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Alternative silvicultural practices with variable retention improve bird conservation in managed South Patagonian forests

María Vanessa Lencinas^a, Guillermo Martínez Pastur^{a,*}, Emilce Gallo^b, Juan Manuel Cellini^c

^a Centro Austral de Investigaciones Científicas (CONICET), Av. Houssay 200 (9410) Ushuaia - Tierra del Fuego, Argentina

^b Administración de Parques Nacionales - Parque Nacional Tierra del Fuego, San Martín 1395 (9410) Ushuaia - Tierra del Fuego, Argentina

^c Facultad de Ciencias Agrarias y Forestales - Universidad Nacional de La Plata, cc 31 (1900) La Plata - Buenos Aires, Argentina

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ABSTRACT

Alternative silvicultural approaches to timber management, such as regeneration treatments with different degrees of stand retention, may mitigate negative effects of clear-cutting or shelterwood cuts in forested ecosystems, including changes in old-growth forest bird communities. The aims of this work were: (a) to compare bird species richness and densities among different silvicultural designs with variable retention (dispersed and/or aggregated) and unmanaged primary forests, and (b) to assess temporal changes at community and species levels before and after treatments. A baseline avian survey was conducted prior to harvesting to evaluate canopy gap presence and forest stand site quality influences. Subsequent to harvesting, data on bird species richness and density were collected by point-count sampling during the summer season for 5 consecutive years (4 treatments × 5 years × 6 sampling points × 5 counts). Bird species richness and density (15 species and 9.2 individuals ha⁻¹) did not change significantly with forest site quality of the stands and canopy gap presence in unmanaged forests. However, both variables were significantly modified in managed forests, increasing over time to 18 species and reaching to 39 individuals ha⁻¹. Inside the aggregated retention, bird communities were more similar to unmanaged primary forests than those observed within the dispersed retention or in clear-cuts. Opting for a regeneration method with dispersed and aggregated retention has great potential for managing birds in *Nothofagus pumilio* forests. This method retained enough vegetation structure in a stand to permit the establishment of early successional birds (at least in dispersed retention), and to maintain the bird species of old-growth forests which could persisted in the retention aggregates.

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1. Introduction

Biodiversity conservation is a main objective of wildlife managers where human activities are responsible for species loss (Vitousek et al., 1997). As a result, when an economic activity is planned it is necessary to make efforts to minimize the impacts (Franklin et al., 1997; Mitchell and Beese, 2002). Among other economic activities, forest management increasingly is being scrutinized by the public on the basis of its effect on non-timber values, including the provision of habitat for forest birds (Aubry et al., 1999). Forest management impacts on biodiversity can be positive or negative and of different intensity, depending on the silvicultural system employed (Willot, 1999). Silvicultural management effects on bird species richness, relative abundance or

density have been analyzed in many forested ecosystems. However, most studies have assessed short-term effects of traditional forest practices (e.g. Costello et al., 2000; King and DeGraaf, 2000; Wardell-Johnson and Williams, 2000), and recently harvesting with different degrees of retention have been evaluated (Rodewald and Yahner, 2000; Vergara and Schlatter, 2006; Waterhouse and Armleder, 2007). Nonetheless, medium- or long-term scale research is lacking. In addition, only a few studies compare forest structure before and after the silvicultural practices (Before-After-Control-Impact or BACI approach) as a way of determining the extent of variation in biodiversity prior to the implemented treatment (Wardell-Johnson and Williams, 2000; Waterhouse and Armleder, 2007).

Variable retention approaches to timber harvesting are a management proposal to mitigate the potentially harmful effects of traditional practices on forest ecosystems, such as clear-cutting or shelterwood cut systems (Franklin et al., 1997; Aubry et al., 1999; Mitchell and Beese, 2002). Species sensitivity to variable retention cuts depends on their individual tolerance to habitat

* Corresponding author. Tel.: +54 2901 422310; fax: +54 2901 430644.
E-mail addresses: vlencinas@cadic.gov.ar (M.V. Lencinas),
cadicforestal@cadic.gov.ar (G.M. Pastur).

alteration (Vanderwel et al., 2007) and could be largely influenced by the interaction between retention types and the spatial-temporal variation in habitat and landscape characteristics. Variable retention harvest is a silvicultural design currently being applied at an industrial scale in *Nothofagus pumilio* forests in the Argentine portion of Tierra del Fuego Island (Martínez Pastur and Lencinas, 2005; González et al., 2006). This proposal leaves 30% of the forest area as aggregated retention and 20% basal area as dispersed retention among aggregates for more than one forest management cycle (70–120 years). This method was designed to minimize the impact on the original biodiversity by maintaining landscape heterogeneity and habitat connectivity (Lencinas et al., 2007).

In *Nothofagus pumilio* forests, as in other forested ecosystems, the most abundant and diverse group of vertebrates is birds (Lencinas et al., 2005). Therefore, they are useful as a broad indicator of biodiversity change under forest management. Here, different retention type effects on avian species richness and density were studied. These effects were compared to an unmanaged primary forest over a 5-year time period. We hypothesized that silvicultural systems with aggregated retention would improve the conservation of bird community structure, compared to dispersed retention, maintaining at least some of the avian diversity observed in unmanaged forests. To enhance the comparison, a baseline was conducted prior to harvesting to evaluate the influence of canopy gap presence and site quality of the stands. Birds were expected to prefer open forests with large gaps, compared to closed forests, and increase their diversity with stand site quality. The second aim of this work was to assess temporal changes of forest birds at the community and species level in harvested and unmanaged primary stands, where we anticipated that bird populations and species richness would be more stable in old-growth forests than in harvested stands.

2. Materials and methods

2.1. Studied forest and structure characterization

An area of 61 ha of pure natural old-growth *Nothofagus pumilio* forest was selected in San Justo Ranch, Tierra del Fuego, Argentina (54°06'S, 68°37'W) with a full range of site qualities: site index at base age of 60 years (SI_{60}) varied between 9.8 and 23.2 m. Stands growing in medium-high site qualities ($SI_{60} = 15.3$ –23.2 m) have a total volume over 650 m³ ha⁻¹ and trees with a total height over 22 m, while stands growing in medium-low site qualities ($SI_{60} = 9.8$ –15.3 m) have a total volume of 300–650 m³ ha⁻¹ and trees with a total height less than 22 m (Martínez Pastur et al., 1997). These forests had remained undisturbed by forest practices before silvicultural regeneration systems were in place.

