Broadscale Outcome and Monitoring Assessment to Evaluate Protected Area Effectiveness in Northern Patagonia

A Dissertation Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

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May 2022

DEDICATION

I dedicate my work to my family for their unstoppable support and love.

ACKNOWLEDGEMENTS

I would like to thank my advisor Dr. Dan Simberloff for his guidance, support, and help. I want to thank to all my field assistants: Ludovico Zeller, Isabela Zeller, Emmanuel Imizcoz, Lucila Amione, Flavia Casinelli, Marlene Zaracho, Edgardo Balverdi, Ana Paula Blazina, Thais Efron, Maria Celeste Lado, Florencia Mallou, Laura Barbieri, Sofia Jones, Julieta D'Amario, Carolina Mansilla Ferro, Maria Belen Dri, Antonio Navarro, Sabrina Ignacio, Mauro Ricci, Carolina Alonso, Natanael Griffa, Francisco Molina; and lab assistants: Brianna Jacobs and Isabella Ritchie. To my collaborators, Juan Morales, Hannah Herrero and Jake Dein, thank you. Finally, this project would not have been possible without the support of the following institutions: University of Tennessee, Ecology and Evolutionary Biology Department, Administracion de Parques Nacionales, Prefectura Naval Argentina, and British Ecological Society.

ABSTRACT

Biomes worldwide have been affected by biodiversity loss and habitat degradation for more than a century. Protected Areas (PAs) have been established in almost every country, as they represent one of the most important tools in biodiversity conservation. Nevertheless, the relentless biodiversity loss trend has not stopped. Concern about PA effectiveness has risen, and several methods to evaluate it have been implemented over the last few decades. Nahuel Huapi National Park (NHNP) is the first PA in Argentina and one of the largest. The area is considered a biodiversity hotspot, and its conservation is essential, as unique ecological and evolutionary processes have resulted in a high degree of endemism and mutualism. Three levels of protection have been designated in NHNP, Strict Natural Reserve (SNR), National Park (NP), and National Reserve (NR), corresponding to IUCN levels Ia, II, and VI respectively. In this study we evaluated NHNP effectiveness, comparing outcomes at each level of protection and the neighboring unprotected area. We assessed the effectiveness using two complementary approaches: broadscale outcome based on remote sensing data, and direct monitoring of the small mammal community. We evaluated broadscale outcome based on 20 years of Normalized Difference Vegetation Index (NDVI) data from period 2000-2020. We included other variables in our analysis such as dominant tree species, precipitation, elevation, temperature, and wildfires. We assessed its small mammal community using a capture-mark-recapture study conducted over two consecutive summers with a total trapping effort of 41,600 trap/nights, resulting in 1259 individuals identified, from eight native species. Both assessments suggested that a key role is played by the highest level of protection, SNR. Nevertheless, lack of investment and the effects of climate change threaten the future of NHNP. We also analyzed variation of small mammal communities by developing multiple occupancy models to understand species distributions, co-occurrence, and habitat use at a small scale, supporting previous findings about differences among effectiveness of the three levels of protection, species-by-species, and providing evidence at a fine scale regarding those differences.

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INTRODUCTION

There are currently 251,922 terrestrial protected areas (PAs) in the world covering 15.73% of the global land surface. Furthermore, 17,721 marine protected areas have been established, accounting for 7.93% of the global sea surface. The number of PAs per country varies greatly; while some countries count thousands of them (United States 42,826 PAs, Australia 11,149 PAs, Ukraine 5,622 PAs), other countries tally only dozens, such as Iraq (23 PAs) and Botswana (22 PAs). Country size is not closely related to the number of PAs. For example, China has 122 PAs while Austria has 1,663 PAs (UNEP-WCMC and IUCN, 2022). Despite this disparity in PA representation per country, the global trend has been toward increasing creation of PAs, since these conservation units remain the cornerstone strategy for biodiversity conservation (Geldmann et al., 2018). While the global extent of land and sea currently protected seems promising, biodiversity continues to decline. Several studies have questioned to what extent PAs are effective at preserving biodiversity (Barnes et al., 2017; Bruner et al., 2001; Coad et al., 2019). Target 11 of the Aichi Biodiversity Targets (CBD, 2010) states that PAs must be effectively and equitable managed (CBD, 2010). Several approaches have been proposed to evaluate PA effectiveness (Leverington et al., 2010). One of the most widely used is Protected Area Management Effectiveness or PAME (Hockings et al., 2006). Currently, there is a Global Database of Protected Areas Management Effectiveness (GD-PAME) that is updated monthly, and it constitutes the most comprehensive database regarding this approach (UNEP-WCMC and IUCN, 2022). At the time this manuscript is being written, only 19,926 PAME are reported in the GD-PAME.

The history of PAs, including times of creation and further effectiveness evaluations, is unique for each country. Argentina is a pioneer nation in Latin America, setting land aside to create a PA as early as 1906 (Rivarola et al., 2021). Despite this apparent early conservation concern in Argentina, the original intention was to delimit an international border with Chile after years of dispute (Rivarola et al., 2021). Argentina was a powerful and promising country at the beginning of the 20th century (Lewis, 2015a), but political and economic instability compromised its future (Lewis, 2015b). Previous research identified the negative effects that frequent Argentinean crises triggered by this instability had on the conservation movement in general and on its PA system in particular (Rivarola et al., 2021)

Nevertheless, there are 463 PAs in Argentina (including national, provincial, municipal, and private designations), a lower number than that of its neighbouring country, Brazil (3,202 PAs) but doubling the number of its western neighbor, Chile (222 PAs). However, Chile has performed effectiveness evaluations for more than half its current PAs (120), while Brazil and Argentina have reported fewer assessments (588 and 74 for Brazil and Argentina respectively) (UNEP-WCMC and IUCN, 2022).

The first PA in Argentina and one of the biggest is Nahuel Huapi National Park (NHNP), located in the northern portion of Patagonia. Patagonian temperate forests are considered a hotspot of biodiversity (BirdLife International 2018), with high rates of endemism (Barnosky et al., 2001) and mutualistic relations among species (Aizen & Escurra, 1998). Two decades ago, a PAME reported that NHNP had "Fairly Satisfactory" management effectiveness (scoring between 51-75% of the optimum) (Rusch, 2002). New data are needed, as effectiveness assessments should be performed regularly, ideally every five years (UNEP-WCMC, 2017). PAME is a popular tool that uses qualitative, perception-based data produced by extensive questionnaires answered by people working in the PAs. It is relatively inexpensive and can readily be applied to multiple sites (Hockings et al., 2006); however, it is not the only possible approach. PA effectiveness can also be assessed by GAP analysis (biodiversity represented within PAs), broadscale outcome (general trends found inside and outside PAs, usually performed with remote sensing data), and monitoring (quantitative information regarding populations or communities within PAs).

For my dissertation, I proposed to evaluate NHNP conservation effectiveness using two approaches. In Chapter 1, I used broadscale outcomes assessment, based on 20 years of remote sensing data. Particularly, I evaluated changes in Normalized Difference Vegetation Index (NDVI) among its three levels of protection (National Reserve, National Park, and Strict Nature Reserve) and neighboring unprotected areas. Furthermore, I incorporated in this analysis precipitation, dominant tree species, and wildfire data. In Chapter 2, I applied a monitoring assessment; specifically, I used a capture-mark-recapture method to investigate its small mammal communities across the four protection categories mentioned above. The high variability reported in Chapter 2led to the research reported in Chapter 3, where I developed seven occupancy models using natural variables as well as anthropogenic

disturbances to shed light on the habitat preferences and distributions of these important, often neglected, native species.

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CHAPTER I

ASSESSING PROTECTED AREAS ZONING EFFECTIVENESS WITH REMOTE SENSING DATA, THE CASE OF NAHUEL HUAPI NATIONAL PARK, ARGENTINA

A version of this chapter is in review process in Frontiers in Remote Sensing, Special Issue Women in Remote Sensing, authored by María Daniela Rivarola, Jacob Dein, Daniel Simberloff and Hannah V. Herrero.

María Daniela Rivarola conducted a search literature in order to gather all the information needed, analyzed the data, and wrote the whole article. Jacob Dein obtained the data. Dan Simberloff revised and edited the article. Hannah Herrero revised and edited the article.

Abstract

Protected areas (PAs) remain the most important tool to prevent biodiversity loss and habitat degradation worldwide, but the formal creation of a PA constitutes only the first step. In recent decades, concerns about PA effectiveness have arisen, and several PAs have been evaluated using different methods. Results show that while some PAs are achieving their conservation goals, others have been less effective. Particularly, assessing broadscale outcomes is a method that allows us to monitor change over time at a large scale, using remote sensing data. In this study, we evaluated the effectiveness of Nahuel Huapi National Park, with particular attention to its three protection categories: Strict Natural Reserve (SNR), National Park (NP), and National Reserve (NR) (IUCN categories Ia, II, and VI respectively). We compared changes in Normalized Difference Vegetation Index (NDVI) among sites in these categories and between them and neighboring unprotected areas, over the period 2000-2020. Overall, habitat degradation was low, and we found no difference among the four categories evaluated. Nevertheless, a greening process has been conspicuous in the entire area, with higher values both in the SNR and in the unprotected area. We propose possible explanations as we take into account variables such as dominant tree species, precipitation, temperature, elevation, and wildfires. This study supports the importance of NHNP at the regional and national levels, particularly its SNR areas.

Introduction

The biodiversity loss occurring nowadays is considered by some to be the worst biological disaster since the last mass extinction 65 million years ago (Soulé, 1987). Although protecting some areas or ecosystems is not enough to stop and reverse this trend, the creation of protected areas (PAs) remains one of the most important measures in conservation biology (Hunter & Gibbs, 2007), as shown by the fact that protected area coverage rapidly achieved the goal of 17% of land and inland water protected set by the Convention of Biological Diversity in 2010 (CBD, 2010; WDPA, 2021).

Establishing a PA is the first step toward ecosystem conservation; however, creating a PA does not by itself guarantee its effectiveness at achieving its conservation and management goals. The need to assess PA effectiveness has been widely noted, resulting in a growing number of studies addressing the outcome from different perspectives (Barnes et al., 2017; Barnes et al., 2016; Coad et al., 2015; Coad et al., 2019; F. Leverington et al., 2010; Nagendra, 2008). Leverington et al. (2010) summarized different approaches used to assess PA effectiveness as follows: Coverage – studies biodiversity representation within PAs, also known as Gap Analysis (Armenteras & Villareal, 2003; Chape et al., 2005; Rodriguez-Cabal et al., 2008; Scott et al., 1993); Broadscale Outcomes – compares environmental changes within and outside protected areas, generally using remotely sensed data (Herrero et al., 2016; Nagendra et al., 2013); Protected Area Management Effectiveness Assessments (PAME) – uses the scoring framework developed by the IUCN (Coad et al., 2015; Hockings, 2003) or a similar approach; and lastly, Detailed Monitoring – generally reporting animal population trends, vegetation conditions, or socioeconomic impacts of a particular PA (Barnes et al., 2016). These different approaches are complementary, as each one addresses the outcome from a singular perspective (Hockings et al., 2006).

The term protected area comprises areas known by different names, often referring to different types of management. The International Union for Conservation of Nature (IUCN) recognizes six management categories organized from more to less strict as follow: Ia-Strict nature reserve, Ib-Wilderness area, II-National Park, III-Natural monument or feature, IV-Habitat/species management area, V-Protected landscape or seascape, and VI-

Protected area with sustainable use of natural resources (Dudley, 2013). While extractive use is forbidden or minimal in categories from I to IV, the restrictions are reduced in categories V and VI. The idea that a stricter management category will yield better habitat preservation has been widely explored in a variety of environments, with contrasting results. A study conducted in Bolivia, Costa Rica, Indonesia, and Thailand found that, although deforestation was generally lower inside the strictest PAs, it was unclear whether this outcome was related to the management category or instead to the remote location of most of the strict PAs (Ferraro et al., 2013). The Royal Chitwan National Park in Nepal allows use by and involvement of local residents, while Celaque National Park in Honduras has a more traditional management approach in which local residents do not participate in this endeavor. Although deforestation rate was lower inside both PAs, the regeneration and conservation of the buffer zones surrounding the PAs were better where local residents were involved, suggesting that a regulated use of PAs could be more effective in the long run (Nagendra et al., 2004). Fire incidence in tropical forest located in strict PAs in Latin America and Asia was lower than in the unprotected area; however, multi-use PAs in these continents sustained an even lower fire incidence (Nagendra, 2008).

While most studies looked at entire units belonging to one particular management category, the division of a PA into zones with differing categories of protection has been less studied (Hull et al., 2011). A common management approach is subdividing a PA into more than one management category, resulting in more strictly regulated areas surrounded by less regulated categories acting as buffer zones between the most highly protected area and the unprotected area (Geneletti & van Duren, 2008). This is the situation in Nahuel Huapi National Park (NHNP), located in the northern portion of the temperate forests in Patagonia, Argentina. This protected area, originally created in 1922 as National Park (NP; category II IUCN), was later subdivided into National Reserve (NR; category VI IUCN) and Strict Nature Reserve (SNR; category I IUCN) (Rivarola et al., 2021a). The National Reserve was established in 1970 as a buffer zone between the National Park (west) and the unprotected area (east); furthermore, most of the private properties that existed at the time were included in this new (lower) category, allowing for regulated extractive use. Finally, in 1990 pristine and remote areas within the National Park were declared Strict Nature Reserve with no human intervention allowed (Martin & Chehébar, 2001; Rivarola et al., 2021a). NHNP has

one city and two small towns on its borders, accounting for a total population of approximately 170,000 people. This region had a low human population density for most of the 20th century, a situation that changed in the 1980s, during which an annual population growth rate above 100% resulted in an unplanned and unregulated urbanization expansion in which social and economic inequity are evident, pressing on natural resources in a complex manner (Madariaga, 2007).

The economic development of this region was historically based on agriculture, livestock, and logging but later switched to tourism, the main source of income nowadays (Nuñez & Vejsbjerg, 2010; Schlüler, 1994). Three biomes are protected by NHNP: high Andes, Patagonian temperate forests, and steppe, with Patagonian temperate forests accounting for the largest extent (Monjeau et al., 2005). These forests have been isolated from other temperate forests since the mid-Tertiary Period (Axelrod et al., 1991; Villagrán & Hinojosa, 1997), and, as a result, 90% of the woody species are endemic (Arroyo et al., 1996) and the region is characterized by one of the highest known rates of plant-animal mutualisms (Aizen & Escurra, 1998). Despite the existence of multiple PAs incorporating Patagonian forests in Chile and Argentina (Armesto et al., 1998; Burkart, 2005), more than 1/3 of the Patagonian forests have been lost since the arrival of Europeans in the 19th century (Tecklin et al., 2002). The assessment of NHNP effectiveness in preserving its biodiversity is crucial. Integral and pluralistic approaches are needed in order to assess PA performance (Caro et al., 2009). Three of the effectiveness assessment methods suggested by Leverington et at (2010) have been implemented in this PA. The first was a PAME assessment that found that NHNP management falls in the fairly satisfactory category (Rusch, 2002). Secondly, a coverage study concluded that the hotspot of Patagonian biodiversity is not fully covered by the current PAs (Rodriguez-Cabal et al., 2008). Lastly, a detailed monitoring of the small mammal community of NHNP concluded that there is no clear evidence that a stricter category preserves this community better, with the exception of the endemic marsupial *Dromiciops gliroides* (Rivarola et al., 2021b). The fourth type of PA effectiveness assessment, broadscale outcome, has not been yet performed, and it is the main goal of the present study.

