

Assessing habitat loss and fragmentation and their effects on population viability of forest specialist birds: Linking biogeographical and population approaches

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Abstract

Aim: Biogeographic approaches usually have been developed apart from population ecology, resulting in predictive models without key parameters needed to account for reproductive and behavioural limitations on dispersal. Our aim was to incorporate fully spatially explicit population traits into a classic species distribution model (SDM) using Geographic Information Systems (GIS), aiming at conservation purposes.

Location: Southern South America.

Methods: Our analysis incorporates the effects of habitat loss and fragmentation on population viability and therefore provides insights into how much spatially explicit population traits can improve the SDM prediction of habitable habitat. We utilized a well-studied focal endemic bird of South American temperate rainforests (*Scelorchilus rubecula*). First, at a large scale, we assessed the historical extent habitat based on climate envelopes in an SDM. Second, we used a land cover change analysis at a regional scale to account for recent habitat loss and fragmentation. Third, we used empirically derived criteria to predict population responses to fragmented forest landscapes to identify actual losses of habitat and population. Then we selected three sites of high conservation value in southern Chile and applied our population model. Finally, we discuss the degree to which spatially explicit population traits can improve the SDM output without intervening in the modelling process itself.

Results: We found a historical habitat loss of 39.12% and an additional forest cover loss of 3.03% during 2000–2014; the latter occurred with a high degree of fragmentation, reducing the overall estimation of (1) carrying capacity by –82.4%, –33.1% and –45.1% and (2) estimated number of pairs on viable populations by –84.1%, –33.0% and –54.6% on the three selected sites.

Main conclusion: We conclude that our approach sharpened the SDM prediction on environmental suitability by 54.4%, adjusting the habitable area by adding population parameters through GIS, and allowing to incorporate other phenomena as fragmentation and habitat loss.

KEYWORDS

focal species, forest change, population parameters, specialist species, species distribution model, temperate rainforest

1 | INTRODUCTION

A great advance in theoretical ecology is the realization that spatial heterogeneity in environmental conditions at larger scales can fundamentally alter the outcome of species interactions and community dynamics (Didham, 2010; Pickett & Cadenasso, 1995). Despite this axiom, large-scale approaches such as spatial distribution of species have been mostly developed separately from ecosystem and species ecology, leading to a lack of biotic components and biological mechanisms in biogeographic studies (Violle, Reich, Pacala, Enquist, & Kattge, 2014; Wittmann, Barnes, Jerde, Jones, & Lodge, 2016). The technical difficulty for integrating biological and ecological characteristics into spatial distribution modelling is the abiotic perspective on which they are based (Guisan & Zimmermann, 2000).

From niche theory, these spatial distribution models rely mostly on abiotic conditions affecting species distributions, such as precipitation and temperature (Phillips et al. 2006). However, the distribution of species is often determined by ecological interactions, for example the presence of specific habitat resources, predators, competitors and dispersal ability, among others, which are difficult to evaluate in a model based only on environmental variables such as climate (Wiszniewski et al. 2013, Violle et al., 2014). In addition, recent studies have discovered significant relationships between the degree of predicted habitat suitability and biological traits, emphasizing the relationship among biogeography, biological and ecological perspectives (Nagaraju et al., 2013; Wittmann et al., 2016). We believe that efforts focused on establishing bridges between large-scale biogeographical studies and biological traits could provide inferences beyond just the spatial distribution of species, which could be far more meaningful for conservation purposes.

We propose a specific modelling approach aiming to link biogeography with the biology and ecology of the species, specifically with traits related to population viability in fragmented forests. The methodology presented here combines classic species distribution models (SDM's) with spatially explicit population measures based on reproductive and behavioural characteristics, as well as species-specific habitat requirements.

We centre our approach on the assessment of fragmentation and habitat loss of a forest specialist species, the chucao tapaculo (*Scelorchilus rubecula* Kittlitz), from highly threatened biodiversity hotspot biome, the Southern South American Rainforest (SATR) (Alaniz, Galleguillos, & Perez-Quezada, 2016; Miranda, Altamirano, Cayuela, Lara, & González, 2017; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). The chucao is a well-studied dense forest-understory bird whose historical distribution range is coincident with the SATR (Carlson, 2000), and with several other forest specialist, endemic, sessile, small-bodied and dispersal limited vertebrates of conservation concern with similar habitat needs, including the long-nosed shrew opossum (*Rhyncholestes raphanurus* Osgood), monito del monte (*Dromiciops gliroides* Thomas), and Chilean tree mouse (*Irenomys tarsalis* Philippi; Castellón & Sieving, 2007). It has been argued therefore that the chucao is a focal species for the biome (Castellón & Sieving, 2012; Willson, 2004; Willson, De Santo, Sabag, & Armesto, 1994) and highly sensitive to fragmentation (Carlson, 2000). Given the robust studies on this species, and the difficulty of getting similarly detailed data on the set of endemic, sessile, small-bodied and dispersal limited vertebrates in SATR with similar habitat needs, chucao represents a strong candidate of the forest ecological community.

