# LANDSCAPE HISTORY, FRAGMENTATION, AND PATCH OCCUPANCY: MODELS FOR A FOREST BIRD WITH LIMITED DISPERSAL

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*Abstract.* We developed and tested patch occupancy models for an endemic understory bird with limited dispersal ability, the Chucao Tapaculo (*Scelorchilus rubecula*), in two South American temperate rain forest landscapes that differed in levels and duration of forest loss. We assessed cover changes since 1961 in each landscape and surveyed patches for Chucao Tapaculo occupancy. We then developed incidence-based predictive models independently for each landscape and tested each model reciprocally in the alternative study area. We thereby assessed the domain of model applicability and identified those predictor variables with general effects and those that varied between the two landscapes. The two models were consistent regarding variable selection, and predictive accuracy of each model was high in the landscape where training data were collected. However, the models differed substantially in the magnitudes of effects related to patch size, with larger unoccupied patches observed in the landscape with the more advanced stage of fragmentation. Due to this discrepancy, each model performed poorly when applied to the alternative landscape, potentially reflecting the contrasting stages of habitat loss. Although it was impossible to dissociate effects of level and duration of forest loss, we viewed the landscapes as representing two extremes along a continuum of fragmentation, providing insights into potential trajectories for portions of the biome where deforestation is occurring. Further, our data suggest that static equilibrium models developed from distribution patterns in recently fragmented landscapes may overestimate persistence when used as a forecasting tool, or when extrapolated to alternative landscapes where fragmentation is more advanced. Thus, we suggest that landscapes used as standards for model building should be selected with caution. We recommend that distribution patterns be obtained from landscapes where fragmentation is advanced, preferably with histories of fragmentation long enough that time-delayed extinctions already would have occurred.

*Key words: Chucao Tapaculo; classification tree; dispersal; fragmentation; landscape history; patch occupancy models; Rhinocryptidae; Scelorchilus rubecula; South American temperate rain forest; tapaculos.*

## INTRODUCTION

Predictive geographical modeling has gained importance in recent decades for examining impacts of land use change and developing conservation strategies (Guisan and Zimmermann 2000). The simplest approach for modeling landscape effects on wildlife populations relies on analysis of species distribution patterns in extant fragmented landscapes (Hanski 1994, ter Braak et al. 1998). Under this "incidence"-based approach, differences in patch occupancy by particular taxa are assumed to reflect the combined effects of landscape factors on population processes, resulting in absence of populations from areas with unsuitable patch- or landscape-context characteristics (Hanski 1994). Incidence-based models are less data intensive than alternative approaches (e.g., dynamic simulation modeling),

but there are several potential drawbacks. For example, independent data are frequently unavailable for model validation. This leads to use of a single data set for both model building and evaluation, resulting in optimistic measures of classification success (Fielding and Bell 1997). Other limitations include the difficulty of documenting species absence (Boyce et al. 2002) and poor model performance at predicting occurrence of rare or secretive species (Manel et al. 2001).

Furthermore, incidence-based models are static in nature and automatically assume equilibrium conditions by statistically relating species distributions to the present environment (Korzukhin et al. 1996, Guisan and Zimmermann 2000). The static character of incidence-based models is problematic because occurrence of a species at a certain moment in time does not necessarily imply persistence, due to potential time lags in equilibration of population processes following landscape alterations ("extinction debt"; Tilman et al. 1994). Therefore, incidence-based models may be valid for interpolating patch occupancies ("filling in" occupancies for non-sampled patches) at the time and place

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PLATE 1. Chucao Tapaculo (*Scelorchilus rubecula*). Photo credit: Steve Morello.

where data were collected. However, they may fail when used as a forecasting tool to predict future distribution patterns, or when extrapolated to alternative landscapes with differing levels or histories of fragmentation (Rykiel 1996).

Despite their limitations, incidence-based models are often the only feasible means for informing conservation planning, because comprehensive data for modeling dynamic responses to environmental change are available for so few species (Guisan and Zimmermann 2000). Nonetheless, models that fail to account for differences in fragmentation levels or extinction time lags may significantly overestimate persistence, with potentially disastrous consequences for conservation planning. Thus, it is critically important that planners recognize the hazards of extrapolating these models beyond their appropriate domains of applicability. If incidence-based models must be extrapolated to address more general conservation questions, they should be validated using independent data from alternative landscapes (Rykiel 1996). In practice, however, such assessment is rarely undertaken.

In this study, we developed and tested patch occupancy models for an endemic understory bird with limited dispersal ability, the Chucao Tapaculo (*Sce-lorchilus rubecula*; see Plate 1), in two South American temperate rain forest landscapes that differed in the level and duration of forest loss. We assessed cover changes since 1961 in the two landscapes and surveyed patches for Chucao Tapaculo occupancy. We then developed incidence-based predictive models independently for each landscape, and tested each model reciprocally in the alternative study area. By testing the models in alternative landscapes, we assessed the range of conditions over which they could properly be applied (Rykiel 1996). Finally, by comparing two landscapes with contrasting fragmentation levels and histories, our research provided insights into potential trajectories of change in portions of the biome currently undergoing deforestation.

## METHODS

### Study system

South American temperate rain forest (SATR) is globally outstanding for its exceptional level of endemism and for being one of the most endangered ecosystems on Earth. The biome is identified as a global biodiversity hotspot (Mittermeier et al. 1998, Myers et al. 2000), a Centre of Plant Diversity (Davis et al. 1997), an Endemic Bird Area (Stattersfield et al. 1998), and a Global 200 Ecoregion (Olson and Dinerstein 1998). Of endemic forest birds, understory insectivores in the family Rhinocryptidae (tapaculos) are among the most sensitive to fragmentation. Relative to other SATR species, tapaculos are lost disproportionately from isolated forest remnants (Willson et al. 1994), they are rarely observed in non-forest habitats, and dispersal among patches is constrained by open matrix (Sieving et al. 1996, Castellón and Sieving 2006).