Ecological applications of satellite remote sensing (SRS) can potentially improve environmental management by providing verifiable and standardized data at a large temporal and spatial scale (Pettorelli et al., 2014). For decades, access to SRS data was very

expensive, limiting its use in many countries and regions. The shift toward free SRS databases provided the opportunity for better and wider use of these data (Woodcock et al., 2008). Concomitantly, advances in processing methods have allowed such data to be used in a more comprehensive manner (Hansen & Loveland, 2012). An increasing number of studies have used SRS to assess PA broadscale outcomes, facilitating the evaluation of large areas that would not have been possible to assess from the ground (Buchanan et al., 2008; Nagendra et al., 2004; Wiens et al., 2009). Among all sensors, Landsat provides the longest consistently calibrated data set registering surface changes since 1972 (Markham & Helder, 2012), providing an excellent source of data for habitat monitoring, allowing detection of habitat fragmentation and disturbances in PAs (Nagendra et al., 2013).

Several vegetation indices have been developed in order to make inferences about vegetation structure, photosynthetic capacity, and leaf water content among other ecological data. Normalized Difference Vegetation Index (NDVI) is the most widely used index and is defined as the ratio of the difference between the spectral reflectance in near-infrared (NIR) and the red (RED) wavelengths divided by the sum of both, where NIR and RED are the light reflected by the vegetation in the NIR and RED wavelength bands respectively (Gandhi et al., 2015; Yengoh et al., 2016). This index is based on the fact that chlorophyll absorbs RED, while the mesophyll disperses NIR (Pettorelli et al., 2005), and its values range between -1 and +1, where negative values correspond to unvegetated areas (Myneni et al., 1995). This index is highly sensitive to changes in canopy photosynthetic activity, and such changes can be used as an early warning of habitat modification (Leisher et al., 2013; Nagendra et al., 2013). In terrestrial ecosystems, the amount and distribution of vegetation directly influence the abundance and distribution of resident and migrant animals; thus, NDVI is a valuable tool not only for assessing photosynthetic activity but also to infer overall ecosystem status at a large spatial and temporal scale (Pettorelli et al., 2005). Time series analysis of NDVI has been used to assess PA effectiveness, allowing researchers to differentiate between seasonal and yearly changes (Herrero et al., 2020; Herrero et al., 2016; Southworth et al., 2016; Waylen et al., 2014).

The research reported here explores vegetation status of NHNP among its three protection categories along with a neighboring unprotected area. We aimed to determine the effectiveness of the three levels of protection in the NHNP during the 21st century by

comparing NDVI time series analyses from 2000 to 2020 of areas under each level of protection to that for "matching" (or "apples-to-apples") unprotected areas in order to reduce variation associated with different land characteristics (Joppa & Pfaff, 2011). Variation in NDVI can be associated with other features including land cover, precipitation, temperature, and elevation. We further analyzed these factors as potential factors determining the observed NDVI.

Methods

Nahuel Huapi National Park is located between the parallels 40° 08' 18" and 41° 35' 19" South and the longitudes 71°50' 52" and 71° 04' 45" West (Fig. 1). It is bordered in the west by Chile, in the north by Lanin National Park, in the east by the Patagonian steppe (a small area of which is included within NR), and in the south by the Manso river. It covers a total area of 7,172.61 km^2 subdivided into different management categories. The eastern 2,253.8 km^2 are designated National Reserve (NR), IUCN category VI, while the western 4,918.81 km^2 are designated National Park (NP), IUCN category II (WDPA, 2021). In 1990, pristine areas within the National Park were declared Strict Nature Reserve (SNR, IUCN category Ia), covering 755.25 km^2; and later in 1994, a new subdivision of the NP was proclaimed Wilderness Natural Reserve (WNR, IUCN category Ib) (Rivarola et al., 2021a). In this study, we investigated NR, NP, and SNR, insofar as we lacked access to shape files that included WNR. Additionally, we evaluated 2,423.8 km^2 of unprotected area located south of the Manso river, using the same NHNP longitudinal range (Fig. 1.1).

NHNP lies within the Valdivian Ecoregion, where High Andean, Patagonian Forests, and Steppe biomes are represented (Burkart et al., 1999). It has a mean annual precipitation of 1,800 mm, with a marked west-east gradient (from above 2,000 mm to approximately 200 mm), owing to the shadow effect of the Andes Mountains (Cabrera, 1976). Most of the NHNP is covered by forest dominated by evergreen or deciduous species of the genus *Nothofagus* (*N. pumilio* - Lenga, *N. antarctica* - Ñire, *N. dombeyi* - Coihue, *N. betuloides* - Guindo, and *N. nitida* - Coihue de Chiloé), and *Araucaria araucana* (Araucaria) in the northern area, and

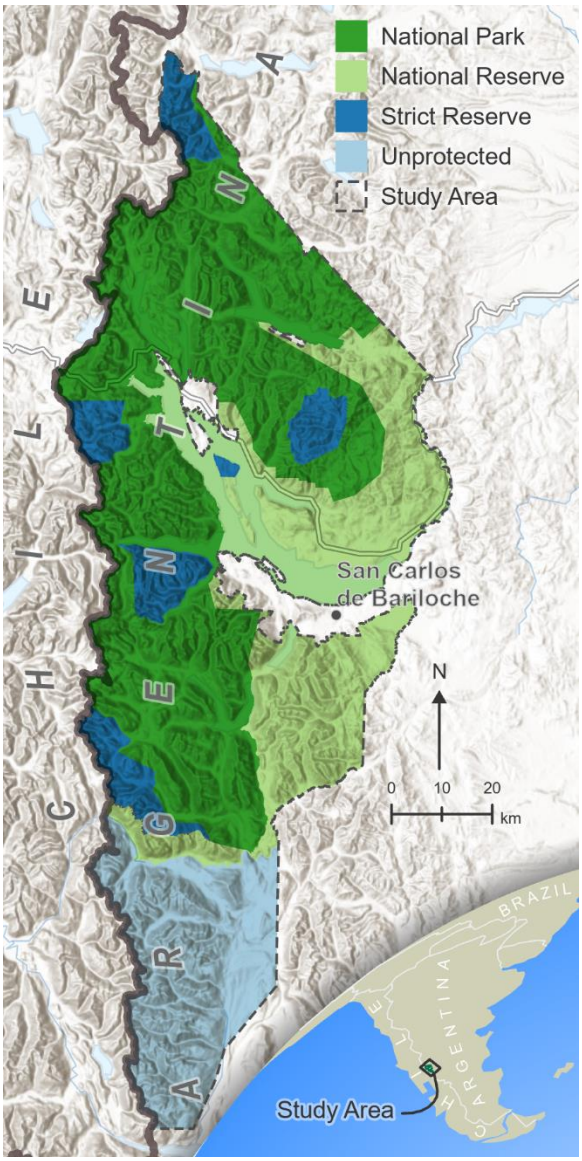

Figure 1.1 Map of Nahuel Huapi National Park. Levels of protection indicated by different colors.

Austrocedrus chilensis -cypress - along the eastern fringe in the ecotone between forest and steppe (Cabrera, 1976).

To quantify NDVI change in the study area in relation to significant environmental variables, we collected satellite imagery, precipitation, and temperature data from available remote sensing products from years 2000 to 2020, leveraging the resources of Google Earth Engine (Gorelick et al., 2017). While limited remote sensing data are available before 2000, sufficient data available starting in year 2000 allowed us to analyze vegetation change from when the strict reserves were first established. In addition to remote sensing data, we also acquired fire history (Mermoz et al., 2005), land cover provided from CIEFAP (Centro de Investigación y Extensión Forestal Andino Patagónico), and tourism data from APN (Administración de Parques Nacionales).

We created cloudless composites using Landsat data by selecting the "greenest" pixel from all scenes captured between December 1 and March 1 of each summer season. We selected only summer data because the presence of evergreen and deciduous forests prevents us from evaluating photosynthetic activity in fall and winter, while frequent presence of snow during the spring would also bias our analysis. The greenest pixel was taken to be that with the highest NDVI, which we computed for each available scene during each season. At least 25 scenes were available for each season. Composites before 2013 were created using Landsat 7[1] scenes, and composites 2013 and after were created using Landsat 8[2].

Selecting the greenest pixel allowed for the best interseason NDVI comparisons. However, while the method works well for creating cloudless composites in areas with vegetation present, pixels containing clouds are often selected over areas with low NDVI values, such as water bodies, urban areas, and areas above the tree line. Because these areas contained little to no vegetation, they were not relevant to our analysis, and we masked them from the resulting composites to exclude them from analysis. The mask was taken from land cover data provided to us by CIEFAP (Centro de Investigación y Extensión Forestal Andino Patagónico) and shown in Fig. 1.2.

[1] Landsat 7 Collection 1 Tier 1 TOA Reflectance courtesy of the U.S. Geological Survey
[2] Landsat 8 Collection 1 Tier 1 TOA Reflectance courtesy of the U.S. Geological Survey

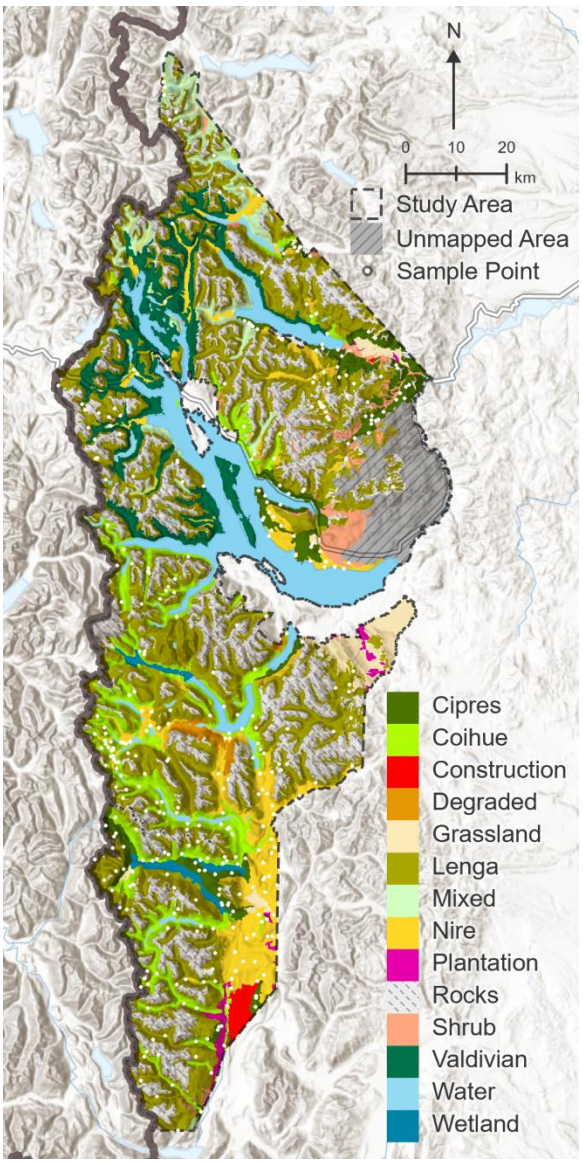

Figure 1.2 Land cover of NHNP and neighboring area.

We collected precipitation data within the study area from the Global Precipitation Measurement (GPM) Integrated Multi-satellitE Retrievals for GPM (IMERG) dataset (Huffman et al., 2019). IMERG provides total precipitation for every month at 0.1 x 0.1 degree (approximately 11.1 x 11.1 km) spatial resolution and calibrates multiple satellite estimates with ground sources.

We collected temperature data within the study area from the MOD11A1 V6 product derived from data collected by satellites equipped with the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument (Wan et al., 2015). The data provide daily (one daytime and one nighttime) land surface temperature estimates at 1 x 1 km resolution. We computed the mean daytime temperature for every year (Jan 1st-Dec 31st) for use in analysis.

We calculated the mean NDVI per austral summer from 2000 to 2020 at each level of protection (SNR, NP, NR, Unprotected). We evaluated the synergistic effect of protection and time on changes in mean NDVI using ANCOVA, followed by a post hoc Bonferroni adjustment test. Level of protection and years (2000-2020) were the categorical and continuous variables, respectively. Since differences in NDVI among the levels of protection do not necessarily mean healthier vegetation, but rather could be related to differences in dominant species cover (e.g., NP mostly dominated by *N. dombeyi* vs NR mostly dominated by *A. chilensis*), precipitation, elevation, or temperature, in a second step we selected random points in each of the Unprotected, NR, NP, and SNR levels. Using the available data regarding dominant species cover across NHNP (Margutti & Arosteguy, 2019), we selected 25 random points per area dominated by one of the four most common dominant tree species: *N. dombeyi*, *N. antarctica*, *N. pumilio*, and *A. chilensis*, accounting for a total of 100 random points each for NP, NR and Unprotected area, and 75 random points for SNR, because no area is dominated by *A. chilensis* within this category (Fig. 2). For these 375 random points we extracted the elevation, and their NDVI values, temperature, and precipitation from 2000 to 2020.

For each random point we ran a linear regression in which we evaluated NDVI change over time, resulting in a total of 375 linear regressions. From each linear regression, we extracted the slope, as it provided us with information regarding the general trend of NDVI change per level of protection. Lastly, we ran an ANOVA test to evaluate if the slopes

(indicating NDVI change over time) varied among the four levels of protection, followed by a Tukey HSD test.

Nothofagus dombeyi, *N. antarctica*, *N. pumilio*, and *A. chilensis* respond differently to disturbances such as wildfire, drought, livestock, and windstorm (Raffaele et al., 2014). To investigate if these species experienced a different trend among the levels of protection, we ran a two-way ANOVA test, grouping by level of protection and dominant species and using as dependent variable the 375 slopes from the random points mentioned above, followed by a Bonferroni test.

Previous studies have indicated that precipitation plays an important role in determining NDVI (Herrero et al., 2020). Other characteristics, such as elevation and temperature, might also affect the NDVI values. In order to reduce the number of physical variables used to explain changes in NDVI, we used Pearson's product-moment correlation to evaluate the correlation between precipitation and elevation (t=2.16, df=7810, p-value=0.03) and correlation between precipitation and temperature (t=-36.20, df=7810, p-value=<1.1e-16). We ran a linear regression to evaluate if annual precipitation in the studied area affected its NDVI. We transformed NDVI values using a Box-Cox transformation to satisfy the normality assumption, then evaluated by ANCOVA whether different levels of protection differed in annual precipitation.

To identify areas where changes in NDVI over the 20-year period were more notable, we filtered those pixels where values changed by more than 1 standard deviation (1 SD), both positive and negative changes. We ran a linear regression to evaluate if increases in NDVI were related to the level of protection, and we ran a second linear regression to analyze the relation between NDVI decreases and level of protection. As mentioned above, total area differs among levels of protection. To standardize the measure among them, we used the percent of area (of each level of protection) where NDVI changed by more than 1 SD. While an increase in NDVI is associated with vegetation growth, it does not necessarily mean that natural vegetation is thriving; in fact, several undesired landscape modifications can induce that change, such as land abandonment and agriculture expansion (Pan et al., 2018). On the other hand, a decrease in NDVI in areas dominated by a particular tree species could reflect disturbances with negative effects on that species. To investigate this situation further, we conducted an ANOVA test to evaluate if decreases in NDVI were related to the type of forest.

We performed the statistical analyses using R 4.0.3 (R Core Team, 2014).

