



Short-term avian responses to experimental variable-density thinning: Initial stand attributes outweigh effects of management in Austral temperate rainforests

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ABSTRACT

Anthropogenic environmental changes have led to secondary forests becoming dominant in many regions. Although ecological or restoration thinnings can help restore old-growth conditions, experimental evidence of their subsequent benefits to biodiversity remains sparse, particularly in Austral Temperate Rainforests in South America. Using mist-net sampling within 1-ha plots in mixed-evergreen and *Nothofagus* secondary forests, we examined short-term effects (4 years) of experimental Variable Density Thinning (VDT) on bird richness, abundance, and the individual body condition of two abundant breeding species: frugivore *Elaenia albiceps* and insectivore *Aphrastura spinicauda*. Based on 518 birds captured, richness and relative abundance were higher in *Nothofagus* than in mixed-evergreen forests, regardless of VDT treatment, except for *E. albiceps* which was more abundant in mixed-evergreen forests. Richness and abundance did not vary with VDT treatment, except for *E. albiceps* which increased in abundance following VDT. However, individual body condition of *E. albiceps* did not change due to VDT management, although it was better in mixed-evergreen than in *Nothofagus* forests, and increased over the course of the study. In contrast, body condition of *A. spinicauda* was not associated to VDT treatment, forest type, or season. Our results suggest that the short-term effects of VDT in secondary Austral Temperate Rainforests upon avian richness, abundance, and individual body condition were minimal, and that initial stand attributes (*i.e.* forest type) more strongly influenced these variables. This is likely due to the region's high diversity of tree species, which drives substantial differences in tree species composition among forest types and affects the food resources available to birds. In this case, most trees in mixed-evergreen forests produce fleshy fruits that are important in the diet of *E. albiceps* and other bird species. Therefore, in geographical regions with a high alpha and beta tree diversity, restoration thinnings in secondary forests should explicitly target tree composition, which appears to be at least as important as vegetation structure in determining short-term avian responses.

1. Introduction

Anthropogenic environmental changes have altered the distribution and status of forests worldwide, with consequences for forest biodiversity (Sekercioglu et al., 2002; Homyack, 2010; Asefa et al., 2017; Betts et al., 2019). For example, harvesting activities, agricultural expansion, and altered disturbance regimes have reduced the extent of old-growth forests (Lindenmayer et al., 2012), leading to secondary forests becoming dominant in many regions (Franklin et al., 2002; Puettmann

et al., 2016; Ponce et al., 2017). Secondary forests differ dramatically from old-growth forests in both structure and composition, ultimately affecting the richness, composition, and abundance of species that a stand can support (Franklin et al., 2002; Ponce et al., 2017). Recent studies and initiatives argue that ecological or restoration thinnings can help restore old-growth conditions (Long, 2009; Franklin and Johnson, 2012; Palik et al., 2021), but experimental evidence of their subsequent benefits to biodiversity remains sparse.