Climate was measured in the study area with two weather stations (Davis Weather Wizard III and accessories, USA) placed in an old-growth forest and in a dispersed retention, harvested stand during years 2002–2005 (Martínez Pastur et al., 2007). The climate was characterized by short, cool summers and long, snowy and frozen winters. Mean monthly temperatures (2 m height from the forest floor) varied from -0.2 °C to 10.4 °C (extreme minimum and maximum from -9.6 °C in July to 24.9 °C in February) in the old-growth forest, while in the harvested stand temperature varied from -1.0 °C to 10.6 °C (extremes from -11.3 °C in July to 25.9 °C in February). Only 3 months per year were free of mean monthly temperatures under 0 °C, and growing season was approximately 5 months (Barrera et al., 2000). Soil temperature (30 cm deep) never froze in the old-growth forest, but soil freezing was observed in the harvested stand (-0.2 to -0.6 °C during June–July). Precipitation including snowfall (2 m height from the forest floor) was 382 mm yr⁻¹ inside the old-growth forest, while it was

639 mm yr⁻¹ in the harvested stand. Annual average wind speed outside forests was 8 km h⁻¹, reaching up to 100 km h⁻¹ during storms.

Three silvicultural regeneration systems were applied during 2001, leaving a unharvested control treatment (C) (22.9 m total height, 528 trees ha⁻¹, 40.6 cm diameter at breast height-DBH, 65.0 m² ha⁻¹ basal area-BA and 727.8 m³ ha⁻¹ total over bark volume-TOBV). The cut treatments were: (i) a dispersed retention (DR), where 30 m² ha⁻¹ BA of overstorey were homogeneously left out as remnants (105 trees ha⁻¹, 54.8 cm DBH and 353.7 m³ ha⁻¹ TOBV), which was comparable with the first intervention of a shelterwood cut (Schmidt and Urzúa, 1982; Martínez Pastur et al., 2000); (ii) an aggregated retention (one aggregate per hectare of 30 m radius) separated by clear-cuts (AR); and (iii) a combined retention with aggregated and dispersed retention (15 m² ha⁻¹ BA of overstorey were homogeneously distributed between aggregates) (CR).

2.2. Bird sampling

Data were collected with the point-count sampling method in each treatment during the summer season (February) for 5 consecutive years: 1 year prior to harvesting (2001) and 4 years after harvesting (2002–2005). Sampling was conducted in a 4-h period following sunrise, which is the time of major social and feeding activity of birds, and under equivalent climatic conditions, discarding days of fog, strong winds or rain (Lencinas et al., 2005).

Prior to harvesting, nine sampling points for medium-low ($SI_{60} = 9.8$ –15.3 m) and medium-high ($SI_{60} = 15.3$ –23.2 m) site quality stands were randomly established and clearly identified in the field. Sampling points were 100 m apart and were visited five times each, reaching 90 total counts. Simultaneously, six forest gaps in the medium-high quality stands (three large gaps - up to 25 m, and three small - less than 20 m diameter) were identified and sampled five times each. After harvesting, six sampling points in each control and regeneration treatments were randomly established and clearly identified in the field. They were at least 100 m apart and were sampled five times during each summer in the following 4 years, reaching 480 total counts. An equal number of samples was taken by each field assistant, while the sampling point order was daily changed to balance the effect of day-time on bird observations (Shields, 1977). This design was used in order to detect the variability in each stand and was successfully implemented in other studies (Deferrari et al., 2001; Lencinas et al., 2005). A 10-min observation period was used in each count. Point-counts consisted of a 2-min period of habituation (time in which birds return to their normal activity) and an 8-min period of counting. A short habituation period was chosen because forest birds of these forests are not at all shy. Sampling considered direct sighting recognition with binoculars. Calls were used as orientation to visually locate individuals to measure the distance between the bird and the center of the plot to calculate density. Taxonomy, observation distance (m) and location (inside, edge or outside gaps) were recorded for each individual. Distance was measured using an IMPULSE laser rangefinder (Laser Technology, USA). Bird taxonomy followed Narosky and Yzurieta (1987) as presented in Table 1.

2.3. Data analysis

Bird species richness and density were determined following Lencinas et al. (2005). This methodology uses the half of the maximum observation distance from each treatment as a radius of a circular area for bird density estimates. These distances for density estimation were 23 m in control plots, 30 m in aggregate plots, 32 m in dispersed retention plots, and 35 m in clear-cuts

Table 1
Trophic and migration status of bird species found in *Nothofagus pumilio* forests.

| Species | Order | Trophic level | Migration level | Code |
|-------------------------------------------|--------------|-------------------------------------------------|---------------------|------|
| <i>Anairetes parulus</i> Kittlitz | Passeriform | I | R, p ⁽⁸⁾ | ANPA |
| <i>Aphrastura spinicauda</i> Gmelin | Passeriform | I, F ⁽³⁾ | R | APSP |
| <i>Campephilus magellanicus</i> King. | Piciform | I | R | CAMA |
| <i>Carduelis barbata</i> Molina | Passeriform | G, H, I ⁽¹⁾ | R, P | CABA |
| <i>Cinclodes patagonicus</i> Gmelin | Passeriform | I | P, R ^a | CIPA |
| <i>Curaeus curaeus</i> Molina | Passeriform | I, G | P, R | CUCU |
| <i>Elaenia albiceps</i> Hellmayr. | Passeriform | I, G, F, N ^(4,10) | M | ELAL |
| <i>Enicognathus ferrugineus</i> Müller | Psittaciform | H, G, F ⁽⁹⁾ | R | ENFE |
| <i>Falco peregrinus</i> Tunstall | Falconiform | C | | FAPE |
| <i>Falco sparverius</i> L. | Falconiform | C | M | FASP |
| <i>Glaucidium nanum</i> King. | Strigiform | C, I | R, p ⁽³⁾ | GLNA |
| <i>Milvago chimango</i> Viellot | Falconiform | C, Sc, I, F ⁽³⁾ , E-N ⁽⁷⁾ | P, R ^a | MICH |
| <i>Muscisaxicola macloviana</i> Garnot | Passeriform | I | M | MUMA |
| <i>Phrygilus patagonicus</i> Lowe | Passeriform | G, F, I, H ^(1,2) , N ⁽⁶⁾ | P | PHPA |
| <i>Polyborus plancus</i> JF Miller | Falconiform | Sc, C, F ⁽³⁾ , E-N ⁽⁷⁾ | R, P ^a | POPL |
| <i>Pygarrhichas albogularis</i> King. | Passeriform | I | R | PYAL |
| <i>Scytalopus magellanicus</i> Gmelin | Passeriform | I, F, G | R | SCMA |
| <i>Tachycineta leucopyga</i> Cabanis | Passeriform | I | M | TALE |
| <i>Theristicus caudatus</i> Boddaert | Ardeiform | I, C, F ⁽³⁾ | M, P ^a | THCA |
| <i>Troglodytes aedon</i> Viellot | Passeriform | I, G ⁽³⁾ | M | TRAE |
| <i>Turdus falcklandii</i> King. | Passeriform | I, F, G, H ⁽²⁾ | R | TUFA |
| <i>Xolmis pyrope</i> Kittlitz | Passeriform | I | M | XOPY |
| <i>Zonotrichia capensis</i> Status Molina | Passeriform | I, G, F, H | M | ZOCA |

