habitat for ground beetles (Carabidae) where native forest is rare. Biodivers. Conserv. 17 (5), 1171-1185.

Bizama, G., Torrejón, F., Aguayo, M., Muñoz-María, D., Echeverría, C., Urrutia, R., 2011. Pérdida y fragmentación del bosque nativo en la cuenca del río aysén (patagonia-chile) durante el siglo xx. Rev. Geogr. Norte Grande (49), 125-138.

Braun Blanquet, J., 1964. Pflanzensoziologie. Grundzüge der Vegetationskunde. Springer, Wien.

Bremer, LL, Farley, K.A., 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. Biodivers. Conserv. 19 (14), 3893-3915.

Brockerhoff, E.G., Berndt, L.A., Jactel, H., 2005. Role of exotic pine forests in the conservation of the critically endangered New Zealand ground beetle Holcaspis brevicula (Coleoptera: Carabidae). N. Z. J. Ecol. 29 (1), 37–43. Brockerhoff, E.G., Ecroyd, C.E., Leckie, A.C., Kimberley, M.O., 2003. Diversity and succession of adventive and indigenous vascular understorey plants in

Pinus radiata plantation forests in New Zealand. Forest Ecol. Manag. 185 (3), 307-326.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J., 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17 (5), 925 - 951

Brooks, T., Mittermeier, R., da Fonseca, G., Gerlach, J., Hoffmann, M., Lamoreux, J., Mittermeier, C., Pilgrim, J., Rodrigues, A., 2006. Global biodiversity conservation priorities. Science 313 (5783), 58-61.

Bustamante, R., Castor, C., 1998. The decline of an endangered temperate ecosystem: the ruil (Nothofagus alessandrii) forest in central Chile. Biodivers. Conserv. 7 (12), 1607-1626

Bustamante, R.O., Simonetti, J.A., 2005. Is Pinus radiata invading the native vegetation in central Chile? Demographic responses in a fragmented forest. Biol. Invasions 7 (2), 243–249.

Camus, P., 2003. Federico Albert: Artifice de la Gestion de los Bosques de Chile. Rev. Geogr. Norte Grande 30, 55-63.

Cawsey, E.M., Freudenberger, D., 2008. Assessing the biodiversity benefits of plantations: the plantation biodiversity benefits score. Ecol. Manage. Restor. 9(1), 42-52

Chey, V., Holloway, J., Speight, M., 1997. Diversity of moths in forest plantations and natural forests in Sabah. Bull. Entomol. Res. 87 (4), 371-385.

Clapp, R., 1995a. Creating competitive advantage: forest policy as industrial policy in Chile. Econ. Geogr. 71, 273–296.

Clapp, R., 1995b. The unnatural history of the Monterey pine. Geogr. Rev. 85, 1-19.

Clapp, R., 2001. Tree farming and forest conservation in Chile: Do replacement forests leave any originals behind? Soc. Nat. Resour. 14 (4), 341-356.

Conget, C., Núñez-Ávila, M., 2008. Hacia un nuevo modelo forestal en chile. Rev. Bosque 47 (2010), 25–35.

Corley, J., Villacide, J., Vesterinen, M., 2012. Can early thinning and pruning lessen the impact of pine plantations on beetle and ant diversity in the Patagonian steppe? South. For.: J. For. Sci. 74 (3), 195-202.

Dube, F., Zagal, E., Stolpe, N., Espinosa, M., 2009. The influence of land-use change on the organic carbon distribution and microbial respiration in a volcanic soil of the Chilean Patagonia. For. Ecol. Manag. 257 (8), 1695-1704.

Echeverria, C., Coomes, D., Salas, J., Rey Benayas, J., Lara, A., Newton, A., 2006. Rapid deforestation and fragmentation of Chilean temperate forests. Biol. Conserv. 130 (4), 481-494.

Estades, C., Grez, A., Simonetti, J., 2012. Biodiversity in monterey pine plantations. In: Estades, C., Grez, A., Simonetti, J. (Eds.), Biodiversity Conservation in Agroforestry Landscapes: Challenges and Opportunities. Editorial Universitaria, Santiago, pp. 77–98.

Estades, C.F., Temple, S.A., 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. Ecol. Appl. 9 (2), 573-585

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34 (1), 487-515.

Faria, D., Mariano Neto, E., Martini, A.M.Z., Ortiz, J.V., Montingelli, R., Rosso, S., Paciencia, M.L.B., Baumgarten, J., 2009. Forest structure in a mosaic of rainforest sites: the effect of fragmentation and recovery after clear cut. Forest Ecol. Manag. 257 (11), 2226-2234.

Ferns, P., Cowie, R., Weir, A., 1992. Managing conifer plantations for the benefit of granivorous birds and mammals. Aspects Appl. Biol. 29, 83-88.

Fischer, J., Lindenmayer, D., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecol. Biogeogr. 16 (3), 265–280.

Fomegas, D., Bayos, N., Atayoc, J., 2004. Phytodiversity under pine (Pinus insularis) forest community in Tadian, Mountain Province. In Regional Sectoral/Commodity Review, ATI-CAR, La Trinidad, Benguet.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Johnson, G., Flemming, S., Gerrow, J., Forbes, G., Woodley, S., 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev. 4 (3), 238-265.