Fragmentation and habitat loss of chucao were assessed in two scales: (1) Regional: estimating the habitat of the chucao and its historical loss, based on the distribution of SATR in a pre-settlement period (before human), and the analysis of the recent habitat loss and fragmentation from 2000 to 2014; (2) Local: in three representative sites, we considered chucao-specific population traits as: (a) reported territory size for a breeding pair to estimate the carrying capacity of forest patches (K) (Willson, 2004), (b) reported minimum size of a viable population (MVP) (Castellón & Sieving, 2007) and (c) patches containing viable populations (potentially source patches), and patches containing non-viable populations (potentially sink patches) according to a and b criteria (Furrer & Pasinelli, 2016; Pulliam, 1998) (Table 1).

The goal of our approach was to estimate the currently remaining suitable habitat for the focal species of SATR chucao tapaculo by incorporating both (1) suitable spatial configurations of remaining patches capable of containing viable populations, with (2) clear understanding

TABLE 1 Population parameters applied in each selected site within the SDM (Appendix S8). These parameters were calculated in 2000 and 2014 in a spatially explicit way

Parameters	Definition
Carrying capacity (K)	Maximum number of territories supported by landscape.
Total area of minimum population size (TAMPS)	Total area of patches >10 ha within landscape
Viable population (VP)	Number of pairs of <i>Scelorchilus rubecula</i> that conform a viable population (>100 territories per patch). This corresponds to the minimum estimated viable population size, considering reproduction, mortality, age structure and environmental stochasticity in a PVA analysis (Castellón & Sieving, 2007).
Non-viable population (NVP)	Number of pairs of <i>S. rubecula</i> that conform to a non-viable population (<100 territories per patch).
Source patches (Source)	Number of patches that support viable populations within landscape. Chucao is a highly sessile bird (<2 m flight range in dense vegetation) and requires a structural corridor to ensure connectivity (Castellón & Sieving, 2006a,b), so the dispersal ability is extremely restricted.
Sink patches (Sink)	Number of patches that don't support viable populations within landscape.

of the suitable climatic range for the species. Essentially, the incorporation of spatially explicit population traits estimates for the currently remaining habitat cover based on a GIS design should reduce the overall estimate of suitable habitat (and estimated population size) of chucaos compared to that based on SDM alone.

2 | METHODS

The methodological approach was constructed by combining SDMs with a GIS landscape ecology analysis (FRAGSTATS 4.2- McGarigal, Marks, Holms, & Ene, 1994), quantifying multiyear changes in landscape structure and integrating spatially explicit population measures (based on population parameters) to analyse the fragmentation and habitat loss.

We generated an SDM of chucao using the maximum entropy technique with MAXENT 3.4.1k software (Phillips, Anderson, Dudík, Schapire, & Blair, 2017). The model is based on two input data sets: environmental layers and species occurrence points (Elith et al., 2011), aiming to predict the environmental suitability for the target species. We used as environmental layers the set of 19 bioclimatic variables of WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) (11 for temperature, eight for precipitation), improved by Pliscoff, Luebert, Hilger, and Guisan (2014) for the Chilean territory. These variables consist of interpolated climate surfaces which aim to characterize climate in SDMs. These specific variables for Chile were generated using the same methodology of WorldClim but integrating a larger number of weather stations in zones 33 and 43 of the Worldclim tile (<http://www.worldclim.org/tiles.php>). Additionally, we included physiographic (aspect, slope, elevation) and anthropogenic layers (human footprint, land use) that complement the bioclimatic variables (SEDAC-NASA 2005; Zhao et al., 2016) (Appendix S1), aiming to incorporate terrain conditions and anthropogenic impacts on the biome. The initial occurrence database considered 1,441 localities of the species compiled from multiple information sources such as Global Biodiversity Information Facility (GBIF), eBird (Sullivan et al., 2009) and our own collection points (Appendix S2).

First, we explore the data through a test model using all environmental variables with the fivefold cross-validation technique in MAXENT. The results show the percentage of contribution and permutation importance of each variable to the model. At the same time, we determined the normality of each variable, applying the Shapiro-Wilk test complemented with Quantile-Quantile plots (Royston, 1983) (Appendix S3). To avoid collinearity among variables, a non-parametric multiple correlation matrix expressed in a correlogram was performed using the absolute correlation coefficients (Bradley, 1985), using a Bonferroni-corrected *p*-value due to the large number of comparisons. We selected the variables with major contribution to the preliminary model and low correlation coefficient (less than ± 0.7), avoiding the "dimensionality curse" (Keogh & Mueen, 2010). Additionally, we applied expert criteria to ensure the correct selection of variables, considering statistical and ecological relevance to the focal species (Appendix S4). Lastly, in a GIS software (Quantum

GIS Development Team 2016), the spatial autocorrelation of occurrences was evaluated using a Spatial Rarefy function (Brown, 2014). This process was applied to point clusters with less than 5 km distance between them, selecting non-spatially autocorrelated points randomly and removing the highly autocorrelated ones. The final distribution model was performed with 661 non-spatially autocorrelated occurrence points, 20-fold cross-validation technique and 95% confidence in the final output. The accuracy of the modelling process was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC), while the importance of variables in the final model was corroborated using a partial least squares regression analysis (PLS) (Appendix S5). Finally, we analysed the contribution of variables and the response curves of environmental suitability (Appendices S5 and S6).

All statistical analyses were performed using the R environment.

