Influence of anthropogenic disturbances on stand-structural complexity in Andean temperate forests

Julián José Caviedes Paúl

11,115 words

Thesis submitted for the degree of MSc Conservation,
Department of Geography,
UCL (University College London)

September 2015

UNIVERSITY COLLEGE LONDON

MSc Conservation

Please complete the following declaration and hand this form in with your MSc Research Project.

I, Julián José Caviedes Paúl hereby declare:

(a) that this MSc Project is my own original work and that all source material used is acknowledged therein;

(b) that it has been prepared specially for the MSc in Conservation of University College London;

(c) that it does not contain any material previously submitted to the Examiners of this or any other University, or any material previously submitted for any other examination.

Signed:

Date: 14/09/2015

Abstract

Despite Chilean temperate forests being one of the 34 biodiversity hotspots, almost 70% or their surface has been lost due to anthropogenic disturbances. I show how anthropogenic disturbances, namely, fire, logging, livestock, and their combined presence, are related to stand-structural complexity in Andean temperate forests in southern Chile. I measured forest structural attributes as well as the presence of anthropogenic disturbances in 505 plots, from 2,011 to 2,013, within the Villarica watershed in the Andean zone of La Araucanía Region, Chile. In each plot, understory density, coarse woody debris volume, snags density, stand basal area, and litter depth were measured to build an index of stand-structural complexity while signs of fire, logging, and livestock were measured to assess the presence of anthropogenic disturbances. Each plot was allocated to one of eight treatments representing anthropogenic disturbance as follows: no disturbance or control (Treatment one, T1), fire (T2), logging (T3), livestock (T4), combined presence of fire and logging (T5), combined presence of fire and livestock (T6), combined presence of logging and livestock (T7), combined presence of fire, logging, and livestock (T8). Ninety-five percent of the plots showed signs of anthropogenic disturbance (N = 475), with the combined presence of fire, logging, and livestock being the most common disturbance (N = 222; 44% of plots). The presence of livestock - alone or in combination with logging or logging and fire - showed the most significant differences in the mean values of the stand-structural complexity index in comparison to the control plots, suggesting that livestock is the disturbance that is most affecting the stand's structural complexity in the southern temperate forests. The highest mean values of the stand-structural complexity index were measured in plots that did not show any signs of anthropogenic disturbance, conversely, the lowest mean values of the stand-structural complexity index were measured in plots showing the combined presence of fire, logging, and livestock. My results suggest that forests should be managed to retain structural attributes such as understory density, coarse woody debris volume, snags density, stand basal area, and litter depth and reduce the presence of anthropogenic disturbances in order to prevent the loss of biodiversity in the southern temperate forests.

Table of contents

List of tables

List of figures

Acknowledgements

I would not have been able to finish my master’s degree and thesis without the kind help, encouragement and support of many people. I would like to thank my tutor Jan Axmacher for all his advice and guidance. I will always be grateful to my parents Francisca Paúl and Iván Caviedes for their unconditional and constant support. Cristóbal Caviedes and Franca Wolf were my companionship during my year in London; I have no idea what I would have done without you both. I would also like to thank my professors Carl Sayer and Sam Randalls for their willingness to help and for their advice every time I requested it. I am especially grateful to my friend and dissertation co-tutor José Tomás Ibarra for his immense patience, endless help and constant encouragement throughout all of these years.

Two people have been essential in my development as a conservationist, Tomás Altamirano and José Tomás Ibarra. I will always feel indebted to them for introducing me to one of my places in the world, the southern temperate forest of Chile. I am also grateful to all my naturalists’ friends and mentors that have been an inspiration throughout all these years, Tomás Altamirano, Cristián Bonacic, Diego Cox, don Juan Gastó, Benito González, José Tomás Ibarra, and Gloria Montenegro. All the conversations and oral teachings that they gave me are more important than they can possibly imagine.

I would also like to thank the Peregrine Fund, Ministry of the Environment (FPA 9-I-009-12), the Interdisciplinary Centre for Intercultural and Indigenous Studies-ICIIS (CONICYT/FONDAP/15110006), Centre of Local Development (CEDEL-Campus Villarrica PUC), Rufford Small Grants for Nature Conservation, Cleveland Metroparks Zoo, Cleveland Zoological Society, and Environment Canada for funding this research. The Chilean Forest Service (CONAF), M. Venegas and R. Sanhueza (Guías-Cañe), Kawelluco Private Sanctuary, and many other landowners allowed us to work in their lands. I am also grateful to the Comisión Nacional de Investigación Científica y Tecnológica de Chile (CONICYT) from which I received a postgraduate scholarship that allowed me to study a master’s program abroad.

“Quién no conoce el bosque chileno, no conoce este planeta. De aquellas tierras, de aquel barro, de aquel silencio, he salido yo a andar, a cantar por el mundo (Neruda, 1974)”.

“Anyone who has not been in the Chilean forest does not know this planet. I have come out of that landscape, that mud, that silence, to roam, to go singing through the world (Neruda, 1974)”.

Para los bosques y el mar de Chile, patrimonio natural invaluable de la humanidad.

To the forests and sea of Chile, priceless natural heritage of humankind.

1. Introduction

1.1. Chilean temperate forests: a Biodiversity Hotspot in southern South America

On a per unit area basis, temperate forests are the world's densest and tallest forests including some of the longest-lived tree species (Pan et al., 2013). These long-lived species, like the Patagonian cypress (*Fitzroya cupressoides*) which has been estimated to achieve an average life of more than 3,000 years, are an invaluable record of climatic variation during the last millennia (Lara and Villalba, 1993; Armesto et al., 2001). In addition, temperate forests are widely acknowledged for their high species diversity and rates of endemism (Olson and Dinerstein, 1998). Moreover, these ecosystems play an essential role as carbon sinks, hosting some of the carbon-densest forests on the planet (Keith et al., 2009; Friedlingstein et al., 2010; Whitman and Hagan, 2007). Different studies have highlighted the biological importance and high biodiversity conservation value of temperate rainforests, and thus have been identified as global conservation priorities (Myers et al., 2000; Brooks et al., 2006; Mittermeier et al., 2003; Olson and Dinerstein, 1998). Nonetheless, the extent of anthropogenic disturbances has reduced the world's temperate forests' biomass by more than 70% of its original surface (Pan et al., 2013).

The temperate forests of South America in Chile and Argentina are the southernmost temperate forests in the world (Armesto et al., 1998). With a total of 13.4 million ha and stretching for over 2,000 km, Chile hosts the largest remaining area of southern temperate forests, representing one-quarter of all temperate ecosystems worldwide (Wilcox, 1996; Conaf et al., 1999; Rozzi et al., 2000). The Chilean temperate forests, found between 35° - 55° south latitude, are considered one of the 34 biodiversity hotspots because of their high rates of endemism and species diversity (Myers et al., 2000; Neira et al., 2002). Even though these forests are considered to be floristically impoverished in comparison with tropical ecosystems, when focusing on evergreen temperate forests, these forests display the highest floristic richness globally (Arroyo et al., 1996). In addition, their high number of endemics especially for plant genera (e.g. *Aextoxicon*, *Lapageria, Philesia*, and *Pitavia*), from which about 80% are monospecific, and the relict family Aextoxicaceae accredits these forests high conservation value (Arroyo et al., 1996).

These forests, which include evergreen and deciduous forests types of diverse life forms with mixed angiosperm and gymnosperm species, are distributed across an elevational gradient from the sea-level to the tree line at 2,400 meters above sea level (masl) (Veblen et al., 1980). In contrast to other temperate ecosystems, since the mid-tertiary, southern temperate forests have developed in isolation - bounded to the north by the Atacama Desert, to the west by the Pacific Ocean, to the south by the Antarctica, and the Andes Mountains to the east - from other forested landscapes (Villagrán and Hinojosa, 1997). This biogeographic island characteristic determines several challenges for biodiversity conservation. On the one hand, the southern temperate forests present high rates of endemism for both flora and fauna, with levels estimated to be 90% for seed plant species (Villagrán and Hinojosa, 1997) and 45% for all vertebrates species (Armesto et al., 1996) that need to be conserved. On the other hand, plant recolonization and vegetation succession after the occurrence of natural or anthropogenic disturbances are considered to be extremely complex and problematic due to the lack of recolonization sources (Armesto et al., 1998). Unfortunately, the conservation of these ecosystems is threatened as southern temperate forests are being subject to extensive and intensive anthropogenic disturbances that are significantly reducing their total surface (Echeverría et al., 2006).

1.2. Stand-scale anthropogenic disturbances on forest ecosystems: fire, logging, and livestock

The reduction of native forests is recognized as a major threat to biodiversity worldwide (Ceballos et al., 2009; Thompson et al., 2009; Laurance et al., 2000). Several studies conducted in different forest biomes have reported the negative impacts of anthropogenic disturbances on forest stands (Dupouey et al., 2002; Ojima et al., 1994; Foley et al., 2005; Sala et al., 2000; Laliberté and Tylianakis, 2012). Anthropogenic disturbances affect forest biodiversity across spatial scales (Echeverría et al., 2007; Mishra et al., 2004; Liira et al., 2007; Ramírez-Marcial et al., 2001). For example, large-scale land use change is the most severe driver of worldwide biodiversity loss (Sala et al., 2000). For its part, small-scale disturbances, particularly logging, fire, and livestock farming, degrade stand-scale distribution and density of structural attributes in forest ecosystems (Mishra et al., 2004; Liira et al., 2007; Ramírez-Marcial et al., 2001). These disturbances are affecting species diversity and composition, leading to floristic homogenization as well as reducing forest structural complexity, hence having detrimental effects on ecosystem functioning (Rüger et al., 2007; Echeverría et al., 2007; Irwin et al., 2010; Lambert et al., 2005; Zamorano-Elgueta et al., 2012; McElhinny et al., 2006a). Ramírez-Marcial et al. (2001) showed that tree species diversity and absolute density as well as stand basal area decreased with increasing disturbance intensity when studying the influence of forest extraction, livestock grassing, and fires in forest structure in Mexico. Moreover, Mishra et al. (2004) indicated that less disturbed forest stands had higher canopy cover values, tree density, and light interception in comparison to disturbed stands in India. These results agree with the ones described by Liira et al. (2007), who showed that anthropogenic disturbances were directly decreasing understory density and stand basal area along a disturbance gradient in hemi-boreal forest stands in Estonia.

Despite their ecological importance, temperate forests of southern South America have experienced a long history of anthropogenic disturbances (fragmentation and degradation) (Echeverría et al., 2006; Neira et al., 2002). Almost 70% of Chilean temperate forests have been lost due to large-scale and small-scale disturbances (Lara, 1996). Early records of anthropogenic disturbances in Chile date back to the 16th century when the Spanish colonizers burned large areas of native forests to prevent the Mapuches from taking refuge there (Neira et al., 2002). Later in the early 19th century, with the settlement of European colonists in the south, vast expanses of temperate forests were cleared and converted to cropland and pasture for commercial exploitation (Rozzi et al., 2000). The extent of this deforestation process is described as one of the most rapid deforestation events ever measured in Latin America (Veblen, 1983). The vast areas of mid-successional stands (< 80 years old) within southern temperate forests originated in the 1,940s, after one of the most recent human-induced catastrophic fires, cataloged as a 'large stand-destroying event' (González et al., 2005:1194; Veblen and Ashton, 1978; Veblen et al., 1992). Nowadays, different authors agree that landscape scale practices such as land use change for intensive agriculture and forest conversion to exotic plantations are the main threats affecting Chilean temperate forests (Echeverría et al., 2007; Armesto et al., 2009; Wilson et al., 2005; Armesto et al., 1998; Neira et al., 2002). These threats have been extensively reported for the southern temperate forests at a landscape scale (Echeverría et al., 2007; Echeverría et al., 2006; Wilson et al., 2005). However, stand-scale studies showing the effects of small-scale anthropogenic disturbances (i.e. logging, livestock farming, and human-set fires) on forest structural complexity are still scarce; thus, at a stand-scale native forest exploitation continues unchanged (Simonetti and Armesto, 1991).

Logging is the most prevalent disturbance in southern temperate forests (Neira et al., 2002). Even though this disturbance is not causing an important reduction in forest surface, logging accounts for the degradation of 75% of current forest area (Neira et al., 2002). This disturbance is directly related to stand-structural complexity, affecting the availability of standing dead trees (hereafter snags) and coarse woody debris (CWD), and reducing the litter depth, stand basal area, and understory density (Neira et al., 2002). For its part, human-set forest fires account for the degradation of 25% of temperate forests' total surface (Neira et al., 2002). Different studies have shown how human-set forest fires have reduced CWD volume, snags density, and litter depth in northern and southern temperate forests (Carmona et al., 2002; Harmon et al., 1986). For example, Carmona et al. (2002) showed that CWD biomass was substantially reduced in sites that had been subject to anthropogenic fires in comparison with undisturbed sites. In addition, other studies have shown the impact of livestock farming in forest composition and structure by altering plant regeneration capacity and reducing understory density (Zamorano-Elgueta et al., 2014; Zamorano-Elgueta et al., 2012). Zamorano-Elgueta et al. (2012) showed that for the endangered monkey puzzle tree (*Araucaria araucana*) regeneration rates dropped to zero when being subject to low livestock intensity. Maintaining structural complexity throughout forests stands has been proposed as a key principle to stop forest degradation at a stand-scale and as an effective way to conserve and enhance biodiversity in temperate forest ecosystems (Franklin, 1988; Lindenmayer et al., 2000).

