Response of temperate forest birds to habitat change in central Chile

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ABSTRACT

Despite the long time since the introduction and spread of pine plantations in southern hemisphere countries there has been no study of the suitability of this exotic and novel type of vegetation on the native avifauna. This thesis aims to add understanding of this habitat replacement and its effects on the forest bird community. This research included a series of studies to assess the quality of mature pine plantations for the forest avifauna in comparison to what is in native forests. The first two studies determine the effects on the forest bird community of the fragmentation and replacement of native forest in a gradient of substitution. The results showed a direct relationship between level of substitution and loss of functional diversity, and that fragmentation predicts the bird assemblage in pine stands. The next two studies used data from an intensive ringing season to assess differences in the condition of populations inhabiting each habitat. Birds, in general, were found in better condition in native fragments than in pine plantations. Moreover, a despotic distribution was determined for a migrant species and a gradient in habitat quality was found in relation to proximity to native forest. The next two studies used information from a nest-box survey set in a gradient of sites with substitution of native forest. The results showed that the type of forest cover and their proportion in the landscape may affect the breeding performance of some species. Finally, in the last study I evaluated the foraging niche of bird species in each habitat. Compared with native forest, niche breath reduced while the niche overlap increased in pine plantations for most species. The results suggest that pine plantations are poor quality habitat for the bird community and that the substitution of native forests increases selective pressure.

Declaration

I hereby declare that this thesis was composed by myself, and the work presented is the result of my own research, carried out by myself unless otherwise stated. The content of this thesis has not been presented in any previous application for a degree.

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Chapter 1

General introduction: **Temperate forests fragmented in a pine plantation matrix — Effects on the forest bird community**

1.1 Fragmentation

Habitat fragmentation and loss, especially of forest, are recognized as the principal causes of biodiversity loss (Brooks *et al.* 2006)[1]. Both processes are directly connected, and they differ in that habitat loss relates to the direct loss of area available for the development of populations (Villard *et al.* 1999), whereas the fragmentation process refers to the loss of habitat connectivity, leaving scattered patches embedded in a matrix which generally dominates the landscape (Andrén 1994). They are caused mainly by the substitution of one habitat type by another. Although this could have a natural cause, currently the most common causes are anthropogenic (Andrén 1994). In this way, habitat matrices of different types can occur in terrestrial environments, which are determined by the land use, e.g.: agricultural crops, forest plantations or urban areas (Shanahan *et al.* 2011).

In the past half century there has been an evolution in the way that studies have considered the matrix of habitat, from a complete binary system to a more graded multi-scale understanding. Hence, early works on fragmentation, based primarily on Island Biogeography Theory (MacArthur 1967) recognized the matrix as a non-habitat where populations cannot penetrate unless the studied species can move to a neighbouring patch. This flow of individuals led to the development of the Metapopulation Theory (Hanski & Gilpin 1991; Pulliam 1988) in which the flow of individuals between patches allows population viability in fragmented environments. However, habitat fragmentation and isolation do not necessarily include very different habitats, these processes can even occur within a forest, if one type of forest habitat becomes fragmented into another (Enoksson *et al.* 1995; Garant *et al.* 2005). In connection to that, McIntyre and Barrett (1992) propose a concept of "variegated" landscape, where there are gradients of habitat and quality condition rather than a

[1] For a review of impacts of temperate forest worldwide see Appendix 1.

binomial state of habitat and non-habitat. Currently, it seems likely that the matrix plays an important role in population dynamics (Ricketts 2001), affecting processes that occur both within and between patches in heterogeneous landscapes (Prevedello & Vieira 2010). Among the best-documented matrix effects is the recognition that the level of fragmentation in the landscape can predict the structure of forest bird communities (Rodewald 2003).

The interaction of the type of matrix, in terms of its composition and structure, with the fragmentation level delineates the fragmentation effect acting on the community. On one hand, it has been recognized that composition of the landscape matrix can determine the extent of edge effects, population size and isolation (Rodewald 2003). On the other hand, structural differences in land use can directly affect the ability of individuals to reach a different patch, find suitable habitat, or find enough resources (Rodewald 2003). Therefore, the type of matrix may affect colonization rates of isolated fragments, movement of animals between fragments, and can also add species to fragments, influencing species composition, abundance and species persistence in fragments (Tubelis *et al.* 2004). In a review, Prevedello and Vieira (2010) noted that in 88% of fragmentation studies, matrices with a similar structure to the patches had a similar quality for the studied organisms as the natural habitat from a functional connectivity point of view. It is proposed that the connectivity between fragments increases with greater similarity in habitat structure, floral composition and microclimate between fragments and matrices (Renjifo 2001). Also, some types of matrix can provide foraging or breeding habitat for some species, and as a result they can influence the local abundance and persistence of forest organisms in fragmented landscapes (Renjifo 2001).

In summary, depending on its nature, a matrix may be an alternative or secondary habitat, source of disturbances and invasive species, and help or deter the dispersal of individuals (Prevedello & Vieira 2010). Nevertheless, to understand the processes by which species are lost when natural habitat is altered or fragmented, we have to relate landscape changes to the species biology (Enoksson *et al.* 1995). Overall response to the surrounding matrices are highly species specific, being related

to the characteristics of individuals such as dispersal ability, area requirements and the degree of habitat specialization that determine which species are affected and how (Enoksson *et al.* 1995).

1.2 Coniferous matrix

Reforestation with fast-growing tree species has reached a significant level of land surface globally, corresponding to 264 million hectares by 2010 (FAO 2010). Pine plantations correspond to approximately 32% of total global forest plantations (Luck & Korodaj 2008), established around the world, and it is expected that the area covered by pine plantations is going to increase dramatically in the coming decades (FSC 2012; Wunderle Jr 1997). While much of the ground now covered with pine plantations include land degraded by intensive agricultural use, it is also true that a significant proportion has directly replaced natural habitats (Kanowski *et al.* 2005; Lara & Veblen 1993). It is also argued that, apart from their economic benefits, pine plantations could provide many ecological benefits, such as carbon sequestration and reducing soil erosion of degraded agricultural lands (Geary 2001). Moreover, as plantations grow faster than natural forests, producing more timber products per year, this reduces the land needed to supply the world demand on wood products, therefore, the pressure on native forests is reduced (Niesten *et al.* 2002). However, this modern forestry practice has changed the structure and composition of natural forest landscapes, affecting the wildlife that resides there (Enoksson *et al.* 1995; Pedersen *et al.* 2010) and ecosystem services provided by native forests (Geldenhuys 1997).

Several studies have shown that coniferous plantations can be colonized and inhabited by different taxa (Brockerhoff, Jactel et al. (2008) since they are more complex structurally than grassland, and so provide greater connectivity for several forest species (Renjifo 2001). Moreover, the matrix of conifer forests can provide greater protection from predators than they would have in other types of matrix, such as open fields or water bodies. In this way, isolation may be less important in this less hostile matrix (Enoksson *et al.* 1995). However, this apparent advantage does not apply in a forest landscape, where bird dispersion requires not only several short flights, but also a need to find food

and the good small or isolated habitat patches (Enoksson *et al.* 1995). In summary, it has been suggested that a soft contrast between matrix and fragments could increase connectivity for local populations and so also their abundance in fragmented forests.

As the edge effect can cause various impacts on native flora and fauna, this type of matrix can have an important influence on the effective area of the fragments (Tubelis *et al.* 2004). Temple (1986) found that core area size of a fragment is more important than the total size of the fragment to explain the response of birds to forest fragmentation. It may be that for forest birds, the core area of a patch of deciduous forest surrounded by a plantation of conifers is more or less like the whole patch, while only the central part of a patch that is surrounded by open fields functions as a core area (Enoksson *et al.* 1995). At the same time, fragmentation studies have usually shown that forest fragment size has a positive relationship with bird species richness, but it seems that coniferous matrices could reverse this relationship (Estades & Temple 1999). Another interesting fragment-matrix interaction effect has been detailed by Tubelis et al. (2004), who found that narrow native forest fragments extend their influence in terms of bird diversity into exotic plantations further than that of wider patches. However, in spite of these documented effects, it is unlikely that any bird species could maintain a viable population in small patches, although these crops may provide a supplement of resources to birds associated with small fragments (Fischer & Lindenmayer 2002).

The ability of certain species to use pine plantations depends on the degree of specialization or generalization of the local fauna (Wunderle Jr 1997). In the same way it has been recognized for several groups of species able to use the surrounding matrix, that they tend to be more tolerant of fragmentation than those species that do not use it (Tubelis *et al.* 2007). Lindenmayer et al. (2003) highlight the wide range of responses at the guild level and how landscapes may be perceived differently across species. Therefore, a review of the situation in different geographic areas is needed to determine the effects of exotic conifer plantations on forest birds. Several studies of the subject have been made, and while the variation in environmental conditions between areas in terms of their breadth and the composition and origin of forest bird communities makes it difficult to find general

patterns, it seems likely that we might identify clear selective effects of conifer plantations on forest bird communities.

Comparisons between bird communities present regionally in a pine plantation and native forest, show that species richness in indigenous forests is greater than that found in conifer plantations, as is the case in France (Barbaro *et al.* 2005), Spain (Díaz 2006), England (Moss 1979), Ireland (Sweeney *et al.* 2010), Australia (Driscoll 1977; Gepp 1976; Tubelis *et al.* 2004) and New Zealand (Clout & Gaze 1984). However, there are exceptions to this condition. Some studies have not found significant differences in species richness between the two forest cover types in Chile (Estades & Temple 1999; Vergara & Simonetti 2004), North Wales (Bibby *et al.* 1989) and New Zealand (Maunder *et al.* 2005). While this may seem strange or contradictory, it is worth noting the differential response of different species of forest birds to the effect of conifer plantations. Thus, forest specialist species and those that depend on resources associated with native broadleaf vegetation are most affected by the habitat replacement. Woodpeckers (Picidae) are often the most sensitive to changes in the tree species composition (Enoksson *et al.* 1995; Gibb 1961) and their local extinction may directly affect populations of cavity nesting species. Closely related to the previous point, the reduced availability of tree holes in pine plantations makes this resource a limiting factor for cavity nesters (Clout & Gaze 1984; Disney & Stokes 1976; Donald *et al.* 1998; Enoksson *et al.* 1995; Sweeney *et al.* 2010). The explanation for this condition is found in the structure and composition simplicity of conifer plantations, which are generally even-aged monocultures subject to short rotation cycles preventing the formation of natural cavities. In this way, the availability of food resources and vegetation structures determine the distribution of species, and the shortage of these resources in forest plantations could make tree monocultures unattractive for various organisms (Renjifo 2001). Frugivorous and nectarivorous foraging guilds are therefore particularly affected by the replacement of natural vegetation with monocultures of conifers (Clout & Gaze 1984; Jackson 1971; Renjifo 2001). However, some insectivorous species can be found using a wide variety of niches in forest plantations (Gibb 1961; Jackson 1971; Maunder *et al.* 2005). It has been suggested that the presence of forest birds in pine plantations could result from the expansion of their foraging areas (Tubelis *et al.* 2004)

using plantations as substitute habitat (Lindenmayer *et al.* 2003). However the condition of habitat substitution by coniferous plantations is still controversial (Carlson 1986; Renjifo 2001).

Consistent with this, a simplification of habitat leads to a simplification of the forest bird community. Most bird species found using forest plantations are generalist species (Sweeney *et al.* 2010) denoting an impoverished avifauna compared to the potential of the regional avifauna at the expense of forest specialist species [South Africa (Allan *et al.* 1997; Armstrong & Van Hensbergen 1995; Armstrong *et al.* 1996), North Wales (Bibby *et al.* 1989), Portugal (Rey-Benayas *et al.* 2010)]. In situations such as Wales and Ireland, much of the bird community is composed of a low number of species, which in general are common in other habitats (Bibby *et al.* 1989; Sweeney *et al.* 2010). According to Jackson (1971), it is common to find facultative forest dwellers, sometimes primary forest dwellers, in Australian pine plantations, and obligate forest dwellers are almost absent from these plantations. For the latter two groups, the author suggests that the plantation matrix would enhance landscape connectivity. However, a generalization of the effect of pine plantations on resident or migratory species it is not possible, finding different answers according to each community and each species. In the forests of northern Europe, resident bird species are strongly affected by the loss of the broadleaf component in the landscape and just about a third of the resident species are found in managed forests of conifers (Enoksson *et al.* 1995). By contrast, in North Wales the community of birds observed in plantations of exotic conifers is mainly composed of resident species, and relatively uncommon migratory species that reach 12% of the community (Bibby *et al.* 1989). A similar condition is reported for pine plantations in Portugal (Galván & Benayas 2011).

Despite the negative impact of conifer plantations for forest birds, there is growing evidence that for some bird species these afforestations have a positive effect. In different latitudes a greater abundance of certain species has been observed than that occurring in surrounding native forests, suggesting a preference of these species for the new habitat (Estades & Temple 1999; Lindenmayer *et al.* 2003; Maunder *et al.* 2005; Vergara & Simonetti 2004). The use of plantations as nesting habitat has also

been recorded for several species of passerines (Estades 1999; Estades & Temple 1999), and for some birds of prey (Estades 1999; Malan & Robinson 2001; Seaton *et al.* 2009; Wilson *et al.* 2009).

To predict accurately the effect of replacement of native forests with plantations of exotic conifers, it is necessary to integrate information across different scales, from sites to landscapes. For example, at a landscape scale there has been a decline in certain populations because of the dominance of exotic plantations and the subsequent loss of the broadleaf component across the landscape (Enoksson *et al.* 1995; Estades & Temple 1999; Tubelis *et al.* 2007). At the same time, it seems essential to carry out a review in relation to how researchers in this field have focused their attention. Studies that seek to determine the effect of the substitution of native forest by plantations of exotic conifers on the bird community should therefore define from the outset the degree of dependence of each species in relation to their natural habitat as well as a description of the prime bird community in the studied habitat. This will eliminate noise generated by the addition of species to the system that are not related to the natural cycle of indigenous forests. For example, industrial forestry that uses clear-cutting as the main harvest method, creates large gaps in the landscape, which allow the arrival of birds associated with grassland habitats to these sites. With the subsequent development of forest plantations, the associated bird community changes through the rotation cycle, and it is precisely this variability, when it is expressed in terms of pooled species richness, that confuses the reader about the real potential of exotic conifers plantations as habitat for forest wildlife.

Finally, despite the many studies of the effect of habitat fragmentation, the status of birds in terms of their success in the exploitation of pine plantations has not been clarified by the characterization of the bird communities (species richness and abundance). All the reviewed information suggests that the proposed role of these artificial forests in the conservation of biodiversity (Lindenmayer *et al.* 2002), has not been thoroughly analysed and is still controversial (Estades & Escobar 2005). It is reasonable to think that pine plantations may act as sink habitats for many forest bird species.

1.3 Aim of this thesis

This thesis aims to clarify what are the real effects of habitat substitution with a novel tree species on a forest bird community, in the context of the mature forest habitat. This is anchored in the fact that there is a huge controversy in Chile about whether pine plantations could be called and treated as forest (Moll-Rocek 2014). This question is not trivial, because according to the last report of Global Forest Watch (FAO 2010), the gain of area covered with forest during the period 2000-2010 was 397,000 Ha, while the loss of primary forest for the same period was 97,000 Ha. Even though these figures reflect the productive forestry cycle, it must also be understood that "if plantations are accepted as forest, there is nothing wrong with replacing natural forests with monocultures"(Putz & Romero 2014).

It is widely recognized that differences in habitat structure may be important in the abundance, diversity and distribution of birds (Cody 1970; Wiens 1989). Accordingly, most of the studies carried out on Chilean temperate forest birds have used them mainly as a tool to explain the effects of fragmentation or habitat lost, not covering the significance of environmental factors for bird populations. However, this information can mask the condition of individuals in terms of health or reproductive rate, as a result of different selective pressures acting on populations. It is important to keep in mind that temporal and geographical variation in adult body size may be related to several factors; climate, intra- and inter-specific competition, predation and environmental variability (Gosler *et al.* 1995; Jakober & Stauber 2000; Yom-Tov *et al.* 2006). In the Great Tit (*Parus major*), Ulfstrand et al. (1981) suggest that variations in body size of individuals inhabiting deciduous forests or alternative coniferous forests, might respond to three possible scenarios. First, birds might nest in the habitat in which they grew, and the birds in suboptimal habitats might therefore be small because they received less food. Second, the birds that inhabit different habitats have different morphological adaptations that allow them to exploit these environments optimally. Third, social dominance might affect habitat selection by individuals (e.g. Gosler 1987). Furthermore, changes in the trophic niche of

the species may well explain temporal and geographical variation in adult body size (Grant & Grant 2002).

In this thesis I assess the effect of habitat substitution with a novel forest cover at a landscape and stand level on forest bird communities, describing them in terms of composition, structure and spatial configuration. I then focus the study on direct responses of individuals belonging to populations associated with each habitat, in terms of behaviour and physiological traits, which, in turn, would influence population parameters such as breeding success. Given the high spatial homogeneity and different disturbance regimes that characterize forest plantations compared with native temperate forests, I suggest that individuals of animal species that inhabit these environments are subject to strong selective pressures. Hence, the research described in the following chapters assesses the habitat quality of pine plantations for the forest bird community by looking at different ecological parameters at different spatial scales.

Each chapter was written so as to a stand alone, including a brief description and introduction to the topic followed by detailed methods. The aim of this approach is to allow each chapter to be judged as a publication. Although this approach leads to some degree of repetition between chapters, it renders this work as a more useful reference tool.

The thesis is organized as follows. In Chapter 2, I investigate the effect of the replacement of native forest with pine plantations at the landscape level on the forest bird community. Specifically, I determine how the fragmentation of natural vegetation affects the functional diversity and species richness in the community. As each species from the community responds individually to habitat disturbances, in Chapter 3, I assess the habitat factors, such as stand vegetation structure and composition, features of neighbouring areas, and fragmentation metrics that explain the abundance of each species.

The remaining chapters are dedicated to comparing the quality of pine plantations against native forest as habitat for bird populations. In Chapter 4, I look for differences in body condition between individuals inhabiting either native forest or pine plantations, while I test habitat

features in explaining those differences. Then, in Chapter 5, I assess how habitat, along with individual's features, determines the health condition of breeding birds. I also compare the ecto-parasite burden and prevalence of blood parasites between individuals captured in either habitat. Chapter 6 assesses the effect of the fragmentation and replacement of native forest on the reproduction of forest birds. There, I evaluate the performance of breeding birds according to habitat descriptors from different spatial scales. It is well known that coniferous forest cause soil acidification (Berthrong *et al.* 2009), reducing the soil concentration of micronutrients, such as Calcium, which is a critical resource for breeding birds (Bidwell *et al.* 2005). Chapter 7 therefore evaluates the environmental effect of pine plantations on the eggshell formation of a passerine species by assessing their pigmentation (Gosler *et al.* 2005). Finally, in Chapter 8 I evaluate how the replacement of the native canopy alters the relationships between species of the forest bird community. I compare the foraging niche of forest bird species in either habitat while evaluating variations in inter-specific competition among species.

The thesis is concluded with a brief general discussion guided by my overall opinion that, based on the results presented in each chapter, the replacement of native forest with pine plantations increases the selective pressures, that discriminate against forest specialists.

Chapter 2

Importance of the amount of native forest in the landscape for bird diversity

2.1. Introduction

Biodiversity is recognized as all the variety of life on earth, at all levels, including their genetic differences, phenotypes, populations, communities, cultures and ecosystems, and the ecological and evolutionary processes that sustain it (UNEP 2007). Habitat loss and fragmentation are known as the principal causes of biodiversity loss (Brooks *et al.* 2006). Many researchers have emphasized the differences between these two processes (Fahrig 1997; McGarigal & Cushman 2002) and while both are directly related, the first one is related to the direct loss of area available for the development of populations (Villard *et al.* 1999), whereas the fragmentation process refers to the loss of habitat connectivity in scattered patches of habitat embedded in a matrix which generally dominate the landscape (Andrén 1994).

Habitat loss and fragmentation are mainly caused by the substitution of one environment with another, and although it could be due to a natural cause, currently the most common causes are anthropogenic (Andrén 1994). In terrestrial environments, therefore, the habitat matrix might differ as it is determined by land use instead (i.e., agricultural crops, forest plantations or urban areas) (Shanahan *et al.* 2011). Early work on fragmentation, based primarily on Island Biogeography Theory (MacArthur 1967), recognized the matrix as a non-habitat where populations cannot penetrate unless the studied species can move to a neighbouring patch. This flow of individuals led to the development of the Metapopulation Theory (Hanski & Gilpin 1991; Pulliam 1988) in which the flow of individuals between patches allows for population viability in fragmented environments.

Reforestation with fast-growing tree species has reached a significant level with substantial land surface globally, corresponding to 264 million hectares by 2010 (FAO 2010). While much of this area includes land degraded by intensive agricultural use, it is also true that a significant

proportion had directly replaced natural habitats (Kanowski *et al.* 2005; Lara & Veblen 1993). This modern forestry practice has changed the structure and composition of natural forest landscapes, affecting the wildlife that reside there (Enoksson *et al.* 1995; Pedersen *et al.* 2010). The difference in structural features between the original habitat and the matrix that dominates the landscape has great relevance in the degree of isolation that habitat replacement generates in the biological populations of the remaining patches (Dunning *et al.* 1992; Fischer & B Lindenmayer 2006; Taylor *et al.* 1993). It has been recognized that the difference in structure between natural forests and forest plantations generates a soft barrier to many populations of vertebrates (Estades & Temple 1999). Several studies have shown that this widespread cultivation could be colonized and inhabited by different taxa (see Brockerhoff *et al*. 2008). However, there is still some controversy regarding the real contribution of forest plantations in conservation, because they select for generalist species at the expense of more specialized ones (Carlson 1986).

In Chile, given its biogeographic history, it is possible to find many types of forests; with deciduous Maulino forest being one of the most threatened in terms of remaining area and the actual state of degradation (Echeverría *et al.* 2006). Forest plantations in Chile have already exceeded 2 million hectares, mainly Monterey pine. Over the last 60 years, this exotic tree species has replaced the natural forest that once covered much of south-central Chile.

There are huge differences between temperate deciduous forest and the evergreen coniferous plantation. Thus, the Maulino forest regeneration strategy, like most broadleaf forests of Chile, is based on canopy openings generated by small perturbations, such as the fall of a dead tree or a landslide, generating a complex stand structure that exhibits all ages and all sizes (Veblen *et al.* 1985). In contrast, pine plantations are under extensive management, where even-aged mono-specific stands are created, varying in size from a few to hundreds of acres that are harvested by clear-cutting at an average age of 22 years (Estades & Escobar 2005). The current management of pine plantations in the study area aims to reconcile the production of timber and pulp. Consequently, stand density used (number of trees per hectare) gives light and moisture conditions

allowing the development of relevant undergrowth in many cases. However, the structure of the vegetation in pine plantations is simpler than that of natural forests and their short production cycles do not allow the development of mature forests.

Forest bird studies on this system have shown no significant differences in the number of species found in continuous natural forests, fragments or pine plantations (Vergara & Simonetti 2004). In addition, small fragments can accommodate more bird species than continuous forests, a fact which contradicts the Island Biogeographic Theory, where the number of species is directly related to the size of the fragment (Estades & Temple 1999; Fischer *et al.* 2006). However, caution must be applied because landscape features, such as the proximity and proportion of open areas, and the fact that small fragments are associated with riparian protection, could alter the assembly of forest birds.

The effect of the evergreen vegetation cover of coniferous plantations during the winter on the forest bird assemblage has not been yet understood. Most of the studies carried out in these systems have considered only the breeding season (Estades & Temple 1999; Vergara & Simonetti 2004). During the winter, forest birds change their behaviour, increasing their tolerance for con-specifics and other species forming multispecies flocks while foraging (Ippi & Trejo 2003). A survey during the non-breeding season is necessary to understand the persistence, dispersion and the use of pine plantation by forest bird species.

There is good evidence that intense fragmentation processes at a landscape level can impact severely on the composition and diversity of bird communities (Magnago *et al.* 2014). According to Bregman et al. (2014), fragmentation processes have a clear and negative impact on species richness of temperate forest birds, which is explained in part by decreased reproductive success in migratory species (Robinson *et al.* 1995).

In recent years, community ecology studies have focused on the relationship of species diversity and functional traits, showing how they influenced ecosystem functioning (Cadotte *et al.* 2011; Petchey & Gaston 2006). The loss of species is not the only change that fragmentation generates on

communities; it also affects ecosystem functions, degrading ecosystem services and ecological processes that support human well-being (Flynn *et al.* 2009; Trindade-Filho *et al.* 2012). Moreover, disturbances causing loss or replacement of species, either degradation or loss of habitat, ultimately produce a functional ecosystem homogenization (Clavel *et al.* 2010), so the use of species richness as the sole measure to quantify changes in the community is insufficient (Cadotte *et al.* 2011; Naeem *et al.* 2012).

The aim of this study is to determine the actual effect of the replacement of natural deciduous forests with mono-specific conifers on the forest bird community. Specifically, I intend to elucidate the effect of fragmentation of native forest in a mature forest matrix, in this study pine plantation, on the forest bird community. I based my research on the hypothesis that the amount of remaining native forest in the landscape has a positive effect on the functional diversity of the forest bird community. In order to do that, I assess how the species richness and the functional diversity of the forest bird assemblage change in a gradient of fragmentation in different seasons, and a comparison of individual bird species abundance in either habitat is also carried out.

2.2. Methods

2.2.1. *Study area*. The study was carried out on the bird community of the temperate forest of South Central Chile, on the administrative region of "Del Maule". The climate in this region is temperate with warm and dry summers (Peel *et al.* 2007), with an average temperature of 13.9 °C, and annual precipitation of 942 mm (Hajek & Di Castri 1975). The study is focused on 7500 km^2 area of the "Roble-Hualo" forest type distribution over the Coastal range, known as Maulino forest, ranging from Tregualemu river (35°58’ S 72°44’ W) in the south to "Altos de Licanten" (34°58’ S 72°02’ W) in the north. One important climatic factor considered in the site selection was the oceanic influence, the extent of which varies with the topography.

2.2.2. *Landscape Units*. The selection of landscape units for the study was based on forest cover database of Arauco S.A., the largest forest company in Chile and South America (Arauco 2012), the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh 2010), and Quickbird™ imagery.

A total of 22 landscape units were defined in the study area considering the following constraints and attributes. To encompass the breeding home range of most species of forest-dwelling passerines, landscape units of 4 km^2 were defined (McGarigal & McComb 1995; Villard *et al.* 1999). The selection process considered continuous forest habitat as a main constraint, selecting only landscape units with at least 85% forest cover. This was necessary to eliminate any disturbing effect made by young or harvested stands. As the majority of pine plantations in the region belonged to Arauco Forest Company, work carried out on their land represented a good sample of the whole area. However, to increase the sample size, I included five landscape units recognized on Satellite images; two natural reserves and three estates that belonged to minor companies (Fig. 1).

2.2.3. *Avian surveys*. During the breeding season 2011, from October to December, I conducted bird counts on every landscape unit, considering every patch type. Bird density and species richness were estimated using the variable circular-plot method with a 50 m maximum observation radius. No observations were conducted on rainy or misty days. All birds seen or heard within the maximum radius were recorded, and their distance from the plot's centre was estimated in 10 m increments to manage differences in detectability in each patch type (Buckland 1987). With the exception of swallows and hummingbirds, birds flying over a plot were not considered.

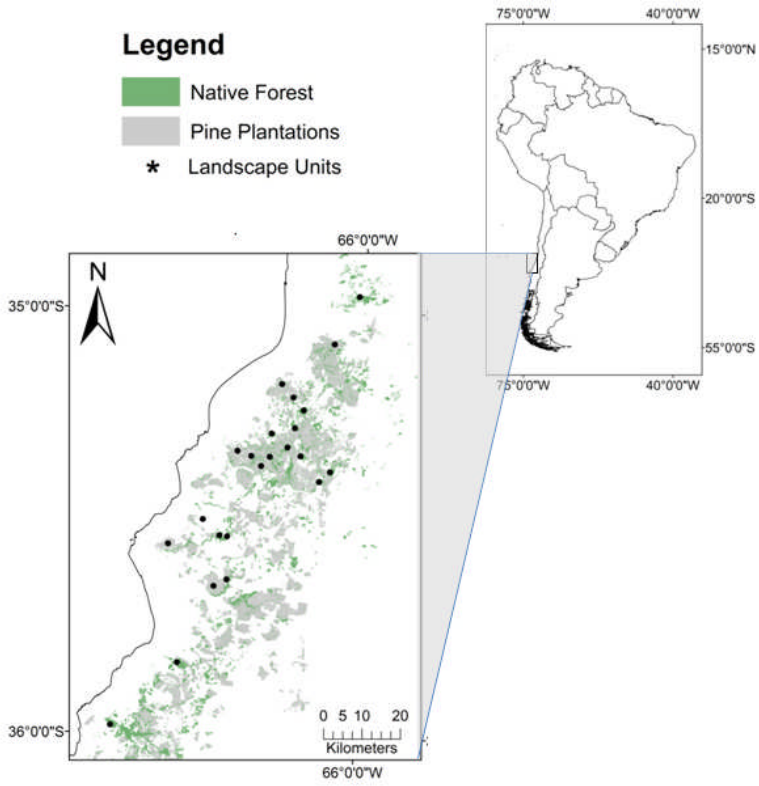

Figure 1. Location of the study area in the Maule Region (Chile). Land covered with native forest and pine plantations are shown along with the landscape units surveyed during the breeding season 2011-2012.

In order to maximize the time spent in the sample plot, in relation to the time travelling between plots, two 5-min counts were conducted at every visit, separated by a 5-min period. I also included a 5-min period before the start of any count to minimize the effects of my arrival at the plots. All counts were carried during the first 5 hours after dawn by a single observer. To control for any season effect between the beginning and the end of the breeding season all plots were visited twice, separated by a month. To assess any possible effect of pine plantation cover on the forest bird community during the winter, I surveyed a subsample of 13 landscape units during July 2014.

Using the software Distance 6.0 (Thomas *et al.* 2010), detectability curves were estimated for individual species in each vegetation type, and data were fitted to a hazard-rate or half-normal model curve accordingly (Buckland *et al.* 1993), considering the understory foliage volume as a covariate. However, detectability was assumed to be uniform (equal to 1) for those species with insufficient sample size (Estades & Temple 1999), to make a more informed decision. This was

completely necessary for including rare species in further analyses, as information indexes calculated using the abundance of species, rather their presence or absence, have more statistical power (avoiding a type II error). Furthermore, correction by species detectability only changes the estimate abundance in decimal values, and never a cero turned into a positive value.

I used stratified sampling design to survey proportionally each forest type in every landscape unit. To ensure independence of samples and to minimize edge effects, point counts were no closer than 300 m from any other point and were located 25 m from stand boundaries for native forest plots. However, for pine plantation plots, they were set at 100 m from another patch type. In summary, distance constraints meant that all landscapes were sampled proportionally to patch types and forest cover, with c.12 points per landscape unit. This sampling effort was adequate to estimate species richness and the density of most Chilean forest bird species, as the number of species and individuals levelled off at 8 points sampled (Jiménez 2000).

2.2.4. *Landscape metrics*. According to numerous studies, the natural habitat patch density would compensate in some way for the lack of a continuous natural fragment (Crozier & Niemi 2003; Olsson *et al.* 2001; Van Dorp & Opdam 1987), and patch shape of remnant native forest has been recognized to have a strong effect on some bird communities (Hawrot & Niemi 1996; Lindenmayer *et al.* 2002). Using ArcGIS (ESRI 2011) over Arauco's forest cover database and the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh 2010) I prepared and constructed geographical information layers to estimate landscape attributes. To describe the landscape units in terms of their composition and fragmentation I worked on Fragstats 3.3 software (McGarigal *et al.* 2002) (Table 1), from which I assessed: (i) the percentage of landscapes covered with native forest; (ii) native forest patch density, which corresponded to the number of native forest patches available to find in 100 Ha of landscape; (iii) Normalized Landscape Shape Index, which represented the perimeter-to-area ratio for the native forest patches, and rescaled to a minimum and maximum value for comparison among landscapes. This landscape metric represented the aggregation of all native forest patches in the landscape, with values ranging from

0 for a non-fragmented landscape, to 1 for a fully disaggregated landscape; (iv) Core Area was defined using a depth-of-edge distance equal to 50m; and (v) Connectivity was defined as the number of functional joining between patches of native vegetation; the joining between each pair of fragments was based on 50-m-distance criterion.

Table 1.Ranges of values for landscape and fragmentation variables obtained through ArcMap 10 and Fragstats 3.3.

Landscape variables	Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Edge density (m/Ha)	0.4867	0.5599	0.8664	0.8542	1.0126	1.5708
Native forest (%)	0.1967	0.4462	0.5781	0.6303	0.9166	0.9911
Core area of native forest (%)	0	0.09778	0.26072	0.33402	0.67697	0.74911
Normalized landscape shape index (native forest)	0.0033	0.0071	0.0099	0.01615	0.0199	0.0796
Native forest patch density	0.6005	10.4077	22.2910	29.6920	45.5537	80.2848
Connectivity of native forest	0	3.0030	5.229	18.203	12.169	66.667

2.2.5. *Statistical analysis*

Mean densities of each landscape unit by habitat type for every forest bird species, as well as the total occurrence of habitat-use-guild-category differences among habitat types were assessed with Wilcoxon Mann-Whitney rank sum tests.

To determine the effect of fragmentation metrics on the functional diversity and composition of the forest bird community, three measures of functional diversity were calculated for each landscape. Functional richness (FRic) that measures the volume of a multidimensional space of species-specific traits (Villéger *et al.* 2008). To measure the functional uniformity of the species assembly, functional evenness (FEve) was calculated (Villéger *et al.* 2008). This index has a value range of 0-1, with small values for aggregate distributions and large values for more uniform distributions. Functional dispersion (FDis) (Laliberté & Legendre 2010) was also calculated. It is a mean distance between species and the centroid of the community in a multivariate functional space, weighted by each species' occupancy.

Due to the high correlation between the proportion of native forest and percentage of core area in the landscape ($r = 0.96$, p-value $<< 0.001$) and connectivity of native forest ($r = 0.77$, p-value $<< 0.001$), as well as the density of native forest patches with edge density ($r = 0.86$, p-value $<< 0.001$), these variables, core area and edge density, were not included in subsequent analyses. Individual responses of species richness and for every functional index were tested separately against landscape fragmentation metrics from a gradient of disturbance. Model selection was done using stepwise multiple linear regressions, checking model assumptions by the use of diagnostic plots and found no significant violations.

Finally, the community-weighted mean of traits (CWM) was computed (Lavorel *et al.* 2008), which corresponded to the mean value for quantitative traits or the dominant value for a categorical variable in each community, weighted by the relative abundance of species in the community. In this case, "habitat user guild" was the trait used to test changes in the assemblage.

The FD indices were calculated using the FD package (Laliberté & Legendre 2010). For all statistical analyses I used R 2.15.3 (R Development Core Team 2012), and a significance level of $\alpha=0.05$ was accepted for all of them.

Selection of Traits. To characterize the role of the species in the community I considered a set of features that included the widest range of ecological functions of each species, as well as characteristics of their autoecology that could imply population limitations. Morphological and feeding traits were included to capture information about demands and strategies of food resource exploitation by species. The interaction of these two types of features strongly defined the trophic niche occupied by the species within a given community. Characteristics of species reproduction, migratory status or particular ecological functions were added as important features describing the ecological functionality of species, since they define limitations for the species itself or other species' dependence on the functions performed by the species in question. The information for these traits was obtained from a literature review. For morphological measurements, records from Johnson et al. (1965) were specifically used. I considered for later analyses only those traits which

did not have a high correlation (< 0.6). However, although body mass was highly correlated with other body measurements, this was included because this trait has a strong relationship with other traits (i.e. metabolic rate or life span) that otherwise would be no longer be represented and could have had a significant effect on the community (see Appendix 2).

Group categorization. Following Zhang et al. (2011) and based on life history and habitat use information for the forest species (Díaz 2005; Díaz *et al.* 2005; Estades 1997), I identified four habitat-use guilds. Large tree users (LTU) included those species that mainly forage and nest in tall trees; Vertical profile generalists (VPG) included species that use all the vertical strata of forest vegetation; Shrub users (SU) included those species that used both shrubs and forest to nest and forage; Understory users (UU) included ground dwelling birds, mainly Tapaculos. Forest specialists (FS), although this category includes species present in other groups, represented bird species that depend strictly on woodlands to nest and forage. Finally, Open-area users, those species that forage and/or nest in non-forest habitats, and raptor species were excluded from subsequent analyses.

2.3. Results

2.3.1. Forest bird abundance under different cover types

In total, 26 forest bird species were recorded in 1025 5-min counts spread throughout the surveyed landscapes. Only one migrant species bred in the area, the White-crested Elaenia (*Elaenia albiceps*), which was the most abundant species in forest landscapes during the breeding season.

Breeding season. Population densities varied greatly between cover types for most of the species (Table 2), and the total number of species recorded under native forest cover was significantly greater than that in pine plantations (Z = 4.24, p-value = 0.026) (Fig. 2). The major differences in abundance were found for the species Thorn-tailed Rayadito (*Aphrastura spinicauda*) (Z = 3.11, p-value < 0.001), White-Throated Treerunner (*Pygarrychas albogularis*) (Z = 3.69, p-value < 0.001), Chesnut-throated Huet Huet (*Pteroptochos castaneus*) (Z = 4.63, p-value <0.001), Ochre-flancked

Tapaculo (Z = 3.00, p-value < 0.001) and for the groups FS (Z = 4.10, p-value < 0.001), UU (Z = 4.32, p-value < 0.001) and LTU (Z = 3.35, p-value < 0.001), all of them with greater abundance under native forest cover. All FS and LTU species with adequate samples showed greater abundance under native cover than in pine plantations.

Three species were significantly more abundant in pine plantations than in native forest. These were Black-chinned Siskin (*Sporagra barbatus*) (Z = -4.15, p-value < 0.001), Rufous-collared Sparrow (*Zonotrichia capensis*) (Z = -2.58, p-value < 0.01) and Southern House Wren (*Troglodytes musculus*) (Z = -2.11, p-value = 0.036). With the exception of Rufous-collared Sparrow, these species plus White-crested Elaenia, Patagonian Sierra-Finch (*Phrygilus patagonicus*) and Tufted-Tit Tyrant (*Anairetes parulus*), were the most common species inhabiting pine plantations and all of them belonged to habitat use guilds SU or VPG.

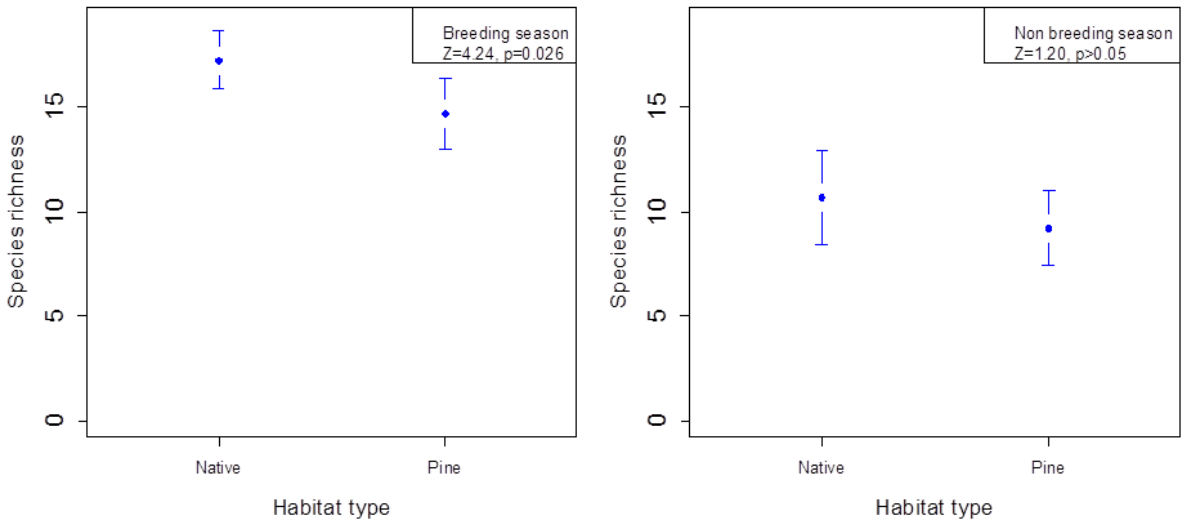

Figure 2. Species richness in native forest and pine plantations during breeding and non-breeding season (Mean ± C.I. 0.95%).

Table 2. Mean densities of each landscape unit ($n_{breeding}$=22; $n_{non\text{-}breeding}$=13) for forest bird species and their categorization in native forest and pine plantation populations. Comparison assessed through Wilcoxon Mann-Whitney rank sum tests;† Species with records for only one landscape.