Trophic levels: C = carnivory; H = herbivory; I = insectivory; F = frugivory; G = granivory; N = nectivory; Sc = scavenger; E-N = eggs and nests predator. Migration level: M = migratory; R = resident; P = partial migratory.

^a Occasional. Based on: (1) Humphrey et al. (1970); (2) Schlatter (1995); (3) Rozzi et al. (1997); (4) Smith Ramírez and Armesto (1998); (5) Clark (1986); (6) Traveset et al. (1998); (7) Donázar et al. (1996); (8) Venegas (1986); (9) Díaz and Kitzberger (2006); (10) Brown et al. (2007).

between aggregate plots. Species richness estimates were obtained from total bird observations at each point count.

For the baseline characterization, two separate one-way ANOVAs were performed with the following main factors: (i) site quality of the stands (medium-low $SI_{60} = 9.8\text{--}15.3$ m, medium-high $SI_{60} = 15.3\text{--}23.2$ m), and (ii) gap presence (closed forest and gap). Then, a two-way ANOVA was carried out with gap size (large and small gaps) and position in the gap (inside, edge or outside) as main factors. The response variables in all the analyses were bird species richness and density.

For comparison of different retention types and control treatments the following analyses were done: (i) a detrended correspondence analysis (DCA) with the 5th year observation bird density data down-weighting for rare species, where rare is a species with less than 20% frequency of the commonest species; (ii) a cluster analysis using a complete linkage amalgamation rule and Euclidean distance measurement based on a matrix of bird species densities of the 5th year observation; (iii) one-way ANOVAs using variable retention and control treatments or sampling year as main factors to analyze bird species richness and density (repeated measure ANOVA was not used due to strong interactions between treatments and years); and (iv) repeated measures ANOVAs for the most abundant nine bird species densities, using treatments (C, RD, inside aggregates in CR-CRI, outside aggregates in CR-CRO, inside aggregates in AR-ARI, outside aggregates in AR-ARO) and years after harvesting as main effects. When the sphericity test was significant, the Greenhouse and Geisser (1959) univariate adjustment was applied to evaluate within-subjects effects. A post hoc Tukey's test, corrected for unequal N, was used for all mean comparisons ($p < 0.05$).

3. Results

Prior to harvesting, 15 bird species and 254 individuals (Table 2) were identified during baseline sampling in 120 point-counts (Table 2). No significant differences were detected in bird species richness ($F = 0.09$, $p = 0.774$; $F = 0.01$, $p = 0.933$, respectively) and density ($F = 0.36$, $p = 0.557$; $F = 1.04$, $p = 0.326$, respectively) based

on site quality of the stands or gap presence. Between medium-high and medium-low site quality stands, 3.8 ± 0.8 S.D. (average \pm standard deviation) species per sampling point and 9.2 ± 7.4 S.D. individuals ha^{-1} were found. Between closed forests and gaps, 3.8 ± 1.2 S.D. species per sampling point and 8.8 ± 6.8 S.D. individuals ha^{-1} were observed. In addition, gap size did not show significant differences either when bird species richness (and $F = 1.19$, $p = 0.297$) or density ($F = 3.77$, $p = 0.076$) were analyzed. When position in the gap was assessed, however, significant differences in bird species richness were found for outside canopy gaps (under closed canopy) and edges, compared to inside gaps ($F = 4.00$, $p = 0.047$), but there was no differences in density ($F = 0.12$, $p = 0.888$). Statistical interactions between position and size were not significant for either variable ($F = 0.76$, $p = 0.488$; $F = 1.41$, $p = 0.282$, respectively). Both bird species richness and density presented the same trend, with lower values inside gaps, medium values in edges and greater values outside gaps.

After harvesting, 23 bird species and 4694 individuals were observed in 480 point-counts (Table 2). A high proportion of bird species was shared between C and retention treatments (56–73%). CR treatment included as a nested subset all the bird species observed in C, in contrast to AR and DR, which lost some bird species (e.g. *Pygarrhichas albogularis* in AR and *Polyborus plancus* in DR). Retention treatments also included species not typically found in C bird assemblages (e.g. *Muscisaxicola macloviana*, *Xolmis pyrope* or *Falco sparverius*). These species were more frequently detected in the harvested sectors (ARO and CRO) than inside aggregates (ARI and CRI). Species highly adapted to C (e.g. *Pygarrhichas albogularis*) were also detected inside aggregates (CRI) in CR treatment.

DCA analysis presented an axis one (eigenvalue = 0.604) more likely related to degree of canopy opening, while axis two (eigenvalue = 0.213) was related with the presence of distinctive bird species (e.g. *Elaenia albiceps*) (Fig. 1A). In the ordination, a closer relationship was shown among plots of CRI, while the others presented greater variability (Fig. 1A). Some plots of C are dissimilar to the harvested stands, while others were more closely related to CRI and ARI treatments. The sampling plots in CRO were intermingled with DR, occupying an intermediate position

Table 2
Bird density (individuals ha⁻¹) in control and harvested stands (dispersed, aggregated and combined retention) of *Nothofagus pumilio* forests prior to harvesting and 1–4 years after harvesting.