1.3. An index of stand-structural complexity for the Andean temperate forest

Stand-structural complexity is defined by McElhinny et al. (2005:5) as 'the measure of a number of different structural attributes present at a stand and the relative abundance of each of these attributes'. Moreover, the combination of different key stand-structural attributes in an index of structural complexity has been recently proposed as a practical biodiversity surrogate that would provide useful information for forest management (McElhinny et al., 2005; Sabatini et al., 2015; Beckschäfer, 2013; Tews et al., 2004). Studies have shown that stands with higher structural complexity generally harbor higher species diversity while promoting ecosystem functioning and greater ecological stability in comparison to the less complex ones (Beckschäfer, 2013; Hansen et al., 1991; Ibarra and Martin, 2015). New sustainable forest management paradigms emphasize creating and maintaining structural complexity at a stand-scale (Lindenmayer et al., 2000); therefore, an index of structural complexity would provide an effective way of classifying stands according to the effects they may have on biodiversity (McElhinny et al., 2005). The rationale behind using an approach based on structural attributes is that forest stands with a complex array of structural attributes would provide greater niches for a broad array of organisms while ameliorating negative relationships between them such as depredation and competition (McElhinny et al., 2006b; Braunisch et al., 2014; Newton, 2008; Franklin and Van Pelt, 2004). Studies on the vegetation regeneration of temperate forests after disturbances have detailed the importance of maintaining original forest remnants for the short-term recovery of the structural characteristics and the maintenance of the biological process in disturbed forest ecosystems (Franklin and Armesto, 1996; Gibbons et al., 2002).

To better conserve the South American temperate forests, efforts should focus on rescuing remaining forests for conservation in high biodiversity areas and those regions which are intensely managed (Armesto et al., 1998). As stated by Franklin (1988:173), 'the objectives of maintaining biodiversity must be incorporated into intensively managed temperate forests'. Anthropogenic disturbances affecting the availability and composition of stand-structural attributes such as understory density, CWD volume, litter depth, snags density, and stand basal area are affecting mammals, birds, reptiles, amphibians, and invertebrates that depend on these key structural attributes for survival (Díaz et al., 2005; Ibarra et al., 2010; Ibarra et al., 2012; Ibarra and Martin, 2015). Even though different studies have highlighted the importance of structural complexity for biodiversity (Tomasevic and Estades, 2006; Owens et al., 2008; Uetz, 1979; Yahner, 1986), there is still a cultural tendency to simplify complex forest structure to single cohort stands (Armesto et al., 1998). Therefore, management practices that enhance structural complexity should be a priority in Chilean native forests where a large proportion of their biodiversity is on private land outside protected areas (Armesto et al., 1992). For example, it has been suggested that the retention of various large, old, and dead trees is successful in the conservation of biodiversity features that are dependent upon them as well as in the increase of the structural complexity of logged forests (Franklin and Armesto, 1996).

For instance, a dense understory of herbs, bamboo, shrubs, and tree samplings in combination with a rich leaf-litter soil would provide different niches for habitat, refuge, and food availability for different organisms. Reid et al. (2004) suggested that retaining a dense bamboo understory was critical for the conservation of four endemic Rhinocryptidae understory birds in the southern temperate forests. Moreover, Meier and Merino (2007) found that the presence of the southern pudu (*Pudu puda*) was significantly associated with a dense bamboo understory. Other studies have proposed that sites with deep leaf litter sustain higher diversity and density of herpetofauna as well as invertebrate species (Fauth et al., 1989; Uetz, 1979). The importance of CWD for birds, amphibians, reptiles, and invertebrates has been demonstrated in several locations (Bowman et al., 2000; Lohr et al., 2002; Owens et al., 2008; Siitonen, 2001). In the southern temperate forest, the presence of CWD provides refuge for small mammals, such as the endemic marsupial Austral opossum (*Dromiciops gliroides*) (Kelt et al., 1994; Kelt and Martínez, 1989; Celis-Diez et al., 2012). Many invertebrates, cavity nesting birds, and mammals depend largely on the availability of snags for their survival (Altamirano et al., 2015; Gibbons et al., 2002; Siitonen, 2001; Ibarra et al., 2012).

1.4. Thesis objectives

As previously detailed, there is some available information about the negative effects that anthropogenic disturbances are having upon stand-structural attributes, and that the importance of those structural attributes is essential to a broad array of organisms inhabiting temperate forests. However, no structural complexity index that could guide management conservation actions has ever been created for the southern temperate forests. My aim is to create a stand-structural complexity index and identify how anthropogenic disturbances (associated with livestock, fire, and logging) and their potential additive effects may influence stand-structural complexity in temperate forests. Additionally, I will develop and discuss the potential role of a stand-structural complexity index for forest conservation and management strategies. I will specifically address the following questions in relation to Andean temperate forest stands: (1) Is it feasible to generate a simple but integrative stand-structural complexity index based on the importance of structural attributes for biodiversity that could be incorporated into forest management?, (2) Is there any relationship between a stand-structural complexity index and stand-scale anthropogenic disturbances?, (3) Which of the three anthropogenic disturbances or the potential additive effects between them are most related to stand-structural complexity? These questions will provide valuable information to enhance the knowledge about southern temperate forests and will contribute with practical information to policy decisions regarding forest conservation and management.

2. Methods

2.1. Study site

The study was conducted between 2,011 and 2,013 within the Araucarias Biosphere Reserve (UNESCO, 2010). Specifically, vegetation surveys were conducted in an area of 2,585 km² within the Villarica watershed in the Andean zone of La Araucanía Region, southern Chile (39° 15’S 71°W) (Fig. 1). The area has a temperate climate with a short dry season (< 4 months) in the summer and mean precipitations of 1,945 mm/year (Di Castri and Hajek, 1976). The mean annual temperature is 1.9 °C for the coldest month (July) and 15.1 °C for the warmest month (January) (Di Castri and Hajek, 1976). The vegetation comprises three vegetation types distributed along an elevational gradient from 200 masl up to the tree line at 1,500 masl. At lower elevations (200 - 500 masl), forests are dominated by deciduous species like *Lophozonia obliqua* and *Nothofagus dombeyi*, mainly associated with *Laurelia sempervirens, Eucryphia cordifolia, Persea lingue,* and *Aextoxicon punctatum*. Mid-elevation forests (500 - 900 masl) are mixed forests dominated by the evergreen species *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *N. dombeyi*. At higher elevations (> 900 masl), forests are dominated by *Araucaria araucana* and *N. pumilio* (Gajardo, 1993). The majority of public protected areas and larger tracks of forests are at high elevations (> 700 masl) with a topography characterized by mountains and volcanoes. Valley floors are mostly used for agriculture in combination with human settlements in small to medium-sized villages and towns. This has caused lowland forest remnants (< 700 masl) to experience intense anthropogenic disturbances, mainly logging, livestock farming, and fires (Veblen et al., 1992). The largest human settlements within the study area are Pucón (227 masl) with a population of 13,925 inhabitants, Caburgüa (700 masl) with a population of 1,731 inhabitants, and Villa San Pedro (380 masl) with a population of 187 inhabitants (Ilustre Municipalidad de Pucón, 2005).

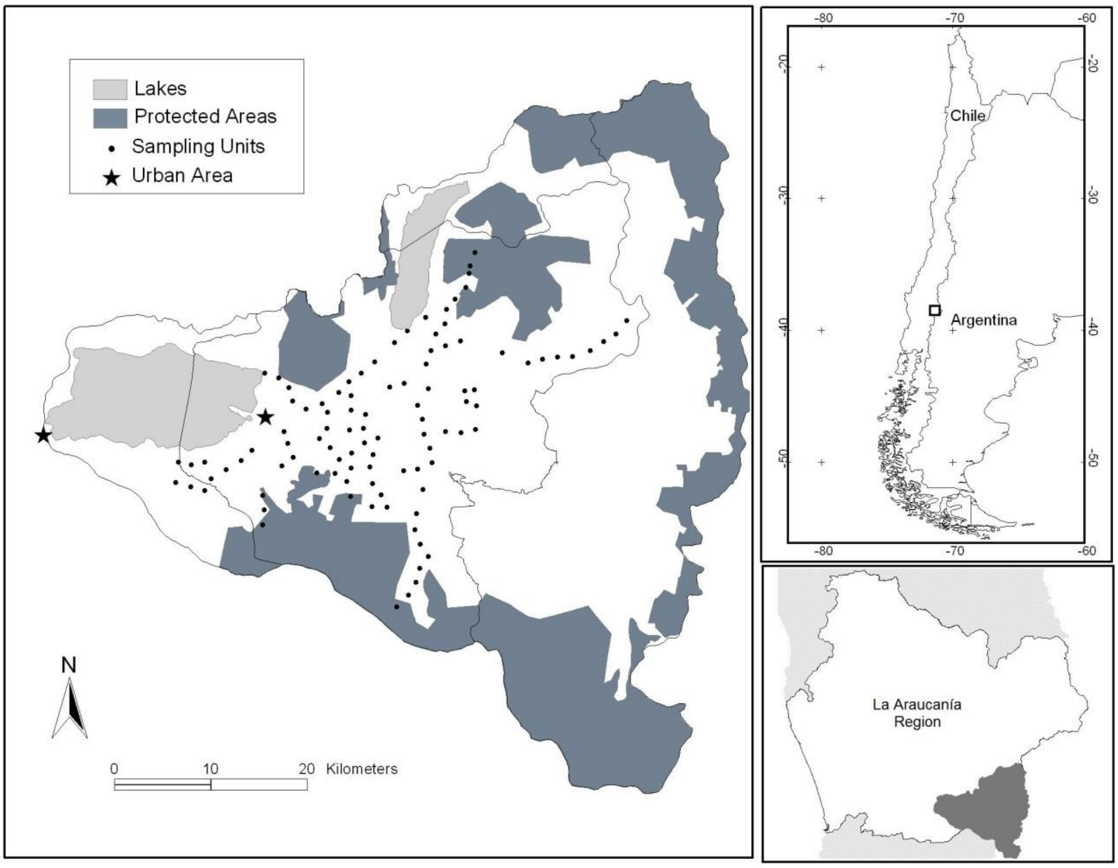

Fig. 1. Spatial distribution of the 101 sites used to build an index of stand-structural complexity in Andean temperate forests at the Villarrica watershed, La Araucanía Region, Chile. The lower right part of the map shows the position and surface occupied by the Villarrica watershed (colored) within the La Araucanía Region.

2.2. Selection of structural attributes to be included in the index

The stand-structural complexity index was constructed adapting the methodology proposed by McElhinny et al. (2006b). Constructing an index of structural complexity requires a four-step approach that involves: (1) establishing a comprehensive suite of stand-structural attributes, (2) identifying the core set of attributes to be included in the index based on the specific purpose of the index, (3) surveying these attributes in a set of different stands, including different vegetation communities and successional stages, and (4) combining the core set of attributes into an additive index. To address point 1, I selected those attributes that were considered a structurally important attribute for the habitat of birds, amphibians, invertebrates, mammals, and reptiles in international and Chilean forest ecosystems (Table 1). The core set of attributes should

(i) have a low kurtosis (< 2), (ii) work as a surrogate for other structural attributes and, (iii) be easily measured in the field (McElhinny et al., 2006b). Each of the five selected attributes, stand basal area, CWD volume, litter depth, snags density, and understory density, were selected as they have demonstrated a high sensitivity to anthropogenic disturbances and because they can be readily surveyed in areas under forest management practices.

Table 1. List of the five core structural attributes selected to be included in the stand-structural complexity index and their ecological importance for different forest ecosystems' faunal groups.

Structural complexity attribute	**Description**	**References for forest ecosystems from elsewhere**	**References for the southern temperate forests**
Understory density	A dense understory provides microclimatic conditions and food supply essential to understory birds. Some mammals require a dense understory for cover while stalking prey and breeding. The shade provided by a dense understory provides critical microhabitat resources for reptiles, as well as regulating the moisture and temperature which are essential for different amphibian species. For invertebrates and understory birds, a dense understory provides an important source of refuge to hide from different predators.	Thiollay, 1993; Aleixo, 2012; Malcolm and Ray, 2000; Dupuis et al., 1995; Whitfield et al., 2007; Fowler et al., 1993	Meserve et al., 1991; Reid et al., 2004; Acosta-Jamett and Simonetti, 2004; Meier and Merino, 2007; Ibarra et al., 2014a
Coarse woody debris volume	Coarse woody debris provides a favorable breeding habitat for several bird species. Small mammals can use CWD for travelling, foraging, and nesting. Moreover, many invertebrate species, especially saproxylic insects, depend on CWD for feeding. The presence of CWD plays an essential role as refuge for different amphibian and reptile species.	Lohr et al., 2002; Bowman et al., 2000; Siitonen, 2001; Owens et al., 2008; Davis et al., 2010	Celis-Diez et al., 2012; Ibarra et al., 2012; Kelt and Martínez, 1989; Kelt et al., 1994; Soto-Azat et al., 2013
Stand basal area	A greater stand basal area provides higher food resources availability to frugivorous and folivorous mammals and birds. In addition, a stand with a large basal area will provide a wide range of suitable microhabitats (e.g. tree cavities) for a series of invertebrate, amphibian, reptile and birds species.	Grove, 2002; Ross et al., 2000; Johns, 1988	Ojeda and Chazarreta, 2014; Dunstone et al., 2002; Carneiro et al., 2013; Ibarra et al., 2014a

Structural complexity attribute	Description	References for forest ecosystems from elsewhere	References for the southern temperate forests
Litter depth	Litter provides refuge for litter-dwelling invertebrates that are foraged by different leaf-litter birds and mammals. This ground level attribute provides moist conditions that are essential for some forests' small mammals. In addition, a deep and dense leaf litter provides diverse habitat niches required by reptile and amphibian species.	Laurance, 2004; Yahner, 1986; Fauth et al., 1989; Uetz, 1979	Crump, 2002; Willson et al., 1996; Kuschel, 1960; Reid et al., 2002; Barbosa and Marquet, 2002
Standing dead trees density (i.e. snags density)	Standing dead trees provide different habitat resources for a range of forest-dwelling animal species. For instance, birds and mammals use snags as shelter and breeding sites. In addition, snags provide shade and litter inputs for amphibians as well as basking areas for reptiles. Moreover, standing dead trees provide high quality habitat and food resources for dead-wood dependent invertebrates.	Smith et al., 1989; Nappi et al., 2010; Bennet et al., 1994; Raphael et al., 1984; MacNeil et al., 2013	Ibarra et al., 2012; Díaz et al., 2005; Tomasevic and Estades, 2006; Ojeda and Chazarreta, 2014; Carneiro et al., 2013; Díaz and Kitzberger, 2013

2.3. Study design and forest sampling

The study design and data used for this dissertation constitute secondary data collected by myself and other researchers as part of the PhD thesis of Dr. José Tomás Ibarra from the University of British Columbia (see Ibarra, 2014b). The selection and calculation of the structural attributes to be included in the index (section 2.2.), their transformations and analysis as well as identifying how anthropogenic disturbances may affect stand-structural complexity in Andean temperate forests (section 2.4.) were all part of my own individual work.