Species	Categorization		Breeding season					Non breeding season				
			Estimated density (Mean Ind/ 100 Ha)		Mann-Whitney-Wilcoxon U test			Estimated density (Mean Ind/ 100 Ha)		Mann-Whitney-Wilcoxon U test		
Scientific name	Habitat Use	Forest Specialist	Native fragment	Pine plantation	U	*Z*	*p* value	Native fragment	Pine plantation	U	*Z*	*p* value
COLUMBIDAE												
Patagioenas araucana	VPG		3.06	1.65	250	1.55	-	0	0	-	-	-
PSITTACIDAE												
Enicognatus ferrugineus †	LTU	FS	1.15	0.00	210	1.00	-	0.66	0.00	84.5	1.04	-
TROCHILIDAE												
Sephanoides galeritus	VPG		34.76	24.11	256	1.51	-	185.12	82.23	117	2.12	*
PICIDAE												
Campephilus magellanicus	LTU	FS	1.61	0.00	220	1.43	-	0.29	0.00	84.5	1.04	-
Colaptes pitius	LTU		3.61	4.83	224	0.74	-	0.53	0.00	84.5	1.04	-
Veniliornis lignarius	VPG		2.56	0.20	314	3.49	0	14.45	0.00	117	2.83	**
EMBERIZIDAE												
Curaeus curaeus	VPG		8.30	6.17	215	0.41	-	0	0	-	-	-
Zonotrichia capensis	SU		0.35	2.90	117	-2.58	**	0	0	-	-	-
FRINGILIDAE												
Sporagra barbatus	SU		9.38	33.54	46.5	-4.15	0	24.48	8.41	77	-0.06	-
Phrygilus patagonicus	VPG		27.89	35.56	149	-1.38	-	365.99	283.20	60	-0.98	-
FURNARIIDAE												
Aphrastura spinicauda	LTU	FS	75.24	27.17	315	3.11	***	194.03	52.99	121	2.34	*
Leptasthenura aegithaloides	SU		15.59	4.60	179.5	-0.57	-	5.33	6.81	66.5	-0.72	-
Pygarrychas albogularis	LTU	FS	12.69	2.43	335	3.69	0	29.17	24.93	103	1.46	-
Pseudasthenes humicola	SU		3.08	4.46	215	0.53	-	0.88	0.00	84.5	1.04	-
Sylviorthorhynchos desmursii	UU		66.27	4.82	363	4.48	0	162.53	13.23	126	2.65	**
HYRUNDINIDAE												
Tachycineta meyeni	LTU		14.26	1.94	271	2.10	*	1.67	1.53	83	0.38	-
RHINOCRYPTIDAE												
Eugralla paradoxa	UU	FS	24.24	6.31	309	3.00	**	12.82	10.79	81	0.18	-
Pteroptochos castaneus	UU	FS	47.81	5.19	370	4.63	0	11.03	7.65	102	1.74	.
Scelorchilus rubecola †	UU	FS	1.64	2.26	223	0.60	-	0	0	-	-	-
Scytalopus fuscus	UU		16.72	10.90	269	1.86	.	24.78	26.79	88.5	0.58	-
TROGLODITIDAE												
Troglodytes musculus	SU		19.40	28.34	122	-2.11	*	14.29	50.71	39.5	-2.14	*
TURDIDAE												
Turdus falcklandii	VPG		22.92	30.21	131	-1.85	.	12.96	17.15	76	-0.11	-
TYRANNIDAE												
Anairetes parulus	SU		85.51	31.01	365	4.46	0	287.54	136.16	113	1.90	.
Colorhamphus parvirostris	VPG		-	-	-	-	-	73.69	13.34	151	3.99	0
Elaenia albiceps	VPG		202.37	152.03	264	1.73	.	0	0	-	-	-
Xolmys pyrope	VPG		20.83	15.68	224	0.66	-	41.54	92.63	44	-1.85	.
LTU	LTU = Σ Ind / Σ(LTU sps)		18.09	5.84	324	3.35	0	37.72	13.24	115	2.01	*
VPG	VPG= Σ Ind / Σ(VPG sps)		40.34	33.20	266	1.78	.	115.62	81.42	92	0.76	-
UU	UU= Σ Ind / Σ(UU sps)		31.26	5.56	360	4.32	0	52.79	14.61	125	2.55	*
SU	SU= Σ Ind / Σ(SU sps)		22.22	17.47	240	1.08	-	66.51	40.42	92	0.76	-
FS	FS= Σ Ind / Σ(FS sps)		23.43	6.06	336	4.10	0	41.33	16.06	121.5	2.36	*
Total Number of Species			17.25	14.68	269	4.24	*	10.66	9.23	100	1.20	-

*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*

Non-breeding season. Out of the breeding season, more bird species were recorded in native forest than in pine plantations, but the difference was not significant (Z = 1.20, p-value > 0.05). It was possible to see dramatic changes in estimated densities for many forest bird species during this season (Table 2); some of them were almost completely absent from the study area (e.g. *Patagioenas araucana*, *Curaeus curaeus*, *Zonotrichia capensis*). Even though these three species were absent from the results, they were nevertheless seen in the study area. However, it was also noticed that there was an exchange of migrant tyrant species between seasons. The White-crested Elaenia left the area for tropical winter grounds, but two austral breeders visited these forests to spend the winter, the Patagonian tyrant (*Colorhamphus parvirostris*) and the Fire-eyed Diucon (*Xolmys pyrope*).

In general, those species that were more abundant in native forest than in pine plantations during the breeding season were still displaying high abundances in native forest in winter time, as was the case for the Thorn-tailed Rayadito (Z = 2.34, p-value = 0.019) and Desmurs' Wiretail (*Sylviorthorhynchos desmursii*) (Z = 2.65, p-value < 0.01). As observed during the breeding season, major differences in abundance were recorded for categories LTU (Z = 2.01, p-value = 0.044), UU (Z = 2.55, p-value = 0.011) and FS (Z = 2.36, p-value = 0.017). Only one species was significantly more abundant in pine plantations than in native forests; Southern House Wren (Z = -2.14, p-value = 0.031). Also, as observed during breeding season, all the species that were more abundant in pine plantations belonged to the SU or VPG categories.

Some species fluctuated greatly in abundance between seasons, and by up to four times their breeding abundance (Table 2), e.g. Thorn-tailed Rayadito, Tufted-tit tyrant or Patagonian Sierra-Finch. Apart from the Green-backed Firecrown (*Sephanoides sephanoides*), whose estimated abundance was exacerbated by regional displacements and high mobility, most of the greater increase in abundance for some species were explained by the constitution of mixed-species foraging flocks that moved around the landscape. In this way, flocks detected in native forest were comprised of more species than those found in pine plantations (Table 3), but the difference was

marginally non-significant (Z = 1.72, p-value = 0.06). Moreover, flock size showed no difference between habitat types (Z = 1.58, p-value = 0.20), ranging from 3 to 40 individuals.

Table 3.Percentage of flocks in which species were recorded in different habitats.

	Habitat type			Habitat type	
Species	Native	Pine	Species	Native	Pine
Veniliornis lignarus	0.30	0.00	*Pygarrychas albogularis*	0.45	0.25
Sporagra barbatus	0.05	0.06	*Sylviorthorhynchos desmursii*	0.05	0.00
Phrygillus patagonicus	0.15	0.56	*Anairetes parulus*	0.50	0.31
Aphrastura spinicauda	0.90	0.43	*Colorhamphus parvirostris*	0.05	0.00
Lepthastenura aegithaloides	0.05	0.12	*Xolmys pyrope*	0.30	0.12
Mean flock size	8.50	13.50			
Mean flock species richness	2.85	1.87			

2.3.2. Effects of landscape features and fragmentation on bird community

Clear differences in species richness of the forest bird community were observed according to the amount and type of fragmentation in forested landscapes (Table 4). The proportion of native forest in a landscape had a positive and significant effect on species richness in forest bird communities during the breeding season (β = 0.0024, p-value << 0.001). Meanwhile, the shape of landscape components showed a strong and negative correlation with species richness. The shape of remnant native forest showed an important effect with forest species richness during the breeding season (β = -2.0924, p-value = 0.02). Such situation did not vary outside the breeding season, but its effect appeared to be stronger (β = -11.9280, p-value = 0.005). The overall model fits were r^2 = 0.52 and r^2 = 0.39, for breeding and non breeding season respectively (Fig. 3).

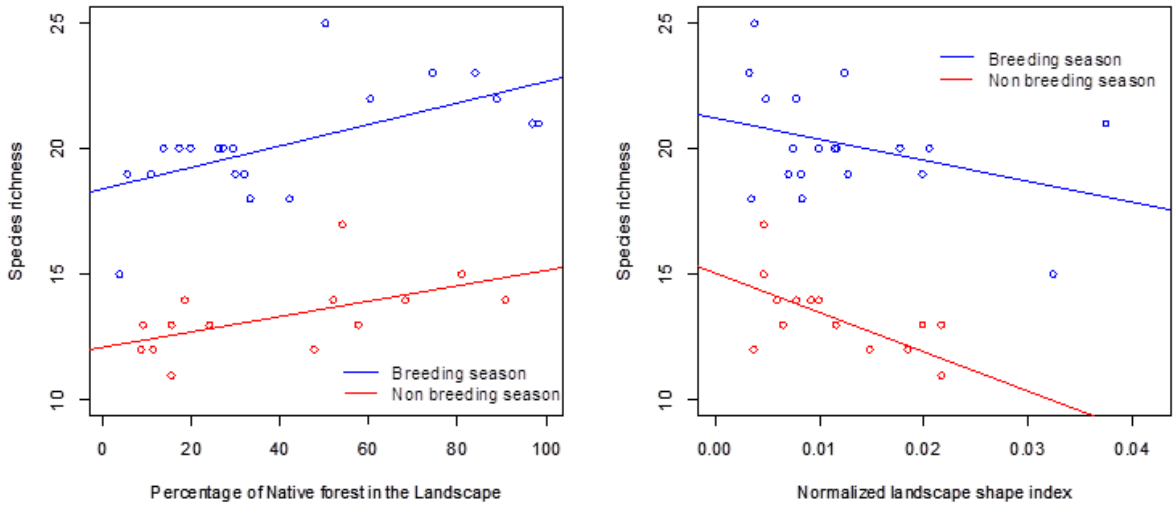

Figure 3.Landscape metrics and their effects on species richness.

Table 4. General linear model (poisson distribution) explaining the species richness during the breeding and non breeding seasons.

Breeding season					
Variable	β	Std error	z-value	p-value	Sig. code
Intercept	2.9315	0.0266	110.195	0	***
Native forest (%)	0.0024	0.0005	4.860	0	***
Normalized landscape shape index	-2.0924	0.9001	-2.325	0.0201	*
r^2 = 0.496					
Non-breeding season					
Variable	β	Std error	z-value	p-value	Sig. code
Intercept	2.7192	0.0493	55.093	0	***
Normalized landscape shape index	-11.9280	4.2493	-2.807	0.005	**
r^2 = 0.395					
*Signifcance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1*					

Functional diversity indices behave differently according to landscape fragmentation metrics and between seasons. Thus, functional richness was conditioned positively by the proportion of the landscape covered with native forest during the breeding season (β= 0.015, p-value = 0.016 in a model with overall fit of r^2 = 0.21). However, during winter, the shape of remnant native forests

showed an effect on this index (β= -111.207, p-value = 0.010 in a model with overall fit of r^2 = 0.41). Results for functional evenness and dispersion showed that the fragmentation effects on these indexes are only seen during the breeding season. The shape of native forest remnants had a positive but marginally non significant effect on functional evenness (β= 1.966, p-value = 0.076 in a model with overall fit of r^2 = 0.10). The proportion of native forest in the landscape showed a negative effect on functional dispersion (β= -2.349, p-value = 0.019 in a model with overall fit of r^2 = 0.20) (Fig 4).

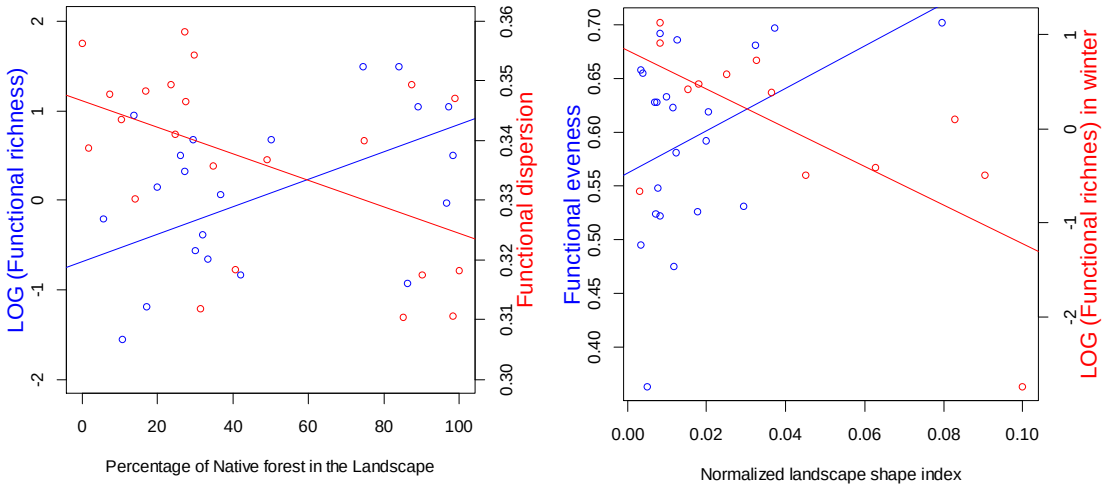

Figure 4. Relationships between functional indexes and landscape metrics.

There is clear variation in traits that dominate the community, and this depends on the degree of substitution or fragmentation of native forests by pine plantations. As shown in Figure 5, there is an obvious dominance of the guild "Large tree users" (LTU) in landscapes with greater cover of native forest, unlike what happened with other categories. A comparison of means indicated that this difference was statistically significant ($F_{3,251}$ = 3.148, p-value= 0.025).

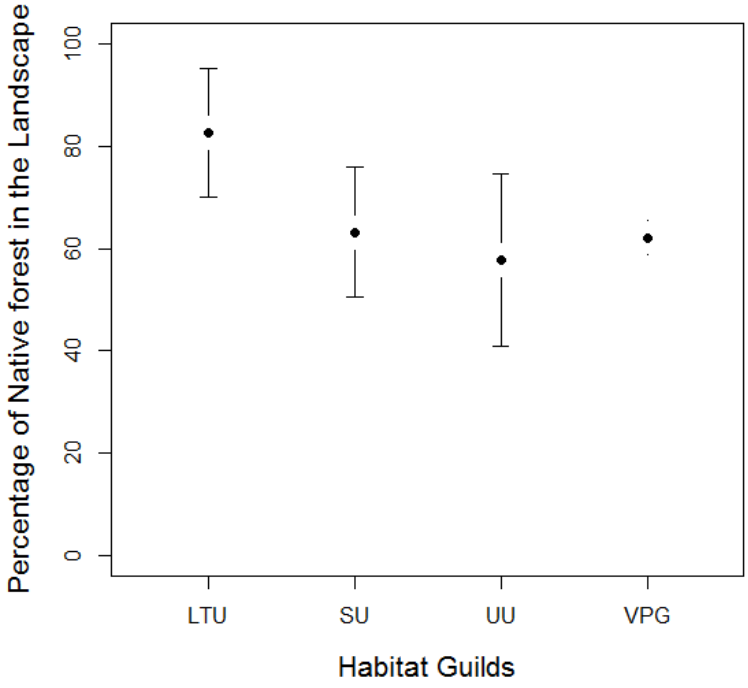

Figure 5. Habitat user guild and their dominance in landscapes according to the amount of native forest.

2.4. Discussion

As expected, species richness of forest birds was higher in native forest than in pine plantations. Analysing the results of individual species, it is clear that the differences in abundance between habitat types are related to the level of specificity of the forest species. Thus, major differences in abundance noted were from the forest obligate species, and some of them were even absent from pine plantations. The absence of forest specialist species in pine plantations could indicate a species filtering process in this new habitat type.

Differences in species abundance values were observed between reproductive and non-reproductive seasons. In this regard, it should be noted that within the bird community of these forests there are several species that migrate and accordingly, their population densities vary seasonally. However, the migratory status of several species was either confusing or there is not enough information about their movements. Thus, I believe the only two strictly migratory species

are the Tyranids; White-crested Elaenia and Patagonian Tyrant. The former leaves these forests every year to spend the winter in western Amazonian forests (Chesser 1994) and returns for the austral spring. For the Patagonian Tyrant, this species breeds in the southern forests and flies to south-central Chile in winter. Although other species perform similar movements, it is possible to observe a substantial number of resident individuals during the breeding season (i.e. Fire-eyed Diucon), suggesting that they are partial migrants (Newton 2010a). In a similar way, there are other species that, while not migrating, do perform seasonal movements at a regional level, either to avoid the harsh winter conditions of the Andes (i.e. Green-backed Firecrown) or because of seasonal habitat selectivity, such as in the case of Black-chinned Siskin and Austral Blackbird that partially leave forest areas for agricultural croplands during winter time. All these patterns contribute to an explanation of the differences in species densities between seasons.

Another reason for the seasonal variation detected in estimated population densities is the fact that, outside the breeding season, individuals do not maintain or defend reproductive territories. This allows individuals of many species to increase their foraging movements within the landscape. At the same time, an increased tolerance to the presence of con-specifics or other competitor species occurs, which together with the previous point, leads to the formation of small mixed-species flocks that forage through the landscape (Ippi & Trejo 2003; Sridhar *et al.* 2009; Wing 1946). These considerations explain the large fluctuations that occur outside the breeding season for some species.

Besides these non-breeding season peculiarities, habitat preferences were maintained consistently for the vast majority of species. This is especially true for "Large tree users" (LTU) and "Vertical profile generalists" (VPG). According to the results, species of these categories were prevalent in native forest and pine plantations, respectively.

Clearly, the nature of the habitat determines the number and abundance of species that can be found in them. However, this local species assemblage potentially reflects the richness of a regional species pool. This study showed how the landscape and its features, in terms of the composition

and distribution of its components, act as a filter over the diversity of the forest bird community. Fragmentation of the native forest in the landscape has a significant effect on the forest bird community. Thus, the degree to which the pine plantations have replaced the natural cover not only affect the species richness of forest birds in terms of sum of individual species, but also adversely affects the functional richness of forest bird assemblage. That is, apart from species loss, replacing native forest also means losing functions and processes associated with those species.

The percentage of native forest remaining in the landscape showed a positive relationship with forest species richness. This fragmentation metric also had an effect on the functional diversity of the community. Thus forest landscapes with a greater proportion of native forest showed higher values of functional richness and lower values for functional dispersion. This implies that landscapes containing a smaller proportion of native forest would have functionally simpler communities. That is, its range of functionality would be reduced, yet functional gaps that appeared would not be fully addressed. Interestingly, the effect of the proportion of native forest in the landscape on the functional dispersion disappears in the non-breeding season. This is explained by the seasonal variation in abundance and species richness. Although the effect of the proportion of native forest on species richness and functional diversity has already been noticed, its effect can also be seen in changes in the dominance of certain traits along the disturbance gradient. Bird communities in landscapes with proportionally more native forest are dominated by LTU species. In conclusion, it has been shown that the loss of forest species increases as the proportion of pine plantation in the landscape increases.

Fragmentation is the replacement of one habitat type by another, leaving the natural habitat as a set of small scattered patches embedded in a matrix of another habitat, in the present case a matrix of pine plantations. In a landscape context, remnant fragments are characterized by their shape and their density. In the case of patch shape, species richness was affected negatively by disaggregated native patches. This also occurred for functional richness during the winter season. Functional evenness, in turn, decreased in landscapes with more aggregated patches. Together, shape and

density of native patches depict the level of fragmentation, with a direct relation to a decrease in the amount or proportion of core area of native forest. So, further fragmentation of forest would also decrease the availability of large trees, and consequently show that fragmentation also involves a process of loss of habitat quality by degradation of the vegetation. In that way, the value of small patches for conservation could be questioned (Fischer & Lindenmayer 2002), given its selectivity for a group of species at the expense of others. Interaction between the amount of native forest in the landscape and shape and density of forest fragments may be revealing the mechanisms that maintain a rich bird assembly in productive landscapes, cushioning the effects of perturbations related to the intensive pine plantation management. Unfortunately, the fragmentation process that these forests have suffered has reduced the amount of Core Area in the study area dramatically. According to Echeverria (2006), in Maulino forests it is no longer possible to find Core Areas with 'edge-of-depth' over 100 m, which in a way also reflects the decrease in patch size. These results are important for temperate forest bird conservation and, through it, to these forests and other communities that inhabit them. Therefore, any conservation or restoration plan management in the area should consider a proper configuration of the landscape components. In conclusion, the importance of native forest cover in the landscape for maintaining the integrity of the forest bird community has been demonstrated, as has the way in which certain features of the landscape influence species groups differently.

Chapter 3

Forest bird species, habitat constraints and preferences

3.1. Introduction

Habitat fragmentation and habitat loss are recognized as the principal causes of biodiversity loss (Brooks *et al.* 2006). Many researchers have emphasized the differences between habitat loss and habitat fragmentation (Fahrig 1997; McGarigal & Cushman 2002). While both are directly related, the first relates to the direct loss of area available for the development of populations (Villard *et al.* 1999), whereas fragmentation refers to the loss of habitat connectivity in scattered patches embedded in a matrix which generally dominates the landscape (Andrén 1994). Habitat loss and fragmentation are mainly caused by the substitution of one environment by another. Although it is known to occur naturally, currently the most common causes are anthropogenic (Andrén 1994). Because of this, in most terrestrial environments the matrix of habitat could be of different types, which are determined by the use of the land, for example agricultural crops, forest plantations or urban areas (Shanahan *et al.* 2011).

Worldwide, more than 264 million hectares has been forested with fast growing tree species (FAO 2010) using degraded lands by intensive agriculture and direct replacement of native habitats (Kanowski *et al.* 2005; Lara & Veblen 1993). The substitution of natural habitats with exotic tree plantations has affected native wildlife by changing the structure and composition of natural forest landscapes (Enoksson *et al.* 1995; Pedersen *et al.* 2010). The structure of the matrix that dominates the landscape defines the degree of isolation of biological populations in the remaining patches of natural habitat (Dunning *et al.* 1992; Fischer & B Lindenmayer 2006; Taylor *et al.* 1993). The similarity between natural forests and forest plantations renders a soft barrier for many vertebrate populations (Estades & Temple 1999; Tomasevic & Estades 2008), allowing them the use of resources that can be found there, colonizing these widespread cultivations (Brockerhoff *et al.* 2008). However, due the fact that exotic tree plantations are selective towards generalist species, at the

expense of more specialized ones, there is controversy regarding the real contribution of forest plantations in conservation (Renjifo 2001).

The biogeographic history of Chile allow us to find many types of forests, being the deciduous Maulino forest the most threatened one in terms of remaining surface and actual state of degradation (Echeverría *et al.* 2006). This forest, that once covered much of the south-central Chile, has been widely replaced by Monterey pine plantations over the last 60 years, which now exceed 2 million hectares in the whole country. There are huge differences between these two types of forests. The deciduous Maulino forest is characterized by a complex stand structure exhibiting all ages and sizes. This is the product of its regeneration strategy, which is based on canopy openings generated by small perturbations, such as the fall of a dead tree or a landslide (Veblen *et al.* 1985). In contrast, the extensive industrial management applied to pine plantations generates even-aged mono-specific stands, varying in size from a few to hundreds of hectares and are harvested by clear-cutting at an average age of 22 years (Estades & Escobar 2005). In the study area, pine plantations are managed to reconcile the production of timber and pulp, thereby stand density used (number of trees per hectare) gives light and moisture conditions allowing the development of relevant undergrowth in many cases. However, the structure of the vegetation in pine plantations is simpler than that of natural forests and the short production cycle does not allow the development of mature forests and related structural features, such as natural cavities, which could limit populations.

The type of matrix of habitat and the configuration of the landscape components determines the assemblage of forest bird species found in any plot of the landscape. It has been suggested that a soft contrast between matrix and fragments could increase connectivity for local populations and also their abundance in fragmented forests. In this mosaic, the edge effect is defined by gradients of conditions that penetrate stands of different land covers, being bird occurrence a consequence of the interaction of this edge effect and the landscape configuration (Tubelis *et al.* 2004). In this way, Lindenmayer *et al*. (2002) found that the effect of the landscape configuration may be more important to explain forest bird abundance in pine plantations than in native forest fragments.

Therefore, the real effect and direction of "edge effect" in these systems may vary for every species and according to every habitat configuration.

The ability of certain species to use pine plantations depends on the degree of specialization or generalization of the local fauna (Wunderle Jr 1997). In the same way it has been recognized for several groups of species able to use the surrounding matrix, that they tend to be more tolerant of fragmentation than those species that do not use it (Tubelis *et al.* 2007). Lindenmayer et al. (2003) highlight the wide range of responses at the guild level and how landscapes may be perceived differently across species. Furthermore, in the bird community of temperate forests of Chile, species differ widely in their morphological characteristics, which are closely related to resource exploitation and energetic needs, so differences in terms of the environmental features that define their niches and limit their numbers are expected.

The aim of this chapter is to determine how native forest substitution with extensive exotic coniferous plantations affects temperate forest bird communities. Under the hypothesis that bird species responses to habitat features from two spatial scales, I look for the factors, from two levels (plot and landscape), that explain forest bird species abundance in these landscapes, considering separately natural deciduous forests and mono-specific coniferous plantations. For ecological reasons, individual species analyses are considered as appropriate to model species abundance in each type of habitat. In addition, due the importance of natural cavities for secondary cavity nesters species, separate analyses are carried out to assess a) the correlation between number of cavities and structural attributes at plot level and b) the relationship between number of cavities and the abundance of secondary cavity nester species.

3.2. Methods

3.2.1. Study area. The study was carried out on the bird community of the temperate forest of South Central Chile, in the "Del Maule" administrative region (Fig.6). The climate in this region is temperate with warm and dry summer (Peel *et al.* 2007), with an average temperature of 13.9 °C and annual precipitation of 942 mm (Hajek & Di Castri 1975). The study is focused on a 7500 km² area of the "Roble-Hualo" forest type distributed over the Coastal range, known as the Maulino forest, ranging from Tregualemu river (35°58' S 72°44' W) in the South to "Altos de Licanten" (34°58' S 72°02' W) in the North. An important climatic factor considered in the site selection was the oceanic influence, whose extent varies with the topography.

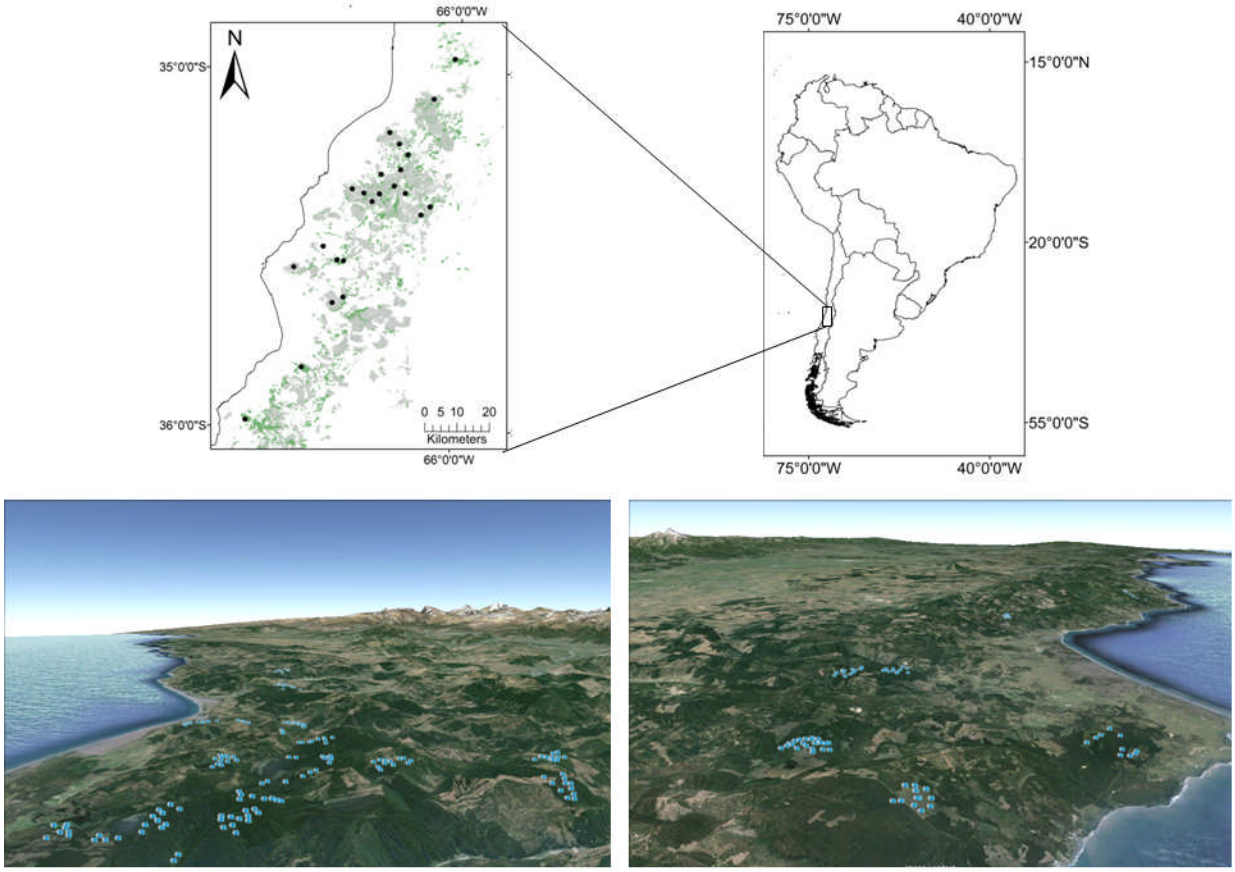

Figure 6. Study area and landscape units selected. Satellite images showing point counts surveyed at the Coastal range to the north of the Maule river (left) and to the South of the Maule river (right).

3.2.2. Landscape Units. Landscape units of 4 km^2 were defined to encompass the breeding home range of most forest-dwelling passerine species (McGarigal & McComb 1995; Villard *et al.* 1999). The selection of landscape units for the study was based on Arauco's forest cover database, the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh 2010), and Quickbird™ imagery. The selection process considered continuous forest habitat as a main constraint, selecting only those landscape units which have at least 85% forest cover. This was necessary to eliminate any disturbing effect made by young or harvested stands. As the majority of pine plantations in the region belongs to Arauco Forest Company, work carried out on their land represents a good sample of the whole area. However, to increase the sample size, I included three landscape units recognized on Satellite images, which belong to minor companies. Finally, I considered all possible landscape units, ending up with 22 landscape units, representing the whole range of percentages of remaining native forest.

3.2.3. Avian surveys. During the 2011-2012 breeding season, from October to December, I conducted bird counts on every landscape unit, using the variable circular-plot method with a 50 m maximum observation radius. No observations were conducted on rainy or misty days. All birds seen or heard within the maximum radius were recorded, and their distance from the plot's centre was estimated in 10 m increments to manage differences in detectability in each patch type (Buckland 1987). With the exception of swallows and hummingbirds, birds flying over a plot were not considered.

In order to maximize the time spent in the sample plot, in relation to the time travelling between plots, two 5-min counts were conducted at every visit, separated by a 5-min period. I also included a 5-min period before the start of any count to minimize the effects of my arrival at the plots. All counts were carried during the first 5 hours after dawn by a single trained observer. To control for any season effect, between the beginning and the end of the breeding season, all plots were visited twice and separated by a month.

Detectability curves were estimated for individual species in each vegetation type and data were fitted to a hazard-rate or half-normal model curve (Buckland *et al.* 1993), considering the understory foliage volume as a covariate while using the Distance 6.0 software (Thomas *et al.* 2010). Detectability was assumed to be uniform (equal to 1) for those species with insufficient data.

I used stratified sampling design to survey proportionally each forest type in every landscape unit. To ensure independence of samples and to minimize edge effects, point counts were no closer than 300 m from any other point and they were located 25 m from stand boundaries for native forests plots. However, for pine plantation plots, they were set at 100 m from another patch type. In summary, distance constraints meant that all landscapes were sampled proportionally to patch types and forest cover, with c.12 points per landscape unit. This sampling effort was adequate to estimate species richness and the density of most Chilean forest bird species as the number of species and individuals levelled off at 8 points sampled (Jiménez 2000).

3.2.4. Landscape and stand variables

Landscape metrics. Using ArcGIS (ESRI 2011) over Arauco's forest cover Database and the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh 2010) I prepared and constructed geographical information layers to assess plot and landscape attributes.

Plot attributes were obtained using that GIS software, characterizing the plot and its vicinity in terms of land use and stream length related to the 200 m radius buffer area of every point count, along with its distance to the nearest creek and native forest patch (Table 5).

Table 5. Range values for plot attributes obtained through ArcMap 10, and landscape and fragmentation variables obtained through ArcMap 10 and Fragstats 3.3.

		Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Plot attributes							
Patch size (Ha)	Patch size	1.41	30.18	66.61	158.87	298.22	566.06
Roads in 200 m buffer (%)	X200RoA	0	0.011	0.025	0.027	0.039	0.124
Other uses in 200 m buffer (%)	X200OtA	0	0.0007	0.0007	0.039	0.040	0.532
Stream in 200 m buffer (m)	X200St_m.ha	0	26.38	52.2	53.52	76.04	146.59
Native forest in 200 m buffer (%)	X200NFA	0	0.016	0.182	0.382	0.816	1
Pine plantation in 200 m buffer (%)	X200PA	0	0.066	0.750	0.551	0.924	1
Distance to the nearest creek (m)	DistQueb_m	2	36.45	69.84	83.41	117.25	255.27
Distance to the nearest native forest patch (m)	Dist_to_NF	0	0	11.18	88.76	146.75	813.98
Landscape variables							
Stream index (m/Ha)	Str_Index	30.15	56.80	67.67	65.31	77.71	94.06
Edge density (m/Ha)	ED_m.Ha	0.486	0.559	0.866	0.854	1.012	1.570
Native forest (%)	PLAND_NF	0.038	0.199	0.298	0.422	0.605	0.982
Pine plantation (%)	PLAND_Pine	0	0.367	0.682	0.554	0.773	0.944
Core area of native forest (%)	Core_Land	0	0.097	0.260	0.334	0.676	0.749
Normalized landscape shape index	NLSI.NF	0.003	0.007	0.009	0.016	0.019	0.079
Native forest patch density	PD.NF	0.6005	10.4077	22.2910	29.6920	45.5537	80.2848
Connectivity of native forest	Connect	0	3.0030	5.229	18.203	12.169	66.667

Composition and fragmentation of landscape units were described through different metrics using the software Fragstats 3.3 (McGarigal *et al.* 2002) (Table 5). "Native forest Patch Density" corresponded to the number of native forest patches available to find in 100 Ha of landscape. Normalized Landscape Shape Index represented the perimeter-to-area ratio for the native forest patches, rescaled to a minimum and maximum value for comparison among landscapes. This represented the aggregation of all native forest patches in the landscape, with values ranging from 0 for an unfragmented landscape, to 1 for a fully disaggregated landscape. Core Area was defined using a depth-of-edge distance equal to 50 m. Connectivity was defined as the number of functional joining between patches of native vegetation; the joining between each pair of fragments was based on 50-m-distance criterion. Percentage of pine plantation and

native forest in the landscape were also estimated along with the density of the drain network in terms of meters per hectare.

Table 6. Range of values for stand level descriptive variables assessed in every plot (n=255). Estimated number of cavities for a subsample of 67 plots (*).Variables associated with specific tree species are described in Appendix 3.

Stand attributes		Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Stand height (m)	Height	5	12	17	16.81	21	35
Mean dbh (cm)	DBH	4.7	13	18.8	19.7	26.7	45.8
Basal area (m^2/Ha)	Basal_Area	0.497	44.264	63.542	63.470	79.537	161.323
Number of cavities (*)	Cavities	0	1	2	3.672	4	23
Vegetation cover (%)	Cover	0.104	0.376	0.449	0.453	0.532	0.793
Volume of native vegetation (m^3/Ha)	Vol_Nat	750	10075	26299	33558	46324	169545
Native vegetation (%)	PorcNat_%	0.009	0.118	0.385	0.522	1	1
Volume of pine (m^3/Ha)	VolPine	0	0	40999	42629	76073	224993
Pine (%)	PorcPine_%	0	0	0.615	0.477	0.881	0,990
First stratum coverage 0-0.3m (%)	Vol_0.3m	5	30	50	47.63	70	100
Second stratum coverage 0.3-2m (%)	Vol_0.3.2m	5	25	45	46.21	67.5	99
Third stratum coverage 2-5m (%)	Vol_2.5m	5	30	45	43.8	60	80
Fourth stratum coverage 5-10m (%)	Vol_5.10m	0	32.5	50	43.91	60	80
Fifth stratum coverage +10m (%)	Vol_.10m	0	10	40	33.25	50	80
First stratum richness	L1Rich	1	3	4	3.733	4	5
Second stratum richness	L2Rich	1	3	4	4.008	4	5
Third stratum richness	L3Rich	1	2	3	3.031	4	5
Fourth stratum richness	L4Rich	0	1	2	1.902	3	5
Fifth stratum richness	L5Rich	0	1	1	1,024	2	5
Number of vine species	Vines	0	0	1	0.654	1	3
Number of species with flowers	Flowers	0	0	1	0.705	1	4

Vegetation description. Because vegetation structure and composition differences between plots offer great help in explaining bird abundances, I characterized the vegetation structure and composition of every census plot. To characterize the vegetation structure, I estimated tree height and measured the diameter at breast height (dbh) of the nearest five trees to the observer point. In order to estimate the basal area of the plot, I counted the number of tree stems belonging to diameter ranges of 10 cm increments. I followed the methodology used by Estades & Temple

(1999) in these forests to describe the vegetation's vertical structure and composition. The total foliage volume and the foliage height diversity were estimated by referring to five vertical strata of the vegetation (see Table 6). This is the proportion of the virtual space of every tier occupied by the foliage. The foliage volume of the main plant species was also assessed, along with the abundance and diversity of flowers and fruits in each plot. In addition, the number of cavities suitable for cavity nester species (over 2.5 cm in diameter) seen from the centre of the plot was assessed for a subset of the sampled plots.

Group categorization. Following Zhang et al. (2011) and based on life history and habitat use information for the forest species (Díaz 2005; Díaz *et al.* 2005; Estades 1997), I identified four habitat-use guilds (Table 7). Large tree users (LTU) included those species that mainly forage and nest in tall trees; Vertical profile generalists (VPG) included species that use all the vertical strata of forest vegetation; Shrub users (SU) included those species that used both shrubs and forest to nest and forage; and Understory users (UU) included ground dwelling birds, mainly Tapaculos. Finally, Open-area users, those species that forage and/or nest in non-forest habitats, and raptor species were excluded from subsequent analyses.

3.2.5. Statistical analysis

In general, populations and communities respond to a different range of scales of environmental heterogeneity (Andrén 1994; Schooley & Branch 2007). Therefore, I used multilevel modelling (GLMM) to assess the effect of landscape and stand level variables on bird abundance. I ran separate analyses using the estimated abundance in every plot as response variable for individual species and for every guild category, for subsets of native forest and pine plantations alone. Only forest species with a sufficient sample size were tested through this protocol. Nevertheless, most rare bird species were included in habitat guild analyses. All statistical analyses were conducted using R (R Development Core Team 2012) and tested at 5% significance level. I used the glmmADMB (Skaug *et al.* 2011) extension for R because it provides a

glmm framework with Negative binomial and/or Quasi-Poisson responses with Zero Inflation, while at the same time allowing control for overdispersion of the data.

Table 7. List of forest non-raptor bird species inhabiting the Maulino forest, showing their habitat-use guild classification.

Species		Categorization	
Scientific name	Common name	Habitat Use	Forest Specialist
COLUMBIDAE			
Patagioenas araucana	Chilean Pigeon	VPG	
PSITTACIDAE			
Enicognatus ferrugineus †	Austral Parakeet	LTU	FS
TROCHILIDAE			
Sephanoides sephanoides	Green-backed Firecrown	VPG	
PICIDAE			
Campephilus magellanicus	Magellanic Woodpecker	LTU	FS
Colaptes pitius	Chilean Flicker	LTU	
Veniliornis lignarius	Striped Woodpecker	VPG	
EMBERIZIDAE			
Curaeus curaeus	Austral Blackbird	VPG	
Zonotrichia capensis	Rufous-collared Sparrow	SU	
FRINGILIDAE			
Sporagra barbatus	Black-chinned Siskin	SU	
Phrygilus patagonicus	Patagonian Sierra-Finch	VPG	
FURNARIIDAE			
Aphrastura spinicauda	Thorn-tailed Rayadito	LTU	FS
Leptasthenura aegithaloides	Plain-mantled Tit-Spinetail	SU	
Pygarrychas albogularis	White-throated Treerunner	LTU	FS
Pseudasthenes humicola	Dusky-tailed Canastero	SU	
Sylviorthorhynchos desmursii	Desmurs' Wiretail	UU	
HYRUNDINIDAE			
Tachycineta meyeni	Chilean Swallow	LTU	
RHINOCRYPTIDAE			
Eugralla paradoxa	Ochre-flanked Tapaculo	UU	FS
Pteroptochos castaneus	Chestnut-throated Huet-huet	UU	FS
Scelorchilus rubecola †	Chucao Tapaculo	UU	FS
Scytalopus fuscus	Dusky Tapaculo	UU	
TROGLODITIDAE			
Troglodytes musculus	Southern House Wren	SU	
TURDIDAE			
Turdus falcklandii	Austral Thrush	VPG	
TYRANNIDAE			
Anairetes parulus	Tufted Tit-Tyrant	SU	
Colorhamphus parvirostris	Patagonian Tyrant	VPG	
Elaenia albiceps	White-crested Elaenia	VPG	
Xolmys pyrope	Fire-eyed Diucon	VPG	

The process of variable selection to include in models began by removing highly correlated variables. Variables to be removed were chosen using correlation coefficient ($r > 0.6$). In the

case of stand effects (level 1), from a total of thirty explanatory variables, a set of nine variables were selected using a Hierarchical partitioning algorithm from the "hier.part" R package (Walsh *et al.* 2013), which is based on partitioning the variances so the total independent contribution of a given independent variable can be estimated (Mac Nally 1996).

With at least nine explanatory variables from stand level, plus four landscape metrics I built full generalized linear mixed models in every case. Following a stepwise backward linear regression approach, I used the “drop1” function for model selection base on Akaike's Information Criterion (AIC), until I obtained the most parsimonious model, checked by its residual distribution. Finally, for selected models a coefficient of determination (r^2) was calculated by comparing the variance of the residuals of the selected models against the residuals variance of the related null model (Xu 2003).

3.3. Results

A total of 26 forest bird species was recorded in the surveyed landscapes. Bird density and species richness were negatively correlated to distance to creeks (β = -0.0075, p-value = 0.009 and β = -0.00087, p-value = 0.0005). The number of species and their density in native fragments showed no effect of patch size. In pine plantations, these parameters were not affected by the distance to native forest fragments.

3.3.1. Large tree user species

Due to the limited amount of presence data for the Magellanic woodpecker (*Campephilus magellanicus*) and Austral parakeet (*Enicognathus ferrugineous*), it was not possible to model their presence (Fig 7). For this group, therefore, results are shown for three species only, and for the group itself (Table 8).