We identified the Chucao Tapaculo as the best subject for intensive research because it is locally abundant and intermediate in both size (40 g) and vagility within the group (Sieving et al. 2000). The Chucao is a year-round resident that is territorial and, like other tapaculos in the biome, strongly associated with understory vegetation (Reid et al. 2004). Although reproductive success is relatively high in fragmented landscapes (De Santo et al. 2002), inter-patch movement is constrained by open habitat, perhaps due to inadequate vegetative cover for predator avoidance. Chucaos are extremely poor flyers and move (even during dispersal) by walking, hopping, or flying short distances (no more than a few meters), usually within or near dense vegetation. Although they are reluctant to enter open habitat, they will use wooded corridors and dense low-stature secondary vegetation for movement (Sieving et al. 1996, 2000, Castellón and Sieving 2006). This sensitivity to movement habitat makes Chucaos potentially valuable focal species for planning the connectivity component of landscape design, because a landscape that provides functional connectivity for Chucaos would probably meet the dispersal requirements of many forest species.
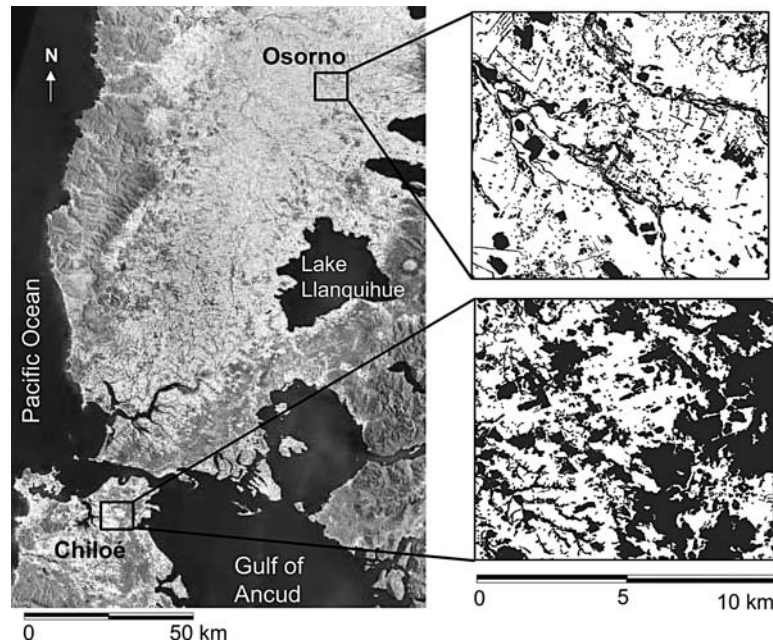
Fig. 1. Satellite image (gray scale) of the study region showing the Osorno and Chiloé study areas, south-central Chile. Darker areas indicate wooded habitats, and lighter areas indicate agricultural land uses. The enlarged areas are thematic maps of 100-km$^2$ subsets of the study areas, showing wooded (gray) and deforested (white) habitats.

We studied patch occupancy by the Chucao in two agricultural landscapes in south-central Chile, one located on northern Chiloé Island, near Ancud (41°55′ S, 73°35′ W; referred to hereafter as Chiloé; Fig. 1), and the other located on the mainland near Osorno (40°35′ S, 73°05′ W; hereafter Osorno). The two landscapes lie within the Valdivian temperate rain forest zone (37°45′ S to 43°20′ S), composed principally of evergreen broad-leaved trees and a few conifers, with dense understory composed of bamboo (*Chusquea* spp.) and shade-tolerant saplings (Veblen et al. 1983). Prior to settlement, this zone was largely covered by unbroken forest, and tapaculos were ubiquitous. At present, 45% of the original forest cover has been lost (Armesto et al. 1998). Tapaculos are still relatively common throughout most of the region, but concern for their long-term persistence is increasing due to their small geographic ranges and the rapid pace of habitat loss.

The two study landscapes were chosen because they represent extremes along a gradient of forest loss and fragmentation occurring in the SATR biome. Large-scale forest fragmentation began relatively recently in the Chiloé study area (within the last 50–100 years; Willson and Armesto 1996) and the landscape is now dominated by small-scale subsistence farming. Forest habitat appears to be relatively well connected in Chiloé, in that most patches are linked by corridors or are isolated by ≤100 m of non-forest matrix. Osorno, in contrast, is more fragmented and has a longer history of human-induced disturbance (100–150 years; Donoso and Lara 1995). This area is located in the Chilean

Central Valley, with the highest human population density and most intensive commercial land use in the biome (Armesto et al. 1998).

*Land cover analysis*

Remote sensing and geographic information system (GIS) analyses were used to evaluate land cover changes in the two study areas and to assess matrix composition surrounding patches censused for Chucao occupancy (described in the following section). Remote-sensing data consisted of panchromatic aerial photographs from 1961 and 1993 (the longest period of photographic data available), each taken during mid-to-late summer. All data were available in orthophotograph format (1:20 000) except the 1961 data for Chiloé, which consisted of non-rectified, partially overlapping photographs (1:70 000). Digital images of each study area were produced as follows using ENVI 3.2 (RSI 1999). All photographs were scanned and the orthophotographs were georeferenced using Universal Transverse Mercator (UTM) grids printed on the photographs as references. The non-rectified 1961 Chiloé photographs were registered to the 1993 orthophotograph, spatially corrected using a rubber-sheet algorithm (root mean square errors < 0.5 m), resampled using a nearest-neighbor algorithm, and arranged to produce a digital photographic mosaic.

Comparison of the Chiloé and Osorno landscapes and change analysis from 1961 to 1993 in each landscape were based on land cover classification within a 100-km$^2$ subset of each study area. Land cover types were hand-

TABLE 1. Metrics describing spatial patterns of forest cover in the Chiloé and Osorno study areas, south-central Chile, in 1961 and 1993.

| Metric | Chiloé | | Osorno | |
|---|---|---|---|---|
| | 1961 | 1993 | 1961 | 1993 |
| Percentage wooded | 50.44 | 44.92 | 21.05 | 17.12 |
| Patch area, mean $\pm$ SE (ha) | 13.25 $\pm$ 8.49 | 6.75 $\pm$ 2.80 | 2.57 $\pm$ 0.45 | 1.44 $\pm$ 0.15 |
| Patch density (no. patches/km$^2$) | 3.85 | 6.65 | 8.20 | 11.84 |
| Patch area /density | 3.44 | 1.02 | 0.31 | 0.12 |

*Note:* The total area of analysis in each study landscape was 100 km$^2$.

digitized with a minimum mapping unit of 0.1 ha using ArcView 3.2 (ESRI 1999) on-screen-digitizing functions. For the 1993 coverages, classification included open, shrubby, and wooded habitats. These classes were selected because prior research indicated that these cover types differed in permeability to Chucao movement, with movement significantly constrained by open matrix (Castellón and Sieving 2006). For the 1961 coverages, only two habitat classes, wooded habitat and non-wooded matrix, were digitized due to lower spatial resolution of the Chiloé photographs, which made it difficult to distinguish shrubby from open matrix types. Wooded patches were defined as continuous areas of woodland separated from surrounding patches by gaps $\geq$10 m, or connected to other patches via wooded corridors or bottlenecks that were at least an order of magnitude narrower than the adjoining patches.

