MULTI-SCALE INFLUENCE OF HABITAT AND DISTURBANCE ON THE SPATIAL

ECOLOGY OF MAGELLANIC WOODPECKERS (*CAMPEPHILUS MAGELLANICUS*)

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MULTI-SCALE INFLUENCE OF HABITAT AND DISTURBANCE ON THE SPATIAL

ECOLOGY OF MAGELLANIC WOODPECKERS (*CAMPEPHILUS MAGELLANICUS*)

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Habitat loss, fragmentation and degradation are major threats to biodiversity, yet

landscapes can be managed in ways that reduce and/or mitigate the severity of such threats.

Effective landscape management, however, requires a sound understanding of ecological

responses to environmental gradients, human activities, and spatial configuration of habitats

elements. A large body of research has established that species perceive, select, and

respond to habitat across a hierarchy of spatial scales – from foraging substrates and micro-

habitats to entire landscapes – as well as through a variety of coarse-grained and fine-

grained processes. Although these processes are poorly understood in many systems, we

urgently need to improve our knowledge in highly threatened places like the Valdivian

Rainforest ecoregion, a global biodiversity hotspot within the South American temperate

forests (SATF) of Chile. Conversion of forest to agriculture and pasture has left only 30%

of the original Valdivian Rainforests, with forest remnants increasingly degraded by

wildfires, unsustainable logging, and firewood extraction. This dissertation examined how

Magellanic woodpeckers (*Campephilus magellanicus*), the primary cavity excavator of

these forests, responded to habitat quality and quantity, social interactions, and landscape

composition and configuration. Our specific objectives were to (1) innovate a remote-sensing method to estimate quality of foraging habitat; (2) investigate how nesting and roosting cavities affected within-territory habitat use; (3) understand the implications of foraging behavior and social interactions on seed dispersal; and (4) estimate the differential contributions of historic deforestation and exotic plantations on genetic population structure. We studied four populations of Magellanic woodpeckers from 2014 to 2017, employing multiple field and computational techniques including remote-sensing, satellite telemetry, surveys of birds, behavioral observations, inventories of cavities or other signs, and spatially-explicit models. We found that decay of Nothofagaceae trees, which is both an important component and indicator of habitat quality for Magellanic woodpeckers, was highly correlated with and estimable from remotely-sensed Plant Senescence Reflectance Index. Although tree decay can profoundly affect quality and use of foraging resources, we found that space use within territories was best explained by the abundance and distribution of previously-excavated cavities for nesting or roosting. In addition, territory size declined with proximity to neighboring families and increased with non-forest cover within individual territories. Our findings also show that both the drivers and consequences of space use were partly determined by social interactions among family members. For example, displacement by adult males expanded the ecological roles of females and juveniles to include seed dispersal across much larger distances than other known dispersers in our study system. The capacity of the species to move over large distances was confirmed, in part, by the low level of genetic differentiation among Northern populations. Nevertheless, we found no evidence that current movement constraints had yet scaled up to affect population structure, which was best explained by historic deforestation.

Overall, our research provides the following insights into the consequences of Patagonian forest loss, degradation, and fragmentation on Magellanic woodpeckers: (1) the quality of foraging resources may be estimated by remote sensing, (2) legacy cavities (i.e., previously excavated) are overlooked but important resources that affect space use and territoriality, (3) social interactions can mediate the delivery of ecosystem services via seed dispersal, and (4) exotic plantations represent a novel barrier to movements that may have long-term consequences for population structure.

BIOGRAPHICAL SKETCH

Gerardo E. Soto was born in San Bernardo in 1989, a large municipality south of Santiago de Chile. He grew up in a car shop and made his own toys using the tools available at the shop as young as he can remember. At the age of 6, he and his siblings joined a Boy Scouts troop, which introduced him to camping in many forested areas in Northern Patagonia. A passion for nature and development of tools motivated him to become an Environmental Engineer at the Universidad de Santiago de Chile (USACH). During his second year at USACH, he volunteered at the Laboratory of Ecology and Plant Biodiversity of Dr. Sergio A. Castro and at the Laboratory of Ecology and Conservation of Dr. Pablo M. Vergara. Gerardo subsequently spent years collaborating with these two laboratories on several research projects related to the landscape ecology and conservation of multiple taxa, such as mammals, birds, insects, and plants, in the Chilean mainland and island territories. After graduating from USACH in 2014, he lectured at USACH's Department of Agricultural Management while serving as a scientific advisor for the Biodiversity Conservation Plan of the Juan Fernández Archipelago, and for the National Conservation Plan for the Magellanic woodpecker (*Campephilus magellanicus*). In 2015, Gerardo began his doctoral studies at Cornell University, with the intention to improve the knowledge about the ecology and conservation of South American temperate forests.

A mi mentor y amigo Dr. Pablo M. Vergara.

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CHAPTER 1

INTRODUCTION

Background

A large body of research has established that species perceive, select, and respond to habitat

across a hierarchy of spatial scales – from foraging substrates and micro-habitats to entire

landscapes (Johnson 1980; Kristan 2006) – as well as through a variety of coarse-grained

and fine-grained processes (Nash et al. 2014). One consequence of these hierarchical

processes is that a species may be absent from patches that provide the necessary habitat

requirements but are embedded within unsuitable landscapes (Vergara and Armesto 2009).

Decisions at small spatial scales also can scale up to influence distribution, activity, and

population persistence at larger spatial scales (Harrison and Taylor 1997, Heffernan et al.

2014). Effective conservation thus requires a sound understanding of how species respond

to habitat and landscape changes across a variety of scales.

Knowledge of the multi-scale effects of forest loss and degradation has never been more

urgently needed than today, given that forests are increasingly under threat yet house more

than half of the world's terrestrial biodiversity (Fischer and Lindenmayer 2007; Newbold et

al. 2016). Though the human activities contributing most to forest degradation vary

globally, drivers usually include unsustainable logging, agroforestry, livestock grazing,

invasive species, fuelwood extraction and wildfires (e.g. van Wilgen et al. 2001; Heilmayr

et al. 2016). Forest degradation can compromise resources (Lindenmayer and Fischer 2007)

and impair growth, reproduction, dispersal, or survival across a wide range of invertebrates

(Heisswolf et al. 2009), vertebrates (O'Dea and Whittaker 2007) and plants (Adriaens et al.

2009). Degraded patches also can reduce rates of occupancy and persistence (e.g., Gyllenberg and Hanski 1997). Forest degradation also can alter species interactions across multiple trophic levels and, in some cases, extirpate species at the highest trophic levels (Lenihan et al. 2001, Sergio et al. 2008). The severity of these potential consequences depends partly upon a species' life history and intrinsic characteristics, such as habitat specialization, movement abilities, perceptual capacities, age or sex, and energetic condition (Nathan et al. 2008).

Study species

The Magellanic Woodpecker is a highly specialized and charismatic species that is well known by local people from various social contexts. Its large size, contrasting colors, sexual dimorphism, association with mature and old-growth forests, and recognition as a hard-working species for its intensive pecking activities, makes people especially attached to them (Arango et al. 2007). This positive perception by local people provides a unique opportunity to use this species as a flagship for the conservation of the remaining Nothofagus forest in the South American Temperate region (Ducarme et al. 2013; Walpole and Leader-Williams 2002).

Magellanic woodpeckers depend upon old-growth forest conditions that provide nesting/roosting sites and wood-boring larvae in dead or decaying trees (Nappi et al. 2015). Although woodpeckers are sensitive to forest loss and degradation (e.g., Virkkala et al. 1993), the mechanisms threatening their persistence in disturbed forest are poorly understood (e.g. Ciudad et al. 2009; Lammertink et al. 2009). Because the main prey of woodpeckers – wood-boring larvae – are not visually conspicuous (Newell et al. 2009,

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Vergara et al. 2016), woodpeckers must make foraging decisions based on the presence of habitat conditions that are favorable for wood-boring larvae. Though woodpeckers possess both innate skill and learned capacity to discern suitable habitat conditions, they could also make maladaptive habitat choices that might negatively impact fitness and population persistence (e.g. Camprodon et al. 2015).

Most scientific knowledge about the ecology of the Magellanic woodpecker comes from relatively intact and contiguous areas of temperate and subpolar Nothofagus forest (e.g. Vergara and Schlatter 2004; Schlatter and Vergara 2005; Ojeda 2004; Ojeda et al. 2007; Soto et al. 2012, 2016, 2017; Ojeda and Chazarreta 2014; Vergara et al. 2016, 2019), with few exceptions (e.g., Espinosa et al. 2016). In these mostly undisturbed forests, woodpecker behavior is consistent with habitat selection and optimal foraging theories (e.g., Charnov 1976), and birds adjust foraging and nesting decisions based on habitat quality. First, woodpeckers select foraging trees based on the quality of trees located within their perceptual range, but also use memorized estimates of habitat quality (Vergara et al. 2016), as predicted from theoretical models (Vergara et al. 2015). Woodpeckers actively select foraging trees with the greatest likelihood of being occupied by beetle larvae, spend 3x more time in high-quality than low-quality trees, seldom visit recently-depleted trees, and orient foraging routes through high-quality woody habitat (Vergara and Schlatter 2004; Vergara et al. 2016; Soto et al. 2017). Second, woodpeckers operate in different behavioral modes while moving through forest, switching from foraging mode to transit mode when they perceive a reduction in the quality of decaying wood patches (Vergara et al. 2019). Third, woodpeckers seem to adjust the size of territories to the quantity of decayed trees that they can exploit and defend from other conspecifics (Ojeda & Chazarreta 2014; Soto et

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al. 2016), as exhibited by other woodpecker species (Tingley et al. 2014). Fourth, woodpeckers excavate cavities for roosting and nesting within large decaying trees (Ojeda et al. 2007). Collectively, these traits and patterns suggest that woodpeckers living in intact forest adjust their behavior based upon their perceptions and evaluations of habitat quality. The ecology of Magellanic woodpeckers living in disturbed forest, presumably with fewer resources (e.g., Ojeda et al. 2007; Ojeda & Chazarreta 2014; Ibarra & Martin 2015), is much less known.

Research Objectives

This dissertation examined how Magellanic woodpeckers (*Campephilus magellanicus*), the primary cavity excavator of these forests, responded to habitat quality and quantity, social interactions, and landscape composition and configuration within the temperate forests of Chile. Specific objectives were to (1) innovate a new method to estimate foraging habitat quality with satellite imagery; (2) investigate how nesting and roosting cavities affected within-territory habitat use; (3) explore the implications of foraging behavior and social interactions on seed dispersal; and (4) understand the differential contributions of historic deforestation and exotic plantations on genetic population structure.

Dissertation Organization

This dissertation is organized as manuscripts written for publication in scientific journals. As such, some introductory material is redundant among chapters. In Chapter 2 (Soto et al. 2017), we investigate how remotely-sensed Vegetation Indices (VI) correlated with tree decay and habitat use on a local population in south Patagonia. In Chapter 3, we explored the contribution of nesting and roosting cavities on within-territory habitat use in two

distinct populations of Magellanic woodpeckers, using these results to discuss on the potential drivers of territory sizes. In Chapter 4 (Soto et al. 2018), we demonstrate in a short note, the possible patterns and mechanisms of seed dispersal by Magellanic woodpeckers using the Valdivian rainforests of North Patagonia. Finally, in Chapter 5, we assessed the possible contribution of historic deforestation and exotic plantations on the genetic population structure of local populations.

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CHAPTER 2

TREE SENESCENCE AS A DIRECT MEASURE OF HABITAT QUALITY: LINKING

RED-EDGE VEGETATION INDICES TO SPACE USE BY MAGELLANIC

WOODPECKERS[1]

Abstract

Accurate estimates of the quality and quantity of remnant habitats is critical for

conservation of threatened species. Although habitat quality usually is understood from a

multidimensional niche space approach, the availability of foraging substrates can be a

suitable and more proximate index of habitat quality for species with specialized habitat

requirements, like woodpeckers that feed almost exclusively on larvae of wood-boring

beetles in the trunks and branches of infested trees. Recent approaches use simple

mathematical algorithms on spectral bands called Vegetation Indices (VI) to identify

infestations, providing a new opportunity to assess habitat quality for woodpeckers. In this

paper, we tested the ability of 102 VI to estimate tree attributes explaining habitat quality

for Magellanic woodpeckers for its usage as a reliable habitat suitability estimator. We

hypothesized that space use of Magellanic woodpeckers is positively associated with the

spatial distribution of decayed trees in the landscape. We developed a methodological

framework based on high-resolution, multispectral imagery with three basic steps. First, we

mapped individual *Nothofagus* trees based on estimates of species composition from a

supervised classification procedure, VI estimates and image segmentation. Second, we

[1] Soto, G. E., Pérez-Hernández, C. G., Hahn, I. J., Rodewald, A. D., & Vergara, P. M. (2017). Tree senescence as a direct measure of habitat quality: Linking red-edge Vegetation Indices to space use by Magellanic woodpeckers. Remote Sensing of Environment, 193, 1-10.

selected the best VI predicting the tree quality for Magellanic woodpeckers. Third, we tested these habitat quality predictors, the species composition and tree age, by using two Synoptic Models of Space Use (SMSU) of Magellanic woodpeckers based on very high-frequency (VHF) radio-telemetry and global positioning system (GPS) telemetry data.

Generalized Linear Mixed Models (GLMM) showed that the VI that best predicted habitat quality at the tree-scale was the Plant Senescence Reflectance Index (PSRI, computed as [Red-Blue]/Red-edge), included in almost all the most parsimonious models. The most parsimonious SMSU included only PSRI as an independent covariate, with a strong positive relation. Although coefficient differences were found between telemetry data (VHF vs. GPS data) both showed a positive overall response. Consequently, Red-edge based PSRI can be considered a reliable estimator of tree-scale foraging habitat quality at landscape extents for future research and management activities including Magellanic woodpeckers living on heterogeneous *Nothofagus* forests.

1. Introduction

Habitat loss and degradation caused by human development represents one of the greatest threats to biodiversity worldwide (IUCN, 2015). Conservation in many human-dominated landscapes is challenged by the lack of accurate estimates of the quality and quantity of remnant habitats needed to support populations of threatened species (Joppa & Pfaff, 2009; Pimm et al., 2014). Yet for certain species assessing habitat at the landscape scale is often a complex task involving high-resolution land cover data measured at the spatial scales over which ecological processes occur (Boyce, 2006; Hölker, 2002; Huston & Huston, 1994). Although habitat quality usually is evaluated from a multidimensional niche

space approach that includes multiple abiotic and biotic factors thought to affect species performance (Wen, Saintilan, Yang, Hunter, & Mawer, 2015), the availability of foraging substrates can be a suitable and more proximate index of habitat quality for species with specialized habitat requirements (Bull, 1978; Walters, Daniels, Carter, & Doerr, 2002). Recent developments of remote sensing systems that can provide fine-grained data (e.g., foraging substrate characteristics such as individual tree's species, height, area, etc.) have made it possible to monitor specific resources in a spatially-explicit manner (Mason et al., 2003). Spatio-temporal changes in vegetation in the landscape, such as leaf pigments, can be assessed by using Vegetation Indices (hereafter VI), which use simple mathematical algorithms to process the spectral reflectance of sunlight (Oumar & Mutanga, 2013; Waser, Küchler, Jütte, & Stampfer, 2014). Indeed, VI have many advantages on other more complex approaches, such as providing information on particular properties of vegetation, including vegetation structure, plant pigments, canopy moisture, Lignin and Cellulose/Plant residues, plant physiology, and photosynthetic metabolism (Bannari, Morin, Bonn, & Huete, 1995; Chuvieco, 2002; Thenkabail, Lyon, & Huete, 2011; Serbin, Dillaway, Kruger, & Townsend, 2012). The Normalized Difference Vegetation Index (NDVI) is one example that is widely heralded as a reliable monitoring vegetation tool (Rouse, Haas, Schell, & Deering, 1974; Pettorelli et al., 2005; Fensholt & Proud, 2012; Wen, Saintilan, Yang, Hunter, & Mawer, 2015), and prevail over other VI, being the more used and studied VI (Kerr & Ostrovsky, 2003). For instance, VI have improved the knowledge about the distribution of threatened species in heterogeneous landscapes through successfully describing the characteristics of suitable habitat at different spatial scales (Kerr & Ostrovsky, 2003; Turner et al., 2003). Therefore, VI are often included in most parsimonious models as predictor covariates for nearly all ecological space use studies

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modeling species' occupancy, richness and abundance, among others (e.g., La Sorte, Fink, Hochachka, DeLong, & Kelling, 2012; Luo et al., 2012; Jathanna, Karanth, Kumar, Karanth, & Goswami, 2015).

In this paper, we developed a remote sensing-based approach to estimate habitat quality based on the availability of foraging substrates for a woodpecker species. Specialist woodpeckers are a particularly appropriate focal group given that they feed almost exclusively on trunks and branches of the trees infested with larvae of wood-boring beetles (Short & Sandström, 1982). Although most remote sensing systems fail to provide information on fine–scale tree features (e.g., individual branches or small trees), satellite-derived images have proved to be useful to quantify the canopy of trees infested by wood-boring saproxylic beetles in hardwood and conifer forests of the north hemisphere (Bright, Hicke & Hudak, 2012; Coops, Johnson, Wulder, & White, 2006; Franklin, Wulder, Skakun, & Carroll, 2003; Hart & Veblen, 2015; Meddens, Hicke, Vierling, & Hudak, 2013; White, Wulder, Brooks, Reich, & Wheate, 2005; Wulder, White, Bentz, Alvarez, & Coops, 2006). For instance, the accelerated tree decay driven by the wood-boring beetles *Dendroctonus* spp., and its coarse-scale impact on timber production and carbon flux dynamics has been studied using remote sensing imagery (Stokland, Siitonen, & Jonsson, 2012; e.g., Kurz et al., 2008; Wulder, Dymond, White, Leckie, & Carroll, 2006).

The introduction of the red-edge band with the launch of RapidEye and WorldView-2 (WV-2) satellite sensors has significantly improved landscape scale assessment of tree senescence and vegetation stress caused by natural factors and environmental disturbances (Adamczyk & Osberger 2015). VI based on the red-edge band (positioned between the 680–750 nm wavelengths) are accurate proxies for the tree senescence resulting from shifts in foliar chlorophyll a and b degradation (Vogelmann,

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Rock, & Moss, 1993; Hörtensteiner, 2006; Eitel et al., 2011). However, estimation of tree senescence based on VI necessitates careful distinction between pixel- (i.e., restricted to some unit area) and tree-based (i.e., restricted to an individual tree) approaches (e.g., Waser, Küchler, Jütte, & Stampfer, 2014). Identification of individual trees in forested landscapes, as required by a proper woodpecker-centered (i.e., tree-based) approach, can be achieved by combining high-resolution multispectral imagery with the image segmentation approach, which uses similarity criteria to group neighboring pixels into regions or segments (Meinel & Neubert, 2004).

Here, we used VI with image segmentation to assess tree habitat quality at the landscape scale for the Magellanic woodpecker (*Campephilus magellanicus*, King 1828), a forest specialist endemic to the temperate forests of southern Chile and Argentina (Short 1970). While IUCN list this species as Least Concern, the local governmental Cattle and Agriculture Service (SAG) list the Magellanic woodpecker as vulnerable across most of its distribution and endangered in the northern limit of the Valdivian Temperate Rainforest, which has been extracted and degraded over the last two centuries, driving to a woodpeckers' decreasing population trend (Chazarreta & Ojeda, 2011; Lara et al., 2012; IUCN, 2015; SAG 2015). Magellanic woodpeckers prefer old-growth Southern beech *Nothofagus* forests with large-diameter and advanced heartwood decayed trees, mostly *N. pumilio* (Ojeda & Chazarreta 2014; Vergara & Schlatter 2004), which is consistent with large woodpeckers in northern hemispheres that also specialize on decaying trees (e.g. Nappi, Drapeau, & Leduc, 2015). Because the Magellanic woodpeckers almost exclusively consume wood-boring larvae of Cerambycidae beetles (Short, 1970), the availability of trees infested with these larvae is perhaps the best proxy of habitat quality for Magellanic woodpeckers. Sapoxylic wood-boring insects play a key role in the dynamics of Chilean

temperate forests by progressively driving *Nothofagus* tree species to death (see Barriga, Curkovic, Fichet, Hernríquez, & Macaya, 1993; Guzman, 1996; Méndez, 2009; Zuñiga-Reinoso, 2013). Therefore, landscape planning designed to promote the conservation of Magellanic woodpeckers requires identifying suitable forest stands based on unbiased estimates of tree quality.

We hypothesized that space use of Magellanic woodpeckers is positively associated with the spatial distribution of decayed trees in the landscape. To test this hypothesis, we developed a methodological framework with the following steps: First, we mapped individual *Nothofagus* trees using high spatial resolution, multispectral imagery-derived estimates of species composition, VI and image segmentation. Second, we selected the best VI predicting tree quality for Magellanic woodpeckers. Third, we tested these habitat quality predictors by modelling the space use of Magellanic woodpeckers based on two sources of telemetry data.