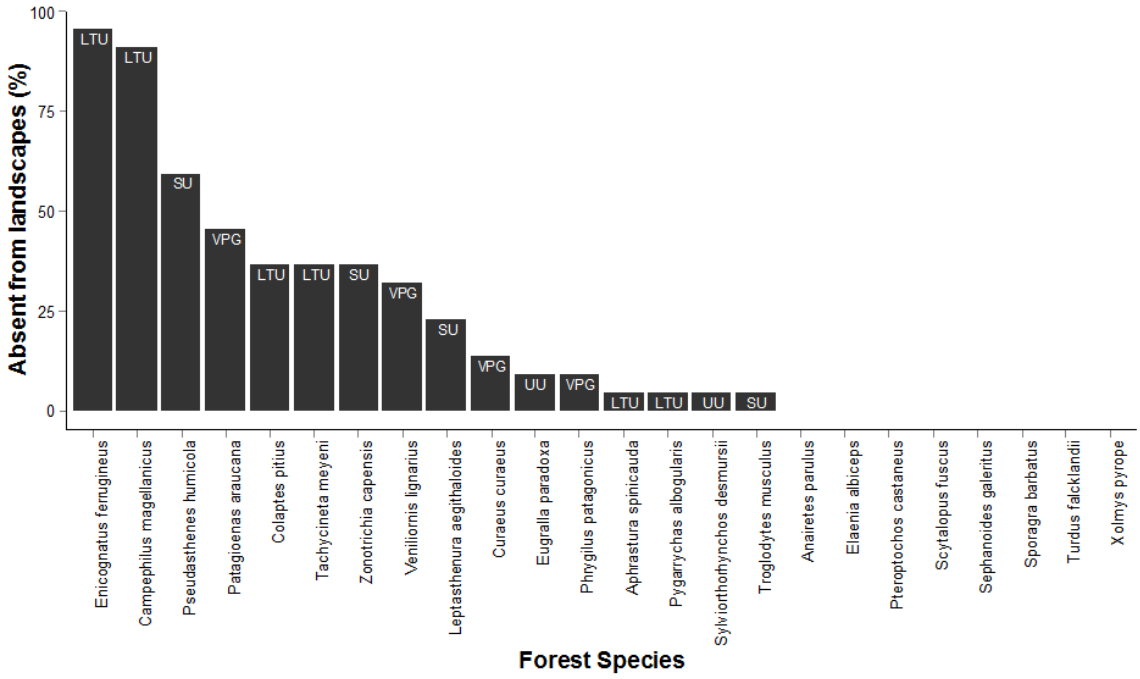

Figure 7. Percentage of the 22 landscapes where the species were not recorded. The list includes only forest non-raptor bird species.

Results showed that for this group of species, the connectivity of native forest fragments was important to explain their abundance in both native forest and pine plantation. Fragmentation effects were more evident in pine stands that in native forest fragments. The proportion of native forest in the landscape negatively affected the abundance of the Thorn-tailed Rayadito (*Aphrastura spinicauda*) in pine plantations. The edge density in the landscape appeared in several selected models to explain the abundance of these species in pine plantations, and in all of them this metric had a negative effect on the species abundance (Fig. 8). The degree of aggregation of native forest remnants in the landscape positively affected the abundance of Chilean Swallow in pine plantations, but did not appear in selected models for other species. Finally, drainage density in landscape was important to explain the abundance of this species group, showing a negative effect on the abundance of the Thorn-tailed Rayadito both in pine plantations and native forest fragments, but a positive effect on the abundance of the Chilean Swallow in pine plantations.

The characteristics of the area surrounding the stands were relevant in the case of the White-throated Treerunner (*Pygarrychas albogularis*), for its abundance in both native forest fragments and pine plantations. In the first case, the proximity of other land uses negatively affected its abundance; in the second, its abundance in pine plantations increased with higher proportion of native forest in the surrounding areas. The latter could also be seen in the model that explained the abundance of the whole species group in pine plantations. Also, the abundance of this group of species, as a whole, in fragments of native forest was positively affected by the distance to streams, but this was not so for the Chilean Swallow whose abundance decreased with increasing distance from the streams.

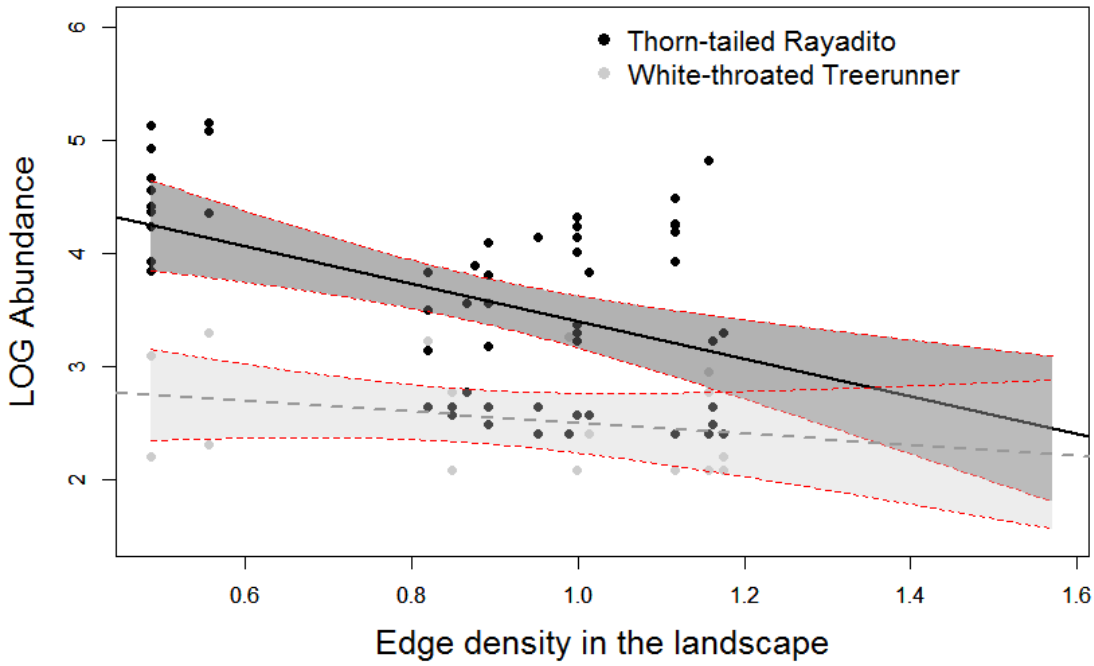

Figure 8. Effect of Edge density in the landscape on the Log abundance of Thorn-tailed Rayadito and White-throated Treerunner in pine plantation stands. Alternate lines show 95% confidence intervals.

Table 8. Mixed models explaining large tree user (LTU) species abundance in native forest and pine plantations

Species	Native forest subset				Pine plantation subset			
LTU								
Model AIC	772.1				571.6			
Model r^2	0.537				0.645			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.148	0.385			0.477	0.691	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	Connect	0.011	0.006	0.066	Str_Index	-0.034	0.016	0.037
					Connect	0.043	0.021	0.043
Stand level variables								
Vicinity variables	DistQueb_m	0.003	0.001	0.026	X200NFA	4.865	1.176	0.00003
Veg Structure variables					Vol_0.3.2m	0.015	0.005	0.003
Veg Composition variables	LCausVol	-0.00017	0.00006	0.014	Patch size	0.007	0.002	0.017
	CQuiVol	0.00003	0.00001	0.007				
	L4Rich	0.221	0.085	0.009				
Aphrastura spinicauda								
Model AIC	924.0				692.2			
Model r^2	0.395				0.516			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.002	0.053			2e-09	4e-05	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	Str_Index	-0.021	0.006	0.001	Str_Index	-0.024	0.007	0.001
					ED_m.Ha	-0.975	0.353	0.006
					PLAND_NF	-0.007	0.004	0.088
Stand level variables								
Veg Structure variables					Vol_0.3.2m	0.010	0.004	0.017
Veg Composition variables	CQuiVol	0.00002	0.00001	0.078	PlinVol	0.00011	0.00005	0.034
	L5Rich	0.175	0.081	0.030				
Pygarrychas albogularis								
Model AIC	617.7				219.9			
Model r^2	0.376				0.398			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.042	0.206			2e-09	4e-05	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables					ED_m.Ha	-0.650	0.334	0.052
Stand level variables								
Vicinity variables	X200OtA	-1.180	0.802	0.143	X200NFA	2.170	0.540	0.000
Veg Composition variables	NGlaucaVol	0.000003	0.000001	0.039	LApicVol	0.0001	0.00005	0.014
Tachycineta meyeni								
Model AIC	530.3				171.7			
Model r^2	0.286				0.134			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		8.684	2.947			3e-07	5e-04	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	PLAND_NF	0.001	0.017	0.951	Str_Index	0.108	0.036	0.003
					NLSI.NF	-190.75	91.29	0.037
Stand level variables								
Vicinity variables	DistQueb_m	-0.002	0.0002	0.000				
Veg Structure variables	Vol_.10m	0.001	0.000	0.006	Vol_0.3.2m	0.043	0.015	0.003
	*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*							

The vegetation structure at the site had a clear role in explaining the abundance of these species. In native fragments, the volume of vegetation in the upper level of canopy had a positive effect on the abundance of Chilean Swallow. Whereas, for the abundance of this whole species group in pine plantations, the volume of vegetation in the understory had a positive effect on each of the selected models, with the exception of the White-throated Treerunner.

Finally, vegetation richness had a positive effect on the abundance of this species group, both in pine plantations and native vegetation fragments. Overall, the volume of plant species included in selected models had a positive effect on the abundance of the large tree user species. However, for the White-throated Treerunner, the volume of Quila (*Chusquea quila*) had a negative effect on its abundance in native forest fragments. In addition, fragments of native vegetation with high proportion of Litre (*Lithraea caustica*) had fewer individuals of this species group.

3.3.2. Vertical profile generalists

For this group of species, with the exception of Striped Woodpecker (*Veniliornis lignarius*) in the pine plantation data subset, it was possible to model species abundance in both habitats. However, most of the models, especially those related to pine plantations had a low coefficient of determination (Table 9).

In terms of fragmentation and native forest replacement, the proportion of native forest in the landscape had a significant effect on the abundance of this group as a whole, and individually for the Austral Thrush (*Turdus flacklandii*) in native fragments. Similarly, the proportion of core area of native forest in the landscape was the main variable explaining the abundance of Chilean Pigeon (*Patagioenias araucana*) in pine plantations. The density of patches of native vegetation favoured the abundance of Austral Blackbird (*Curaeus curaeus*), both in pine plantations and in native vegetation fragments. For Fire-eyed Diucon (*Xolmys pyrope*), edge density in the landscape had a negative effect on its abundance in pine plantations. Some fragmentation

metrics worked in opposite way in the abundance of some species in pine plantations. For example, the aggregation of native vegetation favoured the abundance of White-crested Elaenia (*Elaenia albiceps*) but not the abundance of Fire-eyed Diucon in pine plantations, while the connectivity of native vegetation in the landscape had a positive effect on the abundance of Austral Thrush but a negative effect for that of Green-backed Firecrown (*Sephanoides sephanoides*). Finally, the density of streams in the landscape explained the abundance of Green-backed Firecrown and Fire-eyed Diucon in forest plantations.

The results showed that neighbourhood characteristics were important in explaining the abundance of vertical generalist species. In all cases, a greater variety of environments in the vicinity of the sampled sites showed a positive effect on the abundance of these species. Overall, the proportion of other types of land use in neighbouring areas prevailed over other variables. But in the case of the Striped Woodpecker the quantity of streams in the vicinity of native forest sites favoured its abundance.

The structural characteristics of vegetation were relevant to explain the abundance of these species in both pine plantations and native forest fragments. The pooled group of species, and particularly the White-crested Elaenia, were more abundant in pine stands with a higher basal area, dense understory but with less vertical vegetation volume (see Fig. 9). Similarly, in native forests, this group of species preferred less vegetation volume in the canopy, or possibly gaps in it. As expected, results showed individual species preferences for vegetation structure features in each environment. However, certain patterns were distinguishable; as was shown by the species group model but varying according to species natural history. For example, the Chilean Pigeon and Patagonian Sierra-Finch (*Phrygilus patagonicus*) showed a preference for clear grounds, associated with their foraging behaviour. A clear avoidance of sites with greater vegetation volume in the intermediate vertical strata could be seen for White-crested Elaenia, Fire-eyed Diucon and Austral Blackbird.

In relation to the vegetation composition, a preference for more diverse sites could be seen for the aggregate group of species, and for the Patagonian Sierra-Finch in the native forests data subset. Furthermore, the abundance of some vertical profile generalist species was explained by the volume of certain plant species. That could be explained either by their importance as foraging resource, such as the Maqui (*Aristotelia chilensis*) for the White-crested Elaenia, or because their presence denotes certain site characteristics.

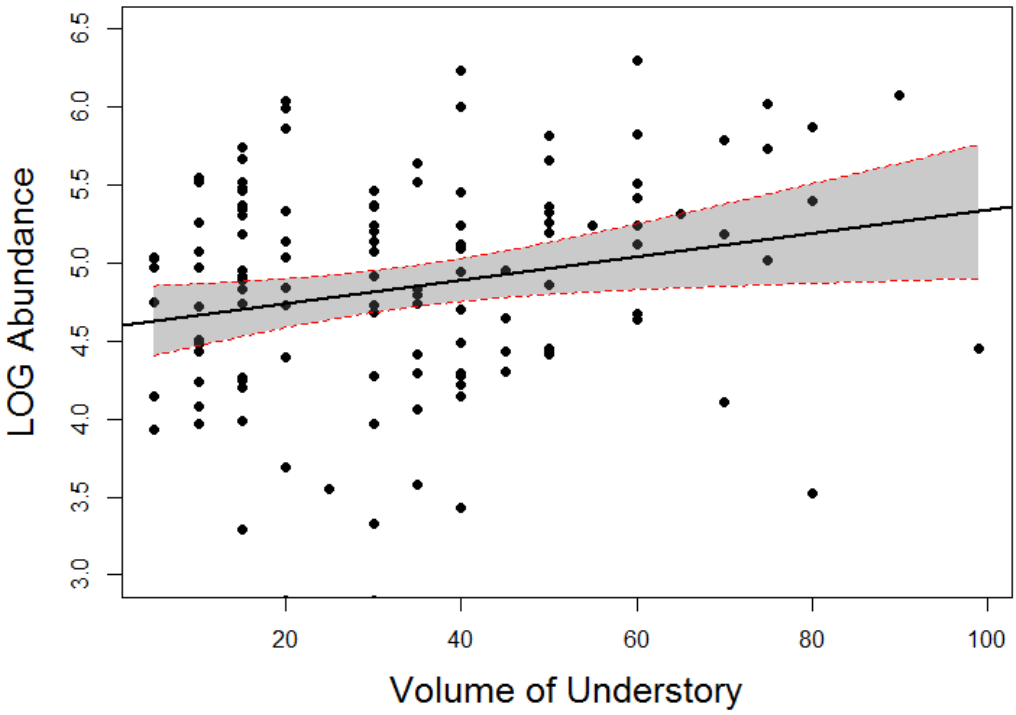

Figure 9. The positive effect of the understory vegetation volume on the Log abundance of White-crested Elaenia in pine plantation stands. Alternate lines show 95% confidence intervals.

Table 9. Mixed models explaining the abundance of Vertical Profile Generalist (VPG) species in native forest and pine plantations.

Species	Native forest subset				Pine plantation subset			
VPG								
Model AIC	834.8				1007.9			
Model r^2	0.310				0.543			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		3e-08	1e-04			0.030	0.175	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	ED_m.Ha	-0.632	0.196	0.0012	PLAND_NF	0.005	0.002	0.052
	NLSI.NF	-5.570	1.540	0.0002				
Stand level variables								
Vicinity variables					X200OtA	1.310	0.552	0.018
Veg Structure variables	Vol_.10m	0.006	0.002	0.0002	Basal_Area	0.003	0.001	0.022
					Cover	-0.933	0.394	0.018
					Vol_0.3.2m	0.006	0.002	0.001
Veg Composition variables	VolPine	-6e-06	2e-06	0.014	LApicVol	0.00009	0.00004	0.019
	NGlaucaVol	-2e-06	1e-06	0.035				
	PBolVol	0.00007	0.00002	0.009				
Patagioenas araucana								
Model AIC	194.1				166.2			
Model r^2	0.278				0.165			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		2e-09	5e-05			6.649	2.579	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables					Core_Land	4.361	0.322	0.000
Stand level variables								
Veg Structure variables	Vol_0.3m	-0.023	0.011	0.035				
Curaeus curaeus								
Model AIC	322.9				491.9			
Model r^2	0.362				0.121			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.106	0.326			0.033	0.184	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	pvalue
Landscape level variables	PD.NF	0.475	0.290	0.102	PD.NF	0.920	0.450	0.041
Stand level variables								
Veg Structure variables	Vol_5.10m	-0.014	0.005	0.012				
Elaenia albiceps								
Model AIC	1222				1466.8			
Model r^2	0.497				0.510			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.046	0.214			0.064	0.253	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables					NLSI.NF	-21.000	10.300	0.041
Stand level variables								
Vicinity variables					X200OtA_.	1.430	0.755	0.058
Veg Structure variables	Vol_5.10m_.	-0.014	0.005	0.012	Basal_Area	0.005	0.002	0.020
Veg Composition variables	VolPine	-6e-06	3e-06	0.100	AChilVol	0.00003	0.00001	0.001
	LCausVol	-0.00006	0.00002	0.019	LApicVol	0.00016	0.00004	0.0004
	GAveVol	0.00002	9e-06	0.016				
	L3Rich	0.076	0.037	0.041				

Phrygillus patagonicus								
Model AIC	526.1				1033.6			
Model r^2	0.286				0.162			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		3e-09	6e-05			0.011	0.104	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	NLSI.NF	-58.100	13.000	7e-06				
Stand level variables								
Vicinity variables	X200NFA	-1.530	0.360	0.00002				
Veg Structure variables					Cover	-1.360	0.704	0.053
					Vol_0.3m	-0.005	0.003	0.088
					Vol_0.3.2m	0.009	0.003	0.010
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Veg Composition variables	NGlaucaVol	-12e-05	6e-06	0.050	PlinVol	0.00007	0.00003	0.057
	LCausVol	0.00012	3.1e-05	0.00012				
Sephanoides sephanoides								
Model AIC	764.2				798.7			
Model r^2	0.218				0.256			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.018	0.134			0.012	0.112	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables					Str_Index	0.013	0.005	0.001
					Connect	-0.015	0.007	0.048
Stand level variables								
Vicinity variables								
Veg Structure variables								
Veg Composition variables	APuncVol	0.00001	6e-06	0.020	L4Rich	0.193	0.091	0.035
Turdus falcklandii								
Model AIC	785.1				1061.4			
Model r^2	0.208				0.150			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		4e-08	2e-04			1e-08	1e-04	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	PLAND_NF	0.002	0.001	0.091	Connect	0.014	0.006	0.040
Stand level variables								
Vicinity variables	X200OtA	1.630	0.452	0.0003	X200NFA	1.650	0.633	0.009
					Patch size	0.003	0.001	0.000
Veg Structure variables	Vol_2.5m	0.006	0.003	0.026	Basal_Area	-0.005	0.002	0.008
	Basal_Area	0.003	0.002	0.032				
Veg Composition variables	CAlbaVol	-1.8e-05	9e-06	0.038	L5Rich	-0.456	0.208	0.028
					NGlaucaVol	-0.00005	0.00001	0.010
Veniliornis lignarius								
Model AIC	278.2							
Model r^2	0.131							
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		5e-09	7e-05					
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	Str_Index	-0.014	0.008	0.073				
Stand level variables								
Vicinity variables	X200St_m.ha	0.011	0.005	0.026				
Veg Composition variables	CAlbaVol	-0.00005	0.00003	0.097				
Xolmys pyrope								

Model AIC	663.6				778.6			
Model r^2	0.167				0.075			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		9e-09	9e-05			0.009	0.096	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables					Str_Index	0.015	0.007	0.026
					ED_m.Ha	-0.766	0.365	0.036
					NLSI.NF	42.600	13.200	0.001
Stand level variables								
Vicinity variables	X200OtA	1.940	0.525	2.20E-04	X200RoA	7.760	2.480	0.002
Veg Structure variables	Vol_.10m	-0.017	0.010	0.094	Vol_2.5m	-0.007	0.003	0.028
Veg Composition variables	CQuiVol	-0.00004	0.00002	0.042	EPulVol	0.000	0.000	0.127
	GAveVol	-0.00025	0.00009	0.009	L2Rich	0.101	0.052	0.052
	L5Rich	0.376	0.179	0.035				
	*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; ' ' 1*							

3.3.3. Understory users

As in the previous group of species, models related to pine plantations showed a lower coefficient of determination than those obtained for models explaining the abundance of these species in fragments of native forest (Table 10).

Fragmentation metrics did not show the marked effect observed in other groups of species. The proportion of native forest in the landscape had a negative effect on the pooled abundance of this species group in fragments of native vegetation. However, this landscape feature positively affected the abundance of the Chestnut-throated Huet-huet (*Pteropthochos castaneus*) in pine plantations. Meanwhile, the abundance of the pooled species and the Ochre-flanked Tapaculo (*Eugralla paradoxa*) in pine plantations was positively affected by the connectivity of native vegetation patches. Interestingly, all species, with the exception of the Dusky Tapaculo (*Scytalopus fuscus*), showed a negative response in their abundances in relation to the density of the drainage network in the landscape.

The size of the native forest fragment had a positive effect on the pooled species group abundance. Another clear effect of the site surrounding area was that the abundance of the Dusky Tapaculo in

pine plantations decreased with increasing distance to the nearest fragment of native forest. However, the opposite effect was observed for the Ochre-flanked Tapaculo, whose abundance in native forest fragments also increased in relation to the density of streams in the vicinity of the site.

This group of species showed a clear preference for certain structural vegetation characteristics, such as dense undergrowth, a smaller volume of foliage in the intermediate canopy and lower basal area. These features were observed both in models that explain the abundance of these species in native forests and in pine plantations (Fig. 10).

In general, a positive association was observed between the abundance of these species and the vegetation richness present on sites. This link was evident for the Ochre-flanked Tapaculo and the Dusky Tapaculo in pine plantations. In addition, plant species included in models referred to wet and open canopy environments.

Table 10. Mixed models explaining abundance of Understory User (UU) species in native forest and pine plantations.

Species	Native forest subset				Pine plantation subset			
UU								
Model AIC	809				629.7			
Model r^2	0.684				0.666			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		2e-08	1e-04			0.382	0.618	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	Str_Index	-0.019	0.005	0.000	Connect	0.028	0.017	0.099
	PLAND_NF	-0.016	0.005	0.001				
Stand level variables								
Vicinity variables	Patch size	0.002	0.001	0.014	Vol_0.3.2m	0.018	0.004	0.00002
Veg Structure variables	Basal_Area	-0.010	0.003	0.003				
	Vol_0.3.2m	0.008	0.004	0.054				
	Vol_5.10m	-0.009	0.004	0.030				
Veg Composition variables	CQuiVol	0.00002	0.00001	0.023	CAlbaVol	0.00007	0.00002	0.011
	L3Rich	0.180	0.078	0.021				
Eugralla pardoxa								
Model AIC	536.8				356.0			
Model r^2	0.666				0.561			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		7.151	2.674			4.444	2.108	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables					Str_Index	-0.118	0.052	0.025
					Connect	0.148	0.068	0.029
Stand level variables								
Vicinity variables	X200St_m.ha	0.002	0.00035	0.0000	Dist_to_NF	0.001	0.000	0.026
Veg Structure variables	Basal_Area	-0.002	0.0002	0.0000	Vol_5.10m	-0.021	0.011	0.068
Veg Composition variables					L4Rich	0.540	0.203	0.007

Pteroptochos castaneus								
Model AIC	750.7				294.5			
Model r^2	0.213				0.156			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		1e-07	3e-04			6e-08	2e-04	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	Str_Index	-0.019	0.005	0.0004	PLAND_NF	0.010	0.004	0.023
Stand level variables								
Veg Structure variables	Vol_0.3.2m	0.018	0.004	6e-06	Vol_0.3.2m	0.010	0.005	0.039
Veg Composition variables	CQuiVol	0.00002	0.00001	0.076				
Scytalopus fuscus								
Model AIC	638.6				696.7			
Model r^2	0.233				0.237			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		6e-09	7e-05			0.034	0.186	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Stand level variables								
Vicinity variables					Dist_to_NF	-0.001	0.001	0.024
Veg Structure variables	Vol_0.3.2m	0.008	0.004	0.052	Vol_0.3.2m	0.006	0.003	0.061
Veg Composition variables	PBolVol	0.00007	0.00004	0.095	L3Rich	0.160	0.080	0.046
	CQuiVol	0.00002	9e-06	0.030				
	GAveVol	-0.0003	0.0001	0.002				
Sylviorthorhynchos desmursii								
Model AIC	696.2				214.4			
Model r^2	0.538				0.213			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		4e-08	2e-04			30.210	5.496	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	Str_Index	-0.018	0.007	0.007				
Stand level variables								
Veg Structure variables	Vol_0.3.2m	0.012	0.005	0.006	Vol_0.3.2m	0.014	0.005	0.006
	Vol_5.10m	-0.011	0.004	0.005				
Veg Composition variables	VolPine	-2e-05	0.00001	0.061				
	NGlaucaVol	-7e-06	3e-06	0.035				
	AChilVol	0.00011	0.00002	2e-05				
	*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*							

3.3.4. Shrub users

For only four species it was possible to model their abundance due to the low number of records. Moreover, for the Black-chinned Siskin (*Sporagra barbatus*) only a model to explain its abundance in native forests was obtained. Also, models explaining species abundance in pine plantations showed lower coefficient of determination than those for native vegetation (Table 11).

Native forest fragmentation did not affect equally to all species in this group. For the Tufted Tit-Tyrant (*Anairetes parulus*), its abundance in fragments of native vegetation was favoured by a

higher proportion of area covered by native forest in the landscape, while this fragmented native forest showed a high aggregation level. The disaggregation of native forest remnants reduced the abundance of the Plain-mantled Tit-Spinetail (*Leptasthenura aegithaloides*) in pine plantations. However, the abundance of this species in fragments of native vegetation is greater when the patchiness of this type of habitat was higher in the landscape. Interestingly, the edge density in the landscape equally favoured the abundance of the Tufted Tit-Tyrant in both native forest and pine plantation.

The characteristics of the neighbouring areas are important to explain pooled Shrub User species abundance in pine plantations. For example, the presence of "Other land use" in the neighbouring areas of pine stands favoured higher abundance of this species group. This land use also affected the abundance of Black-chinned Siskin in larger fragments of native vegetation. Besides that, the abundance of the Tufted Tit-Tyrant in pine plantations increased with increase in the distance to fragments of native vegetation.

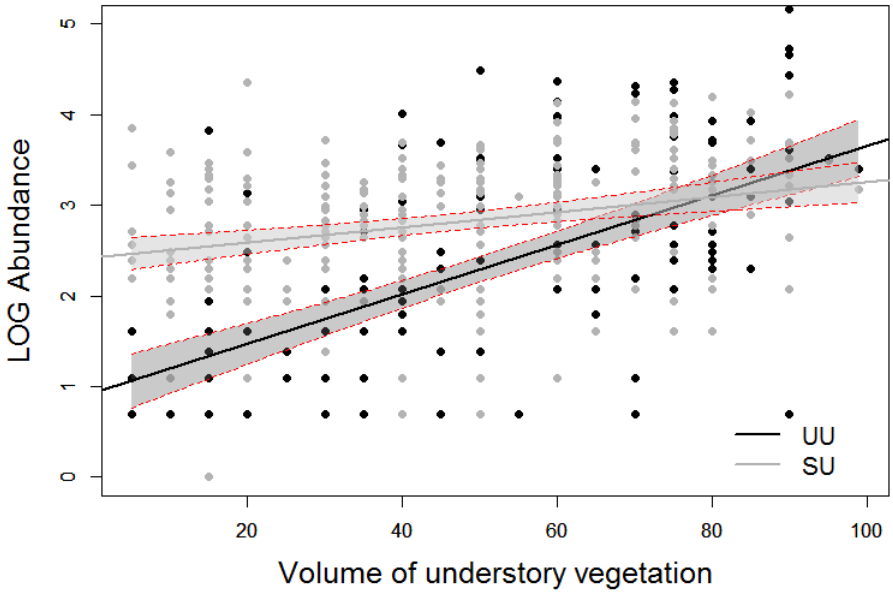

Figure 10. Effect of the understory volume at plot level on the Log abundance of Understory (UU) and Shrub User (SU) species in pine plantation stands. Alternate lines show 95% confidence intervals.

In relation to vegetation structure, Shrub User species preferred sites with greater ground cover, well developed understory and less foliage volume of the intermediate canopy (Fig. 10). These characteristics explained the abundance for most of these species both in native forest and in pine plantation. However, the effect of basal area on Shrub User species abundance differed accordingly to both habitat type and bird species. Thus, the abundance of the Tufted Tit-Tyrant was higher in native forest fragments with lower values of basal area but with an important understory volume. However, only the volume of the understory explained the abundance for this species in pine plantations. Furthermore, the abundance of the Plain-mantled Tit-Spinetail and Southern House Wren (*Troglodytes musculus*) was greater in pine plantation stands with higher values of basal area and dense undergrowth.

Table 11. Mixed models explaining abundance of Shrub Users (SU) species in native forest and pine plantations.

Species	Native forest subset				Pine plantation subset			
SU								
Model AIC	780.6				941			
Model r^2	0.525				0.383			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		1e-08	1e-04			0.035	0.189	
	Fixed effects	estimate	st error	P value	Fixed effects	estimate	st error	P value
Landscape level variables	PLAND_NF	0.00871	0.00288	0.0025				
	NLSI.NF	-9.59	2.78	0.00056				
Stand level variables								
Vicinity variables					X200OtA	1.33	0.821	0.1067
Veg Structure variables	Basal_Area	-0.0060	0.00237	0.01095	Vol_0.3m	0.00436	0.00212	0.0403
	Vol_0.3.2m	0.0109	0.00304	0.00035	Vol_0.3.2m	0.00784	0.00284	0.0058
	Vol_5.10m	-0.0052	0.00299	0.08128	Vol_2.5m	-0.0061	0.00348	0.0763
	Vol_.10m	-0.0089	0.00412	0.03021				
Veg Composition variables	LApicVol	0.00004	0.00002	0.03611	NGlaucaVol	0.00003	0.00001	0.0245
Anairetes parulus								
Model AIC	194.1				877.5			
Model r^2	0.548				0.466			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		0.005	0.070			6e-08	2e-04	
	Fixed effects	estimate	st error	pvalue	Fixed effects	estimate	st error	pvalue
Landscape level variables	ED_m.Ha	1.000	0.282	0.0003	ED_m.Ha	1.010	0.284	0.0004
	PLAND_NF	0.00911	0.00451	0.0435				
	NLSI.NF	-6.1619	3.1103	0.0475				
Stand level variables								
Vicinity variables					Dist_to_NF	0.00112	0.00047	0.0193
Veg Structure variables	Basal_Area	-0.0074	0.00226	0.00093	Vol_0.3.2m	0.0189	0.00309	0.0000
	Vol_0.3.2m	0.00915	0.00286	0.0014				
Veg Composition variables	L4Rich	-0.140	0.0636	0.02773	NGlaucaVol	0.00002	0.00001	0.0154
	L5Rich	0.135	0.0816	0.0975	CAlbaVol	0.00003	0.00001	0.0532

Sporagra barbatus								
Model AIC	453.4							
Model r^2	0.12							
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		4e-08	2e-04					
	Fixed effects	estimate	st error	pvalue	Fixed effects	estimate	st error	pvalue
Stand level variables								
Vicinity variables	X200OtA	0.34	0.694	0.624				
	Patch size	0.00081	0.00040	0.046				
Veg Structure variables	Vol_5.10m	-0.0079	0.00353	0.025				
Veg Composition variables	LCausVol	-0.0000	0.00008	0.24				
Lepthasthenura aegithaloides								
Model AIC	235.9				328.6			
Model r^2	0.699				0.143			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		7.141	2.672			0.286	0.535	
	Fixed effects	estimate	st error	pvalue	Fixed effects	estimate	st error	pvalue
Landscape level variables	PD.NF	0.0467	0.00521	0.00000	NLSI.NF	-21.000	10.300	0.041
Stand level variables								
Veg Structure variables	Vol_5.10m_.	-0.0052	0.00007	0.00000	Basal_Area	0.00739	0.00359	0.0397
					Vol_0.3.2m_.	0.0124	0.00351	0.0003
Veg Composition variables	LApicVol	0.00002	0.00000	0.00000	LApicVol	0.00019	0.00008	0.0260
Troglodytes musculus								
Model AIC	631.4				1037.8			
Model r^2	0.248				0.132			
Random effect		Variance	StdDev			Variance	StdDev	
Landscape		2e-09	4e-05			4e-09	7e-05	
	Fixed effects	estimate	st error	pvalue	Fixed effects	estimate	st error	pvalue
Landscape level variables								
Stand level variables								
Vicinity variables								
Veg Structure variables	Cover_.	-1.53	0.544	0.005	Basal_Area	0.00424	0.00218	0.0519
	Vol_0.3m_.	0.00611	0.0035	0.081	Vol_0.3m_.	0.00627	0.00207	0.0025
Veg Composition variables	APuncVol	-0.0000	0.00002	0.095				
	L1Rich	-0.119	0.0641	0.063	CQuiVol	0.00002	0.00000	0.002
	*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*							

The inclusion of plant species variables in models explaining Shrub Users abundance were related to either structural characteristics of vegetation or source of foraging resources. For example, the presence of the native bamboo Quila (*Chusquea Quila*) in pine plantations produces dense understory conditions that allow greater abundance of Southern House Wren. Similarly, this bird species is more abundant in native forest fragments with fewer volume of the tree species Olivillo (*Aextoxicum punctatum*), which is associated with mature and less disturbed stage of these forests. In addition, Tufted-tit Tyrant showed a preference for a couple of tree species growing in the understory under pine plantations, for what they seem to have a clear role in the species foraging.

3.3.5. Cavity availability and birds. In order to avoid losing analysis power due to sample size, I didn't include the number of cavities seen in the plot in the statistical analyses. Nonetheless, I tested the relationships between this variable and plot and stand attributes through linear regressions.

The number of cavities detected in native forest patches was greater than in pine plantations ($F_{1,65}$ = 92.45, p-value < 0.001). For native forest plots, the number of cavities had a significant and positive relationship ($F_{4,7}$ = 27.81, p-value < 0.001, r^2 = 0.907) with the medium height of the canopy (β = 0.242, p-value < 0.05) and the distance to creek (β = 0.077, p-value < 0.01). However, pine plantation stands showed no association between stand attributes and the number of cavities.

The number of cavities had a clear effect on the occurrence of secondary cavity nester species ($F_{1,65}$ = 91.46, p-value < 0.001, r^2 = 0.57*).* Individually, the number of cavities showed a positive and significant effect on the abundance of the Thorn-tailed Rayadito ($F_{1,65}$ = 55.29 , p-value < 0.001), White-throated Treerunner ($F_{1,65}$ = 76.12, p-value < 0.001) and the Chilean Swallow ($F_{1,65}$ = 17.52, p-value < 0.001), but not for Southern House Wren ($F_{1,65}$ = 0.395, p-value = 0.531) and Plain-mantled Tit-Spinetail ($F_{1,65}$ = 0.541, p-value = 0.464).

3.3.6. Plant species and birds. Many models explaining abundance of species included plant species as explanatory variables. Eleven bird species showed either a positive or negative relationship with one or two native plant species. The more frequent plant species appearing in bird abundance models were Hualo, Luma and Quila.

Hualo (*Lophozonia glauca;* Nothofagaceae). This tree is the dominant species of the Maulino forest, and it also could be found in the understory growing in pine plantations. The abundance of White-Throated Treerunner in native forest patches was clearly associated with its presence (β = 3.70e-06; p-value = 0.039 in a model with r^2 = 0.376). But for some bird species this tree had a negative effect on their abundance in native forest. This adverse effect was related to either a more open forest as for the Patagonian Sierra-Finch (β = -1.21e-05; p-value = 0.049 in a model with r^2 =

0.280) or to a different forest composition like it was for the Desmur's Wiretail (*Sylviorthorhynchus desmursii*) (β = -7.40e-06; p-value = 0.035 in a model with r^2 = 0.53). The volume of this tree under pine plantations showed a positive and significant relationship with the occurrence of Tufted Tit-Tyrant (β = 2.61e-05; p-value < 0.01 in a model with r^2 = 0.165). The opposite relationship was shown by Austral Thrush, whose abundance slightly decreased in pine plantations where this tree species dominated the undergrowth (β = -3.69e-05; p-value = 0.038 in a model with r^2 = 0.128).

Maqui (*Aristotelia chilensis;* Elaeocarpaceae). Maqui is a small tree, with a wide distribution in Chile. It is well known for its small, purple and fleshy fruits that give in the middle of summer season. The White-crested Elaenia showed a marked preference for pine plantation sites where this plant is the main species of the understory (β = 3.47e-05; p-value = 0.0005 in a model with r^2 = 0.51). A similar preference is shown by Desmurs' Wiretail in native forest fragments (β = 1.11e-04; p-value = 2.1e-05 in a model with r^2 = 0.53).

Luma (*Luma apiculata;* Myrtaceae). Luma is a small flowering evergreen tree widely spread in temperate forests of Chile and Argentina. Pine plantations with a high proportion of this species in their understory showed higher abundance of the White-crested Elaenia (β = 1.68e-05; p-value < 0.001 in a model with r^2 = 0.51), White-throated Treerunner (β = 1.31e-04; p-value = 0.014 in a model with r^2 = 0.398) and the Plain-Mantled Tit-Spinetail (β = 1.97e-04; p-value = 0.026 in a model with r^2 = 0.143). For this last bird species, results also showed that its abundance in native forest is greater in fragments with high proportion of Luma (β = 2.70e-05; p-value < 0.001 in a model with r^2 = 0.69).

Litre (*Lithraea caustica;* Anacardiaceae). Litre is a common understory and sub-canopy tree in Maulino forests. Litre foliage volume had a positive effect on the abundance of Patagonian Sierra-Finch in native forests (β = 1.20e-05; p-value = 0.0001 in a model with r^2 = 0.28). However, native forest sites with high proportion of this tree species showed lower

abundance of the White-crested Elaenia (β = -6.70e-05; p-value = 0.019 in a model with r^2 = 0.497) and Black-chinned Siskin (β = -9.90e-05; p-value = 0.024 in a model with r^2 = 0.12).

Quila (*Chusquea quila;* Poaceae). This evergreen bamboo grows associated to humid creeks or invasively covering any gap in mature forests. In general, Understory User species showed a marked preference for sites covered with this bamboo, but individually only the abundance of the Dusky Tapaculo in native fragments is explained by this understory species (β = 2.16e-05; p-value = 0.03 in a model with r^2 = 0.233). Furthermore, the Southern House Wren abundance was positively affected by the presence of this plant species in the understory of pine plantations (β = 2.68e-05; p-value = 0.002 in a model with r^2 = 0.132).

Lingue (*Persea lingue*; Lauracea). Lingue is a threatened evergreen tree species from temperate South America. Greater abundance of the Thorn-tailed Rayadito in pine plantations was associated with the presence of Lingue in the undergrowth (β = 1.18e-04; p-value = 0.034 in a model with r^2 = 0.516).

3.4. Discussion

This research only examined the effect of pine plantation as a forest matrix in landscapes with at least 85% of forest cover. This has not been done before as previous studies included pine at different ages and even harvested areas (Estades & Temple 1999; Vergara & Simonetti 2004). I found that landscape features affected almost every forest bird species, and those unaffected (3) were generalist species that are found in a wide range of habitat. Responses to landscape features were species specific (for a summary of significant variables for every species see Appendix 4); the amount of native forest and core area in the landscape explained the abundance of 5 out of 19 modelled species. This figure should increase considering that some species, related to late-seral forests, were detected too infrequently to run analyses for them. Not only the natural habitat replacement affects forest birds, but also the way that

fragmentation shapes the landscape; native forest connectivity, edge density, native forest aggregation and patch density determined abundance for many forest bird species. Moreover, the abundance of many bird species, mostly vertical profile generalist, was affected by the features of the surrounding at local scale. The proportion of different land use in the vicinity had an effect on the abundance of some bird species either in native forest or pine plantations.

The configuration of landscape components, at different scales, determines bird communities that inhabit forest landscapes. In this way, my results matched Estades and Temple's (1999) findings in that different land-use cover in the vicinity had an effect on the assemblage of birds found in a plot. Bird occurrence is part of the edge effect in this mosaic, allowing or deterring some species to use some areas in the landscape defined by gradients of conditions that penetrate stands of different land covers. The last could be seen for Australian forested landscapes, where birds penetrate further into the pine matrix according to the shape or narrowness of the fragment of native forest (Tubelis *et al.* 2004). My results differed greatly from those from Estades and Temple (1999) in that they found that bird density increased as one moves away from native forest fragments. But they agreed in that bird density and species richness are associated with the proximity to creeks. The heterogeneity of the surrounding area had an effect on the abundance of vertical profile generalist species. This largely represents the generalist nature of the species in this group and, at the same time, its relationship with greater environmental heterogeneity which might represent greater resource opportunities. In addition, it may also reflect the mobility that characterizes these species.

My results suggest that the effect of patch size on the abundance and species richness depends both on the type of matrix and the species ecology. I found that the abundance of only one species (Black-chinned Siskin) was affected by the patch size. No effect was found for the overall bird density or species richness, but the pooled abundance of understory user species was positively related to fragment area. Similar results have been shown by Vergara and

Armesto (2009), where at least four understory user species showed that fragment size has a positive effect on their abundance. However, the abundance of three other species was negatively affected by this variable. The abundance of Black-chinned Siskin is negatively affected by patch size in landscapes dominated by pasture matrix (Vergara & Armesto 2009), and interestingly, the sign of the effect changed with a forested matrix. Results from other studies suggest that more diverse matrices, like pine plantations of different ages, could allow small fragments to harbour a richer bird assemblage (Estades & Temple 1999; Fischer & B Lindenmayer 2006; Vergara & Simonetti 2004), but they included species from the whole pine cycle in the pooled abundance. Furthermore, the real effect of pine plantation matrix on the forest bird community may be blurred by both the effect of different land cover on the proximity and by the inclusion of raptors in the analyses. However, this could also suggests that many species prefer more diverse landscapes (McGarigal & McComb 1995).