The resulting cover maps were used to quantify landscape metrics and estimate extents of deforestation over the referenced period (measured directly from the shapefiles or using FRAGSTATS 3.3; McGarigal et al. 2002). Landscape-scale metrics regarding wooded habitat included the mean patch area in each study landscape, patch density, and patch area-to-density ratio (a measure of habitat contiguity). The percentages of area covered by wooded, shrubby, and open matrix habitats were also recorded (Table 1). Ground truth data were unavailable for the 1961 photographs, and no quantitative accuracy assessment was undertaken for the 1993 land cover classification, but interpretations of photographs were verified extensively in the field. The Chiloé landscape had changed relatively little since 1993, but several patches in the Osorno landscape had been cleared since that time. The effect on model building of differences between the photographic data and current conditions was minimized by selecting census patches that had changed little since the photographs were taken. However, landscape-scale comparison between Chiloé and Osorno reflects the status of the landscapes in 1993.

### Patch occupancy surveys

A subset of patches selected from an area of ~300 km$^2$ in each landscape was surveyed for Chucao occupancy. To randomize patch selection, each study area was subdivided into grids of 4-km$^2$ blocks. Then, isolated patches were censused within blocks selected using a random number table. In Chiloé, 100 patches were censused during the 2000–2001 breeding season (November to February). Thirty-eight of the censused patches were within the 100-km$^2$ study area used for landscape analysis (see preceding section). Then, following the same protocol, 62 patches were censused in Osorno during early 2004. Twenty-four of these patches were within the 100-km$^2$ area analyzed in the Osorno landscape. Fewer patches were visited in Osorno because the landscape was more fragmented there, increasing travel times between patches and the number of landowners that had to be contacted. Further, most patches in Osorno were unoccupied, requiring more intensive surveys to verify absence. Although bird surveys in the two landscapes were not conducted during the same year, confounding effects were minimized by censusing only for patch occupancy. Given Chucaos' high reproductive success in forest fragments (De Santo et al. 2002), few extinctions were expected to have occurred during the intervening period.

Censused patches consisted principally of mixed-age wooded stands that were either selectively logged or entirely secondary. Such patches were assumed to be adequate for Chucaos because reproductive success is similar in continuous forests and fragments, and there is no evidence of significant edge-related effects on nest fate (De Santo et al. 2002). During the initial visit to each patch, censuses were conducted at a maximum density of one census point/10 ha of patch area. Census points were located $\geq$50 m from the forest edge (unless patches were prohibitively small) and were separated from each other by $\geq$100 m. Because the objective was only to document occupancy, once a Chucao was recorded in an individual patch, no further censuses were conducted. However, if a Chucao was not encountered during the initial visit, a more intensive census was conducted on a subsequent day ($\geq$5 days later), at a sampling density of one point/ha.

At each census point, an 8-min passive census was conducted (after Willson et al. 1994) in which any Chucao heard or seen within the patch boundary was recorded. Following the passive census, song playback was used to increase detectability by eliciting vocal responses (Jimenez 2000, Sieving et al. 2000). Playbacks were conducted by sequentially broadcasting tape-recorded Chucao territorial and contact calls. A maximum of eight calls were played, each followed by

TABLE 2. Metrics (mean ± SE) describing focal wooded patches censused for Chucao, shown separately for occupied and unoccupied patches in Chiloé and Osorno.

| | Chiloé | | Osorno | |
|---|---|---|---|---|
| Variable (units) | Occupied ($n = 67$) | Unoccupied ($n = 33$) | Occupied ($n = 13$) | Unoccupied ($n = 49$) |
| Patch area (ha) | 14.07 ± 3.74 | 1.11 ± 0.25 | 13.22 ± 4.00 | 4.09 ± 0.64 |
| Change in patch size (%) † | −12.59 ± 5.58 | −42.33 ± 35.58 | 0.46 ± 0.45 | −0.97 ± 0.22 |
| Nearest patch ≥ 5 ha (m) | 148.82 ± 27.29 | 341.97 ± 47.16 | 51.77 ± 79.87 | 226.69 ± 35.06 |
| Connectivity index ($S_i$) | 238.97 ± 77.10 | 96.13 ± 19.48 | 54.56 ± 7.69 | 28.29 ± 1.80 |
| Mean patch area (ha) | | | | |
| 100-m buffer | 0.96 ± 0.18 | 0.25 ± 0.04 | 1.82 ± 0.39 | 1.11 ± 0.15 |
| 300-m buffer | 0.91 ± 0.14 | 0.78 ± 1.95 | 1.38 ± 0.15 | 0.87 ± 0.07 |
| Percentage wooded | | | | |
| 100-m buffer | 17.17 ± 1.14 | 10.76 ± 1.34 | 42.72 ± 3.76 | 28.52 ± 1.68 |
| 300-m buffer | 26.76 ± 2.23 | 20.84 ± 2.38 | 29.97 ± 1.40 | 23.00 ± 1.08 |
| Percentage open | | | | |
| 100-m buffer | 47.00 ± 3.42 | 65.60 ± 5.53 | 56.56 ± 3.75 | 71.17 ± 1.70 |
| 300-m buffer | 45.22 ± 2.73 | 62.24 ± 4.69 | 67.70 ± 1.12 | 76.51 ± 1.10 |
| Percentage shrubs | | | | |
| 100-m buffer | 35.83 ± 3.38 | 23.64 ± 5.61 | 0.72 ± 0.40 | 0.31 ± 0.19 |
| 300-m buffer | 29.28 ± 2.77 | 16.92 ± 3.55 | 2.32 ± 0.79 | 0.49 ± 0.26 |

*Notes:* The percentage change in patch area was measured from 1961 to 1993; distance was measured to the nearest patch of ≥5 ha; and landscape context variables (mean wooded patch area and percentages of wooded, open, and shrubby habitats) were measured within 100-m and 300-m buffers around each patch. The habitat connectivity index is after Hanski (1994). Wooded habitat is the preferred habitat type. Open habitat is avoided and constitutes a movement barrier at distances of more than ~50 m. Shrubby habitat is permeable to movement but does not serve as living or breeding habitat. Sample size ($n$) refers to the number of patches.