2.1 | Regional analysis

First we selected the significant environmental suitability applying a 10-percentile threshold, excluding suitability values under 0.334 from the analysis (Appendices S7A and S7B). To improve the quality of the prediction, we only considered as suitable habitat the suitability above the threshold, so this reclassified SDM represents the "potential" distribution of the species.

To estimate the historic habitat, we used GIS to overlap the historic distribution of the SATR with the reclassified SDM, obtaining the sites with bioclimatic suitability and presence of forest. We used as historic forest the map of potential vegetation (Lara, Solari, Prieto, & Peña, 2012; Luebert & Pliscoff, 2006), which represents the original extension of forest in a pre-settlement period.

To estimate the habitat of chucao in the years 2000 and 2014, we used a spatial intersect geoprocessing in GIS to overlap the forest extent in 2000 and 2014 with the reclassified SDM. We used the layers of Hansen et al. (2013) which mapped the global forest extent, loss and gain between 2000 and 2014. Because Hansen et al. (2013) do not differentiate between native and exotic forests in Chile, we used a raster calculator tool to subtract the areas corresponding to exotic plantations where the presence of the species is highly uncertain, according to National Native Forest Cadaster (CONAF-CONAMA-BIRF 1999), also calibrating the forest prediction of Hansen et al. (2013) for Chile. Hansen et al. (2013) identified the loss of forest cover between 2000 and 2014 using a large satellite database; therefore, we subtract the cumulative forest losses to the native forest extent at year 2000, estimating the area of native forest in 2014. We determined the habitat of chucao as native forest patches with significant environmental suitability given by MaxEnt model (>10-percentile of environmental suitability predicted by SDM), which was quantified and analysed using landscape metrics in FRAGSTATS software 4.2 (McGarigal et al., 1994). Finally, using map algebra, we linked the historic habitat (based on the potential vegetation map) and 2000 habitat (based on current vegetation) by quantifying the changes in the forest cover extent, considering this as historical loss. We also determined the loss and fragmentation

between 2000 and 2014 applying landscape metrics, which allowed us to quantify structural changes in the configuration and the area of chucao habitat. These metrics were analysed dividing the complete habitat extent into three zones; north from 35°S to 39°S, centre from 39°S to 43°S and south from 43°S to 47°S.

2.2 | Population viability assessment applied to conservation

We spatialize a series of population parameters of chucao obtained on a previous population viability analysis (PVA) (Castellón & Sieving, 2007) and biological studies on fragmented forest landscapes (Castellón & Sieving, 2006a,b, 2012; Rueda & Figueroa, 2003; Willson, 2004). These parameters were spatialized through GIS, applying a series of constraints on the regional SDM acquired in the previous analysis, and considering all the environmental suitability values of the species (from 2000 to 2014).

Then, these criteria were applied as constraints to each habitat map (2000 and 2014) using five main spatial geoprocesses in GIS software: "create fishnet tool," "buffer analysis," "select by location," "spatial join" and "summarize" (Appendix S8). The criteria considered were A) minimum patch size (MPS) estimated from an empirical patch occupancy model (Castellón & Sieving, 2006b); territory size (TS) empirically estimated minimum optimum territory size (1.0–1.3 ha) in forest fragments considering maps of active nests (Willson, Sieving, & De Santo, 2004; Willson unpublished data) and minimum viable population (MPV) obtained from PVA analysis showing long-term persistence populations (Castellón & Sieving, 2007).

We map the territories in each native forest patch using a buffer analysis tool to create a grid of circles of 1 ha of area equivalent to the minimum optimum territory size of a pair of chucacos (representing the maximum amount of pairs per patch) (Castellón & Sieving, 2007, 2012; Willson, 2004; Willson et al., 2004).

The territories of chucao estimated through active nests (Willson unpublished data) ranges in size from 1.0 to 1.3 ha in fragments and 0.4 in continuous forest, based on population density estimations from 2.51 (± 1.71 SD) to 5.69 (± 2.73) individuals per hectare in fragments and continuous forest, respectively (Willson et al., 2004; unpublished data). On the other hand, estimations based on strip censusing (Castellón & Sieving, 2007) ranges territory size from 0.8 ha to 0.34 ha in fragments and continuous forest, respectively. To perform our population analysis, we used the minimum optimum reported territory size of 1.0 ha in fragmented forest based on Castellón and Sieving (2007, 2012) in the mapping process, assuming that this habitat area ensures the viability of a functional demographic unit.

To avoid edge effects, we excluded the territories clipped by patch edges, applying a selection by location to select only the buffers that are completely within the forest patches. We note that the territories (represented by buffers of 1 ha) did not overlap, because chucao has been described as a highly territorial bird (Castellón & Sieving, 2012); hence, the territory size of 1 ha of habitat was respected for each breeding pair.

Traits, such as the poor flying ability (no more than a few meters; Willson, 2004; Castellón & Sieving, 2007; Sieving, personal observations), high resistance to enter into the matrix (Sieving, Willson, & De Santo, 1996), and the marked territorial behaviour (Willson, 2004), make the dispersion for chucao very difficult. However, previous studies identified that chucacos could disperse through densely vegetated corridors or shrubby second growth of 11–25 m wide to move around remnant native forest patches (Castellón & Sieving, 2012). The scale of the remote sensing product used here (30 m) (Hansen et al., 2013) may constitute a limitation on the detection of these small corridors. Considering this background, dispersion was not included in this study.