The amount of native habitat in the landscape explained the abundance of many forest bird species, as was found in other studies (McGarigal & McComb 1995; Vergara & Armesto 2009), but see (Luck & Korodaj 2008). Moreover, the habitat configuration resulting from fragmentation processes had a notorious impact on the abundance of forest bird species in the landscape. However, the effect of the landscape configuration may be more important to explain forest bird abundance in pine plantations than in native forest fragments, which was also reported for forest birds in Australia (Lindenmayer *et al.* 2002). The forest matrix may have a cushioning effect on fragmentation effects acting on populations, in terms of connectivity and providing extra foraging areas to native fragments inhabitants (Estades & Temple 1999; Tubelis *et al.* 2007).

The structure and vegetation composition, in both native forest and the understory beneath pine plantations, has a large influence on the assembly of birds (Estades & Temple 1999; Vergara & Armesto 2009; Vergara & Simonetti 2004). Indeed, the occurrence of birds in pine plantations is explained mainly by the volume of native vegetation growing under the pine

canopy. However, it is possible to distinguish two vegetation effects on the abundance of some species. First, some plant species are source of foraging resources, providing either insects or fruits to some bird species. A remarkable example is the association of the White-crested Elaenia with Maqui for fruits and insects (De La Vega *et al.* 2012; Garcia *et al.* 2010; Rodriguez-Cabal *et al.* 2013). The presence of this plant species in the understory explained in great manner the abundance of this bird species in pine plantations. Secondly, some plant species provide structure features that are essentials for bird species. The abundance of Huet-Huet species (Rhinocryptidae) is associated with dense thickets of bamboo Quila in wet ravines (Vergara & Armesto 2009). These shady, wet and impenetrable formations may provide shelter and foraging resources to these ground dwelling species. Nevertheless, some plant species could denote other site features, like forest degradation or even different temperature and humidity conditions.

Sustainable management of industrialized pine plantations should work at landscape level. The forest bird abundance in mature pine plantations was explained chiefly by the native undergrowth. However, the landscape configuration, primarily the area covered with natural forests, had a great impact on bird communities. In order to preserve temperate forest bird communities, conservation measures should be planned and implemented at landscape scale (Vergara & Armesto 2009). Most of the pine plantations in Chile are certified under international standards, including in their commitments the reduction of their negative effects on the environment (Arauco 2012). These results provide information for demanding a review of the land-use planning to land-managers and accreditation companies.

Chapter 4

The effect of pine plantations on the body condition of forest birds

4.1. Introduction

Habitat loss and degradation are the greatest threats to wild birds (Johnson 2007). Changes in habitat quality can impact population sizes through their effects on demography, physiological conditions and survival of birds (Latta & Faaborg 2002). Local variations in habitat affect the fitness of animals through variations in resources and environmental conditions, generating strong selection pressures on habitat selection (Cody 1985). Indeed, site quality is one of the major determinants of fitness for territorial species (Newton 1998).

Several papers on forest avifauna using exotic coniferous plantations indicate that, based on the presence and abundance of forest bird species, these monocultures could represent an alternative and suitable habitat for sustaining populations (Brockerhoff *et al.* 2008; Estades & Temple 1999; Vergara & Simonetti 2004). However, the use of local density as a proxy for habitat quality must include first an investigation of how the subject of study is fitted to an ideal distribution, as there are various ecological factors that can lead a bird to select a low quality habitat instead of others (Johnson 2007). Consequently, the density of animals in a habitat could, in some cases, be a misleading indicator of habitat quality (Van Horne 1983). Thus, to determine the habitat quality offered by pine plantations to forest avifauna by comparing estimated densities of bird populations in pine plantations and adjacent native forest, it is too vague and could mask the real situation of populations. For example, Van Balen (1973) working on Great Tits in deciduous and coniferous forests, shows a higher density of breeding pairs in deciduous woods than in coniferous forest, but no differences in clutch size. However, at equal density of breeding pairs, clutch sizes proved to be very different. It is essential, therefore, to assess habitat quality indicators for individuals or populations to determine the condition of the bird populations inhabiting pine plantations that have replaced the native forest in south-central Chile.

Nowadays, it is widely recognized that matrices of pine plantations offer suitable habitat condition to support some taxa (Hall *et al.* 1997). McIntyre and Hobbs (1999) proposed that forest landscapes with replacement of native vegetation by pine plantations must be considered as a gradient of alteration states rather than a non-habitat matrix, as this is the most appropriate way to consider how the birds responded to them (Lindenmayer *et al.* 2003). In this context, an inverse relationship with distance from streams covered with native vegetation has been described for the abundance of the bird and arthropod communities in forest landscapes of Central Chile (Estades & Temple 1999; Venegas 2009).

The use of condition indices, often estimated as the residual variance in body mass after controlling by body size (Gosler & Harper 2000), is limited by the inability to control all the variance in the measures used, especially for body mass. In general, birds' body mass is a sum of different components, such as muscle, fat, gut and water content. While methods to measure fat and muscle reserves are already widely known and used (Gosler 2004), gut and water content are not possible to assess in living birds. Accordingly, Gosler *et al*. (1998) demonstrated that the use of a combination of size measures and the inclusion of fat and muscle reserves reduce significantly the residual variance.

Although fat score is consistently one of the best predictor of mass for many passerine species (Gosler *et al.* 1998), this body mass component (fat) is determined by a starvation-predation trade-off (Lima 1986). Birds have higher body temperature and resting metabolic rate than many other endotherms, being fat depots the most important energy reserve when such requirements cannot be met from environmental sources (Witter & Cuthill 1993). This fact could lead to think in a positive relationship between the amount of fat stored and the condition of the individuals. However, fat affect survival in very different ways. In one hand, birds should increase their fat reserves according to low food predictability or when facing periods of high energy demand (i.e.: harsh weather, migration). In the other hand, birds should be lean as possible to avoid predation; leaner birds are more likely to escape from predators and spend less time exposed to predators

while feeding (Gosler 1996; Lima 1986). Thus, the fat reserve of an individual is determined by a trade-off between eat and being eaten. In this way, McNamara and Houston (1990), by modelling relative levels of starvation and predation, state that "....at the optimal level of fat reserves, the rate of decrease of starvation is equal to the rate of increase predation". Therefore, the interpretation of differences in fat content between individuals is not trivial as many ecological factors in these forest systems could be affecting the trade-off balance (i.e.: abundance of predators, food availability, and competition).

To test any possible density dependent effect in the condition of individuals, I compare the mean density for every site and for the commonest species between native forest and pine plantations. In addition, a comparison between estimated densities and capture rate for every site is done to assess the representation of the bird community in the captures. As sexual dimorphism, in terms of body size, is not well documented for the Chilean avifauna, I test the difference in wing-length for the most common species. By estimating the body condition of individuals from forest birds that inhabit either native forest fragments or pine plantations, I looked for any difference in habitat qualities between these two types of environments. Given the higher diversity of native forest fragments in terms of vegetation structure and composition, I expected to see this reflected in the trophic resources available for birds and, therefore, in the body condition of individuals who maintain territories in native fragments. Under the hypothesis that pine plantations are poorer habitat than native forest for bird populations, I expect that differences in resource availability could be expressed in body condition differences between individuals inhabiting native forests and pine plantations (Garnett 1981; Riddington & Gosler 1995; Ulfstrand *et al.* 1981). Moreover, some habitat features and landscape configuration could determine the possible differences in the body condition of individuals inhabiting either habitat. In that way, some native vegetation variables are expected to improve the poorer habitat. Due the importance of muscle and fat content as main components of body mass, I explore in an independent analysis the values of fat and muscle scores for individuals captured in either habitat. Furthermore, I suggest that there might be a hierarchical

arrangement regarding the site quality, which in this case is within pine plantation must be correlated with the distance to the native forest patch.

4.2. Methods

This study was conducted in the Maulino forests of the coastal range of south-central Chile. These are temperate deciduous forests dominated mainly by the tree species Hualo (*Lophozonia glauca, Nothofagaceae*), and having an understory that generally consists of shrubs or small trees with resistant evergreen leaves. However, in wetter areas evergreen species predominate in the canopy.

Sites. In these forests, ten native forest fragments of at least 3 hectares, surrounded by mature Monterey pine plantations were selected for studying their bird populations. The selection of sites considered mature pine stands, ready to be harvested, beside a fragment of native forest. Geographically, the search for sites was constrained to sites located on the western slope of the Coastal range. This is because the oceanic effect on the climate, giving a wetter environment, influences communities developing in the area (Amigo & Ramírez 1998).

Mist-netting. During the breeding season 2012-2013, birds were mist-netted in both habitats, the native forest fragments and within surrounding pine plantations. The fieldwork began in October 2012 and lasted until the middle of February 2013. For this, 34 mist nets of 6, 9 and 12 m were used, totalling 261 m in length. The nets in pine plantations were located at different distances from the border of the pine stand with the fragment of native vegetation (Fig. 11), recording in Gps their location for later estimation of their distance from the edge of the fragment. In addition, each net was active during 9 hours every day, except for sporadic rains, representing a total effort of 36,199 hr*m in native forest and 45,072 hr*m in pine plantations. In order to avoid a time effect on data, and to reduce the possibility of predation of birds in the nets, capture locations were moved every two days. Sites were visited twice during the breeding season.

Habitat description. Each mist-net point was characterized in terms of vegetation composition and structure. The abundance of insects in every site was surveyed using black-light and Mallaise traps. An index of the availability of insects was assessed using the number of items captured and their dry mass.

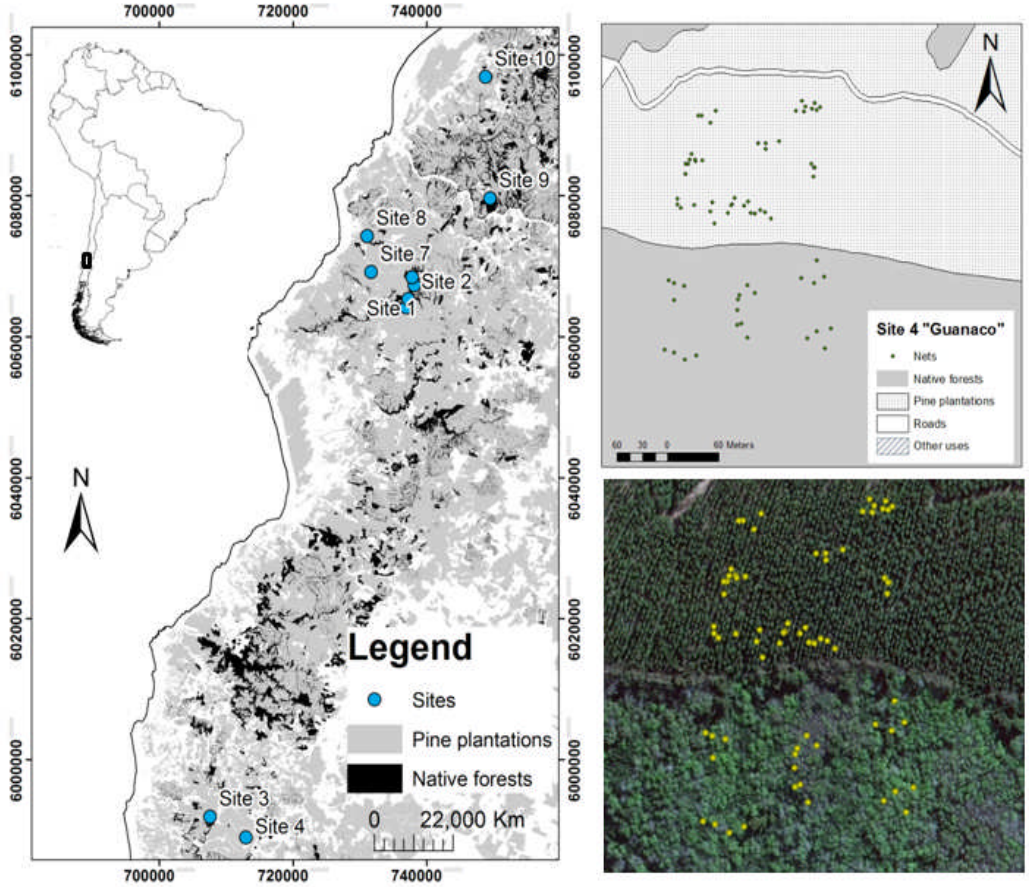

Figure 11. Geographical reference of the study area (Left). Illustrations of the disposition of mist-nets in a surveyed fragment-pine plantation situation, Site 4 "Guanaco": Map of the sites from geographical layers (Top-right) and satellite image depicting the same site, yellow-dots show mist-net positions (Bottom-right).

Ringing and measures. All captured birds were ringed using metal rings provided by SAG-Chile under the ringing permit # 5038 (Servicio Agricola y Ganadero, Gobierno de Chile). The following parameters were measured by a single ringer: maximum wing length was measured using a 1 mm precision stopped rule; maximum tarsus length, depth and length of the bill to 0.1 mm were measured using a vernier calliper; and the weight of the individuals was recorded with a 0.1 g precision digital balance. In addition, I assessed pectoral muscle size (Gosler 2004) and amount of

subcutaneous fat accumulated in the tracheal pit (Gosler 1996), scoring them in ranges of 0-4 and 0-5 respectively. Moult patterns were recorded for every bird and for every wing, in order to find possible asymmetry in this process, following BTO suggested scores (Ginn and Melville 1983). Plumage patterns that differentiate males and females were only used for sexing part of the species in this bird community as most of them have no apparent sexual dimorphism. Therefore, sexing was based on reproductive traits such as cloacal protuberance and presence of brood patch when it was appropriated. However, when no certainty existed regarding the sex of individuals, they were categorized as "not defined". Similarly, for most Chilean species methods have not yet been developed to determine the age of birds on the basis of plumage. Beyond distinguishing juveniles from adults, it is not possible to differentiate the age of adult individuals with certainty (Pyle *et al.* 2015). However, for one species, the White-crested Elaenia (*Elaenia albiceps*), I used the colour of the roof of the mouth as an ageing criterion, discriminating two adult age class: young adults (probably first-year individuals) and older adults (Thomson *et al*., submitted, see also Appendix 5).

Point counts. To estimate bird density in every site where mist-netting were carried out, I did counts using the variable circular-plot method with a 50 m maximum observation radius, following the methodology described in the previous chapters. All birds seen or heard within the maximum radius were recorded, and their distance from the plot's centre was estimated in 10 m increments to manage different detectability in each patch type (Buckland 1987). Birds flying over a plot were not considered, except for swallows and hummingbirds. Due to mist-net locations, counts were not independent of the neighbouring land use. Nevertheless, twelve counts were made per site and no observations were conducted on rainy or misty days.

Data analysis

For ecological reasons, individual species analyses were considered as appropriate. Species in this community differ widely in terms of the environmental features that define their niches and also in their morphological characteristics, which are closely related to resource exploitation and energetic needs. The residuals from a linear regression between weight and body size were used as

a body condition index (BCI); the first axis derived from a principal component analysis of wing, tarsus and bill length was used as a measure of body size (Gosler *et al.* 1998). Yet, I considered the condition in a narrow sense, with the component of body mass independent of the body size , and I controlled the mass of reserve tissues in the models, my body condition index was a relative indicator of mass as it included gut content, which varies through the day (Gosler & Harper 2000). Accordingly, I also tested differences in fat and muscle scores between habitat types. With that index for body condition as a dependent variable, a search for the best model, based on AIC, to explain the body condition was carried out from a full linear mixed model containing the following variables as fixed effects: Muscle score, Fat score, Sex, Age, Time, Season, Habitat type and Understory vegetation volume. Site was included as a random effect. To look for an effect of the distance from capture location to the border of the native fragment on a bird's body condition, the subset of captures made in pine stands was used in mixed linear models. By considering both, a different dataset and a associated non-previously tested variable, I avoid to increase the chances of a Type I error. Analyses were done only for species with more than ten ringed individuals, and all statistical analyses were performed using R (R Development Core Team 2012), with the package lmerTest (Kuznetsova *et al.* 2013) for the mixed model analyses, and all of them considered a level of significance $\alpha=0.05$.

4.3. Results

In total, 732 individuals were ringed of 22 bird species. Three species accounted for almost three quarters of all captures: Green-backed Firecrown (97), Thorn-tailed Rayadito (99) and White-crested Elaenia (339). Only ten species had more than ten captures each, and for those species, with the exception of White-throated Treerunner, no difference in estimated density was seen between pine stands and native fragments. Capture rate in native fragments was significantly higher than in pine plantations for Green-Backed Firecrown and Austral Thrush, and marginally

non-significant for the forest specialists Thorn-tailed Rayadito and White-throated Treerunner (Table 12).

Table 12. Estimated densities and capture rates for site units (n = 8) and for species with more than ten captures. Showing *U* test for both estimated densities and capture rates between native forest and pine plantations, and chi-squared test from contingency tables of values of counts against captures.

Species	Density Estimate (ind/Ha) ± SE		Mann-Whitney-Wilcoxon U test		Capture Rate (ind/1000 h m) ± SE		Mann-Whitney-Wilcoxon U test		Pearson's Chi-squared test (df = 1)	
	Native	Pine	U	p value	Native	Pine	U	p value	Chi-sqd	p value
Tufted Tit-Tyrant (*Anairetes parulus*)	4.51 ± 1.63	2.03 ± 1.11	42	0.111	0.16 ±0.10	0.41 ± 0.18	21	0.427	0.383	0.535
Thorn-tailed Rayadito (*Aphrastura spinicauda)*	6.29 ± 1.83	2.19 ± 0.84	43	0.093	1.44 ± 0.38	0.53 ± 0.29	45	0.055	0.011	0.973
White-crested Elaenia (*Elaenia albiceps)*	7.28 ± 1.79	8.75 ± 2.77	26	0.866	2.87 ± 0.67	3.70 ± 1.26	33	0.612	0.006	0.938
Patagonian Sierra-Finch (*Phrygilus patagonicus)*	0.32 ± 0.22	1.27 ± 0.52	15	0.127	0.39 ± 0.14	0.38 ± 0.25	36	0.370	0.224	0.635
White-throated Treerunner (*Pygarrychas albogularis)*	0.85 ± 0.17	0.29 ± 0.10	49	**0.016**	0.31 ± 0.10	0.07 ± 0.05	43	0.068	0.007	0.930
Green-backed Firecrown (*Sephanoides sephanoides*)	1.04 ± 0.35	0.32 ± 0.13	41	0.151	1.57 ± 0.30	0.72 ± 0.16	47	0.037	0.026	0.870
Black-chinned Siskin (*Sporagra barbatus*)	3.71 ± 1.50	4.81 ± 1.90	24	0.631	0.22 ± 0.15	0.03 ± 0.02	31	0.710	0.185	0.666
Des Mur's Wiretail (*Sylviothorhynchos desmursii*)	0.40 ± 0.30	0.69 ± 0.20	17	0.200	0.08 ± 0.05	0.24 ± 0.13	23	0.490	0.015	0.899
Southern House Wren (*Troglodytes musculus*)	1.02 ± 0.94	0.27 ± 0.17	27	0.890	0.06 ± 0.04	0.14 ± 0.10	27	0.940	0.202	0.653
Austral Thrush (*Turdus falcklandii*)	1.57 ± 0.42	0.59 ± 0.17	43	0.092	1.20 ± 0.31	0.34 ± 0.13	47	0.031	0.013	0.908

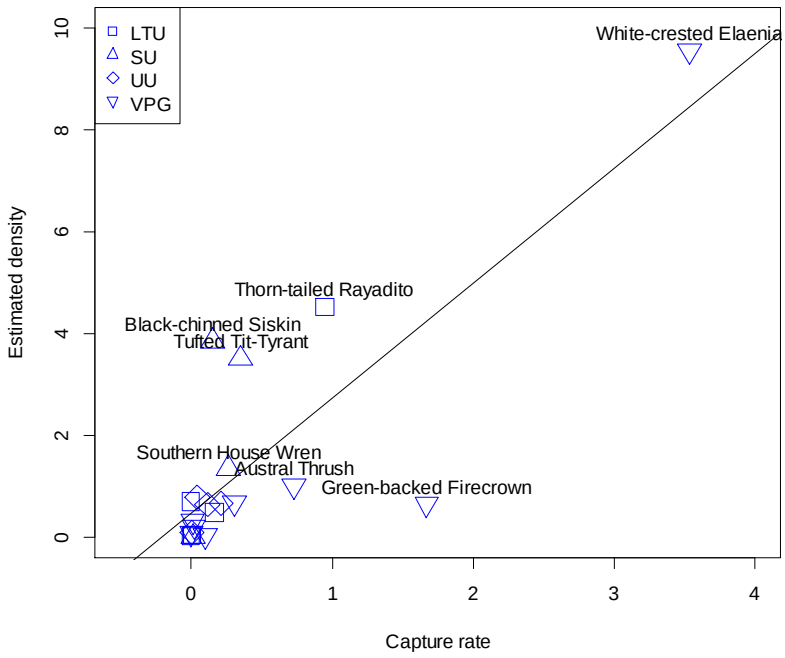

Figure 12. Departure from the linear relationship between estimated densities from point counts and the capture rate obtained using mist-netting.

A difference in size among sexes in terms of wing length was found for five species. These included those species with larger samples (Table 13), which for the White-crested Elaenia and Thorn-tailed Rayadito confirmed that sexing through cloacal protuberance was accurate.

Table 13. Wing length (mm) for adult males and females of forest bird species.

	Females				Males				t-test		
	n	Range	Mean	CV	n	Range	Mean	CV	t	df	p
Tufted Tit-tyrant	11	46-51	47.55	3.0	10	46-50	48.50	3.0	-1.301	15.38	0.212
Thorn-tailed Rayadito	27	57-64	59.62	3.4	21	56-64	60.96	3.1	-2.933	48.67	**0.005**
White-crested Elaenia	162	70-81	74.95	3.1	104	72-82	77.49	2.5	-9.452	242.07	**0.000**
Patagonian Sierra-Finch	11	70-78	74.09	4.0	10	72-82	77.25	3.8	-2.415	18.85	**0.026**
White-throated Treerunner	7	78-82	80.92	1.7	2	80-81	80.75	0.4	0.305	6.90	0.768
Green-backed Firecrown	45	53-65	58.30	4.3	34	56-66	62.72	3.3	-8.441	76.50	**0.000**
Black-chinned Siskin	11	70-72	71.57	1.1	4	71-74	72.87	2.2	-1.473	3.90	0.216
Des Murs' Wiretail	10	50-55	52.60	3.2	2	54-55	54.75	0.6	-3.576	9.44	**0.005**
Southern House Wren	8	50-53	51.75	2.4	2	50-53	51.5	4.1	0.159	1.18	0.896
Austral Thrush	36	126-148	136.19	4.0	13	126-143	137.65	3.4	-0.912	25.09	0.370

With the exception of Austral Thrush, models explaining the body condition of individuals were fitted for each species (Table 14). However, using mixed models did not contribute alone to explaining the variance of the data in the case of Black-chinned Siskin (*Sporagra barbatus*) and Patagonian Sierra-Finch (*Phrygillus patagonicus*). Furthermore, the survey of flying insects was incomplete due to lack of experience and anticipation of operational difficulties, collecting information for only 40% of the sites, for that reasons I decided not include them in the analyses (see Appendix 6 for more details). In general, the selection or inclusion of variables to explain the body condition of individuals was species specific.

As expected, fat and muscle scores predicted body condition for most species. The size of the pectoral muscle was positively correlated with body condition of individuals of Tufted Tit-Tyrant, Thorn-tailed Rayadito, White-crested Elaenia and White-throated Treerunner, with a significant effect for the first three species. Fat scores had a positive and significant effect in the body condition of three species, but in the case of Desmurs' Wiretail fat score correlated negatively with the body condition of individuals. This could possibly happen if gut content was negatively correlated with fat score.

By exploring direct measures of condition, fat and protein reserves (Gosler & Harper 2000), I found significant differences in fat scores between individuals from native and exotic forests (see Appendix 7). Tufted-tit Tyrant and Thorn-tailed Rayadito individuals showed higher fat scores in native forest than those individuals captured in pine plantations. In contrary, Southern House Wren individuals captured in indigenous vegetation had lower fat score values. In terms of protein reserves, only Black-chinned Siskin showed a significant difference between mean values of pectoral muscle score from individuals captured in either habitat type.

For five species of forest bird a time effect was observed at two scales; time of the day and day during the breeding season. The time of day was included in models for Black-chinned Siskin, White-crested Elaenia and Southern House Wren. For these three species, the body condition of individuals increased over the day, or in other words, individuals showed a substantial difference in body condition by comparing the status of individuals captured early in the morning and later in the day. The foraging intake, expressed as gut content, build up through the day, which might explain time variation in the BCI. Likewise, the course of the season had a positive and significant effect on body condition of two forest furnarids; Thorn-tailed Rayadito and White-throated Treerunner.

Table 14. Mixed models explaining the body condition (BCI) of forest bird species.

Species				
Anairetes parulus				
Model: BCI ~ Sex + Age + Muscle + Vol_Understory + (1 | Site)				
Model r^2 (marginal - conditional)		0.373	0.579	
Random effect	Variance	Std.Dev.		
Site	0.035	0.189		
Residual	0.073	0.270		
Fixed effects	estimate	st error	p-value	
Sex (m)	0.294	0.136	**0.049**	*
Sex (ndf)	-0.453	0.277	0.145	-
Age (j)	0.394	0.168	**0.033**	*
Muscle	0.262	0.094	**0.016**	*
Vol_Understory	0.013	0.009	0.176	-

Aphrastura spinicauda				
Model: BCI ~ Sex + Muscle + Season + Cover + (1 | Site)				
Model r^2 (marginal - conditional)		0.334	0.381	
Random effect	Variance	Std.Dev.		
Site	0.019	0.141		
Residual	0.262	0.512		
Fixed effects	estimate	st error	p-value	
Sex (f)	-0.084	0.167	0.617	-
Sex (m)	0.471	0.166	**0.005**	**
Muscle	0.327	0.087	**0.000**	***
Season	0.011	0.002	**0.000**	***
Cover (Pine)	-0.287	0.132	**0.034**	*
Elaenia albiceps				
Model: BCI ~ Time + Fat + Muscle + Cover + (1 | Site)				
Model r^2 (marginal - conditional)		0.155	0.199	
Random effect	Variance	Std.Dev.		
Site	0.064	0.254		
Residual	1.078	1.038		
Fixed effects	estimate	st error	p-value	
Time	1.545	0.574	**0.008**	**
Fat	0.456	0.096	**0.000**	***
Muscle	0.333	0.123	**0.007**	**
Cover (Pine)	-0.331	0.144	**0.022**	*
Phrygillus patagonicus				
Model: BCI ~ Fat + (1 | Site)				
Model r^2 (marginal - conditional)		0.397	0.397	
Random effect	Variance	Std.Dev.		
Site	0.000	0.000		
Residual	0.963	0.981		
Fixed effects	estimate	st error	p-value	
Fat	1.129	0.296	**0.001**	**
Pygarrychas albogularis				
Model: BCI ~ Sex + Fat + Muscle + Season + (1 | Site)				
Model r^2 (marginal - conditional)		0.576	0.712	
Random effect	Variance	Std.Dev.		
Site	0.035	0.188		
Residual	0.074	0.273		
Fixed effects	estimate	st error	p-value	
Sex (m)	0.141	0.270	0.624	-
Sex (ndf)	-0.565	0.235	0.061	.
Fat	-0.234	0.223	0.341	-
Muscle	0.352	0.220	0.171	-
Season	0.014	0.005	**0.027**	*
Sephanoides sephanoides				
Model: BCI ~ Sex + (1 | Site)				
Model r^2 (marginal - conditional)		0.252	0.320	
Random effect	Variance	Std.Dev.		
Site	0.017	0.131		
Residual	0.172	0.414		
Fixed effects	estimate	st error	p-value	
Sex (m)	0.510	0.118	**0.000**	***
Sex (ndf)	-0.054	0.146	0.715	-

Sporagra barbatus				
Model: BCI ~ Time + Sex + Fat + Cover + (1 | Site)				
Model r^2 (marginal - conditional)		0.525	0.525	
Random effect	Variance	Std.Dev.		
Site	0.000	0.000		
Residual	0.690	0.831		
Fixed effects	estimate	st error	p-value	
Time	5.400	2.578	0.070	.
Fat	-1.080	0.661	0.141	-
Muscle	0.449	0.252	0.113	-
Cover (Pine)	0.729	0.578	0.243	-
Sylviorthorhynchos desmursii				
Model: BCI ~ Age + Fat + (1 | Site)				
Model r^2 (marginal - conditional)		0.546	0.564	
Random effect	Variance	Std.Dev.		
Site	0.004	0.067		
Residual	0.114	0.337		
Fixed effects	estimate	st error	p-value	
Age (j)	-0.669	0.221	**0.010**	*
Age (ndf)	-1.066	0.353	**0.011**	*
Fat	-0.844	0.353	**0.034**	*
Troglodytes musculus				
Model: BCI ~ Time + Fat + Cover + Vol_Understory + (1 | Site)				
Model r^2 (marginal - conditional)		0.808	0.975	
Random effect	Variance	Std.Dev.		
Site	0.143	0.378		
Residual	0.021	0.146		
Fixed effects	estimate	st error	p-value	
Time	2.932	0.490	**0.030**	*
Fat	0.807	0.070	**0.020**	*
Cover (Pine)	-2.220	0.563	**0.032**	*
Vol_Understory	-0.110	0.018	**0.017**	*
*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*				

Differences in the BCI of individuals according to their sex were found for five of the nine species of birds with fitted models. In general, males had higher BCI than females or of unsexed individuals. In relation to the age of individuals, only two species included this variable in their best model; Tufted Tit-Tyrant showed a higher BCI in young individuals, and the opposite is observed for Desmurs' Wiretail, where juveniles and unsexed individuals showed a lower BCI than adults.

Analyses showed that environmental variables determined the BCI of three birds species tested. Hence, individuals captured in pine plantations were in poorer body condition than those inhabiting native forest (Fig. 13). The species with this difference were: Thorn-tailed Rayadito, White-crested Elaenia and Southern House Wren. For the latter species, interestingly, the volume of

understory vegetation also affected its BCI negatively. Furthermore, the distance from native forest had a negative effect on the body condition of most species, but for two species body condition improved as they moved away from native forest. However, the effect of the distance from native forest had a statistical significance for only two species; White-crested Elaenia (β= -0.003, p-value = 0.024) and Green-backed Firecrown (β= 0.004, p-value = 0.053).

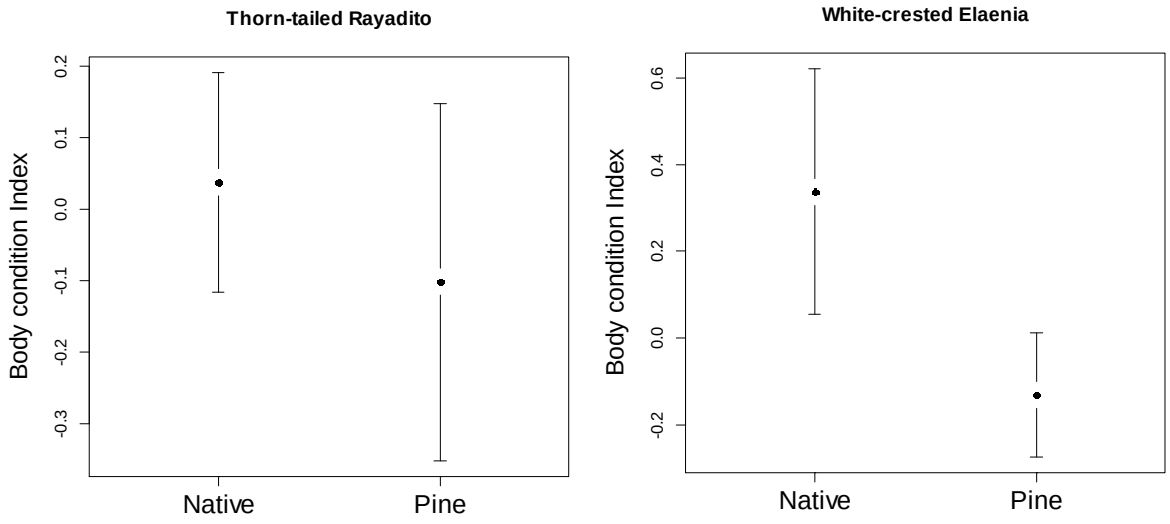

Figure 13. Difference in the body condition of the populations of Thorn-tailed Rayadito and White-crested Elaenia inhabiting native forests and pine plantations before controlling by other effects.

Finally, through ageing White-crested Elaenia individuals as "young adults" and "adults", a difference in the Age structure for populations that inhabit the native forest fragments and pine plantations was found. In native forest, the population of this bird species was constituted evenly with adults and young adults (Fig. 14), but the population in pine plantations had a large proportion of young adults over the other age class (χ^2 = 5.62, df = 1, p-value = 0.017). No differences in age structure among populations were found contrasting the proportions of adults and juveniles in any other species.

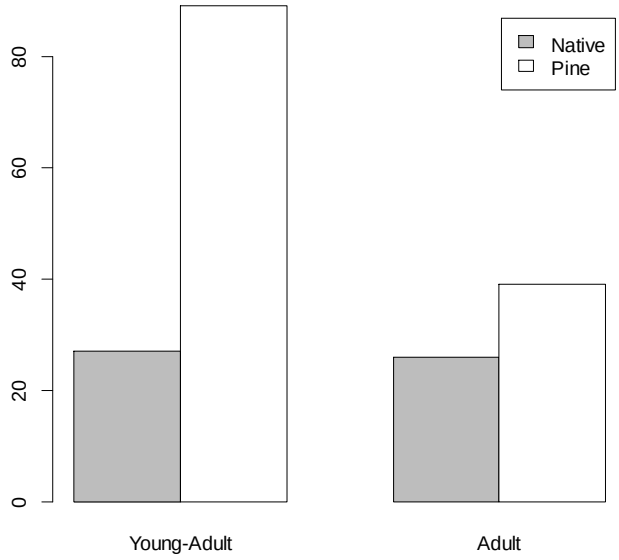

Figure 14. Age structure in native forest and pine plantation populations of White-crested Elaenia ($\chi^2 = 5.62$, df = 1, p-value = 0.017).

4.4. Discussion

Pine plantations may be a poor quality habitat for forest bird species. This could be seen on forest specialists and migrant species. In the case of the forest specialist species, two forest ovenbirds showed that pine plantations have an adverse effect on their populations. The lack of captures in the exotic coniferous plantations could be taken as evidence for the avoidance of this type of vegetation by the White-throated Treerunner. For Thorn-tailed Rayadito, individuals captured in native forest fragments showed a higher BCI than those inhabiting pine plantations. This is also seen for White-crested Elaenia, an austral migrant, that birds holding territories in pine plantations had lower BCI than those in native forests. Furthermore, it was possible to see that the body condition of White-crested Elaenia individuals inhabiting pine plantations worsened as their territories were located farther from native forests. This comes to illustrate McIntyre and Hobbs (1999) idea that forested landscapes dominated by pine plantations are a gradient of alteration

states. And in that way, disturbances in Chilean temperate forest means a diminishing habitat quality for forest specialist species.

I acknowledge that these results are dependent of the starvation-predation trade-off, which is also species dependent. However, as the fluctuations in body mass occur greatly in the fat depots, I tried to reduce this variance by accounting this factor in the models explaining the body condition of individuals. Nonetheless, the findings and conclusions of this research should be taken with caution due to the difficulty to interpret the ecological meaning of lower or higher values of residual mass. Accordingly, the body condition for most species was explained positively by the size of their pectoral muscle or by their fat accumulation. However, for Desmurs' Wiretail higher fat scores were associated with lower BCI, which could be interpreted as a sign of insurance due to lack of predictability on food resources (Gosler 1996). Interestingly, for Desmurs' Wiretail, fat reserves were seen only in individuals captured in pine plantations, this might suggest that for this species food resources are sparsely distributed in this type of habitat.

The difference in body condition between individuals captured in these habitats did not correspond to a density dependent effect, as no differences were found in estimated densities of bird species in either habitat[2]. Local densities seem to be a poor predictor of habitat quality, which could have misled results in previous studies that didn't look at population level, highlighting the importance of assessing population parameters in order to have a thorough understanding of disturbance effects on populations. There is no better example to illustrate that than the social dominance pattern that has been found for White-crested Elaenia, where populations inhabiting pine plantations were made up of a large proportion of younger adults, suggesting that young and less dominant individuals are forced to find territories in coniferous plantations. This despotic distribution of younger or smaller individuals has been described for Great Tits (*Parus major*) (Ulfstrand *et al.* 1981) and Pied Flycatcher (*Ficedula hypoleuca*) (Lundberg *et al.* 1981) in Sweden, where dominant and larger males hold territories in the best quality habitat, deciduous forests,

[2] As point counts were set inside the polygon used for mist-netting, estimated densities in pine stands are biased by their proximity to native fragments (see chapter 3).

forcing young males to use coniferous stands. Nonetheless, in the White-crested Elaenia, individuals inhabiting pine plantations had lower BCI than those holding territories in native fragments which strengthened the selective pressure acting on these populations.

Habitat disturbances that could diminish habitat quality are expected to have cascade effects on various population parameters. According to Van Horne (1983), habitat quality has a clear effect on the survival rate of bird populations. A previous study in this forest community has shown that body condition has a clear effect on the survival rate of some forest passerines inhabiting these forests (Thomson & Estades 2012), with lower survival for individuals showing poor body condition. In this study, it would be expected that forest specialists and migrant species captured in pine plantations would have lower survival rates than those inhabiting native forests. In addition, differences in food availability seem to be the key factor to explain lower BCI in individuals inhabiting the exotic coniferous plantations, which has a strong influence on reproduction and survival rates (Newton 1998). There is enough evidence to consider pine plantations as poor quality habitat for forest bird species, even to think that the pine plantation matrix may well be a sink habitat for some species in a metapopulation context (Hanski & Gilpin 1991; Pulliam 1988).

These results reveal the impact that human-altered environments have on wildlife, in this case, the replacement of natural forest with exotic coniferous plantations. First, the occurrence and use of pine plantations by some species does not necessarily mean that there is preference for that habitat, but, as has been shown, they represent a less suitable habitat that could be used as an alternative for individuals of lower social rank. Resources in pine plantations seem to be inadequate in number and quality to sustain forest bird populations by themselves. Second, the importance of natural forest for native wildlife stands out from these findings. It has been demonstrated not only that the proportion of native vegetation in the landscape has an enormous impact on the forest bird community but also that the distance from native forests has a negative effect on the body condition of a flycatcher species. This corresponds with differences in the abundance and diversity of the arthropod community in these forests (Venegas 2009). Hence, the

contribution of small fragments to the conservation of wildlife in this ecosystem (Grez *et al.* 2005; Simonetti *et al.* 2012) could only be effective when the proportion and distribution of landscape components minimize the negative effect that exotic pine plantations pose for forest bird species.

Chapter 5

Parasites in forest bird populations

5.1. Introduction

In recent decades, the globalization of markets has put increasing pressure on natural resources, leading indirectly to biodiversity loss and habitat degradation (Fahrig 2003). The effect that the decline of habitat quality has on wild populations goes further than just reducing the number of species or individuals, but also altering ecological processes which in turn destabilize the balance of inter-specific relationships in the environment (Ryall & Fahrig 2006), including those between hosts and parasites (Lüdtke *et al.* 2013; Sebaio *et al.* 2010; Walsh *et al.* 1993). Hence, wild populations inhabiting degraded habitats are expected to be under stressful conditions, which could be reflected in the condition or immunity of individuals (Harvell *et al.* 2009; Suorsa *et al.* 2003). Thus, the extent to which human disturbances are affecting wild populations cannot be deduced from just one population parameter (Dhondt 2010; Krams *et al.* 2010), such as density: other condition indicators must be explored too. Fragmentation and habitat loss, therefore, affect wild populations in diverse ways and at different levels, for which a broader assessment therefore needs to be made to understand the impact of habitat alteration over populations.

Selective pressure caused by the decline in habitat quality can be exerted on wild populations by different actors, either biotic or abiotic. Land cover changes may involve negative effects on wild communities (Villard *et al.* 1999), and in the case of bird populations, habitat specialists, migrant species, or those that show a strong philopatry for breeding grounds should be the species most vulnerable to this type of disturbance (Clavel

et al. 2010). Physiological stress in individuals can suppress the immune system, increasing the susceptibility to diseases and parasites (Santiago-Alarcon *et al.* 2012b; Suorsa *et al.* 2003). However, habitat disturbances and alteration of ecological dynamics in the community could also affect parasites or their vectors, regardless of the condition of their hosts (Santiago-Alarcon *et al.* 2012a). The replacement of native forest with exotic coniferous plantations may strongly alter the environmental conditions for both bird populations and their parasites; from microclimatic conditions to availability and diversity of resources (Lüdtke *et al.* 2013). Therefore, it is clear that habitat alteration, such as afforestation, may alter host-parasite relationship either by suppressing the immune system of the host or by favouring the spread of parasites or their vectors.

Even though there has always been interest in understanding the effect of parasitism in birds, in recent decades the number of studies of parasitism has risen due to the increasing incidence of outbreaks of emerging infectious diseases (EID) (Garamszegi 2011; To *et al.* 2014). Parasites are animals or plants that live at the expense of another species, the host, deriving food or protection from them (Arnall & Keymer 1975). Most studies of parasitism in birds are based specifically on protozoa (blood parasites) and arthropods (ecto-parasites). The negative effects that parasites may have on their hosts are many, ranging from reduced reproductive success (Galvan & Sanz 2006; Møller 2010), plumage degradation (Harper 1999; Thompson *et al.* 1997), reduced body condition (Bueter 2005; Harper 1999; Møller 1991), skin lesions (Arnall & Keymer 1975; Philips 1993), immuno-suppression and even death (Santiago-Alarcon *et al.* 2012b). Although Price (1980) points out that by definition all parasites are harmful, this generalization might not be entirely correct; the real effect of the interaction of ecto-parasites with their hosts still holds an unresolved controversy as some studies suggest a positive effect of mite burden on

individual fitness (Blanco *et al.* 1997; Blanco *et al.* 2001; Rozsa 1997). Considering that habitat disturbance can trigger outbreaks of infectious diseases and that there are still unanswered questions about the effects of some parasites on their hosts, it is clear that more studies are needed to understand the ecology of host-parasite interactions in relation to habitat quality.