† Those patches that are currently unoccupied showed greater percentage decrease in size since 1961 than patches that are currently occupied.

a 1-min period of silence. Because sampling occurred during the breeding season, responsiveness to taped calls was high (e.g., Sieving et al. 1996, 2000). All censuses were conducted between dawn and 11:00 hours (EST) on mornings without strong wind or rain.

### Landscape predictors of patch occupancy

Patch- and landscape-context metrics were quantified from GIS maps for each patch surveyed for Chucao occupancy. Patch-scale metrics included censused patch area, percentage change in patch area from 1961 to 1993, presence or absence of corridor linkages, and understory vegetation density (see the following section for details). Landscape-context metrics (quantified within 100-m and 300-m buffers surrounding each censused patch) included the proportional cover of each habitat type, mean area and density of wooded patches, and two additional metrics potentially linked to landscape connectivity (Table 2). These were Euclidean distance to the nearest patch ≥5 ha (assumed large enough to serve as a potential source of immigrants), and Hanski's (1994) connectivity index ($S_i$). Hanski's index was calculated as $S_i = \Sigma\, p_j \exp(-\alpha d_{ij})A_j$, where $p_j = 1$ for source patches (i.e., patches ≥5 ha) and $p_j = 0$ for all other patches; $d_j$ is the Euclidean distance between patch $i$ and $j$; $A_j$ is the area of source patch $j$; and $\alpha$ is a constant scaling the distribution of dispersal distances, with $1/\alpha = 1$ km (the assumed mean dispersal distance). Finally, because the censused patches were nested within 4-km$^2$ blocks, and may not have been spatially independent, we included locational covariates (UTM easting, northing, and easting × northing) as potential predictors in the model-building process (Knapp et al. 2003). We also assessed the potential significance of these factors using stepwise backward-elimination logistic regression (removing all nonsignificant predictors except the locational covariates), and evaluated the distributions of patches misclassified by the resulting models for spatial biases.

### Understory vegetation density

Habitat quality for Chucaos is determined largely by understory vegetation density (Reid et al. 2004). To incorporate this variable in the model-building process, we visually classified understory density for each censused patch using three categories ("sparse," "dense," and "very dense") defined by stem density and the degree of contact among branches. Very dense understory had many stems in contact with each other, at places forming impenetrable tangles. Dense understory had many stems but less contact among plants overall, although patchy areas of very dense vegetation were sometimes present. Sparse understory was easy to walk through, had few stems in contact, and generally lacked dense patches. Given previous knowledge of habitat suitability for Chucaos (Sieving et al. 2000, Willson et al. 2004, Reid et al. 2004), only patches with understory vegetation classified as "dense" or "very dense" were considered in the analysis.

To test the assumption that visual characterizations were unbiased (i.e., that we did not unconsciously bias habitat quality classifications of patches based on our knowledge of their occupancy status), we quantitatively assessed understory vegetation density in a subset of occupied and unoccupied patches (10 each, ranging in size from 0.1 to 3.7 ha) in the Chiloé study area. In each patch, circular sampling stations (5-m radius) were established at random locations with a sampling density of four stations/ha. For each station, understory vegetation density was indexed at four points (located at right angles from each other on the perimeter of the circle) and then averaged. Density was measured by standing a 3-m pole (2 cm diameter) perpendicular to the ground and counting the number of leaves or stems that touched the pole. A $t$ test showed no statistically significant difference in mean understory density between occupied and unoccupied patches ($t_{18} = -1.72$, $P = 0.10$), although density was somewhat higher in occupied (107.60 ± 27.11 leaves and stems, mean ± SE) vs. unoccupied (70.60 ± 17.92) sites. Based on this result, we accepted the visual classifications as reasonably accurate and unbiased measures of understory vegetation density in the censused patches.

### Predictive models

We used classification tree analysis to develop predictive patch occupancy models for Chucaos in the two study landscapes. Classification tree modeling involves recursively partitioning (splitting) a data set into increasingly homogeneous subsets (nodes), with each split defined by a simple rule based on the value of a single predictor variable (Breiman et al. 1984, De'ath and Fabricius 2000). At each split, each predictor variable entered into the model is assessed independently and the one variable that generates the greatest improvement in homogeneity of the two resulting daughter nodes is selected as the node splitting criterion. Then the value for this variable is identified that minimizes heterogeneity in the daughter nodes when used as a threshold value for segregating the data.

Classification tree analysis has been shown to produce better prediction of species distributions than other popular modeling approaches, such as generalized linear models and generalized additive models (Franklin 1998, Vayssieres et al. 2000). The method is appropriate for complex ecological data sets that include imbalance, nonlinear relationships, and high-order interactions, which are dealt with by partitioning the observations and then analyzing each group separately. Further, model building is not hindered by colinearity because each split is based on the value of a single predictor variable. Predictors also may be used repeatedly at different points in the tree; thus the method is inherently context specific.

Classification tree models were built using DTREG (Sherrod 2003). Data sets for Chiloé and Osorno were analyzed independently to build two separate predictive models. In both models, the area of the censused patch was specified as the first variable used to split the data set, which facilitated model comparison. This was appropriate because patch area was consistently identified as a significant predictor of occupancy during exploratory analysis. Subsequent selection of variables for node splitting was automated. Potential predictors used in the model-building process included two qualitative variables, the category describing understory vegetation density (dense or very dense) and corridor presence, along with 12 quantitative patch and landscape-context variables (Table 2) and three locational covariates (UTM northing, easting, and easting × northing).