2. Methods

2.1. Study area

The study area was located on Navarino Island, encompassing approx. 58 km^2 including the coastal town of Puerto Williams, Chile (Fig. 1). This area is part of the Cape Horn Biosphere Reserve (55°S), which is dominated by oceanic climate with a mean annual temperature of 6°C, precipitation of nearly 500 mm, and climatic conditions typical of isothermal tundra (Rozzi et al., 2006). The habitat largely consisted of a forest mosaic of three *Nothofagus* species (*N. antarctica, N. betuloides, N. pumilio*), which are mostly infested by the wood-boring Cerambycid *Microplophorus magellanicus*, as reported in the

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Navarino Island (Cerda, 1986; Huerta, 2013¸ Zuñiga-Reinoso, 2013). Other land cover

classes include mixed forests of *Nothofagus* and *Drymis winterii* stands, scrub, grasslands,

tundra formations and other land uses (Table 1). The spatial extent, composition and quality

of the forest mosaic vary according to past and current human activities, including fires,

clearing forest for livestock, firewood extraction, and introduced beavers (*Castor*

canadensis) (Rozzi et al., 2006). Despite increasing pressure from urban growth, introduced

species and tourism (Arango, Rozzi, Massardo, Anderson, & Ibarra, 2007, Soto et al.,

2012), these forest stands represent the southernmost remnant of pristine forests in the

world.

Fig. 2.1.

Table 2.1.

2.2. Remote sensing

2.2.1 WorldView-2 image and pre-processing

We used a radiometrically corrected, georeferenced and orthorectified high-

resolution WorldView-2 satellite image in bundle modality (panchromatic + 8-band

multispectral; see Table S1 in Supplementary Material). The image covered the entire study

area (lower panel in Fig. 1), and was taken during the Austral Spring, approx. 20 days after

Nothofagus spp. had fully flushed their leafs, thereby permitting the identification of the

main tree species (Wang, Adiku, Tenhunen, & Granier, 2005). The preprocessing of the

imagery consisted of three steps: 1) processing raw image digital count values (DCs) to

physical values of radiance and reflectance, 2) contrast enhancement by decorrelation (only

used for the digital supervised classification scheme, see Section 2.2.2), and 3) pan-sharpening to obtain high-resolution image.

We obtained radiance values by using the parameters from metadata file (.XML) and the calibration equations presented by Updike & Comp (2010). Radiance values from 8-bands were corrected and transformed to canopy reflectance using Fast Line-of-Sight Atmospheric Analysis of Spectral Hypercubes algorithm (FLAASH considering Sub-Arctic summer atmospheric and Maritime aerosol models; Adler-Golden et al., 1999, see Fig. S1A in Supplementary Material).

We used decorrelation stretch to enhance the contrast (exaggerate color saturation) of RGB color compositions in order to facilitate the subsequent digital supervised classification scheme (see Section 2.2.2). Contrast enhancement aims to reduce the uncertainty on the definition of training areas, which raise from the big similarities among the three dominant *Nothofagus* species present in our study area. We applied a three-stage multivariate Principal Component Analysis (PCA; see Campbell, 1996), using ENVI 5.0 (Exelis Visual Information Solutions, Boulder, CO, USA) on the 8-bands reflectance values (Gillespie, Kahle, & Walker, 1986; Richards & Jia, 2006). First, we transformed spectral bands to their principal components. Then, we contrast enhanced the datasets by equalizing bands, except the near-infrared band. Last, we used the inverse of the PCA transformation to get contrast enhanced color compositions for their use in the digital supervised classification scheme (see Section 2.2.2).

We increased the spatial resolution of the 8-band bundle by using pan-sharpening, combining the lower-resolution multispectral bands with the high-resolution panchromatic band (2.0 m and 0.5 m pixel size respectively, see Table S1 in Supplementary Marerial). Image fusion methods allowed us to obtain high spectral and spatial resolutions using the

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Hyperspherical Color Space algorithm (Padwick, Deskevich, Pacifici, & Smallwood, 2010), which allows to incorporate unlimited bands (Johnson, Tateishi, & Hoan, 2012), available on ERDAS IMAGE 2013 (Erdas, Norcross, GA, USA).

2.2.2 Pixel-based image analysis

We identified vegetation types and other land uses using a digital supervised classification scheme in ENVI 5.0 (Chuvieco 2002; Lillesand, Kiefer, & Chipman, 2014). Definition of the classes was according to meaningful habitat structures for Magellanic woodpeckers (e.g. forest and non-forest types; Soto et al., 2012; see Table 1). We used field data from October to December 2014 and contrast enhanced color compositions RGB 532 and 865 to build learning areas. After the three-step PCA, we used these compositions to train the spectral signatures for the classes of interest based on the Jeffries-Matusita distance with a threshold value of 1.8 (Richards & Jia, 2006). We used a Bayesian Maximum Likelihood algorithm to determine the probability of each pixel to belong to each class. Last, in order to evaluate the quality and accuracy of the classification process we calculated the overall accuracy from the corresponding confusion matrix built with 336 ground-truth data points (Chuvieco 2002; Lillesand, Kiefer, & Chipman, 2014).

We selected a set of 102 VI from the Index Database developed by Henrich, Krauss, Götze, & Sandow (2012), including 21 red-edge VI (Table S2 in Supplementary Material). In order to relate the ecologically significant habitat conditions to VI, we measured the tree-scale attributes relevant for Magellanic woodpeckers of five *Nothofagus* trees within a total of 47 20 x 20 m systematically established plots, distanced by 800 m from each other. These plots were sequentially selected from a 41 by 9 grid of 400×400 m cells, including just the cells with centroids located in forest land cover. We included 258 randomly

distributed trees across the study area, spaced by at least 50m to avoid spatial

autocorrelation. Following Vergara & Schlatter (2004), we measured the diameter, height,

decay stage, and woodpecker pecking signs of every sampled tree. We incorporated the

presence of holes generated by the entrance and emergence of adult wood-boring beetles

along the trunk as a direct measure of infestation (see Table 2). The inclusion of the

pecking and entrance/emergence holes covariates respond to the need to test for the

possible bias that this two visual cues represent for the woodpeckers in their search for food

(Vergara et al., 2016).

Table 2.2.

2.2.3 Object-based image analysis

     We applied object-based image analysis on the eight pan-sharpened bands to

identify individual tree crowns belonging to each classified forest type. We used a multi-

resolution segmentation algorithm based on scale and homogeneity criteria using

eCognition Developer 8.7 Object Based Image Analysis software (Trimble Germany

GmbH, Munich, Germany). We iteratively used several combinations of scale and

homogeneity parameters until segmented polygons became visually congruent with actual

tree crowns. Then, to evaluate these results from the segmentation procedure, we photo-

interpreted and digitized 150 randomly selected crowns of individual trees using a scale of

1:1500. We measured and log-transformed the areas of these digitized crowns and the areas

of the spatially matching crowns resulted from the segmentation procedure. Last, the

evaluation of the segmentation process consisted in comparing these areas applying a

Pearson's chi-square test (χ^2) using R 3.1.2 (R Foundation for Statistical Computing,

Vienna, Austria).

2.2.4 Adjusting spatial scale

Tree-scale attributes were obtained by modal selection for vegetation classes (i.e., assigning the class with more pixels within each segmented crown from the supervised classification), and by averaging the values of each VI. We identified specific crowns (n=446 trees) using visual inspection and their coordinates while attributing them with the collected field data.

2.3. Statistical analysis

2.3.1 Relating VI to habitat quality field data

In order to find specific VI related to habitat quality for woodpeckers, we assessed the association between the values of single VI and field measures of trees by using Generalized Linear Mixed Models (GLMM). In other words, we fitted an individual model for each combination of VI and tree measures. In order to reduce the number of candidate models, we only considered tree metrics that were correlated with VIs (i.e., with a Pearson's correlation coefficient $r \geq 0.30$). In the GLMMs, we considered the plot location as a random effect factor. We used different link functions depending on response-model variables. We used the Gaussian distribution as the identity link function for normalized tree height (h) and *DBH* (see Table 2). The presence of entrance and emergence holes in the trunks (*eme*; see Table 2) was analyzed using a logit link function. Decay stage and pecking variables (*dec* and *pec*; see Table 2) were considered as ordinal variables, and thus modeled using Mixed-effects ordinal regressions (Bolker et al., 2009). We performed GLMM and ordinal regression models using *MASS* and *ordinal* packages in R 3.1.2 (Christensen,

2015). Competing models were ranked by their Akaike Information Criterion (AIC) and relative AIC importance (AIC weight), and differences in AIC (ΔAIC) were used to interpret the strength of evidence for each model.

2.4. Woodpecker space use and habitat quality predictions

In order to test the performance of the aforementioned methods as habitat quality estimators, we related the space use of Magellanic woodpeckers to the estimates from our previous analyses using the Synoptic Model of Space Use (SMSU; Horne, Garton, & Rachlow, 2008). SMSU structure assumes that environmental changes are proportional to changes in the use of a specific area in the space (see description in the Appendix; Horne, Garton, & Rachlow, 2008). The null model in the SMSU is a quantitative assessment of the use of space in terms of the time spent in a determined area, often called utilization distribution (UD; Jennrich & Turner, 1969; Van Winkle, 1975; Katajisto & Moilanen, 2006). These models were specifically developed to address habitat selection with both temporally independent and dependent data, and were implemented here using the validated estimates of tree quality derived from our previous analyses (see above) and two sources of telemetry data for the estimation of the UD (null model of space use). Telemetry data has been traditionally used for home-range and habitat use estimations, and current technology ranges from the least expensive very high-frequency (VHF) radio-telemetry transmitters to the more recent and costly GPS data-loggers (Kie et al., 2010). Here, we supplemented the VHF data from individuals whose territories have been monitored in the study landscape (Soto et al., 2012), with more recent VHF and GPS data from Soto et al., (unpublished), which collectively correspond to 30 male Magellanic woodpeckers, 8 VHF and 14 GPS totalizing 516 and 4120 locations respectively during the post-breeding season (Austral

late-spring and summer). We only used males because they guide the daily foraging activities of the family groups, exerting dominance over the other family members (Ojeda & Chazarreta, 2006; Chazarreta, Ojeda & Lammertink, 2012). VHF data were sampled using homing method once daily to avoid spatial autocorrelation (see Soto et al., 2012 for sampling methods). GPS data were acquired using ATS G10 GPS-loggers equipped with a VHF transmitter for its later recovery, and were attached to the backs of woodpeckers. All devices were scheduled to get locations every 5 min throughout the battery life (approx. 4 days), and from 7am to 10pm. After dropped by birds, the GPS loggers were located using radio-telemetry, and spatio-temporal data were downloaded. We examined habitat selection by woodpeckers by applying to the following appropriate null models: a bivariate normal distribution for the SMSU with VHF data (following Horne, Garton, & Rachlow, 2008) and a Brownian bridge movement model (BBMM) for our temporally correlated GPS data (following Wells et al., 2014). We used the *adehabitatHR* package in R 3.1.2 to calculate the BBMM input parameter σ^2, the spatial variance associated with the speed of the sampled woodpeckers, using an average sampling error of 4m (δ in BBMM), calculated during field tests before deployment of the loggers. Log-likelihood functions of SMSU were minimized using the optimization algorithm provide by the *optimx* function in R (Nash, 2014). Last, we obtained standardized averaged coefficients from the SMSU fitted to each individual to identify the best spatial habitat quality estimator for Magellanic woodpeckers.

3. Results

Preprocessing and habitat composition

Preprocessing of the image facilitated the process of definition of training areas for

the subsequent digital supervised classification scheme as decorrelation stretch visually highlighted the young classes of forests, as can be seen in Fig. S1 in the Supplementary Material. The digital supervised classification scheme classified 49.91% of the image as lacking vegetation, which included urban cover (*Ua*), dense cloud cover and snow (*Cs*), shadows (*Sd*), water (*Wt*) and bareland (*Bl*) classes (see Table 3, Fig. 2). Among the classes of interest, old growth forest of *N. betuloides* (*OgNb*) had the most classified pixels (12.71%, see Fig. 1). Saplings and old growth forest of *N. pumilio* (*SpNp* and *OgNp*, respectively), and old growth forest of *N. antarctica* (*OgNa*) represented the 8.36%, 6.15%, and 5.70% of pixels, respectively. Open habitats of shrub and peatlands, dominated by *Chilliotrichium diffussum* and *Berberis buxifolia* (*Sh*), and *Sphagnum* spp. (*Pt*), respectively, represented the 4.79% and 3.90% of the scene. Scrubby deciduous forests of *N. pumilio* and *N. antarctica* (*ScNpNa*) in areas of higher elevation and slope represented 3.43 % of pixels, with saplings of *N. betuloides* (*SpNb*) and coeval forest stands of *N. betuloides* (*IgNb*) representing only 1.92% and 1.75% respectively. Grassland (*Pg*) was the least represented class with 1.32% of classified pixels (see Fig. 1). From the results of the confusion matrix, we estimated an overall accuracy of 86.61% for this pixel-based approach (Table S3). F_c and F_p values showed high values of good performance for classes different to forests-related classes. Most misclassification events occurred between forest classes, with the least-represented *N. Pumilio* (*OgNp*) class having the higher associated errors.

Table 2.3.

Fig. 2.2

Identifying crowns of trees

Evaluation of the segmentation process by area comparison showed that tree crowns (segmented polygons) were successfully identified. When assessed by species and age, the estimated and observed tree crowns were not statistically different, thus supporting a successful segmentation algorithm (see Table 4).

Table 1.4.

Data analysis and statistical modelling

In the preliminary analysis of both, the correlation among field measures of tree quality for Magellanic woodpeckers and the association between them and VI values, only DBH was eliminated from subsequent analysis due to its low correlation values with VI estimates (see Fig. S2 and S3 in Supplementary Material). However, tree height had significant correlation coefficients with NDVI, GI2, ARVI and NORMNIR (see Table 5, 6). The best supported candidate models ($\Delta AIC \leq 2$) for the decay, pecking and emergence/entrance signs always retained PSRI as the best index accounting for the tree quality (Table 5; PSRI = [Red-Blue]/Red-edge, see Table S2 in Supplementary Material). In all GLMMs PSRI had a positive and significant effect on the field measures of tree quality (Table 6).

Table 2.5.

Table 2.6.

Fig. 2.3

Woodpecker's preferences and habitat quality predictions

SMSU including the effect of PSRI had greater support than SMSU incorporating

compositional and forest type, which had higher AIC values (Table 7). VHF- or GPS-based

SMSU differed in the coefficient values associated to the same covariates, with GPS-based

SMSU showing stronger selection (25.2 times the VHF-based PSRI coefficient value).

However, SMSU estimated with both data sources (VHF and GPS data) indicated that

space use by Magellanic woodpeckers responds primarily to decayed wood within

territories, as reflected by the positive averaged coefficient for the PSRI model of 2.596

(SE=0.965, p=0.007). The resulting map of the PSRI estimates, proportional to the

probability of occurrence of woodpeckers in the study landscape, indicates that the space

use by woodpeckers vary markedly in the landscape, responding to the heterogeneous

distribution of trees with advanced decay (Fig. 2 and 3).

Table 2.7.

4. Discussion

Our results showed the potential of multi-spectral high spatial-resolution imagery

for the estimation of habitat quality for a woodpecker species. As presented here, VI can be

used as a direct measure of tree senescence and is a suitable proxy for the estimation of the

abundance of wood-boring larvae at the tree trunks, thus providing support for our

proposed hypothesis.

Even though contrast enhancement is highly dependent on the scene (Gillespie, 1992; Gillespie, Kahle, & Walker, 1986), it facilitated the process of training the classes considered for digital supervised classification (see Table 1 and 3; see also Fig. S1, panel C). The posterior classification results reflected a good performance of the proposed methods, with the confusion matrix revealing null misclassification between the three dominant *Nothofagus* species: *N. betuloides, N. pumilio,* and *N. antarctica* (see Table S3 in Supplementary Material).

Among the fitted GLMMs used to explain variation in the field measures of tree quality (*DBH*; height *hei*; entrance/emergence signs *eme*; decay *dec*; and pecking signs *pec*; see Table 5), we identified more than one VI predictor for three of these tree quality estimates (Table 6). Broadly, the VI predictors can be separated in three main groups: the red-edge related VI (PSRI; VIRE; NDRE), the NDVI related VI (NDVI; ARVI; $NDVI_{8,4}$), and Greenness Index 2 and Normalized NIR. While the red-edge group of VI was developed to address biochemical features of plants such as pigments and chlorophyll for PSRI and VIRE, the other VI focused more on structure of plants (e.g. Leaf Area Index, Green Biomass, Fraction of Absorbed Photosynthetically Active Radiation; Thenkabail, Lyon, & Huete 2011). Although previous studies showed that NDVI-related VI are poor predictors of tree structure, we found that the most parsimonious models explaining variance in tree height included NDVI-related VI. Thus, relationships among VI and structural attributes of *Nothofagus* forests should be further explored.

Although several indirect measures of habitat quality for woodpeckers are available (e.g., decay stage of tree, pecking signs, and emergence holes from wood-boring beetles; Walters, Daniels, Carter & Doerr 2002; Soto et al., 2012; Nappi, Drapeau & Leduc 2015; Ojeda & Chazarreta 2014; Nappi, Drapeau & Leduc 2015; Ojeda & Chazarreta 2014; Soto

et al., 2012), we found red-edge indices performed best. Those most strongly correlated with tree senescence PSRI outperformed other red-edge VI. Moreover, the PSRI was the only VI explaining emergence signs (Table 4), though this does not necessarily represent an unbiased approach to estimate larvae abundance given that signs of entrance/emergence could be below the bark in older trees or otherwise hidden from the observer sight (Barriga et al. 1993; Zuñiga-Reinoso 2013). We also recognize that the lack of ecological studies on Cerambycids in *Nothofagus* forests makes difficult to know if the differences in the distribution of larvae along different trees, atmospheric changes, and nutrient availability can affect the biochemistry of the tree canopy and thereby add a new source of bias to our estimates (e.g., Couture, Meehan, & Lindroth, 2012; Couture, Servi, & Lindroth, 2010). Despite these limitations, both emergence/entrance and pecking signs were successfully accounted for by PSRI. These features represent a putative memory-related attribute, possibly guiding woodpeckers to forage in known previously successful trees (Vergara, Saura, Pérez-Hernández, & Soto, 2015). Finally, the field measure of the decay stage of trees had two main predictors, PSRI and $NDVI_{8,4}$ with similar Akaike's weight values.

Even though our study did not explore how non-forest variables affect space use of woodpeckers (i.e. elevation, slope, distance to roads, distance to beaver meadows, etc.), the expected within-forest selection pattern was confirmed by the use of the SMSU and VI. Although we found an overall positive effect of PRSI on the occurrence probability of woodpeckers, the strength of such an effect was dependent on the nature of telemetry data (i.e., VHF vs. GPS data) and the probability density functions used to analyze these data sources (i.e., Bivariate Normal vs. BBMM). The grain at which these two methods estimates the utilization distributions can explain such difference (see Börger et al., 2006; Fieberg & Börger 2012), because GPS data has an increased temporal resolution (5min)

compared to VHF data (one point per day). The temporally independent VHF-based SMSU used the classic bivariate-normal probability density function assuming data independence. However, even though this method is widely used for home-range estimation, it unbalances the accuracy of habitat use estimates because it can over-smooth the spatial distribution of occurrence probabilities, assigning disproportionately high probability values to the less used resources. Thus, Bivariate-normal kernels underscore the resource selection estimates when using a resource availability dataset with higher resolution than the resolution under which locations of animals are recorded. In the other hand, GPS-based SMSU provide more accurate estimates of occurrence probabilities when using high-resolution habitat maps (as used in this study), since habitat preferences are based on a tree-by-tree selection pattern, accurately resembling the foraging behavior exhibited by woodpeckers.

Like other recently published papers using high-resolution satellite imagery (e.g. Immitzer, Atzberger, & Koukal, 2012; Mutanga, Adam, & Cho, 2012; Novack, Esch, Kux, & Stilla, 2011; Oumar & Mutanga 2013; Ozdemir & Karnieli 2011; Waser, Küchler, Jütte, & Stampfer, 2014), WV-2 data allowed us to identify and count individual tree crowns, and determine their species, structure and decay stage in *Nothofagus* forests, as supported by our results. In general, in each step the proposed model was sufficient to estimate habitat quality for Magellanic woodpeckers. Red-edge VI, specifically PSRI, was closely associated with field measures of tree quality and woodpecker's space use, and therefore PSRI might be a reliable approximation of habitat quality. In order to increase the precision of these PSRI estimates, we recommend the validation of them by using improved field sampling techniques to assess the prevalence of wood-boring larvae in trees, such as Ultrasonic and/or Stress wave timer detectors and even Radars. One important limitation of our approach is that it fails to account for standing or felled dead wood, which represent a

small portion of the foraging substrate for woodpeckers (Jiménez et al. 2014; Stokland, Siitonen, & Jonsson, 2012). Recently, Nappi, Drapeau, & Leduc (2015) used Light Detection and Ranging (LiDAR) to explore successfully the relation of dead wood and woodpeckers' foraging activities among different species. Therefore, we highly recommend the combination of red-edge VI as PSRI and LiDAR methods to provide better assessments of habitat attributes required by specialized woodpeckers.