The study area is highly visited during the summer months, when the risk of wildfire is higher owing to low seasonal precipitations. Campsites distributed in NP, NR, and in the neighboring unprotected area receive thousands of visitors, increasing the risk of wildfires. We performed a colocation analysis to determine if fires were more likely to occur near designated campsites. Colocation analysis yields a colocation quotient for each fire centroid, where values less than 1 indicate isolation and values greater than 1 indicate spatial correlation (Leslie & Kronenfeld, 2011). We performed the analysis using the Spatial Statistics toolbox in ESRI ArcGIS Pro version 2.8 using the four nearest neighbors. Fire data were provided by INIBIOMA (Instituto de Investigaciones en Biodiversidad y Medioambiente) and campsite data were provided by NHNP.

Results

We performed an ANCOVA to determine the effect of level of protection on the NDVI after controlling for time (years). There was a statistically significant difference in NDVI between the groups ($F(3,91)=170.43$, $p<0.0001$). Mean NDVI in the Strict Nature Reserve (0.724 ± 0.003) significantly exceeded that in the National Park (0.711 ± 0.003), Unprotected area (0.707 ± 0.003), and National Reserve (0.642 ± 0.003), $p < 0.001$ (Fig. 1.3).

Linear regressions based on the 375 random points showed an overall NDVI increase over time (Fig. 1.4). We analyzed differences in slope per protection category with ANOVA. The greening process (NDVI increase over time) was significantly higher in the unprotected area than in the Natural Reserve ($p=0.022$), the National Park ($p=0.01$), and the Strict Nature Reserve ($p=0.03$) (Fig. 1.5).

We further investigated if dominant tree species had a different trend of NDVI change over time in each protection category with a two-way ANOVA. The interaction term between level of protection and dominant tree species was not significant ($DF= 8, 357$, $F= 0.283$, $p=0.971$), indicating that the tree species did not follow different trends over time in different protection categories (Fig. 1.6). Nevertheless, the "Group" term indicated that different species did follow a different trend without accounting for the protection level ($DF=$

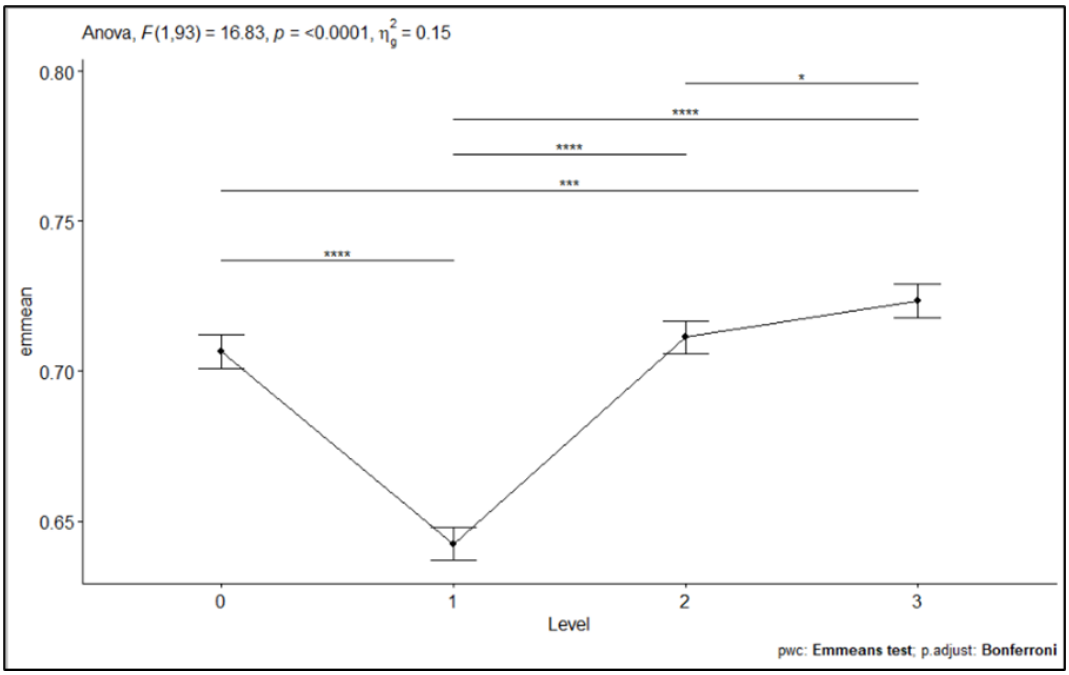

Figure 1.3 Variation in mean NDVI at different levels of protection (0: Unprotected area, 1: National Reserve, 2: National Park, 3: Strict Nature Reserve). Horizontal lines on top indicate statistical differences between paired levels of protection.

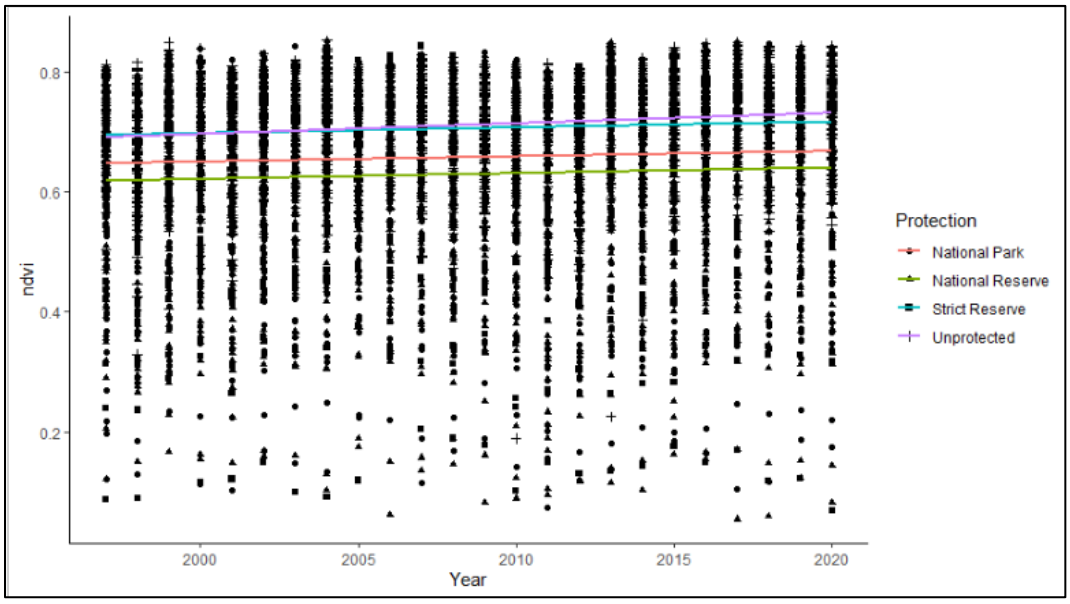

Figure 1.4 NDVI values over time recorded for a total of 375 random points equally distributed among the four levels of protection and four dominant tree species (Nothofagus dombeyi, N. antarctica, N. pumilio, and Austrocedrus chilensis).

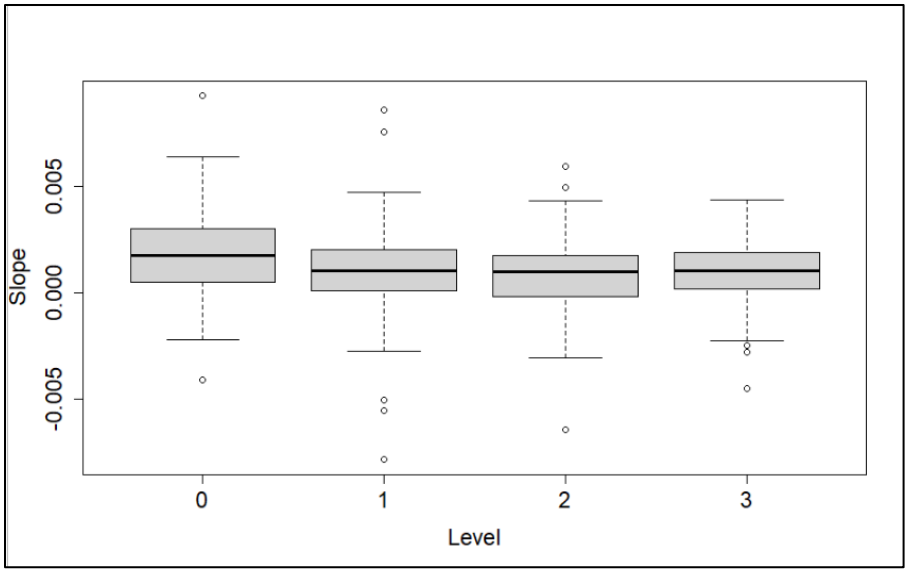

Figure 1.5 Comparison of the NDVI increases over time, indicated as positive slope values, among the different levels of protection (DF=3, 368, F=4.366, p=0.005, ges=0.034). 0: unprotected area, 1: National Reserve, 2: National Park, and 3: Strict Nature Reserve.

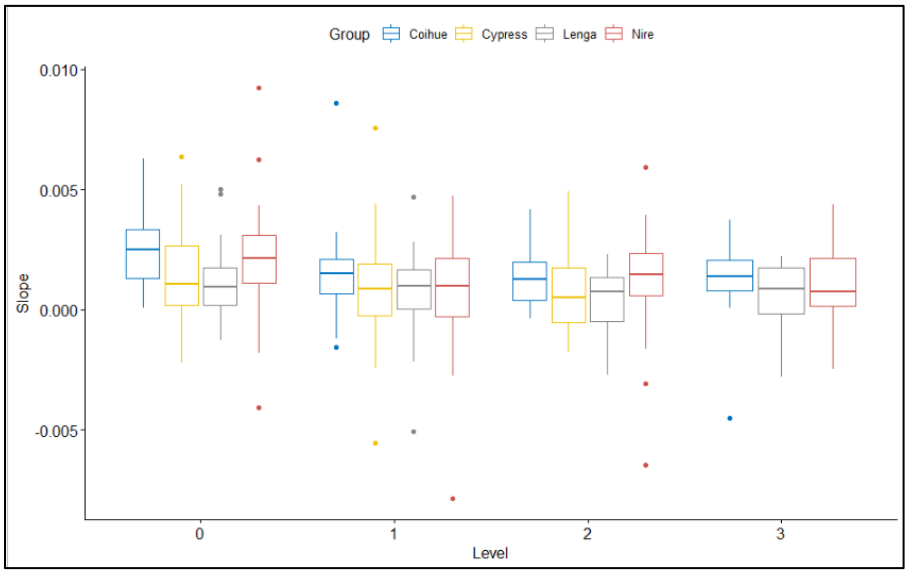

Figure 1.6 Comparison among the NDVI increases over time, indicated as positive slope values, for each of the four most common dominant tree species, among the different levels of protection. 0: unprotected area, 1: National Reserve, 2: National Park, and 3: Strict Nature Reserve.

3, 357, F= 4.036, p=0.008). We then computed a pairwise comparison using a Bonferroni test and found that the trend of NDVI change over time was more pronounced in *N. dombeyi* than in *N. pumilio* (p=0.0009), with no differences among the other species.

Precipitation and temperature were negatively correlated (t = -36.198, df = 7810, p-value < 2.2e-16, r= -0.38), and areas with higher temperature had lower NDVI. On the other hand, precipitation and elevation were positively correlated (t = 2.1616, df = 7810, p-value = 0.03, r=0.02). We further analyzed the effects of precipitation on NDVI, since it was the physical variable that explained the highest fraction of the variation. We found a positive correlation between annual precipitation and NDVI (F(1,82)=17.87, p=6.1e-05). We conducted an ANCOVA in order to determine if annual precipitation has changed in the studied area, and furthermore, if this change is consistent among the different levels of protection. We found an overall decrease in annual precipitation (F(1,79)=38.428, p=2.42e-08), although this decrease differed among levels of protection (F(3,79)=21.469, p=2.88e-10) (Fig. 1.7). In addition, a post-hoc Bonferroni analysis showed that estimated mean annual precipitation in the National Reserve was significantly lower than in the other three categories and that the estimated mean precipitation in the Strict Nature Reserve was higher than in the unprotected area (Table 1.1, Fig. 1.8).

Areas where NDVI changed by more than 1 standard deviation (both positive and negative) are indicated in Fig. 1.9. The percent of greening areas in the unprotected area significantly exceeded that in the NR (Adj. R-squared=0.435, F(4, 91)=19.26, p=1.666e-11), while no significant differences with and among the other categories were found (Fig. 1.10). On the contrary, the same analysis applied to percent of areas with a decreased NDVI yielded no relationship with years or level of protection (Adj, R-squared=0.001, F(4, 91)=1.039, p=0.392) (Fig. 1.11).

To evaluate if negative changes in NDVI were more frequent in forests dominated by a particular tree species, we conducted an ANOVA. We found a significant difference between the number of pixels with a decreased NDVI and the type of forest (F(4,15)=3.922, p=0.023, ges=0.511). Forests dominated by *N. pumilio* contained larger proportional areas with a decreased NDVI than did mixed forests (p=0.0339) and forests dominated by shrub species (p=0.026) (Fig. 1.12).

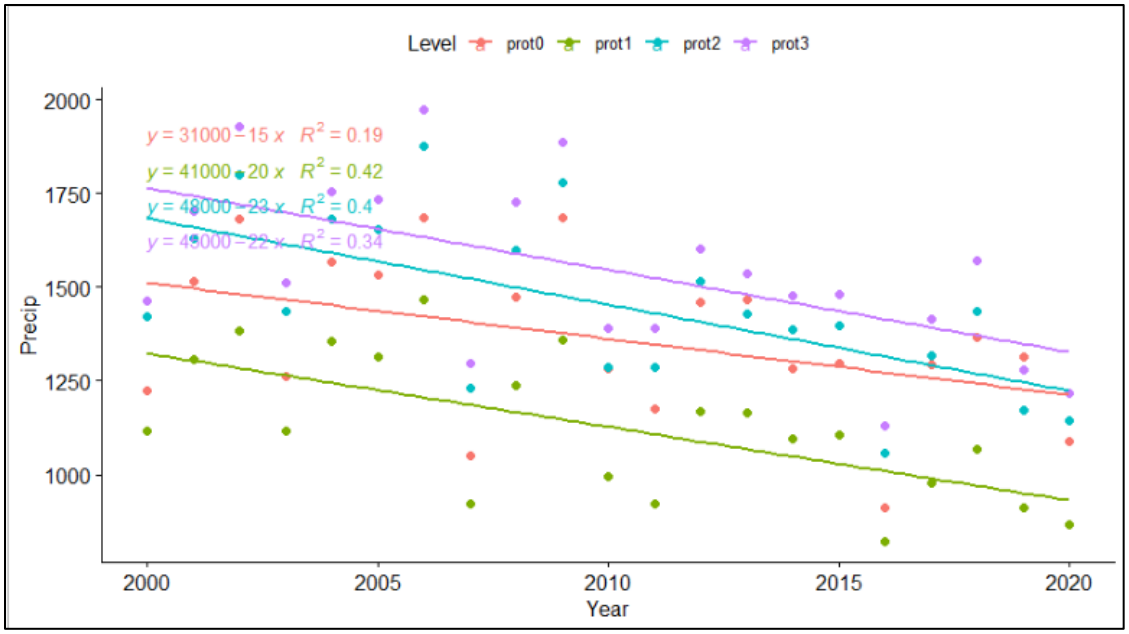

Figure 1.1 Annual precipitation change for each level of protection. prot0: unprotected area, prot1: National Reserve, prot2: National Park, prot3: Strict Nature Reserve.