Gini goodness-of-fit measures were used to determine optimum splits. To avoid model over-fitting, a minimum node size of 10 observations was required to perform a split and trees were constrained to the number of nodes producing the minimum relative validation error (cross-validation error cost relative to a one-node tree), which was calculated using $v$-fold cross-validation. $V$-fold cross validation is performed by splitting the data set into $v$ subsamples, then producing $v$ trees, each time leaving one of the subsamples out of the training set and using it as a test sample for validation (for our analysis, $v = 10$). Cross-validation error costs are then computed for each node of each tree, and these costs are used to statistically determine the optimum tree size. In addition, we interactively removed splits with minimal value for discerning between occupied and unoccupied patches (see *Results* for further explanation).

Model adequacy was assessed in three ways. Predictive accuracy was assessed based on the percentages of the training data that were correctly classified and, because classification accuracy is sensitive to the relative frequency of occupied patches, the models were also assessed using Cohen's Kappa ($K$) statistic. Kappa adjusts for bias associated with random model agreement by measuring the actual agreement minus the agreement expected by chance, given the frequency distribution within the training data set (Cohen 1960, Fielding and Bell 1997). Values of $K$ can be used to classify model agreement as poor ($K < 0.4$), good ($0.4 \leq K < 0.75$), or excellent ($K \geq 0.75$), following Landis and Koch (1977). Finally, to assess model generality, we applied each model reciprocally in the alternative landscape to determine the predictive accuracy of the models when extrapolated beyond the specific landscape where data were collected.

### RESULTS

#### Land cover analysis

By 1961, deforestation in Osorno was advanced, with only 21.05% wooded habitat remaining, and habitat contiguity (patch area to density ratio; Table 1) was already quite low. From 1961 to 1993, an additional 3.93% of the study area was deforested, leaving 17.12% wooded cover in 1993. Over this time period, habitat

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┌─────────────────────────────┐
│ Node 1                      │
│ Occupancy = 1               │
│ N = 100 patches             │
│ Misclassification = 33.00%  │
└─────────────────────────────┘
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┌─────────────────────────────┐          ┌─────────────────────────────┐
│ Node 2                      │          │ Node 3                      │
│ Patch area ≤ 3.80 ha        │          │ Patch area > 3.80 ha        │
│ Occupancy = 0               │          │ Occupancy = 1               │
│ N = 63 patches              │          │ N = 37 patches              │
│ Misclassification = 49.21%  │          │ Misclassification = 2.70%   │
└─────────────────────────────┘          └─────────────────────────────┘
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┌──────────────────────────────────────┐   ┌──────────────────────────────────────┐
│ Node 4                               │   │ Node 5                               │
│ Open matrix in 100-m buffer ≤ 77.50% │   │ Open matrix in 100-m buffer > 77.50% │
│ Occupancy = 1                        │   │ Occupancy = 0                        │
│ N = 40 patches                       │   │ N = 23 patches                       │
│ Misclassification = 32.50%           │   │ Misclassification = 17.39%           │
└──────────────────────────────────────┘   └──────────────────────────────────────┘
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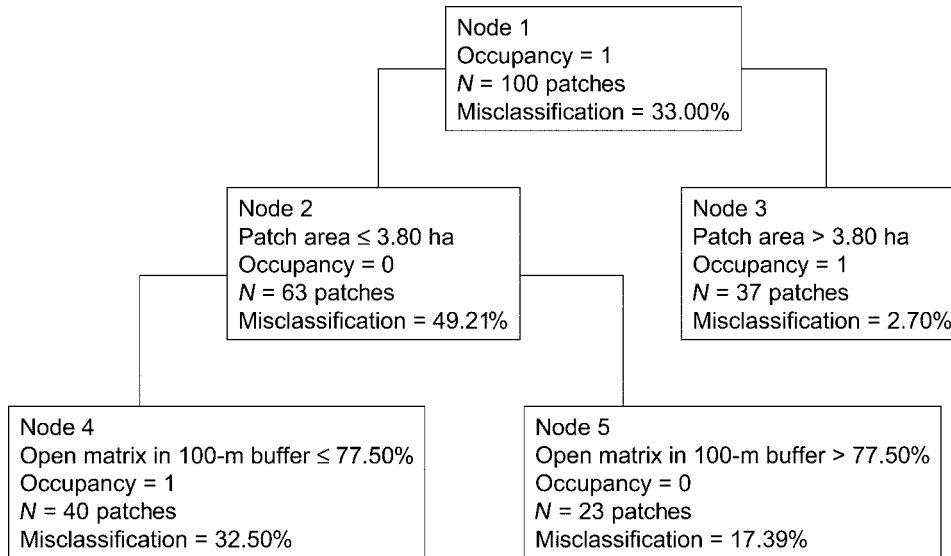
FIG. 2. Classification tree for predicting patch occupancy by Chucao Tapaculos (*Scelorchilus rubecula*) in the Chiloé landscape. Total classification accuracy for this tree was 82.00%.

contiguity (which approaches zero asymptotically with increasing fragmentation) decreased relatively little. Over the same period in Chiloé, forest cover decreased 5.52% (from 50.44% to 44.92%), but habitat contiguity decreased dramatically as large, continuous forest blocks were fragmented into smaller remnants. Within the non-forest matrix, the Chiloé study area was composed of 35.56% open habitat and 19.52% shrubby secondary vegetation (principally *Baccharis magellanica*, a persistent shrubby invader of poorly drained soils). In contrast, Osorno was dominated by open habitat (80.16%), with only 2.73% sparse or shrubby vegetation.

### Chucao distribution patterns

In Chiloé, Chucaos occupied 67% of censused patches. The smallest occupied patch was 0.64 ha and the largest unoccupied patch was 5.29 ha. In Osorno, only 21% of censused patches were occupied. The smallest occupied patch was 0.19 ha and the largest unoccupied patch was 21.78 ha. In both landscapes, very small patches (<1 ha) were usually occupied only if they were near larger patches, surrounded by dense secondary vegetation, or connected by corridors to other wooded habitat. In general, occupied patches in both

landscapes were also larger and less likely to have undergone a major reduction in area since 1961. Further, occupied patches were nearer other patches ≥5 ha, were better connected (i.e., $S_i$ was higher), and had larger percentages of wooded habitat but smaller percentages of open habitat in the surrounding matrix (Table 2). In Chiloé, occupied patches also had higher percentages of dense shrubs in the surrounding matrix, but this trend was not observed in Osorno, where shrub matrix was uncommon.