Acknowledgments

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Figure 2.1. Map showing the study area localized within the Cape Horn Biosphere Reserve. In the lower panel, the WorldView-2 image in false color composition encompassing a landscape of 58 km^2 including Puerto Williams town (Chile).
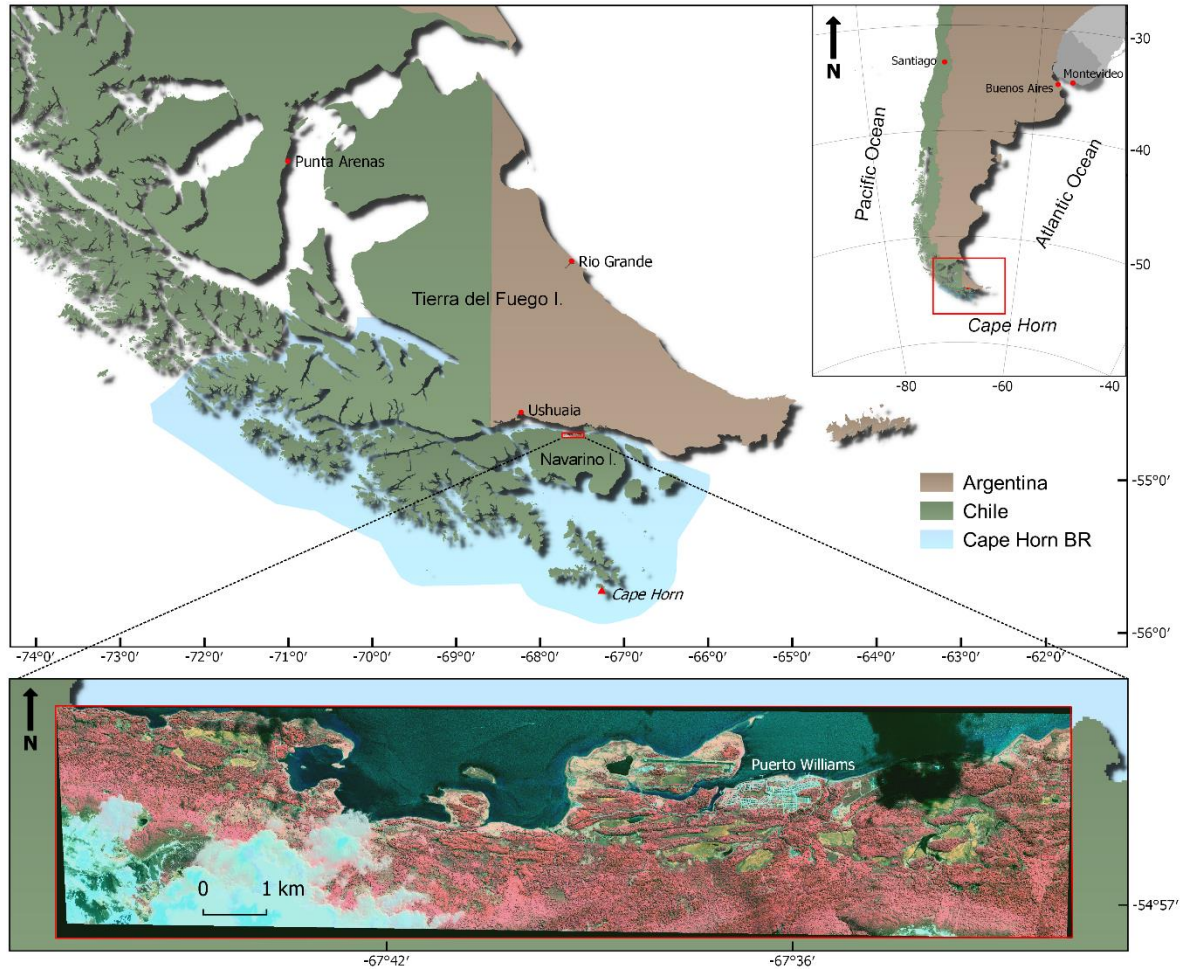
Figure 2.2. Different maps created from the outputs of the analyzed WorldView-2 scene. A) Plant Senescence Reflectance Index - PSRI, calculated as [Red-Blue]/Red-edge, included in supported candidate models (ΔAIC ≤ 2) for decay, pecking and emergence/entrance signs, representing the best vegetation index accounting for tree quality; B) forest species and age of *Nothofagus* trees extracted from a supervised classification. Dark and light colors represent Old-growth and saplings forests classes, respectively. 100-m isoclines, coastline and sea (spaced dots) are included.
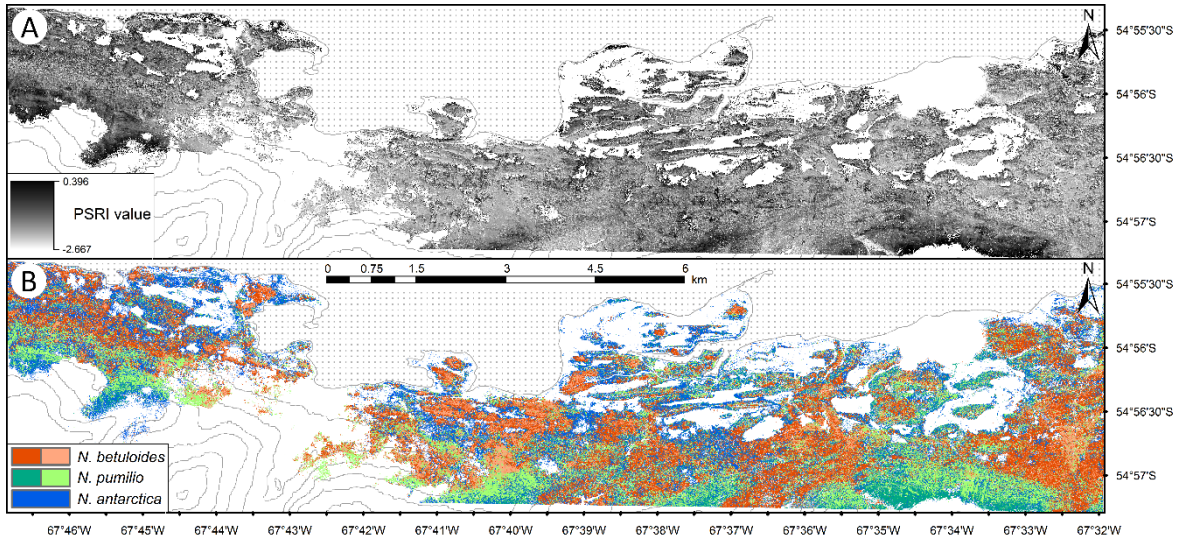
Figure 2.3. Plot of the relationship between PSRI values and decay stage of the two dominant *Nothofagus* tree species present in the study area. Kernel density functions (z-axis) helps understand the domain on PSRI values of the sampled decay stages.
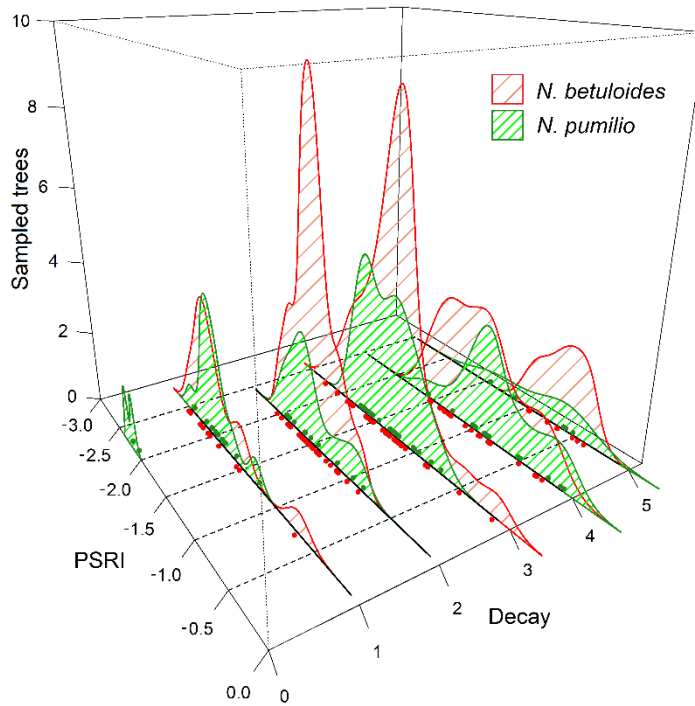
Figure 2.4. Plot of woodpecker locations sampled using two different methods for two dominant males on the study area. Locations are overlaid on PSRI estimates of trees (PSRI values are inherited from Fig. 2.2). A) Successful GPS locations sampled every 5 min of a male woodpecker showing its approximate movement path (lines) during the course of a day. B) Locations of a male woodpecker visited daily using a VHF radio transmitter and homing technique during the course of a year.
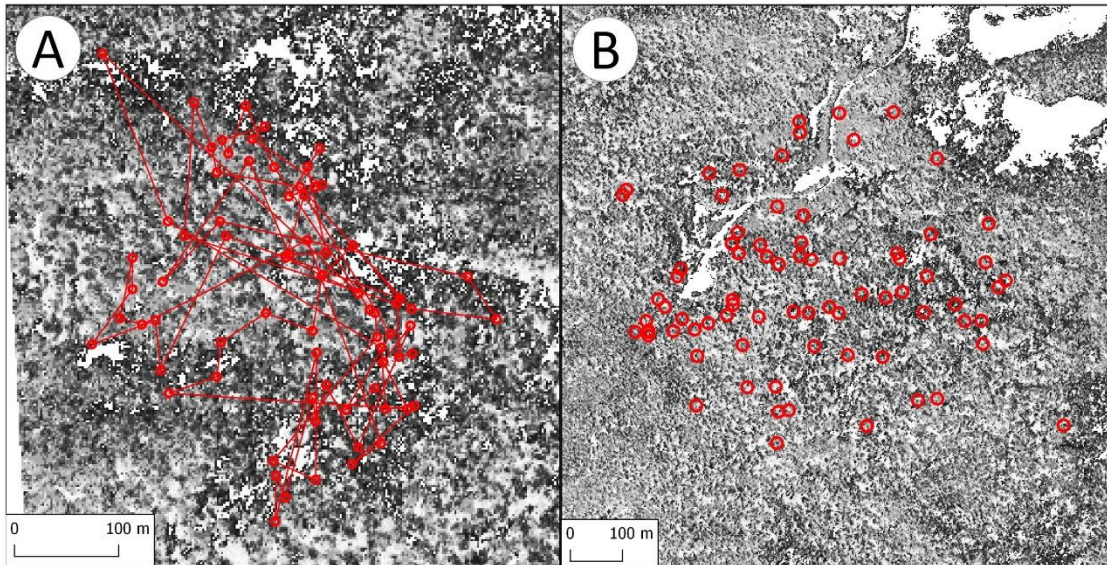
Table 2.1. Description of the vegetation types and land cover classes present in Navarino Island.

Land cover class and description	Code	References
Old growth forest and evergreen emergent trees of *Nothofagus betuloides* (Mirb.) Oerst., usually associated with *Drimys winteri* J. R. et Forst & G. Forst.	*OgNb*	Holdgate, 1961; Moore, 1983; Soto et al., 2012.
Coeval forest stands of *N. betuloides* with intermediate growth, characterized by forming a smooth continuous canopy.	*IgNb*	Holdgate, 1961; Moore, 1983.
Saplings (trees with thin trunk and low height) of *N. betuloides* caused by anthropic disturbances (e.g. firewood extraction).	*SpNb*	-
Old growth forest and deciduous emergent trees of *N. pumilio* (Poepp. & Endl.) Krasser.	*OgNp*	e.g. Lara et al., 2005; Moore, 1983; Soto et al., 2012.
Scrubby deciduous forests of *N. pumilio* and *N. ntarctica* (G. Forst.) Oerst. In areas of high elevation and slope.	*ScNpNa*	Moore, 1983; e.g. Méndez et al., 2013.
Saplings (trees with thin trunk and low height) of *N. pumilio* caused by anthropic and natural disturbances (e.g.wind and slope effects)	*SpNp*	Soto et al., 2012.
Deciduous forests of *N. Antarctica*, preferably in low areas with poorly drained soils and flooded.	*OgNa*	e.g. Ibarra, Anderson, Altamirano, Rozzi, & Bonacic, 2010; Moore, 1983.
Peatlands dominated by *Sphagnum* spp.	*Pt*	e.g. Ibarra, Anderson, Altamirano, Rozzi, & Bonacic, 2010.
Prairie grasses (unidentified species of the family Poaceae) associated with isolated human settlements.	*Pg*	e.g. Ibarra, Schüttler, McGehee, & Rozzi, 2010.
Shrub (e.g. coastal scrub and forest margins) dominated by *Chiliotrichum diffussum* ("Mata negra") y *Berberis buxifolia* ("Calafate").	*Sh*	e.g. Ibarra, Anderson, Altamirano, Rozzi, & Bonacic, 2010; Ibarra, Schüttler, McGehee, &

		Rozzi, 2010.
Water including Canal Beagle, rivers and ponds.	*Wt*	-
Bareland including rocks, bare rivers beds and degraded land.	*Bl*	-
Urban areas including Puerto Williams, main and secondary roads.	*Ua*	-
Dense cloud cover and snow in the higher areas of the Patagonian massif.	*Cs*	-
Shadows caused by clouds and trees, and zones outside the scene.	*Sd*	e.g Arenas, Haeger, & Jordano, 2011.

Table 2.2. Tree-scale covariates explaining the habitat quality for Magellanic woodpecker in each sampled plot.

Code	Description
DBH	Diameter at the breast height in cms.
hei	Height of trees in meters, measured using a hypsometer.
dec	Decay stage, measured as the proportion of dead branches. Stages correspond to: 0) 0% dead branches and no dieback evidence on the trunk; 1) <10% dead branches; 2) 10 to 30% dead branches; 3) 30 to 50% dead branches; 4) 50 to 70% dead branches; 5) >70% dead branches.
pec	Presence of pecking signs on wood surface, ranging from 0 to 50% in 10% intervals.
eme	Binary covariate accounting for the presence/absence of wood-boring beetles' entrance and/or emergence holes in the trunk. It was measured from the ground level to approximately 6 m height.

Table 2.3. Summary of the classified vegetation types and other land cover classes in terms of their area (ha) and % pixels, to the study area.

Landcover	Code	Area (*ha*)	% of pixels
Vegetation types (50.08%)	*OgNb*	743.68	12.71
	IgNb	102.93	1.76
	SpNb	112.87	1.93
	OgNp	359.89	6.15
	ScNpNa	200.8	3.43
	SpNp	489.33	8.36
	OgNa	333.86	5.71
	Pt	228.47	3.91
	Pg	77.65	1.33
	Sh	280.55	4.80
Other land covers (49.92%)	*Wt*	1205.10	20.60
	Bl	152.03	2.60
	Ua	466.65	7.98
	Cs	556.91	9.52
	Sd	539.78	9.23
	Total	5850.50	100

Table 2.4. Summary of Pearson's chi-square test (χ^2) parameters from the evaluation of the segmentation process on the identification of individual crowns of trees.

Type	Species	χ^2	df	p-value
Forest	*N. betuloides*	863.50	875	0.603
	N. pumilio	2165.60	2107	0.183
	N. antarctica	532.20	513	0.270
Saplings	-	2000.80	2014	0.578

Table 2.5. Best supported candidate models (ΔAIC<2) explaining the correspondence between Vegetation Indices and tree-scale attributes (see Table 3).

Model	Covariates	AIC	ΔAIC	w
Height	NDVI	1226.330	0.000	0.364
	GI2	1226.974	0.644	0.263
	ARVI	1227.537	1.207	0.198
	NORMNIR	1227.813	1.483	0.174
Decay	PSRI	549.390	0.000	0.607
	$NDVI_{8,4}$	550.260	0.870	0.393
Pecking	PSRI	562.100	0.000	0.561
	VIRE	563.900	1.800	0.228
	NDRE	564.060	1.960	0.210
Emergence	PSRI	206.900	0.000	1.000

Table 2.6. Model-averaged coefficients, standard errors and *p*-values from models explaining the correspondence between Vegetation Indexes and tree-scale attributes (see Table 5).

Model	Covariate	Name	Coefficients	SE	*p-value*
Height	NDVI	Normalized Difference Vegetation Index	9.441	4.664	0.045
	GI2	Greenness Index 2	11.439	7.162	0.113
	ARVI	Atmospherically Resistant Vegetation Index	3.939	1.794	0.030
	NORMNIR	Normalized NIR	7.108	4.275	0.099
Decay	PSRI	Plant Senescence Reflectance Index	7.042	0.776	<0.001
	NDVI$_{8,4}$	NIR-yellow ratio	-8.828	1.665	<0.001
Pecking	PSRI	Plant Senescence Reflectance Index	3.030	0.449	<0.001
	VIRE	Vegetation Index based on Red edge	-0.457	0.111	<0.001
	NDRE	Red edge NDVI	-5.004	1.222	<0.001
Emergence	PSRI	Plant Senescence Reflectance Index	2.925	0.803	<0.001

Table 2.7. AIC values for the Synoptic model of space use explaining use based in different predictors of habitat quality, and fitted with VHF and GPS data of male territorial Magellanic woodpeckers.

Model	Covariates	VHF-based SMSU		GPS-based SMSU	
		AIC	ΔAIC	AIC	ΔAIC
Decay	PSRI	656.310	0.000	1933.923	0.000
Forest type	Old-growth	699.238	42.928	1957.178	23.255
Null	-	705.733	49.423	1910.000	-23.923
Full	Old-growth, Species, PSRI	709.220	52.910	1942.690	8.767
Composition	Species	762.563	106.253	1940.901	6.978

CHAPTER 3

EXCAVATED CAVITIES AS FOREST LEGACIES THAT AFFECT SPACE USE OF

MAGELLANIC WOODPECKERS

Abstract

Spatial configuration of resources directly affects the occurrence and abundance of

organisms in ways that can influence long-term population dynamics, especially when

space for territories is limited. In this study we explored how the spatial distribution of

cavities affected habitat use within territories of Magellanic woodpeckers (*Campephilus

magellanicus*), a territorial resident of the South American temperate forests that specializes

on decayed wood within mature forests. Unlike many primary excavators, Magellanic

woodpeckers roost, though rarely nest, in previously used cavities. We hypothesized that

the availability of cavities, along with quality of foraging habitat, would determine where

individuals would establish territories. From 2010 to 2015 we assessed the spatial

configuration of roosting trees with cavities within the northern and southern portions of

the woodpecker's range in the temperate forests of Chile. Weighted distribution models

were used to measure the individual and combined effects of the tree decay and cavity

availability on space use within individual territories. In both study areas, activity, or use of

specific areas within territories as indicated by utilization probability distributions,

increased as distance to the nearest excavated cavity declined. Secondarily, individuals also

avoided neighboring woodpecker family groups and preferred to use areas with high levels

of tree decay. Our results provide the first insights into the ways that cavity availability and

distribution can influence territoriality of primary excavators in the South American

temperate forests.

1. Introduction

As forest ecosystems continue to be threatened by changing climate, disturbance regimes, and human activities, we face a growing imperative to manage forests in ways that protect ecosystem function, sustain the services they provide, and safeguard biodiversity (Vose et al. 2012; Maxwell et al. 2016). Whereas most traditional efforts to conserve or sustainably manage forests have focused on maintaining or increasing forest cover, ecologists and managers alike now recognize the importance of specific, and sometimes subtle, features required by certain species and communities. Ecological processes that promote the development of these critical features span a wide range of spatial and temporal scales yet remain poorly understood and, hence, are seldom considered explicitly in planning and management (Daniel et al. 2017). The persistence of such knowledge gaps, especially for systems in the Southern hemisphere (Li et al. 2015), limits our ability to effectively conserve forest ecosystems (Puettmann et al. 2015).

Ranking high among threatened but poorly understood ecosystems are South American temperate forests (SATF), which represent more than half of the temperate forest in the Southern Hemisphere. As a whole, SATF cover has declined by more than 46% since 1700 (Armesto et al. 2001; Donoso 1993), with Chilean Mediterranean forests (34 - 37° S) having less than 4% of pre-colonial cover remaining, the Valdivian rainforest (35 - 48º S) with only 30% remaining, and the Subpolar Magellanic forests (55° S) with most of its extent still remaining (Armesto 2009; Rozzi 2006). Since European colonization and the establishment of the Chilean state, SATFs have been profoundly modified by human activities, such as extensive burning, logging, cattle grazing and conversion to exotic plantations (Donoso 1996; González 2014, Veblen 1996). Despite calls for protection, many forests remain intensively and/or illegally harvested as well as converted to exotic

plantations, which are comprised of highly flammable species (i.e., *Eucalyptus*) that increase the risk of fire when planted adjacent to native forest (Heilmayr et al. 2016).

Management of SATFs is largely governed by the national forest regulatory agency CONAF (Corporación Nacional Forestal - Chile) in relation to policies that focus exclusively on soil and water protection, rather than the defining floristic and structural attributes of native forests (Lara et al. 2006, Reyes et al. 2014, Heilmayr and Lambin 2016; Chilean law 20.283 on Recovery of the Native Forest and Forestry Development). Consequently, most forest attributes are seldom measured or purposefully maintained, in part due to limited information about their roles safeguarding ecosystem structure and function, spatial configuration of resources, and population densities and interactions among associated species (e.g. Essen 1997; Kuuluvainen 2002). Understanding the interplay between spatial configuration of resources and population dynamics requires scaling up individual-level processes to social groups and landscapes (Hooten et al. 2017, Ovaskainen et al. 2016, Fuller 2012).