| Species code | Year 0 | | Year 1 | | | | | | Year 2 | | | | | | Year 3 | | | | | | Year 4 | | | | | |
|--------------|---------------|-------|--------|-------|-------|-------|-------|-------|--------|-------|-------|-------|-------|-------|--------|-------|-------|-------|-------|-------|--------|-------|-------|-------|-------|--|
| | CF (Gaps) | C | DR | CR | | AR | | C | DR | CR | AR | | C | DR | CR | AR | | C | DR | CR | AR | | | | | |
| | | | | CRI | CRO | ARI | ARO | | | | CRI | CRO | | | | ARI | ARO | | | | CRI | CRO | ARI | ARO | | |
| ANPA | - | - | - | - | 0.21 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | | | |
| APSP | 2.47 (2.01) | 4.01 | 1.45 | 1.65 | 1.87 | 2.36 | 1.21 | 4.01 | 2.80 | 4.48 | 1.11 | 0.47 | 0.69 | 4.01 | 3.00 | 7.07 | 5.80 | 3.07 | 1.73 | 1.00 | 4.35 | 8.25 | 1.24 | 2.83 | 2.77 | |
| CABA | 3.54 (1.60) | <0.01 | 3.63 | 1.89 | 2.28 | 4.48 | 2.25 | 0.20 | 0.83 | 2.59 | 1.78 | 0.47 | 2.77 | 0.60 | 3.83 | 4.24 | 9.33 | 3.30 | 21.48 | <0.01 | 3.63 | 1.89 | 2.28 | 4.48 | 2.25 | |
| CAMA | <0.01 (0.20) | <0.01 | <0.01 | - | <0.01 | - | - | <0.01 | <0.01 | - | - | - | - | - | <0.01 | - | <0.01 | <0.01 | - | - | - | - | - | - | - | |
| CIPA | 0.07 (-) | - | - | - | - | - | - | - | - | - | <0.01 | - | - | - | - | - | - | - | - | - | - | - | - | - | <0.01 | |
| CLUCU | - | - | - | - | - | - | <0.01 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| ELAL | 0.74 (0.80) | 1.60 | 0.52 | 2.36 | 0.21 | 0.24 | 0.35 | 1.40 | 0.31 | 0.94 | 0.22 | 0.24 | - | 0.80 | 1.14 | - | - | 0.94 | 0.35 | 2.01 | - | 0.47 | - | 0.47 | <0.01 | |
| ENFE | 1.20 (0.60) | <0.01 | 0.21 | 1.65 | 0.21 | - | <0.01 | <0.01 | 0.83 | 0.24 | 1.11 | 1.89 | <0.01 | <0.01 | 0.21 | 0.47 | - | 1.18 | 0.69 | 0.40 | 1.35 | 3.54 | <0.01 | - | 0.35 | |
| FAPE | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | <0.01 | <0.01 | 0.47 | 0.52 | - | - | - | - | - | <0.01 | |
| FASP | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| GLNA | - | - | - | <0.01 | - | <0.01 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | |
| MICH | <0.01 (-) | <0.01 | <0.01 | - | - | - | <0.01 | <0.01 | <0.01 | - | - | - | - | <0.01 | - | <0.01 | - | <0.01 | 0.17 | - | 0.21 | - | <0.01 | - | - | |
| MUMA | - | - | - | - | - | - | - | - | <0.01 | - | <0.01 | - | <0.01 | - | - | - | - | - | - | - | - | - | - | - | - | |
| PHPA | 0.20 (-) | 0.40 | 0.21 | - | 0.41 | - | 0.17 | - | 0.31 | <0.01 | - | <0.01 | 0.35 | - | 0.83 | <0.01 | 0.21 | 1.18 | 1.73 | 0.40 | 0.31 | - | 1.04 | 0.94 | 3.46 | |
| POPL | - | - | - | - | <0.01 | - | <0.01 | 0.40 | <0.01 | - | <0.01 | - | <0.01 | - | - | - | - | - | - | <0.01 | - | <0.01 | 0.24 | <0.01 | <0.01 | |
| PYAL | <0.01 (-) | 1.81 | 0.10 | - | - | <0.01 | - | - | - | - | - | - | <0.01 | - | - | - | - | - | - | - | - | 0.47 | - | <0.01 | - | |
| SCMA | <0.01 (0.20) | - | <0.01 | 0.24 | <0.01 | - | 0.17 | - | <0.01 | 0.24 | - | - | <0.01 | - | 0.10 | 0.24 | 1.04 | - | 0.17 | - | 0.21 | <0.01 | <0.01 | - | - | |
| TALE | <0.01 (<0.01) | - | <0.01 | 0.94 | 0.21 | 0.24 | 0.35 | - | 0.10 | - | 0.67 | <0.01 | 1.73 | 0.20 | 1.24 | 7.55 | 6.22 | 3.77 | 7.80 | - | 0.52 | - | <0.01 | 0.94 | 0.69 | |
| THCA | <0.01 (-) | <0.01 | - | - | <0.01 | - | - | - | <0.01 | - | - | <0.01 | - | <0.01 | <0.01 | - | - | - | <0.01 | - | - | - | - | - | - | |
| TRAE | 0.27 (0.60) | <0.01 | 0.52 | 0.94 | 0.62 | 0.24 | 1.56 | 0.80 | 0.52 | 1.18 | 0.67 | 0.47 | 0.69 | 0.80 | 1.04 | 0.71 | 3.11 | 1.41 | 1.56 | 0.20 | 1.76 | 1.18 | 2.90 | 1.89 | 3.29 | |
| TUFA | 0.60 (0.20) | <0.01 | 0.10 | 0.47 | 0.41 | 0.24 | 1.91 | 3.21 | 0.93 | 1.18 | 0.44 | 0.24 | 0.35 | 1.81 | 0.41 | 1.41 | 0.83 | 2.59 | 0.87 | 0.20 | <0.01 | 2.12 | 0.21 | 0.24 | 1.21 | |
| XOPY | - | - | - | - | - | - | - | - | - | - | - | - | - | <0.01 | - | <0.01 | - | <0.01 | - | - | - | <0.01 | - | - | 0.17 | |
| ZOCA | 0.13 (0.40) | <0.01 | <0.01 | 1.18 | 1.24 | 0.24 | 3.29 | <0.01 | 3.94 | 0.94 | - | 0.24 | 4.33 | <0.01 | 1.04 | 0.24 | 2.28 | 4.95 | 16.11 | 0.80 | 3.94 | 0.71 | 6.22 | 6.60 | 30.14 | |

CF = closed forest; C = control; DR = dispersed retention; CR = combined retention with aggregated and dispersed retention; AR = aggregated retention; CRI = inside aggregates in CR; CRO = outside aggregates in CR; ARI = inside aggregates in AR; ARO = outside aggregates in AR.