### Predictive models

The relative validation error for the Chiloé model was minimized at a tree size of four terminal nodes, but we removed one node that added little information to the model (distinguishing patch occupancy by a difference of <1% wooded habitat cover), producing a tree with three terminal nodes (Fig. 2). This model accurately classified 82.00% of the training data, and the Kappa statistic ($K = 0.56$, SE $= 0.09$, $P < 0.0001$) indicated good model agreement with the data. Most classification errors were errors of commission (empty patches misclassified as occupied; Table 3) regarding small patches surrounded by shrub-dominated matrix, or

TABLE 3. Classification tree model confusion matrices for Chiloé and Osorno.

| Actual category | Chiloé | | | Osorno | | |
|---|---|---|---|---|---|---|
| | Predicted category | | | Predicted category | | |
| | 0 | 1 | Misclassified (%) | 0 | 1 | Misclassified (%) |
| 0 | 19 | 14 | 42.42 | 43 | 6 | 12.25 |
| 1 | 4 | 63 | 5.97 | 1 | 12 | 7.69 |

*Notes:* Categories are 0, unoccupied; 1, occupied. Misclassified refers to the number of incorrect predictions within the referenced occupancy category.
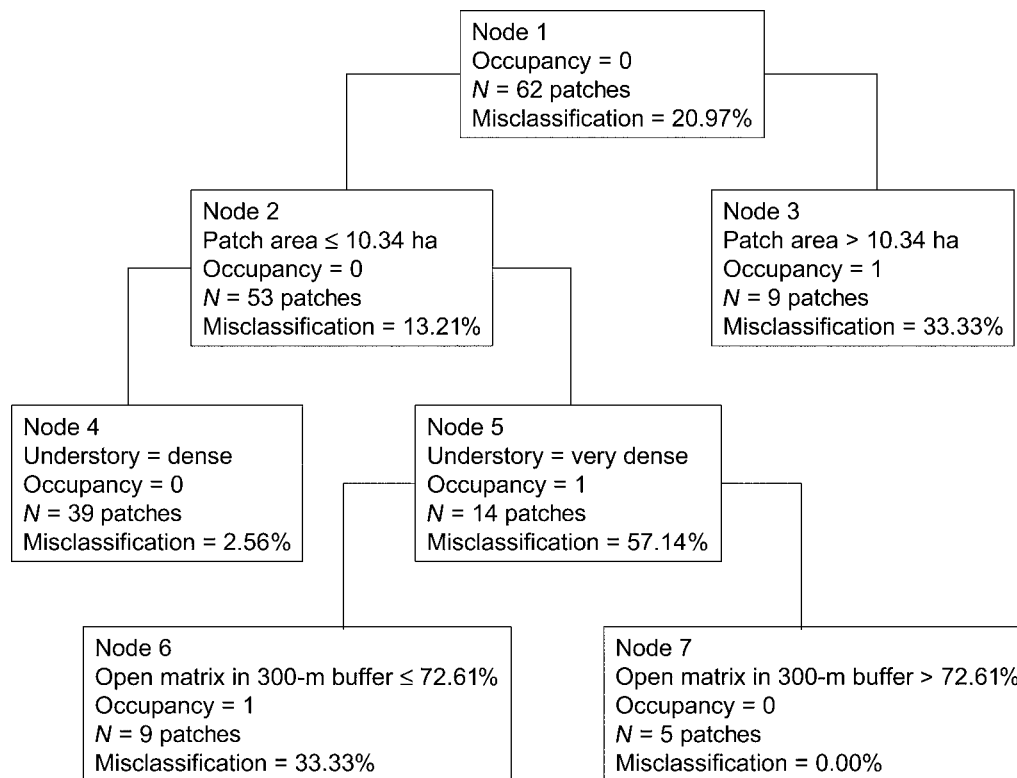
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                        ┌─────────────────────────────┐
                        │ Node 1                      │
                        │ Occupancy = 0               │
                        │ N = 62 patches              │
                        │ Misclassification = 20.97%  │
                        └─────────────────────────────┘
          ┌─────────────────────────────┐     ┌─────────────────────────────┐
          │ Node 2                      │     │ Node 3                      │
          │ Patch area ≤ 10.34 ha       │     │ Patch area > 10.34 ha       │
          │ Occupancy = 0               │     │ Occupancy = 1               │
          │ N = 53 patches              │     │ N = 9 patches               │
          │ Misclassification = 13.21%  │     │ Misclassification = 33.33%  │
          └─────────────────────────────┘     └─────────────────────────────┘
    ┌─────────────────────────────┐   ┌─────────────────────────────┐
    │ Node 4                      │   │ Node 5                      │
    │ Understory = dense          │   │ Understory = very dense     │
    │ Occupancy = 0               │   │ Occupancy = 1               │
    │ N = 39 patches              │   │ N = 14 patches              │
    │ Misclassification = 2.56%   │   │ Misclassification = 57.14%  │
    └─────────────────────────────┘   └─────────────────────────────┘
        ┌────────────────────────────────────┐   ┌────────────────────────────────────┐
        │ Node 6                             │   │ Node 7                             │
        │ Open matrix in 300-m buffer ≤ 72.61%│   │ Open matrix in 300-m buffer > 72.61%│
        │ Occupancy = 1                      │   │ Occupancy = 0                      │
        │ N = 9 patches                      │   │ N = 5 patches                      │
        │ Misclassification = 33.33%         │   │ Misclassification = 0.00%          │
        └────────────────────────────────────┘   └────────────────────────────────────┘
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Fig. 3.   Classification tree for predicting patch occupancy by Chucao Tapaculos in the Osorno landscape. Total classification accuracy for this tree was 88.71%.

relatively large, but isolated, patches located in areas with a longer fragmentation history than other parts of the study area (e.g., coastal areas). Relative validation error for the Osorno tree was minimized at four terminal nodes (Fig. 3). This model correctly classified 88.71% of the training data, and the Kappa statistic ($K = 0.70$, SE $= 0.10$, $P < 0.0001$) indicated good model agreement with the data. In this case, most misclassifications were errors of omission (occupied patches classified as unoccupied) pertaining to small patches located along riparian corridors.