Ecosystem processes in SATF are complex and depend upon direct and indirect roles that species play in energy exchanges and transformations (Waring and Running 2010). Unlike photosynthesis and transpiration, both heavily regulated by species-specific responses of trees to the environment, other processes are more strongly shaped by species interactions (Aber and Melillo 2001; Stockland et al. 2012). In the case of decomposition, for example, numerous saproxylic species decompose wood and form the base of saproxylic forest food webs, with woodpecker species usually acting as top predators (Stockland et al. 2012). As in many systems, top predators are among the species most sensitive to forest degradation (Drossel and McCane 2003). For this reason, birds like woodpeckers can be useful indicators of forest function, a galvanizing focus for

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conservation, and guiding sentinels used to develop sustainable forest practices (Angelstam et al. 2004; Drever et al. 2008; 2010; McClelland et al, 1999; Ruggera et al. 2016). Despite some debate about value or adequacy (e.g. Prendergast and Eversham 1997; Sætersdal et al. 2005), indicator species can serve as important tools in regions with large knowledge gaps about ecosystem functions and responses to anthropogenic and natural disturbance, as is the case for the SATF.

In this study, we used the Magellanic Woodpecker (*Campephilus magellanicus*) to examine how the spatial distribution of resources shaped space use and territory establishment. Magellanic Woodpeckers are primary excavators (i.e., they excavate their own cavities) and, as such, possess several morphological and behavioral adaptations that allow them to excavate, nest, and roost in tree cavities (Short & Sandström 1982). Cavities provide refuge from severe weather, protection or escape from predation, and favorable conditions for reproduction and survival of cavity nesters (Martin 1993, 1995; Zanette et al. 2011). Though woodpeckers tend to excavate or modify cavities in ways that enhance these benefits (e.g., size of entrance hole, addition of wood chips; Maziarz & Wesołowski, 2013), they are constrained by the availability and distribution of suitable trees for excavation. As such, cavities may play an important role in population regulation through density-dependent mechanisms (Scott et al. 2002; Ram et al. 2017; Angelstam et al. 2004) related to breeding, cooperation, space use, and territoriality (Wisz et al. 2013).

Territoriality, in particular, can affect and be affected by the spatial distribution and availability of cavities for which woodpeckers compete (Adams 2001; Giuggioli et al. 2011). Territorial behavior plays out in several ways, from indirect cues (e.g. scent-marking in mammals; Giugglioli et al. 2011; Moorcroft et al. 2006) to conspecific avoidance and antagonistic interactions including displays and physical aggressions (e.g. fights with

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deadly outcomes; e.g. Soto et al. 2016). Territorial behaviors are influenced by many factors, including densities of territorial conspecifics, the proportion of floaters (i.e. wandering or dispersing individuals that do not hold a territory), and the availability of breeding mates (López-Sepulcre and Kokko 2005). As the costs of cavity construction are high and may extend anywhere from 3 months to 4 years (Ojeda 2004; VO pers. observation), the availability of existing cavities and those under construction should strongly shape space use of and interactions among territorial individuals. Choosing to nest in areas containing previous nests also might reduce the need to patrol and defend newly occupied areas (Nathan 2008). In cases where individuals develop strong preferences for the location and attributes of nesting trees, the consequences of these interactions can scale up to affect population dynamics.

In this study, we examined how the spatial configuration of nesting and roosting cavities influenced the space use and territory establishment of Magellanic woodpeckers in the SATF. Whereas our previous research indicates that tree decay affected foraging activities of the species at multiple temporal scales (Vergara et al. 2019; Soto et al. 2017), we hypothesized that space use of Magellanic woodpeckers within their territories would be largely determined by cavity locations and the proximity to neighboring families. Specifically, we expected that territories would become smaller as nesting and roosting resources improved and/or the numbers of neighboring families increased.

2. Methods

2.1 Study area

We studied two distinct populations of Magellanic woodpeckers in Patagonia's temperate forests that are mostly dominated by *Nothofagaceae* trees (Armesto et al. 2001).

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Study areas were separated by ~1500 km and represented the northern and southern range

of the Magellanic woodpecker (Fig. 1).

Fig. 3.1

The northern site, which supports roughly 8 family groups of woodpeckers (see

Ojeda & Chazarreta 2014), is a ~1200 ha area of relatively continuous *N. pumilio* forest

interspersed with native bamboo (*Chusquea* spp.) located along several ridges and steep

slopes near Bariloche, Argentina within the Challhuaco valley (41°S). Forests extend from

treeline at high elevations to pasture at low elevations and are adjacent to the Argentine

Pampa biome (~72°W).

The southern site, which supports approximately 7 family groups (Soto et al. 2012;

Soto et al. *unpublished*), is located on Navarino Island (~55°S) near the town of Puerto

Williams and it contains the world's southernmost extent of temperate forests (Rozzi et al.

2006). The site includes an area of approximately 1200 ha of mixed forests of *N. pumilio*,

N. betuloides, *N. antarctica* and *Drimys winterii* (Soto et al. 2017) with limited or absent

understory but peat bogs at low elevations and flatlands. Unlike the northern site, Navarino

Island has relatively little topography but still supports forests extending from treeline to

pasture, albeit with extensive degradation and/or deforestation along waterways due to

introduced beavers (*Castor canadensis*; Soto et al. 2012).

2.2 Study species

The Magellanic woodpecker (*Campephilus magellanicus*) is a South American

Nothofagaceae forest specialist (Short 1982). The species lives in family groups comprised

of a breeding pair and up to three immature and juveniles, defending a year-long territory of 100 ha on average (Ojeda & Chazarreta 2014, Soto et al. 2012). Movements of family groups are usually guided by the dominant male, who also segregates microhabitat from females and juveniles (Chazarreta et al. 2012; Duron et al. 2018). At the same time, use of space also should be affected the distribution of nesting, roosting, and foraging resources, the latter of which are biased towards trees with advanced decay and senescence (Soto et al. 2017). Nesting and roosting resources, on the other hand, are strongly related to the presence of large-diameter *Nothofagaceae* trees that can accommodate the large cavities (mean depth ~45 cm; Ojeda 2004).

2.3 Data surveys

Because our study occurred within the context of two complementary projects (e.g. Ojeda 2004; 2007; Soto et al. 2017), different sampling techniques were used in our two study areas.

2.3.1 Nesting and roosting cavities

Northern site. From August through May 1998-2017, we searched for the locations and characteristics of trees with roosting and/or nesting cavities within eight known woodpecker territories. Surveyors were trained to develop "search images" for cavities (sensu Dudley and Saab 2003) and actively scanned all trees to locate them. In addition to working within territories, we systematically searched for cavities in between territories. For the purpose of this study, we only inventoried roosting or nesting cavities that were present at the time of the woodpecker space use sampling (see below).

Southern site. From August to May 2012-2013, we recorded the locations and tree

characteristics of cavities that had been excavated by Magellanic woodpeckers along 40 m wide linear transects oriented in the North-South axis. The 56.3 km of linear transects, each separated by 40 m in order to observe all trees from both sides, covering the entire study area. Transects were bounded at North with the coastline, and South with an altitude of 350 m.a.s.l. were trees have diameters smaller than 40 cm, resulting on transects of different length.

Even though the conspicuous behavior of woodpeckers made us confident that sites were completely censused, we analyzed sites separately due to the different durations of fieldwork at sites and the imperfect detectability of cavities.

2.3.2 Woodpecker territories

At the northern study site, we used the data from Ojeda & Chazarreta (2014), in which family groups were followed using visual and auditory cues from dawn to dusk (07:00-20:30 hrs, +3 GMT). These observations were made during the post-reproductive period (late February to late May) for eight to nine nonconsecutive days from 2010 to 2012. Roosting locations were detected by following individuals until nightfall (further details in Ojeda & Chazarreta 2014). In order to increase our sample size, we included first-detected locations of opportunistic encounters with these known woodpeckers outside of the focal observation periods if they occurred on different days. This dataset was filtered in order to reduce spatial autocorrelation between subsequent sampled locations by subsampling locations in intervals of two hours after a test of "time to independence" (sensu Swihart & Slade 1985, see Appendix A).

At the southern study site, we recorded the locations of family groups using radio telemetry during the post-breeding season (late January to late April) of 2012 and 2013 (see

Soto et al. 2017). We captured seven adult dominant males using mist nets and while broadcasting territorial calls and a drumming device (see details in Vergara et al. 2017). Individuals were fitted with VHF transmitters (Advanced Telemetry Systems, model A1250; 11.5 g) and relocated once daily using the homing technique to avoid spatial autocorrelation, recording the locations where families were first spotted (see details in Soto et al. 2017). We also incorporated data from GPS tags from Vergara et al. (2017) corresponding to other individuals from the same studied families plus a family on the northern extent of our study area. We used an autocorrelation function on both spatial axes to sample temporally independent locations for this latter family (See Appendix A), sampling a total of 94 locations from a dataset of 417 locations.

2.3.3 Habitat features

We used radiometrically-corrected, georeferenced and orthorectified high-resolution WorldView-2 and -3 satellite images covering the total extent of both study areas. Images were acquired during the Austral Spring when the leaves of *Nothofagaceae* trees are fully flushed. We used the methods from Soto et al. (2017) to calculate the Plant Senescence Reflectance Index (PSRI). PSRI values represent the best available measure of tree decay for *Nothofagus*-dominated areas (Soto et al. 2017, Vergara et al. 2019), such that PSRI values increase with tree decay. A multi-resolution segmentation algorithm was used to identify individual tree crowns using the parameterization described in Soto et al. (2017). Subsequently, each segmented crown was assigned the mean PSRI value of all 0.5 m pixels within them in order to be used as a covariate for the models (see below). In this work, we use the term "decay" to refer to the scaled PSRI values for each of the study areas.

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2.4 Modeling

2.4.1 Spectral traits of nesting and roosting trees

In order to characterize the spatial structure of roosting/nesting cavities made by Magellanic woodpeckers, we first explored how their spectral traits summarized by the decay of trees differed from those of random trees distributed across the whole study areas. We used a homogeneous random point process to select 1000 random trees per study area. We compared the means and distributions of decay values of trees with cavities with the randomly selected trees using a t-test.

2.4.2 Spatial structure of nesting/roosting trees

We examined nest site selection by determining the extent to which nesting location was associated with proximity of neighboring cavities potentially reflecting biases on the nesting site selection process of woodpeckers (Wiegand et al. 2007).

In order to determine the best predictors of spatial clustering of nest locations was tested using the second-order Ripley's $K(r)$ score (Ripley 1988), which represents the cumulative occurrence probability of other nest locations within buffers of increasing radius r centered in a given sample of locations (i.e. the nesting/roosting trees). To explore clustering, the $K(r)$ score is computed based on a set of points generated by a point process and is graphically compared to the $K(r)$ measure generated by the desired data set (i.e. the sampled nest locations) through a plot of radius values r, versus the values of the function $K(r)$.

For this analysis, we used two sets of point processes, homogeneous and inhomogeneous. The homogeneous point process is used to describe interactions of points assuming that points are clustered only based on the proximity to other points. In contrast,

inhomogeneous point processes assume that points not only interact with each other but are also a function of spatially-explicit covariates. For the latter point process, we modeled clustering as a function of both, proximity to other nest locations and the decay of trees. This approach allows explicit incorporation of decay in our examination of the spatial clustering of nests.

2.4.3 Roosting and nesting locations as covariates

We related cavities to observed locations of woodpeckers using two complementary but distinct abstractions of spatial patterning – (1) the distance to the nearest cavities over the extent of the study area and (2) a bivariate normal distribution of cavity density. We avoided using ad-hoc methods to calculate the bandwidth or smoothing factor for the kernel estimation (e.g. Gitzen et al. 2006; Kie 2013), because this would not match the parameters for woodpecker space use and would thus provide inadequate model fit. Instead, we simultaneously estimated these distributions with the parameters derived from the use of space by individual woodpeckers (see below).

2.4.4 Response of woodpeckers to habitat features

Relationships between cavities and space use were assessed with a weighted distribution formulation of a point process model called Synoptic Model of Space Use (SMSU), originally proposed as a way to calculate space use given environmental covariates and home range or territory size (Horne et al. 2008). This model generates utilization distributions (UD, sensu Jennrich & Turner 1969) which are bivariate normal probability density functions fitted to sampled locations. We used UDs as response variables to indicate the relative proportion of time spent by individuals within defined

areas (i.e. pixels in a grid) as a function of spatial covariates (Horne et al. 2008). The model formulation is based on the calculation of a probability distribution for the UD, multiplied by a linear weighting function containing the covariates and effect parameters (often referred to as resource selection function), and then divided by a normalizing factor, forcing the previous two components to sum one over the study area, as required to become a probability distribution.

Two basic assumptions of our space use model underlie our comparisons among territories. First, and based on our knowledge of the two local populations, we assumed a fixed number of territories at each site for the study period (i.e., 8 and 7 family groups for the northern and southern sites respectively). Second, as the ecologically-relevant spatial scale for this study is the territory of individuals (3rd order; *sensu* Johnson 1980), and because territory size usually declines as habitat quality improves (Klopfer 1969), we scaled the bandwidth parameters of the nesting/roosting covariate as a function of the bandwidth of the UD estimation. Because woodpeckers behave as central-place foragers only during breeding seasons, we were unable to explicitly model seasonal changes in territory size. Accordingly, we assumed no seasonal changes in the sizes of territories and modeled the UDs under the same bandwidth parameter as if it were annual estimates, thereby removing a bias from central-place foraging strategy. Because Magellanic woodpeckers are highly territorial, we incorporated distance to the calculated centroid of neighboring families as a covariate. In cases where we lacked sufficient data to calculate a neighbor's UDs, we defined a centroid using ancillary observations of those other families. All neighboring families were observed and located at least four times.

We modeled four alternate hypotheses, represented by three groups of covariates including (1) Null model with the decay covariate only (PSRI), (2) two nesting/roosting

models with distance to nesting/roosting cavities and a bivariate kernel of nesting/roosting sites (see above), (3) a model with distance to the neighboring territory centroids, and (4) interactions models using combinations of the covariates in an additive setting.

2.4.5 Observed territory area and habitat features

We examined the contributions of territory-scale covariates on the territory sizes (2nd order habitat selection) using linear models explaining territory size with summary measures of the used spatial covariates (see above). First, territory size was calculated as the mean area of the 95% probability surface of the UD estimates for 20 random subsets of 20 locations per individual. Then, we used territory boundaries to calculate the sum and mean distance to cavities, the total number of cavities, the sum, mean and standard deviation of decay values, the proportion of non-forest cover. To link these results with the clustering of cavities, we used the ratio of the Ripley's K function value for the cavity locations and random point pattern at a radius of 500 m, as this seemingly arbitrary distance represented half of the minimum width of an average territory. Given the small sample size of 15 territories, linear models were restricted to contain a maximum of two covariates in addition to the intercept. Models were ranked and averaged using AICc values and derived model weights.

3. Results

Spectral traits of nesting/roosting trees

In both study areas, cavities were excavated in trees with lower mean decay values than of randomly sampled trees (Northern: t = -18.712, df = 752.11, p-value = 2.2e-16; Southern: t = -2.857, df = 189.03, p-value = 0.005; Figure 2). The Northern site showed a

more constrained distribution of decay values for cavity trees than the Southern site.

Fig. 3.2

Spatial structure of nesting/roosting trees

Cavity trees were strongly clustered spatially (Ripley's K [L(r) – r > 0] for any given radius; Fig. 3), indicating that new nesting cavities were established near previously excavated ones. In both study areas, clustering was unrelated to tree decay, as coefficients for the inhomogeneous point processes models were small and not statistically significant. However, both model formulations (homogeneous, and inhomogeneous point processes incorporating decay) resulted in highly clustered patterns for cavity trees in both study areas.

Fig. 3.3

Response of woodpeckers to habitat features

Results from the models explaining the observed woodpecker locations for each individual supported the hypothesis that presence of cavities promoted use by woodpeckers. Though used as a major cue for daily foraging activities (Vergara et al. 2016; 2017; 2019), tree decay was absent from the best-supported models for roughly one-third of tracked individuals (n = 5 individuals – 3 in North, 2 in South). All top models included distance to cavities, and roughly two-thirds included the territories of neighbor families (see Table 1). The negative values of the coefficients for the distance to cavities indicate that as cavity distance increases, the probability of use (or UD values) declines, with effects strongest at

the Northern site. Interestingly, only one model for a single individual included the density of cavities as a covariate, but its coefficient was not statistically significant.

Table 3.1.

Territory size and habitat features

Results from the models explaining territory size included three candidate models with delta AICc < 2 (Table 2). All models included a positive effect of non-forest land cover area on the territory size of woodpeckers (average effect estimate = 0.91, SE = 0.13) along with a second covariate that varied across models. In all cases, intercepts were close to zero (average intercept estimate = 0.00, SE = 0.08). The best model included the effect of mean tree decay with a negative effect on territory size (effect estimate = -0.37, SE = 0.08). The second model included mean distance to excavated cavities, also with a positive effect on territory size (effect estimate = 0.38, SE = 0.09). The last model included the number of neighboring families with a negative effect on territory size (effect estimate = -0.35, SE = 0.08).

Table 3.2.

4. Discussion

Legacy features of forests, like cavities, have long been recognized to influence ecological communities (e.g. Roth et al. 2014; Mazurek and Zielinski 2004; Cockle et al. 2011), particularly in cases where species cannot create the required features through their own activity (Wiebe 2011). Our results are surprising because they show that the spatial

distribution of previously excavated cavities, rather than the availability of decaying trees (i.e., trees suitable for excavation or foraging) alone, influenced space use and territory size of primary excavators. Specifically, Magellanic Woodpeckers preferentially used areas closer to, rather than farther from, existing cavities, even though they have the ability to create new cavities. A key corollary was that tree decay, which is well-known to affect space use and foraging behavior of Magellanic woodpeckers (Soto et al. 2017; Vergara et al. 2016; 2017; 2019), is not the only important feature explaining variation in size of or location of territories. Despite the relative importance of foraging substrates on the territoriality of primary cavity nesters (e.g. Kilham 1958), other woodpecker species show strong biases towards roosting and nest locations (Bull et al. 1992; Garabedian et al. 2018). A key difference between our findings and other studied species like the Red-cockeaded woodpecker (*Leuconotopicus borealis*) and Pileated woodpeckers (*Dryocopus pileatus*; Tomasevic and Marzluff 2018), is that the latter two species exhibit central-place foraging behavior, in which individuals reduce energetic costs by concentrating activities around a single location (e.g., nest) such that activity declines with increasing radial distance from that point, repeatedly returning to it after foraging in different areas (Rosenberg and McKelvey 1999). Our study shows that Magellanic woodpeckers do not bias their activities based on a single location, but instead, to multiple excavated cavities within their territories. To our knowledge, this is the first study incorporating multiple excavated cavities as explanatory features for habitat use in a woodpecker species.

We found that territory size was positively related to both non-forest cover and distance to excavated cavities, which is consistent with previous work showing that territory size is inversely related to habitat quality and competition (Cody 1981; 1985).Individuals respond to the cost and benefits of learning familiar areas (e.g. for

predation avoidance; Stamps 1995) and reducing competition (e.g. conspecific avoidance; Hyman et al. 2004). However, territories are limited by movement abilities and how quickly an individual covers the territory (Giuggioli and Kenkre 2014), with territory size being proportional to the time needed to patrol the territory (Giuggioli et al. 2011). Our results show that mean tree decay and the number of neighboring families are important predictors for territory size with a negative effect following ecological predictions. However, non-forest land cover was the most important covariate affecting territory size of Magellanic woodpeckers. Despite being a forest specialist, Magellanic woodpeckers are able to use and incorporate in their territories unique habitats (e.g., small ponds, peat bogs, rocky outcrops) and even specific structural elements in certain types of non-forest areas (e.g., areas impacted by wildfire or degraded by exotic North American beavers (*Castor canadensis*) ; Soto et al. 2012). Although beaver activity initially promotes infestation of trees by wood-boring larvae species, beaver-impacted stands are unsuitable as foraging habitat for woodpeckers over the long-term (Soto et al. 2012). Instead, Magellanic woodpeckers will continue to use standing dead trees for signaling and territory defense, as double-taps resonate especially well on snags. Scattered standing dead trees present in non-forest areas also can be useful as stepping stones facilitating the movement between forest patches.

The combined effects of excavated cavities, neighbor families and landscape features on territory size supports the hypothesis of territoriality as a limiting factor for the carrying capacity of local populations (Wolff and Cicirello 1990; Cockle et al. 2010), as found in other cavity nesters (e.g. Brown-headed Nuthatches *Sitta pusilla*; Stanton et al. 2014). The absence of the total number and clustering measures of excavated cavities as explanatory variables for territory size highlights the low relative importance of the raw

availability of cavities for territorial individuals. Magellanic woodpeckers thus seem to attribute high value to and base their decisions about territory establishment upon the presence of previously-excavated cavities (as in Pakkala et al. 2017).

Fig. 3.4.