One hundred and one sites were established along an elevational gradient from 221 masl to 1,361 masl (Fig. 1) across a disturbance gradient which included openfields, shrublands, exotic plantations, secondary forests, and old-growth forests. The sites were selected using ArcGIS 10.1 by identifying all the headwaters of smaller basins representing a variety of habitat conditions that could be accessed either by rural roads or hiking trails. Thirteen out of the total 19 basins were randomly selected, placing the first site near the headwater of each basin. The remaining sites were systematically located every 1.5 km descending from the headwaters (Ibarra et al., 2014c). At each of the 101 sites, five vegetation plots (22.4 m diameter; 0.04 ha; N = 505 plots) were set using an L-shaped transect (Fig. 2a). Each plot was separated by a distance of 125 m between them and at least 50 m away from the nearest road or hiking trail (Affleck et al., 2005).

In each vegetation plot a set of structural attributes was measured, including: (1) understory density, (2) CWD volume, (3) litter depth, (4) tree diameter at breast height (DBH), and (5) number of standing dead trees. Two 11.2 m linear transects were established north to south from the center of the plot. Along this transect, understory density and litter depth were measured at five points: the center of the plot and at 5.6 m and 11.2 m to the north and south from the center of the plot as shown in Fig. 2b. Understory density was measured by the number of contacts by the vegetation from the ground level to 3 m height at each of the five points as well as litter depth (Díaz et al., 2006; Yahner, 1986). For each CWD with a diameter ≥ 7.5 cm, the length and diameter were measured (Ibarra et al., 2014a). Tree DBH was measured using a diameter tape for all trees with DBH ≥ 12.5 cm (Ibarra et al., 2014a). All dead standing trees with DBH ≥ 12.5 cm and height ≥ 1.3 m were counted (Ibarra et al., 2014a). Structural attributes were averaged within each plot in order to emphasize the stand's unique structural conditions that differentiate it from adjacent areas (Lindenmayer and Franklin, 2002). In addition, the presence or absence of anthropogenic disturbances (fire, logging, and livestock) was measured in each plot. Anthropogenic disturbances were defined as the disturbances that occurred within the last 80 years. According to different authors, a series of high-severity human-set fires, that destroyed a large amount of stands in the southern temperate forests, occurred in the early 20th century - with the last stand-destroying event occurring between 1,944 and 1,945 (Veblen and Ashton, 1978; Veblen et al., 1992; González et al., 2005). Hence, and based on the impossibility of identifying signs of logging or livestock that were older than 80 years, fire was considered as the oldest disturbance. Fire was measured every time there were signs of fire-scars in a plot. Logging was measured when a plot showed stumps without resprouts of tree species or rests of logged wood, while the presence of livestock was measured when any signs of manure, pats or browsed vegetation were present at each plot. Eight different habitat categories were used to visually define each plot and the surrounding area in a 50 m radius as: (1) Old-growth forest (> 200 years old), (2) Mid-successional forest (< 80 years old with bamboo understory), (3) Mid-successional forest (< 80 years old with understory different than bamboo), (4) Mid-successional forest (< 80 years old without understory), (5) Early successional forest (< 20 years old), (6) Mixed shrubland, (7) Openfield, and (8) Exotic plantation.

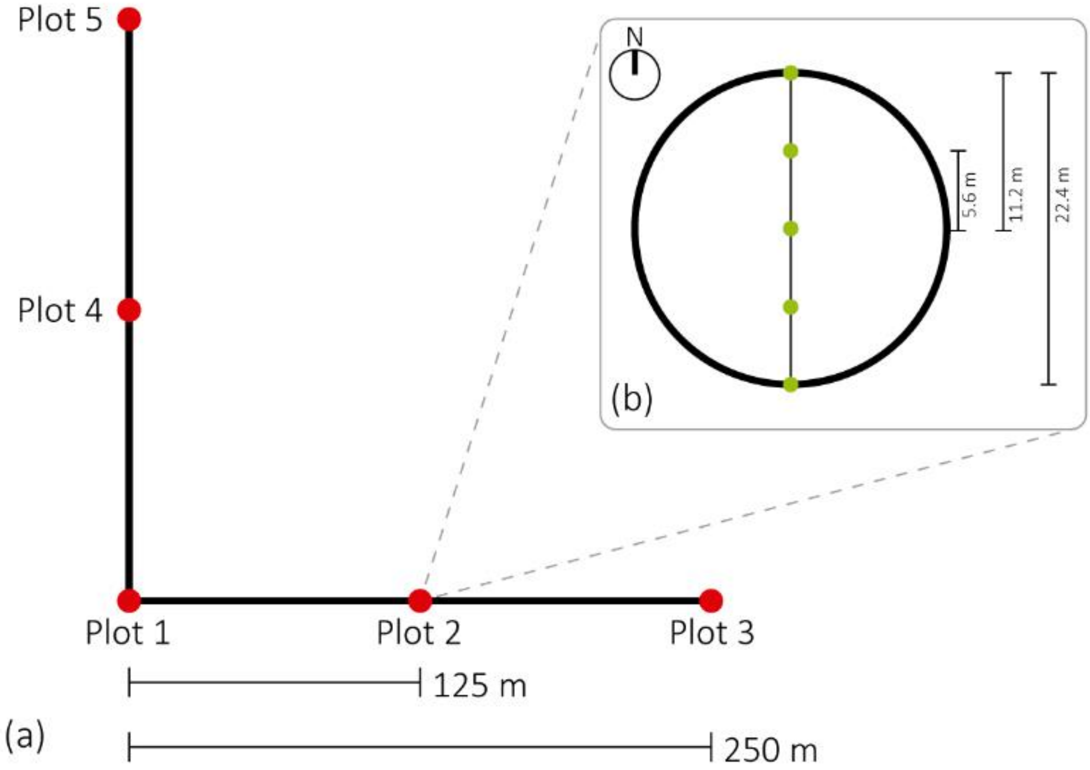

Fig. 2. (a) Scheme of the L-shaped transect with five vegetation plots (red dots) surveyed at each of the 101 sites. Plot 1 was located at the vertex of the L-shaped transect, the remaining plots were separated with a distance of 125 m between them along two 250 m transects starting from plot 1. (b) Scheme of a vegetation plot. Green dots represent each of the five points, distributed north to south along a 22.4 m transect, at which understory density and litter depth were measured.

2.4. Data analysis

2.4.1. Developing an index of stand-structural complexity

In order to improve the distribution of the attributes showing a high kurtosis (< 2), the raw data was subject to logarithm (x+1) transformations. A regression analysis through quartiles was performed to rescale each of the five selected stand-structural attributes to a score ranging from 0 to 10. A score of 2.5, 5, 7.5 and 10 was set to the quartile midpoints corresponding to the 12.5, 37.5, 62.5 and 87.5 percentiles of the raw data distribution (McElhinny et al., 2006b; Sabatini et al., 2015). A maximum score of 10 was attributed to the 87.5 percentile while the equation was constrained so that the minimum score was 0. The structural complexity index was obtained by adding all the rescaled values, with 0 being the minimum and 50 being the maximum additive value. Thus, the total value of a stand with high structural complexity would be closer to 50, while the total value of a less structurally complex stand would be closer to 0. Finally, the index was expressed as a percentage (McElhinny et al., 2006b; Sabatini et al., 2015).

2.4.2 Relationship between disturbances and stand-structural complexity

Exotic plantations covered only < 2% of the study area; therefore, plots categorized as exotic plantations (N = 6) were considered marginal and excluded from all analyses. Each of the remaining plots (N = 499) were allocated to one of eight treatments representing anthropogenic disturbance. The eight treatments included plots that were subject to: no disturbance or control (Treatment one, T1), fire (T2), logging (T3), livestock (T4), combined presence of fire and logging (T5), combined presence of fire and livestock (T6), combined presence of logging and livestock (T7), combined presence of fire, logging, and livestock (T8). Given the lack of normality for the whole dataset, I performed a non-parametric Kruskal-Wallis test to test if there were significant differences in the mean values of the stand-structural complexity index between the eight different disturbance treatments and a multiple comparison post hoc test to test the different relationships between the eight treatments and the structural complexity index for the 499 vegetation plots. In addition, I performed a non-parametric Kruskal-Wallis test to test for significant differences in the mean values of the stand-structural complexity index between the seven habitat categories and a Holm-Sidak post hoc test to test the different relationships between the seven habitat categories and the structural complexity index. All statistical analyses were performed using the statistical software R (R Core Team, 2014).

3. Results

3.1. Stand-structural attributes as determinants of stand-structural complexity

The mean values of the five selected stand-structural attributes - understory density, CWD volume, litter depth, stand basal area, and snags density - varied according to the habitat category (Table 2). The highest mean values of understory density, CWD volume, litter depth, and stand basal area were measured in old-growth forest plots while the highest mean value of snags density was measured in mid-successional forest with bamboo understory plots. Conversely, the habitat category openfield showed the lowest mean values of each of the five structural attributes. The values of understory density ranged from 0.0 contacts per plot measured in old-growth, mid-successional forest without understory, mixed shrubland, and openfield plots to 20.2 contacts in an old-growth forest plot (Appendix 1). The minimum value of CWD volume (0.0 m^3/ha) was measured in all the habitat categories while the maximum value (188.5 m^3/ha) was measured in a mixed shrubland plot. Litter depth values ranged from 0.0 cm in mid-successional forest without understory, early successional forest, mixed shrubland, and openfield plots to 22.0 cm in a mid-successional forest with bamboo understory plot. Stand basal area values ranged from 0.0 m^2/ha in early successional forest, mixed shrubland, and openfield plots to 310.50 m^2/ha in a mid-successional forest with bamboo understory plot. Finally, snags density values ranged from 0.0 (stems/ha) in all the habitat categories to 482.4 (stems/ha) in a mid-successional forest with bamboo understory plot.

Table 2. Results showing the mean values (SD) of the five structural attributes included in the stand-structural complexity index and the structural complexity index expressed in percentage in relation to the seven different habitat categories.

	Understory density (n° contacts)	Coarse woody debris (m^3/ha)	Stand basal area (m^2/ha)	Litter depth (cm)	Snags density (stems/ha)	Structural complexity index (%)
Old-growth forest	7.55 ± (3.87)	13.74 ± (23.79)	75.28 ± (35.62)	6.57 ± (3.7)	46.02 ± (33.20)	80.03 ± (9.10)
Mid-successional forest (bamboo understory)	5.49 ± (2.13)	11.34 ± (16.88)	41.67 ± (33.07)	6.31 ± (3.36)	55.01 ± (75.62)	73.18 ± (11.82)
Mid-successional forest (other understory)	4.72 ± (2.61)	4.41 ± (8.68)	34.76 ± (19.24)	5.23 ± (2.63)	44.11 ± (68.58)	65.18 ± (10.32)
Mid-successional forest (no understory)	1.70 ± (1.24)	5.85 ± (15.01)	35.22 ± (17.95)	2.98 ± (2.43)	35.20 ± (53.15)	55.66 ± (13.75)

	Understory density (n° contacts)	Coarse woody debris (m³/ha)	Stand basal area (m²/ha)	Litter depth (cm)	Snags density (stems/ha)	Structural complexity index (%)
Early successional forest (< 20 years old)	3.58 ± (2.87)	2.30 ± (6.74)	16.71 ± (13.11)	4.30 ± (2.33)	17.26 ± (32.10)	54.21 ± (11.04)
Mixed shrubland	2.39 ± (2.13)	3.11 ± (20.32)	8.71 ± (13.91)	1.65 ± (1.83)	12.55 ± (38.11)	43.91 ± (11.24)
Openfield	0.42 ± (0.41)	1.18 ± (1.23)	2.21 ± (2.27)	0.41 ± (0.41)	0 ± (0)	34.38 ± (3.27)

The mean values of the stand-structural complexity index varied with the habitat category (Fig. 3). The least structurally complex plots were measured in mixed shrubland and openfield habitats with a stand-structural complexity index value of 31.82%. On the other side, the most structurally complex plot was measured in a mid-successional forest with bamboo understory with a stand-structural complexity index value of 100.00% (Appendix 1). A Kruskal-Wallis test showed significant differences in the mean values of the stand-structural complexity index between the seven habitat categories ($X^2 = 302.0071$, df = 6, p-value = 2.2e-16). In addition, a Holm-Sidak post hoc test revealed significant differences ($p < 0.005$) between each of the seven habitat categories.