*Table 1.1 Results from a Bonferroni test indicating differences between changes in annual precipitation at each protection category. Statistical significance is indicated with *.*

Levels compared	**DF**	**F**	**p**
Unprotected vs NR	79	4.28	5.16e-5 ***
Unprotected vs NP	79	-1.66	0.100
Unprotected vs SNR	79	-3.35	1.24e-3 **
NR vs NP	79	-5.97	7.07e-8 ****
NR vs SNR	79	-7.63	4.5e-11 ****
NP vs SNR	79	-1.69	0.096

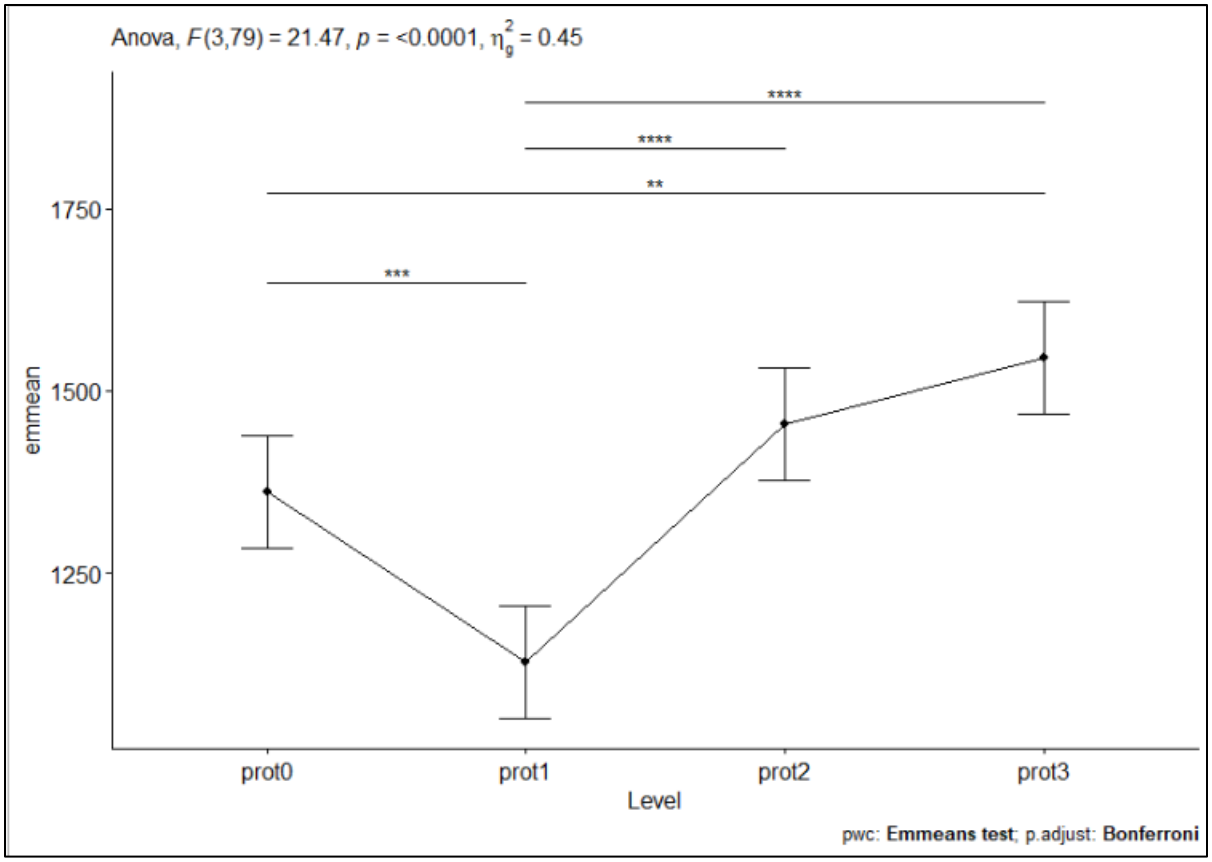

*Figure 1.2 Estimated mean annual precipitation for each level of protection based on 20 years of precipitation data (period 2000-2020). Statistical differences among the protection categories are indicated with *. prot0: unprotected area, prot1: National Reserve, prot2: National Park, prot3: Strict Nature Reserve. Horizontal lines on top indicate statistical differences between paired levels of protection.*

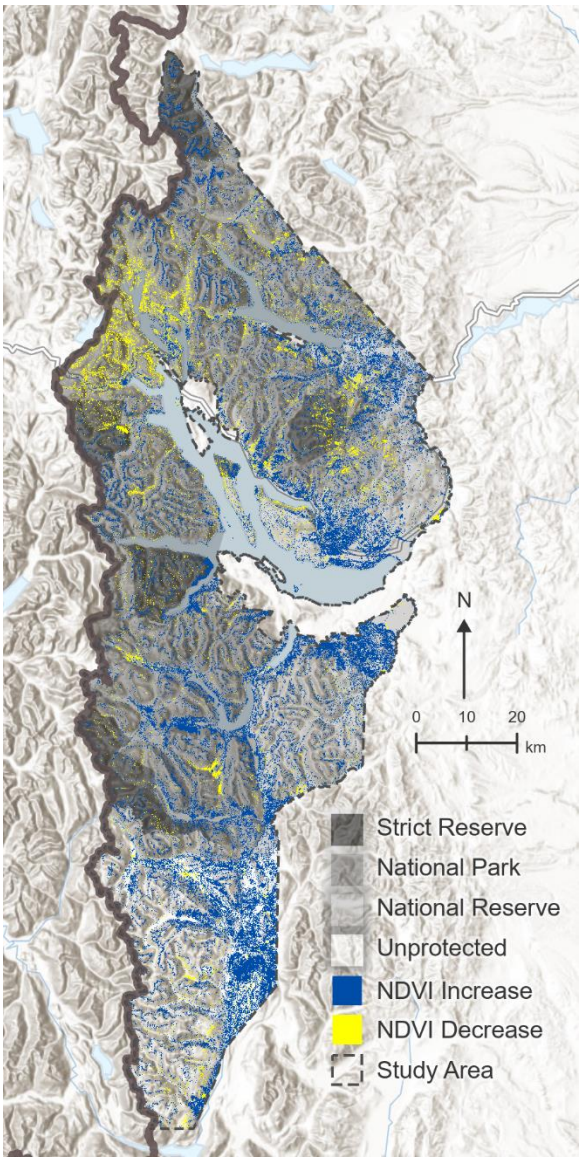

Figure 1.3 Map with areas with NDVI increase (blue) and decrease (yellow) in the period 2000-2020.

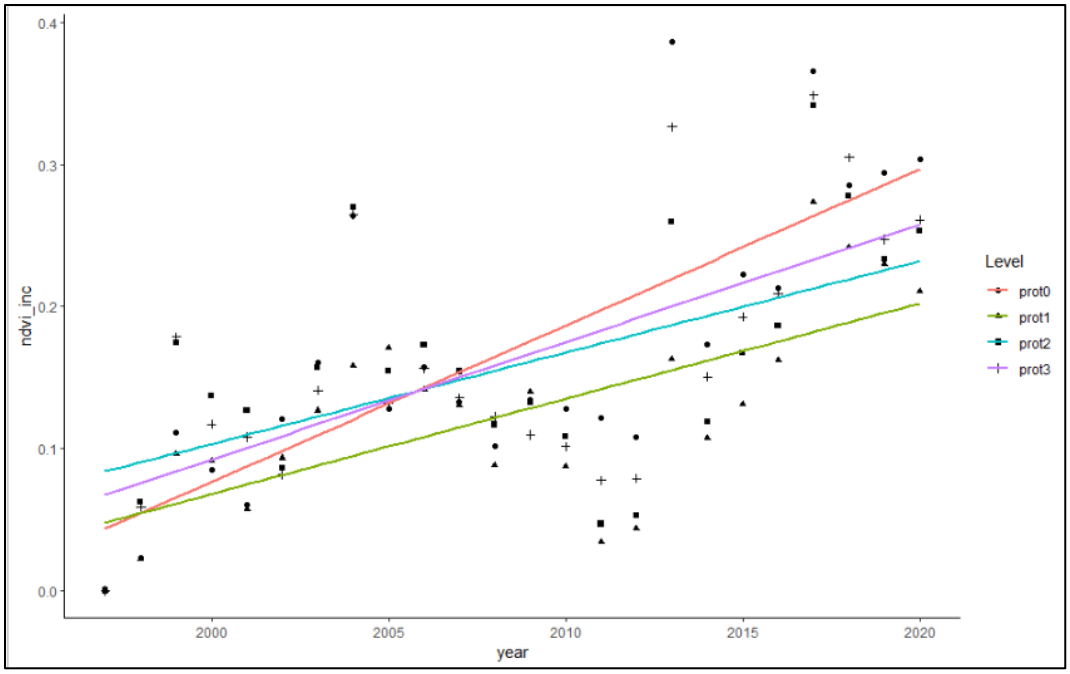

Figure 1.4 Percent of area with an increase in NDVI, per level of protection, over time. prot0: unprotected area, prot1: National Reserve, prot2: National Park, prot3: Strict Nature Reserve.

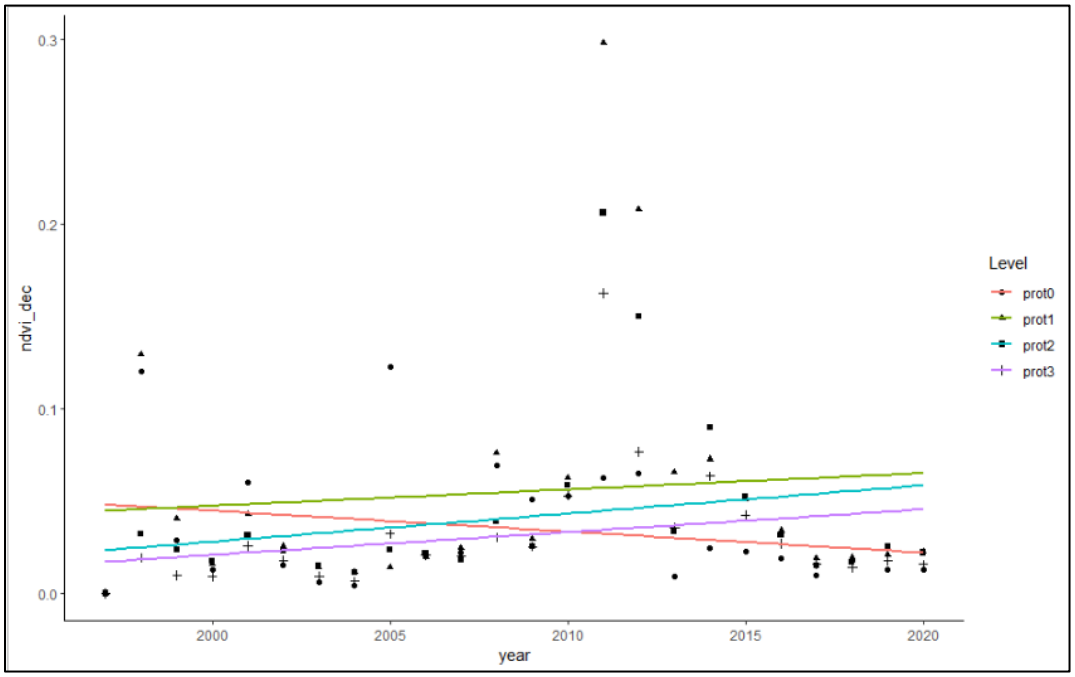

Figure 1.5 Percent of area with a decrease in NDVI, per level of protection, over time. prot0: unprotected area, prot1: National Reserve, prot2: National Park, prot3: Strict Nature Reserve.

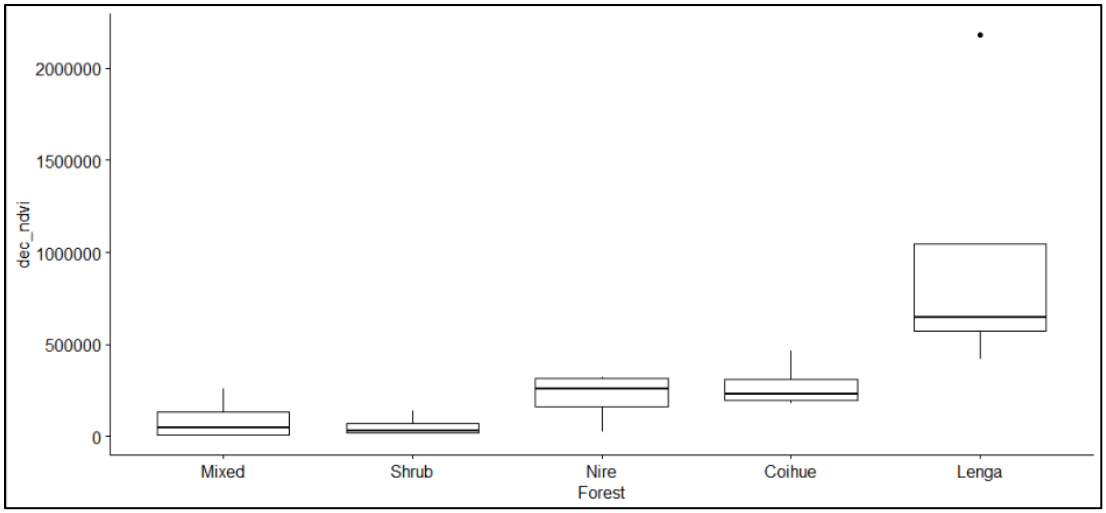

Figure 1.6 Total number of pixels where NDVI decreased over a 20-year period for each type of forest.

As shown in Figure 1.13 and Table 1.2, colocation analysis suggests that some fires were more likely to occur near campsites than if they were randomly distributed. However, none of the quotients are statistically significant, which could be due to the low number of both fires (n=23) and campsites (n=28). Overall, approximately 1.7% of the land within the study area burned between 2000 and 2020.

Discussion

Remote sensing data provide an excellent opportunity to evaluate land surface changes over time at different scales, from local to global assessments, and they have been widely used to evaluate fragmentation and degradation within protected areas (Nagendra et al., 2013). Leisher et al. (2013) analyzed land and forest degradation in 1788 PAs in Latin America between 2004 and 2009, concluding that the rate of degradation increased from 0.04% to 0.10% per year, resulting in 1,097,618 hectares degraded. They evaluated 166 Argentinean PAs, concluding that almost 20% of them have experienced land and forest degradation, despite having a funding level three times the average for the Latin American countries (US$ 8.60 versus US$ 2.50 per hectare). In this study, we evaluated in detail the conservation status of the oldest and one of the largest of the Argentinean PAs, Nahuel Huapi National Park (NHNP). The second NHNP Management Plan published in 2019 (Margutti & Arosteguy, 2019) highlighted the importance of unifying the criteria used to subdivide the PA following its formal and legal delimitation between different conservation categories (Strict Nature Reserve, Wilderness Natural Reserve, National Park, National Reserve; IUCN categories Ia, Ib, II and VI respectively) rather than by zoning categories based on its uses, as the first management plan proposed (Gil et al., 1986). Because the strictest category was created in 1990, our study spanning from 2000 to 2020 provides the best up-to-date evidence regarding the effectiveness of this high conservation category. NDVI values were consistently higher in the SNR compared to the other protection categories and the unprotected area with an assessment based on the average NDVI per category per year.