The high degree of spatial clustering of cavities in our system provides preliminary evidence that Magellanic woodpeckers actively prefer to construct cavities in forest stands that contain previously excavated cavities. Non-uniform distribution of excavated cavities by woodpecker species is not uncommon (e.g. Black Woodpecker *Dryocopus martius*; Bocca et al. 2007), with the observed clustering of cavities denoting use and maintenance of areas used by family groups. In fact, Magellanic woodpeckers may inherit cavity clusters and territories from family members, as is suggested by previous observations (e.g. after a dominant male was predated by an introduced American mink, Jimenez et al. 2014; and after a deadly confrontation of two territorial males, Soto et al. 2016), a behavior also described in Pileated (*Dryocopus pileatus*) and Red-cockeaded woodpeckers (*Picoides borealis*) in North America (Bull and Holthausen 1993; Copeyon et al. 1991; Carrie et al. 1998). This might be an important feature for population stability, as shown by the weak variability in population sizes within two national parks (Vergara et al. 2017).

Our results also show that the availability of nesting substrate was not the main factor guiding nest-tree selection within Magellanic woodpecker territories. Interestingly, decay estimates of trees with excavated cavities were lower than available trees, thus woodpeckers might be investing on resources and not preferring "softer" trees as woodpecker literature often suggest (Conner et al. 1976; Blanc and Martin 2012), even for

this same species (e.g. Ojeda et al. 2007). Though polyporous fungi are thought to facilitate decay of trees, which may then be preferentially selected for cavity construction (Robles et al. 2007; Wesołowski and Tomialojc 1986), evidence suggests that cavities excavated in fungi-infected wood are less likely to persist over long periods than cavities in other substrates (Wesołowski 2011). This fact, along with the bias towards constructing cavities within clusters, suggests that Magellanic woodpeckers perceive and defend excavated cavities as a valuable resource. The value of excavated cavities might well be learned through social interactions (Gibson 1977; van Schaik 2010), though this requires additional study. The extended period (at least two years) of parental care of Magellanic woodpeckers prior to juvenile dispersal (Chazarreta et al. 2011, Ojeda 2004) provides opportunity for learning, as family groups seek refuge from harsh weather within excavated cavities and often perform territorial double-taps close to the entrance of excavated cavities (G.E. Soto *pers. observation*).

Our study provides evidence that legacy features, like existing cavities, are important attributes for species that are able to create them – a finding that has implications for forest management and wildlife conservation. We also show that tree decay, though an important factor in excavation (Zahner et al. 2012; Ojeda et al. 2007), is an inadequate indicator of preferred cavity trees, which were less decayed than available trees. As such, we strongly recommend that in addition to providing forest patches that exceed the mean territory size (~100 ha), managers incorporate legacy features into harvesting guidelines and best management practices, as has been done for other species like the Red-cockaded woodpecker (e.g. Carrie et al. 1998).

Contrary to the widespread belief that decayed trees are most important to breeding woodpeckers (Edworthy et al. 2012; this study), our results suggest that even healthy and

partially-decayed trees may be critical resources. Moreover, cavities excavated in trees with less advanced decay may persist much longer, especially amid forestry practices (e.g., thinning) that raise for the likelihood of windthrow (Edworthy and Martin 2013). Therefore, the retention of living trees, especially those with multiple cavities, may support the long-term persistence of woodpeckers (Cockle et al. 2011).

Acknowledgments

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Figure 3.1: Location of study areas (stars) within the distribution of the Magellanic Woodpecker (purple). Inset maps show the locations of sampled cavities (dots) and scaled tree decay estimations from satellite imagery (red indicating greater decay; see methods for description of this estimation).
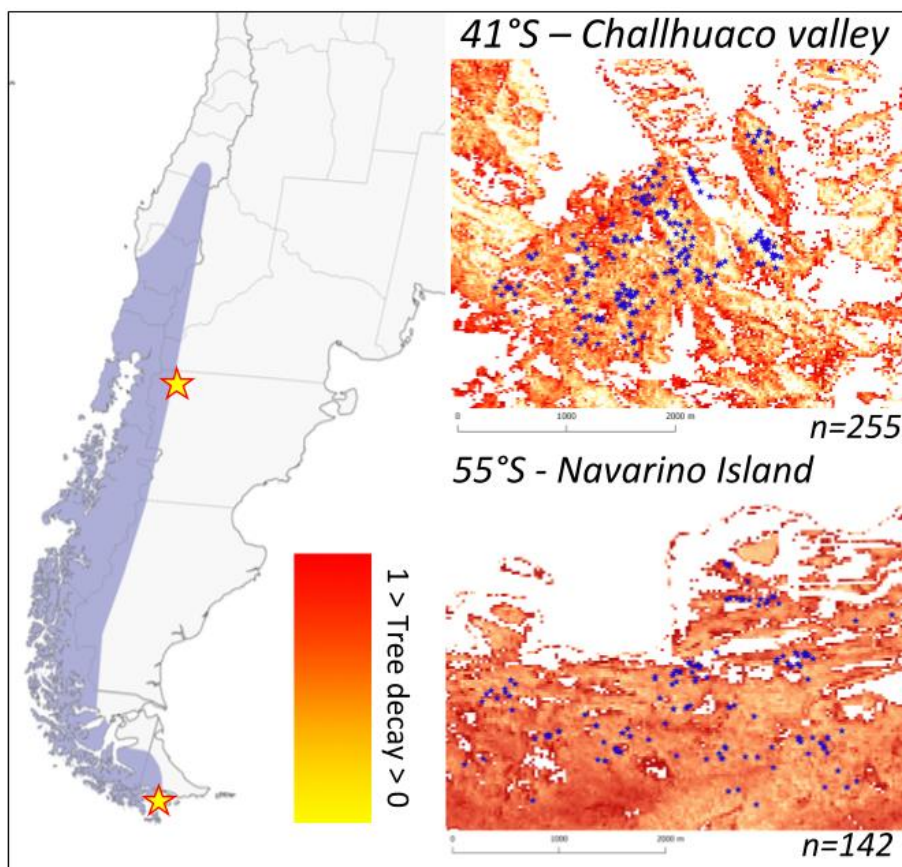
Figure 3.2: Decay values for nesting/roosting trees and randomly-selected trees for the Northern (left) and Southern (right) study areas.

Scaled PSRI values for Northern and Shouthern study areas
Codes: cav = Nesting/Roosting trees, ran = Random trees
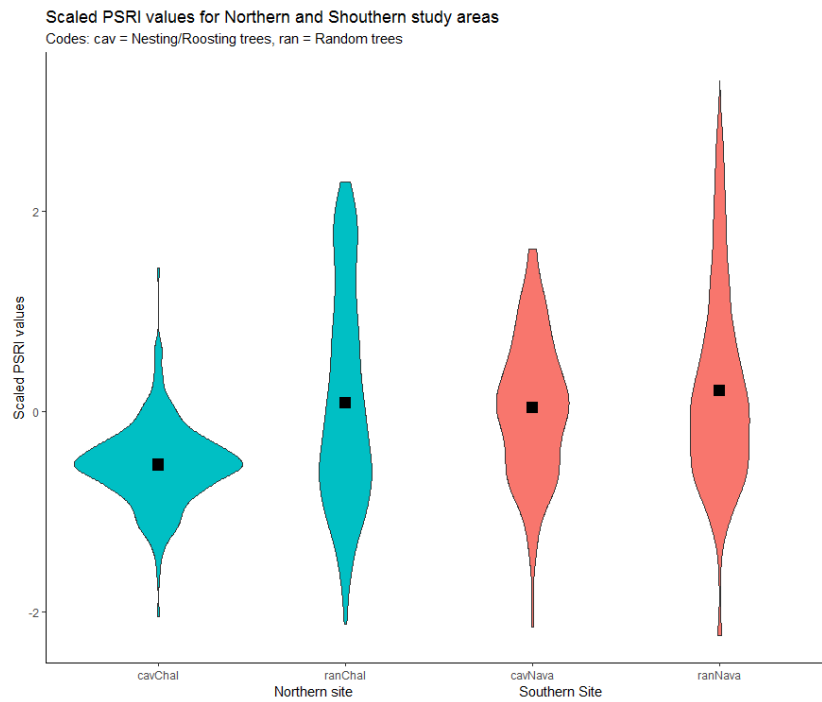
Figure 3.3: Ripley's K function estimation for the Northern (left) and Southern (right) study areas for a range of radiuses from 0 to 1000 meters. Values from data are shown in a continuous black line, values with border corrections are shown in a dashed red line, and values for a completely random point pattern are shown in a dotted green line. Values that are bigger than the random point pattern denotes clustering at a spatial scale, given by a search radius r.
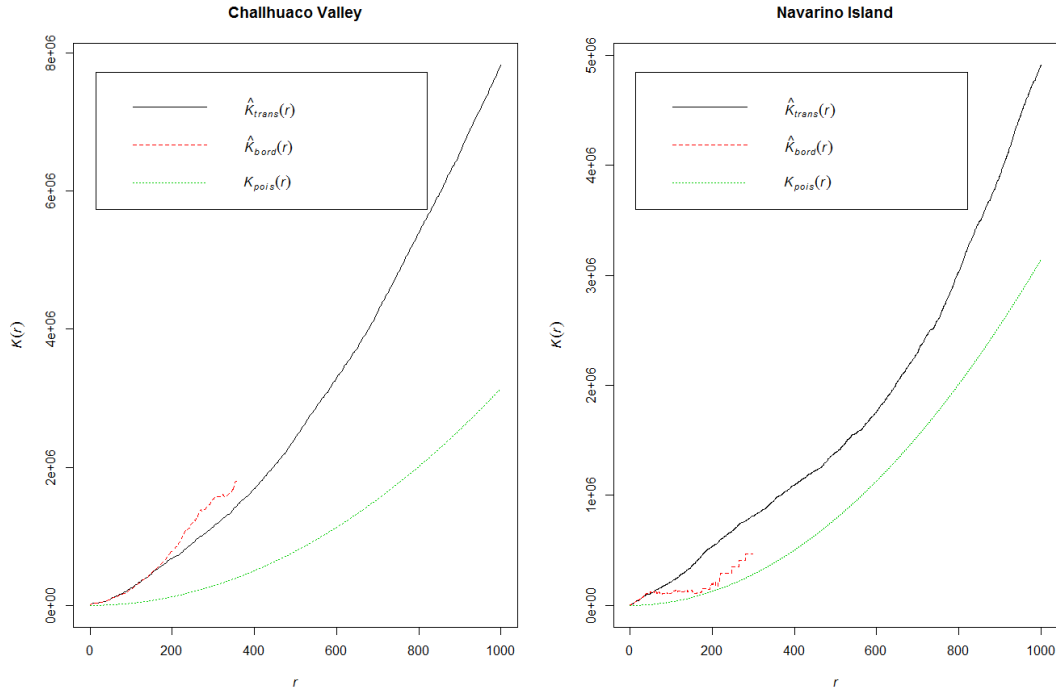
Figure 3.4: Contour plots of the best supported models shown in Table 2 showing estimated territory size (ha) as a function of two covariates. The left panel includes the mean tree decay and non-forest land cover area (ha). The center panel includes mean distance to cavities and non-forest land cover area (ha). The right panel includes the number of neighboring families and non-forest land cover area (ha). Absolute value of residuals from the models are plotted following a color scale (see legend), and labels correspond to individuals from the North (N) and South (S) study sites following codes used in Table 1.

Table 3.1: Best-supported models (Delta AIC < 2) explaining observed locations of territorial Magellanic woodpecker individuals in two separate local populations. Explanatory covariate codes correspond to cavDist = Distance to nesting/roosting cavities, cavDen = Density of nesting/roosting cavities, Decay = tree decay (PSRI value), famDis = Distance to other families.

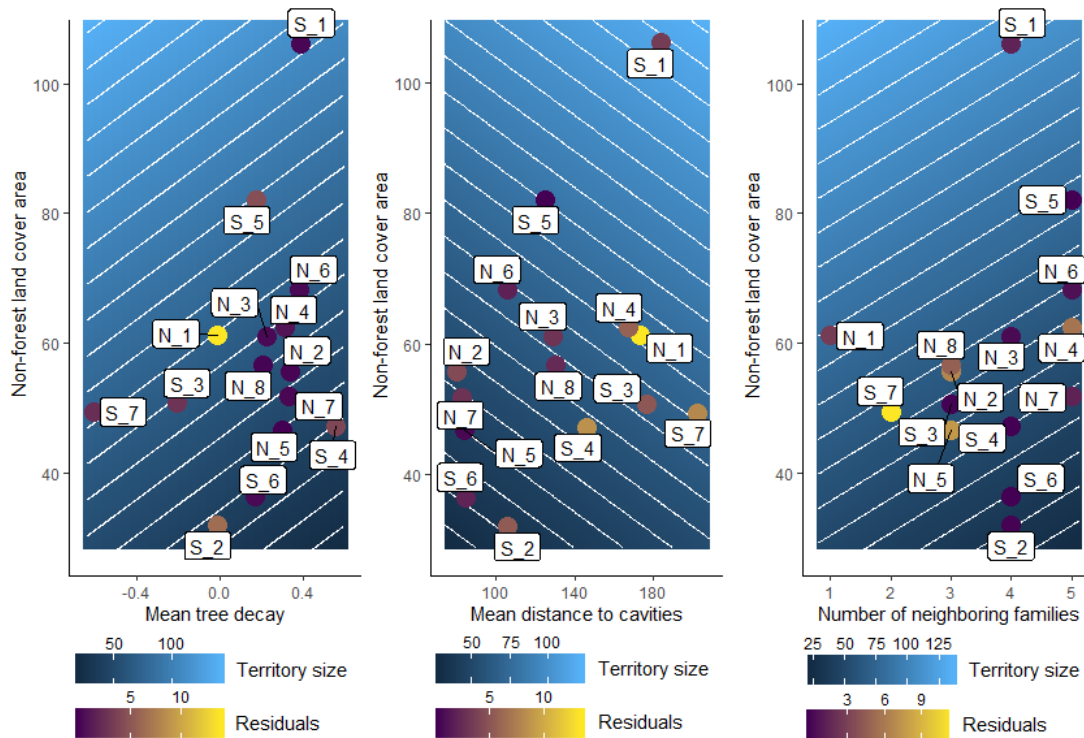| Individual	Model	Delta AIC	Covariate	Estimate	P-value
N_1	Best supported	0.000	cavDis	-7.742	<0.001
N_2	Best supported	0.000	Decay	-0.352	0.060
			famDis	1.282	<0.001
			cavDis	-8.121	<0.001
	Candidate	1.128	famDis	1.362	<0.001
			cavDis	-8.152	<0.001
N_3	Best supported	0.000	Decay	-0.313	0.232
			cavDis	-7.548	<0.001
N_4	Best supported	0.000	Decay	-0.623	0.001
			cavDis	-3.133	<0.001
N_5	Best supported	0.000	Decay	-0.596	0.033
			famDis	3.339	<0.001
			cavDis	-12.522	<0.001
N_6	Best supported	0.000	cavDis	-7.528	<0.001
N_7	Best supported	0.000	famDis	3.161	<0.001
			cavDis	-7.389	<0.001
N_8	Best supported	0.000	Decay	-1.003	0.006
			famDis	0.614	0.342
			cavDis	-6.678	<0.001
S_1	Best supported	0.000	cavDis	-2.280	<0.001
S_2	Best supported	0.000	Decay	-0.061	0.560
			famDis	0.306	0.475
			cavDis	-1.176	0.008
S_3	Best supported	0.000	Decay	0.116	0.112
			famDis	3.145	<0.001
			cavDis	-1.222	<0.001
S_4	Best supported	0.000	Decay	-0.333	0.010
			famDis	4.247	<0.001
			cavDis	-5.200	<0.001
S_5	Best supported	0.000	cavDis	-1.815	0.003
S_6	Best supported	0.000	famDis	2.811	<0.001
			cavDis	-4.089	<0.001
	Candidate	0.649	Decay	0.134	0.182
			famDis	2.790	<0.001

			cavDis	-4.136	<0.001
S_7	Best supported	0.000	Decay	-0.194	0.067
			cavDis	-1.158	0.007

Table 3.2: Best-supported models (Delta AICc < 2) explaining observed territory size of Magellanic woodpeckers in two separate local populations. Covariates used in these models represent measures at the territory-level. AICc value of best model was 16.02.

Delta AICc	Weight	Covariate	Estimate	P-value
0	0.45	Mean decay	-0.371	0.001
		Non-forest land cover area	0.992	<0.001
0.82	0.30	Mean distance to cavities	0.378	0.001
		Non-forest land cover area	0.748	<0.001
1.11	0.26	Number of neighboring families	-0.355	0.002
		Non-forest land cover area	0.962	<0.001

CHAPTER 4

THE FRUIT OF COMPETITION: SEED DISPERSAL BY MAGELLANIC

WOODPECKERS IN THE THREATENED VALDIVIAN RAINFOREST[2]

The endemic Magellanic Woodpecker (*Campephilus magellanicus*), the southernmost and

largest extant congener of the Ivory-billed woodpecker (*C. principalis*), is among the most

iconic species of the Valdivian forest ecoregion. Threatened by habitat loss and

fragmentation and with less than one-third of its original extent remaining, the Valdivian

ecoregion is one of the world's 32 biodiversity hotspots (Olson et al. 2001). Within these

forests, Magellanic Woodpeckers are foraging specialists and use their long, harpoon-

tipped tongues to extract saproxylic insect larvae from the bark and heartwood of decayed

Nothofagaceae trees. The woodpecker is not considered an important consumer of fruit or

seed disperser, though anecdotal reports indicate that birds occasionally consume

vertebrates and fruit (Willson et al., 1994; Ojeda & Chazarreta 2006). Importantly, these

previous observations did not specifically indicate if seeds were consumed intact and only

described that the woodpeckers pecked at small fruits (i.e., < 1 cm diameter) to the point of

potentially destroying seeds. Here, we provide new evidence that females and juveniles,

when competitively displaced from preferred foraging microhabitat by males, regularly

consume fruits and may act as an important seed disperser in the threatened Valdivian

forests.

During the Austral Spring (September to December) of 2015 and 2016, we

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conducted two expeditions to the center of the Valdivian ecoregion to investigate the effects of deforestation and land use changes on this bird species, assessing over 500 forest plots including surveys and focal observations of individuals when found (see Fig. 2A & B). We detected 25 social groups and directly observed 39 individuals from 20 social groups. Of these, we observed 8 individuals from different social groups (5 adult females, 2 juvenile females and 1 juvenile male) carefully handling fleshy fruits of native plant species and apparently swallowing seeds intact, thereby raising the possibility that the seeds remain viable after dispersal by birds. We observed four adult females and one juvenile female foraging on flowers and fruits of Canelo (*Drimys winteri*, see Fig. 1), one juvenile female and the juvenile male consuming fruits of Calafate (*Berberis buxifolia*), and one adult female foraging on fruits of Luma (*Amomyrtus luma*). Based on resights and GPS data from tagged individuals, we also documented fruit-consuming individuals traversing distances of up to 5 km in their daily activities. Seed dispersal during the peak fruiting period (Austral Fall) of native trees in South American temperate forests is performed primarily by small (<100 g) passerines, such as Austral thrush (*Turdus falcklandii; Turdidae)* and Fire-eyed Diucon (*Xolmis pyrope; Tyrannidae)* (Vergara et al. 2010; Morales-Paredes et al. 2018). These species typically move seeds across relatively short distances (<100 m; e.g., Núñez-Ávila et al. 2013) when foraging within forest fragments, but also are capable of transporting seeds over longer distances (100 - 400 m) when moving between forest patches (Pérez-Hernández et al., 2014; Vergara 2011; Vergara et al., 2013, 2014). Our observations suggest that Magellanic Woodpeckers have the potential to disperse and transport seeds over relatively long distances, beyond which has been described for passerines. In addition, these observations are among the first to implicate campephiline woodpeckers as potential seed dispersers.

Intraspecific competition seemed to mediate the extent to which Magellanic Woodpeckers act as seed dispersals. Like many species, Magellanic Woodpeckers sexually segregate microhabitat as a consequence of behavioral dominance by the sexually-dimorphic and much larger and aggressive males (Chazarreta et al. 2012; Duron et al. 2018). At the peak of niche segregation, most females and juveniles are competitively displaced to smaller woody substrates (e.g. branches) and to less decayed trees, or to tree species that lack relatively large wood-boring larvae (e.g. Cerambycidae) that comprise the majority of the male diet (Chazarreta et al. 2012; Duron et al. 2018). Though this segregation had been widely observed, the pattern had not yet been associated with shifts in diet and ecological roles. These foraging shifts suggest that Magellanic Woodpeckers play a previously undocumented ecological role in the Valdivian Rainforests by consuming flowers and fruits of Canelo (*Drimys winteri*, see Fig. 1), Calafate (*Berberis buxifolia*), and other non-*Nothofagaceae* species.