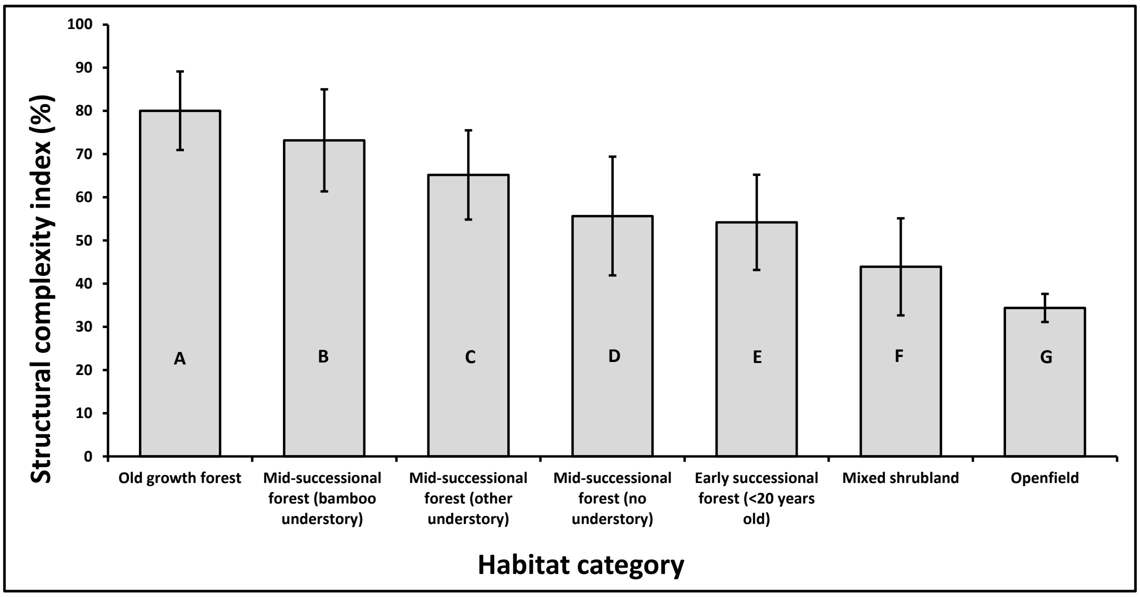

Fig. 3. Relationship between the mean values of the stand-structural complexity index and the seven habitat categories. Bars with different letters were significantly different according to a Holm-Sidak post hoc test. Small bars are ± standard deviation.

3.2. Presence of stand-scale anthropogenic disturbances (fire, logging, and livestock) in an Andean temperate forest

The habitat category mid-successional forest with bamboo understory accounted for the highest number of plots (N = 102), while the lowest number of plots was measured for openfield (N = 28). Ninety-five percent of the plots showed signs of anthropogenic disturbances (N = 475), with the combined presence of fire, logging, and livestock being the most common disturbance (N = 222; 44% of plots), and the combined presence of fire and livestock being the least common disturbance (N = 20). Only 24 plots did not show any signs of anthropogenic disturbances from which 92% of these plots (N = 22) corresponded to old-growth forests (Table 3).

Table 3. Results showing the distribution of the number of plots (N = 499) from each of the eight different disturbance treatments along the seven habitat categories.

	No disturbance	Fire	Logging	Livestock	Fire + Logging	Fire + Livestock	Logging + Livestock	Fire + Logging + Livestock
Old-growth forest	22	2	1	5	22	1	2	9
Mid-successional forest (bamboo understory)	0	8	2	1	39	9	6	37
Mid-successional forest (other understory)	1	10	14	2	33	6	7	26
Mid-successional forest (no understory)	0	0	6	2	9	1	10	16
Early successional forest (< 20 years old)	1	3	11	11	17	3	10	19
Mixed shrubland	0	0	0	0	0	0	0	87
Openfield	0	0	0	0	0	0	0	28
N (total number of plots per treatment)	24	23	34	21	120	20	35	222

The percentage of plots showing signs of anthropogenic disturbance varied according to the habitat category (Table 4). Fifty three percent of old-growth forest plots showed signs of fire or logging, 27% of them showed signs of livestock and 34% of them did not show any signs of disturbance. The proportion of plots showing signs of fire, logging or livestock increased to 100% for the habitat categories mixed shrubland and openfield. No plots without disturbance were measured in mid-successional forest with bamboo understory, mid-successional forest without understory, mixed shrubland, and openfield habitats.

Table 4. Table showing the presence of stand-scale anthropogenic disturbances, expressed by percentage (SD), in 499 plots where signs of fire, logging, and livestock were measured along the seven habitat categories. N is the number of plots per habitat category.

Habitat category	Fire	Logging	Livestock	No disturbance	N
Old-growth forest	53 ± (50)	53 ± (50)	27 ± (45)	34 ± (48)	64
Mid-successional forest (bamboo understory)	91 ± (29)	82 ± (38)	52 ± (50)	0 ± (0)	102
Mid-successional forest (other understory)	76 ± (43)	81 ± (40)	41 ± (50)	1.01 ± (10.5)	99
Mid-successional forest (no understory)	60 ± (50)	93 ± (25)	67 ± (48)	0 ± (0)	44
Early successional forest (< 20 years old)	56 ± (50)	76 ± (43)	57 ± (50)	1.33 ± (11.55)	75
Mixed shrubland	100 ± (0)	100 ± (0)	100 ± (0)	0 ± (0)	87
Openfield	100 ± (0)	100 ± (0)	100 ± (0)	0 ± (0)	28

3.3. Relationship between stand-structural complexity and stand-scale anthropogenic disturbances

The resulting mean values of the stand-structural attributes that were selected to be included in the stand-structural complexity index varied according to the disturbance treatment (Table 5). The highest mean value of the stand-structural complexity index was measured in plots that did not show any signs of anthropogenic disturbances (control plots) while the lowest mean value of the stand-structural complexity index was measured in plots that were subject to the combined presence of fire, livestock, and logging. The highest mean values of understory density, CWD volume, and stand basal area were measured in plots that did not show any signs of disturbance. For its part, the highest mean values of litter depth and snags density were measured in plots that were subject to fire and the combined presence of fire and livestock respectively.

Conversely, plots that were subject to the combined presence of logging and livestock showed the lowest mean values of understory density and CWD volume. Plots that were subject to the combined presence of fire, logging, and livestock showed the lowest mean values for litter depth and stand basal area while the lowest mean value for snags density was measured in plots that were subject to livestock alone (Table 5). The minimum and maximum individual values of the five stand-structural attributes as well as the stand-structural complexity index varied differently according to the disturbance treatment (Appendix 2).

Table 5. Results showing the mean (SD) values of both the stand-structural attributes and the stand-structural complexity index for the eight disturbance treatments.

	Understory density (n° contacts)	Coarse woody debris (m^3/ha)	Stand basal area (m^2/ha)	Litter depth (cm)	Snags density (stems/ha)	Structural complexity index (%)
No disturbance (control)	6.18 ± (2.87)	15.75 ± (30.35)	68.15 ± (28.34)	6.27 ± (3.49)	40.20 ± (35.84)	77.67 ± (11.15)
Fire	5.89 ± (2.84)	2.96 ± (4.40)	45.33 ± (31.78)	7.04 ± (3.10)	48.57 ± (42.56)	72.51 ± (13.44)
Logging	5.11 ± (3.53)	2.87 ± (8.72)	27.88 ± (18.60)	5.50 ± (2.85)	41.82 ± (67.28)	62.70 ± (13.72)
Livestock	4.01 ± (4.03)	3.38 ± (9.84)	32.36 ± (49.08)	3.57 ± (1.97)	18.13 ± (33.24)	54.74 ± (18.79)
Fire + Logging	5.60 ± (2.95)	7.84 ± (12.66)	44.31 ± (34.99)	6.31 ± (3.26)	50.78 ± (73.52)	71.63 ± (11.82)
Fire + Livestock	4.98 ± (2.39)	5.23 ± (7.32)	48.05 ± (19.81)	4.53 ± (1.69)	60.93 ± (61.88)	70.42 ± (12.16)
Logging + Livestock	2.72 ± (2.58)	1.23 ± (2.24)	30.18 ± (20.79)	3.58 ± (3.70)	23.94 ± (52.95)	53.48 ± (12.94)
Fire + Logging + Livestock	2.99 ± (2.81)	6.77 ± (19.04)	20.23 ± (24.46)	2.89 ± (2.76)	21.73 ± (44.32)	52.47 ± (16.28)

A Kruskal-Wallis test shows that the mean values of the stand-structural complexity index were significantly different between the eight disturbance treatments (X^2 = 148.8512, df = 7, p-value = 2.2e-16) (Fig. 4). A multiple comparison post hoc test does not show significant differences in the mean values of the stand-structural complexity index between the control plots and the plots that were subject to the singular presence of fire ($p = 0.73$). However, the mean values of the stand-structural complexity index are significantly lower in all the other six disturbance treatments compared to the control plots. For its case, the presence of logging alone shows a significant difference with the control plots ($p < 0.05$). However, the most significant differences ($p < 0.0000$) are found in plots showing signs of livestock alone, plots showing the combined presence of logging and livestock and plots showing the combined presence of fire, logging, and livestock.

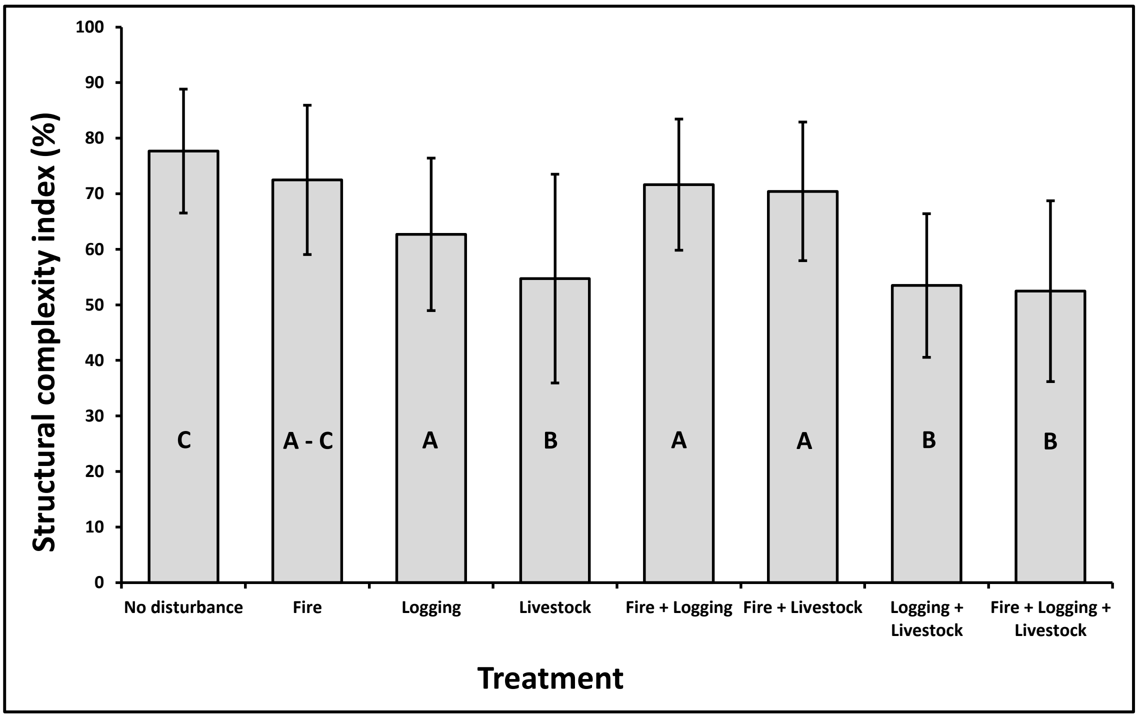

Fig. 4. Relationship between the mean values of the stand-structural complexity index along a disturbance gradient. Bars with different letters were significantly different according to a multiple comparison post hoc test ($p < 0.05$). Small bars are ± standard deviation.

4. Discussion

This work provides the first stand-structural complexity index for the southern temperate forests based on the measures of understory density, CWD volume, litter depth, stand basal area, and snags density. My results indicate that stand-structural complexity is related to the presence of anthropogenic disturbances such as fire, logging, livestock, and the combined additive effects between them. The stand-structural complexity index is more strongly related to the combined presence of fire, logging, and livestock whereas fire alone is the anthropogenic disturbance that showed lowest relation to stand's complexity. In addition, I found a positive correlation between the five selected stand-structural attributes and stand age. I suggest that specific forest management practices regarding the maintenance of structural attributes and the reduction of anthropogenic disturbances should be considered to enhance stand-structural complexity in order to conserve the southern temperate forests' biodiversity.

4.1. Stand-structural attributes' variation among stand age helps to determine stand-structural complexity

It has been stated that in order to best conserve the biodiversity of temperate ecosystems, the maintenance of all forest successional stages must become a priority for forest managers (Franklin, 1988). However, as in most temperate forests early successional stages are well represented due to the impact of anthropogenic disturbances in the forests' structure, there is an increasing awareness for conserving old-growth stands (Zenner, 2004; Franklin and Spies, 1991; Franklin and Van Pelt, 2004). For its case, old-growth forests are proposed to present a larger proportion of specific structural attributes such as CWD volume, litter depth, understory density, snags density, and stand basal area that distinguish them from other successional stages (Zenner, 2004; Franklin, 1988; Armesto et al., 2001; Hansen et al., 1991). The mean values of the stand-structural attributes considered in this study were positively correlated with old-growth stands with the exception of snags density which was higher in mid-successional forest stands. However, the maximum values of the stand-structural complexity index and the individual stand-structural attributes did not show a specific trend regarding stand age. These results are of high importance as they support the conclusion reached by McElhinny et al. (2006b) who stated that there is no single ideal stand structure, but instead, a combination of different attributes could produce a variety of structurally complex stands.