We selected three representative sites of Chilean temperate forest that have been seriously affected by deforestation, influenced by human activities. We included two protected areas: Tolhuaca National Park/Malleco National Reserve (–38° 08' S, –71° 47' W) and Cayumanqui Hill, a "Priority site of Biodiversity" (–36° 42' S, –72° 31' W) and a non-protected area affected by deforestation, "Huíte" near the town of Los Lagos, XIV Administrative Region (–39° 57' S, 72° 43' W). The area of these sites was 233.5 km², 68.2 km² and 202.5 km², respectively. In these sites, we analysed the habitat loss and fragmentation effect at the population level in chucacos between 2000 and 2014. We estimated six population and landscape parameters, analysing their dynamics between 2000 and 2014. The parameters were carrying capacity of forest patches in the landscape (K), total patch area >10 ha (TAMPS), number of pairs of chucacos within viable populations (VP), number of pairs of chucacos within non-viable population (NVP), number of patches that support viable populations (Source), number of patches that do not support viable populations (Sink). We defined as source patches the patches that contains viable populations, so the growth rate is expected to be positive ($\lambda > 1.0$), allowing to export individuals to sink patches that does not contain viable populations (Table 1).

3 | RESULTS

3.1 | Regional analysis

The final SDM reached an AUC of 0.952 ± 0.006 , predicting a potential distribution area of 123,353 km² (based only on environmental variables). The variables in the SDM with highest importance reported by MAXENT were Precipitation of coldest quarter (BIO19), Precipitation of driest quarter (BIO17) and mean temperature of warmest quarter (BIO10), with percentage contributions of 76.5%, 8.2% and 6.4%, respectively. The PLS analysis showed high importance of variable BIO19, validating the prediction of MAXENT (Appendices S1 and S4) through a *post hoc* statistical approach. The response curve of environmental suitability according to BIO19 showed an increase from 200 mm precipitation, reaching a peak at 1,100 mm and decreasing over this amount. Suitability in relation to BIO17 showed a unimodal Gaussian curve with a peak at 300 mm. Finally, the suitability of BIO10 showed a peak at 15 °C, decreasing with higher and lower temperatures (Appendix S9).

The historical distribution range of chucao is mainly located between 35°S and 47°S, including an area of 110,150.1 km². The

habitat was 69,191.2 km² in 2000 and 67,121.2 km² in 2014, which represents a loss of 3% between these years (2070 km²). If we compare the historic habitat with the habitat extent in 2000, there was a loss of 38.29% (44,458.9 km²) (Figures 1 and 2). The historic loss per zone was 54.51% in the north, 32.71% in the centre and 22.65% in the south zone. In addition, we found that between 2000 and 2014, the northern zone was the most affected by habitat loss with 5.3%, while the centre zone lost 3.10% and the southern zone was the least affected with a decrease of 0.09% (Table 2).

Analysing the fragmentation between 2000 and 2014, we found that the number of patches (Nump) and the edge densities (ED) increased in the northern and centre zones, but decreased in the south zone. The mean shape index (MSI) decreased in all zones, while the number of patches increased in the northern and centre zones; the latter was the most affected with an increase of 12.31%, indicating a high influence of fragmentation (Table 2). The most affected area in the north zone was the coast from 35°S to 40°S (Figure 1).