Friend, G., 1982. Bird populations in exotic pine plantations and indigenous eucalypt forests in Gippsland, Victoria. Emu 82 (2), 80–91.

Fuentes Ramirez, A., Pauchard, A., Cavieres, L., Garcia, R., 2011. Survival and growth of Acacia dealbata vs. native trees across an invasion front in southcentral Chile. Forest Ecol. Manag. 261, 1003-1009.

García, R., Pauchard, A., Escudero, A., 2014. French broom (teline monspessulana) invasion in south-central chile depends on factors operating at different spatial scales, Biol. Invasions 16 (1), 113-124.

- Gill, A.M., Williams, J.E., 1996. Fire regimes and biodiversity: the effects of fragmentation of southeastern Australian eucalypt forests by urbanisation, agriculture and pine plantations. Forest Ecol. Manag. 85 (1), 261–278.
- Gomez, P., Hahn, S., San Martin, J., 2009. Estructura y composicion floristica de un matorral bajo plantaciones de pinus radiata d. don en chile central structure and floristic composition of a shrub under pinus radiata d. don plantation in central chile. Gayana Bot. 66 (2), 256–268.
- Grime, J., 2006. Plant Strategies, Vegetation Processes, and Ecosystem Properties. John Wiley & Sons.
- Guerrero, P.C., Bustamante, R.O., 2007. Can native tree species regenerate in Pinus radiata plantations in Chile?: Evidence from field and laboratory experiments. Forest Ecol. Manag. 253 (1), 97-102.
- Gut, B.J., Guzzetti, M.P., Diaz, A.E., 2008. Trees in Patagonia. Springer.
- Gwynne, R., 1996, Direct foreign investment and non-traditional export growth in chile: the case of the forestry sector, Bull, Lat, Amer, Res, 15 (3), 341–357. Hildebrand Vogel, R., Godoy, R., Vogel, A., 1990. Subantarctic-andean Nothofagus pumilio forests. Vegetatio 89 (1), 55-68.
- Holmgren, M., Aviles, R., Sierralta, L., Segura, A., Fuentes, E., 2000. Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil, nutrients, and fire. J. Arid Environ. 44 (2), 197–211. Instituto Nacional de Estadisticas, 2002. Censo 2002: Sintesis de Resultados. Santiago de Chile, Chile. Report of Chilean Statistical Authorities.
- Kanowski, J., Catterall, C.P., Wardell-Johnson, G.W., 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes

of tropical and subtropical Australia. Forest Ecol. Manag. 208 (1), 359-372

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J.e.a., 2010. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol. Lett. 13 (5), 597-605.

Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. Oikos 7, 5–13.

- Lande, R., DeVries, P.J., Walla, T.R., 2000. When species accumulation curves intersect: implications for ranking diversity using small samples. Oikos 89 (3), 601_60
- Langdon, B., Pauchard, A., Aguayo, M., 2010. Pinus contorta invasion in the Chilean Patagonia: local patterns in a global context. Biol. Invasions 12 (12), 3961-397
- Lennon, J.J., Koleff, P., Greenwood, J., Gaston, K.J., 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. J. Anim. Ecol. 70 (6), 966-979.
- Lin, Y., Augspurger, C., 2008. Impact of spatial heterogenity of neighborhoods on long-term population dynamics of sugar maple (Acer saccharum). Forest Ecol. Manag. 255, 3589-3596

McGarigal, K., Čushman, S., Neel, M., Ene, E., 2002. Fragstats: spatial pattern analysis program for categorical maps. Technical Report.

- Ministerio De Agricultura, 1974. Decreto Ley 701. Fija Regimen Legal de los Terrenos Forestales o Preferenmente Aptos para la Forestacion, y Establece Normas de Fomento sobre la Materia.
- Murphy, M., Balser, T., Buchmann, N., Hahn, V., Potvin, C., 2008. Linking tree biodiversity to belowground process in a young tropical plantation: Impacts on soil co2 flux. Forest Ecol. Manag. 255 (7), 2577-2588.
- Murphy, H.T., Lovett Doust, J., 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105 (1),

Myers, N., Mittermeier, R., Mittermeier, C., Da Fonseca, G., Kent, J., et al., 2000. Biodiversity hotspots for conservation priorities. Nature 403 (6772), 853–858. Oberdorfer, E., 1960. Pflanzensoziologische Studien in Chile: Ein Vergleich mit Europa. Vol. 2. J. Cramer Weinheim.