Studies conducted within different forest ecosystems have widely acknowledged stand basal area as a reliable indicator of structural complexity (Peck et al., 2014; Zenner, 2004; Zenner et al., 2012; Kane et al., 2010). For example, Peck et al. (2014) concluded that structural complexity in even-age stands was highly influenced by basal area when studying stand-structural complexity in Switzerland. These findings support my results as the higher - mean and individual - values of stand basal area were measured in old-growth plots. Other researchers have also observed a positive correlation between stand basal area and stand age. For example, Armesto and Figueroa (1987) showed for the southern temperate forests that stand basal area was directly correlated with stand age and suggested that higher values of stand basal area were possible in old-growth forests due to the absence of natural and anthropogenic disturbances. In addition, the range of the stand basal area values reported in this study are similar to the ones reported by Carmona et al. (2002), Echeverría et al. (2007), and Díaz et al. (2005) whose values were considerably higher in old-growth stands in comparison to early and mid-successional stands in the southern temperate forests. For the northern temperate forests, Spies and Franklin (1991) reached the same conclusion stating that basal area was one of the most important structural attributes to discriminate among stand age when comparing forest structure in the United States. Moreover, my findings also support the conclusions of Zenner et al. (2012) who stated that stand-scale structural complexity could be increased by retaining an important proportion of larger trees in Norway spruce-dominated forests in Finland.

Various studies around the globe have demonstrated how CWD volume increases structural complexity (Pasher and King, 2011; McElhinny et al., 2005), having a positive effect on forests' biodiversity (Christie and Armesto, 2003; Kelt et al., 1994; Soto-Azat et al., 2013). My results also show a positive relation between the mean values of CWD volume and stand age. This concurs with the results reported in previous researches which stated that CWD volume tends to accumulate in relation to stand age (Harmon et al., 1986; Franklin, 1988; Spies and Franklin, 1991; Christie and Armesto, 2003). For example, CWD volume was found to be higher in old-growth stands in comparison to younger stands when studying CWD characteristics in relation to stand age in the northern temperate forest (Franklin, 1988; Spies and Franklin, 1991). Moreover, Carmona et al. (2002) indicated that old-growth forest stands had higher CWD volume values in comparison to early and mid-successional forests in a coastal temperate forest in the lowlands (50 - 100 masl) of Chiloé Island, Chile.

A similar trend is reported in this study for understory densities whose mean values were markedly higher in old-growth plots than in successional stages' plots. This is in line with findings by Díaz et al. (2005) and Hansen et al. (1991) who found that structural complexity was maximized by understory density in the southern and northern temperate forests respectively. For instance, the high values of understory density measured in this study can be explained as the understory of southern temperate forests is mainly dominated by the native *Chusquea* bamboos (Poaceae: Bambusoideae) which forms highly dense thickets (Veblen, 1982). The high levels of structural complexity shown in this study regarding understory density are of great conservation importance for some endemic species of the southern temperate forest such as the endangered Rufous-legged Owl (*Strix rufipes*) and the Des Murs' Wiretail (*Sylviorthorhynchus desmursii*), which have been positively associated with dense understory vegetation (Ibarra et al., 2012; Ibarra et al., 2014a; Díaz et al., 2006).

Moreover, a high understory density can be correlated with high litter depth. For instance, the high mean values of litter depth measured in this study for old-growth and mid-successional forest with bamboo understory plots illustrate the importance of bamboo plants for the stand-structural complexity of the southern temperate forests. This supports conclusions by other researchers who also observed changes in the stand structure with higher litter depth produced by the bamboo leaves (Armesto and Fuentes, 1988; Christie and Armesto, 2003; Veblen et al., 1977). For its case, Reid et al. (2002) showed that invertebrates' abundance was higher in plots with higher litter biomass when studying the importance of native bamboos for understory birds in Chile. On the other side, Spies and Franklin (1991) reported higher values of litter depth in old-growth stands in comparison to young or mature stands for the northern temperate forests. However, even though litter depth is an easily measurable attribute, few studies have been undertaken in the southern temperate forests. thus making it difficult to make a quantifiable comparison between my results and previously reported studies.

As expected, I found that old-growth forest stands accounted for the highest mean values of understory density, CWD volume, litter depth, and stand basal area. However, the highest mean values of snags density between the seven habitat categories were measured in mid-successional forest with bamboo understory plots. This result is similar to the ones reported by Franklin (1988), Carmona et al. (2002), and Veblen et al. (1996), in two ecologically comparable environments, who stated that even though disturbances kill trees, they do not consume the wood structure, hence, a large proportion of trees remain standing after disturbance. These structural attributes that persist through disturbances have been described as biological legacies, being subject to increase stand-structural complexity post disturbance (Franklin et al., 2002). Still, there is not a defined correlation between snags density and stand age. For instance, Díaz et al. (2005) reported that the highest values of snags density in the southern temperate forests were measured in early-successional stands. Conversely, in the northern temperate forests, Spies and Franklin (1991) stated that snags density increased dramatically with stand age while Hansen et al. (1991) concluded that snags density was negatively associated with stand age.

For its part, the lowest mean values of the five structural attributes measured in openfield plots are a direct consequence of land clearance for agriculture and livestock farming (Veblen and Ashton, 1978; Veblen et al., 1980; Armesto and Figueroa, 1987). Openfield stands within the southern and the northern temperate forests have been described to be mainly concentrated in lowlands near human settlements. There, a recurrent practice is to remove logs and snags for usage as timber-derived products or firewood, leaving the land cleared for livestock farming (Franklin, 1988; Carmona et al., 2002). Overall, the stand-structural complexity index built for the Andean temperate forest shows similar results to the ones reported by McElhinny et al. (2006b) and Sabatini et al. (2015) who adapted the same methodology used in this study - with similar structural attributes - to build two different structural complexity indexes in Australia and Italy respectively.

4.2. Anthropogenic disturbances in the Andean temperate forest: a long-lasting but disruptive relationship

Stand structure in southern temperate forests has been shaped by a continuous history of anthropogenic disturbances (Veblen and Ashton, 1978; Veblen et al., 1980). The extent of these disturbances helps to explain the high proportion of plots that were subject to anthropogenic disturbances and the consequently high amount of plots representing successional forest stages (Veblen et al., 1992). For instance, the large presence of mid-successional forest plots are a direct consequence of the fire history of the southern temperate forests (Veblen et al., 1992). This can be inferred as the age of the mid-successional stands concurs with the elapsed time since the last catastrophic fire, that burned large areas of southern temperate forests, occurred (Veblen and Ashton, 1978). Different studies have shown how fire, logging, and the presence of livestock are generally presented on a successive way with the presence of one disturbance typically involving a continuity of disturbances such as logging and livestock grazing (Lusk, 1996; Szeicz et al., 1998; Aravena et al., 2002; Hansen et al., 1991). This sequence of anthropogenic disturbances supports the result showing a high number of plots that were subject to the combined presence of the three anthropogenic disturbances considered in this study (Lusk, 1996; Veblen et al., 1992).

Different authors suggest that the intensity of anthropogenic disturbances is higher at lower elevations (Armesto and Figueroa, 1987; Veblen et al., 1980). For instance, the acquisition of firewood for heating in both rural and urban housing areas continues to be the driving factor behind logging within the southern temperate forest, standing out as the main degrading activity especially in rural areas near forest remnants (Carmona et al., 2002). This is similar to what has happened in other temperate ecosystems. For example, the temperate forests of the Pacific Northwest of the United States are mostly secondary forests that have developed during the last 100 - 150 years due to logging and land abandonment for agriculture (Franklin, 1988). On the other side, my results show that old-growth forests were the least disturbed habitat.

This result may be explained by the distribution of public protected areas within the southern temperate forests which are mostly (> 90%) located at elevations above 600 masl (Armesto et al., 1998). Thus, it can be inferred that non-disturbed, old-growth forest stands are more prone to be present at higher elevations away from human settlements. Similar results were previously reported for the southern temperate forests (Gutiérrez et al., 2004; Veblen et al., 1992) where old-growth also showed none or very few signs of anthropogenic disturbances.

4.3. Stand-scale anthropogenic disturbances are differentially affecting stand-structural complexity in the southern temperate forests

Different studies have shown how anthropogenic disturbances are significantly reducing forest structure around the globe (Harmon et al., 1986; Hansen et al., 1991; Hitimana et al., 2004). Consequently, the loss of forest structure is responsible for losses of biodiversity across different ecosystems (Thiollay, 1993; Jaña-Prado et al., 2007; De Santo et al., 2002). However, as far as I know, this is the only study that has assessed the influences of anthropogenic disturbances on stand-structural complexity for the southern temperate forests. My results are of high importance for the conservation of southern temperate ecosystems where it has been proposed that the effects of anthropogenic disturbances such as fire, logging, and livestock on forest structure have superimposed the natural regime (Carmona et al., 2002). Willson and Armesto (1996), when comparing the writings of Charles Darwin about the Chilean temperate forests with the present forests' condition 150 years after, stated that the forests' structural complexity described by Darwin is greatly absent nowadays because of logging, burning, and land clearing for agriculture.

The lack of significant differences in the mean values of the stand-structural complexity index between the control plots and the plots that were subject to the sole presence of fire suggest that temperate forests that have been subject to fire are highly resilient. Despite the small reduction in structural complexity caused by fire, my results show that these plots can still achieve high to moderate levels of structural complexity sometime after disturbance. Similar results were found for the structure of abandoned pastures in Puerto Rico (Aide et al., 2000), where the density, basal area, aboveground biomass, and species richness of secondary forest achieved similar values to those of the old-growth forest 40 years after fire, concluding that restoration in tropical forests can be achieved by protecting areas from fire and allowing natural regeneration. Different authors have widely acknowledged the resilience capacity of temperate forests to moderate levels of anthropogenic disturbances (Franklin, 1988; Aravena et al., 2002; Neira et al., 2002). For instance, a greater array of structural attributes would provide greater ecosystem resilience (Peck et al., 2014) and recovery after anthropogenic disturbances (O'Hara, 2006). This hypothesis is in line with previous results reported for the southern temperate forests (Díaz et al., 2005) where it was shown that the values of basal area and understory density increased in relation to the elapsed time since the disturbance. In addition, the unexpected high mean values of understory density post-fire disturbances reported in this study are due to the proliferation of a dense bamboo understory. Following fire events, bamboos have been described to dominate these forests' understory, forming extensive thickets impeding the regeneration of other vegetative species (Veblen, 1982; Veblen and Ashton, 1978).

However, my results do show that logging alone and the combined action of logging and fire are indistinctively reducing stand-structural complexity. The continuous cutting of snags and removal of logs for firewood, which are actually reducing the structural legacies (Hansen et al., 1991), may be a potential explanation of the reduction of the stand-structural complexity index in plots subject to fire and logging. For instance, the low values of CWD volume measured in this study for plots that were subject to fire may be explained by the removal of logs and snags by landowners to be used or sold as firewood - which is a very common practice in southern Chile (Aravena et al., 2002; Carmona et al., 2002; Smith-Ramírez et al., 2014). In addition, logging practices have resulted in the alteration and elimination of the understory due to the opening of roads for timber extraction with animals and machinery (Jaña-Prado et al., 2007). Studies in northern temperate forests have demonstrated that snags were three to five times more dense in undisturbed plots in comparison with logged plots (Hansen et al., 1991). Similarly, Aravena et al. (2002) indicated that basal area increased significantly in undisturbed plots in comparison to plots that showed the combined presence of fire and logging in the southern temperate forests. This supports conclusions from other researchers around the globe who also observed a reduction in stand-structural attributes such as snags density, CWD volume, and understory density in plots that were subject to logging (Hansen et al., 1991; Harmon et al., 1986; Carmona et al., 2002; Thiollay, 1993; Youngblood, 2010; Hitimana et al., 2004).

Interestingly, there was not a significant difference in the mean values of the stand-structural complexity index when subject to the presence of logging alone or in combination with fire. This result is in line with previous studies on the southern temperate forests (Aravena et al., 2002; Gutiérrez et al., 2004; Carmona et al., 2002; Seaman et al., 2015), in which mean values of basal area, CWD volume, and snags density showed little differences between plots showing signs of fire in comparison to plots showing the combined presence of fire and logging. However, when assessing the difference between the mean values of the structural attributes reported in those studies with my findings, the results should be viewed with caution because the elapsed time since the disturbance may have been different. For instance, the post-fire plots measured in this study may have been immediately abandoned after the occurrence of the last catastrophic fire (80 years ago), having a longer recovery time since the disturbance.

The introduction of livestock by the European colonists has had a detrimental effect on the structure of the southern temperate forests by reducing stand-structural attributes such as understory density, basal area, and litter depth (Zamorano-Elgueta et al., 2012; Veblen et al., 1992; González et al., 2005; Veblen et al., 1996). My results correspond with this statement as they suggest that the presence of livestock - solely or in combination with logging or logging and fire - is the most important anthropogenic disturbance related to a decrease in the structural complexity of southern temperate forests. This is similar to what was reported by Tasker and Bradstock (2006) who concluded that livestock - followed by logging and fire - was the disturbance that was affecting the complexity of understory vegetation strongest when studying the influence of livestock grazing on forest understory structure in New South Wales, Australia. Similarly, livestock was shown to have a more negative effect on forest regeneration in comparison to logging when studying the impacts of forests fragmentation in the composition and structure of the southern temperate forests (Zamorano-Elgueta et al., 2014).