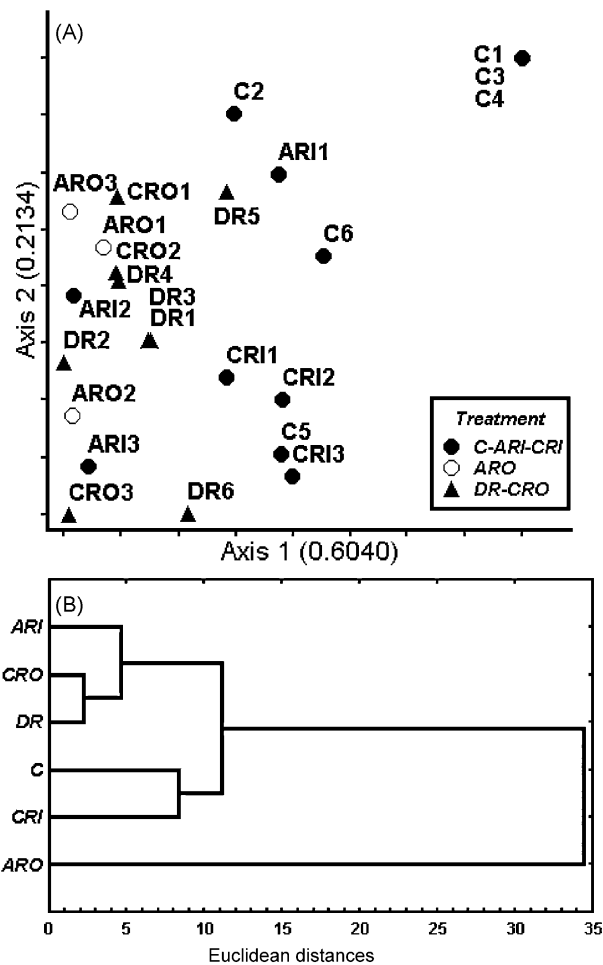


Fig. 1. DCA ordination (A) and cluster analysis (B) based on the 4th year after harvesting for bird density data of control and harvested stands of *Nothofagus pumilio* forests. C = control; DR = dispersed retention; CRI = inside aggregates in combined retention; CRO = outside aggregates in combined retention; ARI = inside aggregates in aggregated retention; ARO = outside aggregates in aggregated retention.

between control C and ARO. Cluster analysis (Fig. 1B) presented comparable results to those described for DCA, where C and CRI were closer related (8.5 Euclidean distances) than a second group composed of ARI, CRO and DR. Clear-cuts outside aggregates (ARO) represented the most different treatment regarding bird assemblages (34.0 Euclidean distances).

Harvest with variable retention significantly affected bird species richness and density (Table 3). Bird species richness significantly increased in variable retention treatments compared to C (3–5 species), being higher in AR (6–10 species) than in CR and DR (5–8 species). Bird density showed significant differences only in the 4th year after harvesting (Table 3), with higher density in the AR (39 individuals ha⁻¹) compared to DR and CR (16–17 individuals ha⁻¹) or C (5 individuals ha⁻¹). No significant temporal changes in forest bird species richness and density were evident in C (Table 3), with 3.9 ± 1.4 S.D. species per sampling point and 7.8 ± 7.0 S.D. individuals ha⁻¹ for the studied period. Harvested forests showed greater variations in both variables. AR presented the greatest changes with a maximum of 10 species per sampling point and 39 individuals ha⁻¹. DR presented differences in bird species richness among years reaching eight species per sampling point, but no difference in density (7–16 individuals ha⁻¹). In CR significant differences among years were observed in bird density reaching to 25 individuals ha⁻¹, but bird species richness did not change with time (6–8 species per sampling point).

Table 3

One-way ANOVA for bird species richness (species per sampling point) and density (individuals ha⁻¹) in control and harvested stands (dispersed, aggregated and combined retention) in *Nothofagus pumilio* forests. Each year after harvesting was compared among silvicultural treatments (rows), and each silvicultural treatment was analyzed among years (columns).

| Years | C | DR | CR | AR | F (p) |
|-----------------|---------------|---------------|---------------|---------------|----------------|
| Richness | | | | | |
| 1 | 3.5 | 5.2 | 7.5 | 6.5 | 12.27 (0.0001) |
| 2 | 4.7 | 5.2 | 6.2 | 6.0 | 1.18 (0.3436) |
| 3 | 4.0 | 7.5 | 7.2 | 9.8 | 18.56 (0.0000) |
| 4 | 3.7 | 6.2 | 6.5 | 8.3 | 14.27 (0.0000) |
| F (p) | 0.80 (0.5109) | 4.31 (0.0168) | 1.45 (0.2584) | 8.50 (0.0008) | |
| Density | | | | | |
| 1 | 7.82 | 6.74 | 9.49 | 9.64 | 0.37(0.7845) |
| 2 | 10.03 | 10.57 | 9.00 | 7.46 | 0.25 (0.8631) |
| 3 | 8.22 | 12.85 | 25.37 | 38.03 | 3.02 (0.0541) |
| 4 | 5.01 | 16.16 | 17.00 | 39.15 | 6.65 (0.0027) |
| F (p) | 0.48 (0.6981) | 1.69 (0.2013) | 8.03 (0.0010) | 3.89(0.0242) | |

C = control; DR = dispersed retention; CR = combined retention with aggregated and dispersed retention; AR = aggregated retention; F = F test; p = significance level.

Changes in bird species richness and density were greater in the harvested zones (ARO and CRO) than inside the aggregates (ARI and CRI) when compared with C annual temporal variation, with the greatest differences in the AR treatment (Fig. 2). These differences significantly increased after the 3rd year post-harvesting. CRO and ARO had 5 and 7 more species than C, while bird densities were 21 and 54 more individuals ha⁻¹ in C than in CRO and ARO, respectively.

Repeated measures ANOVAs of the densities of the most abundant birds (eight Passeriformes and one Psittaciformes) showed significant differences in six species (Table 4). One small bird (*Aphrastura spinicauda*), one thrush (*Turdus falcklandii*) and one parrot (*Encicognathus ferrugineus*) did not show significant differences in density among treatments. *Elaenia albiceps* had differences among treatments but not among years. Density was higher in C (1.45 individuals ha⁻¹) than in harvested stands, but this was more frequent in the aggregates (ARI and CRI) than open adjacent areas (ARO and CRO) where density drastically decreased to 10% of the original value.