This result would provide an optimistic assessment of the effectiveness of the strictest category. However, differences in area, location (affecting precipitation,

Table 1.2 Colocation Analysis Summary: relation between wildfires and campsites.

ID	Year	Area (ha)	Colocation Quotient	p-value	Colocation label
2	2013	201.2	1.4	0.5	Colocated
3	1999	99.4	0.0	0.06	Isolated
4	2002	14.8	1.1	0.96	Colocated
9	1999	593.8	1.2	0.86	Colocated
10	1999	2.1	1.4	0.76	Colocated
11	1999	145.0	0.3	0.2	Isolated
12	1999	3830.6	1.4	0.48	Colocated
13	1999	513.4	0.0	0.06	Isolated
15	2002	191.8	1.4	0.42	Colocated
19	2015	459.9	0.9	0.74	Isolated
20	1999	123.1	1.4	0.72	Colocated
21	1999	8.6	1.4	0.52	Colocated
1	1999	1933.2	Not analyzed		
22	1999	177.8	Not analyzed		
23	2004	272.4	Not analyzed		
5	2013	1.0	Not analyzed		
6	2006	246.8	Not analyzed		
7	2012	322.3	Not analyzed		
8	2009	2160.0	Not analyzed		
14	2012	39.6	Not analyzed		
16	2002	2364.4	Not analyzed		
17	2002	317.0	Not analyzed		
18	2004	278.6	Not analyzed		

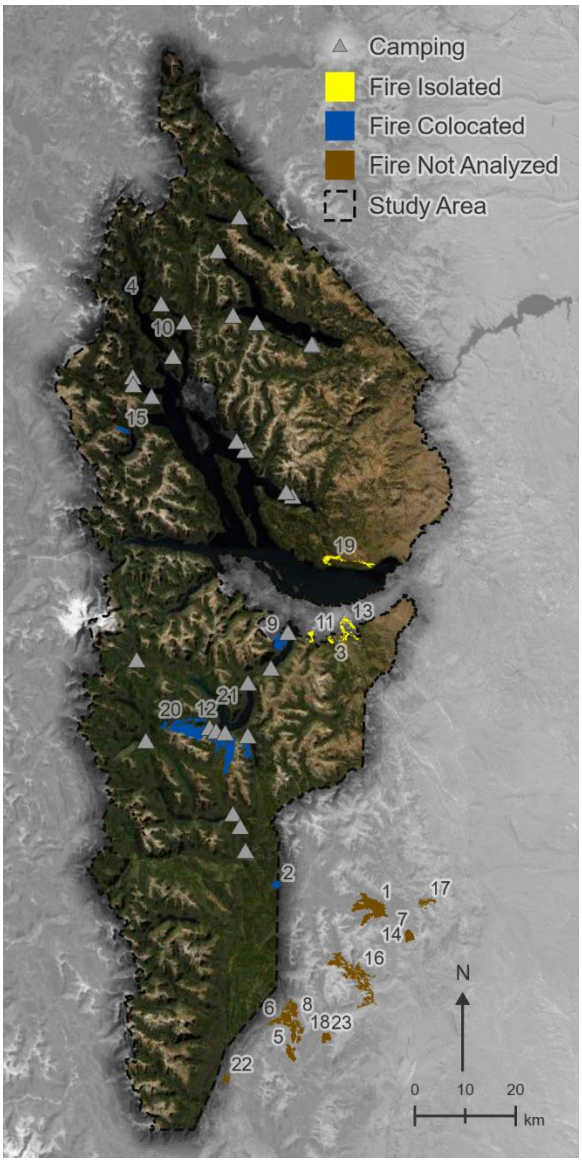

Figure 1.7 Fires and campsites within the study area.

temperature, elevation), and dominant tree species among the protection categories might bias our understanding of differences among them in effectiveness. To address this situation, we re-evaluated NDVI changes based on the selection of 375 random points, with an equal representation of different dominant tree species among the four levels. Surprisingly, with this second analysis, the unprotected area shows the highest values of NDVI, which differ statistically from those values reported in the three categories inside the PA. A common approach is to compare vegetation inside and outside PAs. However, the border of a PA may coincide with a natural change in habitat type leading to misinterpretation regarding the effectiveness of such a PA (Ferraro et al., 2013; Joppa & Pfaff, 2011; Mas, 2005). We purposely selected as unprotected area the neighboring southern region based on landscape, climatic conditions, and floral similarities with the PA, since the eastern area transitions into steppe and the western area is in a different nation, Chile. Finally, NDVI values within NHNP coincided with the levels of protection (NDVI values SNR>NP>NR).

The general NDVI change trend was positive for all four categories. We found similar results with both assessments (average NDVI per category and using 375-pixel values). The observation of increasing NDVI values agrees with the greening phenomenon reported globally (Zhu et al., 2016). There is not a direct interpretation of the process; greener does not necessarily mean better conserved. Seasonal or annual changes in NDVI could be associated with an increase in leaf size, number of leaves per plant, plant density, and crop grown per year, but it can also reflect replacement of natural ecosystems by agricultural lands, or non-native species colonization after disturbances (Piao et al., 2020). Interpreting positive NDVI changes remains challenging because no rigorous method has yet been validated (Leisher et al., 2013). In the case of NHNP, no forest has been replaced by agricultural land. Presence of non-native species, extensive livestock, logging, and wildfires were identified as the main threats in this PA (Margutti & Arosteguy, 2019). While a compelling body of evidence depicts negative effects associated with non-native plant species in NHNP (Franzese & Ghermandi, 2014; Nunez, 2008; Simberloff et al., 2002; Svriz et al., 2013), where 25% of the plant species are non-native (Raffaele et al., 2014), further studies are needed to evaluate if this colonization is related to the increased NDVI values reported here. Furthermore, introduced animals have also impacted forest structure and regeneration in NHNP (Barrios-Garcia & Simberloff, 2013; Martin-Albarracin et al., 2015;

Nunez et al., 2013; Rodriguez-Cabal et al., 2013). The combination of cattle and wildfires negatively affected regeneration of *Nothofagus dombeyi* - *Austrocedrus chilensis* mixed forests in NHNP, facilitating a post-fire transition from forest to bamboo-dominated shrubland (Blackhall et al., 2008), which could increase NDVI values (Franco et al., 2020). Specific studies addressing this question are needed.

We found a positive relationship between NDVI and precipitation, supporting previous findings (Herrero et al., 2020). Furthermore, the variation in precipitation among the levels of protection resembles the differences found among their NDVI values (SNR>NP>Outside>NR, see Fig. 3 and Fig. 8), suggesting that precipitation might be the cause of these differences in NDVI rather than levels of protection. However, mean annual precipitation fluctuated over time across this region, but the overall trend manifests a decreasing pattern. Precipitation therefore cannot explain the increasing NDVI trend.

Despite the general greening pattern explained above, we further investigated this process by extracting pixels where the NDVI changed more than 1 SD during the period studied. The unprotected area accounted for a larger increase compared to the NR, while this difference was not evident between unprotected and NP, unprotected and SNR, or within the three levels of protection inside NHNP. As stated above, interpretation of increasing NDVI is difficult; however, as a similar pattern or tendency was observed inside and outside the PA, the greening process could be a consequence of a global phenomenon such as climate change and increased CO_2 (Ogunkoya et al., 2021), further exacerbated in the unprotected area where extensive livestock and logging are common.

Negative NDVI change could be more easily related to degradation and habitat fragmentation (Leisher et al., 2013; Morton et al., 2005). We found no evidence that degradation was more extensive in the unprotected area compared to that in areas under any level of protection. Interestingly, during the year 2012 there was a peak in the percentage of area with a negative NDVI change inside the PA (NR ~ 30%, NP ~ 20% , SNR ~ 16%), but this value remained low in the unprotected area (~5%), which could be explained by the massive ash deposit as consequence of the Puyehue-Cordón Caulle volcanic eruption that dispersed about 100 million metric tons of ash, covering 7.5 million ha in Patagonia (Wilson et al., 2013). While the central and northern area of NHNP were severely affected by ash deposition, the southern portion of NHNP and the unprotected area

evaluated in this study remained free of ash. The area more severely affected by ash deposition (Bignami et al., 2014) coincides with the red area observed in the NW section of Fig.9.

Fragmentation or degradation were more striking in areas dominated by *Nothofagus pumilio* (both inside and outside the PA) compared to areas dominated by mixed forests and shrublands. *Nothofagus pumilio* forests are distributed at high elevations along approximately 3,000 km of the southern Andes Mountain chain (Mathiasen & Premoli, 2010). A previous study found a positive correlation between *N. pumilio* growth and precipitation, and a negative correlation with mean annual temperature (Lara et al., 2005). Severe droughts in the 20th century following relatively wet and cool years have been associated with a persistent decline in *N. pumilio* growth, suggesting that current and future trends with lower precipitation and higher temperatures associated with climate change would further promote the decline of these forests (Rodríguez-Catón et al., 2016). Furthermore, wildfires have historically affected forests of *N. pumilio* by direct burning (Veblen et al., 2003) and also by reducing root ectomycorrhizal colonization after fire (Longo et al., 2011).

Wildfires in the region are common between September and April, with record numbers in January and February, due to the combination of low precipitation and high temperatures during the austral summer months. The causes of most of these wildfires remain unknown owing to lack of trained personnel and low budgets. However, human activities are thought to be closely related to their occurrence (Margutti & Arosteguy, 2019; Monjeau et al., 2005). Although tourists arrive in NHNP throughout the year, more than 23% of the total annual visitation occurs during two summer months (Área Técnica y Estadística, 2015). Campsites are distributed in NP, NR, and the unprotected area, and camping during summer is one of the favorite activities for both residents and tourists. Since the establishment of campsites within the PA is regulated by the APN (National Park Administration), we explored if the locations of wildfires were associated with the authorized campsites. We used available data (date, location, and area burnt) for 22 wildfires that occurred between 1999 and 2015 within NHNP. Although we found no relationship between these two variables, it is important to notice that there were a total of 239 fires recorded in this period, most of which (150) affected less than 0.5 ha (Margutti & Arosteguy,

2019), and no location data were available, so we could not include such data in our analysis. Furthermore, illegal campfires are common across the region, and the low number of personnel and lack of appropriate vehicles make it difficult for authorities to prevent them (Rivarola et al., 2021a). On the other hand, the current trend of warmer and drier summers following unusually dry springs (phenomena associated with La Niña events), uncommon electrical storms during the summer, and the massive accumulation of fuel material in the forests constitute a permanent threat for these forests, across all levels of protection. The remote and isolated location of most of the SNR areas makes them particularly vulnerable to fires, since ground access is difficult, preventing prompt response to many fires. Thousands of hectares are affected. On December 7th, 2021, lighting ignited a wildfire in the southern area of NHNP, within the SNR. The initial, small fire could not be controlled because firefighters could not access the area. The wildfire is spreading and remains active at the time this manuscript is being written, one and half months after the initiation of the fire. It is estimated that more than 6,000 ha of pristine native forests within NHNP (both in SNR and NP) have been burned (ADN SUR, 2022; Sala de Noticias, 2022).

Effective management of PAs is essential to conserve natural ecosystems. Their role in ecosystem services and preserving biodiversity goes beyond the limits of a PA, and they constitute a substantial fraction of a country's national capital, supporting national sustainable development and human well-being (Bovarnick et al., 2010). The Argentinean PA system has a long history, and despite political and economic instability in the country, the general trend of PA establishment and management by the APN is promising (Rivarola et al., 2021a). Weaknesses and threats were well identified in the latest management plan for NHNP, and general and specific goals were established for both the short and the long term. This study provides further evidence supporting the regional importance of NHNP and particularly the strict nature reserve component.

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CHAPTER II

CONSERVATION STATUS OF SMALL MAMMALS IN NORTHER PATAGONIAN TEMPERATE FOREST

A version of this chapter was published by María Daniela Rivarola, Christy Leppanen and Daniel Simberloff in 2021 in PARKS, 27(2), 15-26.

María Daniela Rivarola conducted a search literature in order to gather all the information needed and wrote the whole article, designed and carried on the fieldwork, analyzed the data and wrote the article. Christy Leppanen revised and edited. Dan Simberloff revised and edited the article.

Abstract

Protected Areas are the cornerstone of conservation strategies, but their effectiveness is increasingly questioned. In Argentina's Nahuel Huapi National Park (NHNP) we compared small mammals in unprotected areas and areas with three protection levels: (1) human activity forbidden, (2) recreation can be authorized, and (3) authorized tourism and extractive uses. A capture-mark-recapture study on five plots in each type of area included a trapping effort of 41,600 traps/night. In 2015, we trapped seven native rodent species and an endemic marsupial. In 2016, we captured the same species except for one rodent. Species richness did not vary among protection levels. However, greatest abundances were in the highest protection level and lowest abundances in the lowest level. We found no evidence that the NHNP protection system substantially conserves small mammals. However, higher abundances in the highest protection level suggest direct human interaction negatively affects this assemblage.

Introduction

Protected areas (PAs) are a key component of biodiversity conservation (Mascia and Pailler, 2011). Target 11 of the Aichi Biodiversity Targets proposes that they must be effectively and equitably managed (CBD, 2010), yet recent publications increasingly question the success of PAs in conserving biodiversity (Barnes et al., 2016; Bruner et al., 2001; Carey et al., 2000; Chape et al., 2005; Coad et al., 2015; Coetzee et al., 2014; Gardner et al., 2009).

We assessed the effectiveness of Nahuel Huapi National Park (NHNP) in northwestern Argentinian Patagonia. Its 750,000 ha are subdivided into three categories or protection levels (Martin and Chehébar, 2001):

a. Strict Nature Reserve: Category I, World Database of Protected Areas (WDPA 2017): In these areas, surrounded by National Park, human activity, apart from scientific research, is forbidden.

b. National Park: Category II, World Database of Protected Areas (WDPA 2017): Extractive use and tourist infrastructures are disallowed. Recreational use can be authorized.

c. National Reserve: Category VI, World Database of Protected Areas (WDPA 2017): These areas, with tourist infrastructure allowed, are buffer zones between protected and unprotected lands. Extractive use may be authorized.

NHNP, including Strict Natural Reserve, National Park, and National Reserve, aims to protect an ecological gradient comprising high Andean Forest, Valdivian temperate forest, and steppe. While large and medium-sized mammals are poorly represented in NHNP's forests (Barnosky et al., 2001), small mammal diversity equals that found in temperate forest elsewhere (Pearson, 1983).

Agricultural economies conflict with natural area protection (Raffaele et al., 2014). Additionally, tourism constitutes a risk; the number of visitors increases annually in NHNP and generates a service demand and consequent economic-ecosystem conflicts (Martin and Chehébar, 2001; Monjeau et al., 2005). Introduced plants, vertebrates, and invertebrates have substantially affected NHNP forests (Arbetman et al., 2012; Barrios Garcia Moar, 2012; Correa et al., 2012; Franzese and Ghermandi, 2014; Nunez et al., 2013; Rodriguez-Cabal et al., 2013; Simberloff et al., 2002; Svriz et al., 2013). Also, a combination of natural and anthropogenic factors has increased wildfire severity in Patagonia (Davis et al., 2019; Godoy et al., 2019; Paritsis et al., 2013; Raffaele et al., 2014; Tiribelli et al., 2019; Urretavizcaya and Defossé, 2019).