In order to assess the quality of pine plantations for species members of the temperate forest bird community in South-Central Chile, the health condition of individuals captured in native forest fragments against those captured in exotic coniferous plantations will be compared. This will be done by scoring ecto-parasite burden in flight feathers of every ringed individual. However, as the mite-host interaction is not well understood yet, the prevalence of blood parasites was also assessed (Galvan & Sanz 2006). Nonetheless, it is recognized that the prevalence of haemasporidians as a habitat quality indicator could lead to misleading conclusions since habitat disturbances could favour or eradicate parasites or their vectors (Chasar *et al.* 2009). With this in mind and under the hypothesis that pine plantations are poorer quality habitat for forest bird species, a higher burden of ecto-parasites and prevalence of blood-parasites in individuals inhabiting exotic coniferous forests is expected there.

5.2. Methods

The study was carried on the Coastal range forests of South-Central Chile, in what is called the "Maulino forests". This temperate deciduous forest extends 200 km over the Coastal range in Chile, from the northern limit of the administrative region of "del Maule" (34°45' S) to the Itata river (35°25' S) in the "del Bio-Bio" region. These forests have gone through

a history of alteration that started 300 years ago, and nowadays have been reduced to small fragments embedded in a matrix of exotic pine plantations.

Sites. In these forested landscapes ten sites were selected to assess the health condition of populations inhabiting either native or exotic forests. The selection of sites considered fragments of native forest of at least 3 ha surrounded by mature pine stands soon to be harvested. In addition, only sites located on the western slope of the Coastal range were considered. This geographical factor has great importance for the environment, as the oceanic influence models the entire community through regulating climate conditions; wetter conditions, as mist and more rainfall, and less extreme temperatures.

Mist-netting. During the breeding season of 2012-2013, birds were mist-netted in both habitats, the native forest fragments and within surrounding pine plantations. The fieldwork began in October 2012 and lasted until mid February 2013. For this, 34 mist nets of 6, 9 and 12 m were used, totalling 261 m in length. The nets in pine plantations were located at different distances from the border of the pine stand with the fragment of native vegetation (Fig. 15), recording in Gps their location to estimate their distance from the edge of the fragment. In addition, each net was active during 9 hours every day, except for sporadic rains, representing a total effort of 36,199 hr*m in native forest and 45,072 hr*m in pine plantations. In order to avoid a time effect on data, and to reduce the possibility of predation of birds in the nets, capture locations were moved every two days. Sites were visited twice during the breeding season. Finally, each mist-net point was characterized in terms of vegetation composition and structure.

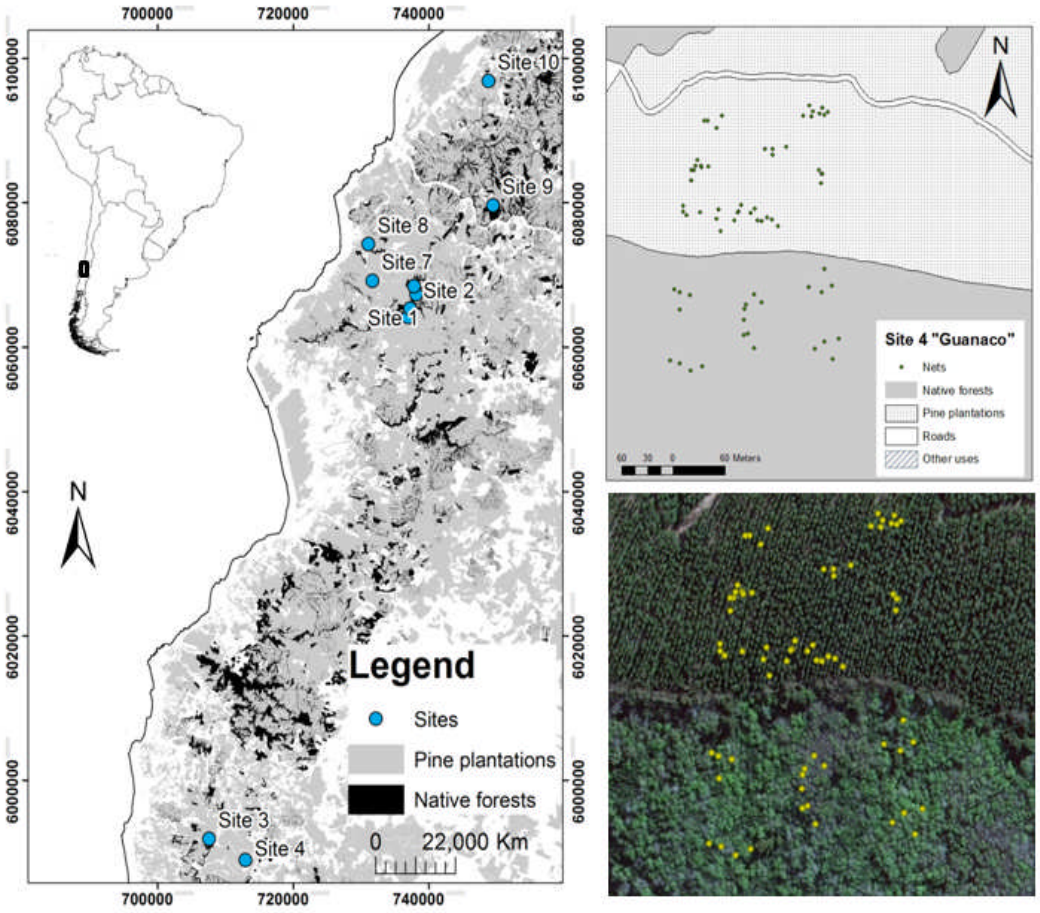

Figure 15. Geographical reference of the study area (Left). Illustrations of the disposition of mist-nets in a surveyed fragment-pine plantation situation, Site 4 "Guanaco": Map of the sites from geographical layers (Top-right) and satellite image depicting the same site, yellow-dots show mist-net positions (Bottom-right).

Ringing and measures. All captured birds were ringed using metal rings provided by SAG (Servicio Agricola y Ganadero, Gobierno de Chile). The following parameters were measured by a single ringer (RT): maximum wing length were measured using a 1 mm precision stopped rule; maximum tarsus length, depth and length of the bill to 0.1 mm were measured using a vernier calliper; and with a 0.1 g precision digital balance the weight was estimated. At the same time, scores for pectoral muscle size (Gosler 2004) and amount of subcutaneous fat accumulated in the tracheal pit (Gosler 1996) were given in ranges of 0-4 and 0-5 respectively. Plumage patterns that differentiate males and females were only used for sexing part of the species in this bird community as most of them have

not apparent sexual dimorphism. Therefore, sexing was based on reproductive traits such as cloacal protuberance and presence of brood patch when it was appropriated. However, when no certainty existed regarding the sex of individuals, they were categorized as "unsexed". Similarly, the knowledge about plumage pattern for ageing birds has not been developed for most Chilean bird species. Beyond distinguishing juveniles from adults, it is not possible to differentiate the age of adult individuals with certainty (Pyle *et al.* 2015). However, for one species, White-crested Elaenia (*Elaenia albiceps*), I used the colour of the roof of the mouth as ageing criterion, discriminating two adult age class (Thomson *et al*., submitted).

Parasite sampling. The number of mites seen on the primary feathers of the right wing was recorded (Behnke *et al.* 1999). A 5-point score (0-4) was assigned to mite densities as follows: 0 = no feather mites; 1 = 1-10; 2 = 11-100; 3 = 101-1000 and 4 = Over 1000. Blood samples were obtained by brachial venipuncture using disposable syringe needles. Blood smears were made, air dried and fixed with 100% methanol (Owen 2011). All blood smears were stored in a slide box for later analysis. Once in the laboratory, blood smears were stained with 3% GIEMSA solution in buffered water diluted 1:10. To inspect for blood parasites, all blood smears were scanned at 400X, counting the number of infected cells on 4000 blood cells in every blood smear, obtaining the percentage of infected cells or morbidity, which is a measure of the level of infection for every sampled individual.

Statistical analysis

Statistical models were built to explain the presence and parasite load in bird populations inhabiting this fragmented forest system. For this, generalized linear mixed models were used because of the hierarchical structure of data, where catches were made in situations fragment-pine plantation nested in several sites. Analyses were performed for each species

independently, and when the data distribution allowed quantitative analyses of parasite load were made. However, by transforming quantitative into qualitative data, models explaining the presence of parasites were fitted for each species, analysing the error through a binomial distribution. Nonetheless, due the small sample size, by either low number of captures or few infected individuals, analyses were performed for only seven species.

In model building the following descriptive variables of the capture location were considered; type of vegetation cover, distance to nearest fragment of native vegetation, and volume of vegetation in the understory. Information on each individual in terms of age, sex and body condition was also included (see chapter 4), as was the day within the breeding season when the catch took place. The search and selection for the model that best explains the abundance and presence of parasites began with a full model that included the aforementioned variables as fixed effects and the identification of the sites as a random effect. The selection of the best model was based on Akaike information criterion values (AIC) and the coefficients of determination for each model (Barton 2014). For all statistical analyses the software R was used (R Development Core Team 2012), and a minimum statistical power $\alpha = 0.05$ was considered acceptable. All mixed models were run on Lmer.test package (Kuznetsova *et al.* 2013), except for data with a negative binomial distribution where the glmmADMB package (Skaug *et al.* 2011) was used instead.

5.3. Results

Mites

In total, 710 birds belonging to 20 species were captured and inspected for mites. All these species carried such parasites, except for the single individuals captured of Rufous-legged Owl (*Strix rufipes*) and Bicolored Hawk (*Accipiter bicolor*).

Models explaining the presence or parasite burden were fitted for only seven species due to characteristics of the data; mainly due to small number of infested individuals for some bird species. In terms of the variables included, these models showed that the host-parasite relationship was species specific. In general, the most common variable explaining the burden or presence of parasites was the day of the season when the individual was captured (Season) (Table 15). Parasite burden decreased along with the season, as it happened for the Patagonian Sierra-Finch, Austral Thrush and marginally non-significant for Desmurs' Wiretail.

The individuals' features of three forest species explained the prevalence of parasites. Parasite load in Desmurs' Wiretail was predicted by the body condition of individuals, which *post hoc* analyses showed a positive correlation between Fat and mite burden (r=0.23; df=15; p-value=0.36), but negative for Mucle score (r=-0.11; df=15; p-value=0.64), in both cases correlations were non-significant. Sex categories had a significant effect on mite burden for the White-throated Treerunner and marginally insignificant on the presence of parasites for White-crested Elaenia. Also for this last species, differences were found in mite infestation according to the age of individuals. Finally, the moulting process plays an important role in variation of mite load; from all birds moulting, only 10 individuals showed the presence of mites in flying feathers.

Table 15. Models explaining mite burden or its prevalence in forest bird species.

Species				
Tufted-tit Tyrant (*Anairetes parulus*)				
Model: Mites prevalence ~ Season + Distance to NF + Vol_Understory + (1 | Site)				
Family: binomial (logit)				
Model r^2 (marginal - conditional)		0.533	0.533	
Random effect		Variance	Std.Dev.	
Site		0.000	0.000	
Residual				
	estimate	st error	p-value	
Season	0.026	0.019	0.182	
Distance to NF	0.016	0.008	0.068	*
Vol_Understory	0.157	0.088	0.075	*
Thorn-tailed Rayadito (*Aphrastura spinicauda*)				
Model: Mites prevalence ~ Cover + Vol_Understory + (1 | Site)				
Family: binomial (logit)				
Model r^2 (marginal - conditional)		0.115	0.381	
Random effect		Variance	Std.Dev.	
Site		1.069	1.034	
	estimate	st error	p-value	
Cover (Pine)	1.047	0.644	0.104	
Vol_Understory	-0.050	0.026	0.052	*
White-crested Elaenia (*Elaenia albiceps*)				
Model: Mites ~ BCI + Sex +Cover + Age + Dist to NF * Vol_Understory + (1 | Site)				
Family: binomial (logit)				
Model r^2 (marginal - conditional)		0.092	0.185	
Random effect		Variance	Std.Dev.	
Site		0.380	0.617	
	estimate	st error	p-value	
Age (young adults)	-0.056	0.317	0.858	
Age (older adults)	**0.891**	**0.385**	**0.020**	**
Sex (males)	0.361	0.288	0.211	
Sex (ndf)	0.843	0.494	0.088	*
BCI	0.082	0.118	0.485	
Cover (Pine)	-0.387	0.511	0.447	
Vol_Understory	0.010	0.017	0.570	
Dist to NF	-0.015	0.010	0.133	
Dist to NF : Vol_Understory	0.0002	0.0001	0.148	
Patagonian Sierra-Finch (*Phrygillus patagonicus*)				
Model: Mites ~ Season + Cover + (1 | Site)				
Family: binomial (logit)				
Model r^2 (marginal - conditional)		0.222	0.271	
Random effect		Variance	Std.Dev.	
Site		-	-	
	estimate	st error	p-value	
Season	**-0.016**	**0.006**	**0.010**	**
Cover (Pine)	**1.218**	**0.020**	**0.000**	***

White-throated Treerunner (*Pygarrychas albogularis*)				
Model: Mites ~ Vol_Understory + Sex +Cover + (1 | Site)				
Family: poisson (log)				
Model r^2 (marginal - conditional)		0.454	0.454	
Random effect		Variance	Std.Dev.	
Site		0.000	0.000	
	estimate	st error	p-value	
Vol_Understory	-0.014	0.011	0.196	
Sex (m)	-0.170	0.496	0.730	
Sex (ndf)	**-1.104**	**0.496**	**0.026**	**
Cover (Pine)	1.438	0.780	0.065	*
Desmurs' Wiretail (*Sylviorthorhynchos desmursii*)				
Model: Mites ~ Season + BCI + Cover + (1 | Site)				
Family: poisson (log)				
Model r^2 (marginal - conditional)		-	0.526	
Random effect		Variance	Std.Dev.	
Site		0.000	0.000	
	estimate	st error	p-value	
Season	-0.024	0.013	0.064	*
BCI	**0.950**	**0.459**	**0.038**	**
Cover (Pine)	0.004	0.004	0.316	
Austral Thrush (*Turdus falcklandii*)				
Model: Mites prevalence ~ Season + BCI + Sex + Dist. to NF + (1 | Site)				
Family: binomial (logit)				
Model r^2 (marginal - conditional)		0.857	0.864	
Random effect		Variance	Std.Dev.	
Site		0.157	0.397	
	estimate	st error	p-value	
Season	**-0.044**	**0.021**	**0.037**	**
BCI	-0.001	0.101	0.993	
Sex (males)	0.630	1.357	0.642	
Sex (ndf)	21.730	2048	0.991	
Distance to NF	-0.013	0.015	0.385	
*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; ' ' 1*				

In terms of habitat variables, habitat type predicted the presence of mites in Patagonian Sierra-Finch, and marginally insignificant, in the forest furnarids White-throated Treerunner (Fig. 16) and Thorn-tailed Rayadito. In all these cases, the parasite load, or presence of parasites, was greater in pine plantations than in fragments of native forest. Furthermore, although non-significant, the distance to the fragment of native forest had a positive effect on the presence of mites in Tufted Tit-Tyrant.

Figure 16. Mites in the flying feathers of one individual of White-throated Treerunner (*Pygarrychas albogularis*).

Blood parasites

Blood samples were taken from 186 individuals belonging to 10 bird species (see Appendix 8). Only four species showed prevalence of haemosporidians (Fig. 17), these were the tyrant White-crested Elaenia (*Elaenia albiceps*), the Patagonian Sierra-Finch (*Phrygillus patagonicus*), the Austral Thrush (*Turdus flacklandii*) and the Southern House Wren (*Troglodytes musculus*). No juveniles from White-crested Elaenia appeared to be infected with blood parasites. Haemo-parasites identified through visual inspection of blood smears were *Haemoproteus sp*. and *Plasmodium sp*. However the latter was detected in only one female individual of White-crested Eleania, which was also infected with *Haemoproteus sp*. Due to the small sample size for Patagonian Sierra-Finch, Southern House Wren and Austral Thrush, models explaining the prevalence and morbidity of blood parasites were fitted only for White-crested Elaenia (Table 16).

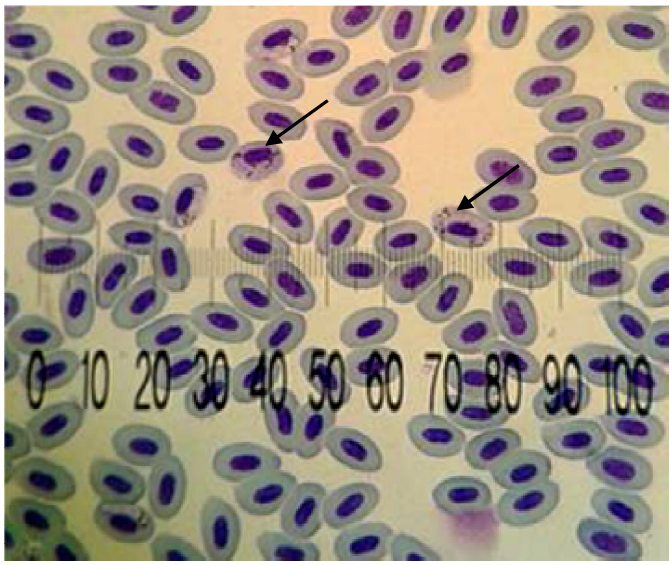

Figure 17. Haemosporidians in blood cells of White-crested Elaenia (*Elaenia albiceps*)

According to models explaining prevalence and morbidity of blood parasites in White-crested Elaenia, there is a clear difference between age groups for these parameters. Older adults showed a higher prevalence and morbidity than young adults did. However, this was only statistically significant in the morbidity model. Infected individuals with better body condition showed lower morbidity of blood parasites, and as the body condition of individuals improves along with the season so did the health of infected individuals. There was no difference in the prevalence of haemosporidians among sexes, but males had a higher morbidity than females. Interestingly, the mite burden correlated positively with the prevalence and morbidity of blood parasites.

Table 16. Models explaining the prevalence and morbidity of blood parasites in White-crested Elaenia.

Species				
White-crested Elaenia (*Elaenia albiceps*)				
Model: Prevalence ~ Mites + Age + Vol_Understory + (1 | Site)				
Family: binomial				
Model r^2 (marginal - conditional)		0.275	0.325	
Random effect		Variance	Std.Dev.	
	Site	0.243	0.493	
	estimate	st error	p-value	
Age (young adults)	-0.776	0.663	0.241	
Age (older adults)	0.559	0.640	0.382	
Mites	1.126	0.631	0.074	
Vol_Understory	**-0.056**	**0.023**	**0.014**	
White-crested Elaenia (*Elaenia albiceps*)				
Model: Morbidity ~ Season * BCI + Age + Sex + Dist. to NF * Vol_Understory + Mites + (1 | Site)				
Family: Negative binomial				
Model r^2 (marginal - conditional)		-	0.316	
Random effect		Variance	Std.Dev.	
	Site	21.52	4.63	
	estimate	st error	p-value	
Season	**-0.010**	**0.005**	**0.045**	*
BCI	**-3.770**	**0.609**	**0.000**	***
Sex (males)	**0.176**	**0.072**	**0.014**	*
Age (young adults)	**-0.447**	**0.121**	**0.0002**	***
Age (older adults)	**0.353**	**0.122**	**0.003**	**
Mites	**1.664**	**0.093**	**0.000**	***
Distance to NF	**0.066**	**0.003**	**0.000**	***
Vol_Understory	0.0005	0.004	0.900	-
Season : BCI	**0.027**	**0.005**	**0.000**	***
Dist. to NF : Vol_Understory	**-0.001**	**0.0001**	**0.000**	***
*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; ' ' 1*				

Variables related to habitat features appeared in both models, and they may have an indirect effect on the prevalence and morbidity of blood parasites. Therefore, the prevalence of blood parasites in White-crested Elaenia was higher in sites with less understory vegetation. In spite of the fact that this variable lose power to explain morbidity by itself, its interaction with the variable "distance to native forest fragment" revealed its effect in the habitat quality for pine plantations; while the distance to the nearest native fragment had a positive effect on the morbidity of blood parasites, its effect was inverted when the pine plantations hold an important understory under their canopy.

5.4 Discussion

This study revealed how the substitution of natural habitat with exotic pine plantations affects the health of forest bird populations, demonstrating that these plantations are low quality habitat for forest bird species. Parasite loads of birds are sign of poor health state and for most vulnerable species this was explained by habitat variables. Forest specialists and migrant species showed a poor health condition for individuals captured in pine plantations. Mite burden was higher in pine plantations for White-throated Treerunner and Thorn-tailed Rayadito, which is closely related to the negative habitat effect found for the body condition of these forest specialists, even though models explaining mite burden didn't include body condition as an explanatory variable. This parameter, body condition, was only a significant predictor of the parasite burden of Desmurs' Wiretail, although it showed a positive effect. This seems confusing but in line with results of the previous chapter; for this small insectivorous species a negative relationship was found between fat accumulation with the body condition, where fat reserves are explained as insurance for individuals in poor quality habitat due to lower predictability of food resources (Gosler 1996), which might be acting on the weight, and in turn, in the estimated body condition of individuals. Similarly, a gradient in the body condition already found for White-crested Elaenia individuals holding territories in these exotic plantations (see Chapter 4) was also seen in their blood parasite morbidity, which increases with the distance from native forest fragment. Interestingly, the understory vegetation improves the habitat quality of pine plantations for these forest species, as all the mentioned parasite parameters were softened by the presence and importance of the native undergrowth. Thus, there is a clear effect of habitat quality on the health of forest bird populations.

There is an important effect of season on the health condition of forest bird populations. Results showed that parasite burden and blood parasite infection decreased through the breeding season. This could be explained by a depressed immune system during the breeding process of some bird species, which recover after rearing their brood. The impact that reproductive effort could have on the physiological condition may allow an increase in feather mites (Gustafsson *et al.* 1994). In the case of migratory species, above the reproductive cost, long-distance migration added a huge energetic cost for migrants (Newton 2010b), which must have consequences for their physiological condition. However, another explanation seems also to be plausible for ecto-parasites: A positive correlation between abundance of feather mites and the size of the uropygial gland has been reported (Møller 2010). This gland shows a seasonal size variation, growing larger after the mating season to regain its regular size by the end of the breeding season (Pap *et al.* 2010), mite burden might therefore vary along with the seasonal size variation of the uropygial gland. Although, Pap et al. (2010) found no significant correlation between the uropygial gland size and the parasite load for House Sparrows (*Passer domesticus*), this proposed relationship may apply for some temperate South American host-mites systems: a detailed study is clearly needed. In conclusion, seasonal variation in health condition of forest bird populations may respond to physiological changes that occurred in individuals during the breeding season.

Differences in health status, given by the age and sex of the individuals, also respond to changes in their physiological condition. First, the lower mite burden in unsexed White-throated Treerunners could be explained by the fact that these were non-breeding individuals which were not subjected to the energetic cost that reproduction implies. The absence of features for ageing this species, apart from juveniles versus full-grown

individuals, prevented me from subdividing this group of individuals by age classes that would reveal a possible social dominance acting on these populations. A determining factor in the number of non-breeder individuals would be the availability of cavities in these environments, which would limit the reproduction of this and other secondary cavity nesters species (Cornelius *et al.* 2008; Estades & Temple 1999; Tomasevic & Estades 2006). Second, since it was possible to age White-crested Elaenia, it is highly probable that those individuals that were not sexed due to lack of reproductive traits (after controlling by age), were either from a lower social rank or were individuals in such poor physiological condition that they couldn't invest in reproduction. A greater burden of ecto-parasites was observed in them. In relation to the age of individuals, as mentioned above, White-crested Elaenia was the only species where adult birds were aged with a criterion developed in this study (Thomson *et al*., submitted). This age classification showed that older individuals had both a higher burden of mites and also, for individuals infected with blood parasites, a higher morbidity. Blood parasites can cause chronic infections that relapse during stressful situations, such as the breeding season (Bennett *et al.* 1995; Merino *et al.* 2000). Therefore, the physiological stress involved in reproduction might trigger an increase in morbidity for breeding birds, in this case older adults. Nevertheless, it is also necessary to consider in this analysis the greater immune-competence that juvenile birds have (Møller & Erritzøe 1998), which could influence the results obtained. Differences in demographic structure of populations could therefore mask the effect of habitat quality; in this study it was observed that populations of White-crested Elaenia inhabiting pine plantations had a larger proportion of adult individuals from the youngest class (see Chapter 4). Therefore, no statistically significant differences appear when their health condition is compared against populations inhabiting the native forest fragments without controlling by age classes. So, behind the inclusion of age and sex in models

explaining parasite infection and infestation, there must be physiological factors playing a chief role determining bird health status and susceptibility to contagion.

Habitat disturbances may alter the dynamics of vector populations, allowing the outbreaks of diseases in the environment, which raises the question of whether pine plantations harbour larger vector populations indeed or whether the transmission actually happens in these forests? Working with the Siberian Tit (*Poecile cinctus*) in Finland, Krams et al. (2010) found no effect of the type and intensity of the forest management on the abundance of blood parasites, but instead it was explained by the distance of the nearest stream where the vectors were abundant. In Chile, protective indications for basin and creeks from the Chilean Forest Service have modelled the forest landscapes in the Coastal range of Central Chile. This regulation has resulted in many of the creeks and streams being covered by native forest, intermingled with the surrounding pine plantations. So, one would expect a higher morbidity of blood parasites in birds captured in native forests. However, the opposite is observed, with higher morbidity in individuals holding territories away from native fragments, which would suggest either the absence of the vector in the environment and/or a difference in habitat quality. Considering that White-crested Elaenia is a migratory species, spending the winter in tropical areas, I propose that the main parasite transmission occurs in the winter grounds, where climatic conditions are more suitable for vector populations. Moreover, no juvenile was found to be infected by haemosporidians, although the sample size was negligible. A contagion in tropical areas is the most plausible explanation regarding the lower, or even absent, prevalence of blood parasites in resident species.

This research has shown that parasites could be used as a habitat quality indicator for this bird community. This study has also exposed the fact that mite burden is a consequence

rather than a cause of health condition, which in turn is concatenated with environmental degradation. I acknowledge that more detailed studies are needed to sustain and defend some arguments used in the discussion. However, all of them were used in a conservative way. I believe that this is the first study assessing the impact, in terms of habitat quality through parasite burden, of the replacement of native forest with exotic pine plantations in temperate areas. This work has important implications for the conservation of temperate forest bird communities and their habitats, illustrating through health parameters the effect of the substitution of natural habitats has on wildlife.

Chapter 6

Pine plantations as a breeding habitat for forest bird species

6.1 Introduction

The replacement of natural forests with plantations of fast-growing species has affected much of the world's forest formations, from the tropics to high latitudes (Myers *et al.* 2000). Temperate forests have been one of the biomes most affected by human activities since they are near to densely populated areas that have a long history of resource exploitation (Ovington 1983). In the reforestation with fast-growing species, there is a preference for coniferous species because, apart from their virtue for the industry, many of them are more resistant to adverse environmental conditions than are hardwoods (Clapp 2001). The big difference between deciduous and coniferous forests may have a negative effect on wildlife (Pedersen *et al.* 2010) and ecosystem services provided by forests (Núñez *et al.* 2006). Although, many studies have reported the use of exotic plantations by native wildlife (Brockerhoff *et al.* 2008; Fischer & B Lindenmayer 2006; Saavedra & Simonetti 2005), the real value or impact of pine plantations for the conservation of wildlife is still controversial (Clapp 2001; Kanowski *et al.* 2005). The occupation of pine plantations by forest wildlife has been explained mainly by the similarity in the habitat structure that exists between native forests and mature pine plantations (Renjifo 2001); i.e. the forest structure doesn't deter the movement of forest wildlife. However, there is a clear loss of forest-dependent species and a decrease in the densities of the remaining forest species (Estades 1994). This could be explained by the poorer quality of habitat represented by pine plantations for forest avifauna. There is enough evidence to suggest that, even in their native lands, coniferous forests represent poor habitat for forest passerines when compared to broadleaf forests (Lundberg *et al.* 1981; Riddington & Gosler 1995).

The fragmentation of native forests in a matrix of pine plantation may limit the breeding success of forest bird populations. Different factors could have an effect on the reproductive success of populations in modified habitats. The most acknowledged factors are population density,

availability of nutrition resources, breeding timing, nest sites, predation and parasitism, among others. Accordingly, higher population densities could diminish the quality of native forest fragments as breeding habitat for forest bird populations. In small native forest patches, a density-dependent relationship might regulate bird populations, impairing the fitness of those individuals that inhabit them (Newton 1998). The individuals' dispersion in this type of environment would inevitably tend to be directed toward neighbouring pine plantations, which may be a preferable option as the likelihood of finding a breeding territory within the populated fragment might be lower. However, forest breeding birds would have to deal with other limiting factors. First, the availability of cavities is a limiting resource for secondary cavity nesters in temperate forests degraded by logging and fragmentation (Cornelius *et al.* 2008), yet this is more pronounced in pine plantations (Maicas Catalan & Fernández Haeger 1996). Second, food and nutritional resources is maybe the most important factor controlling reproduction in birds (Martin 1987). The food abundance, timing and its distribution affect not only the development and survival of nestlings, but also the survival and body condition of adult birds (Tinbergen & Dietz 1994). Therefore, the fragmentation of native forests in a matrix of pine plantation might have a negative impact on the breeding success of forest bird populations.

In central Chile at least nine species of forest passerines have been reported nesting in pine plantations (Escobar 2004; Estades 1999), but most of the observed nests in pine plantations were located in the native undergrowth (Estades & Temple 1999). There are few studies of the effect of fragmentation of Chilean temperate forests in a matrix of pine plantation on the reproduction of forest birds; they suggest that only the scarcity of cavities limits the use of pine plantations during the breeding season (Quilodrán *et al.* 2014). This study aims to determine the fragmentation effect on reproductive traits of forest passerines in South-Central Chile. Under the hypothesis that both the replacement of native forest with pine plantations, and its configuration at different scales, may have a negative effect on the breeding performance of bird populations, I expect to find higher breeding success in nests located in sites with higher a proportion of native forest. Moreover, as it has suggested that the presence or abundance of other cavity nesters (including conspecific) could

deter the use of available territories (Quilodran *et al*. 2014), I tested the interaction between the proportion of native forest and the abundance of cavity nester species.

6.2 Methods

The study was carried out on the bird community of the temperate forests of the Coastal range of South-Central Chile. The climate of this region is temperate with warm and dry summers (Peel *et al.* 2007), and an oceanic influence. This study is focused in the "Roble-Hualo" forest type distributed over the Coastal range, known as the Maulino forest. These forests have gone through a history of alteration, and nowadays they have been reduced to small fragments embedded in a matrix of exotic pine plantations.

Sites. In these forests, I selected 29 landscape units of 21.09 ± 16.5 Ha. The selection process considered continuous forest habitat as a main constraint, selecting only landscape units with at least 85% of forest cover. Another important characteristic considered in the site selection was to cover the whole range of replacement of native forest in the landscape; from 0 to 100%. All sites were located in the western slope of the Coastal range in the commune of Constitución (Fig 18).

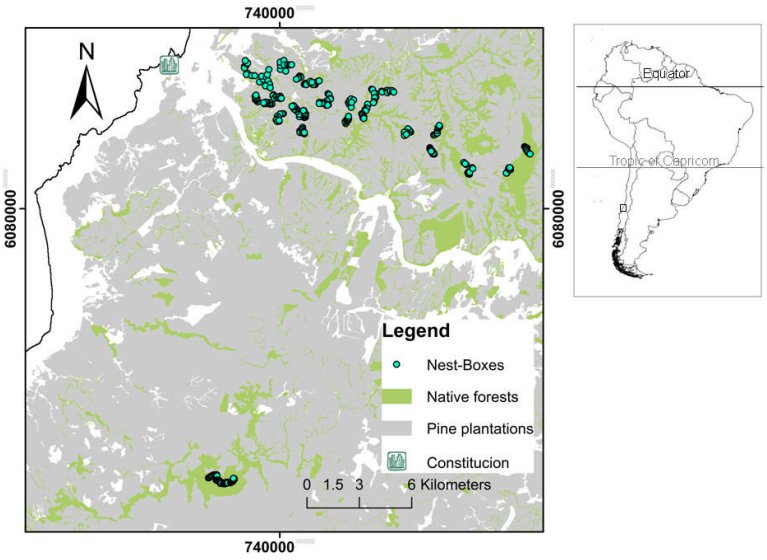

Figure 18. Map of the study area, showing the location of nest-boxes in the commune of Constitución (Chile).

In order to assess the breeding of forest bird species, I considered two separate surveys according to the bird species in the community. I planned the study focused on migrant and forest specialist, which are the most vulnerable species. First, cavity availability is a limiting resource in fragmented and managed forest (Cornelius *et al.* 2008; Maicas Catalan & Fernández Haeger 1996), and this is especially true for two forest specialist species (Tomasevic & Estades 2006). Second, there is only one strict migrant species breeding in these forests, White-crested Elaenia (*Elaenia albicpes*), which is an open nester that breeds late in the season, between November and February (Altamirano *et al.* 2012). Therefore, I intended firstly to run a survey for secondary cavity nester species using nest boxes, and later in the season, to look for nests of White-crested Elaenia by using radio transmitters, awarded by IdeaWild.org, attached to females with brood patches. However, in the early days of 2014 a forest wildfire was declared in the vicinity of Constitución (mainly surface fire, not crown fire). Aided by high temperatures and strong prevailing winds in the area, the fire affected a large area of forest and residential areas taking about a week to be controlled. Unfortunately, a significant number of the sites included in this research were hit by the fire, eliminating virtually all the understory vegetation. This unforeseen situation changed site conditions dramatically and stopped the search for open nests that I had recently started (Fig. 19).

Nest-boxes. I used nest-boxes made of medium-density fibreboard (MDF) 5.5 mm thick, and their dimensions were 10 X 12 X 20 cm with a circular 3-cm-diameter entrance. A mobile top allow access to the nest. Nest-boxes were attached to single trees at a height of 2-2.5 m and entrance facing northeast.

Preliminary survey. In the experimental field station "Dr Justo Pastor Leon" from the Universidad de Chile, located in the commune of Constitución, I erected 50 nest-boxes in pine plantation stands and another 50 in native fragments during the breeding season 2012-2013. Nest-boxes were inspected every three weeks for signs of occupancy. The aim of this preliminary survey was to get an assessment of the occupancy rate that this type of nest-box would have from the secondary

cavity nester species. An occupancy rate of 32% in both types of habitat was found, with no significant difference in the occupancy rate between species in the two habitat types.

Figure 19. Photographs taken during the breeding survey 2013-2014. A) Adult female of White-crested Elaenia (*Elaenia albiceps*) with a radio tag attached to her rump. B) Remains of a nest-box burnt during the wildfire. C) Fire-fighters of the national forest service (CONAF) in action.

Nest monitoring. At the beginning of the breeding season, September 2013, ten nest-boxes were erected in every site. Nest-boxes were placed proportionally in pine stands and native fragments, and never closer than 50 m from each other. I considered that erecting a low number of nest-boxes

per site would be more appropriate as the aim of the study is to assess the habitat quality for breeding birds; adding nest-boxes could alter the breeding densities in the study sites (Mänd *et al.* 2009; Mänd *et al.* 2005). Nest-boxes were visited every five days, as this was the time needed to complete a 290 nest-box round in these landscapes. In every visit I recorded the nest stage, number of eggs and the species using the nest-boxes. Eggs were weighed and measured before the incubation started. Egg length and breadth were measured to the nearest 0.1 mm with a vernier caliper, and the egg mass was recorded to the nearest 0.1 g on a portable digital balance (Myco™, model MZ-100). Egg volume was estimated using Hoyt's (1979) formula: volume = 0.51 X (length X breadth^2). After hatching, in every visit I weighed chicks with a portable digital balance to the nearest 0.1 g, and the parents visiting the nest were recorded with digital video cameras (Samsung F30 SD Flash Camcorder). When the pin feathers in the wing of the pulli were fully formed, and their tips were sprouting (Redfern & Clark 2001), chicks were ringed with metal leg bands provided by the ringing authority in Chile (Servicio Agricola y Ganadero). The tarsi of ringed chicks were measured to the nearest 0.1 mm with a vernier calliper, and their weights were recorded with a portable digital balance to the nearest 0.1 g. The survey was interrupted and ended by a wildfire that affected the area.

Avian surveys. While visiting the nest-box sites, between October and November, I conducted 5 min bird counts using the variable circular-plot method with a 50 m maximum observation radius. All counts were carried out within the first 5 hours after dawn by a single trained observer (RT). No observations were conducted on rainy or misty days. All birds seen or heard within the maximum radius were recorded, and with the exception of swallows and hummingbirds, birds flying over a plot were not considered.

Habitat and land use description. I characterized the vegetation structure around every nest-box. I estimated tree height, the number of natural cavities and I measured the diameter at breast height (dbh) of the nearest five trees to the observer point. I followed the methodology used by Estades & Temple (1999) in these forests to describe the vegetation's vertical structure; the total foliage

volume was estimated by referring to five vertical strata of the vegetation. To estimate the insect abundance, three 300 cm^2 yellow sticky traps were left in every site and the number of insects was counted after a week. Using ArcMap 10 (ESRI 2011) over Arauco's forest cover database and the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh 2010) I prepared geographical information layers to assess plot and landscape unit attributes. The proportion of every land use in landscape units and in the 50 m radius buffer area around each nest-box was obtained using that GIS software (Table 17).

Data analysis. The information collected during the breeding survey was used to fit models explaining the occupancy of nest-boxes, breeding success, weight of ringed chicks and frequency of parental visits to nests for each species. Due to the hierarchical structure of the data, with nest-boxes nested in sites, all these response variables were modelled in a mixed model framework, with landscape units as random effects. The response variable used to model the frequency of parental visits to nests was the number of visits per hour. Because many videos were recorded for every nest, and the individual weights of fledglings from a clutch are not independent, clutch identification was also included as a random effect in those analyses. All response variables showed a binomial distribution, either with a categorical (occupancy) or with a continuous type response with upper and lower limits. In all cases, modelling procedures start with a full model, including all habitat and landscape variables, following a step-down model simplification. In addition, the interaction between species abundance (TRO, APH, SCN) and the proportion of native forest at landscape level (PLAND_NF) or in the 50m-buffer area (X50NFA) terms are also considered. The best models were selected using the AIC values, checked by their residual distribution. All statistical analyses were tested at 5% significance level and conducted using the package lmerTest (Kuznetsova *et al.* 2013) in R statistical software (R Development Core Team 2012).

Table 17. Range values for plot attributes and landscape variables obtained through ArcMap 10.

Stand attributes		Min.	1st Qu.	Median	Mean	3rd Qu.	Max.
Number of trees	Ntree	3	29	45	53.37	65	200
Mean dbh (cm)	DBH	6.60	15.90	19.40	20.14	24.00	42.60
Height (m)	Height	7	15	17	17.54	20	28
First stratum coverage 0-0.3m (%)	Vol_0.3m	0	7	15	19.03	25	90
Second stratum coverage 0.3-2m (%)	Vol_0.3.2m	0	10	20	24.23	30	80
Third stratum coverage 2-5m (%)	Vol_2.5m	0	7	15	19.7	30	75
Fourth stratum coverage 5-10m (%)	Vol_5.10m	0	15	20	22.91	30	75
Fifth stratum coverage +10m (%)	Vol_.10m	0	5	20	24.62	40	60
Number of cavities	Cavities	0	0	0	1.5	2	12
Landscape and surrounding variables							
Roads in 50 m buffer (%)	X50RoA	0	0.023	0.056	0.067	0.088	1.000
Other uses in 50 m buffer (%)	X50OtA	0	0	0	0.007	0	0.947
Native forest in 50 m buffer (%)	X50NFA	0	0	0.003	0.277	0.536	1.000
Pine plantation in 50 m buffer (%)	X50PA	0	0.283	0.883	0.647	0.949	1.000
Native forest (%)	PLAND_NF	0	0.049	0.120	0.291	0.409	0.954
Pine plantation (%)	PLAND_Pine	0	0.460	0.754	0.619	0.891	0.966
Insect abundance index	Insect	10	14	19	21.9	26	49
Southern House Wren Abundance (ind/Ha)	TRO	0	0	0.318	0.482	0.954	1.273
Thorn-tailed Rayadito Abundance (ind/Ha)	APH	0	0.636	0.636	0.889	1.273	2.864
Secondary cavity nesters Abundance (ind/Ha)	SCN	0	1.273	1.591	1.624	1.910	3.820

6.3. Results

Occupancy.- From 290 nest-boxes erected in the study area, 151 (52%) were used by different secondary cavity nester species; Southern House Wren (*Troglodytes musculus*) (136), Thorn-tailed Rayadito (*Aphrastura spinicauda*) (13) and White-throated Treerunner (*Pygarrychas albogularis*) (2). White-throated Treerunner was excluded from further analyses as the sample size was too small. A large proportion of nest-boxes were used in pine plantations (χ^2 = 7.143, df = 1, p-value = 0.007). This difference in the proportion of occupancy between habitats is mainly explained by Southern House Wren (χ^2 = 10.324, df = 1, p-value = 0.001), and not by Thorn-tailed Rayadito (χ^2 =

0.791, df = 1, p-value = 0.373) neither by White-throated Treerunner (χ^2 = 0.004, df = 1, p-value = 0.944).

Although part of the variance is explained by "Landscape" (random effect), the occupancy of nest-boxes by Southern House Wren is chiefly explained by structural features of the habitat, and by the abundance of the species in the site, and all these fixed effects are statistically significant (Table 18). The occupancy of nest-boxes by this species showed a positive association with the diameter of the trees in the stand and with Southern House Wren abundance on the site. However, a lower occupancy occurred in stands where the availability of natural cavities was higher and the volume of understory vegetation was larger. For Thorn-tailed Rayadito, the type of habitat and structural characteristics of the plot explained the occupancy of nest-boxes. A higher occupancy occurred in native fragments than in pine stands, and also the number of natural cavities in the plot had a negative effect on the occupancy of nest-boxes by Thorn-tailed Rayadito, and both effects were statistically significant. The ground vegetation cover had a negative, but marginally non-significant, effect on the use of nest-boxes by this species. Volume of vegetation in the canopy and proportion of native forest in the landscape were included in the model to explain nest-box utilization but they neither were statistically significant.