Birds are key components of forest biodiversity and are also excellent

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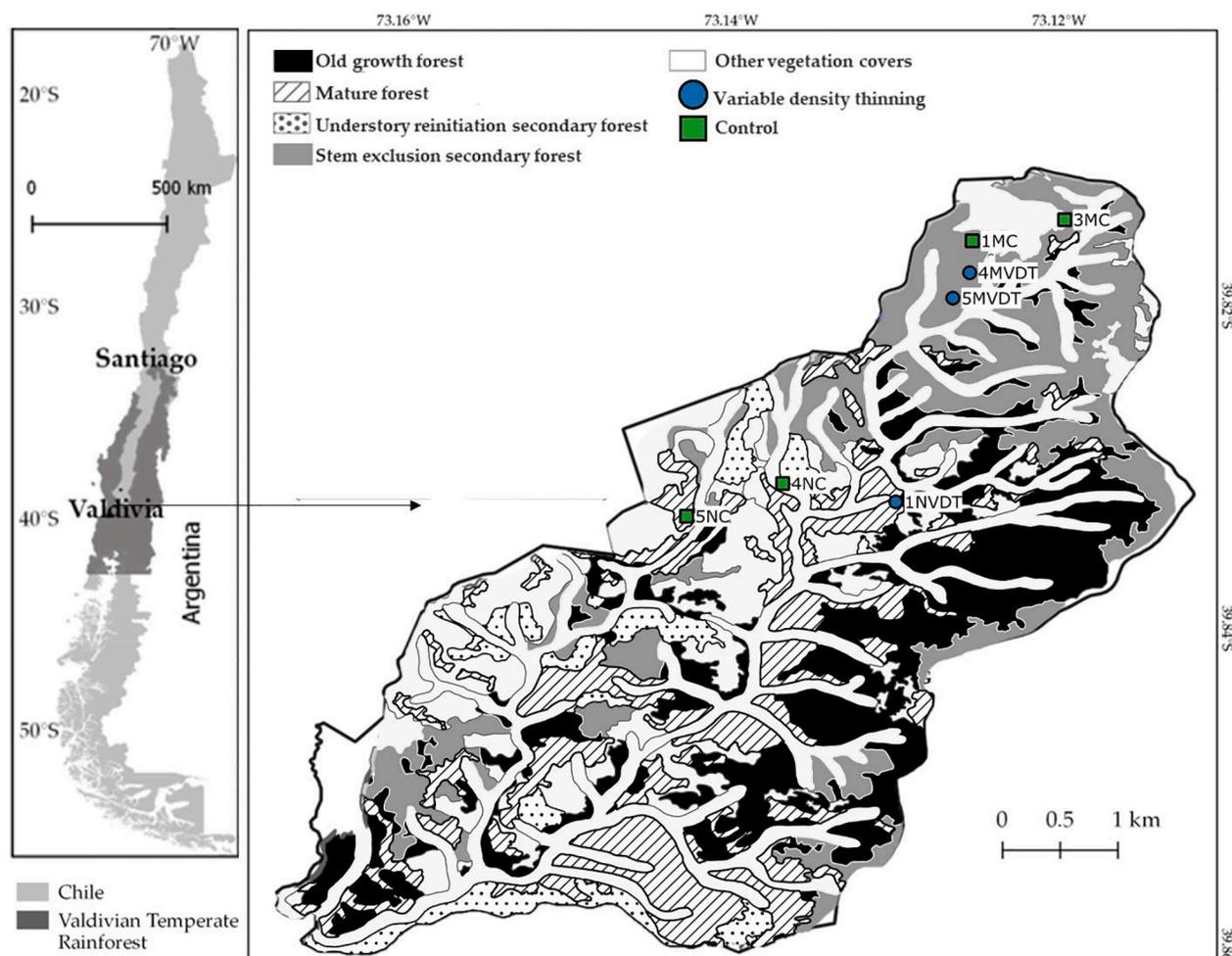


Fig. 1. Location of the Llancahue experimental forest within the Valdivian Temperate Rainforest in Chile (left panel), showing the 7 study plots (right panel). Plots treated with VDT are in blue, and those untreated in green (modified from Donoso et al., 2020).

indicators of environmental change (Díaz et al., 2005; Sekercioglu, 2006; Wenny et al., 2011). Given their well-known sensitivity to changes in vegetation structure (e.g., MacArthur, 1964; Gabbe et al., 2002), birds may be useful in assessing the performance of restoration thinnings for promoting diversity. Birds are also important contributors to numerous ecological functions and services (Sekercioglu, 2006), and so improved habitat conditions for bird communities would further contribute to the restoration and rewilding of secondary forests. However, while birds are sensitive to changes in vegetation structure, resulting changes in bird populations and community composition may take years to manifest themselves. Instead, indicators of individual body condition may offer an early detection system for revealing the effects of forest management (Latta and Faaborg, 2002).

Individual body condition is defined as the capital energy that can be stored in the body of an individual at a given time (Peig and Green, 2009), thus representing the ability of an environment to provide resources for a particular species or population (Hall et al., 1997; Johnson, 2007). Because the amount of energy that an individual can acquire in different habitats is modulated by different factors (e.g. availability of resources, number of consumers, and individual competitive abilities), body condition is closely linked to individual fitness and has consequences for the survival of populations (Brown, 1996; Schulte-Hostedde et al., 2001; Milenkaya et al., 2013; Werner et al., 2019). Therefore individual body condition can be used as an honest proxy for how variation in habitat conditions affects forest biodiversity (Stevenson and Woods, 2006; Johnson, 2007; Homyack, 2010; Milenkaya et al., 2013).

Variable-density thinning (hereafter VDT) is a type of ecological

thinning that is frequently recommended as a forest management technique for accelerating the recovery of old-growth characteristics in secondary forests (Donoso et al. 2020; Brodie and Harrington, 2020). VDT aims to accelerate the development of late-successional habitat in secondary forests by thinning at different intensities, creating gaps and skips (Brodie and Harrington, 2020), and leaving and promoting coarse woody debris and standing dead trees, therefore generating a mosaic of tree densities and stimulating the development of a structurally and compositionally complex forest (Carey et al., 1996; Haveri and Carey, 2000; Harrington et al., 2005; Eyre et al., 2015; Willis et al., 2018; Donoso et al. 2020). A study on the short-term effects of VDT on wildlife in North American temperate coniferous forest found that bird species richness during the non-breeding season increases in the short-term (*i.e.* 4 years) due to understory development (Haveri and Carey, 2000). Another study in the same region reported that abundance of small mammals also increased in the short-term (*i.e.* 3 years), but mammal community composition and structure were different than that observed in old-growth forest (Carey and Wilson, 2001b). These promising though somewhat variable findings in temperate forests within the Boreal Hemisphere suggest that VDT may have a high potential conservation value in Austral temperate forests (Gutiérrez et al., 2009), but reported studies dealing with VDT effects on austral bird communities are lacking.