Many problems in NHNP have been identified through scoring or PA management effectiveness evaluations (Rusch, 2002), but no clear evidence shows to what extent they impact resident small mammals. In an ecosystem with low vertebrate diversity like NHNP, small mammals (particularly rodents) affect forest dynamics and constitute the main food of

many other species (Raffaele et al., 2014). Nevertheless, because rodents are small and fecund, the general perception is that they occur in high density and require little area, so they can persist in a fragmented landscape, which may not be true for all species (Lidicker, 1989). Small mammal species extinctions and distribution contractions have been reported in Northern Patagonia (Teta et al., 2014).

We aimed to assess the conservation effectiveness of NHNP by monitoring its small mammals. We proposed that communities inhabiting Strict Nature Reserve Areas will be richer and more abundant because they lack human intervention. Increasing contact with human activities and presence along the gradient National Park-National Reserve-unprotected area could be reflected in impoverished small mammal communities.

Methods

We conducted our study in 2015 and 2016 in NHNP in the Andean foothills of Argentina (Fig. 2.1). Average temperatures range from 3°C (July) to 15°C (January). Precipitation is greatest in autumn and winter, averaging 1,800 mm annually. The area lies within the southern temperate forest in the sub-Antarctic biogeographic province, with the Patagonian Steppe Ecoregion also represented along the eastern, drier fringe (Mermoz and Martin, 1986). Southern beeches (Nothofagus dombeyi, N. pumilio, N. antarctica) and Chilean cedar (Austrocedrus chilensis) dominate the canopy, and bamboo (Chusquea culeou) and several species of shrubs and smaller trees the understory (Dimitri, 1977). Elevation (from 3554 to 500 m a.s.l.), water availability, and dominant species are inter-related. Differences in biological outcomes measured in different ecological conditions might reflect variation of those conditions rather than the management approach (Barnes et al., 2017). To reduce such variation, we worked entirely in N. dombeyi-dominated forest between 500 and 700 m a.s.l.

We implemented a widely used strategy to assess PA effectiveness, comparing communities inside and outside of PAs (Coetzee et al., 2014). We conducted a capture-mark-recapture study to evaluate small mammal communities across different protection levels

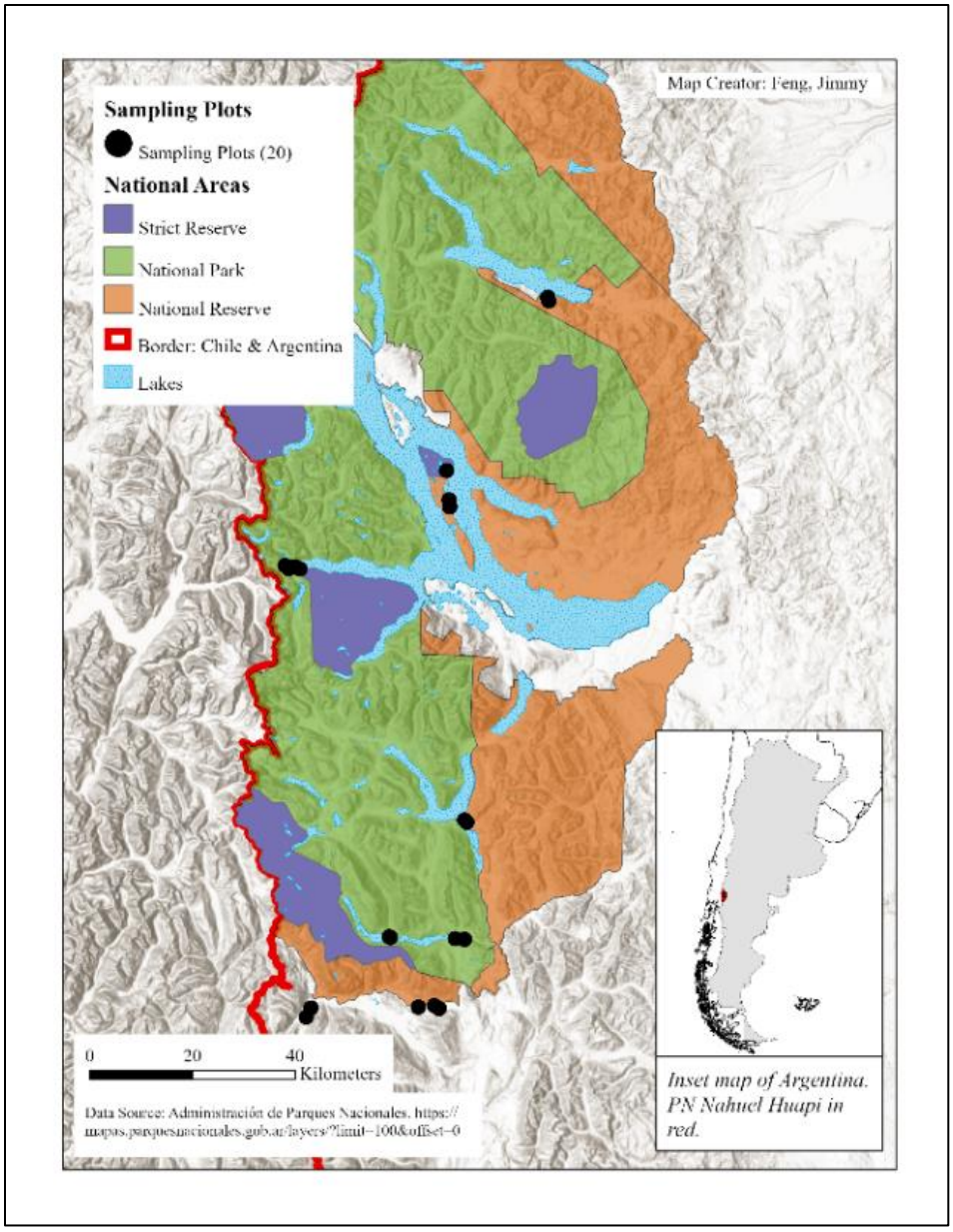

Figure 2.1 Study site map. Map of NHNP with its protection categories indicated with different colors. Purple: Strict Nature Reserve, Green: National Park, Orange: National Reserve. Dots indicate sampling plots. Overlapping dots does not mean overlapping sampling plots. Sampling plots were at least 1,000 m apart.

and outside of NHNP, establishing 20 plots (60 x 60 m) at least 1 km apart, five each in the Strict Nature Reserve, National Park, National Reserve, and outside PAs (Fig. 2.1).

In 2015 we also established two extra plots on Isla Victoria (largest island in Nahuel Huapi Lake) in an area where natural forest was replaced by Douglas fir (*Pseudotsuga menziesii)* plantations approximately 70 years ago. To assess sampling area equivalences, we measured vegetation cover and plant species composition in 100 squares (1 x 1 m) per plot both years; we classified the species based on native or non-native status. To estimate forest structure we superimposed over each plot a 13 x 13-transect grid, with transects 5 m apart. We defined 169 nodes (one at each transect intersection) where we measured the diameter at breast height (DBH) of the nearest tree (within 1 m radius) or recorded zero for treeless nodes. We estimated tree density by the number of trees over the plot area (3,600 m^2). We converted DBH values to obtain basal area per plot (G):

$$G = \frac{\sum g_i}{S_T}$$

Where g_i is the stem cross-section area of tree i in m^2 and S_T is the plot area in hectares.

Invertebrates are components of small mammal diets in Patagonian temperate forests (Pearson, 1983). We established nine pitfall traps per plot: plastic containers 10 cm in diameter and 15 cm deep half-filled with a water/dishwashing liquid solution. We activated pitfall traps simultaneously with small mammal trapping sessions. We preserved samples in 70% ethanol and recorded abundances.

We used a star design for each plot, establishing 25 trap stations 10 m apart, georeferencing the central trap station with a Garmin GPS60. At each station, we activated a Sherman trap (10 x 10 x 29 cm) baited with oats and peanut butter (Pearson and Pearson, 1982) on the ground and a Tomahawk trap (30 x 14 x 14 cm) baited with apple and banana slices (Fonturbel and Jimenez, 2009; Rivarola, 2010) in vegetation 1 m above the ground. We conducted monthly capture sessions during austral summers in 2015 and 2016, activating traps four consecutive nights and checking them at sunrise and at sunset, yielding a total capture effort of 41,600 traps/night. Trap success was calculated as number of small mammals caught divided by number of active traps.

We identified to species each individual captured. Before releasing individuals, we marked marsupials with Passive Integrated Transponders (PIT-Tags, TXP148511B model, Biomark 8.5 mm X 2.12 mm, 134.2 kHz ISO, 0.067g) by subcutaneous implantation on the back and rodents with ear-tags (National Band and Tag Company, style 1005-1). We handled captured animals following UTK-IACUC protocol # 2409-0116 (Institutional Animal Care and Use Committee, University of Tennessee).

To compare small mammal diversity between sites under different protection levels, we used species richness (S), assemblage abundance, and abundance of each species. We used Kruskal-Wallis tests to compare each index across protection levels and conducted post-hoc Tukey's Honest Significance Differences analyses with 95% confidence level when an index varied in response to protection level. To evaluate habitat equivalence between plots, we used ANOVA and Kruskal-Wallis tests to compare vegetation cover, plant species richness, tree basal area, tree density, and arthropod abundance. Finally, we analyzed these environmental variables with Principal Component Analysis (PCA) to evaluate clustering of plots within protection levels.

Small mammals can deter the colonization of non-native plant species, a process known as biotic resistance (Pearson et al., 2014). We analyzed the proportion of non-native plants (both richness and cover) across the different levels of protection, with Kruskal-Wallis test followed by post-hoc Dunn test. Furthermore, we used a generalized linear model to explore the relationship between the abundance of small mammals and the richness and cover proportions of non-native plant species.

Results

We had a higher capture effort in 2016 but higher capture success in 2015 (Table 2.1). We trapped no small mammals in the two plots established in 2015 in areas dominated by Douglas fir, despite a capture effort of 2,100 traps/night.

In 2015, we trapped seven rodents – long-haired mouse *Abrothrix hirta*, olive grass mouse *A. olivacea*, long-tailed pygmy rice rat *Oligoryzomys longicaudatus*, long-clawed mole mouse *Geouxus valdivianus*, Andean long-clawed *mouse Chelemys macronyx*, Chilean climbing

mouse *Irenomys tarsalis*, southern big-eared mouse *Loxodontomys micropus* – and the endemic marsupial monito del monte *Dromiciops gliroides* (Fig. 2.2).

In 2016, we captured the same species except for *C. macronyx*. *Abrothrix hirta*, *D. gliroides* and *O. longicaudatus* were by far most abundant across the four protection levels both years (Fig. 2.3).

Species richness did not vary among protection levels in 2015 or 2016 (Table 2.2). However, assemblage abundances were greatest in the highest protection level and lowest in the lowest protection level each year (Table 2.2; Tukey test [p=0.0287 for 2015 and p=0.0399 for 2016]). Finally, abundance by species across the NHNP system and outside PAs differed only for *L. micropus* and *D. gliroides* (Appendix, Table 1). *Loxodontomys micropus* was trapped only outside the PA in 2015; this difference did not persist in 2016.

A Kruskal-Wallis test on abundance of *D. gliroides* vs protection level yielded p = 0.0381 in 2016; however, the subsequent Tukey test did not indicate a significant difference between any pair; thus those results should be cautiously interpreted. Nevertheless, *D. gliroides* abundances appeared greater in National Park and Strict Nature Reserve than in National Reserve and outside PA. To evaluate these unequal abundances further, we combined capture numbers from the Strict Nature Reserve and National Park as "High protection" and National Reserve and outside NHNP as "Low-no protection." Each year saw a difference between these groups (2015, t=3.2188, df=9.4882, p-value=0.0098; 2016: t=2.8567, df=10.16, p-value=0.0168).

Most environmental variables showed no differences among treatments, suggesting habitat equivalence. We evaluated forest structure with two variables (tree basal area and tree density). While the former manifested no difference among protection levels (F= 2.162, DF 3, 16, p=0.1324), the latter showed a marginal difference between National Reserve and National Park (F=3.218, DF=3, 16, p=0.051, Tukey test p=0.049). Ground vegetation cover and plant richness were analyzed separately by year. While vegetation cover did not differ among treatments both years (F=1.801, DF 3, 16, p=0.187, and KW chi-squared=3.549, DF=3, 16, p=0.314 for 2015 and 2016, respectively), plant species richness was consistently higher in the unprotected area (F=7.813, DF= 3, 16, p=0.002 for 2015, and KW chi-squared=13.16, DF= 3, 16, p=0.004 for 2016, Appendix, Fig. 1).

Table 2.1 Capture summary. Small mammals captured during 2015 and 2016. Capture effort for two extra plots located in an area dominated by Douglas fir during 2015 not included here.

	Summer 2015	Summer 2016
Capture effort	20,600 traps/night	21,000 traps/night
Number of individuals caught	727	532
Total number of captures	2102	1894
Capture Success	10.20%	9.02%

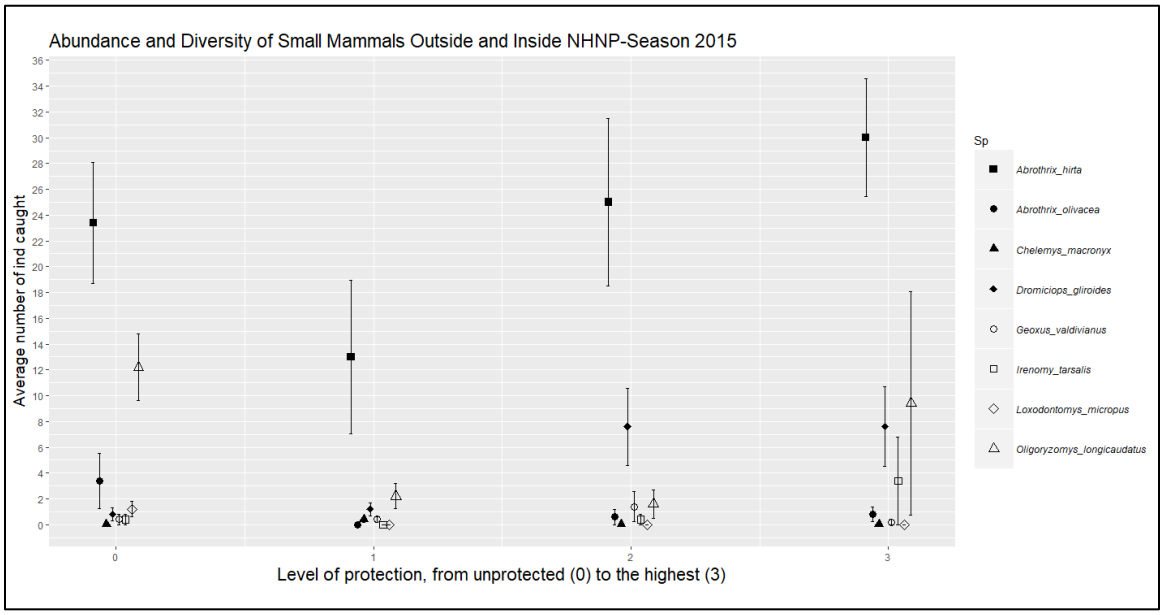

Figure 2.2 Season 2015. Diversity and average abundance of small mammals caught across different protection levels in NHNP during summer 2015. (0) outside NHNP, (1) National Reserve, (2) National Park, (3) Strict Nature Reserve.