Ogden, J., Braggins, J., Stretton, K., Anderson, S., 1997. Plant species richness under Pinus radiata stands on the central North Island volcanic plateau, New Zealand, N. Z. J. Ecol. 21 (1), 17-29

- Ovalle, C., Avendaño, J., Aronson, J., Del Pozo, A., 1996. Land occupation patterns and vegetation structure in the anthropogenic savannas (espinales) of central Chile. For. Ecol. Manag. 86 (1-3), 129-139.
- Paritsis, J., Aizen, M., 2008. Effects of exotic conifer plantations on the biodiversity of understory plants, epigeal beetles and birds in Nothofagus dombeyi forests. For. Ecol. Manag. 255 (5), 1575-1583.
- Pauchard, A., Aguayo, M., Peña, E., Urrutia, R., 2006. Multiple effects of urbanization on the biodiversity of developing countries: the case of a fast-growing metropolitan area (Concepcion, Chile). Biol. Conserv. 127 (3), 272-281.
- Pauchard, A., Alaback, P., 2004. Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central chile. Conserv. Biol. 18 (1), 238-248.
- Pauchard, A., Garcia, R., Pena, E., González, C., Cavieres, L., Bustamante, R., 2008a. Positive feedbacks between plant invasions and fire regimes: Teline monspessulana (l.) k. koch (fabaceae) in central chile. Biol. Invasions 10 (4), 547-553.
- Pauchard, A., Garcia, R.A., Pena, E., Gonzalez, C., Cavieres, L.A., Bustamante, R.O., 2008b. Positive feedbacks between plant invasions and fire regimes: Teline monspessulana (L.) K. Koch (Fabaceae) in central Chile. Biol. Invasions 10 (4), 547-553.
- Pawson, S.M., Brockerhoff, E.G., Didham, R.K., 2009. Native forest generalists dominate carabid assemblages along a stand age chronosequence in an exotic Pinus radiata plantation. Forest Ecol. Manag. 258, S108-S116.
- Pellissier, V., Gallet, S., Roze, F., 2004. Comparison of the vegetation and seed bank on hedge banks of different ages in Brittany, France. Environ. Manag. 34 (1), 52–61.
- Perley, C., 1994. Biodiversity, sustainability and a land ethic. New Zealand For. 39. 2–3.

Potton, C., 1994. A public perception of plantation forestry. New Zealand For. 39, 2–3.

- Program, A. G. S. J. V. A., RIRDC, Canberra A., 2004. Trees and Biodiversity; A Guide for Australian Farm Forestry. Agroforestry Guideline Series. Joint Venture Agroforestry Program and RIRDC, Canberra, ACT.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria,
- Saavedra, B., Simonetti, J.A., 2005. Small mammals of Maulino forest remnants, a vanishing ecosystem of south-central Chile. Mammalia 69 (3–4), 337–348. Sanchez Jardon, L., Acosta, B., delPozo, A., Casado, M., Ovalle, C., Elizalde, H., Hepp, C., deMiguel, J., 2010. Grassland productivity and diversity on a tree cover gradient in Nothofagus pumilio in NW Patagonia. Agric. Ecosyst. Environ. 137 (1), 213-218.
- Schmithusen, J., 1956. Die raumliche Ordnung der Chilenischen Vegetation. In: Bonner Geograpische Abhandlungen, vol. 17. Geographisches Institut Universitt Bonn, Bonn.
- Senbeta, F., Teketay, D., 2001. Regeneration of indigenous woody species under the canopies of tree plantations in Central Ethiopia. Trop. Ecol. 42 (2),
- Simberloff, D., Nuñez, M., Ledgard, N., Pauchard, A., Richardson, D., Sarasola, M., Van Wilgen, B., Zalba, S., Zenni, R., Bustamante, R.e.a., 2010. Spread and impact of introduced conifers in south America: lessons from other southern hemisphere regions. Austral Ecol. 35 (5), 489-504.
- Simonetti, J., Grez, A., Celis-Diez, J., Bustamante, R., 2007. Herbivory and seedling performance in a fragmented temperate forest of chile. Acta Oecol. 32 (3). 312-318.
- Simpson, E., 1949, Measurement of diversity, Nature 163, 11-13,
- Smith, B., Wilson, J.B., 1996. A consumer's guide to evenness indices. Oikos 76, 70–82.
- Smith-Ramirez, C., 2004. The Chilean coastal range: a vanishing center of biodiversity and endemism in South American temperate rainforests. Biodivers. Conserv. 13 (2), 373–393.
- Stephens, S., Wagner, M.R., 2007. Forest plantations and biodiversity: a fresh perspective. J. Forest. 105 (6), 307–313. Taki, H., Inoue, T., Tanaka, H., Makihara, H., Sueyoshi, M., Isono, M., Okabe, K., 2010. Responses of community structure, diversity, and abundance of understory plants and insect assemblages to thinning in plantations. Forest Ecol. Manag. 259 (3), 607-613.
- Tomasevic, J.A., Estades, C.F., 2008. Effects of the structure of pine plantations on their softness as barriers for ground-dwelling forest birds in south-central chile. Forest Ecol. Manag. 255 (3), 810-816.
- Vergara, P.M., Simonetti, J.A., 2004. Avian responses to fragmentation of the Maulino Forest in central Chile. Oryx 38 (4), 383–388. Williams, M.C., Wardle, G.M., 2005. The invasion of two native Eucalypt forests by Pinus radiata in the Blue Mountains, New South Wales, Australia. Biol. Conserv. 125 (1), 55-64.