Egg and Clutch Size.- The clutch size of unpredated and undeserted nests was 4.1 ± 0.6 eggs (n = 94) for Southern House Wren and their eggs measure 17.3 ± 0.7 mm in length and 13.2 ± 0.3 mm in width (n = 518), with an egg volume of 1,543.9 ± 127.8 mm^3. For Thorn-tailed Rayadito, mean clutch size was 2.9 ± 0.3 eggs (n = 10), and the egg dimensions were 18.3 ± 0.7 mm in length and their width was 14.5 ± 0.3 mm (n = 29), with a volume of 1,986.3 ± 169.3 mm^3. These results did not differ from those obtained in previous studies in populations of Southern House Wren in Chiloe Island (Chile) (Ippi *et al.* 2012), and Thorn-tailed Rayadito populations from the Chiloe Island (Moreno *et al.* 2005) and from one of the landscape included in this very study (Quilodrán *et al.* 2012).

Table 18. Models explaining the occupancy of nest-boxes and the breeding success of Southern House Wren, and the nest-box occupancy of Thorn-tailed Rayadito.

Species				
Southern House Wren (*Troglodytes musculus*)				
Occupancy ~ DBH + Vol_0.3.2m + Cavities + TRO + (1 | Landscape)				
Family: binomial				
Model r^2 (marginal - conditional)		0.235	0.294	
Random effects	Variance	Stand. Dev.		
Landscape	0.273	0.522		
Fixed effects				
	estimate	st error	p-value	
DBH	0.066	0.026	0.0131	*
Vol_0.3.2m	-0.024	0.009	0.0131	*
Cavities	-0.188	0.072	0.0087	**
TRO	0.897	0.359	0.0126	*
Breeding success ~ DBH + Vol_0.3.2m + X50RoA + (1 | Landscape)				
Family: binomial				
Model r^2 (marginal - conditional)		0.391	0.391	
Random effects	Variance	Stand. Dev.		
Landscape	0.000	0.000		
Fixed effects				
	estimate	st error	p-value	
DBH	0.070	0.034	0.0398	*
Vol_0.3.2m	0.033	0.017	0.0510	.
X50RoA	15.111	4.793	0.0016	**
Thorn-tailed Rayadito (*Aphrastura spinicauda*)				
Occupancy ~ Cover + Vol_0.3m + Vol_.10m + Cavities + PLAND_NF + (1 | Landscape)				
Family: binomial				
Model r^2 (marginal - conditional)		0.541	0.586	
Random effects	Variance	Stand. Dev.		
Landscape	0.356	0.597		
Fixed effects				
	estimate	st error	p-value	
Cover (Pine)	-2.204	1.033	0.0329	*
Vol_0.3m	-0.096	0.056	0.0909	.
Vol_.10m	0.051	0.036	0.1589	-
Cavities	-0.528	0.259	0.0419	*
PLAND_NF	1.991	1.522	0.1908	-
*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*				

Predation.- Twenty seven of 136 Southern House Wren active nests (19.8%) were depredated and 15 were deserted (11%), giving an overall reproductive failure of 30.8% for this species. The proportion of predation was larger in pine plantations (20%) than in native forest (12%), but the

difference was not significant (χ^2 = 0.696, df = 1, p-value = 0.404). In the case of Thorn-tailed Rayadito, 7 of 13 active nests (53.8%) were depredated but no desertion was recorded. No difference in predation between pine plantation and native forest was found (χ^2 = 0.036, df = 1, p-value = 0.848). However, the proportion of predation was larger for Thorn-tailed Rayadito than for Southern House Wren (χ^2 = 4.002, df = 1, p-value = 0.045).

Breeding success.- The breeding success, calculated as the proportion of fledglings from the number of eggs laid per clutch, was similar for both species, with overall values of 51.5% and 48.7% for Southern House Wren and Thorn-tailed Rayadito respectively. Model explaining the breeding success for Southern House Wren showed a major effect of vegetation structure variables and land use surrounding the nest-box. Table 18 shows the positive and significant association of the breeding success with the average tree diameter (DBH) and a marginally non-significant effect of the understory vegetation. The proportion of secondary roads in the 50 m buffer area around the nest-boxes had a positive and significant effect on the reproductive success of the species. No landscape level effect on the breeding success was found for Southern House Wren. Due to sample size, no model was fitted for Thorn-tailed Rayadito.

Weight of fledglings.- Clutch (Nest-box) identity explains most of the variance in the weight of 188 fledglings of Southern House Wren ringed (Table 19). The weight of the fledglings was negatively affected by the brood size and the proportion of secondary roads in the nest-boxes' surroundings. The interaction of two landscape level variables had a positive effect on the weight of the chicks of Southern House Wren.

Only 10 fledglings of Thorn-tailed Rayadito were ringed before they have fledged. The small sample size limited the number of variables possible to include in the candidate models. Random effects (Landscape and Nest-box) were unable to explain the variance in the weight of Thorn-tailed Rayadito chicks. The type of habitat and the average tree diameter had a negative effect on the weight of the fledglings (Table 19).

Table 19. Mixed models explaining the weight of chicks for the Thorn-tailed Rayadito and the Southern House Wren.

Species				
Southern House Wren (*Troglodytes musculus*)				
Weight of Fledglings ~ Brood size + X50RoA + PLAND_NF * SCN + (1 | Landscape)				
Family: binomial				
Model r^2 (marginal - conditional)		0.329	0.721	
Random effects	Variance	Stand. Dev.		
Landscape	0.019	0.139		
ID Box	0.235	0.484		
Fixed effects				
	estimate	st error	p-value	
Brood size	-0.317	0.100	0.0160	*
X50RoA	-5.473	1.705	0.0133	*
PLAND_NF	-4.339	1.098	0.0000	***
SCN	-0.137	0.161	0.3946	-
PLAND_NF: SCN	1.275	0.434	0.0033	**
Frequency of parent visits ~ Age pulli + Height + X50RoA + (1 | Landscape) + (1 | ID Box)				
Family: binomial (logit)				
Model r^2 (marginal - conditional)		0.200	0.200	
Random effects	Variance	Stand. Dev.		
Landscape	0.000	0.000		
ID Box	0.000	0.000		
Fixed effects				
	estimate	st error	p-value	
Age pulli	-0.075	0.047	0.1069	-
Height	-0.198	0.066	0.0029	**
X50RoA	-38.823	15.302	0.0111	*
Thorn-tailed Rayadito (*Aphrastura spinicauda*)				
Weight of Fledglings ~ Cover + DBH + (1 | Landscape) + (1 | ID Box)				
Family: Gaussian				
Model r^2 (marginal - conditional)		0.635	0.635	
Random effects	Variance	Stand. Dev.		
Landscape	0.000	0.000		
ID Box	0.000	0.000		
Fixed effects				
	estimate	st error	p-value	
Cover (Pine)	-1.373	0.698	0.0491	*
DBH	-0.179	0.070	0.0109	*
Frequency of parent visits ~ Height + APH + (1 | Landscape) + (1 | ID Box)				
Family: Gaussian				
Model r^2 (marginal - conditional)		0.145	0.145	
Random effects	Variance	Stand. Dev.		
Landscape	0.000	0.000		
ID Box	0.000	0.000		
Fixed effects				
	estimate	st error	p-value	
Height	0.018	0.008	0.0251	*
APH	0.085	0.059	0.1511	-
*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; '-' 1*				

Parental visits.- A total of 58 hours of video was recorded during the nest-box survey. Southern House Wrens visited their nests with a frequency of 9.53 ± 5.79 times per hour. Differences in visit frequency were explained by the average height of trees in the plot and the proportion of secondary roads in the surrounding 50 m buffer area. There was a negative but not significant association among the parental visiting and the age of the pulli, or days since hatching. For Thorn-tailed Rayadito, the mean frequency of nest-box visiting was 16.88 ± 9.80 times per hour. The factors explaining the differences in visit frequency were the average height of trees in the plot and the abundance of the species itself in the landscape, but only tree height had a significant effect (Table 19).

6.4. Discussion

The number of suitable cavities for nesting is a limiting resource for secondary cavity nester species in these modified forested landscapes. Nest-boxes were used mostly by Southern House Wren and Thorn-tailed Rayadito, two insectivorous species with a wide distribution range, including temperate and Mediterranean forests. These species differ greatly in terms of their habitat guild; Thorn-tailed Rayadito is recognized as a forest specialist (Moreno *et al.* 2005) and Southern House Wren is associated to shrubland and marginal forests (Ippi *et al.* 2012). Accordingly, different factors govern the occupancy of nest-boxes by these two bird species (Table 18). Pine plantations showed a negative effect on the occupancy rate for Thorn-tailed Rayadito, which is mainly explained as the use of this mono-specific crop as an alternative habitat due to its low quality for forest specialist species. However, for Southern House Wren the occupancy of nest-boxes was explained by the species abundance in the site, which is higher in pine plantations (see Chapter 2). Consequently a large proportion of the nest-boxes set in pine plantations were used by Southern House Wren. Even though there are clear differences in terms of niche for these two secondary cavity nester species, both were affected negatively by the number of natural cavities available; the occupancy of artificial nesting structures was higher in sites where natural cavities

were scarce. Hence, this fact clearly illustrates how shortage of nesting cavities could prevent breeding for a part of secondary cavity nester species populations.

The breeding site quality is determined by vegetation structure features in the stand, and they affect species differently. The average tree diameter had a positive effect on the occupancy of nest-boxes and the breeding success of Southern House Wren, suggesting that older pine stands are preferable and better breeding habitat for this species. Regardless of this, the clear effect of tree diameter on both parameters, the age of the pine stand is generally associated with different stage of development of the undergrowth (Estades & Escobar 2005), suggesting that tree diameter could have an indirect rather than a direct effect on the occupancy and breeding success for Southern House Wren. This proposed indirect effect of tree diameter is playing a similar role in explaining the weight of fledglings of Thorn-tailed Rayadito; heavy chicks were associated with lower average tree diameter that, in turn, may be related to a more diverse forest structure and composition. Interestingly, Southern House Wrens have to trade off between concealment and visibility in their nesting site selection (Götmark *et al.* 1995), understory vegetation provides cover and foraging resources but decrease the detection of potential predators and rivals. This trade off was shown in the positive effect of understory vegetation on the breeding success but negatively on the selection of nesting site, a situation also reported for the House Wren (*Troglodytes aedon*) in North America (Finch 1989), from which *T. musculus* was previously considered the same species (Young 1994). Moreover, the tree height in the plot was the only structural variable with an effect on the frequency of parental visits to the nest. This feature affected both species, yet in a contrary way; while Thorn-tailed Rayadito increased the frequency visiting the nest in plots with higher trees, Southern House Wren would require more time to search for food at the same plot. The reason for the different response lay mainly in the particular niche, and its breadth, that these species exploit.

Fragmentation may alter the breeding of natural populations by the loss of preferable nesting habitats and structures, alteration of the prey communities, and by adding edge effects to breeding grounds (Faaborg 1995). The replacement of the natural vegetation with pine plantations had a

negative effect on the weight of the fledglings and the occupancy rate of nest-boxes for Thorn-tailed Rayadito, suggesting that pine plantations are poor breeding habitat for forest specialists, not only for the lack of natural cavities, but also for a low quality and abundance of insect prey (Estades & Escobar 2005). Thus, Thorn-tailed Rayadito avoided nesting in pine plantations, and when they did, their offspring weighed less than those raised in native forests. Moreover, at a landscape level, the amount of replacement of native forest and its degradation also affected the weight of the Southern House Wren's offspring, which may be understood in terms of the advanced impoverishment of the habitat, with higher level of environmental simplification that affects even a generalist species. For the Southern House Wren, the ambivalent effect of secondary roads in the vicinity of nesting sites suggests that a factor, derived from the interaction of the species' breeding strategy and some forestry practices may be disturbing their breeding process. The proportion of secondary roads in the nest surroundings had a negative relationship with both the frequency of parental provisioning visits and the weight of the chicks. However, nest-boxes with a high proportion of secondary roads in their surroundings showed better breeding success. While secondary roads may introduce diversity in terms of plant species, they also reduce the foraging area available for the breeding birds, forcing them to travel farther to find prey. Furthermore, the increasing plant diversity and volume of the edge vegetation may not be available for the birds if the roads are in use, because most of the vegetation would be covered with dust from the roads. Fragmentation and especially edge effects, such as roads, raise the intensity of nest predation (Vergara & Simonetti 2003), and in these forest systems five potential predators are recognized for cavity nesters: the Long-tailed Snake (*Philodryas chamissonis*), the introduced and invasive Black Rat (*Rattus rattus*), the Elegant Fat-tailed Mouse Opossum (*Thylamys elegans*), the Lesser Grison (*Galictis cuja*), and the Kodkod (*Leopardus guigna*) (Escobar & Vukasovic 2003) and T. Altamirano *pers.com.*). Despite the fact that a higher predation rate would be expected in nest-boxes associated with a high proportion of roads, the opposite occurred, which may be explained by the avoidance of disturbed areas by some predators (Acosta-Jamett & Simonetti 2004), but see (Vergara & Simonetti 2003). As a result, a large part of the recruitment of cavity nester species from landscapes dominated with pine

plantations would be formed by individuals raised in poor conditions, which could be considered as a sort of ecological trap for the breeding population as the weight of the offspring predict their later survival (Maicas Catalan & Fernández Haeger 1996; Reynolds & Perrins 2010).

Even though they have some limitations, these results showed how fragmentation affects the breeding of forest bird populations in a species specific manner. Therefore, these findings should not be generalized but considered, as they report general factors affecting the normal offspring development. Conducting the research across several landscape units has allowed me to demonstrate that the impact and extent of the native forest replacement with pine plantations is correlated with the degree of species specialization. I acknowledge that the sample size for Thorn-tailed Rayadito is too small for the results to be considered definitive, but they reflect the real situation for the forest species in these systems.

Finally, the usefulness of nest-boxes as a mitigation practice in pine plantations is questioned. First, offspring of birds nesting in pine plantations fledge in poorer conditions, and therefore with poorer chances of survival. Second, increasing the size of breeding populations artificially in temporal habitats could have severe consequences for the bird community; depending on land configuration of the pine plantations, the harvest of mature pine stands could mean a massive spill over of birds to neighbouring fragments.

Chapter 7

Pine plantations and their soil acidification effect on the egg formation process

7.1. Introduction

Globally, due to their greater economic returns, fast-growing tree plantations have been replacing native forests at increasing rate. Nowadays, more than 260 million hectares of land is covered with plantations of fast-growing species (FAO 2010), mainly of *Pinus* and *Eucalyptus*. The majority of these plantations are located in temperate areas, creating large forest industries whose expansion demands more land to be converted into plantation, and therefore exerting great pressure on the temperate forest communities (Ovington 1983). In general, a large part of native fauna has been reported using exotic pine plantations elsewhere, especially birds (Brockerhoff *et al.* 2008). The occupancy of pine plantations by native forest birds has been explained by the structural similarity between native forest and coniferous plantations (Renjifo 2001), perceived as a soft barrier for the displacement of forest avifauna (Tomasevic & Estades 2008). Some forest birds venture into pine plantations using them as a subsidiary source of foraging (Tubelis *et al.* 2004), but most of them are forced to move to neighbouring plantation from over-populated fragments. However, pine plantations could be a poor quality habitat for breeding bird populations, as they could not find the resources they need to breed.

Pine plantations may alter the soil chemistry, and therefore affect the food webs and add more selective pressure on bird communities. This modern forestry, with fast-growing species, demands large amounts of nutrients from the soil (Merino *et al.* 2004), which are removed frequently through harvesting in short rotations (Adams 1999). Another negative effect of pine forestry is the soil acidification, which has been explained by both the continuous removal of nutrients (base cations mainly) and by the releasing of organic acids from the pine needle litter, thereby enhancing the cation leaching from the mineral soil (Lilienfein *et al.* 2000; Messenger 1980). Calcium is an important nutrient for plants and animals and is one of the elements more susceptible to depletion from forest soils by modern pine forestry (Schaberg *et al.* 2001). As a consequence of soil

acidification and calcium deficiency, soil fauna has declined in sites where coniferous plantations have replaced deciduous forests (Wäreborn 1992), especially affecting snails and other land molluscs that require Calcium for their reproduction and development (Johannessen & Solhøy 2001). Similarly, forest passerine species rely on land molluscs to obtain the Calcium they need for reproduction (Graveland & Van der Wal 1996). Hence, inadequate levels of Calcium in the soil trigger a concatenated effect on the food web of the ecosystem.

Calcium is a critical and limiting resource for shell formation in small passerines, and its deficiency affects the normal reproduction of birds (Bidwell *et al.* 2005; Graveland & Drent 1997). In the early stages of reproduction, egg production requires an adequate supply of water, micro and macro nutrients (Reynolds & Perrins 2010). Besides protein and energy, reproduction requires a large amount of calcium for both egg formation and bone growth (Graveland & Drent 1997; Johnson & Lombardo 2000), and its deficiency can result in abnormal egg formation, nest desertion or even poor skeletal development in nestlings (Reynolds & Perrins 2010; Tilgar *et al.* 1999).

Some small passerine species, breeding in Calcium deficient sites, are able to compensate for the lack of this element by depositing greater quantities of pigment during the egg formation process. The evolution of the ancestral white eggshell (Solomon 1997) in the current diversity of patterns and colours could have been influenced by many factors, such as crypsis, structural strength or brood parasitism (Kilner 2006). The eggshell pigmentation patterns are determined by both genetic and environmental effects; for example, in wild birds, the eggshell patterns are subject to female sex-linked inheritance (Gosler *et al.* 2000). However, in small passerines the pigmentation of maculated eggs is associated with thinner areas of the shell, where the pigments (protoporphyrins) are deposited as a way to compensate the lack of calcium (Gosler *et al.* 2005). Protoporphyrins have two distinctive physical properties that allow them structurally to replace Calcium; they act as a shock-absorber and by reflecting the infra-red they create cool spots that may reduce the water loss during incubation (Gosler *et al.* 2011; Gosler *et al.* 2005). Therefore, variation in egg pigmentation would be found between clutches from rich and poor soils sites.

It is well known that conifer plantations cause soil acidification, reducing the soil concentration of calcium and other nutrient cations (Berthrong *et al.* 2009). Consequently breeding territories in pine stands may be of poor quality in terms of calcium availability. To see whether the replacement of native forests with pine plantations in South-Central Chile has an effect on the calcium availability, the speckled pattern of maculated eggs of Southern House Wren (*Troglodytes musculus*) nesting in forested landscapes was scored by a single observer.

7.2. Methods

The study was carried out in the commune of Constitución, in the coast of the administrative region "Del Maule", Chile. The climate of this region is temperate with warm and dry summers (Peel *et al.* 2007), with an oceanic influence. The study was carried out in the temperate deciduous forests of the Coastal range, known as the Maulino forest. These forests have gone through a history of alteration, and nowadays they have been reduced to small fragments embedded in a matrix of exotic pine plantations. The parent material of the soil in this area is Palaeozoic metamorphic rocks covered with sedimentary sequences from the Triassic and Tertiary periods (Mardones 2005).

In these forests, I selected 29 landscape units of 21.09 ± 16.5 Ha in size (Mean ± SD). The selection process considered continuous forest habitat as a main constraint, selecting only landscape units with at least 85% forest cover. Another important characteristic considered in the site selection was to cover the whole range of replacement of native forest in the landscape; from 0 to 100%. All sites were located in the western slope of the Coastal range in the commune of Constitución (Fig 20).

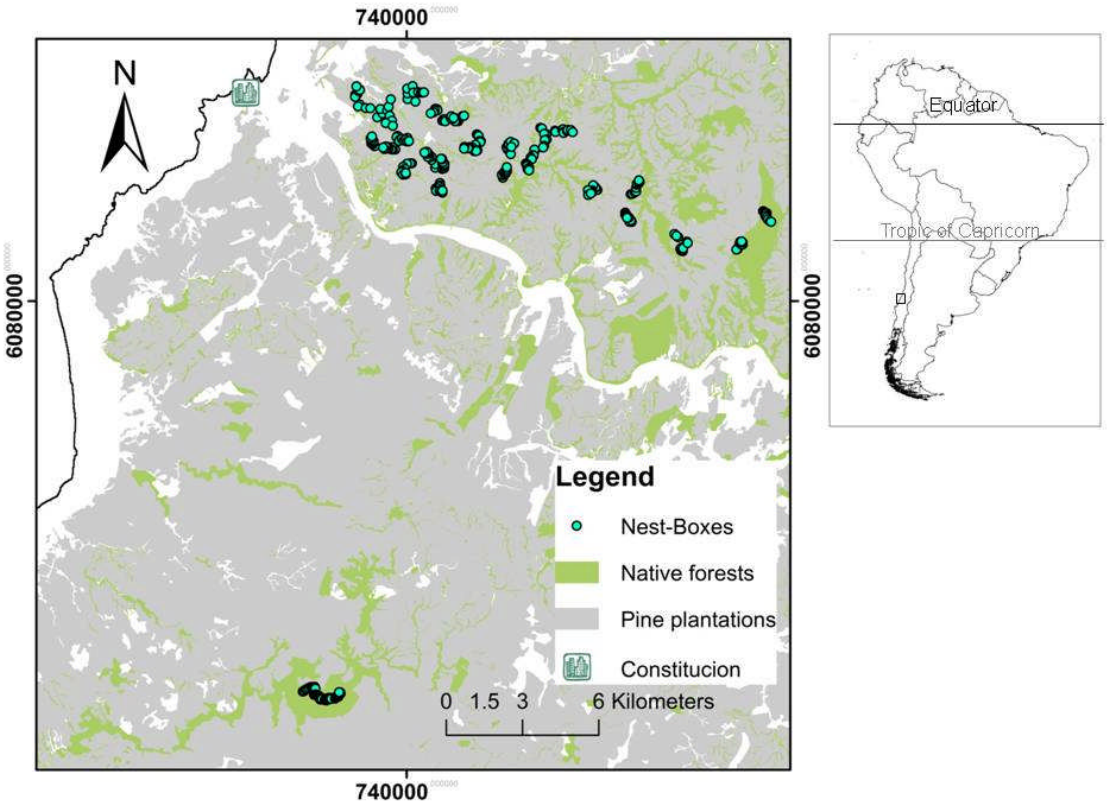

Figure 20. Map of the study area, showing the location of nest-boxes in the commune of Constitución (Chile).

Egg sampling. During the austral spring of 2013 I carried out a survey on the reproduction of secondary cavity nester (SCN) species of the bird community. Ten nest-boxes were erected in every site, they were placed proportionally in pine stands and native fragments, and never closer than 50 m from each other. Because of the three SCN species using the nest-boxes, Southern House Wren is the only one with maculated eggs, this study is focused on that species. Nest-boxes were visited every five days, as it was the time I needed to complete 290 nest-box rounds in these landscapes. Eggs were weighed and measured before incubation started. Egg length and breadth were measured to the nearest 0.1 mm with a vernier caliper, and the egg mass was recorded to the nearest 0.1 g on a portable digital balance (Myco™, model MZ-100). Egg volume was estimated using Hoyt's (1979) formula: volume = 0.51 X (length X breadth^2). For every egg, a photograph was taken in natural light conditions, and avoiding direct sunlight.

As the intensive afforestation program with exotic pine species in Chile started around 1950, Southern House Wren eggs collected in South Central Chile before that date might differ from modern eggs in speckling pattern if soil acidification is responsible for eggshell patterning. Eggs from 17 clutches of Southern House Wrens from the collection of the Museum of Natural History (Tring), dated between 1858 and 1962, were therefore also scored and used to assess the historic environmental effects on the habitat quality for birds.

Habitat and land use description. I characterized the vegetation structure around every nest-box. I estimated tree height, the number of natural cavities and I measured the diameter at breast height (dbh) of the nearest five trees to the observer point. I followed the methodology used by Estades & Temple (1999) in these forests to describe the vegetation's vertical structure; the total foliage volume was estimated by referring to five vertical strata of the vegetation. Using ArcMap 10 (ESRI 2011) over Arauco's forest cover Database and the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh 2010) I prepared geographical information layers to assess plot and landscape unit attributes, including the proportion of every land use in landscape units and in the 50 m radius buffer area around of each nest-box (see Table 17 in Chapter 6 for more details).

Scoring the eggs. Following the methodology described in Gosler *et al*. (2005), the eggshell spot-pattern of 517 eggs from 123 clutches was scored by a single observer (J. Bustos-Weisser) who was trained by double blind scoring methods and consistency checks. The egg scoring was done according to three simple score series that are illustrated in Figure 21: Intensity of the spots (I), their distribution in the surface of the eggshell (D), and the average spot size (S). The ground-colour pigmentation (biliverdin) (Jagannath *et al.* 2008) was not considered for scoring.

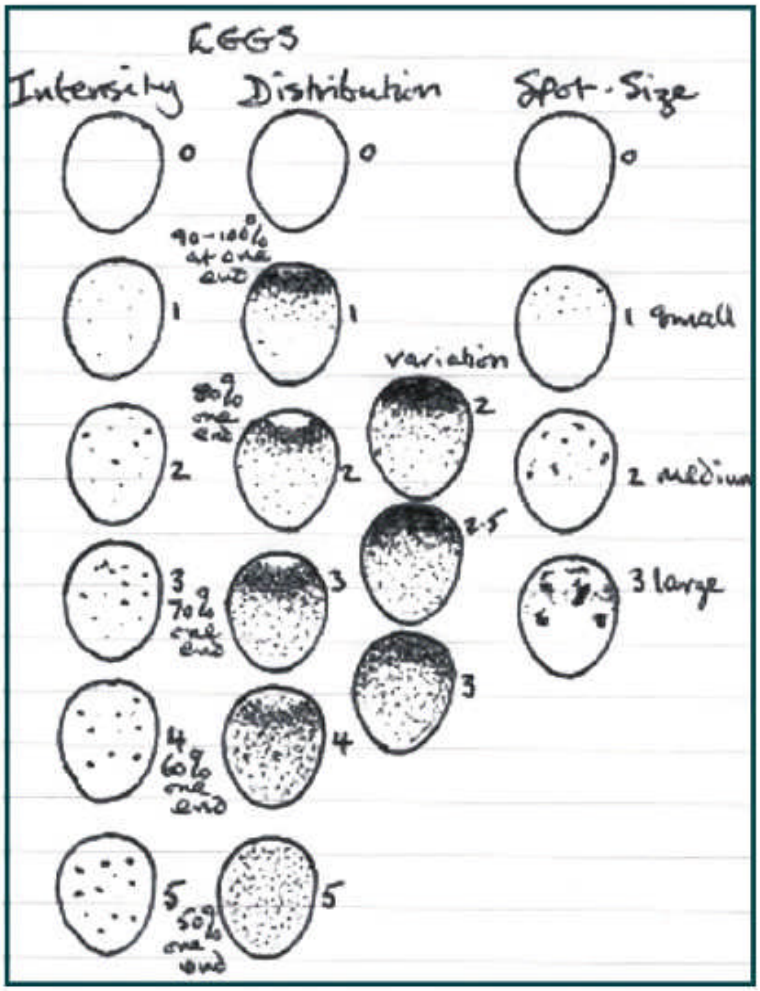

Figure 21. Egg sketch diagrams used to score the Southern House Wren eggs (Source: Gosler (2006), page 344).

A principal component analysis was carried out to summarise the variation contained in the three score series and to eliminate the correlation among the scores (Gosler *et al.* 2000; Gosler *et al.* 2005). As PC1 showed a positive loading of all three scores (eigenvectors: Intensity = 0.68, Distribution = 0.59, and Spot size = 0.41), it is referred to "darkness" of the egg; with higher values of PC1 representing an increase of pigments throughout the entire eggshell surface. The loading of PC2 was strong and positive with Spot size, but the loading with Distribution was negative (eigenvalues Spot size = 0.83, Distribution = -0.54). Therefore, PC2 is referred to "spread", where higher values of PC2 correspond to larger spots gathered near the blunt end of the egg, forming a

dark ring around the polar area (Fig. 22). PC1 and PC2 explained 47.3% and 32.0% respectively of the total variance in Intensity, Distribution and Spot size.

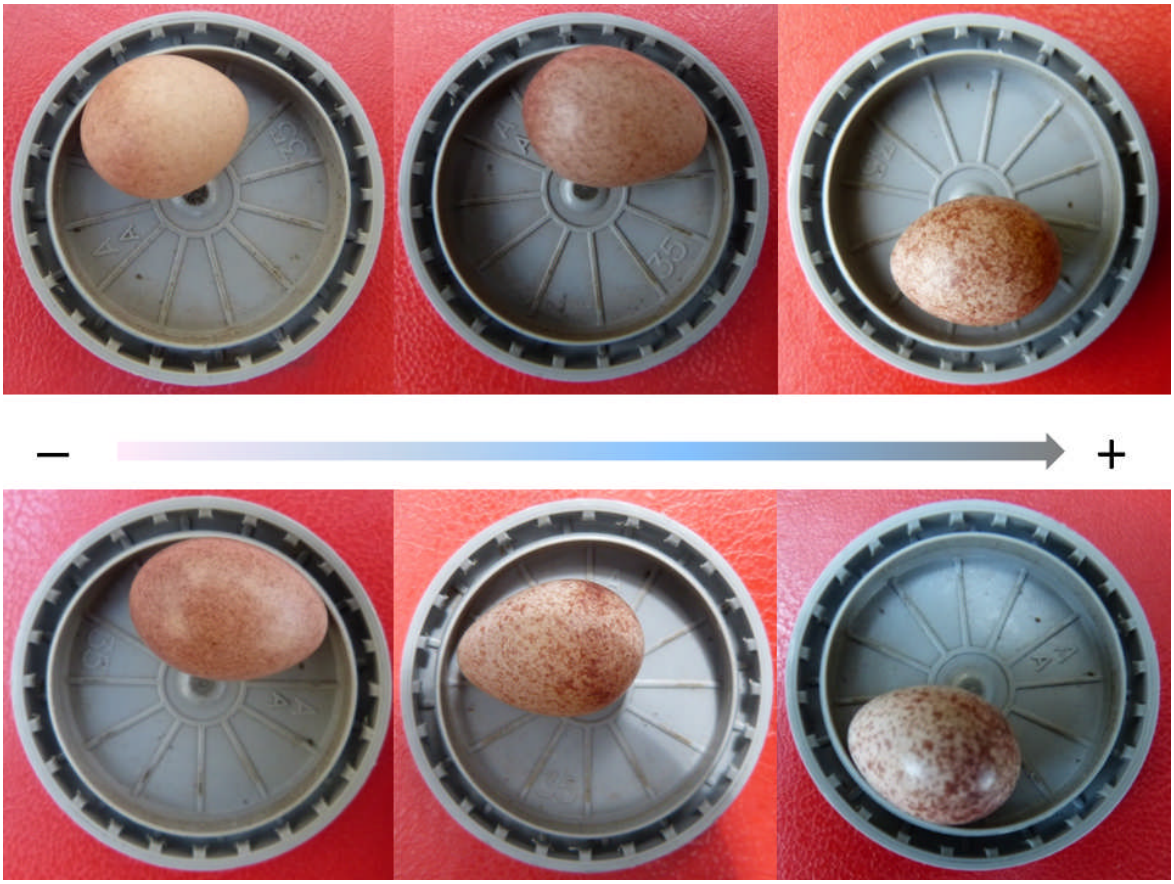

Figure 22. Illustration of eggs through the PCA1 (top) and PCA2 (bottom) gradient of values.

Statistical analyses. In a wild Great Tit (*Parus major*) population, Gosler *et al*. (2000) found that "darkness" (PCA1) of the eggshell's pigment pattern is female sex-linked heritable, but not the "spread" (PCA2) of the maculation. As the level of inheritance of the speckled pattern for Southern House Wren is unknown, environmental effects on the maculation pattern were tested on both features darkness and spread. Using multilevel modelling I assessed the effect of landscape and stand level variables on the speckled pattern of the eggs. As eggs from a clutch are not statistically independent, and nest-boxes were nested in landscape units, both clutch and landscape unit were considered as random effects. Independent analyses were carried out with darkness (PC1) and spread (PC2) as response variables, and the search for the best models, based on AIC values, was

done from a full linear mixed model containing all non-correlated variables describing habitat and landscape as fixed effects. To test the temporary effect of industrial afforestation on the speckled pattern I include the eggs from the museum collection in the statistical analyses as a third level of the factor "Egg Source". All statistical analyses were tested at 5% significance levels and conducted using the package lmerTest (Kuznetsova *et al.* 2013) in R statistical software (R Development Core Team 2012).

7.3. Results

Most of the variation in the spot pattern of Southern House Wren eggs was associated with the Nest-box, location and clutch membership for the eggs. This could be seen on the amount of variance explained by the random effects and the marginal coefficient of determination (see Table 20). Egg features had low power in explaining the variation in the values of PCA1 and PCA2. The volume and weight of the egg had a non-significant effect on PCA1 and PCA2 respectively.

The variation in the maculation pattern of Southern House Wren eggs was strongly associated with landscape configuration and its association with vegetation features of the nesting location. Eggs from nest-boxes erected in pine stands showed higher values for PCA2 than those from native fragments. In general, the volume of the canopy showed an association with both components; the upper canopy had a positive and significant effect on PCA2 and the lower canopy had a negative but insignificant effect on PCA1. The proportion of pine plantation in the landscape explained PCA1 and PCA2 values in a negative and significant manner.

Independent Pearson's correlation tests showed that PCA2 and Distribution of the spots had a negative ($r = -0.111$, p-value = 0.009) and positive ($r = 0.108$, p-value = 0.012) correlation with the number of fledglings from the clutch, respectively.

Table 20. Mixed models explaining the variation in spot patterns.

Southern House Wren (*Troglodytes musculus*)				
PCA1 ~ Egg volume + Lower canopy volume + % Pine landscape + (1 | Box) + (1 | Landscape)				
Family: gaussian				
Model r^2 (marginal - conditional)		0.025	0.366	
Random effects	Variance	Stand. Dev.		
Box	0.444	0.666		
Landscape	1e-18	1e-09		
Fixed effects				
	estimate	st error	p-value	
Egg volume	0.0004	0.0004	0.366	-
Lower canopy volume	0.0085	0.0058	0.145	-
% Pine in landscape	0.6398	0.2679	0.016	*
PCA2 ~ Weight + Cover + Tree density + Upper canopy volume + % Native forest in landscape + (1 | Site) + (1 | Landscape)				
Family: gaussian				
Model r^2 (marginal - conditional)		0.063	0.376	
Random effects	Variance	Stand. Dev.		
Box	0.278	0.527		
Landscape	1e-16	1e-08		
Fixed effects				
	estimate	st error	p-value	
Weight	0.5940	0.3932	0.253	-
Egg Source (Pine)	0.7220	0.2672	0.005	**
Tree density	0.0047	0.0029	0.073	.
Upper canopy volume	0.0063	0.0030	0.030	*
% Native forest in landscape	0.9083	0.3439	0.007	**
*Signif. codes: 0 ; '***' 0.001 ; '**' 0.01 ; '*' 0.05 ; '.' 0.1 ; ' ' 1*				

The eggs from the museum collection differed clearly from those that were recorded during the fieldwork survey (Fig. 23). There was a great and significant difference between modern and museum eggs for PCA1 ($F_{1,587}$ = 40.85, p-value < 0.001) and PCA2 ($F_{1,587}$ = 9.63, p-value = 0.002) values. This was related to the original scores of the spot pattern (Intensity, Distribution and Spot size), where the difference was given by the distribution ($F_{1,587}$ = 40.80, p-value < 0.001) and size ($F_{1,587}$ = 90.57, p-value < 0.001) of the spots in the eggs. In general, the maculation pattern of the eggs from the museum collection was well spread through the whole eggs, whereas modern eggs showed a marked trend for lower values in their spot distribution.

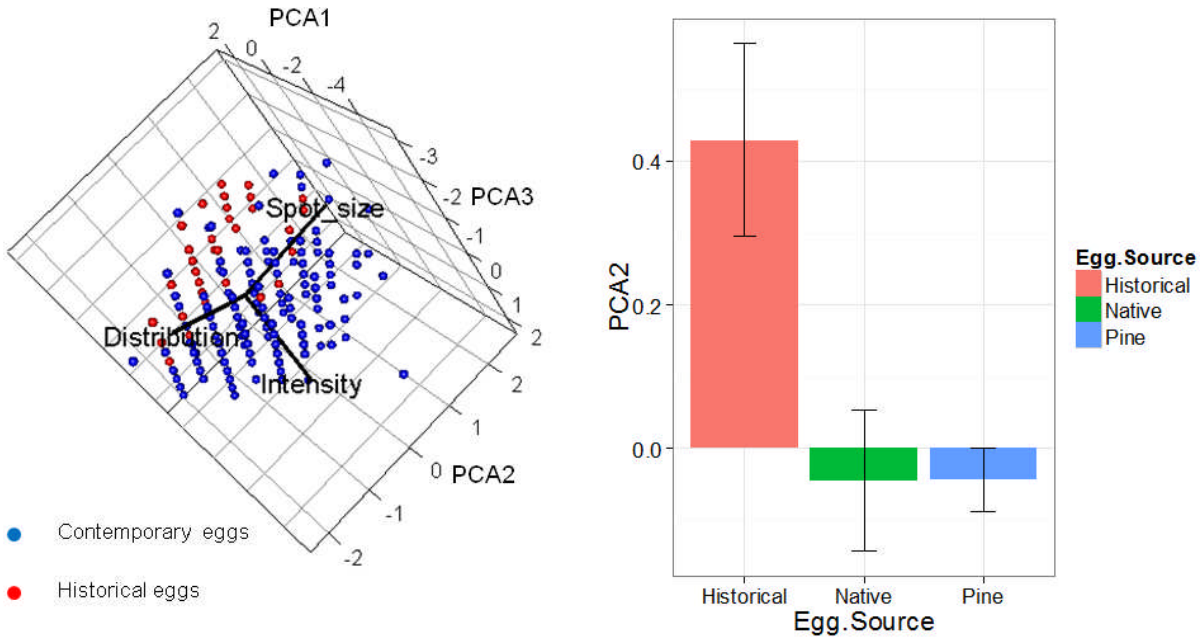

Figure 23. Left: PCA values for historical and modern eggs and they relationship with the initial scores. Right: Comparison of PCA2 ± SE values between eggs from native forest, pine plantations and the museum collection.

7.4. Discussion

The replacement of native forest with exotic pine plantations has caused soil acidification where this land-use change has taken place, and consequently the Calcium available for forest birds has decreased. According to the results, females breeding in territories associated with pine plantations laid darker eggs, and their maculation pattern differed from those eggs laid in native forests. Similarly, the inclusion of museum egg specimens in the analyses revealed the impact that 50 years of the afforestation program with exotic coniferous has had on the soil chemistry. The maculation pattern from museum eggs differed greatly from those now found in landscapes dominated by pine plantations. The absence of the dark crown pattern in eggs collected prior to the expansion of pine plantations is the clearest difference from modern eggs. The Calcium deficiency during the egg formation process was evident in large deposits of protoporphyrin in the shoulder of the eggs, depicting a sort of dark crown around the blunt end of the egg. This region is one of the thinner parts of an eggshell (Gosler *et al.* 2005), a fact that explains the tendency for reinforcement with pigment deposits when the calcium is scarce (Gosler 2006).

Pine plantations had an effect on both egg pattern descriptors used in the analyses, PCA1 and PCA2. In general, it was possible to find darker eggs (PCA1), with greater protoporhyrin visibility, in landscapes where the substitution of native forests with pine plantations has been more extensive. In a similar way, the eggs from nest-boxes erected in pine stands frequently had a marked crown pigmentation pattern (PCA2). In both cases, the increase of pigment deposits would indicate Calcium deficiency in forest soils. Interestingly, native forest had a similar effect on PCA2 values, but at landscape level rather than locally. The process behind this two-scale response is not clear, although some explanation may be given by habitat preference; Southern House Wrens are more abundant in pine plantations than in native forests (see chapter 3), and the interaction between the proportion of native forest in the landscape with the abundance of secondary cavity nester species affects the weight of their fledglings (see chapter 6). This information suggests that, along with habitat features, intra- and inter-specific competition may determine the selection of breeding sites for this species.

Soil acidification indirectly decreases the reproductive success of forest passerines. In line with previous studies in Europe (Graveland & Van der Wal 1996; Tilgar *et al.* 2002), the effects of soil acidification by coniferous plantations alters the normal reproduction of forest birds, which in this study is shown through the negative correlation between number of fledglings and the dark-crown pattern. The lower reproductive success in forest passerines associated with poor Calcium sites is the result of either an abnormal egg formation or impaired skeletal development in chicks (Wilkin *et al.* 2009). Even though females are able to mobilize part of their skeletal Calcium to egg production (Simkiss 1967), this process is much less significant in small passerine species, which depend strongly on daily intake of food items rich in Calcium (Graveland & Van Gijzen 1994). The main source of Calcium for insectivorous birds are fragments of bone, eggshell, and mainly snail shell (Reynolds & Perrins 2010), therefore, the abundance and diversity of soil fauna would, in turn, limit the reproduction of forest birds. Not only does the leaching of Calcium from forest soils constrains the soil fauna that depends on Calcium to complete their life cycles (Graveland & Van der Wal 1996; Wäreborn 1992), but also the quality of the litter material; in this study the pine

needle litter that is considerably less suitable for detritivores than the leaf litter from broad-leaved trees (Scheu *et al.* 2003).

In addition, regarding the lower reproductive success observed in the preferred habitat, pine plantations could be considered as an ecological trap for Southern House Wren. The Calcium deficiency in landscapes dominated by pine plantations would mean an extra selective pressure on those populations, but it does not necessarily mean a conservation problem for this generalist species; as it is a wide spread and regional abundant species, and eggshell speckling is a partial compensation mechanism. However, this situation raises questions about the condition of forest specialist species inhabiting these forest systems, and also about the mechanisms used by white-egg species to palliate the shortage in Calcium.

There is a need for more studies of gastropods and their interactions with other taxa in these temperate and fragmented ecosystems. Most of the studies done in recent decades have been focused on marine ecosystems and temperate rainforest of Southern Chile (Valdovinos *et al.* 2005). Hopefully, these findings will promote new studies on land molluscs, which is one of the less studied groups in these ecosystems (Stuardo & Vega 1985), and maybe one of the most threatened by modern forestry. In this regard, special attention should be given to the chemistry of fresh water in landscapes dominated by pine plantations (Lilienfein *et al.* 2000).

As far as I know, this is the first study that has used the speckled pattern of a small passerine species to demonstrate the soil acidification by coniferous plantations. I acknowledge that a complete and robust answer would be given by assessing the amount of Calcium in the eggshells and the soil Calcium-content. However, the simple and direct tests, using both spatial and temporal analyses to test the hypothesis, supported by a respectable sample size, give confidence in the results. These findings will contribute to increasing knowledge about South-American temperate forest community, and should encourage new studies focused on the conservation of forest specialist species.