Knowing that Magellanic Woodpeckers move across large areas each day, we quantified potential seed dispersal distances of Magellanic woodpeckers. We used mechanistic dispersal kernel models parameterized with data from VHF and GPS tracked individuals, as part of a larger study of habitat selection and movement patterns across different geographic areas (41-55°S) (Soto et al. *unpublished*; Soto et al. 2017; Vergara et al. 2016). Although only adults were outfitted with GPS devices (>4,500 relocations), juvenile movements were also captured given that birds usually travel in family groups. We modeled seed dispersal distance based on woodpecker displacement distances predicted by state-space models fitted with relocation data. Because gut retention times of seeds (GRT; i.e., the time before regurgitation or defecation) of woodpeckers are unreported in the literature, we specified GRT in increments from 5 to 140 min in our dispersal kernel

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models. Across this range of GRT, 95% of seeds dispersed by woodpeckers were within

630 m (Fig. 2C), which is ca. 50% farther than the maximum distance predicted in southern

temperate forest of Chile and Argentina for passerines, whose GRT average 25.4 minutes

(Pérez-Hernández et al., 2014; Vergara 2011; Vergara et al., 2013). As GRT increased,

dispersal distances increased by ~20 m per each min increment (Fig. 2C). If GRT are twice

longer, seeds dispersed by females and juveniles likely travel >900 m, ca. 114% farther

than the previously studied seed-dispersing passerines in Valdivian forests (Pérez-

Hernández et al., 2014; Vergara 2011; Vergara et al., 2013).

Young woodpeckers might disperse seeds even longer distances when prospecting

or dispersing from natal sites, during which they travel across the matrix and use different

habitats; i.e., not the core nesting areas in old-growth *Nothofagaceae* forest fragments (Cox

& Kresler 2012). Based on surveys of Magellanic woodpecker signs (i.e., pecking marks),

we estimate that dispersing individuals can travel at least 100 km to reach a different local

population. Notably, many signs were found in forest remnants of mixed-*Nothofagaceae*

second-growth in the agriculture-dominated Central Valley of southern Chile and low hills

between mountain ranges – areas that are typically unsuitable for nesting (Fig. 2A). These

second-growth fragments, however, may function as regional corridors and possibly serve

as a temporary habitat for non-breeding individuals.

We further suggest the possibility that woodpeckers contribute to the maintenance

of genetic connectivity of trees within the highly fragmented Valdivian forests. That said,

we recognize that genetic diversity within these forests is primarily accounted for by

abundant bird species dispersing pollen, such as the Green-backed Firecrown (*Sephanoides

sephaniodes*) and White-crested Elaenia (*Elaenia albiceps*; Aizen et al. 2002). Our

observations provide novel insights into the potential of woodpeckers to transport seeds for

long distances in the Valdivian forest and such a seed dispersal service may depend on intraspecific competition and subsequent segregation of foraging niches between males and females/juveniles. Conceivably, seed dispersal by Magellanic Woodpeckers could affect population demography and genetic connectivity of plants in the threatened and highly fragmented Valdivian forests. A thorough assessment of seed dispersal by woodpeckers in these forests is warranted and requires the study of fruit-intake rates, GRT and post-transit seed viability, along with a characterization of natal dispersal dynamics.

Our observations underscore how our incomplete understanding of the ecology of even highly charismatic species may result in a failure to recognize their importance in maintaining ecosytems. For example, one might expect to find similar ecological roles played by other campephiline species, including the presumably extinct Ivory-billed woodpecker, that are sexually dimorphic and segregate microhabitats, especially in regions with greater plant diversity – and correspondingly more potential for symbiotic relationships – than our study system. Although natural history studies often attract less attention and funding, the current biodiversity crisis makes imperative the need to describe potentially important ecological roles provided by extant species.

Acknowledgements

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Figure 4.1. A) Map of the study area showing *Nothofagaceae*-dominated forest stands on orange and non-*Nothofagaceae*-dominated forest stand on red, with the locations of the surveyed forest plots. B) Map showing the extent of the Valdivian Ecoregion and the study area on panel A. C) Probability distributions of seed dispersal distance for gut retention times of 30, 60 and 120 min. Each curve represents the upper 95% CI from predictions based on a Weibull distribution; the colored heatmap on the base is the calculated distribution from movement data.
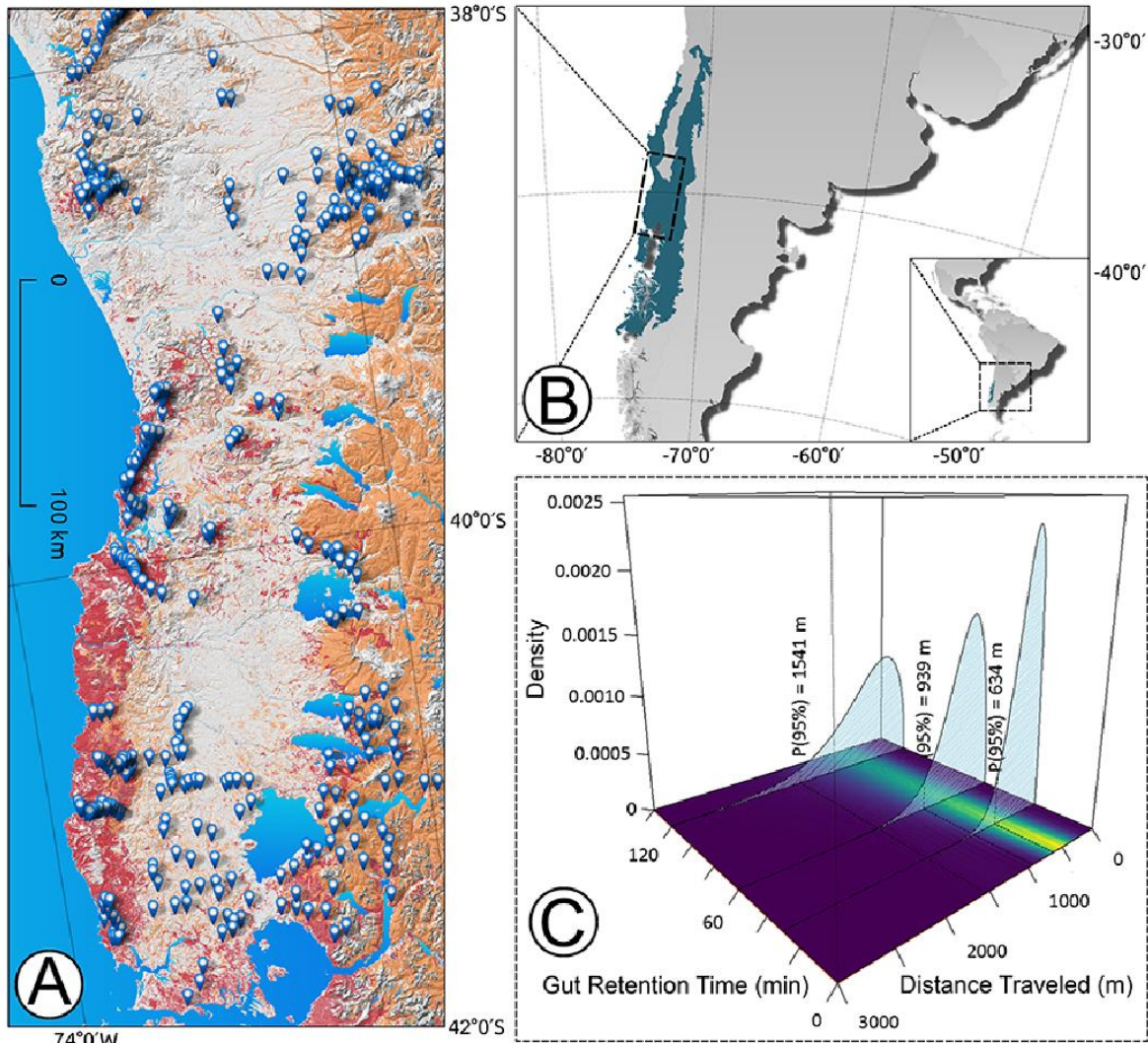
Figure 4.2. Juvenile female Magellanic woodpecker carefully removes a seed from a fruiting *Drimys winteri* before ingesting.

CHAPTER 5

DEFORESTATION AND EXOTIC AFFORESTATION IN NORTHERN PATAGONIA

AND CONSEQUENCES FOR GENETIC DIFFERENTIATION OF MAGELLANIC

WOODPECKERS

Abstract

Fragmentation and habitat loss threaten biodiversity through a wide variety of genetic and

demographic mechanisms. As landscapes change in ways that restrict movement of

individuals, populations can become isolated in ways that affect genetic and population

structure. Although deforestation (i.e., conversion of forest to non-forest habitat) is

traditionally considered to have the greatest impact on forest species, populations also can

be isolated by more nuanced shifts in the structure and composition of the landscape

matrix. Thus, afforestation by exotic plantations, which some regard as one remedy to

deforestation and fragmentation, might actually exacerbate isolation. Exotic plantations

have since transformed the South American temperate forest (SATF), particularly the

Valdivian ecoregion, being reduced to just 30% of its original extent over the last century.

Here we test the extent to which deforestation versus exotic afforestation has influenced

population structure, and specifically genetic divergence, of Magellanic woodpeckers

(*Campephilus magellanicus*) in the northern extent of the Valdivian ecoregion. Our results

showed that Magellanic woodpeckers presented low to moderate levels of population

structure in the North extent of their population, with historic deforestation as the main

driver of the observed differentiation. Our analysis provides evidence that historical land

use change contributed to current levels of differentiation – presumably by reducing

connectivity of populations, as deforestation resulted in isolated remnant forest patches within landscapes with varying levels of fragmentation and degradation. Contrary to our expectations, exotic afforestation did not explain observed genetic variation, possibly because of its relatively recent presence in the study area.

Introduction

Fragmentation and habitat loss threaten biodiversity through a wide variety of genetic and demographic mechanisms (Butchart et al. 2010; Kokko and López-Sepulcre 2006). As landscapes change in ways that restrict movement of individuals, populations can become isolated in ways that affect genetic and population structure. In some cases, isolation can facilitate adaptation to local conditions by restricting gene flow that counteracts natural selection (e.g. Stankowski et al. 2015). However, isolation may result in negative outcomes for small or remnant populations due to genetic drift and inbreeding, which can reduce genetic diversity, fitness, and evolutionary potential (e.g. Mäki-Petäys et al. 2005; Cooper and Walters 2002). The sensitivity of a species and/or population to isolation depends upon life history (e.g. dispersal, sex bias, and social behavior; e.g. Beck et al. 2008; Temple et al. 2006), behavior, interactions with other species, and environmental conditions, but usually is most prominent in habitat specialists (Daniels et al. 2000; Cooper and Walters 2002). The extent to which dispersal is constrained also depends partly on the ability of individuals to acquire and use information about environmental features and social interactions (Harris and Reed 2002; Van Houtan et al. 2007; Nathan et al. 2008).

The consequences of isolation for forest-associated species are better documented than for taxa associated with other habitats (e.g. Browne and Bowers 2004; Bierregaard

et al. 1992). Although deforestation (i.e., conversion of forest to non-forest habitat) is traditionally associated with the greatest impacts, populations also can be isolated by more nuanced shifts in the structure and composition of the landscape matrix (Rodewald and Yahner 2001; Rodewald 2003). Exotic tree plantations are one such example of a forest cover type that can restrict movement of individuals, depending upon site and species attributes (Estades and Temple 1999; Tomasevic and Estades 2008; Bremer et al. 2010 but see Brockerhoff et al. 2008). Thus, afforestation by exotic plantations, which some regard as one remedy to deforestation and fragmentation, might actually exacerbate isolation.

Exotic plantations have been expanding globally and at an average annual rate of 2.75% in temperate regions since 1990 (FAO 2015). Following a wave of political and economic reforms (Decree Law 701), exotic plantations in Chile have expanded by 3.46% annually since the mid-1980s. Exotic plantations have since transformed the South American temperate forests (SATF), particularly the Valdivian ecoregion, which is the smallest of five biodiversity hotspots in South America (~250,000 km^2 in size). After being reduced to just 30% of its original extent over the last century (Lara et al. 2005), the Valdivian rainforests are now largely restricted to mountain slopes and lack meaningful legal protection (Smith-Ramírez 2004). The northern extent of the ecoregion, which is known to support many endemic species, has the largest area of exotic plantations in Chile (>3 million ha and >17% of forest in the country; CONAF 2011).

The ecological consequences of land-use changes in the Valdivian ecoregion have not been studied extensively, making it difficult to plan and manage landscape-scale approaches to conserve biodiversity (Smith-Ramírez 2004). Previous studies demonstrate that forest degradation and loss reduce species richness and functional diversity, alter population dynamics, and impair dispersal abilities of forest specialists (Vergara and

Armesto, 2009; Ibarra et al. 2017; Ramirez-Collio et al. 2017). The ecological implications of exotic plantations at the landscape scale, however, remain poorly understood. Although recent studies have explored how within-stand characteristics affect species richness and abundance (e.g. Moreira-Arce et al. 2015; 2016; Fierro et al. 2017; 2019), determining the influence of plantations on biodiversity at landscape and regional scales remains a priority for ecological research (but see Alaniz et al. 2018; Carvajal et al. 2018).

Here we test the extent to which deforestation versus exotic afforestation has influenced population structure and genetic divergence of Magellanic woodpeckers (*Campephilus magellanicus*) in the northern extent of the Valdivian ecoregion, a region transformed by post-colonial forest loss as well as expansion of exotic plantations (Smith-Ramírez 2004, Heilmayr et al. 2016). Exotic plantations, though technically a forest cover, are not used as habitat by Magellanic woodpeckers and might actually impair the ability of individuals to visually locate isolated patches of native forest.

We modeled optimal dispersal routes and accumulated costs of moving among locations in three scenarios reflecting historical and current forest cover: 1) historical forest cover (late 1800s), 2) post-colonial forest cover (early 1970's) and 3) current forest cover with exotic plantations considered to be non-habitat. We tested the alignment of our estimated costs of dispersal with the genetic differences among subpopulations, as indicated by measures of relatedness.

Methods

We studied the Magellanic woodpecker because of its potential to serve as a flagship species for the conservation of the SATF in this ecoregion, both because of its ecological specialization and high regard by local communities (Arango et al. 2007). The

species prefers mature Nothofagaceae forests (Short 1970) and is sensitive to forest

degradation, a desired feature on indicator species to inform conservation (Mikusiński et al.

2001; Ojeda 2009; Soto et al. 2017). Socially monogamous pairs defend large territory

sizes (~100 ha) around the year, making the species a candidate for acting as an umbrella

species (sensu Roberge and Angelstam 2004). Increased interest from ecologists over the

last decade has elucidated many aspects of the species' breeding biology (Ojeda 2004;

Ojeda et al. 2007), home ranging behavior and territoriality (Chazarreta et al. 2011; Ojeda

and Chazarreta 2014; Soto et al. 2016), sexual segregation (Chazarreta et al. 2012; Duron et

al. 2018), variability of population sizes on local populations (Vergara et al. 2017), use of

information on daily movements (Vergara et al. 2016), seed dispersal (Soto et al. 2018),

and foraging ecology (Soto et al. 2017). This body of work confirms that the Magellanic

woodpecker, with the exception of isolated instances of foraging on exotic trees (M.

Saavedra *pers. communication*), does not use exotic plantations as habitat. Little is known

about its dispersal abilities or even more generally, its ecology at the landscape and

population levels.

Our research focused on the North extent of the Valdivian ecoregion between 37°

and 42° S on the Chilean territory, emphasizing two forested regions where Magellanic

woodpeckers are known to have high densities (Vergara et al. 2017). We originally selected

20 study sites located in mature forest on relatively gentle terrain and with known territorial

woodpeckers (Figure 1; Soto et al. 2018). At each site, we captured territorial adult birds

using mist-nets and decoys over a period of 3 to 5 days, in most cases. Our complementary

research at two sites within Nahuelbuta and Conguillío National Parks involved more

extensive efforts, exceeding 100 days of capture. We targeted adult territorial individuals in

adult forest based on a previous survey of territories on each site. Captures were performed

by attracting territorial males and accompanying family using a Drumming Device (a wooden box, developed to perform Campephiline territorial double knocks), a decoy and a mist net (see Vergara 2017). We collected blood samples from captured individuals by performing a venipuncture in the brachial vein (Campbell and Ellis 2007), while storing samples on FTA cards (Whatman™).

Birds were successfully captured at the following seven sites (Fig. 1): Nahuelbuta National Park (NAH; 37°47′ S 72°59′ W), Conguillío National Park (CON; 38°40′ S 71°39′ W), Icalma (ICA; 38°50′ S 71°23′ W), Huerquehue National Park (HUE; 39°08′ S 71°42′ W), Mocho-Choshuenco National Reserve (MOC; 39°56′ S 72°04′ W), Alerce Costero National Park (ACO; 40°00′ S 73°23′ W), and Alerce Andino National Park (AAN; 41°30′ S 72°35′ W). In total, we captured 41 individuals; 14 from Nahuelbuta NP (NAH), 19 from Conguillío NP (CON), one from a mature *Nothofagus pumilio* stand near the town of Icalma (ICA), one from Huerquehue NP (HUE), three from Mocho-Choshuenco National Reserve (MOC), one from Alerce Andino National Park (AAN), and one from Alerce Costero National Park (ACO).

Landscapes surrounding study sites varied widely. The Nahuelbuta National Park is considered an 'island' of 6,832 ha of a relatively continuous old-growth forest within a more extensive band heavily fragmented Valdivian forest in the Nahuelbuta mountains (CONAF 2011). The population of Magellanic woodpeckers at this National Park is the largest and most isolated (>100 km from others) in the region, we studied and is >100 km from other populations and ~90 km from the nearest patch of mature forest (Fig. 1).

The Conguillío National Park is located on the slopes of Llaima volcano (38° 41′ 45″ S, 71° 43′ 54″ W), in the Andes. It features mixed and pure forests of *Nothofagaceae* trees, and the oldest *A. Araucana* trees found in its entire distribution (Aguilera-Betti et al.

2017). Conguillío is relatively well-connected with the Andean forests in the surrounding landscapes.

Fig. 5.1

Whereas Nahuelbuta and Conguillío NPs are mostly covered by Nothofagaceae and monkey puzzle trees, the other sites were comprised by highly diverse forests that were characteristic of the Valdivian ecoregion. The habitat diversity, in part, explains the difficulty we had capturing birds at those sites.

Genetic methods

We used a reduced-representation next generation sequencing approach. We followed the protocol described in Thrasher et al. (2018) to perform a double-digest restriction site-associated DNA sequencing (ddRAD-seq) analysis, known to outperform microsatellite loci for relatedness estimations in birds. Restriction site-associated DNA sequencing techniques produce "reduced representations" of the genome for polymorphism discovery, allowing genotyping populations with a high number of markers, usually starting at a couple of hundreds, and up to thousands (Peterson et al. 2012). Following Thrasher et al. (2018), lab work consisted of the digestion of DNA with two restriction enzymes at the same genomic regions across individuals, a size-selection step, and the amplification of the library and its sequencing on Illumina HiSeq 2500. After trimming sequences to a final length of 147 bp, filtering and demultiplexing, we used the STACKS pipeline version 1.48 (Catchen et al. 2013) to conduct a denovo assembly of RAD loci as described in detail in Thrasher et al. (2018).

To understand the contribution of the historical landscape to population genetic

differentiation, we calculated genetic differentiation to be included in a regression

approach. We performed a Discriminant Analysis of Principal Components (DAPC;

Jombart et al. 2010) as an estimation of relatedness in R (*adegenet* package; Jombart et al.

2008). DAPC differs from other approaches in that it optimizes the variance between

groups of individuals (as in Principal Component Analysis; PCA) while minimizing the

variation within groups (unlike PCA). DAPC also provides an alternative to assess

population genetic structure (Jombart et al. 2010). For this section of the study, we selected

two principal components (PC), because of our small sample size and because regardless of

the number of PCs selected, the first two PCs always explained most of the variation. The

contribution of individual alleles is measured by the so-called loadings, which act as

weights in the Discriminant Analysis (DA). The resulting loadings from the DAPC

performed in this study can be found in Figure A1. The output of this model also allows

calculating the posterior distributions of the probabilities of individuals to belong to each

sampled population. For this analysis, we only used 1092 loci, which resulted from using

trim lengths of 147 base pairs, 80% missing data; 5% minimum minor allele frequency, and

a stack depth of 10 for the assembling STACKS pipeline. In total, we used 38 samples

corresponding to adult woodpeckers. We did not include juveniles because they can

potentially induce unwanted biases on within-population variabilities due to their high

relatedness values.

Landscape abstractions

We used different data sources to characterize the landscapes explaining the genetic

differentiation of woodpeckers. For the late 1800's forest cover, we used the reconstruction

of forest cover by Lara et al. (2012), based on Luebert et al (2006), and refined by Carvajal et al. (2018), which are based on bioclimatic modeling, historical inventories and chronicles. For the early 1970's forest cover and present land cover including exotic plantations, we used the National forest inventory (CONAF 2011).

In order to link the historical landscape changes to the genetic differentiation of the population through limited dispersal, we performed simulations of propagating radial waves with travel cost surfaces, an agent-based model that outperform least-cost path models in the abstraction of motion through the geographical space when using resistance gridded layers (Tomlin 2010). This model resembles the gradient fields resulting from velocity-based movement modeling (Hanks et al. 2011). We performed these simulations using Google Earth Engine^{TM} (Gorelick et al. 2017), using resistance layers corresponding to each of the landscapes representing historical transformations (see above). The scenarios included the pre-settlement native forest extension with each pixel given a resistance value of one, and a high value of 10 to non-habitat open areas. The early 1970's scenario including extensive deforestation, corresponding to the period prior to the expansion of exotic plantations with the same values as the previous scenario. And the last scenario, corresponding to the extent of exotic plantations at the time of the genetic sampling, with conservative values of resistance for exotic plantations of 2, which is comparatively bigger than native forest, as these plantations do not contain the same food resources as native forests and completely lacks natural or excavated cavities that allow woodpeckers to refuge.