Grazing activity by livestock not only affects vegetation regeneration but other structural attributes. For example, Echeverría et al. (2007) reported lower values of stand basal area in patches showing higher presence of livestock in comparison to less disturbed forest stands. This is in line with the findings of Veblen et al. (1993) who concluded that livestock grazing was decreasing the size and abundance of woody plants as well as inhibiting the regeneration of common tree species of the southern temperate forests. Similarly, Zamorano-Elgueta et al. (2012) revealed that monkey puzzle trees' regeneration was significantly affected by the presence of livestock. In addition, livestock also affects understory structure by grazing and trampling the herbaceous layer (Belsky and Blumenthal, 1997). For example, Rummell (1951) showed that grazing by livestock reduced understory vegetation by 45 - 61% when studying ponderosa pine's forest dynamics that had been subject to grazing in the Unites States. Similar results were found for tree communities in the southern temperate forest of Argentina (Veblen et al., 1993) in which understory density - mainly of bamboo - was significantly reduced in highly grazed stands in comparison to less disturbed stands.

There was not information available about the effects that livestock was having upon CWD volume or snags density in the southern temperate forests. However, my results suggest that the reduction of understory density and basal area by livestock is indirectly affecting other structural attributes such as CWD volume, litter depth, and snags density. For instance, the lowest mean values of litter depth reported in this study were measured in plots that were subject to the presence of livestock; this may be because the livestock's grazing activity of plant biomass located above ground minimizes the quantity of biomass for litter conversion (Belsky and Blumenthal, 1997). Similarly, Hayes and Holl (2003) reported that litter depth was significantly lower in grazed sites in comparison to ungrazed sites when investigating the impact of cattle grazing on a coastal prairie plant community in California. On the other side, the low mean values of CWD volume and stand basal area in plots that were subject to livestock may be due to the tradition of local farmers to remove the bamboo understory as well as other woody residues for aesthetic and productivity reasons (Reid et al., 2004).

4.4. Recommendations for management

Southern temperate forests are not an exception when studying the effects that anthropogenic disturbances are having upon forest ecosystems (Liira et al., 2007; Irwin et al., 2010; Ramírez-Marcial et al., 2001). My results suggest that anthropogenic disturbances are having significantly negative effects on the stand-structural complexity of Andean temperate forests. Different studies have shown how the structural attributes measured in this study - CWD volume, snags density, stand basal area, litter depth, and understory density - are of significant importance for a great array of organisms inhabiting the southern temperate forests (Ibarra et al., 2012; Ibarra et al., 2014a; Crump, 2002; Díaz et al., 2005). Thus, a reduction in the availability of those structural attributes by means of anthropogenic disturbances may have negative implications for biodiversity conservation in southern temperate ecosystems. This study contributes to the understanding of the influence that anthropogenic disturbances are having upon the structure of southern temperate forests at a stand level and provides some guidelines for policymakers and forest managers regarding forest conservation.

Even though my results suggest that high levels of structural complexity and the presence of logging and livestock are incompatible, total disturbance eradication is not feasible within the study area. Thus, I propose that in order to better conserve the temperate forests' biodiversity, the retention of structural attributes must be incorporated into forest management plans. My results also show that there is no single ideal stand structure that maximizes structural complexity. However, the lowest values of stand-structural complexity were measured in openfield and early-successional plots whereas the highest values of structural complexity were measured in mid-successional and old-growth forest plots. In addition, the lowest - individual and mean - values for the five structural attributes and the stand-structural complexity index were measured in plots subject to livestock - alone or combined with logging or logging and fire. These results indicate that a higher focus should be put on the reduction of livestock-associated disturbances and the retention of stand-structural attributes in openfield and early-successional plots to increase their structural complexity. The construction of a stand-structural complexity index with structural attributes that can be readily recognized and measured by researchers or managers provides a great opportunity to rank stands in terms of their structural complexity in order to guide conservation efforts.

5. Conclusion

My results demonstrate that it is feasible to generate a simple stand-structural complexity index for the southern temperate forests based on structural attributes that are important for biodiversity. This study is the first attempt to build an index of stand-structural complexity as well as the first study to assess the relationship between anthropogenic disturbance and stand-structural complexity in the southern temperate forests. The analyses conducted show that the mean values of the stand-structural complexity index were significantly related to anthropogenic disturbances. The presence of livestock - alone or in combination with logging or logging and fire - showed the most significant differences in the mean values of the stand-structural complexity index in comparison with the control plots, suggesting that livestock is the disturbance that is most affecting the stand’s structural complexity in the southern temperate forests. Moreover, the highest mean values of the index of stand-structural complexity were measured in plots that did not show any signs of anthropogenic disturbance, conversely, the lowest mean values of the stand-structural complexity index were measured in plots showing the combined presence of fire, logging, and livestock. In addition, my results also suggest a positive relationship between the mean values of the stand-structural complexity index and stand age.

The conservation importance of the southern temperate forests demands the incorporation of biodiversity conservation as an objective into intensively managed ecosystems. Therefore, it is necessary to conserve the structural complexity of forest fragments minimizing additional anthropogenic disturbances. If the current rates of anthropogenic disturbances are maintained, the ability of the remnant forests to maintain their structure will be reduced, having a concomitant negative effect on the southern temperate forests’ biodiversity. My results suggest that forests should be managed to retain structural attributes such as understory density, CWD volume, snags density, stand basal area, and litter depth and to reduce the presence of anthropogenic disturbances in order to prevent the loss of biodiversity in the southern temperate forests. The findings reported in this study provide valuable information to enhance the knowledge about southern temperate forests and contribute with practical information to policy decisions regarding forest conservation and management.

List of references

Acosta-Jamett, G., Simonetti, J. A. (2004). Habitat use by Oncifelis guigna and Pseudalopex culpaeus in a fragmented forest landscape in central Chile. *Biodiversity and Conservation*, 13(6), 1135–1151.

Affleck, D. L. R., Gregoire, T. G., Valentine, H. T. (2005). Design unbiased estimation in line intersect sampling using segmented transects. *Environmental and Ecological Statistics*, 12(2), 139–154.

Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., Mercado-Vega, H. (2000). Forest regeneration in a chronosequence of tropical abandoned pasture: implications for restoration ecology. *Restoration Ecology*, 4(4), 328–338.

Aleixo, A. (2012). Effects of selective logging on a bird community in the Brazilian Atlantic forest. *The Condor*, 101(3), 537–548.

Altamirano, T. A., Ibarra, J. T., de la Maza, M., Navarrete, S. A., Bonacic, C. (2015). Reproductive life-history variation in a secondary cavity-nester across an elevational gradient in Andean temperate ecosystems. *The Auk*, *132*(4), 826–835.

Aravena, J. C., Carmona, M. R., Pérez, C. A., Armesto, J. J. (2002). Changes in tree species richness, stand structure and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Revista Chilena de Historia Natural*, 75(2), 339–360.

Armesto, J. J., Aravena, J. C., Villagrán, C., Pérez, C., Parker, G. (1996). Bosques templados de la cordillera de la costa, in: Armesto, J. J., Villagrán, C., Kalin, M. (Eds.), *Ecología de los Bosques Nativos de Chile*. Editorial Universitaria Santiago, Chile, pp. 199–213.

Armesto, J. J., Rozzi, R., Caspersen, C. (2001). Temperate forests of North and South America, in: Chapin, F. S., Sala, O. E., Huber-Sannwald, E. (Eds.), *Global Biodiversity in a Changing Environment. Scenarios for the 21st Century*. Springer-Verlag, New York, pp. 223-249.

Armesto, J. J., Figueroa, J. (1987). Stand structure and dynamics in the temperate rain forests of Chiloé archipelago, Chile. *Journal of Biogeography*, 14(4), 367–376.

Armesto, J. J., Fuentes, E. R. (1988). Tree species regeneration in a mid-elevation, temperate rain forest in Isla de Chiloé, Chile. *Vegetatio*, 74(2-3), 151–159.

Armesto, J. J., Smith-Ramírez, C., Carmona, M. R., Celis-Diez, J. L., Díaz, I. A., Gaxiola, A., Gutiérrez, A. G., Núñez-Avila, M., Pérez, C., Rozzi, R. (2009). Old-growth temperate rain forests of South America: conservation, plant-animal interactions, and baseline biogeochemical processes, in: Wirth, C. H., Gleixner, G., Heimann, M. (Eds.), *Old-*

Growth Forests. Function, Fate and Value, Ecological Studies, vol. 207. Springer, Berlin, Germany, pp. 367–390.

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

Armesto, J. J., Smith-Ramírez, C., León, P., Arroyo, M. (1992). Biodiversidad y conservación del bosque templado en Chile. *Ambiente y Desarrollo*, 19–24.

Arroyo, M., Riveros, M., Peñaloza, A., Cavieres, L., Faggi, A. M. (1996). Phytogeographic relationships and regional richness patterns of the cool temperate rainforest flora of Southern South America, in: Lawford, R. G., Fuentes, E., Alback, P. B. (Eds.), *High-latitude rainforests and associated ecosystems of the west coast of the Americas*. Springer, New York, pp. 134-172.

Barbosa, O., Marquet, P. A. (2002). Effects of forest fragmentation on the beetle assemblage at the relict forest of Fray Jorge, Chile. *Oecologia*, 132(2), 296–306.

Beckschäfer, P. (2013). Enhanced structural complexity index: An improved index for describing forest structural complexity. *Open Journal of Forestry*, 03(01), 23–29.

Belsky, A. J., Blumenthal, D. M. (1997). Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conservation Biology*, 11(2), 315–327.

Bennett, A. F., Lumsden, L. F., Nicholls, A. O. (1994). Tree hollows as a resource for wildlife in remnant woodlands: spatial and temporal patterns across the northern plains of Victoria, Australia. *Conservation Biology*,1(3), 222-235.

Bowman, J. C., Sleep, D., Forbes, G. J., Edwards, M. (2000). The association of small mammals with coarse woody debris at log and stand scales. *Forest Ecology and Management*, 129(1-3), 119–124.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Zellweger, F., Bollmann, K. (2014). Temperate mountain forest biodiversity under climate change: Compensating negative effects by increasing structural complexity. *PLoS ONE*, 9(5), e97718.

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A. B., Gerlach, J., Hoffmann, M., Lamoreux, J. F., Mittermeier, G., Pilgrim, J. D., Rodrigues, A. S. L. (2006). Global biodiversity conservation priorities. *Science*, 313(5783), 58–61.

Carmona, M. R., Armesto, J. J., Aravena, J. C., Pérez, C. A. (2002). Coarse woody debris biomass in successional and primary temperate forests in Chiloé Island, Chile. *Forest Ecology and Management*, 164, 265–275.

Carneiro, A. P. B., Jiménez, J. E., Vergara, P. M., White, T. H. (2013). Nest-site selection by Slender-billed Parakeets in a Chilean agricultural-forest mosaic. *Journal of Field Ornithology*, 84(1), 13–22.

Ceballos, G., Vale, M. M., Bonacic, C., Calvo-Alvarado, J., List, R., Bynum, N., Medellín, R., Simonetti, J. A., Rodrígues, J. P. (2009). Conservation challenges for the austral and neotropical America section. *Conservation Biology*, 23(4), 811–817.

Celis-Diez, J. L., Hetz, J., Marín-Vial, P. A., Fuster, G., Necochea, P., Vásquez, R. A., Jaksic, F. M., Armesto, J. J. (2012). Population abundance, natural history, and habitat use by the arboreal marsupial Dromiciops gliroides in rural Chiloé Island, Chile. *Journal of Mammalogy*, 93(1), 134–148.

Christie, D. A., Armesto, J. J. (2003). Regeneration microsites and tree species coexistence in temperate rain forests of Chiloé Island, Chile. *Journal of Ecology*, 91(5), 776–784.

Conaf, Conama, Birf, Universidad Austral de Chile, Pontificia Universidad Católica de Chile, Universidad Católica de Temuco. (1999). *Catastro y Evaluación de los Recursos Vegetacionales Nativos de Chile. Informe Nacional con Variables Ambientales.* Santiago, Chile.

Crump, M. L. (2002). Natural History of Darwin´s frog, Rhinoderma Darwinii. *Herpetological Natural History*, 9(1), 21–30.

Davis, J. C., Castleberry, S. B., Kilgo, J. C. (2010). Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain. *Forest Ecology and Management*, 259(6), 1111–1117.

De Santo, T. L., Willson, M. F., Sieving, K. E., Armesto, J. J. (2002). Nesting biology of Tapaculos (Rhinocryptidae) in fragmented south-temperate rainforests of Chile. *The Condor*, 104(3), 482-495.

Díaz, I. A., Armesto, J. J., Reid, S., Sieving, K. E., Willson, M. F. (2005). Linking forest structure and composition: Avian diversity in successional forests of Chiloé Island, Chile. *Biological Conservation*, 123(1), 91–101.

Díaz, I. A., Armesto, J. J., Willson, M. F. (2006). Mating success of the endemic Des Murs’ Wiretail (Sylviorthorhynchus desmursii, Furnariidae) in fragmented Chilean rainforests. *Austral Ecology*, 31(1), 13–21.

Díaz, S., Kitzberger, T. (2013). Nest habitat selection by the Austral parakeet in north-western Patagonia. *Austral Ecology*, 38(3), 268–278.

Di Castri F., Hajek E. R. (1976). *Bioclimatología de Chile*. Ediciones de la Universidad Católica de Chile, Santiago, Chile.

Dunstone, N., Durbin, L., Wyllie, I., Freer, R., Acosta-Jamett, G., Mazzolli, M., Rose, S. (2002). Spatial organization, ranging behaviour and habitat use of the kodkod (Oncifelis guigna) in southern Chile. *Journal of Zoology*, 257(1), 1-11.

Dupouey, A. J. L., Dambrine, E., Laffite, J. D., Moares, C. (2002). Irreversible impact of past land use on forest soils and biodiversity. *Ecology*, 83(11), 2978–2984.

Dupuis, L. A, Smith, J. N. M., Bunnell, F., Bunnellt, F. (1995). Relation of terrestrial-breeding amphibian abundance to tree-stand age. *Conservation Biology*, 9(3), 645–653.