Here we evaluate short-term avian responses to experimental VDT in Austral Temperate Rainforests in southern Chile from 2015 to 2019. We examined the effects of VDT and forest type on bird richness, abundance, and individual body condition of two abundant species with contrasting

Table 1

Stand structure variables for seven 1-ha secondary forest plots, corresponding to two forest types. Values for plots treated with Variable Density Thinning are reported for both Pre- and Post-management.

Forest type	Management	Density (trees)	Basal area (m ²)
Mixed Evergreen forest	Pre	4,453	53.8
	Post	–	–
	Pre	3,744	60.3
	Post	–	–
	Pre	3,890	59.2
	Post	2,667	44.1
	Pre	4,513	61.6
	Post	3,208	44.9
<i>Nothofagus</i> forest	Pre	2,593	72.2
	Post	1,565	52.9
	Pre	1,958	66.3
	Post	–	–
	Pre	1,511	64.3
	Post	–	–

Table 2

Number of birds captured by species in *Nothofagus* forest and Mixed-evergreen forest. Note that a higher capture effort was made in Mixed-evergreen forest (see text for more details).

Species	Scientific name	<i>Nothofagus</i> forest	Mixed-evergreen forest
Green-backed	<i>Sephanoides</i>	120	74
Firecrown	<i>sephanoides</i>		
White-crested	<i>Elaenia albiceps</i>	48	120
Elaenia			
Thorn-tailed	<i>Aphrastura spinicauda</i>	51	25
Rayadito			
Austral Thrush	<i>Turdus falcklandii</i>	19	31
White-throated	<i>Pygarrhichas albigularis</i>	–	6
Treerunner			
Tufted Tit-Tyrant	<i>Anairetes parulus</i>	4	–
Magellanic	<i>Scytalopus magellanicus</i>	4	–
Tapaculo			
Patagonian Tyrant	<i>Colorhamphus parvirostris</i>	2	–
Des Murs's	<i>Sylviorthorhynchus desmursii</i>	2	–
Wiretail			
Fire-eyed Diucon	<i>Pyrope pyrope</i>	–	1
Austral Pygmy-owl	<i>Glaucidium nana</i>	1	–
Chucazo Tapaculo	<i>Scelorchilus rubecula</i>	1	–
Black-Throated	<i>Pteroptochos tami</i>	1	–
Huet-huet			
Eared Dove	<i>Zenaidia auriculata</i>	–	1
Patagonian Sierra-Finch	<i>Phrygilus patagonicus</i>	–	1
Rufous-collared Sparrow	<i>Zonotrichia capensis</i>	1	–

diets, forest vertical profile use, and migratory strategies. White-crested Elaenia (*Elaenia albiceps*) (hereafter elaenias) is a frugivorous vertical profile generalist and the most abundant austral migratory passerine in southern Chile (Díaz et al., 2005; Bravo et al., 2017). By contrast, Thorn-tailed Rayadito (*Aphrastura spinicauda*) (hereafter rayaditos) is a resident insectivore and secondary cavity nester that is mainly associated with large trees (Díaz et al., 2005). VDT leads primarily to increasing structural heterogeneity within managed stands, at least in the short-term (Willis et al., 2018; Donoso et al., 2020; Palik et al., 2021). As such, we predicted that avian richness and abundance would not be affected in the short-term, but that body condition would indicate individual species responses to VDT. In this light, we expected forest specialist rayaditos to be more sensitive to modification in habitat features towards old-growth forest attributes, and thus would increase in body condition after VDT, while forest generalist elaenias would maintain similar body condition before and after VDT.