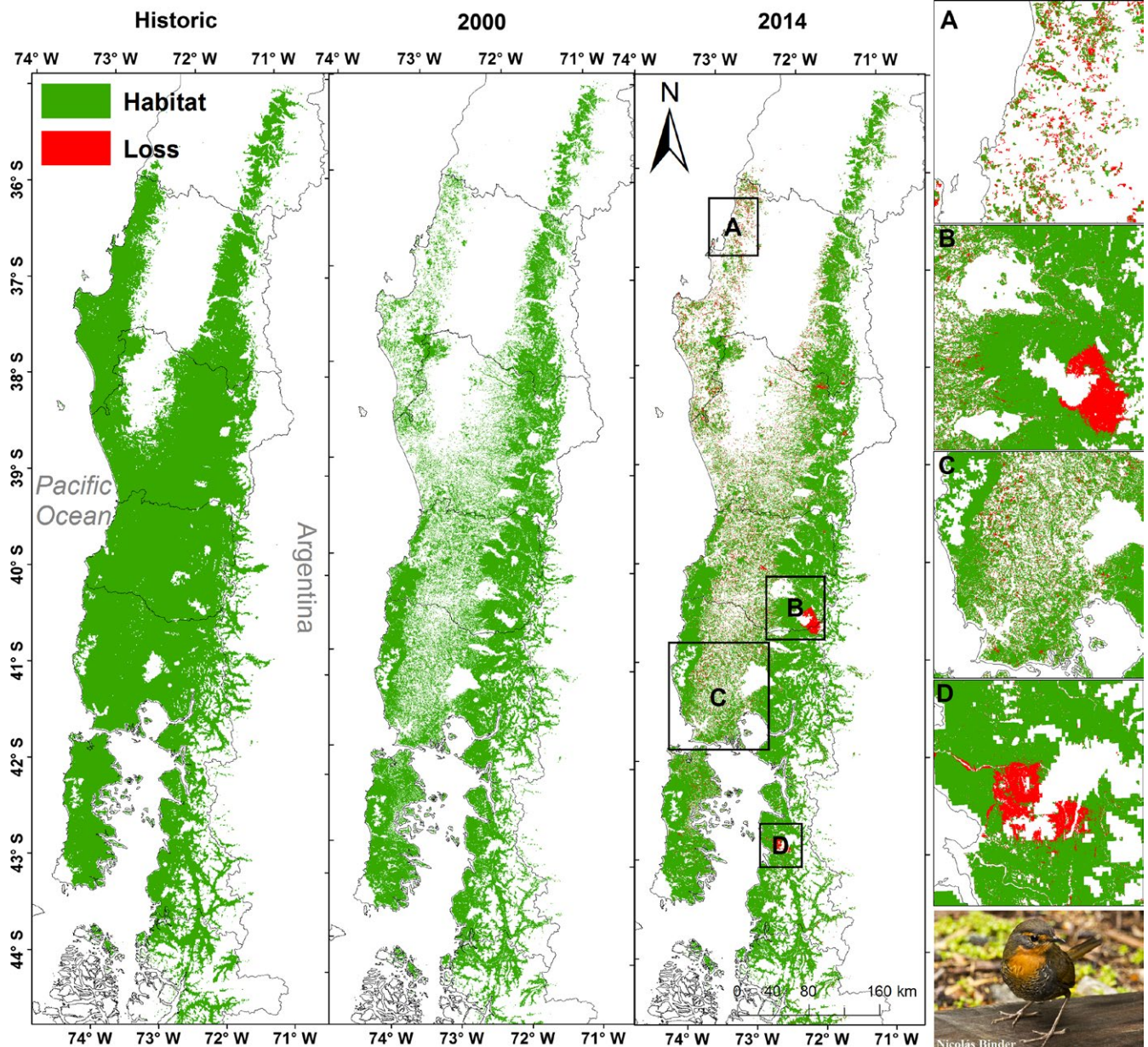


FIGURE 1 Potential habitat of *Scelorchilus rubecula* (left), habitat in year 2000 (centre) and habitat in year 2014 with losses. Potential habitat was generated by MAXENT algorithm, with 20-fold cross-validation technique based on climatic, topographic and human variables. We consider only medium, high and very high environmental suitability (See Appendix S6). Habitat in 2000 and 2014 were generated through the spatial interaction in GIS of the SDM, the native forest extension in each year (2000 and 2014) and the selection of >10 ha patches according to the minimum patch size for the species. Habitat loss, obtained through Global Forest Change platform was added to the habitat 2014 cover. Right boxes (A, B, C and D) shows zooms of the losses in years 2000 and 2014. Photography by Nicolás Binder (available at https://commons.wikimedia.org/wiki/File:Chucao_-_Flickr_-_jackripper.jpg wileyonlinelibrary.com] under CC-BY-SA-2.0 license) [Colour figure can be viewed at wileyonlinelibrary.com]