Echeverría, C., Coomes, D., Salas, J., Rey-Benayas, J. M., Lara, A., Newton, A. (2006). Rapid deforestation and fragmentation of Chilean temperate forests. *Biological Conservation*, 130(4), 481–494.

Echeverría, C., Newton, A. C., Lara, A., Benayas, J. M. R., Coomes, D. A. (2007). Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecology and Biogeography*, 16(4), 426–439.

Fauth, J. E., Crother, B. I., Slowinski, J. B. (1989). Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica*, 21(2), 178–185.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., Snyder, P. K. (2005). Global consequences of land use. *Science*, 309:570–574.

Fowler, H. G., Silva, C. A., Venticinque, E. (1993). Size, taxonomic and biomass distributions of flying insects in Central Amazonia: forest edge vs. understory. *Revista de Biologia Tropical*, *41*(3), 755–760.

Franklin, J. F. (1988). Structural and functional diversity in temperate forests, in: Wilson, E. O., Peters, F. M. (Eds.), *Biodiversity*. National Academy Press, Washington, DC, pp. 166–175.

Franklin, J. F., Armesto, J. J. (1996). Una alternativa de manejo para los bosques nativos chilenos. *Ciencia y Ambiente*, 12, 69–79.

Franklin, J. F., Spies, T. A., Van Pelt, R., Carey, A. B., Thornburgh, D. A., Berg, D. R., Lindenmayer, D. B., Harmon, M. E., Keeton, W. S., Shaw, D. C., Bible, K., Chen, J. (2002). Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, 155(1-3), 399–423.

Franklin, J. F., Spies, T. A. (1991). Composition, function, and structure of old-growth Douglas-fir forests, in: Ruggiero, L. F., Aubry, K. B., Carey, A. B., Huff, M. H. (Eds.), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. Portland, USA, pp. 71–80.

Franklin, J. F., Van Pelt, R. (2004). Spatial aspects of structural complexity in old-growth forests. *Journal of Forestry*, 12(3), 22–28.

Friedlingstein, P., Houghton, R. A., Marland, G., Hackler, J., Boden, T. A., Conway, T. J., Canadell, J. G., Raupach, M. R., Ciais, P., Le Quéré, C. (2010). Update on CO2 emissions. *Nature*, 3(12), 811–812.

Gajardo, R. (1993). L*a vegetación natural de Chile: clasificación y distribución geográfica*. Editorial Universitaria, Santiago, Chile.

Gibbons, P., Lindenmayer, D. B., Barry, S. C., Tanton, M. T. (2002). Hollow selection by vertebrate fauna in forests of southeastern Australia and implications for forest management. *Biological Conservation*, 103(1), 1–12.

González, M. E., Veblen, T. T., Sibold, J. S. (2005). Fire history of Araucaria-Nothofagus forests in Villarrica National Park, Chile. *Journal of Biogeography*, 32(7), 1187–1202.

Grove, S. J. (2002). Tree basal area and dead wood as surrogate indicators of saproxylic insect faunal integrity: a case study from the Australian lowland tropics. *Ecological Indicators*, 1(3), 171–188.

Gutiérrez, A. G., Armesto, J. J., Aravena, J. C. (2004). Disturbance and regeneration dynamics of an old-growth North Patagonian rain forest in Chiloé Island, Chile. *Journal of Ecology*, 92(4), 598–608.

Hansen, A. J., Spies, T., Swanson, F. J., Ohmann, J. L. (1991). Conserving biodiversity in managed forests. *BioScience*, 41(6), 382–392.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K. J., Cummins, K. W. (1986). Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research,* 15, 133–302.

Hayes, G. F., Holl, K. D. (2003). Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology*, 17(6), 1694–1702.

Hitimana, J., Kiyiapi, J. L., Njunge, J. T. (2004). Forest structure characteristics in disturbed and undisturbed sites of Mt. Elgon Moist Lower Montane Forest, western Kenya. *Forest Ecology and Management*, 194(1-3), 269–291.

Ibarra, J. T., Martin, K., Drever, M., Vergara, G. (2014a). Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: a multi-scale approach. *Forest Ecology and Management*, 1(604), 1–35.

Ibarra, J. T. (2014b). *Andean temperate forest owls: detectability, habitat relationships and reliability as biodiversity surrogates*. PhD Dissertation. Faculty of graduate and postdoctoral studies, University of British Columbia.

Ibarra, J. T., Martin, K., Altamirano, T. A., Vargas, F. H., Bonacic, C. (2014c). Factors associated with the detectability of owls in South American temperate forests: Implications for nocturnal raptor monitoring. *Journal of Wildlife Management*, 78(6), 1078–1086.

Ibarra, J. T., Altamirano, T. A., Gálvez, N., Rojas, I., Laker, J., Bonacic, C. (2010). Avifauna de los bosques templados de Araucaria araucana del sur de Chile. *Ecología Austral*, 20, 33–45.

Ibarra, J. T., Gálvez, N., Gimona, A., Altamirano, T. A., Rojas, I., Hester, A., Laker, J., Bonacic, C. (2012). Rufous-legged Owl (Strix rufipes) and Austral Pygmy Owl (Glaucidium nanum) stand use in a gradient of disrupted and old growth Andean temperate forests, Chile. *Studies on Neotropical Fauna and Environment*, 47(1), 33–40.

Ibarra, J. T., Martin, K. (2015). Beyond species richness: an empirical test of top predators as surrogates for functional diversity and endemism. *Ecosphere*, 6(8), p.142.

Ilustre Municipalidad de Pucón. (2005). Actualización del plan regulador comunal de Pucón, Chile. http://www.municipalidadpucon.cl/index.php/plan-regulador/197 Accessed 22 Jun 2015.

Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J. L., Raherilalao, M. J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L., Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*, 143(10), 2351–2362.

Jaña-Prado, R., Celis-Diez, J. L., Gutiérrez, A. G., Cornelius, C., Armesto, J. J. (2007). Diversidad en bosques fragmentados de Chiloé ¿son todos los fragmentos iguales?, in: Grez, A., Simonetti, J., Bustamante, R. (Eds.), *Biodiversidad en ambientes fragmentados de Chile: patrones y procesos a diferentes escalas*. Editorial Universitaria, Santiago, Chile, pp. 59-189.

Johns, A. D. (1988). Effects of ‘‘selective’’ timber extraction on rain forest structure and composition and some consequences for frugivores and folivores. *Biotropica* 20(1), 31–37.

Kane, V. R., McGaughey, R. J., Bakker, J. D., Gersonde, R. F., Lutz, J. A., Franklin, J. F. (2010). Comparisons between field- and LiDAR-based measures of stand structural complexity. *Canadian Journal of Forest Research*, 40(4), 761–773.

Keith, H., Mackey, B. G., Lindenmayer, D. B. (2009). Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proceedings of the National Academy of Sciences of the United States of America*, 106(28), 11635–11640.

Kelt, D., Martínez, D. (1989). Notes on distribution and ecology of two marsupials endemic to the Valdivian forests of southern South America. *Journal of Mammalogy*, 70(1), 220–224.

Kelt, D., Meserve, P., Lang, B. (1994). Quantitative habitat associations of small mammals in a temperate rainforest in southern Chile: empirical patterns and the importance of ecological scale. *Journal of Mammalogy,* 75(4), 890-904.

Kuschel, G. (1960). Terrestrial zoology in southern Chile. *Proceedings of the Royal Society of London: Biological Sciences*, 152(949), 540–550.

Laliberté, E., Tylianakis, J. M. (2012). Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology*, 93(1), 145–155.

Lambert, T. D., Malcolm, J. R., Zimmerman, B. L. (2005). Effects of mahogany (Swietenia macrophylla) logging on small mammal communities, habitat structure, and seed predation in the southeastern Amazon basin. *Forest Ecology and Management*, 206(1), 381–398.

Lara, A., Villalba, R. (1993). A 3620-year temperature record from Fitzroya cupressoides tree rings in southern South America. *Science*, 260(5111), 1104–1106.

Lara, A. (1996). La conservación del bosque nativo en Chile: problemas y desafíos, in: Armesto, J. J., Villagrán, C., Arroyo, M. (Eds.), *Ecología de Los Bosques Nativos de Chile*. Editorial Universitaria, Santiago, Chile, pp. 335-362.

Laurance, S. G. W. (2004). Responses of understory rain forest birds to road edges in central Amazonia. *Ecological Applications*, 14(5), 1344–1357.

Laurance, W. F., Vasconcelos, H. L., Lovejoy, T. E. (2000). Forest loss and fragmentation in the Amazon: implications for wildlife conservation. *Oryx*, 34(1), 39–45.

Liira, J., Sepp, T., Parrest, O. (2007). The forest structure and ecosystem quality in conditions of anthropogenic disturbance along productivity gradient. *Forest Ecology and Management*, 250(1-2), 34–46.

Lindenmayer, D. B., Margules, C., Botkin, D. (2000). Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology*, 14(4), 941–950.

Lindenmayer, D. B., Franklin, J. F., (2002). *Conserving Forest Biodiversity: A Comprehensive Multi-Scaled Approach*. Island Press,Washington, DC.

Lohr, S. M., Gauthreaux, S. A., Kilgo, J. C. (2002). Importance of coarse woody debris to avian communities in Loblolly Pine forests. *Conservation Biology*, 16(3), 767–777.

Lusk, C. H. (1996). Gradient analysis and disturbance history of temperate rain forests of the coast range summit plateau, Valdivia, Chile. *Revista Chilena De Historia Natural*, 69(3), 401–411.

Macneil, J., Macgowan, B. J., Currylow, A., Williams, R. N. (2013). *Forest management for reptiles and amphibians: A technical guide for the midwest*. Purdue extenssion, Indiana, USA.

Malcolm, J. R., Ray, J. C. (2000). Influence of timber extraction routes on Central African small-mammal commnunities, forest structure, and tree diversity. *Conservation Biology*, 14(6), 1623–1638.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J. (2006a). Fauna-habitat relationships: A basis for indentifying key stand structural attriutes in temperate Australian eucalypt forests and woodlands. *Pacific Conservation Biology*, 12, 89–110.

McElhinny, C., Gibbons, P., Brack, C. (2006b). An objective and quantitative methodology for constructing an index of stand structural complexity. *Forest Ecology and Management*, 235(1), 54–71.

McElhinny, C., Gibbons, P., Brack, C., Bauhus, J. (2005). Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management*, 218, 1–24.

Meier, D., Merino, M. L. (2007). Distribution and habitat features of southern pudu (Pudu puda Molina, 1782) in Argentina. *Mammalian Biology*, 72(4), 204–212.

Meserve, P. L., Lang, B. K., Murua, R., Muñoz-Pedreros, A., González, L. A. (1991). Characteristics of a terrestrial small mammal assemblage in a temperate rain-forest in Chile. *Revista Chilena De Historia Natural*, 64(1), 157–169.

Mishra, B. P., Tripathi, O. P., Tripathi, R. S., Pandey, H. N. (2004). Effects of anthropogenic disturbance on plant diversity and community structure of a sacred grove in Meghalaya, northeast India. *Biodiversity and Conservation*, 13, 421–436.

Mittermeier, R. A., Mittermeier, C. G., Brooks, T. M., Pilgrim, J. D., Konstant, W. R., da Fonseca, G. A. B., Kormos, C. (2003). Wilderness and biodiversity conservation.

Proceedings of the National Academy of Sciences of the United States of America, 100(18), 10309–10313.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–8.

Nappi, A., Drapeau, P., Saint-Germain, M., Angers, V. A. (2010). Effect of fire severity on long-term occupancy of burned boreal conifer forests by saproxylic insects and wood-foraging birds. *International Journal of Wildland Fire*, 19(4), 500–511.

Neira, E., Verscheure, H., Revenga, C. (2002). *Chile's frontier forests: Conserving a global treasure*. WRI, CODEFF, UACH, Washington, DC.

Neruda, P. (1974). *Confieso que he vivido*. Seix Barral, Barcelona, España.

Newton, P. F. (2008). Complex stand structures and associated dynamics: Measurement indices and modelling approaches. *Forestry*, 81(5), 573–574.

O'Hara, K. L. (2006). Multiaged forest stands for protection forests: concepts and applications. *Forest Snow and Landscape Research*, 80(1), 45–55.

Ojeda, V., Chazarreta, L. (2014). Home range and habitat use by Magellanic Woodpeckers in an old-growth forest of Patagonia. *Canadian Journal of Forest Research*, 44, 1265–1273.

Ojima, D. S., Galvin, K. A., Turner, B. L. (1994). The global impact of land-use change. *BioScience*, 44(5), 300–304.

Olson, D. M., Dinerstein, E. (1998). The Global 200: A representation approach to conserving the earth's most biologically valuable ecoregions. *Conservation Biology*, 12(3), 502–515.

Owens, A. K., Moseley, K. R., McCay, T. S., Castleberry, S. B., Kilgo, J. C., Ford, W. M. (2008). Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (Pinus taeda) forests. *Forest Ecology and Management*, 256(12), 2078–2083.

Pan, Y., Birdsey, R. A., Phillips, O. L., Jackson, R. B. (2013). The structure, distribution, and biomass of the world's forests. *Annual Review of Ecology, Evolution, and Systematics*, 44(1), 593–622.

Pasher, J., King, D. J. (2011). Development of a forest structural complexity index based on multispectral airborne remote sensing and topographic data. *Canadian Journal of Forest Research*, 41(1), 44–58.

Peck, J. E., Zenner, E. K., Brang, P., Zingg, A. (2014). Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types. *European Journal of Forest Research*, 133(2), 335–346.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ramírez-Marcial, N., González-Espinosa, M., Williams-Linera, G. (2001). Anthropogenic disturbance and tree diversity in Montane Rain Forests in Chiapas, Mexico. *Forest Ecology and Management*, 154(1-2), 311–326.