The other species did differ among treatments and years. *Carduelis barbata*, *Phrygilus patagonicus*, *Tachycineta leucopyga*, *Troglodytes aedon* and *Zonotrichia capensis* were found in low densities in C (0.05–0.45 individuals ha⁻¹), while their density increased in the harvested areas (0.41–13.17 individuals ha⁻¹) more than in the aggregates (<3.42 individuals ha⁻¹). Bird densities significantly increased after the 3rd year post-harvesting, going from 0.11–2.42 individuals ha⁻¹ to 0.66–8.07 individuals ha⁻¹, except for *T. leucopyga* which presented a high density in only 1 year (4.46 individuals ha⁻¹ at the 3rd year compared to 0.29–0.41 individuals ha⁻¹ in the other years). Interactions found in *T. leucopyga* were due this unusual behavior, while the interactions found in *Zonotrichia capensis* were due to the significant density increase with time in ARO compared to the other treatments.

4. Discussion

4.1. Birds in primary *Nothofagus* forests

Bird species richness in old-growth *Nothofagus* forests is naturally lower than more temperate areas farther north (Brown et al., 2007). Climatic factors in the Magellanic Region, such as low temperatures, frequent snowfalls even in summer and strong

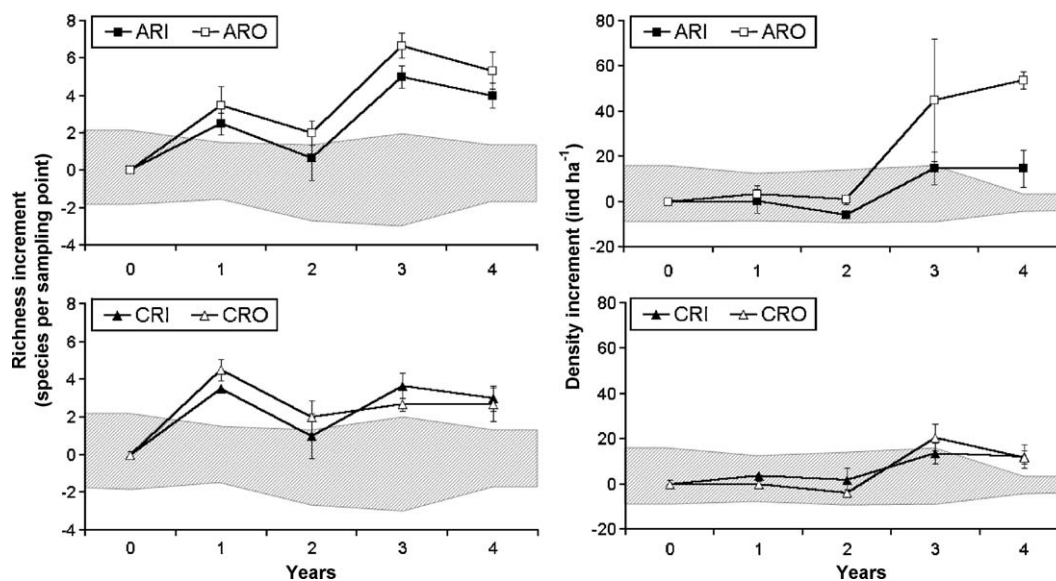


Fig. 2. Increments of bird species richness (species per sampling point) and density (individuals ha⁻¹) of harvested stands compared to C averages in *Nothofagus pumilio* forests prior to harvesting and 1–4 years after harvesting. ARI = inside aggregates in aggregated retention; ARO = outside aggregates in aggregated retention; CRI = inside aggregates in combined retention; CRO = outside aggregates in combined retention. Fill area indicate C variations and bars indicate standard error.

winds, may limit the assemblage of birds to only a subset of all austral temperate forest species that are well adapted to this climate (Vergara and Schlatter, 2006). Only 15 species were detected in this study, as reported by Lencinas et al. (2005), which is more than those described by Deferrari et al. (2001) and Venegas (2000) (12 and 10 species, respectively). Anderson and Rozzi (2000) reported 19 forest bird species on Navarino Island (Chile), with a lower number of species in the closed forests (9 species) compared to forest edge or openings (16 species). The avian density described here for old-growth forests (9 individuals ha⁻¹) was lower than that reported by Lencinas et al. (2005) (12–17 individuals ha⁻¹).

Differences in vertical forest structure (e.g. foliage height or number of layers), as well as gap patches, could influence the number of potential niches that affect bird diversity in a natural, unmodified forested landscape (Costello et al., 2000; Wardell-Johnson and Williams, 2000; Díaz et al., 2005). In our study, birds

did not show a preference in their use of different site quality stands within the old-growth forests, nor for canopy gaps. We might expect a positive relationship between bird species richness and density and understory plant richness and cover. Understory plants were positively related to site quality stands in *Nothofagus* forests, being higher in the medium-high site qualities (23 species and 63% cover) than in the medium-low site qualities (18 species and 11% cover) (Mariottini et al., 2002). Canopy openings due to tree falls generate an increase in the incident light and effective rainfall that reaches to the forest floor (Caldentey et al., 1999–2000), enhancing the floristic richness and cover of the understory plants (Martínez Pastur et al., 2002). This increase in potential food offering was not found to influence birds in our study. Consequently, the hypothesis that birds prefer open forests with large gaps compared to closed forests was rejected, as there is not enough evidence of changes in richness and density. Despite this, it is possible that old-growth forests themselves offer greater insect

Table 4

Repeated measures ANOVA for bird species density (individuals ha⁻¹) in control and harvested stands (dispersed, aggregated and combined retention) in *Nothofagus pumilio* forests.