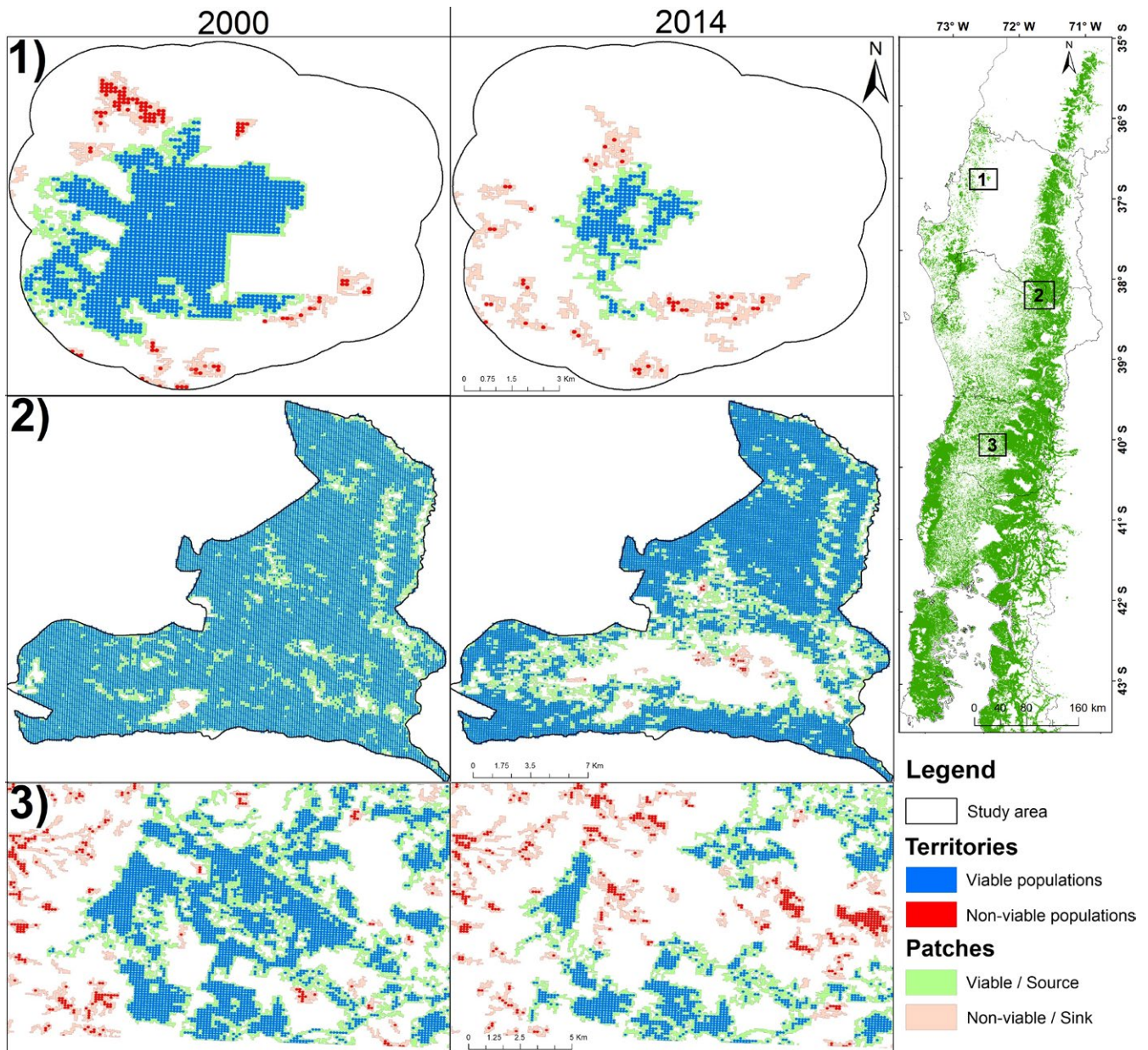


FIGURE 2 Map of the three selected sites where spatial population dynamics were evaluated. Two protected areas, (1) Cayumanqui hill “Priority site of Biodiversity” ($-36^{\circ} 42' S$, $-72^{\circ} 31' O$), (2) Tolhuaca National Park with Malleco National Reserve ($-38^{\circ} 08' S$, $-71^{\circ} 47' O$) and (3) one non-protected area near Los Lagos city ($-39^{\circ} 57' S$, $72^{\circ} 43' O$) were selected as applied cases in Chilean temperate forest. Spatially explicit population dynamics from Table 1 were evaluated in each site. Numeric results from each site are summarized in Table 3 [Colour figure can be viewed at wileyonlinelibrary.com]

The difference between SDM prediction ($123,353 \text{ km}^2$) and 2014 estimated habitat ($67,121.2 \text{ km}^2$) is 54.4%.

3.2 | Population viability assessment applied to conservation

In this section, we describe the population dynamics of chucao in the three selected areas, indicating the temporal (between 2000 and 2014) and spatial variability (through spatially explicit population measures).

3.2.1 | Cayumanqui Hill, priority site for conservation

During the study period, the habitat experienced a decrease in almost all population parameters, reducing the habitat area by 75.9%. In year 2000, the total carrying capacity was 1,795 territories, distributed in a main source patch with 1,687 pairs and 12 surrounding sink patches with 108 pairs. In 2014, the total carrying capacity experienced a loss of 82.4%, which corresponds to a decrease of 84.1% of viable pairs in the main source patch and 56.5% in non-viable

TABLE 2 Results of FRAGSTATS processing of habitat metrics per zone and year appears the percentage of change between 2000 and 2014 (negative and positive). Mean shape index (MSI), edge density (ED, in mt/ha), mean patch size (MPS, in km²), number of patches (Nump), area per habitat suitability level (Area, in km²)

Zone	Metric	2000	2014	Change (%)
North	MSI	3.07	3.06	-0.30
	ED	65.72	69.47	5.71
	MPS	268.00	235.62	-12.08
	NumP	6,145	6,619	7.71
	Area	16,468.56	15,595.96	-5.30
Center	MSI	3.11	3.09	-0.61
	ED	44.74	47.97	7.21
	MPS	756.67	651.12	-13.65
	NumP	5,036	5,671	12.31
	Area	38,105.85	36,925.01	-3.10
South	MSI	2.54	2.31	-8.90
	ED	34.18	33.34	-2.47
	MPS	801.87	804.89	-0.38
	NumP	1,671	1,661	-0.60
	Area	13,399.21	13,369.28	-0.22

patches. The number of sink patches increased by 16.6% and empty patches by 700% (Table 3; Figure 2).

3.2.2 | Tolhuaca National Park and Malleco National Reserve

The total habitat decreased by 22.8% from 2000 to 2014. Almost all the area was covered by available habitat in 2000. However, by 2014 total carrying capacity experienced a loss of 33.1% which corresponds to a decrease of 33.0% on viable pairs. This reduction generated seven sink patches that did not exist in 2000, changing 89 pairs from viable to nonviable populations (Table 3), while empty patches increased from one to four in the study period (Figure 2).

3.2.3 | "Huíte," Los Lagos commune, XIV Los Ríos administrative región

The available habitat decreased by 46.1%. There was a reduction of 45.1% in the carrying capacity from 2000 to 2014, which corresponds to a decrease of 54.6% on viable pairs. Source patches declined by 39.6% and sink patches increased by 83.9%. In 2000, there were 33 sink patches, 10 empty patches and only one source patch. This source patch occupied the core area, connecting viable populations of the northern and southeastern areas through corridors. In 2014, the central patch was removed; only the southern section of the original patch remained, obstructing the connectivity with northern populations. In this period, 13 sink patches and four empty patches were generated, dividing the main source patch into five smaller patches (Table 3).