To address potential spatial autocorrelation of data from patches within close proximity to each other (i.e., within the same 4-km² census block) that may not be accounted for by the other spatial-context variables, locational covariates were included in the model-building process and were assessed using logistic regression. However, none were selected as significant predictors of patch occupancy, and there was no apparent spatial bias in the distributions of misclassified patches. Only three of the 4-km² census blocks in the Chiloé landscape had more than one misclassified patch (two patches were misclassified in each), and only one block in the Osorno landscape had two misclassified patches.

The two models were relatively consistent regarding variable selection, but they performed poorly when applied reciprocally to the alternative landscape (as a test of generality). They differed in that the Chiloé model predicted occupancy for all patches $>3.80$ ha, whereas the Osorno model placed this threshold at 10.34 ha (Figs. 2 and 3). The Osorno model was only 54% accurate when applied to census data for Chiloé patches (98% of the misclassifications were errors of omission pertaining to patches $\leq 10.34$ ha), and the Kappa statistic ($K = 0.12$, SE $= 0.06$, $P = 0.093$) indicated poor agreement with the data. The Chiloé model was only 60% accurate when applied to Osorno data (97% of the errors were errors of commission regarding patches $\leq 10.34$ ha), and the Kappa statistic ($K = 0.22$, SE $= 0.06$, $P = 0.001$) indicated poor agreement with the data.

Patches with adequate habitat quality that were below the referenced threshold sizes in each landscape were predicted to be occupied only if the immediately surrounding matrix consisted of $<72.61\%$ (within buffers of 300-m radius, Osorno) to 77.50% (within 100-m buffers, Chiloé) open habitat. Although the buffer-radius scale (100-m vs. 300-m) at which open habitat influenced patch occupancy differed between models, this metric (percentage of open habitat) was correlated at the two referenced scales in both landscapes (Pearson: Chiloé, $r = 0.92$, $P < 0.0001$; Osorno, $r = 0.68$, $P < 0.0001$). Selection of different-scaled metrics by the model-building algorithm reflected minor peculiarities of the data sets caused by a few patches with atypical disagreement between the two scales. As a

result, the 100-m buffer scale provided better separation of occupied and unoccupied patches for the Chiloé data, whereas measures at the 300-m scale provided better separation for the Osorno data.

## DISCUSSION

Models developed for the two landscapes were relatively consistent regarding variables chosen as important predictors of occupancy, and the predictive accuracy of each model was high in the landscape where training data were collected (Figs. 2 and 3, Table 3). Further, the two models were remarkably consistent regarding the influence of open matrix, both predicting occupancy of small patches only if open habitat composed ≤75% of the surrounding matrix, on average. However, the models differed substantially from each other in the magnitudes of effects related to patch size and, therefore, performed poorly when applied reciprocally to the alternative landscape. As expected, the patch size effect was stronger in the Osorno landscape, which had a more advanced stage and longer history of forest loss.

### Landscape analysis

Analysis of historic land cover data documented substantially different levels of habitat loss and fragmentation in the two study areas by 1961 (the earliest data for which aerial photographs were available; Table 1). This observation supported our assumption that longer periods of relative isolation had elapsed in many Osorno patches by the time our surveys were conducted, allowing more time for population decline to extinction. In Osorno, large-scale deforestation began in the mid-1800s, so that only 21% forest cover remained in 1961 and habitat contiguity was already low. Forest loss and fragmentation continued thereafter and, by 1993, only 17% wooded habitat remained, but contiguity decreased little due to the mathematical characteristics of the index, which approaches zero asymptotically with decreasing patch size. In contrast, deforestation in Chiloé began in the early 1900s, and by 1961 approximately one-half of the original cover remained. Contiguity dropped considerably in Chiloé during the years that followed. Nonetheless, in 1993 the landscape still supported ~45% wooded habitat cover, and much of the deforested matrix was vegetated by dense shrubby habitat, which is relatively permeable to Chucao Tapaculo movement (Castellón and Sieving 2006).

The simultaneous availability of sites that differed in time since initiation of the fragmentation process allowed us to apply a space-for-time substitution approach (Warton and Wardle 2003, Purtauf et al. 2004). Although comparisons between landscapes are problematic because habitat quality often varies clinally with climate, we assumed that pre-fragmentation habitat quality was comparable in the two regions because Chucao densities were similar in Chiloé and mainland parks (Chiloé National Park and Pumalin National Park; Willson et al. 2004). Nonetheless, our analysis is bounded by the caveat that pre-fragmentation densities may have differed, potentially influencing current occupancy patterns. Despite this uncertainty, the Osorno landscape represents the only area in the biome with a substantially longer fragmentation history than Chiloé, and thus provides the best possible reference for comparison.

### Chucao distribution patterns

Results of landscape analysis and a radiotelemetry study of Chucao movement behavior (Castellón and Sieving 2006) indicate that the Chiloé landscape is still relatively well connected with regard to Chucao movement abilities (i.e., few patches isolated by ≥80–100 m, a distance shown to seriously impede movement). Further, with an average patch size of 6.75 ha (Table 1), most patches were still large enough to support several breeding territories (~1 ha each; De Santo et al. 2002). Thus, given that most patches are occupied and well connected, population structure in Chiloé appears to represent a single, patchily distributed population (Ovaskainen and Hanski 2004). Many patches <10 ha that are currently occupied in Chiloé may be highly reliant on immigration from other wooded patches, because populations with fewer than 10 breeding pairs are unlikely to persist without frequent immigration. Nonetheless, occupancy of these patches may serve to augment the regional population and may produce reproductive surplus in some years, further increasing the flow of dispersing individuals through the landscape (Dias 1996). In contrast, Osorno conditions appear to be largely inadequate for long-term sustainability of Chucao populations, with only 17% wooded habitat remaining, a mean patch size of 1.44 ha, and intervening matrix dominated (80.16%) by impermeable open habitat. Most patches <10 ha in Osorno are unoccupied, and patches ≥10 ha are largely isolated from each other by distances that exceed observed Chucao movement abilities (Castellón and Sieving 2006), indicating that immediate conservation action may be required to prevent further population declines or extinction.