| Source | df | APSP F(p) | CABA F(p) | ELAL F(p) | ENFE F(p) | PHPA F(p) | TALE F(p) | TRAE F(p) | TUFA F(p) | ZOCA F(p) |
|--------------------------------------------------------------|------|--------------|---------------|--------------|--------------|--------------|----------------|--------------|--------------|----------------|
| Between subject effects | | | | | | | | | | |
| Treatments | 5 | 2.02 (0.081) | 7.30 (<0.000) | 3.25 (0.009) | 2.16 (0.064) | 3.82 (0.003) | 12.06 (<0.001) | 2.85 (0.018) | 1.11 (0.359) | 12.35 (<0.001) |
| Within subject effects | | | | | | | | | | |
| Years | 3 | 2.41 (0.067) | 5.37 (0.007) | 0.49 (0.658) | 0.99 (0.363) | 4.40 (0.012) | 79.86 (<0.001) | 5.86 (0.002) | 1.25 (0.287) | 3.60 (0.003) |
| Interaction | | | | | | | | | | |
| Treatments × Years | 15 | 1.34 (0.177) | 1.82 (0.064) | 0.81 (0.646) | 1.35 (0.217) | 1.52 (0.131) | 8.93 (<0.001) | 1.24 (0.253) | 1.41 (0.176) | 2.30 (0.021) |
| Density of bird species (individuals ha⁻¹) | | | | | | | | | | |
| Treatments | | | | | | | | | | |
| C | 3.26 | 0.20 a | 1.45 | 0.10 | 0.20 a | 0.05 a | 0.45 | 1.30 | 0.20 a | |
| DR | 2.90 | 2.95 a | 0.49 | 0.65 | 0.41 ab | 0.47 ab | 0.96 | 0.36 | 2.23 a | |
| CRI | 5.36 | 2.30 a | 0.94 | 1.47 | 0.00 a | 2.12 ac | 1.00 | 1.30 | 0.77 a | |
| CRO | 2.54 | 4.61 a | 0.10 | 0.41 | 0.41 ab | 1.76 bcd | 1.81 | 0.47 | 2.43 a | |
| ARI | 2.18 | 3.42 a | 0.47 | 0.77 | 0.53 ab | 1.24 ce | 1.00 | 0.82 | 3.01 a | |
| ARO | 1.60 | 10.74 b | 0.17 | 0.25 | 1.43 b | 2.64 de | 1.78 | 1.08 | 13.17 b | |
| Years | | | | | | | | | | |
| 1 | 2.09 | 2.42 a | 0.88 | 0.34 | 0.20 a | 0.29 a | 0.64 a | 0.52 | 0.99 a | |
| 2 | 2.28 | 1.42 a | 0.52 | 0.73 | 0.11 a | 0.41 a | 0.71 a | 1.05 | 1.57 a | |
| 3 | 4.11 | 7.13 b | 0.54 | 0.42 | 0.66 ab | 4.46 b | 1.44 ab | 1.32 | 4.10 ab | |
| 4 | 3.41 | 5.18 ab | 0.49 | 0.94 | 1.02 b | 0.36 a | 1.87 b | 0.66 | 8.07 b | |

Species codes appear in Table 1; C = control; DR = dispersed retention; CRI = inside aggregates in combined retention; CRO = outside aggregates in combined retention; ARI = inside aggregates in aggregated retention; ARO = outside aggregates in aggregated retention; F(p) = F test with significance level between parentheses. Different letters within columns represent significant differences at p < 0.05 for means.

abundance and richness (Lencinas et al., 2008), while understory plants represent a secondary source (a few grass species and scarce shrub fruit availability for a few weeks during the growing season). On the other hand, *Nothofagus* flowers and fruits are an attractive food resource for some bird species such as *Enicognathus ferrugineus* reported by Díaz and Kitzberger (2006).

4.2. The effect of silviculture on avian biodiversity

Silvicultural activities affect bird diversity through their influence on forest structure (King and DeGraaf, 2000). This varies in proportion to the magnitude of the alteration (Annand and Thompson, 1997) and influences foraging, nesting and breeding of forest birds; e.g. clear-cuts could lead to a complete replacement of the original bird community (Costello et al., 2000). *Nothofagus pumilio* forests managed by shelterwood cuts transformed uneven-aged to even-aged stands (Gea et al., 2004), without regard to forest values such as biodiversity conservation (Deferrari et al., 2001; Spagarino et al., 2001; Martínez Pastur et al., 2002). However, variable retention systems can maintain ecosystem health, resilience, and productivity, as well as compositional, structural, and functional diversity of the old-growth forests (Franklin et al., 1997; McClellan et al., 2000). The retention system proposed for Southern Patagonia (Martínez Pastur and Lencinas, 2005; González et al., 2006) tries to satisfy the need for a new silvicultural approach that maintains biological diversity as well as economic feasibility (Franklin et al., 1997; Mitchell and Beese, 2002). Variable retention harvesting differs from other systems, due to the fact it attempts to permanently maintain live trees and snags in multiple crown and size classes of both commercially and non-commercially trees, to maintain species and structural diversity (Rodewald and Yahner, 2000).

Dispersed retention harvesting (comparable to the first cut of a shelterwood system) provoked major changes in understory plant richness (19–29 species) and biomass (0.3–2.4 ton ha⁻¹) (Martínez Pastur et al., 2002), while the relative abundance of insects dramatically decreased by 30% (Spagarino et al., 2001). The increase in some food resources (e.g. gramineous plant grains) allowed the establishment of early successional birds and the incorporation of several non-typical forest bird species (e.g. *Muscisaxicola macloviana* or *Xolmis pyrope*), as well as increasing the density of other species that live in low density in the old-growth forests (e.g. *Carduelis barbata*) (see also Deferrari et al., 2001). Otherwise, the existence of open sectors and the increase in Passeriformes density offered raptors, such as *Falco sparverius* or *F. peregrinus*, a most favorable environment to perch with good sight distance for hunting. King and DeGraaf (2000) cite a decrease in abundance of several bird species (e.g. *Piranga olivacea*) in shelterwood cuts or clear-cuts compared to mature forests of New Hampshire, while other species (e.g. *Mniotilta varia*) experienced a considerable increase. Other studies found similar trends in bird changes when closed stands were compared to open impacted forest environments (Costello et al., 2000; Wardell-Johnson and Williams, 2000; Rodewald and Yahner, 2000; Aubry et al., 2004; Waterhouse and Armleder, 2007; Lantschner and Rusch, 2007).

The aggregated retention size in this study (30% of the harvested area and up to 100 trees each) was higher than that employed in the study reported by Vergara and Schlatter (2006) (1–20 trees each and 10–20% of the harvested area) conducted in *Nothofagus* forests in Chile. Other studies used nearly 100 live trees ha⁻¹ (23–46 m² ha⁻¹ basal area) as dispersed retention in mixed *Quercus-Acer* forests (Rodewald and Yahner, 2000), or 15% of green tree retention (70% as aggregated of 0.2–1.0 ha and 30% as dispersed) for northwestern United States forests (Aubry et al., 1999, 2004). The aggregate size evaluated in this study was enough

to safeguard some of the original environmental conditions of the primary *N. pumilio* forests (Martínez Pastur and Lencinas, 2005; Lencinas et al., 2007). These results agree with Vergara and Schlatter (2006) opinion, which stated that retention in forests with simple structure and where climate is rigorous, such as *N. pumilio* forests, should involve higher undisturbed areas (up to 20%) in order to mitigate negative effects on bird forest specialists. However, Aubry et al. (2004) and Vanderwel et al. (2007) suggest that not all the bird species significantly respond to different retention types and levels in different forested regions of North America. In our case, some bird species (e.g. *Elaenia albiceps*) maintained their presence and density inside aggregates, which were more similar to old-growth forests when dispersed retention was employed in the harvested areas. Beside this, other species, such as *Falco sparverius*, increased their densities in the edges of aggregates, using aggregates for shelter and foraging in clear-cuts or in open sectors of dispersed retention. Variable retention could be helpful for many species that need special tree requirements for nesting associated with old-growth forests (e.g. *Campephilus magellanicus*) (Ojeda et al., 2007). However, some species of old-growth forest bird community were sensitive to habitat changes, especially *Pygarrhichas albogularis* and *Polyborus plancus*, whose densities drastically diminished in clear-cuts or where the overstory was opened and homogenized in large patches as in DR.