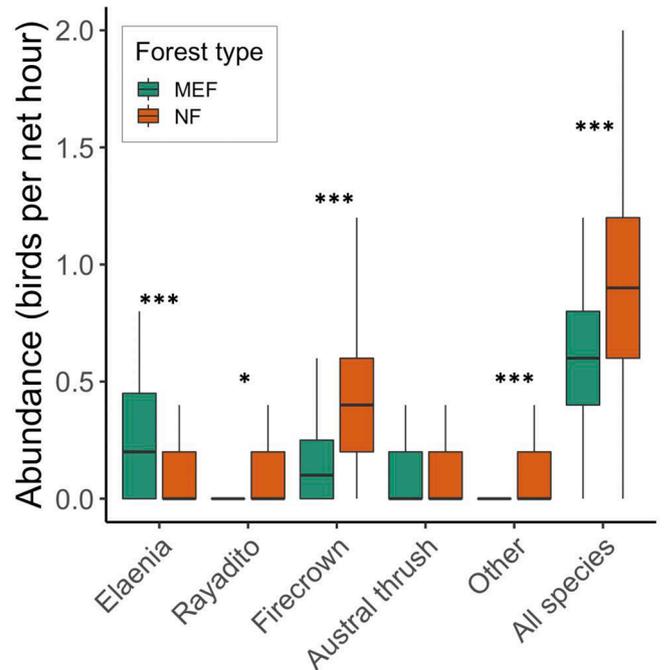


Fig. 2. Relative abundance (birds per net-hour) of species captured in Mixed-evergreen forest (MEF) and *Nothofagus* forest (NF). Lines, boxes, and whiskers indicate the median, first and third quartiles, and 1.5 times the inter-quartile range, respectively. Asterisks indicate significant differences between forest types (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

Table 3

Parameter estimates for linear models examining the effects of forest type and variable density thinning (VDT) on bird richness and the abundance across all bird species, the four most commonly captured species, and other species pooled. VDT effect represents the interaction of treatment (control versus managed plots) and period (before versus after management).

	Forest type (<i>Nothofagus</i>)	VDT effect
Richness	0.66 ± 0.18 ***	NS
Abundance	0.28 ± 0.10 ***	NS
Elaenia	−0.15 ± 0.05 ***	0.32 ± 0.13 *
Rayadito	0.10 ± 0.05 *	NS
Firecrown	0.28 ± 0.07 ***	NS
Thrush	NS	NS
Other species (pooled)	0.07 ± 0.02 ***	NS

(* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; NS = not significant)

2. Methods

2.1. Study area

Fieldwork was conducted in the Llancahue experimental forest (1,270 ha), located within the intermediate depression near the city of Valdivia, Los Ríos Region, Chile (39° 49' S, 73° 07' W; 50 to 410 m a.s.l.; Donoso et al., 2014, 2018, 2020; Oyarzún et al., 2021) (Fig. 1). Llancahue provides freshwater to the city of Valdivia and protects more than 700 ha of old-growth native forests and ~ 300 ha of secondary native forests. Topography (gentle slopes < 20%) and soil type are relatively homogenous throughout the reserve (see Donoso et al., 2018). The climate is moist temperate, with an average annual precipitation of 2,300 mm and average annual temperature of 12 °C (Donoso et al., 2014; Ponce et al., 2017). Two types of secondary forests are found in Llancahue: 1) Mixed-evergreen forest which originated by logging and presumably fire in the early 1930s, dominated by several evergreen hardwood species (*Dassyphyllum diacanthoides*, *Gevuina avellana*, *Drimys winteri*, *Eucryphia cordifolia*, and several species of the Myrtaceae family)

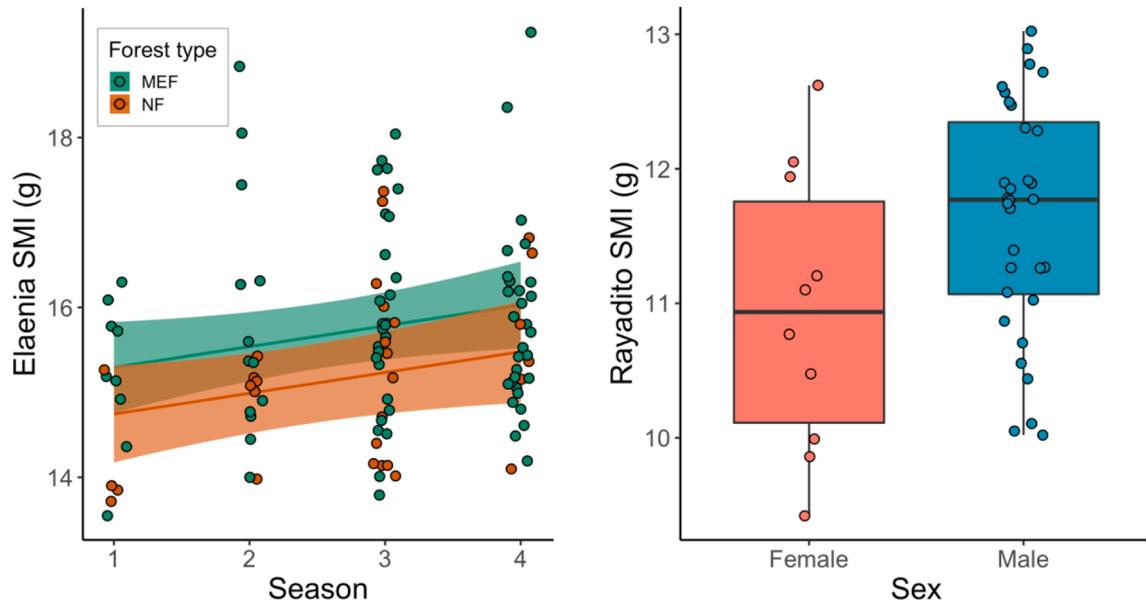


Fig. 3. Left: Elaenia body condition across seasons and between forest types (MEF = Mixed-evergreen forest; NF = Nothofagus forest). Points are slightly jittered to aid interpretation. Lines and shaded colors indicate mean and 95% confidence intervals for linear models. Right: Rayadito body condition by sex. Lines, boxes, and whiskers indicate the median, first and third quartiles, and 1.5 times the inter-quartile range, respectively.