TABLE 3 Results of population analysis calculated to each selected site in 2000 (upper part of table) and 2014 (lower part of table). The explanation of each parameter can be found in Table 1

Year	Population Parameter	Sites		
		Prioritary site Cayumanqui hill	Tolhuaca National Park-Malleco National Reserve	Huíte, Los Lagos commune
2000	K	1,795 territ.	15,310 territ.	4,296 territ.
	TAMPS	2,743.9 há	21,613.4 há	8,352.4 há
	PV	1,687 pairs	15,310 pairs	3,998 pairs
	NPV	108 pairs	0 pairs	298 pairs
	Source	1 patch	1 patch	1 patch
	Sink	12 patches	0 patch	33 patches
	Empty	1 patch	1 patch	10 patches
2014	K	315 territ.	10,241 territ.	2,360 territ.
	TAMPS	660.6 há	16,683.5 há	4,505.5 há.
	PV	268 pairs	10,246 pairs	1,812 pairs
	NPV	47 pairs	89 pairs	548 pairs
	Source	1 patch	1 patch	5 patches
	Sink	14 patches	7 patches	46 patches
	Empty	8 patches	4 patches	14 patches

4 | DISCUSSION

4.1 | Chucao (*S. rubecula*): indicator species for the SATR biome

The climate suitability for chucao is highly determined by the precipitation during the coldest quarter which coincides with winter; the amount of precipitation is closely related to the temperate Chilean climate between 37°S and 45°S (Luebert & Pliscoff, 2006). This responds to the climatic conditions that make chucao a representative species for the entire biome. Loss of chucaos therefore reflects declining health and integrity of the native rainforest ecosystem. It has been argued that the habitat preferences of this species are coincident with many endemic small and medium-sized vertebrates of the SATR; therefore, the implications of our study extend not just to chucaos, but to the guilds of species for which chucao is a focal indicator species (see Castellón & Sieving, 2012). Chucao declines are coincident with the decline and degradation of an entire and highly unique and productive forest biome.

4.2 | Historical versus recent losses

The SATR covered all Southern Chile after the end of the Last Glacier Maximum (Holocene period). Implications are that recolonization by Holocene forest taxa came from the refuge zone in central Chile,

occupying the range from 35°S to 55°S (Lara et al., 2012; Segovia, Hinojosa, Pérez, & Hawkins, 2013; Villagran & Hinojosa, 1997). The potential current distribution of chucao highly overlaps with the historical pre-settlement distribution of forest, which implies that its historical habitat decrease has been 39.12%. In the last 15 years, our analysis estimates 2,070 km² of overall habitat lost, with evidence of fragmentation throughout the current distribution, especially in the northern and central zones. The northern zone is the most affected by losses, mainly due to forest fires and replacement by exotic plantations (CONAF 2014; Miranda et al., 2017). In the central zone, major losses have occurred in two areas. First, in the coast range and central valley, anthropogenic land cover has spread and greatly reduced the forest range, and second, in the Andean zone volcanism is the main cause with around 40% of the total losses of the biome. The southern zone has been less affected due to low human influences and lack of road access (22.65% historic loss and 0.22% in the recent period).

We found that the mean patch size has decreased in all zones, especially in the central zone. Moreover, the edge density and mean shape index increased, and this likely intensifies edge effects on chucao. The dramatic losses of suitable chucao habitat within the past decade that our analyses identified are on a par with post-glacial historical contractions of habitat, brought on by very slow climatic shifts. That means that similar percentages of suitable habitat for SATR wildlife were lost in just 14 years as were lost since human settlement. Furthermore, as the range of the chucao is coincident with healthy, minimally disturbed SATR, these percentages apply to the biome. Our analysis points to dire endangering of a unique and productive forest biome that, for its size, houses a disproportionate stockpile of Earth's endemic, unique biodiversity forms (Myers et al., 2000). Our results reveal an increase in forest loss amounts of the SATR in the last 14 years, in comparison with historic and previous periods, according to the evidence of previous studies (Lara et al., 2012; Miranda et al., 2017).

The most rapid changes in the SATR forest occurred near the coast; an area largely cleared by native forest, due to intensive land use changes (especially agriculture and forest plantations) during the last 30 years (Miranda et al., 2017). Our analysis showed that this process remained rapid during the study period. The three selected sites showed different spatial patterns of deforestation and edge effects with varying consequences for chucaos at the population level (Tuff, Tuff, & Davies, 2016). The most affected sites were Cayumanqui Hill and Huite, with a serious loss of habitat and reduction in all population parameters, to levels suggesting loss of viability in these populations. Similar results were found by Keesen, Silva, Arashiro, and Pinheiro (2017), where the viability of forest specialist primate populations in Brazil was lost, suggesting that (1) the effects of density and patch size (size of the available area) reflects directly in the loss of viability of populations, and (2) population survival, even considering parameters of a metapopulation model (dispersion), depends directly on the minimum area and the geometric conformation of the fragments. When viability is lost, the recovery of populations should come associated with measures to ensure the increase in the area for the species (Keesen et al., 2017).