Chapter 8

Effect of the substitution of native forest with pine plantation on the inter-specific competition of the bird community

8.1. Introduction

Habitat loss and fragmentation are one of the major causes of biodiversity loss, affecting ecological functions and processes. Fragmentation has a detrimental effect on the quality of natural habitats, impacting on population sizes through its effects on demography, physiological conditions and survival of birds (Latta & Faaborg 2002). Local variations in habitat affect the fitness of animals through variations in resources and environmental conditions, generating strong selective pressures on habitat selection (Cody 1985). Furthermore, the alteration and degradation of the forest structure can influence bird communities to a large extent. The number of species in a habitat is directly related to its structural diversity (Cody 1985; MacArthur & MacArthur 1961), in that greater structural diversity gives opportunities for more species or foraging guilds to exploit resources (Robinson & Holmes 1982). The selection or preference for one or other habitat is therefore based chiefly on vegetation physiognomy (Cody 1985; MacArthur & MacArthur 1961). Finally, fragmentation may alter the balance of food webs, either by increased pressure on certain arthropod prey (González-Gómez *et al.* 2006) or by changing the vegetation structure (Whelan 2001).

The contrast between the life forms of broadleaf and coniferous tree species is probably one of the strongest found in temperate forests (Franzreb 1978). The substitution of native forests with exotic coniferous plantations therefore imposes a dramatic change in the foraging substrate for forest birds (Peck 1989), given the diversity of tree species, canopy architecture and features of trunk and bark (Garton 1979; Robinson & Holmes 1984). Moreover, the vegetation role as a source of arthropod prey is critically important as it influences the structure and composition of temperate forest bird communities (Robinson & Holmes 1984). Modern forestry, based on mono-specific

crops, has produced a homogenization and simplification of the environment, resulting in a worldwide decline in specialist species (Clavel *et al.* 2010), particularly birds (Julliard *et al.* 2004). Disturbances, such as habitat loss or its degradation, could increase the level of competition between specialist and generalist species, which could also lead to the extinction of specialists unable to adapt to new and changing conditions (Clavel *et al.* 2010). Thus, the substitution of preferred species of tree as a foraging substrate may influence the composition of the bird community (Holmes & Robinson 1981).

Any modification of the vegetation structure and composition, such as the substitution of tree species, is expected to alter the relationships between species in the forest bird community. It is understood that the foraging behaviour of species, including tree preferences, is an integral part of their biology and may become distinctive for species (Remsen Jr & Robinson 1990). In forest habitats, birds tend to partition resources using different foraging techniques, foraging sites, tree species and canopy height (Airola & Barrett 1985; Recher *et al.* 1985). Coexisting species have evolved to use different resources, reducing the effects of inter-specific competition (Svanbäck & Bolnick 2007). Niche theory has assumed that inter-specific competition, the joint use of a limited resource by two species (Pianka 1981), is an important determinant of niche breadth (Vandermeer 1972). As fragmentation of natural habitats increases competition (Fischer & Lindenmayer 2007), similarly, an increase of trophic niche overlap between species may occur with habitat alteration (Luiselli 2006)). Consequently, the substitution of the broadleaf canopy with coniferous species may affect forest bird species by either directing their foraging activity strongly toward the native undergrowth vegetation, which would increase niche overlap and inter-specific competition, or by shifting their foraging niche, adding the coniferous species as new foraging substrate.

This study aims, therefore, to answer the following questions: a) has the substitution of temperate deciduous forest with exotic pine plantations changed the level of inter-specific competition in the forest bird community? b) is there any change in the exploitation of the vertical profile of the vegetation related to this change? By answering these questions I will compare the habitat quality

of the exotic plantation against native forest, shedding light on the effects of habitat substitution on forest bird ecology.

8.2 Methods

Study area. The study was carried out on the bird community of the temperate forest of South Central Chile, in what is the administrative commune of Constitución. The climate of this region is temperate with warm and dry summers (Peel *et al.* 2007). This study is focused in the temperate deciduous forest, known as the Maulino forest. This is a deciduous forest dominated mainly by the tree species Hualo (*Lophozonia glauca*, *Nothofagaceae*), characterized by having an understory that generally consists of shrubs or small trees with resistant evergreen leaves. These forests have gone through a history of alterations and nowadays they have been reduced to small fragments embedded in a pine plantation matrix.

Foraging data. During January and July 2014 twelve sites, with at least 85% of forest cover, were visited twice, and there many transects were conducted by three observers in every site looking for foraging birds. The transects were carried out ad-libitum in order to maximize the number of detected foraging individuals in relation to the invested effort. After detecting a bird foraging, the follow information was recorded: height at which the bird was foraging, position in the tree (trunk, branch, twig, foliage, and cone), ground (litter, wood debris) or air, tree species (Remsen Jr & Robinson 1990). In addition, for every location at which a bird was recorded, the vegetation structure was described in terms of the volume of vegetation in 5 vertical strata.

Group categorization. Following Zhang et al. (2011) and based on life history and habitat use information for the forest species (Díaz 2005; Díaz *et al.* 2005; Estades 1997), I identified four habitat-use guilds: LTU, VPG, SU and UU. Large tree users (LTU) included those species that mainly forage and nest in tall trees; Vertical profile generalists (VPG), included species that use all the vertical strata of forest vegetation; Shrub users (SU) included those species that used both shrubs

and forest to nest and forage; Understory users (UU) included species associated with dense understory in forest habitats, including ground dwelling birds, mainly Tapaculos.

Data analysis. As the niche space of animals has been conceived as multidimensional (Hutchinson 1957), three foraging niche dimensions (tree species, tree part and height in the vertical profile) were used to calculate multidimensional niche breadths and overlaps (Peck 1989). The niche breadth and niche overlap for every habitat-use guild were estimated considering the use of 95 resource categories resulting from the interaction between plant species, their structures and vertical strata where the birds were recorded foraging. These niche measures were estimated using Levins' (Levins 1968) and Pianka's (Pianka 1973) indexes respectively. Levin's niche breath is calculated over the proportion of individuals using a set of resources available. The proportions of individuals using each resource category, expressed in decimal values, are summed up after being squared. In that way, species with a wide use of resources are punished by the squaring of the small decimal values (proportion of individuals), for then representing a large niche breadth value as it is converted in its reciprocal value. In the case of Pianka's niche overlap, this index is calculated by the sum of the products between proportions of individuals from two species using the same resource category. Thus, when two species have identical use of a set of resource niche overlap is equal to 1.

$B = 1/\sum_{i=1}^{R} p_i^2$ Levin's index for niche breadth, where p_i is the proportion of individuals exploiting the category *i*.

$O_{jk} = \sum_i^n p_{ij} \times p_{ik} / \sqrt{\left(\sum_i^n p_{ij}^2 \times \sum_i^n p_{ik}^2\right)}$ Pianka's index for niche overlap, where p_{ij} is the proportion of resource *i* used by species *j* and p_{ik} is the proportion of resource *i* used by species *k*.

To answer the first question, whether the habitat substitution has changed the level of inter-specific competition in the forest bird community, I tested the effect of the habitat type, native forest or pine plantation, on the niche breadth and the average niche overlap shown by each species in a general linear mixed model. I also compared the intra and extra-guild niche overlap differences estimated for each species in either habitat. Similarly, a general linear mixed model was run to determine possible variations between native forest and pine plantation in the height of the canopy exploited during foraging activities by forest bird species. This model included height at which the bird was foraging as a response variable and three independent variables; season (winter or summer), type of habitat (pine or native) and time of the record. Each mixed model tested included species as a random effect in order to control by differences among them. Finally, both matrices of niche overlap between species in each habitat type are plotted using the R package "popgraph" (Dyer 2014). In this graphs, the niche overlap matrices are represented as a network of species connected by a link that its length correspond to the inverse value of the niche overlap. For all statistical analyses the software R was used (R Development Core Team 2012), and a statistical power $\alpha = 0.05$ was considered. All mixed models were run on Lmer.test package (Kuznetsova *et al.* 2013).

8.3 Results

A total of 498 records of foraging birds, belonging to 19 species were obtained in six weeks of fieldwork. In the analyses I considered only species with more than ten records (10 species), and one of them, Striped Woodpecker (*Veniliornis lignarius*) was not recorded in pine stands (Table 21).

Table 21. Number of records from foraging birds in either habitat, and the number of records of birds foraging specifically in pine. A detailed description of foraging pine substrates is given in Appendix 9.

Species	Code	Records in native forest		Records in pine plantation	
		Total	using pine	Total	using pine
Tufted-tit Tyrant (*Anairetes parulus*)	anapar	31	2	40	26
Thorn-tailed Rayadito (*Aphrastura spinicauda*)	aphspi	83	5	77	53
White-crested Elaenia (*Elaenia albiceps*)	elaalb	30	0	5	1
Patagonian Sierra-Finch (*Phrygilus patagonicus*)	phrpat	32	21	29	10
White-throated Treerunner (*Pygarrhichas albogularis*)	pygalb	26	0	24	21
Black-chinned Siskin (*Sporagra barbatus*)	spobar	10	3	33	19
Southern House Wren (*Troglodytes musculus*)	tromus	2	0	12	5
Austral Thrush (*Turdus falklandii*)	turfal	14	1	5	2
Striped Woodpecker (*Veniliornis lignarius*)	venlig	10	0	0	0
Fire-eyed Diucon (*Xolmis pyrope*)	xolpyr	8	1	4	4

Difference in foraging height. The foraging height was explained by the type of habitat (Cover) and time of the day, after controlling by species differences (Table 23). Birds tended to forage lower down in exotic pine stands than in native forests (Fig. 24), while there was also a temporal pattern explaining the foraging height; in general, birds foraged high in the canopy early in the day to descend to lower vertical strata as the day progress.

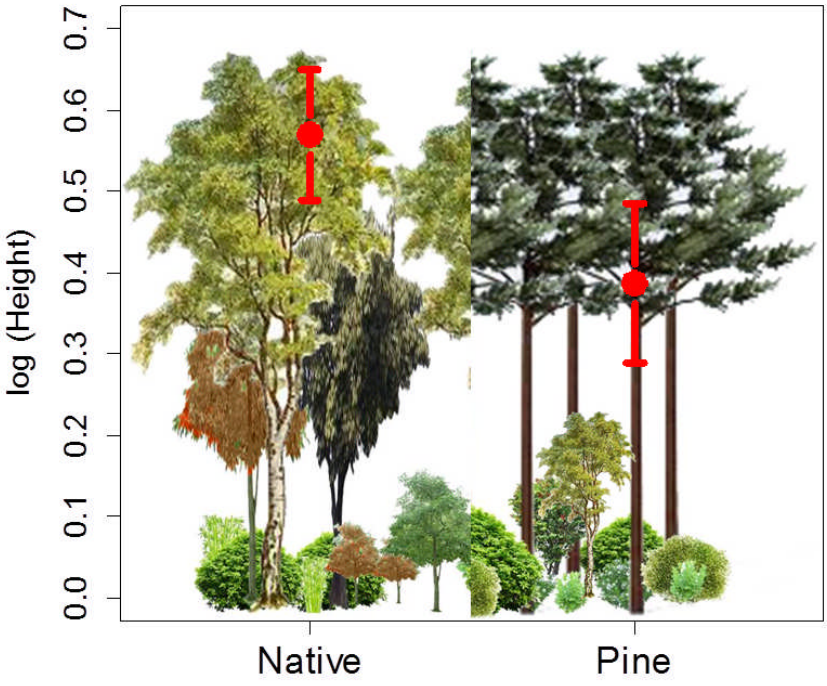

Figure 24. Difference in foraging height recorded in native forests and pine plantations.

Trophic niche shift. A reduction in the trophic niche breadth of bird species could be seen when comparing the values from native forest and pine plantation (Table 22), but the effect of the type of habitat was non-significant (see Table 23). The average value of niche breadth decreased in approximately 60% in pine plantations from what was seen in native forest. The greatest reduction in niche breadth was seen on two vertical profile generalist species, Austral Thrush (*Turdus flacklandii*) and Patagonian Sierra-finch (*Phrygilus patagonicus*). However, for two shrub user species, Tufted-Tit Tyrant (*Anairetes parulus*) and Southern House Wren (*Troglodytes musculus*) the niche breadth values showed a significant increase in pine plantations.

Table 22. Niche overlap between bird species and niche breadth (B) for bird species in either type of habitat.

	Guild	Species	anapar	aphspi	spobar	elaalb	phrpat	piclig	pygalb	tromus	turfal	xolpyr	B
Native	SU	anapar		0.42	0.06	0.26	0	0.26	0.10	0	0	0	64.3
	LTU	aphspi	0.42		0	0.35	0.02	0	0	0.18	0.37	0.17	53.4
	SU	spobar	0.06	0		0	0	0.24	0	0	0	0	5.9
	VPG	elaalb	0.26	0.35	0		0	0	0	0	0	0	36.0
	VPG	phrpat	0	0.02	0	0		0	0	0	0.11	0	102.4
	VPG	piclig	0.26	0	0.24	0	0		0	0	0	0	100.0
	LTU	pygalb	0.10	0	0	0	0	0		0	0	0	112.7
	SU	tromus	0	0.18	0	0	0	0	0		0	0	2.0
	VPG	turfal	0	0.37	0	0	0.11	0	0	0		0.35	24.5
	VPG	xolpyr	0	0.17	0	0	0	0	0	0	0.35		16.0
Pine	SU	anapar		0.37	0	0	0.01		0	0.26	0	0	80.0
	LTU	aphspi	0.37		0.28	0.05	0.17		0.58	0.06	0.09	0	35.3
	SU	spobar	0	0.28		0.67	0.98		0.18	0.28	0.86	0	5.1
	VPG	elaalb	0	0.05	0.67		0.69		0	0.21	0.63	0	12.5
	VPG	phrpat	0.01	0.17	0.98	0.69			0.08	0.33	0.89	0	3.6
	VPG	piclig											0.0
	LTU	pygalb	0	0.58	0.18	0	0.08			0	0.19	0	15.6
	SU	tromus	0.26	0.06	0.28	0.21	0.33		0		0.27	0.21	13.1
	VPG	turfal	0	0.09	0.86	0.63	0.89		0.19	0.27		0.21	2.3
	VPG	xolpyr	0	0	0	0	0		0	0.21	0.21		8.0

In terms of niche overlap, and despite the fact that one species was not recorded in pine plantations, there was a significant increase in their values in pine stands (ANOVA: $F_{1,17} = 13.31$, p-value = 0.001) (Table 22). The average values of niche overlap in pine stands were almost 2.5 times higher than those observed in native forests. The intra-guild overlap showed a stronger increase than was seen for the extra-guild overlap (see Table 23 and Figure 25). Large tree user species, Thorn-tailed Rayadito (*Aphrastura spinicauda*) and the White-throated Treerunner (*Pygarrhichas*

albogularis) were the species that showed the greatest increase in intra-guild overlap in pine stands compared to native forests. According to these results, White-throated Treerunner changed from an unchallenged situation in native forest to a high overlapping use of resource in pine plantations (Fig. 25). Interestingly, the Tufted-tit Tyrant along with the Fire-eyed Diucon (*Xolmis pyrope*) showed higher average values of niche overlap in native forests than in pine plantations.

Table 23. Results from different test carried out in this study. A) Model explaining the variation in foraging height, B, C and D results of individual tests of type of habitat (Cover) on niche breadth and extra and intra guild overlap.

A	Log (Height) ~ Season + Cover + Time + (1 | Species)				
	Family: gaussian				
	Model r^2 (marginal - conditional)		0.014	0.376	
Random effects		Variance	Stand. Dev.		
	Species	0.503	0.709		
Fixed effects					
		estimate	st error	p-value	
	Season	0.0988	0.1031	0.338	-
	Cover (Pine)	-0.2363	0.0908	0.009	**
	Time	-2.0528	0.9063	0.023	*
B	Log (Niche breadth) ~ Cover + (1 | Species)				
	Family: gaussian				
	Model r^2 (marginal - conditional)		0.111	0.111	
Random effects		Variance	Stand. Dev.		
	Species	0.000	0.000		
Fixed effects					
		estimate	st error	p-value	
	Cover (Pine)	-2.632	1.708	0.140	-
C	Log (Extra Guild Overlap) ~ Cover + (1 | Species)				
	Family: gaussian				
	Model r^2 (marginal - conditional)		0.122	0.254	
Random effects		Variance	Stand. Dev.		
	Species	1.042	1.021		
Fixed effects					
		estimate	st error	p-value	
	Cover (Pine)	1.927	1.123	0.120	_
D	Log (Intra Guild Overlap) ~ Cover + (1 | Species)				
	Family: gaussian				
	Model r^2 (marginal - conditional)		0.421	0.421	
Random effects		Variance	Stand. Dev.		
	Species	0.000	0.000		
Fixed effects					
		estimate	st error	p-value	
	Cover (Pine)	6.982	1.929	0.002	**

An extreme change in terms of competition was seen between two Finch species, Black-chinned Siskin and Patagonian Sierra-Finch, when comparing the situation in both types of habitat. These species went from showing no overlap in their trophic niche in native habitat, to an almost complete overlap in pine plantations.

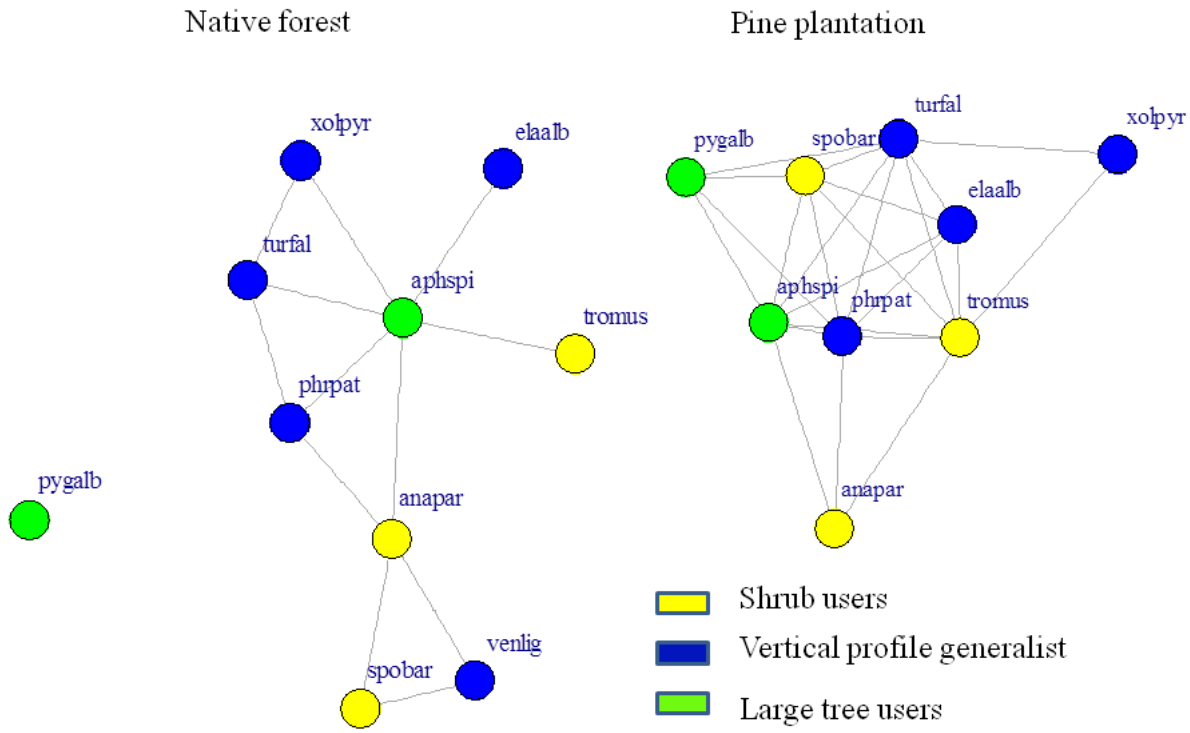

Figure 25. Trophic niche overlaps for bird species in native forests and in pine plantations. Interaction networks are at the same scale and the length of the connection between species is the inverse of the niche overlap value between any two species. Links between species show that their niches overlap, and longer links between species represent a small niche overlap. Habitat-use guilds are depicted in different colours. The R package "popgraph" were used to build this graph (Dyer 2014).

8.4. Discussion

By changing the way they exploit food resources and by unbalancing species interactions, the substitution of native forest with pine plantations impacts on the foraging behaviour of forest bird species. The birds foraging in pine plantations might adapt themselves not only to the different

vegetation structure, which defines the set of resources available, but also to new conditions in the inter-specific relationships. For many species, foraging in pine plantations means an increased competition for a subset of the resources found in native forests. If food in this coniferous habitat is inadequate in quantity or quality, exotic pine plantations could be considered to be poorer quality than the natural habitat in this region as foraging habitat for forest birds.

Most of the foraging activity carried out by birds in pine plantations was concentrated in the native understory growing below the pine canopy. The amount of native vegetation and its structural complexity inside the pine plantations explains the abundance and composition of the bird community (Estades & Temple 1999; Lindenmayer & Hobbs 2004; Poch & Simonetti 2013), which has led to considering the exotic matrix to be a supplementary foraging habitat for birds (Poch & Simonetti 2013; Tubelis *et al.* 2004). However, the mean height at which the birds were recorded foraging differs among type of habitat (Fig. 24); birds in pine plantations foraged at lower heights on average than in native forests. These results showed that birds used the understory vegetation more than the pine canopy, which is in line with observations made by Estades and Temple (1999) in this forest system. This is mainly explained by differences in the arthropod community between pine trees and native vegetation, with higher and similar levels of species richness and abundance of arthropods between native forests and native undergrowth inside pine stands, compared to that in pine canopy (Escobar 2008).

Greater use of the native undergrowth in pine plantations as a source of foraging resources implies greater competition for forest bird species. Competition theory predicts a positive relationship between niche overlap and the intensity of the inter-specific competition (Munday *et al.* 2001). The results showed that for most bird species, the trophic niche overlap increased when foraging in pine stands, compared to what it was seen in native forests. Along with that, a simultaneous and general reduction in niche breadth occurred, showing that birds used fewer resource categories in pine stands. These changes, in both niche metrics, indicate that under similar bird densities, resources in pine plantations would be under higher pressure, which would in turn be translated

into higher competition between bird species. These results are in line with the findings of Luiselli (2006), who shows an increased trophic niche overlap in sympatric predators with forest degradation. Regarding the present research, it is reasonable to think that the poorer body condition found in individuals of Thorn-tailed Rayadito and White-crested Elaenia holding territories in pine stands (see Chapter 4), may be explained by the increased competition in this alternative habitat. The ecological implications of higher competition could easily be translated into impaired survival and breeding success (Newton 1998), and through varying selective pressures, competition could also impact populations at an evolutionary level (Ricklefs 1973).

Nevertheless, while some bird species were unable to benefit from the exotic pine tree species, other members of the forest bird community have found opportunities in this new habitat. It has been reported that Pine shoot Moth larvae (*Rhyacionia buoliana*; Tortricidae), an introduced pest, are consumed by Black-chinned Siskin and Plain-mantled tit-spinetail (*Leptasthenura aegithaloides*) (Simeone *et al.* 1997). The former bird species, and the Thorn-tailed Rayadito, has been seen feeding on pine seeds (Estades 2001; Tomasevic 2004), and all bird species in this study, with the exception of Striped Woodpecker, were recorded foraging on pine substrates (Table 21 see also Appendix 9). The using of foraging resources in the exotic coniferous plantation may well be explained by the plasticity shown by these forest bird species. The species of the bird communities of *Nothofagus* forests are characterized by wide habitat-niches, as they live across different habitat types, elevational and latitudinal ranges (Vuilleumier 1985). This makes them less susceptible to extinction because they are able to shift among alternative food resources (Purvis *et al.* 2000). Interestingly, the new resources seem to become important for some species, triggering competition between them. The two main seedeaters, considered in this study, showed an almost complete niche overlap in pine stands (Table 22), as both foraged on the pine seeds, either taken from the cones or loose on the ground. The huge decrease in niche breadth shown by Patagonian Sierra-Finch suggests that by shifting their foraging habits in pine stands, this species is being most affected by the substitution of native forests. Finally, these results suggest that birds have learnt to

exploit the limited resources available in pine plantations, and have also modified their behaviour by foraging at different heights in the canopy.

Species with wider niches are better adapted to uncertain environments (Rotenberry & Wiens 1980), and can thrive in modified environments by using a wide range of resources. The greater abundance in pine plantations shown by the Tufted-tit Tyrant and the Southern House Wren (see Chapter 3), plus the better body condition of individuals of the former species holding territories in pine stands (see Chapter 4), may well be accounted for by the wider niche breadths estimated for these species in the exotic plantations. These wider niche breadths along with the lower abundances of competing species, mainly Thorn-tailed Rayadito and White-crested Elaenia (see Chapter 4), suggest a competitive release for these two small insectivorous species. In this case, the smaller species shift their foraging behaviour in the presence of individuals of larger or more dominant species (Alatalo & Moreno 1987), and when they are absent, smaller species fill the foraging niche that is vacant (Laiolo *et al.* 2003).

To my knowledge, this is the first study made on the effects of the habitat substitution on the inter-specific competition of temperate forest birds in the Southern Hemisphere. As the abundance and quality of foraging resources are the main factors limiting bird populations (Newton 1998), the results presented here support and explain most of the findings given in previous chapters, showing once again that exotic pine plantation is a habitat of lower quality for most of the forest bird species. Some potential limitations to this study are the effect of predators on the foraging behaviour recorded, which could not considered in the methodology, and that for some species the sample size is not large enough to be conclusive. Finally, I would strongly recommend that ornithologists record this type of information in parallel with their counts, because it is simple and it has shown to be explicative for some population conditions.

Chapter 9

General discussion

In this thesis I investigated the effect of the replacement of temperate native forest with exotic pine plantations in south-central Chile on the forest bird community, and through different ecological parameters I assessed the habitat quality of pine plantations for forest passerines. Here I summarize the main results and conclusions presented in previous chapters, together with their collective significance.

9.1 Motivation for this thesis

Temperate forests are extremely diverse ecosystems and may be even more diverse than the rainforests in terms of variation within some taxa (Dudley 1992), topography, soil characteristics and other environmental properties (Ricklefs 1977). However, temperate zones have been influenced more by anthopogenic modification due to settlement, agriculture, etc. than have other regions. Dramatic examples of the loss of these forests are found elsewhere: perhaps only a third of the original forest cover remains in Europe, and only a fifth of deciduous forests that in ancient times covered vast areas (Moenkkoenen & Welsh 1994). In the early twentieth century the remnant native vegetation in New Zealand corresponded to less than 25% of its natural range (Leathwick 2002). Sixty-seven percent of the area covered by the Maulino forest, a temperate deciduous forest from South Central Chile, has been lost in a period of 25 years (1975-2000) (Echeverría *et al.* 2006). The loss of temperate forests has affected biodiversity at ecosystem, species, population and genetic levels. Accordingly, the distribution range of several species has been reduced, and other species have become extinct (Norton 1996).

Reforestation with fast-growing tree species has reached a significant level of land surface globally, corresponding to 264 million hectares by 2010 (FAO 2010). Pine plantations correspond to approximately 32% of total global forest plantations (Luck & Korodaj 2008), established around

the world, but especially in the southern hemisphere, Australia, New Zealand, South Africa and Chile, where the family *Pinaceae* is not part of the natural vegetation. Several studies have shown that coniferous plantations can be colonized and inhabited by different taxa (Brockerhoff *et al.* 2008). The ability of certain species to use pine plantations depends on the degree of specialization or generalization of the local fauna (Wunderle Jr 1997). Consistent with this, a simplification of habitat leads to a simplification of the forest bird community. Most bird species found using forest plantations are generalist species (Sweeney *et al.* 2010) denoting an impoverished avifauna compared to the potential of the regional avifauna at the expense of forest specialist species.

Despite the many studies of the effect of habitat fragmentation, the status of birds in terms of their success in the exploitation of pine plantations has not been clarified by the characterization of the bird communities (species richness and abundance). Accordingly, most of the studies carried out on Chilean temperate forest birds have used them mainly as a tool to discern the effects of fragmentation or habitat lost. Moreover, the use of local density as a proxy for habitat quality must include first an investigation of how the subject of study is fitted to an ideal free distribution, as various ecological factors can lead a bird to select a low quality habitat instead of others (Johnson 2007). Thus, the density of animals in a habitat could, in some cases, act as an ecological trap and be a misleading indicator of habitat quality (Van Horne 1983).

9.2 Some aspects of the effects of habitat quality of exotic pine plantations on the ecology of forest birds

Divergence in structure and composition between native forest and pine plantation, including not only physical parameters but also chemicals, is translated in differences in foraging resources available for forest avifauna. Chapter 8 shows that the niche breadth of most forest species is reduced in pine plantations, even though new resources are offered and consumed, and while niches are reduced there is an increase of niche overlap among the members of the community. Forest degradation is expected to cause an increase of trophic niche overlap (Luiselli 2006), supporting the

idea that exotic pine plantations could be considered a poor quality habitat for some species. These differences between native forest and pine plantations in the foraging niche reflect higher competition for fewer resources in pine plantations, as a poorer assembly of arthropods has been reported in exotic plantations (Estades & Escobar 2005).

Variation in the richness and abundance of prey might trigger higher levels of intra and inter-specific competition, which must affect the energy balance of individuals and the structure of populations. In Chapters 4 and 5 I reported differences in the health and body condition between individuals captured in the two habitats. In general, my findings show that forest specialist and migrant species are most affected by the poorer habitat quality provided by pine plantations, showing lower values for their body condition index and higher parasite burdens, which might affect the survival rates of forest passerines inhabiting these forests (Thomson & Estades 2012). Moreover, the austral migrant, White-crested Elaenia (*Elaenia albiceps*), shows differences in the age structure of populations inhabiting native fragments and pine plantations. A despotic distribution, where young and less dominant individuals are forced to find territories in pine stands is reported. A similar effect of despotic distribution has been described for Great Tits (*Parus major*) (Ulfstrand *et al.* 1981) and Pied Flycatcher (*Ficedula hypoleuca*) (Lundberg *et al.* 1981) in Sweden, where dominant and larger males hold territories in the best quality habitat, deciduous forests, forcing young males to use conifer stands. This difference in population structure could be a general pattern in the community, but ageing criteria (as is the case for many aspects of the autoecology) have not been studied for these species. Nevertheless, as part of this research, a new ageing criterion for White-crested Elaenia was developed (Thomson et al. submitted).

Although I was not able to collect enough information to assess the breeding success of the forest bird community as a whole, Chapter 6 reported the habitat limitations on the breeding of secondary cavity nester species. For Thorn-tailed Rayadito (*Aphrastura spinicauda*) a higher occupancy rate and heavier fledglings were found in native fragments than in nest-boxes erected in pine stands. These findings are in accordance with European studies in forest cavity nester species, showing that the

development of nestlings of Great Tits is constrained in poor quality habitats (Riddington & Gosler 1995) and that the breeding success of Pied Flycatcher was higher in deciduous forests than in pine habitats in Sweden (Lundberg *et al.* 1981). Moreover, for the first time an additional and more subtle effect of the substitution of native forest with exotic plantations on the breeding of forest birds was investigated here. Evidence was reported of increasing deposits of protorphyrin pigment in Southern House Wren (*Troglodytes musculus*) eggs in conifer plantations, consistent with the calcium-compensation hypothesis (Gosler *et al.* 2005). This is in consistent with reports that the soil acidification is caused by coniferous plantations (Chapter 7), which is known to affect the normal reproduction of forest birds (Graveland & Van der Wal 1996; Tilgar *et al.* 2002).

As has been shown, a wide variety of selective pressures appears to be acting on populations inhabiting these fragmented landscapes, and in most of the cases the alleged effect is correlated with the abundance of the species in either habitat. However, this is not a binary system of high and low qualities, but a mosaic of gradients in which edge effects and site features, such as vegetation, determine the quality of the plot for each bird species.

Vegetation structure. The vegetation structure predicts the abundance of forest species in both native fragments and pine plantations (Chapter 3). Even though, each species and group of species has its own habitat preferences, a general preference for sites with rich understory vegetation has been found, which is in line with previous studies (Estades & Temple 1999; Vergara & Simonetti 2004). The volume of undergrowth explained differences in the body condition and health status of individuals (Chapters 4 and 5). Bird reproduction is also determined by structural features, including the volume of understory, affecting nesting site selection, breeding success and parental provisioning (Chapter 6). Differences in foraging height between native forests and pine stands clearly illustrated the importance of the undergrowth for forest birds in pine plantations, showing that most of the foraging activity is focused in the understory vegetation growing under the pine canopy (Chapter 8). Therefore, this feature appears to be one of the main predictors of habitat quality for this forest community.

Nevertheless, the management of pine plantations, as monocultures with short rotations, prevents them from generating some critical structural features for some forest specialist species. For example, the lack of snags and decaying trees in pine plantations limits the number of woodpecker species and secondary cavity nesters that have difficulty in finding foraging resources and suitable nesting holes, respectively.

Vegetation composition. The composition and species richness of the canopy is one of the major differences between native forests and pine plantations, representing for birds a simplification and impoverishment of the resources found in the natural vegetation. It is this mono-specific canopy that increases the importance of the understory vegetation, directing the foraging activity to lower levels (Chapter 8). The presence of many tree species and the richness of the vertical layer of vegetation were included in many of the species abundance models (Chapter 3). Thus, vegetation composition was as important as the vegetation structure in explaining the habitat quality for birds.

Competition. Evidence for increasing competition in pine plantations has been shown for most of the species in Chapter 8. I also reported a possible release of inter-specific competition in pine stands for a couple of small bird species, Tufted-tit Tyrant (*Anairetes parulus*) and Southern House Wren, whose increasing niche breadth in pine plantations could be explained by the lower abundance of other forest species. Regarding intra-specific competition, I was only able to age adults for one species, finding that young and less dominant adults are forced to find territories in pine stands (Chapter 4). I believe that social dominance must be a general factor for birds in these forestry systems, influencing habitat selection by breeding birds. Consequently, higher levels of forest substitution or less preferred habitat in the landscape would increase intra-specific competition for some breeding populations, which in turn could reduce the quality of native fragments by increasing population density (Fretwell & Lucas 1969).

9.3 Fragmentation effects at different scales acting on the ecology of forest birds

In the previous section I have showed how site features determine the quality of the habitat for forest species in both native forest and exotic plantations. However, the composition of landscapes and the distribution of their components, such as native forest, pine plantation, roads and other land uses, at different scales affect ecological parameters studied in this research, contributing to the definition of the habitat quality of pine plantations for many forest species.

Immediate neighbouring areas, that should encompass breeding territories for most forest passerines, explain the abundance of forest species, especially for their abundance in pine stands (Chapter 3), and most importantly, they influence many of the breeding activities for some species (Chapter 6). These features reflect the edge effect in these forested systems, so that these landscapes could be perceived more as a variegated than as a patchy situation, where gradients of habitat quality occur (McIntyre & Barrett 1992). Edge effects are commonly considered to be a negative consequence of disturbances to natural environments, although, according to the type of disturbance, it may act in either direction. For example, Chapters 4 and 5 showed that the body condition and health status of White-crested Elaenia holding territories in pine plantations improve as their territories were closer to native fragments. Therefore, the proximity of native forest improves the quality of pine stands for some forest bird species, which is perhaps explained by the similar gradient pattern reported for the arthropod community (Venegas 2009).

At a landscape level the substitution of native forest with pine plantations modifies the composition of the forest bird community, and the abundance and presence of species are determined by the habitat configuration resulting from fragmentation. In general, the process of occupancy of pine plantations by forest avifauna is facilitated by fragmentation patterns, chiefly those related to edge effects and allowed by the permeability of pine plantations to the movement of forest birds. This pattern was also reported by Lindenmayer et al. (2002) for forest birds in Australia. It seems that the structure of the pine matrix makes patch isolation less important as has been reported when the matrix is a grassland (Vergara & Armesto 2009), but the connectivity of native fragments is still

important for the abundance of large tree user species in these landscapes. However, fragmentation and the substitution of native forests have negative effects on the populations inhabiting native forests. Those landscapes with a higher proportion of pine plantations show a marked acidification of their soils, making Calcium a critical element for bird reproduction (Chapter 7). Moreover, the functional trait diversity and species richness decreases with higher levels of substitution and fragmentation. As the replacement and fragmentation of native forests increases the bird community shifts into a more simplified one; after losing the species related to the core area of native forests, the number of forest specialist species starts to decline while generalist species become the dominant group in the community.

9.4 Concluding remarks

As has been emphasized in every chapter, pine plantations seem to be a poorer habitat for the bird community of the temperate forest in south central Chile. Even though these bird species are characterized by wide-habitat niches which make them less susceptible to extinction, some of them seem to struggle in this exotic habitat. As no similar study has been carried out in the southern hemisphere, where pines are not part of the natural vegetation, most of the references used in the analyses of my results refer to studies done in Europe, where bird communities have evolved in forests where pines are native species. My results suggest that birds holding territories in pine plantations depend greatly on the native undergrowth to acquire most of the resources needed, although intra-specific competition for those resources may impair even more the quality of exotic plantations and some populations are limited there by the availability of critical resources (e.g. cavities for secondary cavity nesters).

The future of temperate forest ecosystems in the Southern hemisphere doesn't look promising. Today, as native forests are still being lost and exotic plantations are expanding in area (FAO 2010), local governments and global institutions show the positive net gain of area covered with forest between assessment periods, while including mono-clonal stands of exotic fast-growing tree species

in their figures. This generalization also considers naming forest plantations in a "more friendly" way, as planted forest, on what is called the "harmonization" of terms in the outreach policies considered by FAO (FAO 2012). To ensure conservation and integrity of these ecosystems it is necessary to avoid doing this type of generalization and, most importantly, to understand the effects that the substitution of native forest has on wildlife populations, which was the aim of this thesis. Nonetheless, any plan for the conservation of this forest avifauna should be directed to the conservation of the most threatened species, the Austral Parakeet and the Magellanic Woodpecker. These two species are on the brink of regional extinction, and they are not represented in the protected areas of the studied region. Moreover, I have knowledge of only 5 and 2 sites where these species are present in the region respectively. There is no pine plantation management that helps to preserve these species, other than its substitution and native forest restoration in a regional network of big patches of native forest.

From the results of this research, apart from the previously mentioned network of forest reserves required to avoid the regional extinction of area-sensitive species (Magellanic woodpecker and Austral parakeet), the following management recommendations arise:

Maintaining a respectable proportion of native forest at landscape level is critical to preserve the integrity and functionality of the forest bird community. To retain 50% of the functional richness, a productive landscape should maintain 30% of its area covered with native forests. In this study, that it means to have 120 Ha of native forest per 280 Ha of pine plantations. However, this recommendation needs much further work as this study only included mature pine stands and, at the same time, the forest mosaic is dynamic in productive landscapes. To be sure that the recommended proportion would be adequate, a thorough understanding of the effects of pine plantations harvest on the forest bird community is needed.

The configuration of the native forest in the landscape is relevant for both forest specialist and ground-dwelling species. Accordingly, it is important to maintain high levels of connectivity between fragments of native vegetation after the harvest of pine stands.

The volume and diversity of the understory vegetation is the most critical feature in pine plantation stands for the forest bird community. Therefore, any management practices, such as thinning or maintaining native seed trees through pine rotations, could help to improve the undergrowth conditions.

The use of nest-boxes to enhance the quality of pine plantations for secondary cavity nesters is also suggested.

In conclusion, this thesis contributes to knowledge of the Chilean forest avifauna, which has many things yet to study and comprehend about the ecology of these species, but which stands as a model for the impact of forest substitution in the Southern Hemisphere. Here, I have demonstrated that exotic pine plantations are poor habitat for the forest bird community, and it must also be for other taxa, such as the soil fauna. Finally, all the information presented in this thesis shows that pine plantations may be a poorer quality habitat for the forest bird community, by comparing adult stages of native versus exotic pines, although the whole pine forestry cycle must have a stronger impact on the forest bird community as it introduces habitat loss and edge effects through clear-cutting, intensifying selective pressures already acting on forest populations.

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APPENDICES

Appendix 1

Temperate forests and birds— A review

Temperate forest distribution

The main communities on Earth can be classified as biomes according to their predominant vegetation, which is directly related to temperature and precipitation (Campbell 1996). Accordingly, forests are one of the most extensive terrestrial biomes, covering a third of the earth's surface, and their classification varies according to different criteria used. However there is a clear division between tropical, temperate and boreal forests. Similarly, there are different definitions for temperate forests, some more exhaustive than others. Some of these definitions are based on geographical references, others based on physiognomy and vegetation attributes and there are also definitions related to weather conditions and seasonality, the latter being the most widely used. A simple definition states that temperate forests are those forests that are located in geographic areas that have a temperate climate; that is, a marked seasonality with cold winters and warm summers, with rainfall over 300 mm per year, which is concentrated in autumn and winter. Temperate forests occur in latitudinal bands that run between the desert and subtropical areas and tundra and polar deserts, and these forests are generally located at latitudes higher than 30° and less than 60° (Fig. A1). Nonetheless, more detailed definitions generate more ambiguity than certainty due to the long-term dynamics in geo-climatic conditions. For example, it is possible to find plant formations that correspond to definitions based on vegetation characteristics, but that do not match other definitions based on weather conditions. This could be the result of historical changes in environmental conditions, generating a lag in the vegetation response that can potentially lead to the generation of new species as a result of natural selection, or in the constitution of relict forests in unique areas that still maintain conditions for the survival of these forests.