We calculated the accumulated cost distances between populations with each population modeled as a source population under the three landscape scenarios. With these results, we created symmetric matrices of accumulated cost between populations. We

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compared these matrices to the symmetric matrices of genetic relatedness from the previous

DAPC analysis through Generalized Linear Mixed Models (GLMM), with the source

populations as random effects in order to account for within-population variability on the

explanatory variables.

Results

The results from the DAPC analysis showed that individuals from the Nahuelbuta

(NAH) population differed genetically from all other samples, with the first principal

component explaining most variation (Fig. 2), resulting in two main clusters. The

proportion of variance accounted for by principal components was 13.7%, with eigenvalues

of 60.5 and 0.3. Posterior membership probabilities to the sampled populations were mixed

for individuals outside of Nahuelbuta (NAH; Fig. 3), with most individuals showing >15%

membership probability to Conguillío population (CON). Behind Nahuelbuta and

Conguillío, the two individuals from Mocho-Choshuenco (MOC) had the highest

probabilities of membership for its own population (42 and 22%). Populations surrounded

by mixed broadleaf forests (ANN and ACO), showed mixed probabilities with two

individuals above 10% for membership to Mocho-Choshuenco. One interesting aspect is

the apparent similarity between the individuals from AAN and MOC with high levels of

admixture. Also, individuals from ACO and MOC show a lower membership probabilities

for CON than individuals from HUE and ICA. However, individuals from ACO shows

higher memberships probabilities for Conguillío population (CON) than individuals from

AAN and MOC.

Fig. 5.2.

Links between genetics and landscape

GLMMs linking accumulated cost distances between populations under the three modeled landscape scenarios with their genetic differences are presented in Table 1. The model using the effects of historic deforestation on woodpecker movements performed better in explaining the genetic differences. An alternate model containing exotic plantations received little support.

Table 5.1.

Discussion

The increased resolution of next-generation sequencing techniques have improved our understanding of population differentiation across landscapes (Toews et al. 2016; Saenz-Agudelo et al. 2015). Here we show low to moderate levels of population structure in the Northern extent of the range of Magellanic woodpeckers (Fig. 2), with historic deforestation as the main driver of the observed differentiation (Table 2). Our investigation suggests high levels of gene flow between samples, with the exception of the isolated population at Nahuelbuta National Park. Little evidence of population genetic structure was found among Andean populations, as high levels of admixture suggested that populations remained connected in the still highly-forested region. Instead, individuals from Nahuelbuta differed genetically from other populations.

Our findings suggest that historical land use change contributed to current levels of differentiation – presumably because extensive deforestation reduced connectivity among forest remnants. The Nahuelbuta population was severely affected by deforestation, with an

open area of ~90 km between the closest patches of mature forest, located in the Andes. The few remnant native forests in the region were predominantly surrounded by agricultural land without trees (Lara et al. 2005; 2012). Despite being a large bird (~350 g; Sutherland et al. 2000), Magellanic woodpeckers are not adapted for long-distance flights, which would require large amounts of energy to perform in such a deforested environment.

Interestingly, afforestation by exotic plantations was not a supported explanatory variable for the observed genetic variation. Although recent levels of exotic afforestation would presumably help restore connectivity in previously-deforested landscapes for forest specialists, exotic plantations are not comparable to native forests in terms of floristic composition, structure, and resources (Carnus et al. 2006). Since the 1970s exotic plantations have been planted throughout the range of the woodpecker (see Fig. 1), with Nahuelbuta being surrounded by the most extensive exotic plantations. The contrast of our findings with those from parallel studies showing that exotic plantations were movement barriers to woodpeckers in the same region (Soto et al. *unpublished*; Soto et al. 2018) raises the possibility that insufficient time has elapsed to detect population structure, especially for a species with long generation times.

Methodological reasons also may explain our failure to detect genetic structure among northern populations. First, our small sample sizes outside of Conguillío and Nahuelbuta National Parks prevented us from using standard measures of genetic structure such as F_{st} or Phi_{st} (Wright 1965). Second, Nahuelbuta is the only population (to our knowledge) surrounded by exotic plantations, in contrast to northernmost local populations that are bounded by exotic plantations only on the western side, which impacts connectivity less given the North-South orientation of the Andes and remnant habitat patches. Given these constraints, we used a spatially–explicit model to account for the effects of exotic

plantations on the landscape connectivity between local populations of Magellanic

woodpeckers using samples from local populations in a landscape with a gradient of exotic

plantation cover.

We show that the only affected population by deforestation and consequent

isolation examined here is Nahuelbuta. A recent proposal to declare the Nahuelbuta

mountain range as a Biosphere reserve represents an opportunity for a better future for

biodiversity in this landscape. As Pewen (*Araucaria araucana*) populations in this

mountain range are also genetically distinct from other local populations on its distribution

(Bekessy et al. 2002; Ruiz et al. 2007), other endangered species also share space in this

isolated mountain range, including the critically endangered Darwin's fox (*Lycalopex*

fulvipes) and Queule trees (*Gomortega keule*; Yahnke et al. 1996). Conserving these forests

have the potential to protect many other species, including broadleaf tree species, which are

critical for cavity-nesting vertebrates (Cockle et al. 2019). The proposal of a Biodiversity

Reserve becomes clearly beneficial when we account for the fact that the Nahuelbuta

National Park legally protects just 31% of the extent of the mature forest in the range

(3,720 ha) with more than 60% (40,936 ha) belonging to private timber companies. The

pattern of genetic structure presented here provides a basis for considering Nahuelbuta to

be a separate unit for conservation of the Magellanic woodpecker in North Patagonia.

Acknowledgments

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Figure 5.1: Map of the study area including the locations where captures were attempted (dotted circles) and locations were blood samples were collected with their respective name codes used along the manuscript (in black). Native forest corresponds to purple areas, exotic plantations to light brown, and other land covers in grey. Lakes and the Pacific Ocean are represented in blue and light blue, respectively.
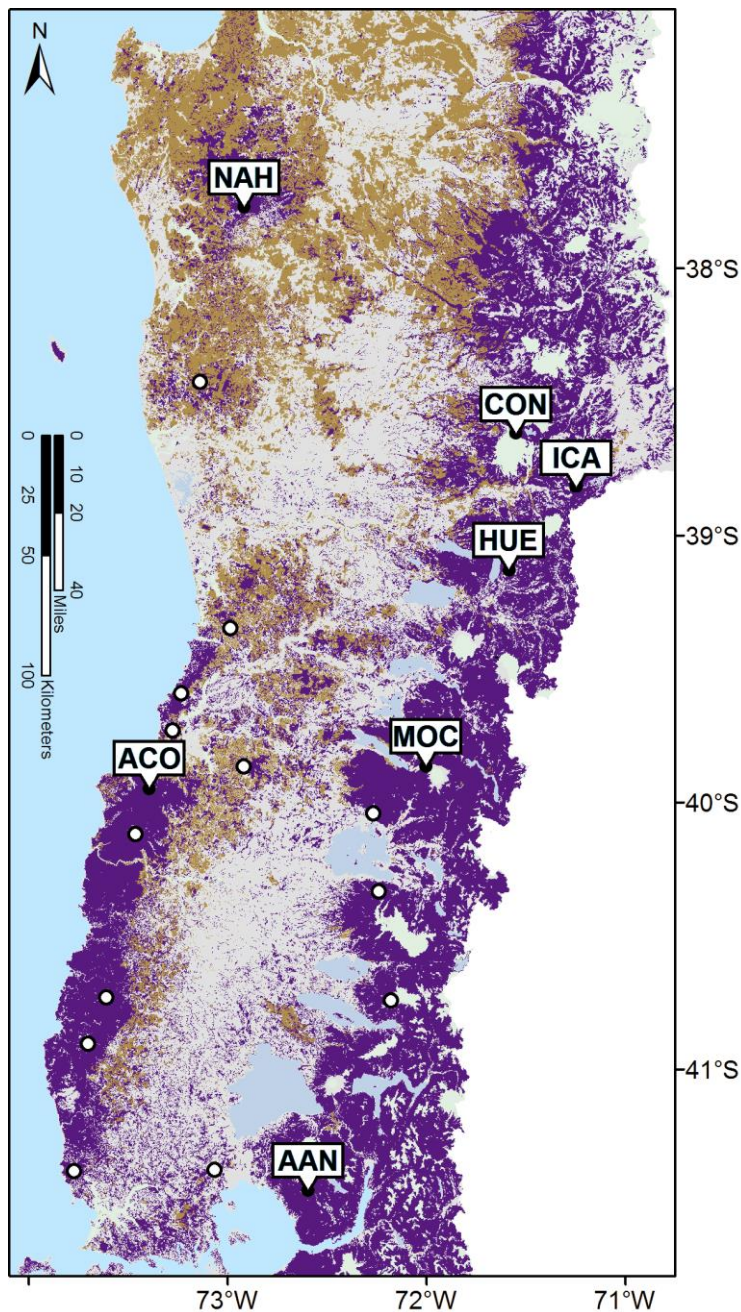
Figure 5.2: Discriminant analysis of principal components (DAPC) of seven Magellanic woodpecker sample regions. See Figure 1 for geographic reference of coded sites. Membership probabilities of each sampled individual to every sampled local population, calculated from the Discriminant Analysis of Principal Components (DAPC) analysis. Local populations are colored following the codenames used in the text. Lower panel shows clustered individuals into two groups approximately.
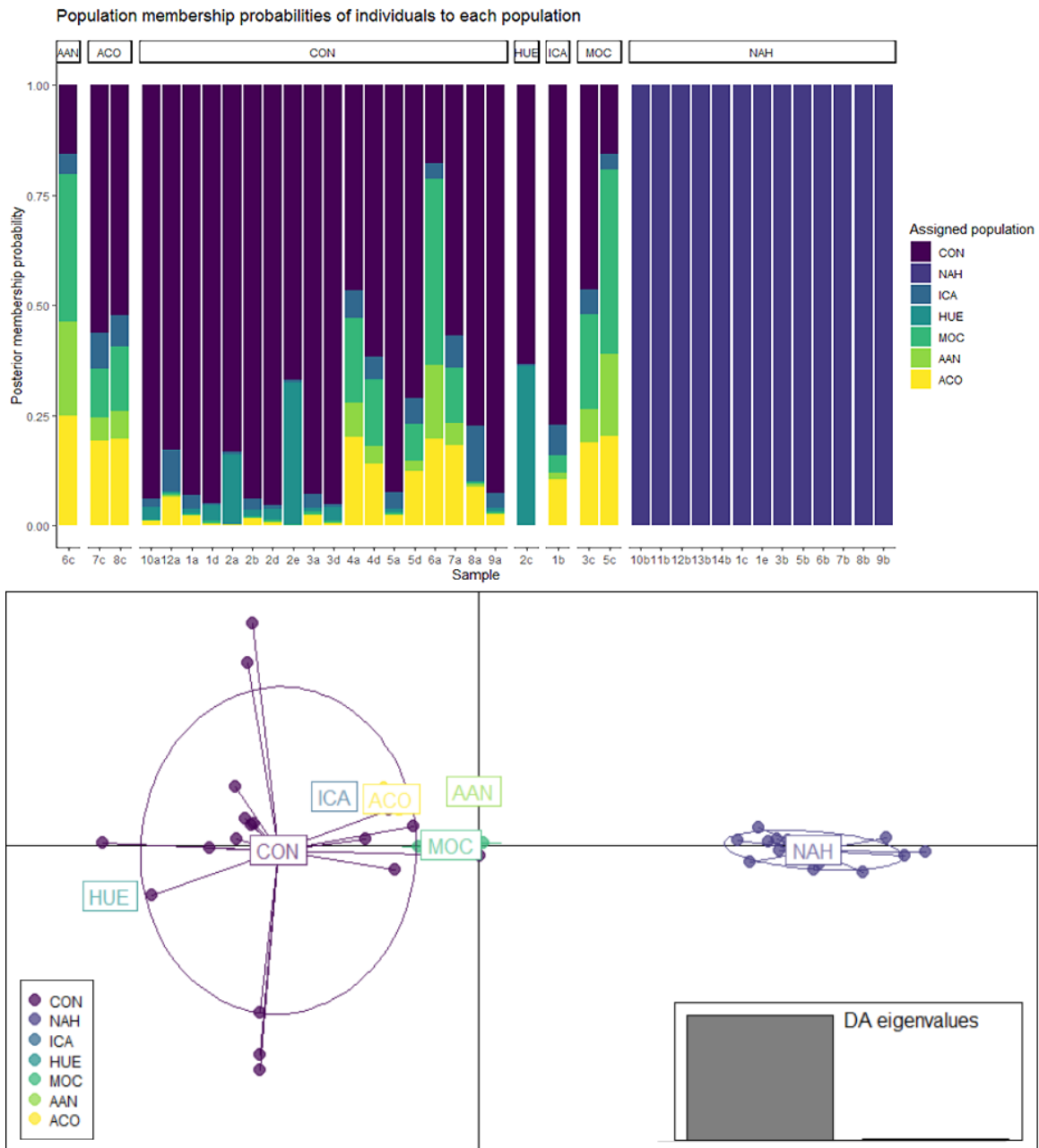
Table 5.1: Generalized linear mixed models with the three proposed hypotheses including geographic distance, historic deforestation and historic deforestation with plantations, explaining the pairwise relatedness of individuals as a measure of genetic differentiation.

Model	AIC	Delta AIC	Intercept	Intercept P-value	Coefficient	Coefficient P-value
Distance	2152.947	85.629	-0.137	<0.001	0.303	<0.001
Deforestation	2067.318	0	-0.067	<0.001	0.463	<0.001
Def. + Plantations	2140.258	72.940	-0.044	<0.001	0.337	<0.001

Description of Synoptic Model of Space Use (Extract from Horne et al. 2008)

Similar to Manly et al. (1974, 2002:77) our model structure is based on the idea that there is a proportional change in use of an area attributable to each environmental covariate. First, we set $f_0(x)$ as the null model of space use in the absence of any effect from environmental covariates. The null model is chosen to describe the utilization distribution resulting from the behavioral and spatial processes in aggregate that give rise to an animal's home range. For example, $f_0(x)$ could be a bivariate normal distribution characterizing the space use of an animal that biases movements towards a central place (Dunn and Gipson, 1977, Okubo, 1980) or the exponential power model that allows for a more uniform distribution of space use (Horne and Garton, 2006).

Next, we assume a proportional increase or decrease in $f_0(x)$ caused by a spatially explicit environmental covariate where $H(x)$ is a function describing the environmental covariate. In the case of categorical variables, $H(x)$ can be an indicator function with $H(x) = 1$ if x is within the category type and 0 otherwise. For continuous covariates, $H(x)$ can equal the value of the environmental variable at position x, suggesting a linear relationship between the proportional change and the value of the variable or be some function of the environmental variable for non-linear relationships. Thus, a synoptic model describing the utilization distribution that incorporates a proportional increase or decrease in f0(x) caused by including one covariate is:

Eq. (1)

$$s(x) = \frac{f_0(x) + \beta H(x) f_0(x)}{\int_x [f_0(x) + \beta H(x) f_0(x)]}$$

where β is an estimated selection parameter controlling the magnitude of the effect. To ensure s(x) ≥ 0 (i.e., non-negative probability) and integrates to one, we set β ≥ −1 and standardize H(x) to range from 0 to 1.

For models with multiple interacting covariates, we assume that any additional covariate results in a proportional change in the utilization distribution. Thus, for i = 1 to k covariates the synoptic model of space use is:

Eq. (2)

$$s(x) = \frac{f_0(x) \prod_{i=1}^{k}(1 + \beta_i H_i(x))}{\int_x \left[f_0(x) \prod_{i=1}^{k}(1 + \beta_i H_i(x)) \right]}$$

The denominator of Eq. (2) is the normalizing factor for a weighted distribution (Patil and Rao, 1978, Lele and Keim, 2006) and for most combinations of initial models and environmental covariates will be analytically intractable. As an approximation, we suggest dividing the landscape into m discrete grid cells and calculating:

$$A \sum_{j=1}^{m} \left[f_0(x_j) \prod_{i=1}^{k}(1 + \beta_i H_i(x_j)) \right] \approx \int_x \left[f_0(x) \prod_{i=1}^{k}(1 + \beta_i H_i(x)) \right]$$

where A is the area of each grid cell. Instead of calculating the approximation across the entire landscape, the extent of the grid can be fixed to incorporate nearly all (e.g., >0.99) of

the cumulative probability.

The synoptic model s(x) is a probability density function with parameters describing the null model of space use f0(x), symbolized by θ, and the k-dimensional vector of selection parameters β describing the selection for or against environmental covariates. These parameters can be estimated for a given a set of q = 1 to n observed locations xq by maximizing the log-likelihood function

Eq. (3)

$$L(\theta, \beta) = \sum_{q=1}^{n} \ln \left[\frac{f_0(x_q|\theta) \prod_{i=1}^{k}(1+\beta_i H_i(x_q))}{\int_x \left[f_0(x|\theta) \prod_{i=1}^{k}(1+\beta_i H_i(x)) \right]} \right]$$

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Table S1. Summary of the satellite data used for habitat quality assessment: Data acquisition details, and Main codes and resolutions of bundle modality (panchromatic + 8-band multispectral) for WorldView-2 imagery (Updike & Comp, 2010).

Data acquisition			
Date	Sunday, 06 November 2011		
Time	14:34:07 GMT+4		
Sun Azimuth	36.3°		
Sun elevation	46.7°		
Cloud cover	0.102%		
Coordinate system	Projection UTM, datum WGS 84, zone 19 S		
Band	Radiometric res.	Spatial res. (m)	Spectral res. (nm)
(Pan) Panchromatic		0.5	450-800
(C) Costal			400-450
(B) Blue			450-510
(G) Green			510-580
(Y) Yellow	16 bits per pixel	2.0	585-625
(R) Red			630-690
(Re) Red edge			705-745
(NIR1) Near Infrared 1			770-895
(NIR2) Near Infrared 2			860-1040

Table S2. List of the 102 Vegetation Indices (VI) used in the assessment of habitat quality for Magellanic woodpeckers with its corresponding formulae. Red-edge VI are listed first and codes for bands follows Table S1.