Given previous knowledge that Chucaos reproduce relatively well in forest patches (De Santo et al. 2002), their absence only from relatively small patches (≤10 ha) surrounded by open habitat (shown to impede movement; Castellón and Sieving 2006) in both study areas indicates that extinction is likely only for very small, functionally isolated populations that are vulnerable to demographic and environmental stochasticity. Thus, conservation of this species appears achievable, given careful landscape management. An additional point important for conservation planning is that an average of ~25% permeable habitat in the matrix surrounding a censused patch was a good predictor of occupancy in both landscapes. Thus, ≥25% permeable habitat cover in the matrix may be an adequate goal for conservation

planning to provide connectivity within patch networks (at the spatial scales tested). This conclusion is supported by a radiotelemetry study documenting successful movement by Chucaos through wooded corridors and dense secondary vegetation in a fragmented landscape, even though permeable habitats often represented a relatively small percentage of the landscape area (Castellón and Sieving 2006).

### Model validation

Accuracy of each model was high in the landscape where data were collected (Figs. 2 and 3, Table 3), but the models performed poorly when applied reciprocally, due to differences in predicted occupancies of patches in the 3.80–10.34 ha size range. The Chiloé model predicted occupancy of all but the smallest and most isolated patches, whereas the Osorno model was more conservative, predicting occupancy only for large patches ($\geq$10.34 ha) and smaller high-quality patches with adequate permeability in the surrounding matrix. Because both models statistically related occupancy to current environmental conditions (i.e., they were static equilibrium-based models), their differences potentially reflected the contrasting stages of habitat loss and fragmentation exemplified by the two landscapes, which were more advanced in Osorno.

The preponderance of errors of commission when applying the Chiloé model to the Osorno landscape indicated that patches used to build the Chiloé model may not reflect equilibrium conditions, potentially due to an extinction debt in Chiloé. Chucao demographic data are suggestive of an extinction debt because reproductive success in forest patches is relatively high. Even though population density (Willson et al. 2004) and pairing success (Willson 2004) in fragments are lower than in continuous forest, breeding pairs still have a relatively high chance (63%) of fledging at least one young per clutch and of producing two or three clutches per season (De Santo et al. 2002). Given this level of in situ reproductive output, small populations could potentially persist in effectively isolated patches for many generations following fragmentation, although long-term persistence of populations with 10 or fewer breeding pairs is unlikely due to environmental and demographic stochasticity.

If an extinction debt existed in Chiloé, we would expect a stronger patch-size effect (i.e., larger unoccupied patches) in Osorno (having a longer fragmentation history), which our data confirmed. However, patches in Osorno were also more isolated than in Chiloé (larger inter-patch distances and a higher percentage of "impermeable" open matrix). This greater isolation may have further reduced immigration rates, thereby reducing time to extinction in Osorno patches (Stacey and Taper 1992, Ovaskainen 2002), which could also explain the larger empty patches. Likewise, the higher percentage of wooded habitat in Chiloé provided more breeding habitat than was available in Osorno, possibly

increasing the flow of dispersers through the Chiloé landscape. Finally, the higher human population density in Osorno may intensify an entire suite of detrimental effects associated with human land uses (e.g., Ford et al. 2001), possibly reducing the Chucao population in Osorno.

Unfortunately, it was impossible to dissociate the potentially interacting effects of duration, extent, and intensity of human land use on patch occupancy, and our interpretation is further constrained because replication at the focal-landscape scale was impossible (no other landscape areas were available with fragmentation histories or levels of habitat loss comparable to those of Osorno). This lack of replication prevented us from quantifying the effect of fragmentation history in a way that would support deterministic predictions of future scenarios. Nonetheless, because the Chiloé and Osorno landscapes represent two extremes along a continuum of fragmentation in the South American temperate rain forest biome, occupancy patterns in the two landscapes are suggestive of possible population trajectories for areas where fragmentation is ongoing (assuming that mechanisms driving landscape change are similar; i.e., human population growth and agricultural intensification).

Clearly, the Osorno landscape represents a more advanced stage of habitat loss and fragmentation (Table 1), and the Chiloé landscape appears to be following a similar pattern. It is, therefore, a reasonable expectation that current conditions in Osorno represent a possible future scenario for Chiloé (or other landscapes currently undergoing fragmentation) if no action is taken to prevent further habitat loss. Evidence that Chucao populations in Chiloé may be following a trajectory similar to those in Osorno includes the following. Although the Osorno model generally failed to predict current occupancy patterns in Chiloé, due to errors of omission for patches in the 3.80–10.34 ha size range, some extremely isolated patches within this size range are, in fact, currently unoccupied. Further, demographic isolation effects are evident in other patches in the size range (e.g., reduced pairing success due to a preponderance of unmated males; Willson 2004). Thus, many of the Chiloé patches predicted by the Osorno model to be unoccupied may be declining toward eventual extinction. If this is true, predictions of the Osorno model may approximate the future distribution of Chucao populations in Chiloé, once localized extinctions have occurred.

Alternatively, the Chiloé model (based on data from the relatively well-connected Chiloé landscape where deforestation is recent), may be prone to errors of commission when applied to alternative landscapes or when used as a forecasting tool. Such forecasting errors might arise if extinction time lags exist or if further habitat loss causes intensified fragmentation effects (e.g., by eliminating demographic sources). Thus, static models developed from distribution patterns in landscapes where habitat loss is recent or ongoing may be

minimally applicable for conservation because they may be overly optimistic when used to forecast future distributions or to predict distributions in more highly fragmented landscapes. Nonetheless, due to lack of time and financial resources for more extensive research, static models probably will continue to serve as the best available information for conservation decision making in many cases (Guisan and Zimmermann 2000).

Given our results, we suggest that landscapes used as standards for building incidence-based models intended for general conservation planning should be selected with caution. We recommend selection of landscapes where fragmentation has reached relatively advanced stages, preferably with histories of fragmentation long enough that time-delayed extinctions would already have occurred. Alternatively, prudent ecologically based criteria, such as estimates of sustainable population sizes and habitat areas needed to support sustainable populations, could be used to augment empirically based predictive models. Such criteria might serve to build additional safeguards into the planning process that would minimize risk of unanticipated extinctions. Of course, it is impossible to validate the predictive accuracy of models used in this way. Nonetheless, such tools will provide planners with conservative estimates of potential outcomes that are credible because they are bounded by empirical observations in real landscapes where fragmentation is advanced. Although imperfect, such tools are critically needed because conservation decisions must be made, and predictive models are necessary to inform these choices (Rykiel 1996).

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