Table 4

Parameter estimates for generalized linear models exploring the effects of two models (full versus null) on body condition (SMI) of Elaenia and Rayadito. We used season, sex, forest type and VDT management as explanatory variables in full models.

Species	Model		$\beta \pm SE$	P value	2.5% CI	97.5% CI	AIC
Elaenia	SMI ~ 1	Intercept	15.62 ± 0.10	***	15.42	15.82	409.78
		SMI ~ all variables	Intercept	15.25 ± 0.37	***	14.52	15.97
		Season	0.25 ± 0.12	0.046	0.01	0.48	
		NF	-0.55 ± 0.24	0.026	-1.03	-0.07	
		Males	-0.20 ± 0.23	0.395	-0.65	0.25	
		VDT	-0.13 ± 0.24	0.587	-0.60	0.34	
Rayadito	SMI ~ 1	Intercept	11.47 ± 0.13	***	11.22	11.71	151.10
		SMI ~ all variables	Intercept	9.98 ± 0.59	***	8.83	11.14
		Season	0.30 ± 0.16	0.078	-0.02	0.62	
		NF	0.21 ± 0.30	0.491	-0.39	0.81	
		Males	0.74 ± 0.33	0.031	0.09	1.38	
		VDT	0.14 ± 0.36	0.698	-0.57	0.85	

(*** p < 0.001).

Table A1

Parameters of Likelihood ratio test for two model species. Full model: SMI = Season + Forest type + Sex + VDT management; Null model: SMI ~ 1.

Species	Model	df	Deviance	P value
Elaenia	Full	4	14.31	0.022
	Null			
Rayadito	Full	4	6.75	0.079
	Null			

and few conifers of the Podocarpaceae family; and 2) *Nothofagus dombeiyi* dominated forests, which originated after a severe fire in ~1914 (González et al., 2015; Donoso et al., 2018, 2020). Prior to these stand-replacing anthropogenic disturbance events, Llancahue was dominated by extensive stands of old-growth Valdivian Temperate Rainforest (Donoso et al., 2020).

2.2. Stand attributes and variable density thinning

Seven one-hectare plots were delimited in November 2015 in Mixed-evergreen (n = 4) and *Nothofagus* (n = 3) forests (Table 1). Distance

between plot limits averaged 1,345 m (range: 216–2,802). During the following year (October–November 2016), three randomly selected plots (two Mixed-evergreen and one *Nothofagus*) were managed using VDT. The specifics of this management are given in Donoso et al. (2020), but briefly, management is driven by the need to create attributes similar to those found in regional old-growth forests, including those associated to their gap-phase dynamics (Veblen, 1985). Therefore, VDT in these one-hectare plots included the creation of eight gaps (four of 100 m² and four of 300 m²) in each plot where all trees were removed, eight reserves of the same dimensions without intervention, and a restoration thinning implemented in the remaining area (6,800 m²). This restoration thinning included girdling of 10–20 trees (>30 cm diameter at breast height, hereafter DBH) in each plot to create standing dead trees, and a similar number of trees of the same characteristics were felled to increase the presence of coarse woody debris.

2.3. Bird sampling

We captured birds using mist-nets once per month in each plot during each of four consecutive breeding seasons (October to March) from 2015 until 2019 (n = 22 surveys per plot). Following a constant capture effort between sites and breeding seasons, we deployed 6 mist-

nets (9 m long; 2.5 m height; 32 mm mesh) at each plot, which were operated for five hours each sampling day beginning one hour after sunrise for a total effort of 80,136 hr·m⁻¹ in Mixed-evergreen forest and 43,740 hr·m⁻¹ in *Nothofagus* forest. This differential effort is due to a higher number of plots monitored in Mixed-evergreen forest, though the number of sampling days per plot were balanced. Due to unforeseen logistical constraints, bird sampling in the managed *Nothofagus* forest plot did not begin until after the VDT treatment was applied. Nets were checked every 30 min and all captured birds were banded with numbered metal rings (with the exception of hummingbirds which we began banding during the third season using hummingbird-specific aluminum bands; following McFadden et al., 2019).