Raphael, M. G., White, M. (1984). Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife monographs*, (86), 3-66.

Reid, S., Cornelius, C., Barbosa, O., Meynard, C., Silva-García, C., Marquet, P. A. (2002). Conservation of temperate forest birds in Chile: Implications from the study of an isolated forest relict. *Biodiversity and Conservation*, 11(11), 1975–1990.

Reid, S., Díaz, I. A, Armesto, J. J., Willson, M. F. (2004). Importance of native bamboo for understory birds in Chilean temperate forests. *Auk*, 121(2), 515–525.

Ross, B., Fredericksen, T., Ross, E., Hoffman, W., Morrison, M., Beyea, J., Lester, M. B., Johnson, B. N., Fredericksen, N. J. (2000). Relative abundance and species richness of herpetofauna in forest stands in Pennsylvania. *Forest Science,* 46(1), 139-146.

Rozzi, R., Silander, J., Armesto, J. J., Feinsinger, P., Massardo, F. (2000). Three levels of integrating ecology with the conservation of South American temperate forests: The initiative of the Institute of Ecological Research Chiloé, Chile. *Biodiversity and Conservation*, 9(8), 1199–1217.

Rüger, N., Gutiérrez, Á. G., Kissling, W. D., Armesto, J. J., Huth, A. (2007). Ecological impacts of different harvesting scenarios for temperate evergreen rain forest in southern Chile-A simulation experiment. *Forest Ecology and Management*, 252(3), 52–66.

Rummell, R. S. (1951). Some effects of livestock grazing on ponderosa pine forest and range in central Washington. *Ecology,* 32, 594–607

Sabatini, F. M., Burrascano, S., Lombardi, F., Chirici, G., Blasi, C. (2015). An index of structural complexity for Apennine beech forests. *iForest*, 8, 314–323.

Sala, O., Chapin, F., Armesto, J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwld, E., Huenneke, L., Jackson, R., Kinzing, A., Lee-mans, R., Lodge, D., Mooney, H., Oesterheld, M., Poff, L. R., Sykes, M., Walker, B., Walker, M., Wall, D. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774.

Seaman, B. J., Albornoz, F. E., Armesto, J. J., Gaxiola, A. (2015). Phosphorus conservation during post-fire regeneration in a Chilean temperate rainforest. *Austral Ecology*, 40(6), 709–717.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organism: Fennoscandian boreal forests as an example. *Ecological Bulletins*, 49(49), 11–41.

Simonetti, J. A., Armesto, J. J. (1991). Conservation of temperate ecosystems in Chile: Coarse versus fine-filter approaches. *Revista Chilena de Historia Natural*, 64, 615–626.

Smith, A. P., Wellham, G. S., Green, S. W. (1989). Seasonal foraging activity and microhabitat selection by echidnas (Tachyglossus aculeatus) on the New England Tablelands. *Australian Journal of Ecology*, 14(4), 457–466.

Smith-Ramírez, C., Maturana, V., Gaxiola, A., Carmona, M. (2014). Salvage logging by indigenous people in a Chilean conifer forest. *Forest Science*, 60(1), 1–7.

Soto-Azat, C., Valenzuela-Sánchez, A., Collen, B., Rowcliffe, J. M., Veloso, A., Cunningham, A. (2013). The population decline and extinction of Darwin’s frogs. *PLoS ONE*, 8(6), e66957.

Spies, T. A., Franklin, J. F. (1991). The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington, in: Ruggiero, L. F., Aubry, K. B., Carey, A. B., Huff, M. H. (Eds.), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. Portland, USA, pp. 91–109.

Tasker, E. M., Bradstock, R. A. (2006). Influence of cattle grazing practices on forest understorey structure in north-eastern New South Wales. *Austral Ecology*, 31(4), 490–502.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), 79–92.

Thiollay, J. (1993). Influence of selective logging on bird species diversity in a Guianan rain forest. *Biological Conservation*, 64(3), 245–246.

Thompson, I., Mackey, B., McNulty, S., Mosseler, A. (2009). Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series no. 43.

Tomasevic, J. A., Estades, C. F. (2006). Stand attributes and the abundance of secondary cavity-nesting birds in southern beech (Nothofagus) forests in South-Central Chile. *Ornitologia Neotropical*, 17(1), 1–14.

Uetz, G. W. (1979). The influence of variation in litter habitats on spider communities. *Oecologia*, 40(1), 29–42.

UNESCO. (2010). World Network of Biosphere Reserves (WNBR). Ecological Sciences for Sustainable Development. <http://www.unesco. org/new/en/natural-sciences/environment/ecological-sciences/biosphere- reserves/wnbr/>. Accessed 22 Jun 2015.

Veblen, T. T., Donoso, C., Kitzberger, T., Rebertus, A. J. (1996). Ecology of southern Chilean and Argentinean Nothofagus forests, in: Veblen, T. T., Hill R. S., Read J. (Eds.), *Ecology and biogeography of Nothofagus forests*. Yale University Press, New Haven, pp. 293-353.

Veblen, T. T., Schlegel, F., Escobar, B. R. (1980). Structure and dynamics of old-growth Nothofagus forests in the Valdivian Andes, Chile. *Journal of Ecology*, 68(1), 1–31.

Veblen, T. T. (1982). Growth patterns of Chusquea bamboos in the understory of Chilean Nothofagus forests and their influences in forest dynamics. *Bulletin of the Torrey Botanical Club*, 109(4), 474–487.

Veblen, T. T., Ashton, D. H. (1978). Catastrophic influences on the vegetation of the Valdivian Andes, Chile. *Vegetatio*, 36(3), 149–167.

Veblen, T. T., Ashton, D. H., Schlegel, F. M., Veblen, A. T. (1977). Distribution and dominance of species in the understorey of a mixed evergreen-deciduous Nothofagus forest in south-central Chile. *Journal of Ecology*, 65(3), 815–830.

Veblen, T. T., Kitzberger, T., Lara, A. (1992). Disturbance and forest dynamics along a transect from Andean rain forest to Patagonian shrubland. *Journal of Vegetation Science*, 3(4), 507–520.

Veblen, T. T., Mermoz, M., Martin, C., Kitzberger, T. (1993). Ecological impacts of introduced animals in Nahuel Huapi National Park, Argentina. *Biological Conservation*, 6(1), 71-83.

Veblen, T. T. (1983). Degradation of native forest resources in southern Chile, in: Steen, H. K. (Ed.), *History of Sustained-Yield Forests: A Symposium*. Forest History Society, Durham, North Carolina, pp. 344-352.

Villagrán, C., Hinojosa, L. F. (1997). Historia de los bosques del sur de Sudamérica, II: Análisis fitogeográfico. *Revista Chilena de Historia Natural*, 70(2), 241–267.

Whitfield, S. M., Bell, K. E., Philippi, T., Sasa, M., Bolaños, F., Chaves, G., Savage, J. M., Donnelly, M. A. (2007). Amphibian and reptile declines over 35 years at La Selva, Costa Rica. *Proceedings of the National Academy of Sciences of the United States of America*, 104(20), 8352–8356.

Whitman, A. A., Hagan, J. M. (2007). An index to identify late-successional forest in temperate and boreal zones. *Forest Ecology and Management*, 246(3), 144–154.

Wilcox, K. (1996). *Chile's Native Forests: A conservation legacy*. Ancient Forest International, Redway, CA.

Willson, M. F., Armesto, J. J. (1996). The natural history of Chiloe: on Darwin's trail. *Revista Chilena de Historia Natural*, 69, 149–161.

Willson, M. F., Sabag, C., Figueroa, J., Armesto, J. J., Caviedes, M. (1996). Seed dispersal by lizards in Chilean rainforest. *Revista Chilena de Historia Natural*, 69(3), 339–342.

Wilson, K., Newton, A., Echeverría, C., Weston, C., Burgman, M. (2005). A vulnerability analysis of the temperate forests of south central Chile. *Biological Conservation*, 122(1), 9–21.

Yahner, R. H. (1986). Microhabitat use by small mammals in even-aged forest stands. *American Midland Naturalist*, 115(1), 174–180.

Youngblood, A. (2010). Thinning and burning in dry coniferous forests of the western united states: Effectiveness in altering diameter distributions. *Forest Science*, 56(1), 46–59.

Zamorano-Elgueta, C., Cayuela, L., González-Espinosa, M., Lara, A., Parra-Vázquez, M. R. (2012). Impacts of cattle on the South American temperate forests: Challenges for the conservation of the endangered monkey puzzle tree (Araucaria araucana) in Chile. *Biological Conservation*, 152, 110–118.

Zamorano-Elgueta, C., Cayuela, L., Rey-Benayas, J. M., Donoso, P. J., Geneletti, D., Hobbs, R. J. (2014). The differential influences of human-induced disturbances on tree regeneration community: a landscape approach. *Ecosphere*, 5(7), 90.

Zenner, E. K. (2004). Does old-growth condition imply high live-tree structural complexity? *Forest Ecology and Management*, 195(1-2), 243–258.

Zenner, E. K., Peck, J. E., Lähde, E., Laiho, O. (2012). Decomposing small-scale structural complexity in even-and uneven-sized Norway spruce-dominated forests in southern Finland. *Forestry*, 85(1), 41–49.

Appendices

Appendix 1. Table showing the range and mean values of the five stand-structural attributes and the stand-structural complexity index for the Andean temperate forest in relation to the seven habitat categories. Asterisks represent the minimum (*) and maximum (**) values of the stand-structural complexity index and of each structural attribute.

	Understory density (n° contacts)		Coarse woody debris (m^3/ha)		Litter depth (cm)		Stand basal area (m^2/ha)		Snags density (stems/ha)		Structural complexity index (%)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Old-growth forest	7.55**	0.0* - 20.2**	13.74**	0.0* - 150.88	6.57**	1.32 - 21.86	75.28**	5.54 - 206.11	46.02	0.0* - 126.94	80.03**	39.47 - 96.14
Mid-successional forest (bamboo understory)	5.49	1.2 - 13.4	11.34	0.0* - 98.0	6.31	0.64 - 22.0	41.67	8.26 - 310.49**	55.01**	0.0* - 482.38**	73.18	41.49 - 100**
Mid-successional forest (other understory)	4.72	0.8 - 14.0	4.41	0.0* - 51.38	5.23	1.04 - 15.82	34.76	1.13 - 102.17	44.11	0.0* - 380.83	65.18	40.8 - 88.23
Mid-successional forest (no understory)	1.7	0.0* - 5.4	5.85	0.0* - 91.41	2.98	0.0* - 9.44	35.22	2.96 - 78.07	35.2	0.0* - 228.50	55.66	34.79 - 85.47
Early successional forest (< 20 years old)	3.58	0.2 - 13.0	2.3	0.0* - 44.16	4.3	0.0* - 10.18	16.71	0.0* - 77.89	17.26	0.0* - 177.72	54.21	35.43 - 82.26
Mixed shrubland	2.39	0.0* - 8.6	3.11	0.0* - 188.4**	1.65	0.0* - 7.82	8.71	0.0* - 106.40	12.55	0.0* - 304.7	43.91	31.82* - 85.03
Openfield	0.42*	0.0* - 3.2	1.18*	0.0* - 33.17	0.41*	0.0* - 23.82**	2.21*	0.0* - 3.34	0.0*	0.0* - 0.0	34.38*	31.82* - 44.82

Appendix 2. Table showing the range and mean values of the five stand-structural attributes and the stand-structural complexity index for the Andean temperate forest in relation to the eight disturbance treatments. Asterisks represent the minimum (*) and maximum (**) values of the stand-structural complexity index and of each structural attribute.

	Understory density (n° contacts)		Coarse woody debris (m^3/ha)		Litter depth (cm)		Stand basal area (m^2/ha)		Snags density (stems/ha)		Structural complexity index (%)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
No disturbance (control)	6.18**	1.60 - 12.20	15.75**	0.00* - 150.88	6.27	1.32 - 13.44	68.15**	7.88 - 123.34	40.2	0.00* - 126.94	77.67**	55.54 - 96.14
Fire	5.89	2.80 - 14.00	2.96	0.00* - 17.20	7.04**	0.00* - 15.14	45.33	0.00* - 113.10	48.57	0.00* - 126.94	72.51	40.48 - 91.85
Logging	5.11	0.40 - 13-00	2.87	0.00* - 40.42	5.5	0.22 - 13.16	27.88	2.96 - 77.89	41.82	0.00* - 304.66	62.7	34.79 - 86.57
Livestock	4.01	0.20 - 14.00	3.38	0.00* - 45.34	3.57	1.00 - 7.66	32.36	0.00* - 206.11	18.13*	0.00* - 126.94	54.74	35.43 - 93.60
Fire + Logging	5.6	0.80 - 13.40	7.84	0.00* - 73.44	6.31	1.56 - 22.00**	44.31	1.13 - 310.49**	50.78	0.00* - 482.38**	71.63	41.49 - 100**
Fire + Livestock	4.98	2.00 - 11.00	5.23	0.00* - 27.98	4.53	1.24 - 7.10	48.05	16.51 - 85.93	60.93**	0.00* - 228.50	70.42	49.76 - 90.66
Logging + Livestock	2.72*	0.00* - 10.20	1.23*	0.00* - 8.90	3.58	0.00* - 21.86	30.18	2.82 - 96.92	23.94	0.00* - 279.27	53.48	35.27 - 80.02
Fire + Logging + Livestock	2.99	0.00* - 20.20**	6.77	0.00* - 188.40**	2.89*	0.00* - 16.46	20.23*	0.00* - 175.58	21.73	0.00* - 380.83	52.47*	31.82* - 94.83