Vegetation Index	Formulae
Blue Ratio	(R-B)×(G/B)×(Re/B)×(NIR1/B)
Canopy Chlorophyll Content Index	((NIR2-Re)/(NIR2+Re))/((NIR2-R)/(NIR2+R))
Chlorophyll Red-edge	(NIR1/Re)^(-1)
Chlorophyll Index Red-edge	NIR2/Re-1
Datt4	R/(G×Re)
Datt6	NIR2/(G×Re)
Leaf Chlorophyll Index	(NIR1-Re)/(NIR1+R)
Maccioni	(NIR1-Re)/(NIR1-R)
Normalized Difference NIR/Red-edge Normalized Difference Red edge	(NIR2-Re)/(NIR2+Re)
Plant Senescence Reflectance Index	(R-B)/Re
Red Ratio	(NIR1/R)×(G/R)×(NIR1/Re)
Red-edge NDVI	(NIR1-Re)/(NIR1+Re)
Red-edge YELLOW Ratio	(Re-Y)/(Re+Y)
Simple ratio 440/740	C/Re
Simple ratio 690/740 Fluorescence ratio2	R/Re
Simple ratio 710/420	Re/C
Simple ratio 710/670	Re/R
Simple ratio NIR/Red-edge	NIR2/Re
Vegetation Index based on Red-edge	(10000×NIR1)/((Re)^2)
Vegetation Index based on Red-edge 2	NIR1/Re
Visible Atmospherically Resistant Index Red-edge	(Re-R)/(Re+R)
Ashbum Vegetation Index	2.0×NIR2-R
Atmospherically Resistant Vegetation Index	(NIR1-R+B-R)/(NIR1+R-B+R)
Atmospherically Resistant Vegetation Index 2	(-0.18)+1.17×(NIR-R)/(NIR2+R)
BLUE-Wide dynamic Range vegetation Index	(0.1×NIR2-C)/(0.1×NIR2+C)
Chlorophyll GREEN	(NIR1/G)^(-1)
Chlorophyll Vegetation Index	NIR2+R/G^2
Chlorophyll Index Green	NIR2/G-1
Coloration Index	(R-C)/R
Difference 800/550	NIR1-G
Difference Vegetation Index	(2×NIR1-R)-(G-B)
Difference NIR/GREEN Difference Vegetation Index	NIR2-G
Enhanced Vegetation Index	2.5×(NIR2-R)/(NIR2+6×R-7.5×C+1)
Enhanced Vegetation Index 2	2.4×(NIR2-R)/(NIR2+R+1)
GREEN Atmospherically Resistant Vegetation Index	(NIR2-G+C-R)/(NIR2-G-C+R)
Greenness Index 2	(B×-0.2848+G×-0.2434+R×-0.5436+NIR1×0.7243+NIR2×0.0840)×5
GREEN-RED NDVI	(NIR2-G-R)/(NIR2+G+R)

GREEN-RED Ratio	$(G-R)/(G+R)$
GRENN-BLUE NDVI	$(NIR2-G-C)/(NIR2+G+C)$
Infrared percentage vegetation Index	$(NIR2/(NIR2+R))$
Intensity	$(1/30.5)\times(R+G+C)$
Modified Chlorophyll Absorption in Reflectance Index 1	$1.2\times(2.5\times(NIR1-R)-1.3\times(NIR1-G))$
Modified NDVI	$(NIR1-R)/(NIR1+R-2\times C)$
Modified Simple ratio	$(NIR1-C)/(R-C)$
Modified Simple Ratio 670,800	$(NIR1-R-1)/(NIR1/R+1)^2$
Modified Soil Adjusted Vegetation Index	$(2\times NIR2+1-((2\times NIR2+1)^2-8\times(NIR2-R)))^2/2)$
Modified Soil Adjusted Vegetation Index hyper	$(0.5)\times((2\times NIR1+1)-((2\times NIR1+1)^2-8\times(NIR1-R)))^2$
Modified Triangular Vegetation Index1	$1.2\times(1.2\times(NIR1-G)-2.5\times(R-G))$
NIR-RED-YELLOW Ratio	$NIR1/(R+Y)$
NIR-YELLOW Ratio	$(NIR2-Y)/(NIR2+Y)$
Normalized Difference 550/450 Plant Pigment ratio	$(G-C)/(G+C)$
Normalized Difference 680/430 Normalized Pigment Chlorophyll Index	$(R-C)/(R+C)$
Normalized Difference 800/500 Pigment specific normalized difference C1	$(NIR1-B)/(NIR1+B)$
Normalized Difference 800/550 Green NDVI hyper 2	$(NIR1-G)/(NIR1+G)$
Normalized Difference NIR/BLUE BLUE-Normalized Difference Vegetation Index	$(NIR2-C)/(NIR2+C)$
Normalized Difference NIR/GREEN NDVI	$(NIR2-G)/(NIR2+G)$
Normalized Difference NIR/Red Normalized Difference Vegetation Index, Calibrated NDVI-CDVI	$(NIR1-R)/(NIR1+R)$
Normalized Difference Red/Green Redness Index	$(R-G)/(R+G)$
Normalized Difference Vegetation Index	$(NIR1-R)/(NIR1+R)$
Normalized Difference Vegetation Index 690-710	$(NIR2-R)/(NIR2+R)$
Normalized Green/Red Difference Index, Visible Atmospherically Resistant Index GREEN	$(G-R)/(G+R)$
Normalized NIR	$NIR1/(NIR1+R+G)$
NormNIR	$NIR2/(NIR2+R+G)$
NormR	$R/(NIR2+R+G)$
Optimized Soil Adjusted Vegetation Index	$(1+0.16)\times(NIR1-R)/(NIR1+R+0.16)$
PanNDVI	$(NIR2-G-R-C)/(NIR2+G+R+C)$
Ratio Vegetation Index	$NIR1/R$
RDVI2	$(NIR1-R)/(NIR1+R)^2$
RED-BLUE NDVI	$(NIR2-R-C)/(NIR2+R+C)$
Reflectance at the inflexion point	$(R-NIR1)/2$
Renormalized Difference Vegetation Index	$(NIR1-R)/(NIR1+R)^2\times 0.5$
Shape index	$(2\times R-G-C)/(G-C)$
Simple ratio 450/550 Blue Green pigment index	C/G
Simple ratio 520/420	G/C
Simple ratio 550/800	$G/NIR1$
Simple ratio 560/658 GRVI hyper	G/R
Simple ratio 605/420	Y/C

Simple ratio 605/670	Y/R
Simple ratio 683/510	R/B
Simple ratio 695/800	R/NIR1
Simple ratio 700	1/R
Simple ratio 800/500 Pigment specific simple ratio C1	NIR1/B
Simple ratio 800/960	NIR1/NIR2
Simple ratio 810/560 Plant Biochemical Index	NIR1/G
Simple ratio 833/658	NIR1/R
Simple ratio NIR/G	NIR2/G
Simple ratio NIR/RED Difference Vegetation Index, Vegetation Index Number (VIN)	NIR2/R
Simple ratio pigment Index	C/R
Simple ratio red/blue iron oxide	R/C
Simple ratio red/green red green ratio	R/G
Simple ratio REED/NIR Ratio Vegetation Index	R/NIR2
Soil adjusted Vegetation Index	(NIR1-R)/(NIR1+R+0.5)×(1+0.5)
Soil and atmospherically Resistant Vegetation Index 2	2.5×(NIR2-R)/(1+NIR2+6×R-7.5×C)
Soil and atmospherically Resistant Vegetation Index 3	(1+0.5)×(NIR1-R)/(NIR1+R+0.5)
Soil background line	NIR2-2.4×R
Structure Intensive Pigment Index1	(NIR1-C)/(NIR1-R)
Structure Intensive Pigment Index3	(NIR1-B)/(NIR1-R)
Surface Albedo	(((Y+R)×0.35)/2)+((0.7×(NIR1+NIR2))/2)-0.69
Transformed Vegetation Index	((((R-G)/(R+G)))+0.5)^2
Visible Atmospherically Resistant Index Green	(G-R)/(G+R+B)
Wide Dynamic Range Vegetation Index	(0.1×NIR2-R)/(0.1×NIR2+R)

Table S3. Confusion matrix showing the accuracy of individual classes for the pixel-based supervised classification. The sampled ground-truth points were 336, while 291 were the coincident points, with an overall accuracy of 86.6%.

		OgNb	IgNb	SpNb	OgNp	ScNpNa	SpNp	OgNa	Pt	Pg	Sh	Wt	Bl	Ua	Cs	Sd	Total	Fc (%)	Commission (%)
								Ground truth reference data											
Classification results	OgNb	30	6	0	1	0	0	1	0	0	0	0	0	0	0	0	38	78.95	21.05
	IgNb	1	19	1	0	0	0	0	0	0	0	0	0	0	0	0	21	90.48	9.52
	SpNb	2	0	16	0	0	0	0	0	0	0	0	0	0	0	0	18	88.89	11.11
	OgNp	2	0	0	21	4	3	5	0	0	0	0	0	0	0	0	35	60.00	40.00
	ScNpNa	0	0	0	2	14	0	0	0	0	0	0	0	0	0	0	16	87.50	12.50
	SpNp	0	1	2	1	0	22	0	0	0	0	0	0	0	0	0	26	84.62	15.38
	OgNa	0	1	0	3	0	0	26	0	0	0	0	0	0	0	0	30	86.67	13.33
	Pt	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	18	100.00	0.00
	Pg	0	0	0	0	0	0	0	0	13	0	0	0	0	0	0	13	100.00	0.00
	Sh	0	0	0	1	0	0	0	1	2	27	0	1	0	0	0	32	84.38	15.63
	Wt	0	0	0	0	0	0	0	0	0	0	13	0	1	0	0	14	92.86	7.14
	Bl	0	0	0	0	0	0	0	1	0	0	0	17	0	0	0	18	94.44	5.56
	Ua	0	0	0	0	0	0	0	0	0	0	0	0	19	0	1	20	95.00	5.00
	Cs	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	16	100.00	0.00
	Sd	0	0	0	0	0	0	1	0	0	0	0	0	0	0	20	21	95.24	4.76
	Total	35	27	19	29	18	25	33	20	15	27	13	18	20	16	21	336	-	-
	Fp (%)	85.71	70.37	84.21	72.41	77.78	88.00	78.79	90.00	86.67	100.00	100.00	94.44	95.00	100.00	95.24	-	-	-
	Omission (%)	14.29	29.63	15.79	27.59	22.22	12.00	21.21	10.00	13.33	0.00	0.00	5.56	5.00	0.00	4.76	-	-	-

Figure S1. RGB band combinations showing the three steps of the decorrelation stretch on a WorldView-2 image; A) Red-Green-Blue original reflectance composition, B) decorrelated Red-Green-Blue composition, and C) contrast-enhanced Red-Green-Blue composition (note the resultant bright yellow for sapling trees).
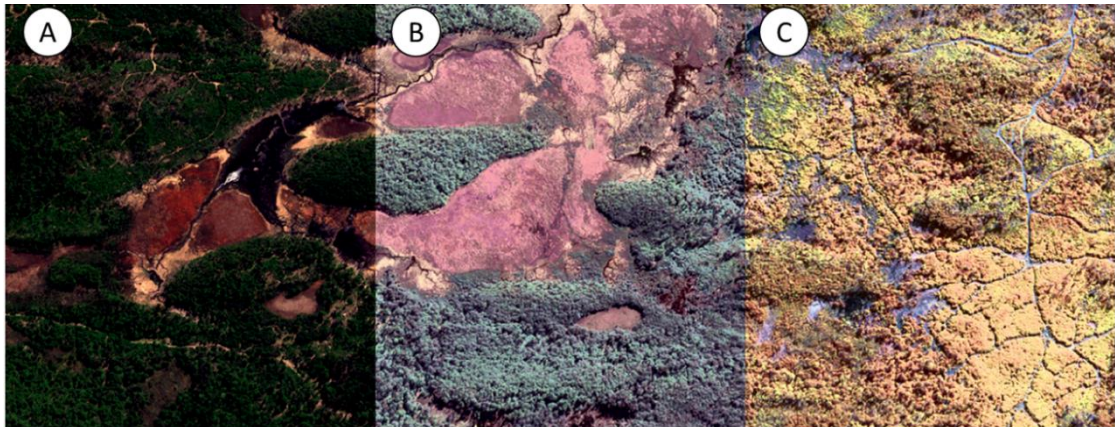
Figure S2. Correlograms showing the correlation between each measured tree-scale covariate (see Table 3). Correlation values are accompanied by its confidence intervals (CI), and are graphically supported by each curve and CI ellipses.
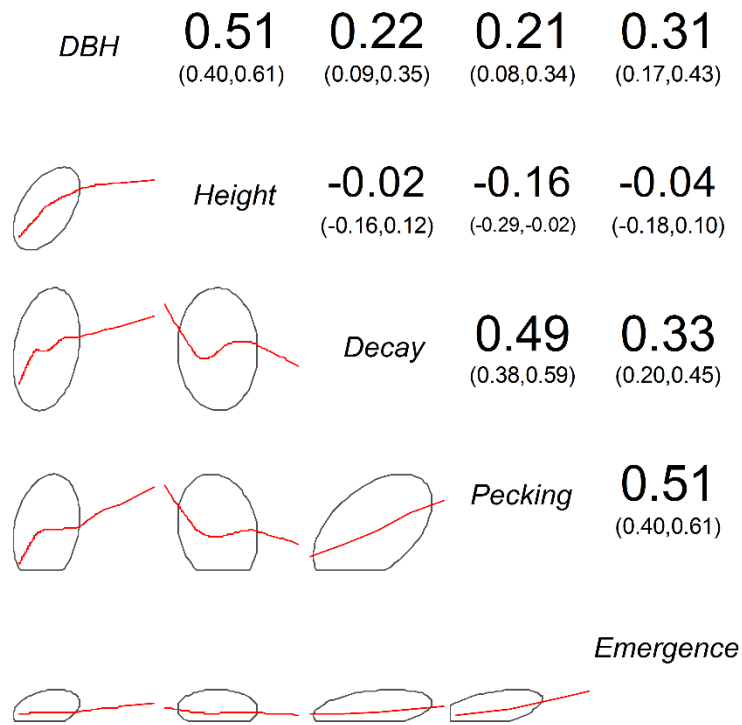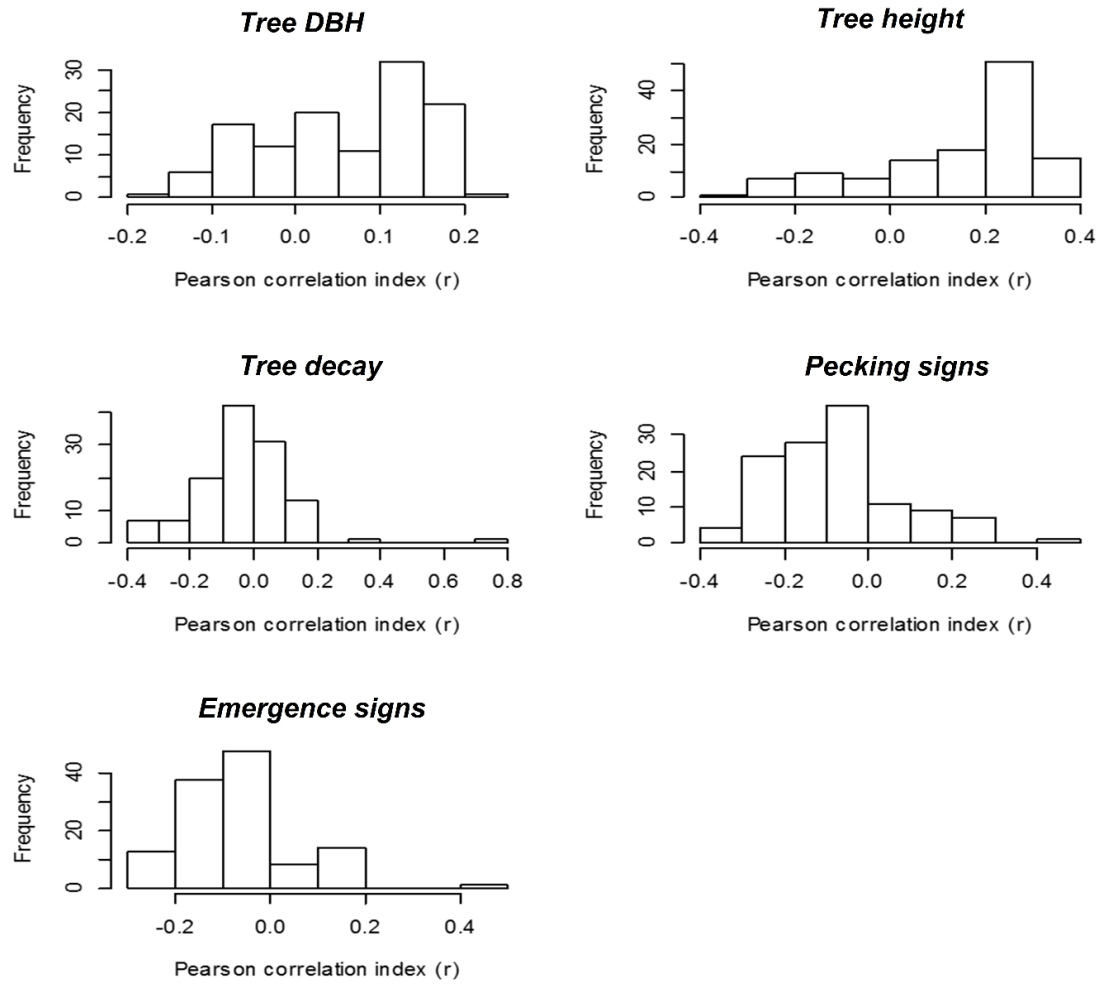
Figure S3. Histograms showing the correlation frequencies of the considered Vegetation Indexes to each tree-scale covariate (see Table 3).

Reducing temporal autocorrelation

We used autocorrelation functions (ACF) to map our temporally correlated data and extract a subset of temporally independent locations from each sampled track (Shumway and Stoffer, 2017). Rather than comparing the ACF from our data to theoretical ACF by setting a fixed limit for the filtering process (e.g. plus/minus two standard errors), we set up a logical rule over the values of temporal correlation in the two major spatial axes (longitude and latitude). This is a conservative estimation that follows the logic of the so-called "time to independence" used in quantitative analysis of movement (Swihart and Slade 1985). Despite there has been debate in using the term "independence" in movement analyses (both temporal and spatial), since the location of individuals in a given time is inherently dependent of the individuals' past locations, when working with territorial species that perform periodic activities such as patrolling, the use of ACFs are considered standard practice for this type of filtering (). For our study, we selected a filtering interval for each GPS dataset as follows:

Pseudo-code:

1: **for** *t* in 1 to T   // T is the maximum sampled time period

2:        **for** *each* coordinate *lat* and *lon*

3:                Calculate the module of ACF_t // autocorrelation function value at time *t*

4:      end **for**

5: end **for**

6: **assign** to FirstMin$_{t, lon}$ and FirstMin$_{t, lat}$ the first minimum values of ACF$_{t, lon}$ and ACF$_{t, lat}$

7: **return** the maximum t between FirstMin$_{t, lon}$ and FirstMin$_{t, lat}$

Formula:

Filtering time interval = max_interval(first(min(|ACF(Easting)|))), min(first(min(|ACF(Northing)|)));

where $| \alpha |$ stands for the module, or distance of any number α, to the x axis. Therefore, selecting the time at which ACF functions for both axes (Easting and Northing) reach their first minimum values, which also corresponds to their first root values of the ACF (i.e. where $y = 0$). By setting up the maximum between both coordinates, we can assure independence in both spatial directions.

Figure D1: Autocorrelation functions (ACF) for Easting (longitude) and Northing (latitude) of one of our sampled GPS tracks. The time lags for this dataset are 5 min. The plotted vertical lines denote the first point at which the ACF crosses zero (40 min for longitude and 50 min for latitude). In this example, the maximum of the first minimum ACF values is 50 min, therefore only 10 locations were used for the UD estimation (see text).
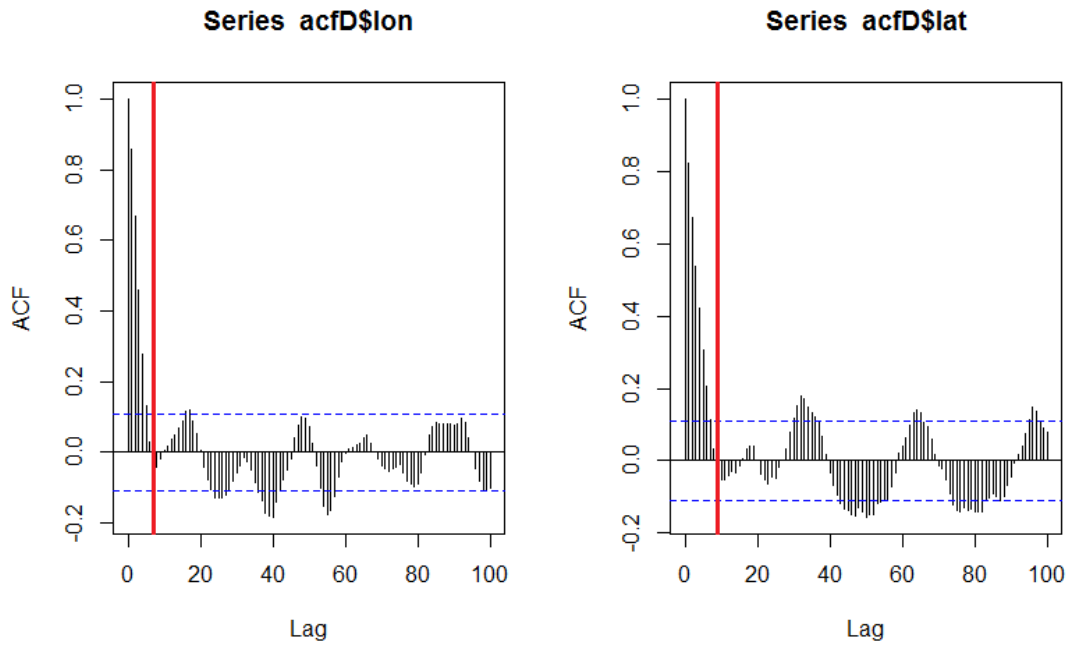
R code:

```
library(sp)


locs  # regular GPS data with longitude, latitude and non-NA values.


# calculate ACF functions for sampled locations:

lagMax <- 100

acfLon <- acf(locs$lon, lag.max = lagMax, plot = F)  # ACF for longitude

acfLat <- acf(locs$lat, lag.max = lagMax, plot = F)  # ACF for latitude


# calculate approx. polynomial functions and calculate their roots:

acfLon_coefs <- lm(acfLon$acf[, , 1] ~ poly(0:lagMax, 5, raw = TRUE))

acfLon_firstMin <- polyroot(acfLon_coefs$coefficients)[1]  # first root

acfLat_coefs <- lm(acfLat$acf[, , 1] ~ poly(0:lagMax, 5, raw = TRUE))

acfLat_firstMin <- polyroot(acfLat_coefs$coefficients)[1]  # first root


# find max value between min values of ACFs for lat & lon:

maxMin <- max(acfLon_firstMin, acfLat_firstMin)


# sample data using the calculated maxMin time interval:

locsFiltered <- locs[seq(1, nrow(locs), by = round(maxmin)), ]
```

References

Shumway, R. H., & Stoffer, D. S. (2017). Time series analysis and its applications: with R examples. Springer.

Swihart, Robert K., and Norman A. Slade. (1985) Testing for independence of observations in animal movements. Ecology 66, 1176-1184.

CHAPTER 5 APPENDIX

Figure A1. Plot of the loading values for the 1092 loci used for the Discriminant Analysis of Principal Components (DAPC) analysis. Labels are shown for loci with loadings above the third quartile (0.00048).