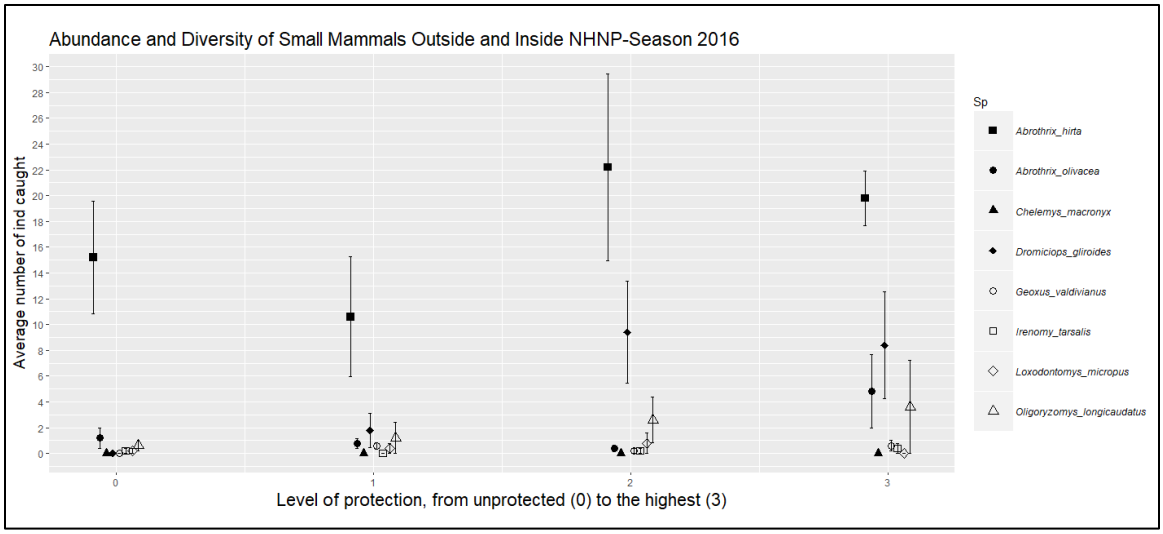

Figure 2.3 Season 2016. Diversity and average abundance of small mammals caught across different protection levels in NHNP during summer 2016. (0) outside NHNP, (1) National Reserve, (2) National Park, (3) Strict Nature Reserve.

*Table 2.2 Community vs Protection. Comparison among small mammal communities across different protection levels in the NHNP system and outside. Each variable (column 1) was analyzed for each year independently (top 2015, bottom 2016) by Kruskal-Wallis's Test. Mean±standard error is indicated in each cell. * Indicates statistical significance.*

	Outside NHNP	National Reserve	National Park	Strict Nature Reserve	KW chi^2	Df	p-value
Species Richness	3.8±0.66 2.2±0.49	3.0±0.74 3.0±0.32	3.0±0.54 2.8±0.66	3.2±0.37 3.0±0.54	0.853 4.1315	3,16 3,16	0.8368 0.2476
Assemblage Abundance	41.8±8.45 17.0±3.99	17.2±5.91 15.4±5.55	36.6±7.86 35.8±7.08	51.4±8.26 37.6±3.75	7.6316 9.2491	3,16 3,16	0.0542* 0.0261*

Finally, arthropod abundance did not vary among protection levels (chi-squared= 1.1102, DF 3, p=0.7746 and chi-squared=5.7657, DF=3, p=0.1236, for 2015 and 2016 respectively).

We evaluated clustering of plots within protection levels using PC1, PC2 and PC3, which accounted for over 80% of environmental variation (Appendix, Table 2). No clear clustering of plots occurred within protection levels (Fig. 2.4).

Native plants had higher richness and cover than non-native plants across the four levels of protection (Fig. 2.5). However, the proportion of non-native richness varied among the levels of protection (KW chi-squared=19.113, df=3, p=0.0002). This proportion was higher in the unprotected area compared to National Reserve (p=0.03) and to National Park (p=0.0004). Furthermore, the proportion was higher in the Strict Nature Reserve compared to National Park (p=0.017) (Fig. 2.6). The same pattern was found for the proportion of non-native species cover (KW chi-squared=21.104, df=3, p=0.0001), with the cover proportion higher in the unprotected area compared to the National Reserve (p=0.016) and to National Park (p=0.00008). As before, the proportion of non-native cover was higher in the Strict Nature Reserve compared to National Park (p=0.03) (Fig. 2.7).

The proportion of non-native plant species cover did not present a significant relationship with the abundance of small mammals (t=-0.915, p=0.366), neither did the proportion of richness of non-native plant species (t=0.424, p=0.673).

Discussion

Several PA effectiveness evaluation methods have been implemented since the 1990s, suggesting need for a generic approach (Hockings, 2003). There are four complementary levels to assessing PA effectiveness: 1) coverage, 2) broad-scale outcomes, 3) protected area management effectiveness assessments (PAME), and 4) biological outcomes obtained from monitoring (Hockings et al., 2006; Leverington et al., 2010).

Biological outcomes inform us to what extent a PA is achieving its goal of biodiversity conservation (Barnes et al., 2017). Quantitative data from population or community

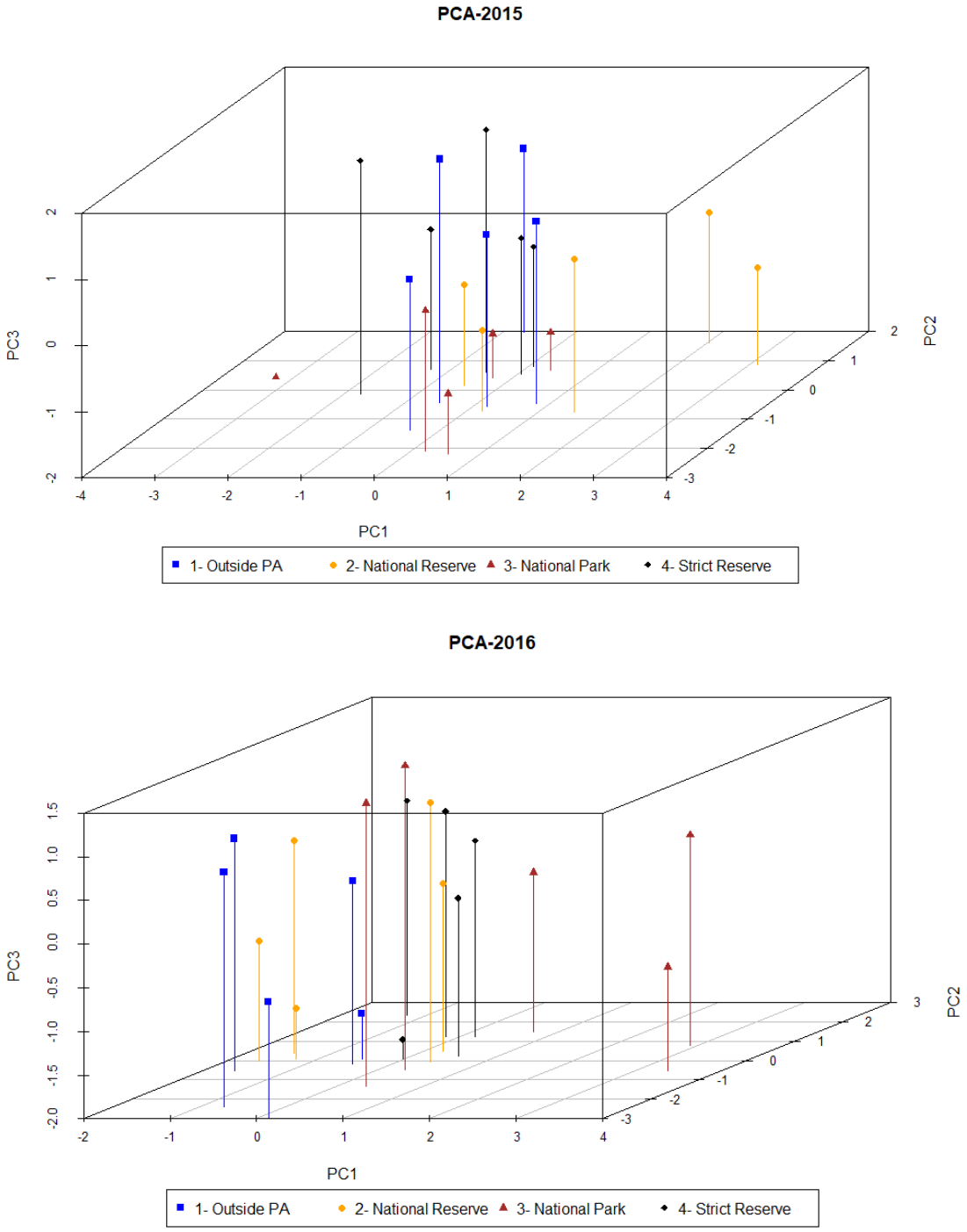

Figure 2.4 Plots vs Principal Components. Lack of clustering of plots within protection levels using PC1, PC2 and PC3. Top 2015, bottom 2016.

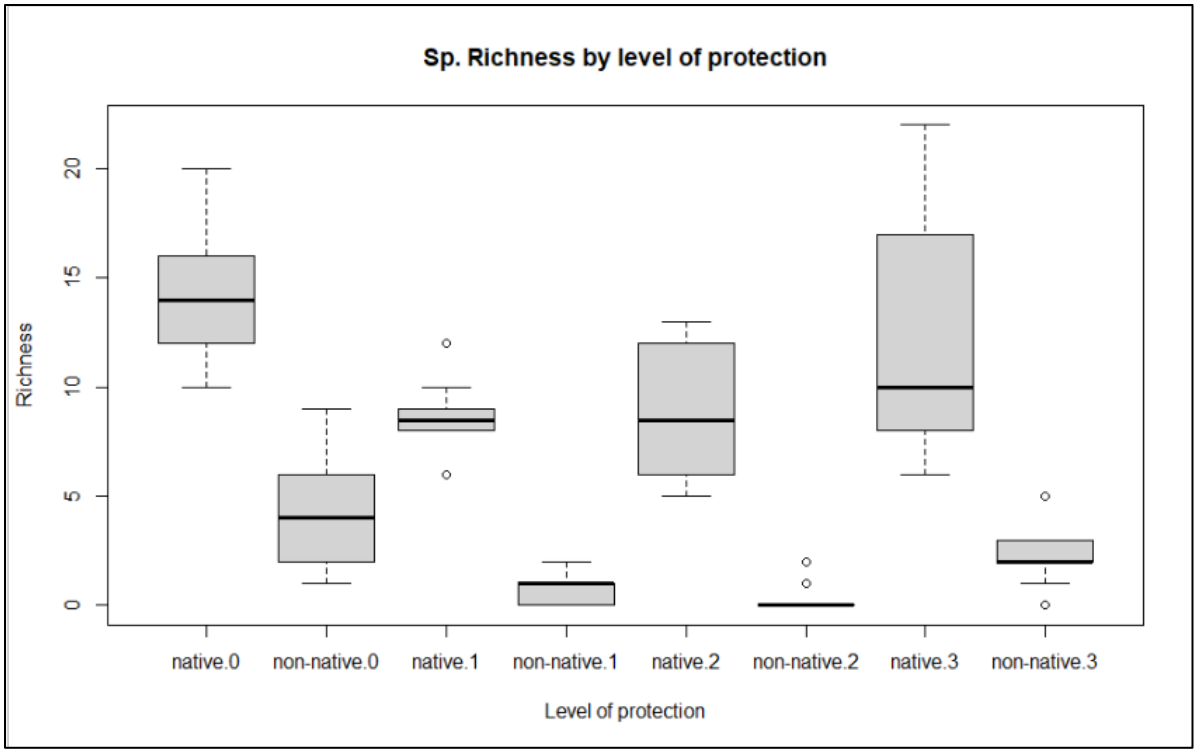

Figure 2.5 Native and non-native plants species richness at each level or protection (0: unprotected area, 1: National Reserve, 2: National Park, 3: Strict Natural Reserve).

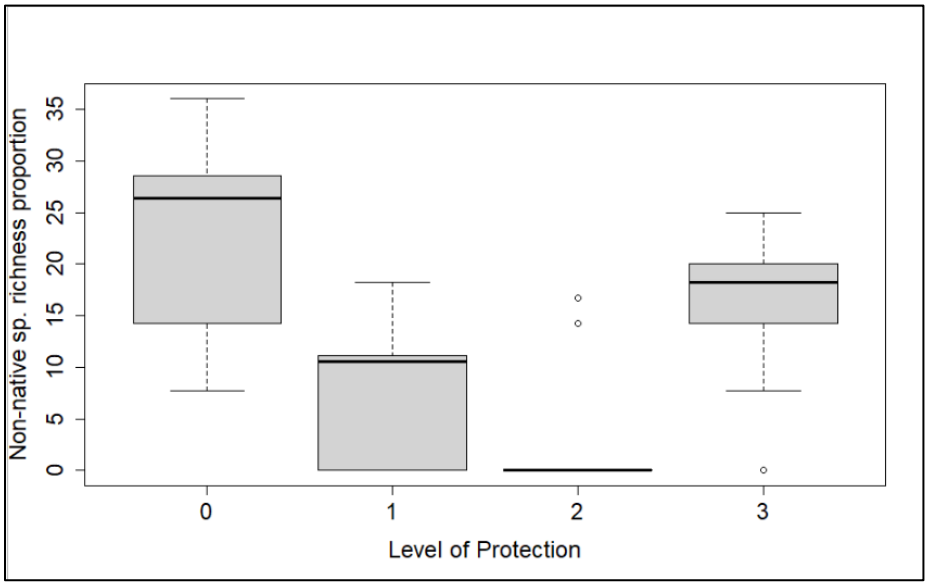

Figure 2.6 Proportion of non-native species at each level of protection (0: unprotected area, 1: National Reserve, 2: National Park, 3: Strict Natural Reserve).

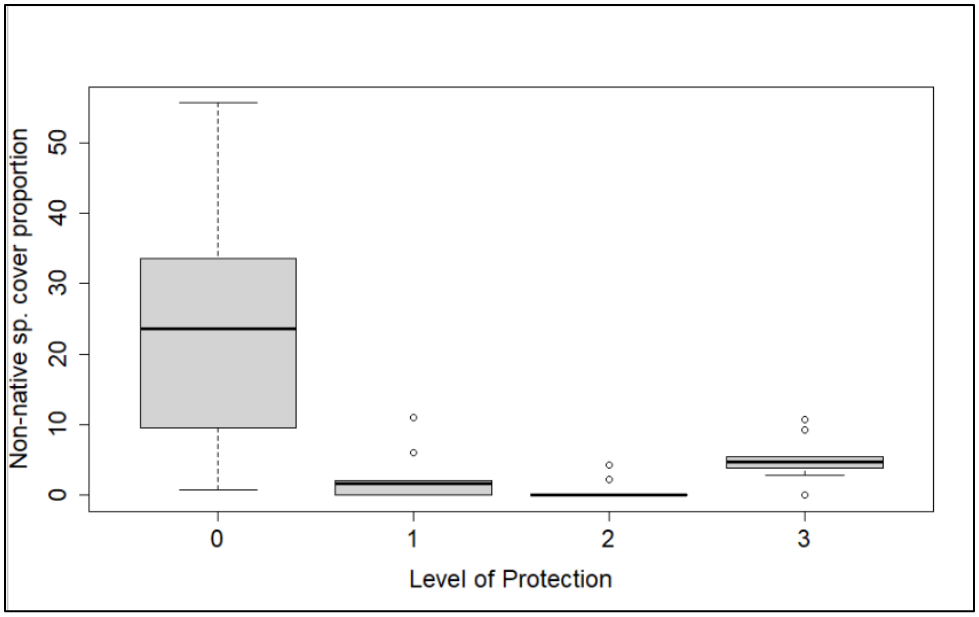

Figure 2.7 Proportion of cover of non-native plant species across the four levels of protection (0: unprotected area, 1: National Reserve, 2: National Park, 3: Strict Nature Reserve).

monitoring complement the overall assessment, providing information regarding the effects of those factors on particular species or groups (Christie, 1984a). A management effectiveness evaluation of NHNP using PAME concluded that performance was "Fairly satisfactory" (scoring 51-75% of optimal) (Rusch, 2002). However, lack of monitoring for most resident species, particularly small mammals, prevents assessment of the effect of current management on these communities.