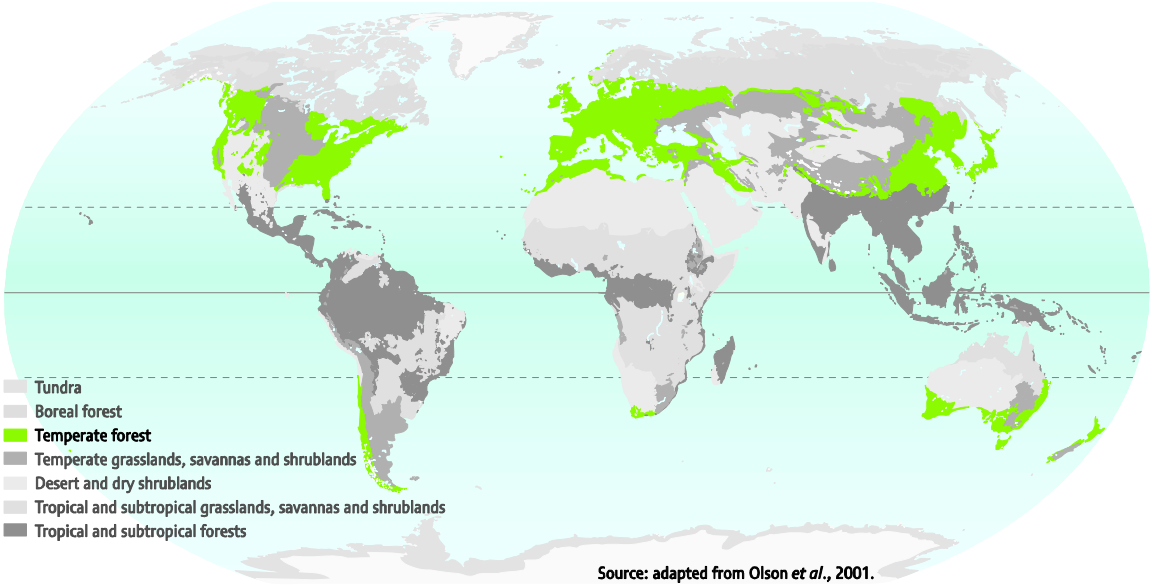

Figure A1. Temperate forests of the world (source: riccardo pravettoni, unep/grid-arendal; http://www.grida.no/graphicslib/detail/temperate-forests_1753).

Physical environment variability in the distribution of temperate forests results in different types of formations (Whittaker 1973). Thus, it is possible to distinguish at least three types of clearly recognizable formations, mixed forests of coniferous and deciduous trees, temperate deciduous forests and temperate evergreen broadleaf forests. Latest estimates note that there are 11 billion hectares of temperate forest worldwide, with a presence in every continent. According to the distribution of land masses on the planet, most temperate forests are found in the northern hemisphere (92%), mainly in Russia (41%) and North America (32%). This proportion of land between hemispheres is also reflected in the characteristics of the types of temperate forests that are possible to find in both areas. Therefore in the northern hemisphere, with a markedly continental influence resulting in colder winters, coniferous and deciduous broadleaf forests dominate landscapes, while in the southern hemisphere with more mild winters evergreen broadleaf forests prevail. In consequence, temperate forests are extremely diverse ecosystems and may be even more diverse than the rainforests in terms of variation within some species (Dudley 1992), topography, soil characteristics and other environmental properties (Ricklefs 1977).

Deciduous temperate forests. These forests are composed mainly of deciduous tree species in the upper canopy and with an understory that generally consists of shrubs with resistant evergreen leaves and seasonal herbaceous cover (Gilliam 2007). Among its main features are the large trees, simple structure and broad-leaved deciduous species.

Mixed coniferous and deciduous trees. Mixed coniferous and deciduous forests correspond to a particular form of temperate deciduous forest that occurs in regions where low temperatures prevail during the non-growing season, at high latitudes and at mid and high altitudes in mountainous areas (Röhrig and Ulrich 1991). Coniferous trees are an important part of these forests with a high diversity of species.

Temperate evergreen broad-leaved forests. These forests occur in completely disjunct areas, and due to very different evolutionary histories they differ greatly in species composition of flora and fauna. However, it is possible to observe affinity in the structures of these forests, with a marked tendency for three tiers in the canopy (Ovington 1983).

Despite its low share of the total global temperate forests, temperate forests of the southern hemisphere are of great importance in relation to its rich biodiversity (Dudley 1992). These forests are home to a greater number of plant forms than their northern hemisphere counterparts and display higher levels of endemism in their vascular plants (Armesto et al. 1994; Villagran and Hinojosa 1997).

Global status and threats for temperate forests

Temperate zones are the regions of the world that have been most influenced by anthopogenic modification due to settlement, agriculture, etc; their impact on local biodiversity has been dramatic (Norton 1996). Thus, areas of the northern hemisphere where temperate forests are the natural vegetation coincide with ancestral human population centres. This has meant that most of these forests have been cleared, and what remains is in a highly modified state (Ovington 1983). This cannot be more evident than it is in Europe, where the first logging of forest seems to have started in the Neolithic period, about 5500 years ago, and the rate of forest loss, either for timber or clearing for agriculture, increased through time with the increase in population (Petty et al. 1990; Wilcove and Dobson 1986). Nevertheless, forest loss has occurred differently according to the different regions of Europe; Forests of southern and central Europe have been subjected to a continuous history of logging and grazing and are currently highly modified from their natural condition (Ovington 1983). In northern Europe, not only did deforestation of vast areas occur, but a further impoverishment of the remaining forests came about due to the loss of the broadleaf component (Poulsen 2002). However, forest loss has nowhere been more extreme than in Britain, where forests that once covered almost the entire land surface have been reduced to fragments, with native forests reaching only up to 7% of the land cover (Hinsley et al. 1995). According to

Moenkkoenen and Welsh (1994), perhaps only a third of the original forest cover currently remains in Europe, and only a fifth of the deciduous forests that once covered vast areas.

In North America, native peoples managed the landscape to create pastures for hunting animals and clearing for agricultural crops. However, extensive deforestation resulted from European settlement in the seventeenth century (Pimm and Askins 1995; Wilcove and Dobson 1986). Forest loss peaked in the late nineteenth century, which was characterized by intense forest clearance and land clearing for agriculture. However, in the last century the amount of deciduous forest has shown sustained increase in the northeast and south of the territory (Pimm and Askins 1995), although some forest types show a worryingly poorer recovery (Noss 1999).

The situation isn't more auspicious in Asia, where most of the world's population is concentrated. Due to the high population pressure, Asian temperate forests have suffered a major setback. Principal causes are also forestry and land clearing for agriculture and livestock (Gaston et al. 1983; Ovington 1983). In general, the remnants of ancient forests have been reduced to fragments scattered along the coast of China and on some nearby islands. A similar situation can be seen in Japan (Ovington 1983).

The South American temperate forests are concentrated in central and southern Chile and adjacent areas of Argentina, extending over two thousand miles. While human modification of these forests dates back ten thousand years, the arrival of European settlers greatly intensified the loss of these forests, through logging and the increased use of fire to clear land for agriculture and grazing (Aagesen 1998; Núñez et al. 2006). Furthermore, in recent decades, these forests have suffered their replacement by plantations of fast-growing exotic species (Lara and Veblen 1993).

The impact of human activities on the biodiversity of non-tropical ecosystems in southern Africa has been significant (Castley and Kerley 1996). According to Feely (1980), South African forests have been exploited during the last 1600 years, with fire as a main tool used for the destruction and fragmentation of forests. With the arrival of European settlers timber extraction began on a large scale, which worsened the situation, leading to the loss of 70-80 % of forest cover in certain areas (Castley and Kerley 1996).

In Australia, a total of 500,000 km2 of temperate forests has been lost to make way for crops, pastures for grazing or for human settlements in the last 150 years (AUSLIG 1990; Yates and Hobbs 2000). In several areas of Australia, temperate forests have been reduced to fragments of different sizes, quality and isolation (Yates and Hobbs 2000).

Prior to the arrival of the first humans, 1000 years ago, temperate forests covered much of New Zealand. The first settlers used fire to clear some areas, which was subsequently done by European

settlers for agricultural crops (Ewers et al. 2006; Ovington 1983). By the early twentieth century the remnant native vegetation corresponded to less than 25% of its natural range (Leathwick 2002).

Effects of the loss of temperate forests on Birds

The loss of temperate forests has affected biodiversity at the ecosystem, species, population and genetic levels. Accordingly, the distribution range of several species has been reduced, and other species have become extinct (Norton 1996).

The forests of Western Europe exhibit great variation in their associated communities, where the number of species and their densities can vary greatly within a small geographic area, and even among neighbouring stands (Fuller and Green 1998). Reviewing particular cases, it can be seen that in the mixed forests of northern Europe, degradation and fragmentation have resulted in the removal of some species (Poulsen 2002). In relation to the extensive deforestation that took place in Britain, there is little evidence as to how anthropogenic changes affected birds, although it certainly must have been dramatic (Petty et al. 1990). A large proportion of the birds inhabiting temperate forests in Britain now occupy relatively small fragments of up to tens of hectares (Hinsley et al. 1995). Among the bird species whose extinction can certainly be attributed to the destruction of forests and hunting in Britain are Capercaillie, Goshawk and presumably Black Woodpecker, although, the first two species have been reintroduced into the territory (Wilcove and Dobson 1986). Nonetheless, Reif et al. (2008) posit that forest bird species associated with deciduous forests show a positive population trend in central Europe in recent years, due to the replacement of coniferous forests by deciduous ones. The latter experienced an increase of 20% in area between 1970 and 2004 in the eastern zone (Czech Republic).

In North America, as the forest ecosystems declined through human activity, so did the species associated with them (Noss 1999), and as a result a large number of species became extinct in certain areas. By the combined action of habitat loss and hunting the Passenger pigeon and the Ivory-billed woodpecker became extinct (Wilcove and Dobson 1986). According to Pimm and Askins (1995), habitat modifications generated in pre -Columbian times were not so extensive as to cause the extinction of forest birds. Furthermore, they note that during the peak period of deforestation in North America, the existence of large forest shelters prevented further loss of forest avifauna.

In Asia, the greatest threat to endemic bird species is habitat loss (Lei et al. 2003). In some areas, the homogenization and anthropogenic influence on habitats have led to the displacement of

indigenous bird species by human commensal species (Oza 2003), and many species are at risk of becoming locally extinct due to forest disturbance (Shahabuddin and Kumar 2007).

Due to habitat loss and the degree of fragmentation of Australian temperate forests, resident forest bird species have been recognized as the group most negatively affected amongst Australian birds (Watson 2004). The loss of these ecosystems has generated widespread extinction of wildlife at local, regional and global levels (Yates and Hobbs 2000). About 25% of Australian forest bird species are currently considered threatened (Taylor 1992).

In relation to the temperate forests of South Africa, the wildlife that inhabits them is 75% more vulnerable to extinction than is the fauna associated with other biomes in the region (Castley and Kerley 1996). The same authors note that 13 of the 102 species of birds that inhabit the temperate forests of South Africa are threatened, and these are mainly forest specialist species.

New Zealand's avifauna has faced extinction through the introduction of several species since the beginning of human settlement in their territory (Diamond and Veitch 1981). In the period of the first human settlements, New Zealand lost almost half of the native bird species (Clout and Gaze 1984), although recent extinctions on islands have been associated with anthropogenic causes, such as habitat destruction and predation, both by humans and by introduced predators (Duncan 1997).

The avifauna of temperate forests of South America is not very diverse compared with temperate forest elsewhere; Rozzi et al (1996) described only 30 species of birds that perform basic functions commonly or exclusively in forests. However, this avifauna is characterized by a high degree of endemism (Vuilleumier 1985). Habitat loss, fragmentation and degradation of forests are the main threats to forest birds in Chile and Argentina (Díaz 2005), causing local extinctions of those forest specialist species that have large area requirements (Estades and Temple 1999).

To understand how loss of native vegetation, or its replacement with coniferous plantations, could affect forest bird communities, it is necessary to keep in mind the uniqueness of every environment. Temperate forest bird communities, as any bird community, are the product of many different historic processes; either at the origin of the forest or the avifauna. These communities differ in their species composition and the range of niches they exploit.

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Appendix 2

Traits

Scientific name	Habitat Use	Feeding strategy	Prim. trophic source	Sec. trophic source	Prim. trophic stratum	Sec. trophic stratum	Diet
COLUMBIDAE							
Patagioenas araucana	VPG	Fruit and grains	F	G	medium stratum	terrestrial	Herbivore
PSITTACIDAE							
Enicognatus ferrugineus †	LTU	nutter	G		canopy	terrestrial	Herbivore
TROCHILIDAE							
Sephanoides sephanoides	VPG	flower	N	I	canopy	air	Omnivore
PICIDAE							
Campephilus magellanicus	LTU	woodpecker	I		medium stratum		Carnivore
Colaptes pitius	LTU	woodpecker	I		medium stratum	terrestrial	Omnivore
Veniliornis lignarius	VPG	woodpecker	I		medium stratum		Carnivore
EMBERIZIDAE							
Curaeus curaeus	VPG	all	I	G	terrestrial	canopy	Herbivore
Zonotrichia capensis	SU	seedeater	G	I	terrestrial	medium stratum	Herbivore
FRINGILIDAE							
Sporagra barbatus	SU	seedeater	G		terrestrial	canopy	Herbivore
Phrygilus patagonicus	VPG	seedeater	G		terrestrial	canopy	Herbivore
FURNARIIDAE							
Aphrastura spinicauda	LTU	gleaner	I	F	canopy	medium stratum	Carnivore
Leptasthenura aegithaloides	SU	gleaner	I		canopy		Carnivore
Pygarrychas albogularis	LTU	barker	I		medium stratum		Carnivore
Pseudasthenes humicola	SU	gleaner	I		medium stratum	terrestrial	Carnivore
Sylviorthorhynchos desmursii	UU	gleaner	I		canopy		Carnivore
HYRUNDINIDAE							
Tachycineta meyeni	LTU	swallow	I		air		Carnivore
RHINOCRYPTIDAE							
Eugralla paradoxa	UU	litter	I	G	terrestrial	understory	Omnivore
Pteroptochos castaneus	UU	litter	I	G	terrestrial		Omnivore
Scelorchilus rubecola †	UU	litter	I	G	terrestrial		Omnivore
Scytalopus fuscus	UU	gleaner	I	G	terrestrial	understory	Omnivore
TROGLODITIDAE							
Troglodytes musculus	SU	gleaner	I		understory		Carnivore
TURDIDAE							
Turdus falcklandii	VPG	all	F	I	terrestrial	canopy	Omnivore
TYRANNIDAE							
Anairetes parulus	SU	flycatcher	I	F	canopy		Carnivore
Colorhamphus parvirostris	VPG	flycatcher	I		medium stratum		Carnivore
Elaenia albiceps	VPG	flycatcher	I	F	canopy	air	Omnivore
Xolmys pyrope	VPG	flycatcher	I	F	air	canopy	Omnivore

Scientific name	Body mass	Wing length	Bill length	Regional Abundance	Migratory status	Clutch size	Engineer	Nest
COLUMBIDAE								
Patagioenas araucana	200	209.8	15.5	low	Migrant	1	Dispersion	Open
PSITTACIDAE								
Enicognatus ferrugineus †	200	198	23.6	medium	Resident	6	No	SCN
TROCHILIDAE								
Sephanoides sephanoides	5.6	60.4	25.4	medium	Migrant	2	Polinization	Open
PICIDAE								
Campephilus magellanicus	260	214.9	50.4	very low	Resident	2	Cavity	Cav
Colaptes pitius	125	159.1	39.3	low	Resident	5	Cavity	Cav
Veniliornis lignarius	39.97	93.7	23.2	low	Resident	4	Cavity	Cav
EMBERIZIDAE								
Curaeus curaeus	90	126	33.7	medium	Resident	4	No	Open
Zonotrichia capensis	20.75	71	11.6	medium	Resident	3	No	Open
FRINGILIDAE								
Sporagra barbatus	22.3	72.7	15.1	high	Migrant	4	No	Open
Phrygilus patagonicus	20.13	76	16.7	high	Resident	3	No	Open
FURNARIIDAE								
Aphrastura spinicauda	10.57	60.1	15.1	high	Resident	4	No	SCN
Leptasthenura aegithaloides	9.1	56.6	8.7	medium	Resident	3	No	Open
Pygarrychas albogularis	13	80.8	23.9	very low	Resident	2	No	Cav
Pseudasthenes humicola	21	62	12.6	medium	Resident	4	No	Open
Sylviorthorhynchos desmursii	10.5	52.3	18.3	medium	Resident	4	No	Open
HYRUNDINIDAE								
Tachycineta meyeni	15.35	114	12.1	high	Migrant	4	No	SCN
RHINOCRYPTIDAE								
Eugralla paradoxa	29	63.2	19.34	medium	Resident	2	No	Hole
Pteroptochos castaneus	185	105.2	20.8	medium	Resident	2	No	Hole
Scelorchilus rubecola †	53.7	81	22.5	high	Resident	2	No	Hole
Scytalopus fuscus	11.93	50.8	14.8	high	Resident	2	No	Hole
TROGLODITIDAE								
Troglodytes musculus	9.47	52	15.9	high	Resident	6	No	SCN
TURDIDAE								
Turdus falcklandii	86.27	135.5	27.3	medium	Resident	2	Dispersion	Open
TYRANNIDAE								
Anairetes parulus	7.2	47.6	13	high	Resident	2	No	Open
Colorhamphus parvirostris	9.7	61.8	8.1	low	Migrant	3	No	Open
Elaenia albiceps	15.6	75.7	14.47	high	Intracontinental	2	Dispersion	Open
Xolmys pyrope	30.45	109.3	15	high	Migrant	2	No	Open

Appendix 3

Variables associated with the foliage volume of particular tree species

Variable name	Scientific name	Family	Common name	IUCN status
LCausVol	Lithraea caustica	Anacardiaceae	Litre	
CQuiVol	Chusquea quila	Poaceae	Quila	
PLinVol	Persea lingue	Lauraceae	Lingue	Near Threathened
NGlaucaVol	Lophozonia glauca	Nothofagacea	Hualo	Vulnerable
LApicVol	Luma apiculata	Myrtaceae	Luma (Chilean myrtle)	
PBolVol	Peumus boldus	Monimiaceae	Boldo	
GAveVol	Gevuina avellana	Proteaceae	Gevuin (Chilean hazel)	
AChilVol	Aristotelia chilensis	Elaeocarpaceae	Maqui (Chilean wineberry)	
APuncVol	Aextoxicon punctatum	Aextoxicaceae	Olivillo	Data deficient
CAlbaVol	Cryptocarya alba	Lauraceae	Peumo (Chilean acorn)	
EPulVol	Escallonia pulverulenta	Escalloniaceae	Corontillo	

Appendix 4

Summary of significant variables explaining species abundance in native forest

	Chilean Pigeon	Green-backed Firecrown	Striped Woodpecker	Austral Blackbird	Black-chinned Siskin	Patagonian Sierra-Finch	Thorn-tailed Rayadito	Plain-mantled Tit-Spinetail	White-throated Treerunner	Desmurs' Wiretail	Chilean Swallow	Ochre-flanked Tapaculo	Chestnut-throated Huet-huet	Dusky Tapaculo	Southern House Wren	Austral Thrush	Tufted Tit-Tyrant	White-crested Elaenia	Fire-eyed Diucon	Large Tree Users	Vertical profile generalist	Understory users	Shrub users	Number of species
Str_Index			-				-			-			-									-		5
ED_m.Ha																	+							1
PLAND_NF																+	+					-	+	4
PLAND_Pine																								0
Core_Land																								0
NLSI.NF						-											-						+	3
PD.NF								+																1
Connect																				+				1
Patch size					+																	+		2
X200RoA																								0
X200OtA																+			+					2
X200St_m.ha			+									+												2
X200NFA						-																		1
X200PA																								0
DistQueb_m											-									+				2
Dist_to_NF																								0
Height																								0
DBH																								0
Basal_Area												-				+	-					-	-	5
Cover															-									1
Vol_Nat																								0
PorcNat_%																								0
VolPine										-								-			-			3
PorcPine_%																								0
Vol_0.3m	-														+									2
Vol_0.3.2m										+			+	+			+					+	+	6
Vol_2.5m																+								1
Vol_5.10m				-	-			-		-								-				-	-	7
Vol_.10m											+								-		+		-	4
L1Rich															-									1
L2Rich																								0
L3Rich																		+				+		2
L4Rich																	-			+				2
L5Rich							+										+		+					3

Summary of significant variables explaining species abundance in pine plantations

	Chilean Pigeon	Green-backed Firecrown	Austral Blackbird	Patagonian Sierra-Finch	Thorn-tailed Rayadito	White-throated Treerunner	Plain-mantled Tit-Spinetail	Desmurs' Wiretail	Chilean Swallow	Ochre-flanked Tapaculo	Chestnut-throated Huet-huet	Dusky Tapaculo	Southern House Wren	Austral Thrush	Tufted Tit-Tyrant	White-crested Elaenia	Fire-eyed Diucon	Large Tree Users	Vertical profile generalist	Understory users	Shrub users	Number of species
Str_Index		+			-				+	-							+	-				6
ED_m.Ha					-	-									-		-					4
PLAND_NF					-						+								+			3
PLAND_Pine																						0
Core_Land	+																					1
NLSI.NF							-		-							-	+					4
PD.NF			+																			1
Connect		-								+				+				+		+		5
Patch size														+				+				2
X200RoA																	+					1
X2000tA																+			+			2
X200St_m.ha																						0
X200NFA						+								+				+				3
X200PA																						0
DistQueb_m																						0
Dist_to_NF										+		-			+							3
Height																						0
DBH																						0
Basal_Area							+						+	-		+			+			5
Cover				-															-			2
Vol_Nat																						0
PorcNat_%																						0
VolPine																						0
PorcPine_%																						0
Vol_0.3m				-									+								+	3
Vol_0.3.2m				+	+		+	+	+		+	+			+			+	+	+	+	12
Vol_2.5m																	-				-	2
Vol_5.10m										-												1
Vol_.10m																						0
L1Rich																						0
L2Rich																	+					1
L3Rich												+										1
L4Rich		+								+												2
L5Rich														-								1

Appendix 5

THE COLOR OF THE PALATE: AN ADDITIONAL AGEING CRITERION FOR THE WHITE-CRESTED ELAENIA (*ELAENIA ALBICEPS*)

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El color del paladar: un criterio adicional para la caracterización de la edad en Fío-Fío Chileno (*Elaenia albiceps*)

Key words: Elaenia, age, palate, Chile, color, tyrant, mouth.

INTRODUCTION

Many ecological processes and relationships in natural populations are influenced by the age of individuals, which, for example determines population rates such as survival and reproductive success (Temple & Wiens 1989). In the same way, social relations within populations could be expressed as variation in proportions and spatial distribution of age classes (Newton 1998). Furthermore, as a basic principle in population ecology it is assumed that the relative number of individuals within an age class will remain stable in a population if conditions do not change (Ricklefs 1973). It follows then that knowing the age structure of a population should allow a researcher to detect evidence of environmental disturbance. For these and other reasons it is valuable to be able to determine the age of individuals in population studies.

In the Northern Hemisphere methods have been described to determine the age of full-grown birds of many species. Methods include morphological characters, molt patterns (affecting color, shape and wear of feathers), skull ossification, and tongue marks or the color of other bare parts (Svensson 1992, Pyle 1997). However, comparatively little is known about ageing neotropical birds (Ryder & Wolfe 2009, Wolfe & Pyle 2012); at best, for most of the passerine species, only anecdotal methods are available to separate juveniles from full-grown individuals. The inability to distinguish first-year individuals from adults might mask the real state of neotropical passerine populations, which might be stressed due, for example, to high rates of habitat fragmentation and loss. It is therefore important to develop this fundamental ornithological knowledge in this region and other parts of the world.

In this paper we investigate whether scoring the color of the palate might be used to determine the age of individual White-crested Elaenias (*Elaenia albiceps*); a species which is being studied as part of a broader ecological study. The nestling palate color in many passerine species aids the parent birds in feeding the chicks (Kilner 2006, Wiebe & Slagsvold 2009), but this changes with age after fledging. Although some studies have found that the palate color of nestlings may signal the chick's

health (De Ayala *et al.* 2007), that variation is less than the changes that occur post-fledging, and so this character has been found to be helpful in ageing birds of several taxa including corvids, parids, and the European Robin (*Erithacus rubecula*) and related muscicapids (Svensson 1992, Pyle 1997). Based on findings in these other taxa, we hypothesised that the soft tissue covering the palate might change gradually in color due to its keratinization as the bird ages. If correct, we should find a yellowish palate in young full-grown (probably first-year) birds, and pale-greyish palate in older individuals. To test our hypothesis, we hypothesized that we might expect a high correlation between palate color and the wing length, since in many passerine species this increases through the years (Alatalo *et al.* 1984).

METHODS

This study was conducted in the Maulino forests of the coastal range of south-central Chile. Once a continuous cover of native forest, these temperate deciduous forests are now highly fragmented and persist only in a matrix of intensive managed exotic pine plantations. During the breeding season of 2012-2013, birds were mist-netted in both the native forest fragments and the surrounding pine plantations.

All captured birds were ringed and their maximum wing length was measured by a single ringer using a stopped rule to a precision of a 1 mm. As with many other species in Chilean forests, the White-crested Elaenia has no apparent sexual dimorphism (Pyle *et al.* 2015). Although recent studies point out that males are larger than females (Brown *et al.* 2007), sexing individuals through this criterion is not possible in the field as ranges overlap. Therefore, sexing was based on reproductive traits such as the presence of a cloacal protuberance or of a brood patch when appropriate. However, it was not always possible to determine the sex of individuals due to a lack of reproductive features; all unsexed individuals were categorized as "Ndf".

White-crested Elaenias were aged as either "juvenile" (hatched during the 2012–2013 season), "first-year" (approximately one year old), or "adult" (older than first-year). We differentiated with certainty all juveniles. Although it is possible to age first-year individuals on the color of the primary coverts (Pyle *et al.* 2015), only 8 out of 315 individuals were aged using this method. To test the applicability of the palate color as an ageing criterion we therefore photographed the palate of most captured individuals in the field under natural light. The upper mandible color of non-juvenile White-crested Elaenia individuals was assessed using the following criteria by a single observer (RT) (see also Figure 1):

0. The whole upper mandible was yellow-reddish or yellow.

1. The distal third of the upper mandible was grey or pale-pink

2. Half or more of the upper mandible was grey or pale pink.

We tested the score given to the color of the palate against the wing length of every sexed bird, since wing-length is known to be sexually dimorphic in this species (Brown *et al.* 2007), and that, in general, older individuals might be expected to have longer wings (Alatalo *et al.* 1984, Gosler *et al.* 1998). These two factors, sex and wing length, were included in an analysis of variance.

RESULTS

In total four juveniles and 335 non-juvenile individuals were ringed during the whole season. The color of the palate in all of the juveniles was reddish-yellow; scoring "0" but with gape flanges still visible. Of the non-juveniles, we were able to score the mouths of 246 birds, of which 187 had been sexed in the field (Table 1).

Taking only the data subset of sexed individuals (Fig. 2), a significant and consistent difference was found in the wing length of non-juvenile individuals scored in classes 1 and 2 (F 1–185 = 18.71, $P < 0.0001$) after controlling by sex (F 1–185 = 38.59, $P < 0.0001$).

DISCUSSION

There is a clear relationship between the color of the palate and wing length in full-grown White-crested Elaenia. The soft tissue in the palate of individuals of this species is reddish yellow when they are juveniles. As the birds age the fleshy tissue is absorbed, and in White-crested Elaenia this gradual morphological change appears to be accompanied by a change in the color of the palate, which gradually turns to a greyish-pink.

While we recognize that there are limitations in a one-year survey, mainly due to the lack of recaptures to see a progression within individuals of the studied pattern, and the true period over which the change in palate color occurs, we believe that our results are compelling. We suggest that it is unlikely that our findings could have arisen through any other mechanism than that they have distinguished between first-year birds and adults, and this was one of our main goals. However, classifying post-juvenile birds as first-years and adults, according to scores 1 and 2 respectively, allowed us to document important facts and effects acting on the study populations. For example, a significant difference in age structure was found in populations inhabiting native and exotic forests (Thomson & Gosler in prep.). Furthermore, adults had a significantly higher prevalence of blood parasites, a pattern that has been reported for many forest bird species (Norris *et al.* 1994, Deviche *et al.* 2001). However, we are confident that differences in palate color were not caused by differences in the level of infection because infection was a much weaker predictor of palate color (F 1–64 = 5.64, $P = 0.02$) than was the age (see above).

The results of our study have clear implications for future studies of the neotropical avifauna. We suggest that this finding should be considered as a basic foundation for further studies among the 18 species comprising the genus *Elaenia* (Fitzpatrick *et al.* 2004); considering their close relatedness (Fjeldså & Krabbe 1990) it is expected that this pattern for ageing White-crested Elaenia may be applicable to other species.

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Tables

TABLE 1. Number of individuals for every palate score class, and wing lengths (mm) for sex categories. Palate scores: 0 -The whole upper mandible was reddish yellow; 1-The distal third of the upper mandible was grey or pale-pink; 2 -Half or more of the upper mandible was grey or pale pink. Unsexed individuals were categorized as "Ndf".

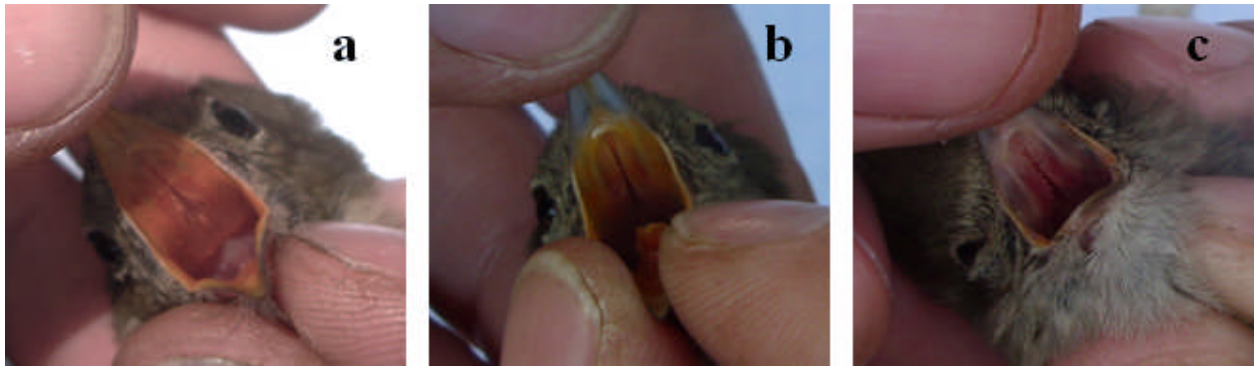
.

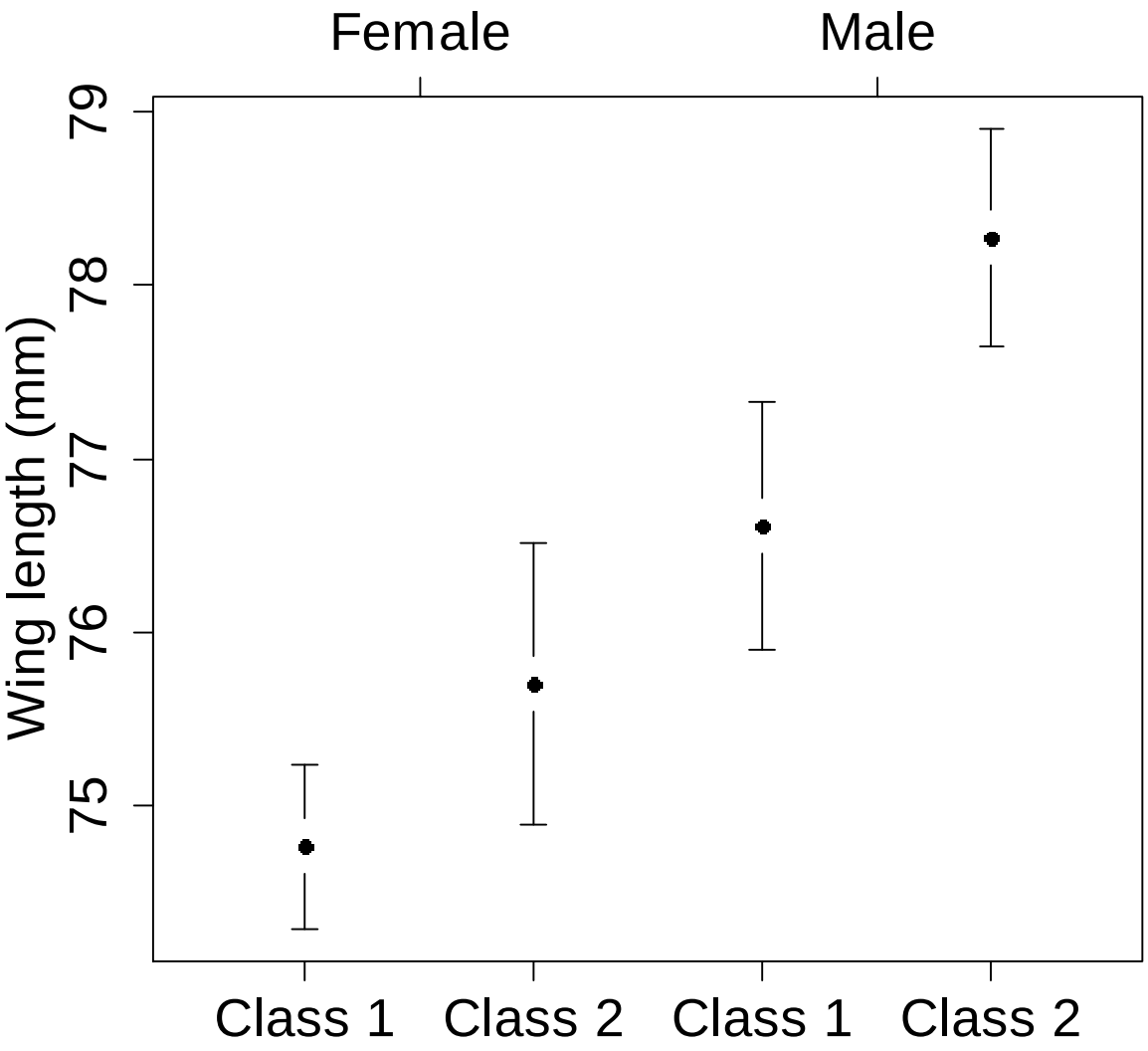
	Palate score			Wing length		
Sex	0	1	2	Range	Mean	CV
Female	0	83	40	71-81	75.04	3.1
Male	0	35	29	72-82	77.35	2.7
Ndf	8	26	19	70-82	76.22	4.1

Figure captions

FIG. 1. Change in the color of the palate in White-crested Elaenia, showing illustrations for a) class 0, the whole upper mandible was reddish yellow; b) class 1, the distal third of the upper mandible was grey or pale-pink; c) class 2, half or more of the upper mandible was grey or pale pink.

FIG. 2. Mean values and 95% CI bars for Wing length of White-crested Elaenia classified as different age groups by the color of their palate and controlled by Sex.


a
b
c


Female
Male
Wing length (mm)
75
76
77
78
79
Class 1
Class 2
Class 1
Class 2

Appendix 6

Insect survey during breeding season 2012-2013 (Chapter 4)

The survey was conducted during the first visits to each mist-netting site, from October to December of 2012. I used black light and malaise traps made by myself (see Fig A5-1).

Figure A5-1. Black light trap made by the author

Traps were set in native forest and in pine plantations at different distance from the border of the native fragment (Fig A5-2). Black light traps were set during three consecutive nights and malaise traps were opened for 72 hours.

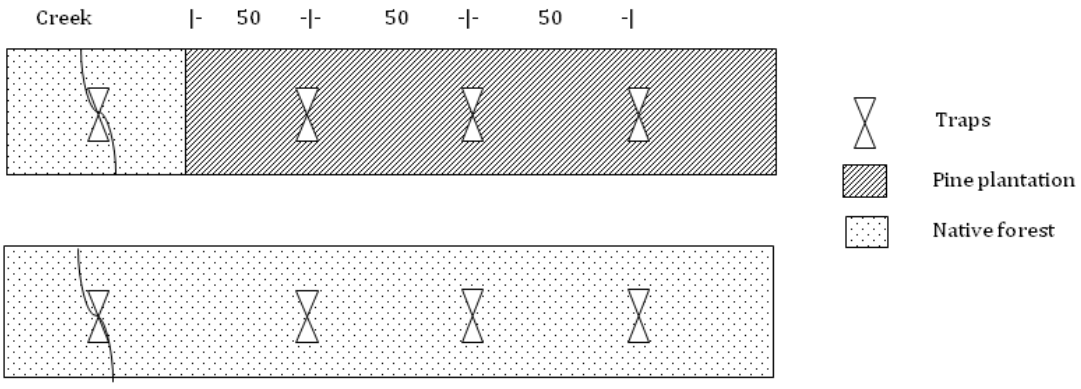


Figure A5-2. Diagram depicting the locations for the insect survey traps.

Operational difficulties. The main problem I had during the operation of the traps was the uncertainty of the capture effort. In the case of the black light traps, the operative length of the lead batteries was not possible to estimate as they were not consistent for unknown reasons. With malaise traps I experienced a similar situation, but in this case was related to the wind that closed

or moved the traps, introducing bias in the surveys. Finally, some samples were not managed appropriately.

The results are presented in the Figure A5-3. Without considering the pick in the mean values for 50-m-traps and their variance, a slight decrease in the mean mass of insects can be seen in the graphs, from a higher value in native forest declining as the traps were set further into pine plantations.

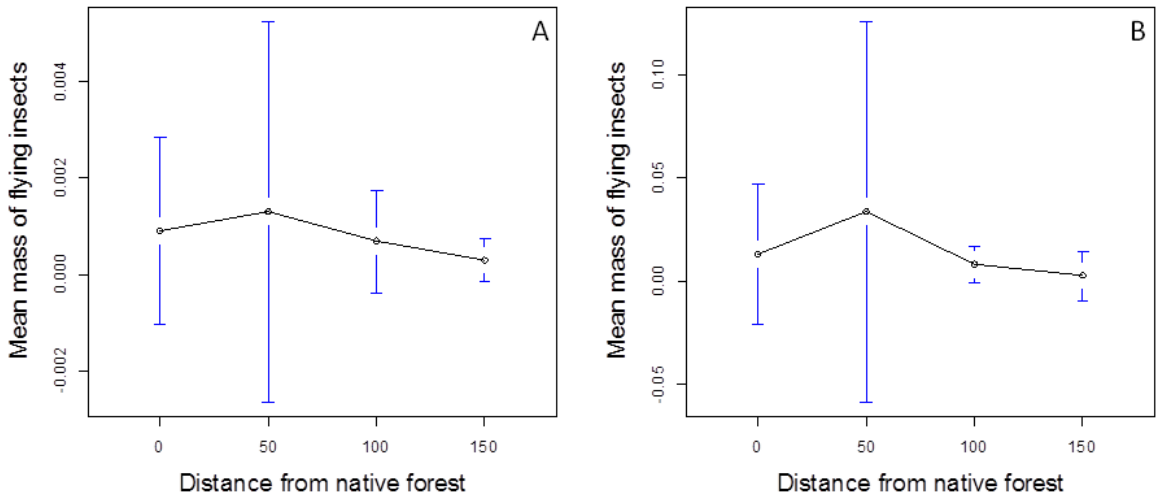


Figure A5-3. Results from the flying insect survey. A) Malaise traps and B) Black light traps

Appendix 7

Differences in fat and protein reserves of birds captured in either habitat

Species	Fat						
	Mean		Range		t-test		
	Native	Pine	min	max	t	df	p
Tufted Tit-tyrant	1.0	0.4	0	2	2.868	21.3	**0.009**
Thorn-tailed Rayadito	0.266	0.033	0	4	3.062	116.1	**0.002**
White-crested Elaenia	0.424	0.394	0	3	0.409	216.8	0.682
Patagonian Sierra-Finch	0.850	0.535	0	2	0.988	17.4	0.336
White-throated Treerunner	0.321	0.000	0	1			
Green-backed Firecrown	0.000	0.000	0	0			
Black-chinned Siskin	1.000	1.000	0	2	0	1.1	1.000
Des Murs' Wiretail	0.000	0.090	0	1	-1	10.0	0.340
Southern House Wren	0.000	1.000	0	3	-2.449	8.0	**0.039**
Austral Thrush	0.194	0.166	0	1	0.247	35.5	0.806

Species	Muscle						
	Mean		Range		t-test		
	Native	Pine	min	max	t	df	p
Tufted Tit-tyrant	2.708	2.966	1	4	-1.323	35.0	0.194
Thorn-tailed Rayadito	2.822	2.900	1	4	-0.51	44.3	0.612
White-crested Elaenia	2.030	1.948	0	4	1.162	193.0	0.246
Patagonian Sierra-Finch	2.100	2.115	1	3	-0.089	20.2	0.929
White-throated Treerunner	2.678	4	2	4			
Green-backed Firecrown	1.790	1.729	0	3	0.411	44.1	0.682
Black-chinned Siskin	2.333	2.000	2	3	2.309	8.0	**0.049**
Des Murs' Wiretail	2.750	3.318	2	4	-1.673	7.0	0.137
Southern House Wren	1.500	3.055	1	4	-2.8	1.514	0.145
Austral Thrush	2.000	1.861	1	3	0.92	36.4	0.363

Appendix 8

Species sampled for blood parasites

Species	Number of samples	Number of positives
Tufted-tit Tyrant	8	0
Thorn-tailed Rayadito	36	0
Black-chinned Siskin	4	0
White-crested Elaenia	142	34
Ochre-flancked Tapaculo	1	0
Austral Pigmy Owl	1	0
Patagonian Sierra Finch	7	2
White-throated Treerunner	7	0
Desmurs' Wiretail	7	0
Southern House Wren	5	1
Austral Thrush	22	1

Appendix 9

Foraging substrates in pine trees

Species	Twig		Foliage		Branch		Cone		Trunk		Others	
	n	%	n	%	n	%	n	%	n	%	n	%
Tufted-tit Tyrant (*Anairetes parulus*)	14	54	3	12	9	34	0		0		0	
Thorn-tailed Rayadito (*Aphrastura spinicauda*)	23	45	0		24	47	4	8	0		0	
White-crested Elaenia (*Elaenia albiceps*)	1	100	0		0		0		0		0	
Patagonian Sierra-Finch (*Phrygilus patagonicus*)	0		0		4	40	6	60	0		0	
White-throated Treerunner (*Pygarrhichas albogularis*)	2	9	0		6	29	3	14	10	48	0	
Black-chinned Siskin (*Sporagra barbatus*)	0		0		12	63	6	32	1	5	0	
Southern House Wren (*Troglodytes musculus*)	2	40	0		1	20	0		0		2	40
Austral Thrush (*Turdus falklandii*)	0		0		0		0		1	50	1	50
Striped Woodpecker (*Veniliornis lignarius*)	0		0		0		0		0		0	
Fire-eyed Diucon (*Xolmis pyrope*)	1	25	0		1	25	0		0		2	50