Banded birds were aged (adult/juvenile) based on plumage characteristics, and sex was recorded for species with apparent sexual dimorphism. We collected the following measurements: body mass (± 0.1 g), maximum tarsus (± 0.01 mm) following Redfern and Clark (2001), wing chord (± 0.5 mm) and bill-head length (± 0.01 mm). All measurements were taken by two bird banders (GB & JR) and no significant differences in morphometric measurements were found (Wilcoxon test: maximum tarsus length ($V = 224$, $p = 0.10$), wing length ($V = 77$; $p = 0.29$) and bill-head length ($V = 14$; $p = 0.58$)). For two model species we collected a blood sample (<1% body weight) from a puncture in the brachial vein following standard procedures (e.g., Owen, 2011) and then stored in Eppendorf tubes containing ethanol (96%). Individuals with highly irrigated brooding patch were not bled.

2.4. Molecular sexing

Molecular methods were used to sex adult elaeenias ($n = 109$) and rayaditos ($n = 42$). Blood samples obtained in the field were separated for DNA extraction with a commercial kit (E.Z.N.A. Tissue DNA Kit Quick Guide, OMEGA biotek). We subsequently used polymerase chain reactions (PCR) and employed the primers P0, P2 and P8 for the amplification of the CHDW gene. An initial denaturation at 94 °C for 3 min was followed by 35 cycles of 45 °C for 30 seg, 72 °C for 45 seg and a final run at 72 °C for 5 min. The PCR product was separated by electrophoresis at 80 V for 50 min on 2% agarose gel and stained with ethidium bromide for visualization of the bands under ultraviolet light. Males were identified by the presence of a single band Z chromosome, whereas females showed two bands corresponding to the W and Z chromosomes (Han et al., 2009).

2.5. Data analysis

We used linear models to evaluate the drivers of bird richness and overall abundance, as well as the abundance of the four most common bird species, and the pooled abundance of the remaining other species. Our models included the following explanatory variables: forest type, experimental treatment (control vs. VDT plots), period (before vs. after management), and the interaction between treatment and period, which represents the effect of VDT.

We calculated Scaled Mass Index (SMI) as an index of body condition (Peig and Green, 2009) for the two model species:

$$Mi_i = Mi \left(\frac{Lo}{Li} \right)^{bSMA}$$

where Mi_i and Li are the body mass and the linear body measurement of individual i respectively; $bSMA$ is a scaling exponent, which we calculated indirectly by dividing the slope from an OLS regression (bOLS) by the Pearson's correlation coefficient r of Mi and Li (both log-transformed); Lo is the arithmetic median of the linear body measurement for the population and Mi_i is the predicted body mass for individual i when the linear body measurement is standardized to Lo .

We performed a correlation analysis between each structural measurement and body mass (*cor* function in R version 2.14.1; R

Development Core Team, 2012). We used maximum tarsus length as a structural measure (elaenias: $n = 129$; $r = 0.41$; $p < 0.001$; rayaditos: $n = 55$; $r = 0.50$; $p < 0.001$). $bSMA$ and Lo values were 1.83 and 21.50 mm for elaeenias and 2.20 and 22.74 mm for rayaditos, respectively. We calculated SMI only for adult individuals and excluded all recaptures from the analysis to avoid pseudo-replication.

We used generalized linear models (family = "gaussian") to explore the drivers of SMI for elaeenia and rayaditos separately. As explanatory variables, we included breeding season (as a continuous variable), sex, forest type, and experimental management (managed or unmanaged). We used the explanatory variable 'experimental management' as an indicator of VDT effect because we did not have sufficient pre-management samples to conduct a typical BACI-style analysis. Plots were considered 'managed' if they had received the VDT treatment. We compared the full model (all variables) for each species with a null model using a likelihood ratio test and calculated 95% confidence intervals using the *confint* function. Explanatory variables were considered statistically significant if the 95% confidence interval did not include zero.

All analyses were conducted in RStudio version 1.1.447 - © 2009–2018.

3. Results

A total of 518 birds were captured, with 265 in the *Nothofagus* forest and 253 in the Mixed-evergreen forest, during the four breeding seasons. In both forest types the most abundant species were Green-backed Firecrown (*Sephanoides sephanioides*), rayadito, elaeenia, and Austral Thrush (*Turdus falcklandii*) (Table 2). We recaptured a total of 11 elaeenias (out of 168 (6.5%)), 5 rayaditos (out of 76 (6.6%)) and 4 Austral Thrush (out of 50 (8%)) in different years, and another 10 elaeenias and 2 rayaditos within the same year. Notably, all individuals recaptured were in the same plot where they were first captured.