The hypothesis that silvicultural systems with aggregated retention would improve the conservation of bird community structure more than other silvicultural proposals was supported by these data, due to greater similarity being observed between C and CRI or ARI, than with DR or CRO or clear-cuts. Bird species-dependent of the structure of old-growth forests (e.g. *E. albiceps*) were favored by the variable retention, while generalist species which usually live in the old-growth forests also were favored in the harvested stands due to the major food offering (e.g. *Troglodytes aedon*).

4.3. Temporal changes

Limited year-to-year changes were observed in the bird communities of old-growth forests during the 5 years of this study. This was probably because most of the main species were resident or partially migratory, and few of them are fully migratory (e.g. *E. albiceps*) (Brown et al., 2007). Some changes that were observed could be attributed to variable arrival of migratory species that nest in Tierra del Fuego, which usually depends on annual or periodic climate and vegetation variations that occur at larger scales. For example, *Tachycineta leucopyga* arrived in great numbers during the 4th year of the study, but returned to their normal values during the following year. On the other hand, some reductions in bird abundance could be attributed to annual temperature decrease and snowfall increase, which was also cited by Vergara and Schlatter (2006) for bird communities in similar forests.

For forest birds, short- and medium-term effects of variable retention cuts may depend mainly on the amount of residual, late-succession structures such as a multilayered canopy, stumps, understory cover, logs, snags (standing dead trees) and cavities (Merrill et al., 1998; Chambers et al., 1999). Canopy-dwelling species may experience a reduction in foraging efficiency with the thinning of the canopy (Franzreb and Ohmart, 1978). In contrast, ground and shrub-dwelling species may be affected by increases in understory biomass, which change the availability of suitable foraging and nesting habitat (Annand and Thompson, 1997). Wardell-Johnson and Williams (2000) reported considerable variation in year-to-year and season-to-season bird abundance in southwestern Australian forests associated with logging activities, although considerable replication is necessary before

changes can be reliably assigned to disturbance impacts. In our study, avian richness and density varied considerably among the years in the harvested areas (dispersed retention and clear-cuts), which could be related to the food offering as was discussed above. In these areas, bird density did not greatly change during the 1st years after harvesting although certain species did diminish (e.g. *A. spinicauda* or *Phrygilus patagonicus*) (see also Vergara and Schlatter, 2006). *Elaenia albiceps*, *Pygarrhichas albobularis* and *Turdus falcklandii* decreased in density as well, due to the fact they could also be negatively affected by fragmentation (Estades and Temple, 1999; Vergara and Simonetti, 2004). However, since the 3rd and 4th year after harvesting, bird diversity considerably increased compared to old-growth unmanaged forests, as observed by Deferrari et al. (2001), who study the full *Nothofagus pumilio* forest management cycle under shelterwood cut. Venegas and Schlatter (1999) and Venegas (2000) also found an insignificant effect on bird diversity in a short-term period after harvesting and a significant increase after longer periods (e.g. 8 years).

Bird species richness in aggregates increased with time compared to old-growth forests perhaps due to the fact that some predatory species, like *Falco sparverius*, use the edges of these patches. However, density did not vary inside aggregates as the understory maintained low levels of richness and biomass, which were comparable to those found in old-growth forests. The increase in bird richness inside aggregates was related to both described factors: (a) the density of migrant birds that arrived in harvested stands, and (b) food availability in each forest area. Density of birds that foraged in the understory of harvested stands significantly increased after the 3rd and 4th year post-harvesting, as the grass cover and biomass significantly increased at this time, compared to the previous years (Martínez Pastur et al., 2002). For this, the hypothesis that annual changes are more stable in old-growth forests than in harvested stands was accepted. Some studies have indicated that bird communities in forests are less variable year-to-year than those found in open ground habitats at local scale (Rotenberry and Wiens, 1980), which could be explained for their simpler habitat structure. However, the assemblage composition may also be more stable on the regional than on the local scale (Virkkala, 1991).

5. Conclusions

There is no single management system that will provide habitat for all species of forest birds in a single stand. Different management strategies are suited for sustaining different components of an entire forest ecosystem, and choosing the appropriate system will depend on specific goals (Costello et al., 2000). Partial cutting, such as variable retention, appear to have great potential for managing forest birds in southern Patagonian forests, because it alters the vegetation structure in a stand enough to permit the establishment of at least the early successional birds in dispersed retention, without eliminating all of the old-growth forest bird community, which could survive in retention aggregates. However, variable retention is relatively recent in Tierra del Fuego, so the beneficial effects of this management system on birds or other vertebrate species will have to be assessed over the medium- and long-term (Vergara and Schlatter, 2006).

Maximizing within-stand diversity by emphasizing shelterwood cutting may reduce diversity at the landscape scale because it does not appear to accommodate either old-growth forest specialist bird species or early succession specialist bird species (King and DeGraaf, 2000). On the other hand, shelterwood cuts change the structure from an uneven-aged old-growth forest to a more homogenous, secondary even-aged stand (Gea et al., 2004), thereby influencing the foraging, nesting, and breeding resources available to forest birds (Wardell-Johnson and Williams, 2000). For

this, the implementation of variable retention methods can improve bird diversity at the landscape scale by maintaining specialized bird species in both diversity and abundance. This silvicultural regeneration method also must be complemented with a landscape management plan that includes a well-dispersed system of old-growth forests along roads, rivers, and stream zones as well as reserves of old-growth timber-quality forests within the regeneration mosaics (Wardell-Johnson and Williams, 2000). The present study was carried out at a medium scale, and more replications must be conducted to generalize these conclusions at landscape or regional level.

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