The reduction in carrying capacity determined by the decrease of the resources could also influence the biological fitness of individuals, which could lead to an increase in competition and reduction in the viability of populations (Engen & Sæther, 2000). The main causes of this loss in the SATR have been anthropogenic and natural forest fires (Cayumanqui hill and Tolhuaca-Malleco areas; CONAF 2014) and replacement by agriculture in "Huite," Los Lagos commune.

4.3 | Potentialities for population assessment on conservation

The identification of viable populations in potential source patches and non-viable populations in potential sink patches allows the generation of conservation actions such as the identification of priority patches, design of corridors to ensure the viability of populations and dealing with extinction debt in small populations (Furrer & Pasinelli, 2016; Hanski & Ovaskainen, 2002). Spatiotemporal landscape analysis is useful to identify patterns of habitat quality degradation, loss and fragmentation (Sharma, Areendran, Raj, Sharma, & Joshi, 2016). We applied an approach that combines both methods, analysing the spatiotemporal changes on populations (e.g., decreases on viable populations). The estimated population amount could change due to the variability on population parameters (e.g., bigger territory size of single pairs), so we decide to use the minimum reported values on each parameter as a conservative estimation approach. Previous studies have assessed population dynamics using different approaches, based on mathematical modelling of populations or using connectivity analysis, among others (Skarpaas & Stabbetorp, 2011; Xu, Feng, Allen, & Swihart, 2006).

About population analysis, the source-sink structure is mainly defined in terms of the biological adequacy (fitness) within each population (Heinrichs, Lawler, & Schumaker, 2016). Source patches have a high emigration and natality but a low immigration and survival rate. Sink patches are maintained by immigration of individuals from other patches compensating their low natality and high mortality rates (Nystrand, Griesser, Eggers, & Ekman, 2010). This effect is even stronger when the species are density dependent and territorial as the case of chucao (Castellón & Sieving, 2007). In our case, the definition of source-sink patches was linked to the viability of populations, so in non-viable population the fitness is expected to be low, increasing the probability of inbreeding depression, genetic drift and extinction vortex (Fagan & Holmes, 2006; Fietz, Tomiuk, Loeschcke, Weis-Dootz, & Segelbacher, 2014).

One of the main potentialities of the population assessment presented here is the capability to generate population data with a spatially explicit dimension, which could be included into PVA analysis to project future changes on threatened populations for conservation targets. The population estimations could be combined with data of growth rate, survival, natality, mortality, immigration and emigration, to estimate future changes in populations (e.g., it can be attributed an specific λ to source or sink populations depending on the population number estimated here, to predict the population

decrease or increase in a determined time window). Stochasticity could be included to these future estimations, including the probability of occurrence of environmental events (e.g., fires) or applying standard deviation units to the population parameters (e.g., SD units on growth rate).

4.4 | Potentialities and assumptions of the model

The SDM has been widely used in different fields of study, demonstrating great ability to estimate distributions of species and ecological patterns, for example ecological invasions or shifts of species ranges (Elith, 2014; Hill, Gallardo, & Terblanche, 2017; Porfirio et al., 2014). SDMs have been a useful tool for management and conservation planning (Pyke, Andelman, & Midgley, 2005; Zhang et al., 2012). We suggest that using the methodological approach presented here it is possible to produce even more accurate estimations of distribution, so it could be useful for planners to identify zones with high environmental suitability (through MAXENT) and those which have experienced high levels of degradation (GIS to give the population parameters a spatially explicit dimension, Global Forest Change to detect the forest losses and FRAGSTATS to quantify them), so vulnerable zones can be prioritized. This methodology could be applied to other forest specialist species for which habitat requirements are known, as in the case of the chucao, highlighting the usefulness of spatially explicit population measures to sharpen SDM predictions. This could be performed through adapting the population parameters according to the target species, making this methodology useful to other forest taxon assessment. Forest cover represents a valuable tool for calibration of SDMs, due to its global coverage (Hansen et al., 2013). Previous methods of SDM calibration based on life history traits have been performed by adding numerous sets of variables in the modelling process (Chefaoui, Lobo, & Hortal, 2011; Syphard & Franklin, 2010; Wang, Goslee, Miller, Sanderson, & Gonet, 2017; Wogan, 2016). The outcomes obtained here suggest that the high predictive performance of SDMs could be boosted through the use of GIS, which apply *post hoc* treatments to the outputs obtained from the modelling process, not modifying them (by adding more variables or making the model more complex) or extrapolating the results already obtained by the algorithms. According to this, GIS permits sharpening SDM prediction, discriminating areas where the environmental suitability is low or null based on empirical geospatial information and biological knowledge of the species (spatially explicit population measures). We found a difference of 54.4% between the prediction of the SDM with only environmental variables (MAXENT output) and the current GIS-calibrated habitat extent in 2014, which represents the actual habitable area. However, it is important to recognize that the real distribution of species is influenced by many other factors difficult to consider in SDMs (e.g. some specific habitat preferences, co-dependence with other species, interspecific competition) (Vasconcelos, Rodríguez, & Hawkins, 2012), so the inclusion of population parameters could be helpful to deal with

this limitation. Nevertheless, to apply this constraint the existence of previous biological and ecological studies is essential; however, the lack of information on wild species represents a limitation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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