Overall relative abundance (mean capture rate \pm SE) was 0.9 ± 0.1 birds·h⁻¹ and the same four species were the most abundant at both forest types. Relative abundance was significantly higher in the *Nothofagus* forest (1.0 ± 0.1 birds·h⁻¹) than in the Mixed-evergreen forest (0.7 ± 0.1 birds·h⁻¹) ($\beta = 0.28 \pm 0.10$, $p < 0.001$). Elaeenias were more abundant in Mixed-evergreen than in *Nothofagus* forest ($\beta = -0.15 \pm 0.05$, $p < 0.001$), while rayaditos ($\beta = 0.10 \pm 0.05$, $p = 0.049$) and Green-backed Firecrowns ($\beta = 0.28 \pm 0.07$, $p < 0.001$) were more abundant in *Nothofagus* forest (Fig. 2). Relative abundance of Austral Thrush was similar among forest types ($\beta = -0.01 \pm 0.03$, $p = 0.79$) (Fig. 2). Elaeenias increased in abundance following VDT, indicating a positive effect of management ($\beta = 0.32 \pm 0.13$, $p = 0.013$). VDT had no effect on richness, total abundance, or abundance of any other species (Table 3).

Elaenia body condition did not change due to VDT ($\beta = -0.13 \pm 0.24$, $p = 0.587$). However, it increased throughout the study period ($\beta = 0.25 \pm 0.12$, $p = 0.046$) and was lower in *Nothofagus* forests ($\beta = -0.55 \pm 0.24$, $p = 0.026$) (Fig. 3). Molecular analysis of blood samples identified 72 males and 37 females within elaeenias, with no significant differences in body condition among sexes ($\beta = -0.20 \pm 0.23$, $p = 0.395$). The comparison between models (full versus null) showed significant differences ($p = 0.022$) (Appendix A) with a lower AIC value for the full model (Table 4).

We identified 32 males and 10 females in rayaditos. Males showed a higher body condition index ($\beta = 0.74 \pm 0.33$, $p = 0.031$) (Fig. 3), with no differences associated to VDT ($\beta = 0.14 \pm 0.36$, $p = 0.698$), across breeding seasons ($\beta = 0.30 \pm 0.16$, $p = 0.078$), or forest type ($\beta = 0.21 \pm 0.30$, $p = 0.491$). We did not find significant differences among the full and null models (Appendix A), although the former showed a lower AIC value.

4. Discussion

We found a consistently higher bird abundance and richness associated to *Nothofagus* than to Mixed-evergreen forest, with no short-term effect (four years) of VDT management (except for elaeenias relative abundance). Bird communities were characteristic of those recorded elsewhere in South American temperate forests (Willson et al., 1994; Rozzi et al., 1996; Reyes-Arriagada et al., 2015; Ibarra et al., 2017), dominated by one large-tree user and three vertical-profile generalists. However, ground-foraging ‘tapaculos’ (Fam. Rhinocryptidae) were notably absent as a methodological artifact, since they are rarely captured with mist-nets. While overall relative abundance of birds was similar throughout the four breeding seasons, *Nothofagus* forest had higher richness relative bird abundances for all species except for the migratory elaeenias, which were more abundant in Mixed-evergreen forest. In parallel, elaeenias exhibited a higher body condition index in Mixed-evergreen forests. In addition, male rayaditos showed consistently better body condition than females, irrespective of forest type. Notably, no changes in body condition were detected in plots treated with VDT for either species, although elaeenias body condition did increase over the course of the study. Therefore, our results suggest that forest type outweighed short-term effects of VDT in bird communities inhabiting *Nothofagus* and Mixed-evergreen secondary forests.

The dominant effect of forest type is likely related to differences in vegetation composition and structure in *Nothofagus* versus Mixed-evergreen forests, and is linked to their differing successional stages of secondary forest development (Ponce et al., 2017; Donoso et al., 2020). Both compositional and structural attributes of managed forests may drive bird responses, depending on bird species traits and niches (Lindenmayer et al., 2009). For example, vegetation structure may be particularly relevant for insectivorous birds, because large-diameter and emergent trees provide suitable substrate and high abundance of prey by increasing food access (Holmes and Robinson, 1981; Rozzi et al., 1996; Gabbe et al., 2002). On the other hand, vegetation composition may be more relevant for birds that consume fleshy fruits (berries and drupes) (Armesto et al., 1987; Aizen et al., 2002). In secondary Austral temperate rainforest, insectivorous rayaditos would thus better thrive in *Nothofagus* forests, where these larger trees with more furrowed bark provide abundant foraging substrates for these foliage-trunk insectivores. In addition, pre-existing cavities which are more common in *Nothofagus* than in Mixed-evergreen forest (Altamirano et al., 2017) provide an essential micro-habitat feature for second-growth cavity nesters such as rayaditos (Moreno et al., 2005; Altamirano et al., 2015, 2017). By contrast, high fruit availability of *Drimys winteri* and several species of the Myrtaceae family, which are dominant in Mixed-evergreen forest (Donoso et al., 2020) provide foraging opportunities for the mainly frugivorous elaeenias (Brown et al., 2007), where they present a higher body condition index and are indeed more abundant.

As in other studies in Austral temperate forests (Brown et al., 2007; Rozzi and Jiménez, 2014; Botero-Delgado et al., 2017; Bravo et al., 2017), in the present study all birds showed a very high philopatry at the plot scale (1 ha), indicating that changes in body condition were probably related to local resource availability. Previous studies in southern Chile conclude that large-tree users are highly sensitive to modifications in forest structure (Willson et al., 1994; Sieving et al., 2000; Díaz et al., 2005; Vergara and Simonetti, 2006). However, we did not detect differences in abundance or in body condition of rayaditos between plots treated with VDT and untreated plots. Interestingly, we found more males than females, with the former showing a consistently higher body condition index. In parallel, body condition of vertical-profile generalist elaeenias increased throughout the study period. While such inter-annual differences may be related to forest management disturbances during the first season (Lucas et al., 2006) or specific environmental conditions due to inter-annual variability (Haveri and Carey, 2000), we did not see any effect of VDT management.

VDT as a management tool is primarily focused on modifying stand

structure to increase old-growth attributes in secondary forests, and could improve habitat conditions for bird communities in the short term if a homogeneous stand structure is a limiting factor (Haveri and Carey, 2000). However, VDT may be less effective (at least in the short term) for improving habitat conditions for bird communities in situations where tree species composition is important for determining biodiversity outcomes. Most previous studies that evaluated wildlife response to VDT are focused in North American coniferous-dominated forests with low tree richness (including several studies in intensively managed monocultures) (Carey et al., 1996; Haveri and Carey, 2000; Carey and Wilson, 2001; Franklin and Donato, 2020). This low functional and taxonomic diversity of tree species would suggest that stand structure may be more important than composition in these North American forests. In contrast, tree richness is much higher in temperate forests in the southern hemisphere, and dominant tree species are functionally very diverse, including a high proportion of species that produce fleshy-fruits and animal-pollinated flowers (Jaksic and Feinsinger, 1991; Aizen et al., 2002). Thus, forest composition is likely particularly important to determining avian habitat quality in botanically diverse ecosystems such as the Austral temperate rainforests. As such, VDT should be applied with forest composition in mind, considering for example, the availability of seed trees and the time needed for new recruitment to occur in each forest type. Such considerations could expedite the restoration process and support the various ecosystem functions provided by bird communities within secondary forests. However, there are at least two possible alternative explanations for the lack of clear VDT effects in our study. First, avian responses to forest thinning can take several years to develop and are often non-linear as a result of harvest-related disturbances, vegetation development, and demographic or behavioral lags (Cahall et al., 2013; Harris and Betts, 2021). Second, unforeseen logistic constraints prevented our achieved experimental design from being perfectly orthogonal and thus could have reduced the power of the tests conducted to detect VDT effects.

Besides these limitations, our study showed that VDT had surprisingly little effect on bird communities in Austral Temperate Rainforest in the short-term, with initial stand attributes outweighing effects of forest management. In addition, because our sampling design is biased towards the understory up to the first meters due to the height limit of mist-nets (2.5 m), some individuals or species inhabiting the mid-canopy layer could be underrepresented in our results. Furthermore, the lower canopy and denser understory in Mixed-evergreen versus *Nothofagus* forests may affect species-specific capture rates. Nevertheless, since we captured 14 out of the 19 species of Passeriformes reported using point-counts at this area (Authors unpubl. data), with none of the five missing species in our study being canopy specialists, our results provide a decent representation of bird communities inhabiting secondary Austral Temperate Rainforests. Within species, the higher number of males with respect to females in both elaeenias and rayaditos, and the higher body condition index in males of the latter, could represent a sampling bias if each sex differentially used the vertical profile.

In conclusion, while VDT management increases structural complexity in temperate forests, in geographical regions with a high alpha and beta tree diversity, dominant tree composition could be more important for supporting avian communities, at least in the short-term. Further studies of bird communities and habitat features using the same experimental plots (Donoso et al., 2020) should additionally consider survival analyses (Willson and Pendleton, 2008; Thomson and Estades, 2012), specific sampling efforts for ‘tapaculos’ (e.g. Willson et al., 1994), and mist-net captures in the mid-canopy layer (e.g. Derlindati and Caziani, 2005), to better understand the mid- and long-term effects of VDT management in key associated biodiversity to Austral temperate rainforests.

Declaration of Competing Interest

The authors declare the following financial interests/personal

relationships which may be considered as potential competing interests: Pablo Donoso reports financial support was provided by CONICYT.

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Appendix A

Table A1

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