To minimize the effect of landscape variation on species presence/absence and abundance, we restricted our plots to forest dominated by N. dombeyi, between 500 and 700 masl, aiming to relate community and population variation to protection levels. The absence of native small mammals in pine plantation agrees with previous studies in northern Patagonia (Lantschner et al., 2011). Pearson (1983) described nine species in the most comprehensive small mammal study in northern Patagonian forests. We recorded all but Aconaemys fuscus, whose distribution occurs north of NHNP (Roach, 2016). Our analysis yielded no clear evidence that the NHNP different protection categories are effectively conserving small mammals.

Creating a species conservation priority list of Patagonian vertebrates was proposed as an inexpensive, rapid tool to use resources allotted to biodiversity protection efficiently (Christie, 1984a). Detailed monitoring methods such as that presented here could help validate or update such lists. The conservation status of the 32 resident mammal species of NHNP was assessed in 1994 (Úbeda et al., 1994). The study considered two protection levels, National Park (high) and National Reserve (low) and defined 14 variables believed relevant for species survival and conservation, assigning scores to each. However, using variables such as body size, feeding behavior, and reproductive potential yielded low scores for small mammals, which could bias results against this group as suggested for previous studies (Lidicker, 1989). Most species recorded in our study occupy the bottom part of the priority list proposed by Úbeda (1994), except for *D. gliroides*, ranked tenth. *Dromiciops gliroides*, declared vulnerable in Argentina (Diaz and Ojeda, 2000), is listed as Near Threatened because its population is declining mainly owing to habitat changes, especially forest conversion to agriculture and habitat fragmentation (IUCN Red List; (Martin et al., 2015). It is remarkable that *D. gliroides* was the third and second most abundant species in 2015 and 2016 respectively (Appendix, Fig. 2). However, these populations were smaller than those

previously reported in Argentina (Rivarola, 2010) and Chile (Fonturbel et al., 2012). The first long-term study tracking population changes in this species demonstrated yearly variation associated with natural events (Balazote Oliver et al., 2017). Importantly, most individuals were trapped in plots with a high protection level (Strict Nature Reserve and National Park).

Abrothrix hirta exceeded in abundance and distribution all other species (Appendix, Fig. 2 and 3). This result agrees with previous studies (Christie, 1984b; Pearson and Pearson, 1982). Although a typical forest species, A. hirta is found in steppe with sufficient ground cover and bushes (Pearson, 1983). This habitat breadth plus its omnivorous feeding behavior could be associated with its numerical dominance. Oligorizomys longicaudatus has been described as scarce in dense forest (Pearson, 1983). However, it was the second most abundant species trapped during 2015 (Appendix, Fig. 2). Its numbers dropped in 2016, but it was the third most abundant species (Appendix, Fig. 2). As abundance and protection level were unrelated, this decline could be due to a natural process. The remaining species combined accounted for 8.84% of the assemblage abundance in 2015, and 10.17% in 2016. Their low numbers and uneven distribution (Appendix, Fig. 2 and 3) suggest that conclusions based on these data are preliminary (Appendix).

Small mammal populations commonly undergo cycles of different length responding to biotic and abiotic factors (Armas et al., 2016; Murua et al., 1986). Lack of this information for the communities in this area renders tenuous our conclusion regarding NHNP effectiveness and highlights the importance of long-term studies and regularly scheduled monitoring programs.

The higher assemblage abundance recorded both years inside the Strict Nature Reserve suggests that direct human interaction negatively affects this assemblage, a situation particularly important for the marsupial D. gliroides. The different protection categories did not actually differ as much as one might expect in terms of anthropogenic impacts. For instance, we found cattle (domestic, semi-wild, or wild) in almost every plot. Species inhabiting plots near human settlements might suffer predation by domestic cats. Dromiciops gliroides was preyed on by domestic cats in a municipal PA in Bariloche (Di Virgilio et al., 2014). Interestingly, the four plots located in the area of Puerto Blest, where no domestic cats are present, recorded the highest abundances of D. gliroides. Areas where we found more diversity and abundance were located in zones with more difficult access,

possibly implying it is not the protection category but primarily the inaccessibility that is preserving these communities, as has happened in PAs elsewhere (Struhsaker et al., 2005).

Non-native plant species are a threat worldwide, particularly in NHNP where 25% of the flora diversity are non-native species (Raffaele et al., 2014). We found that the proportion of richness and cover of non-native plants were higher in the unprotected area, shielding a positive effect of NHNP at preventing the invasion of non-native species. Interestingly, while no non-native species was identified in National Park, both their richness and cover in the Strict Nature Reserve were higher. The five plots under this higher category were isolated, with no near human settlement, and only accessible by boat. While direct anthropogenic effects seem an unlike reason for the colonization of non-native species, both native and non-native animal species might facilitate this process (Nunez et al., 2013). Small mammals, particularly rodents, have been identified as an effective biotic resistant in central Argentina, where rodent exclusion increased seedling recruitment by 100-300% in eight out of nine non-native species (Pearson et al., 2014). However, we did not find a relation between the proportion of non-native species and small mammal abundance. Further studies are needed to understand this pattern.

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Appendix

This appendix was published as "Supplementary tables, figures and species information" in PARKS https://parksjournal.com/parks-27-2-november-2021

*Table 2.3 Species vs Protection. Comparison among small mammal communities across different protection levels in the NHNP system and outside. Each diversity variable (column 1) was analyzed for each year independently (top 2015, bottom 2016) by Kruskal-Wallis Test. Mean±standard error is indicated in each cell. * Indicates statistical significance.*

	Outside NHNP	National Reserve	National Park	Strict Nature Reserve	KW chi^2	DF	P-value
A hirta	23.4±4.69 15.2±4.37	13.0±5.98 10.6±4.65	25.0±4.46 22.2±7.27	30.0±4.57 19.8±2.11	4.1562 2.9045	3,16 3,16	0.2451 0.4066
O. longicaudatus	12.2±2.59 0.6±0.4	2.2±0.97 1.2±1.2	1.6±1.12 2.6±1.78	9.4±8.66 3.6±3.6	7.1228 0.5515	3,16 3,16	0.0681 0.9074
D. gliroides	0.8±0.49 No capture	1.2±0.49 1.8±1.32	7.6±2.99 9.4±3.95	7.6±3.07 8.4±4.16	5.7734 8.417	3,16 3,16	0.1232 0.0381*
A. olivacea	3.4±2.13 1.2±0.8	No capture 0.8±0.37	0.6±0.6 0.4±0.24	0.8±0.58 4.8±2.85	2.3911 1.4184	3,16 3,16	0.4953 0.7012
G. valdivianus	0.4±0.4 No capture	0.4±0.24 0.6±0.24	1.4±1.16 0.2±0.2	0.2±0.2 0.6±0.4	0.8742 4.3244	3,16 3,16	0.8316 0.2285
C. macronyx	No capture No capture	0.4±0.24 No capture	No capture No capture	No capture No capture	6.3333 -	3,16 -	0.0965 -
I. tarsalis	0.4±0.4 0.2±0.2	No capture No capture	0.4±0.4 0.2±0.2	3.4±3.4 0.4±0.4	1.1333 0.1333	3,16 3,16	0.7690 0.7690
L. micropus	1.2±0.58 0.2±0.2	No capture 0.4±0.4	No capture 0.8±0.8	No capture No capture	9.9805 1.1385	3,16 3,16	0.0187* 0.7678

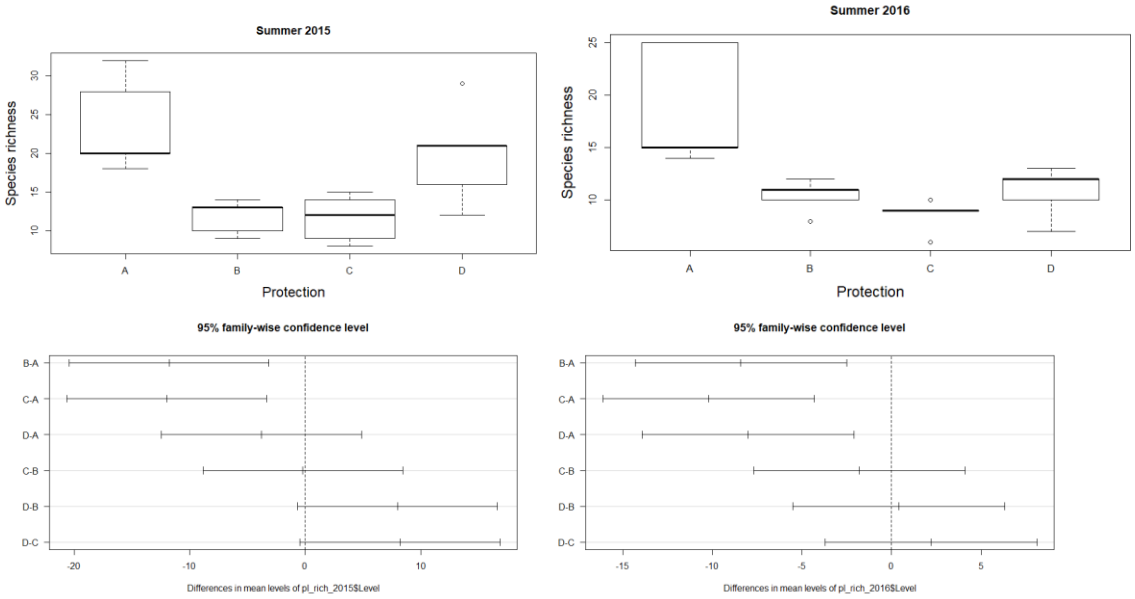


Figure 2.8 Plant species richness. Variations in sites with different protection levels in NHNP. Top left corresponds to 2015, top right to 2016. (A) outside PA, (B) National Reserve, (C) National Park, (D) Strict NatureReserve. Results from Tukey's HSD test at bottom for each year. Differences between group A and B (Outside PA and National Reserve) and A and C (Outside PA and National Park) occurred both years (A-B p=0.0063 for 2015 and p=0.0044 for 2016, A-C p=0.0055 for 2015 and p=0.0007 for 2016). Also, differences between groups A and D (Outside PA and Strict Nature Reserve) were found in 2016 (p=0.0065).

Table 2.4 Principal Component Analysis. Five environmental variables used: vegetation cover, plant species composition, tree density, tree basal area and arthropods abundance. The first three components account for more than 80 percent of the variation.

		PC1	PC2	PC3	PC4	PC5
2015	Standard Deviation	1.3347	1.0880	1.0229	0.7352	0.6693
	Proportion of Variance	0.3563	0.2368	0.2093	0.1081	0.0896
	Cumulative Proportion	0.3563	0.5930	0.8023	0.9104	1.0000
2016	Standard Deviation	1.3097	1.2275	0.9013	0.8440	0.50316
	Proportion of Variance	0.3431	0.3014	0.1625	0.1424	0.05063
	Cumulative Proportion	0.3431	0.6444	0.8069	0.9494	1.0000

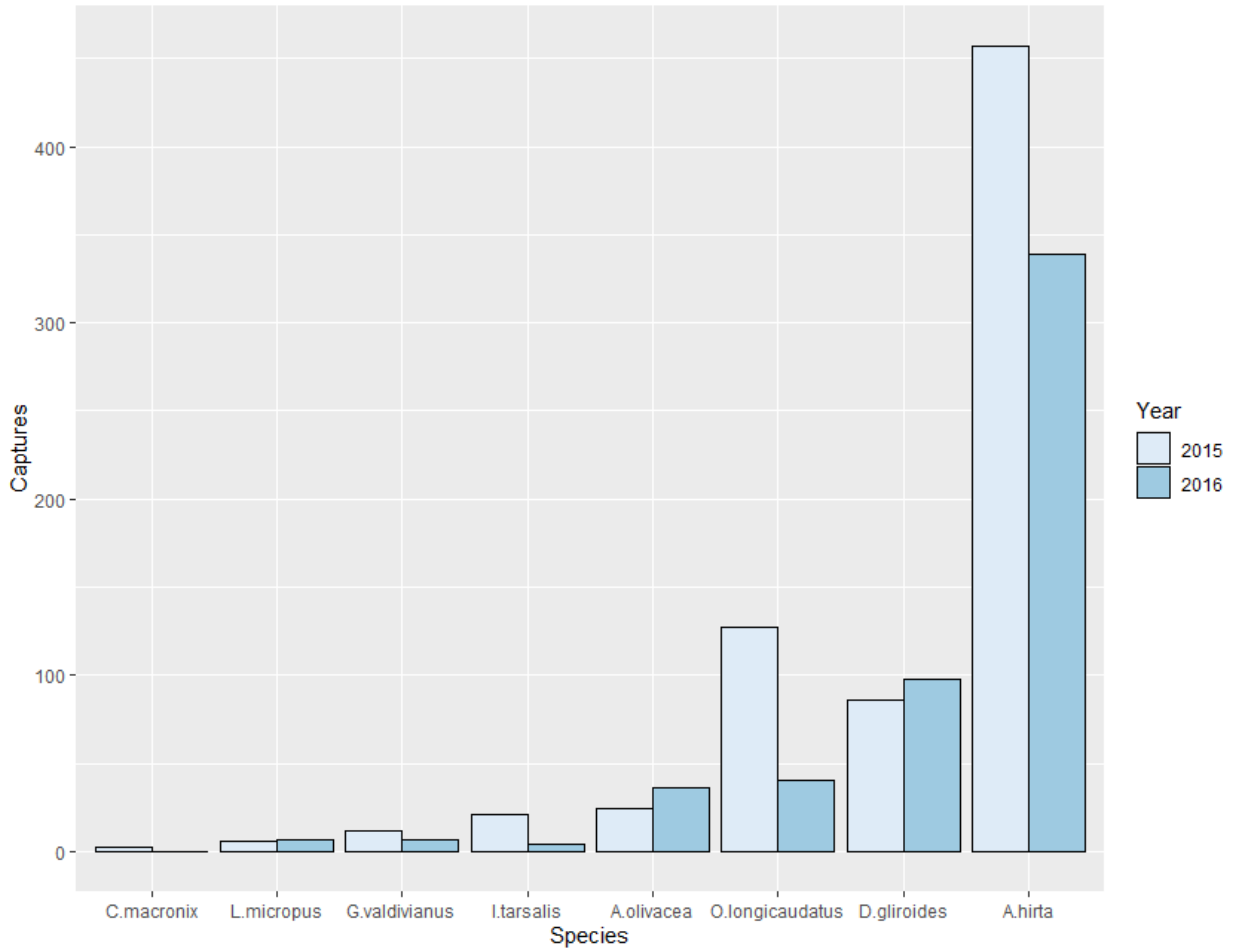


Figure 2.9 Small mammal abundance. Number of small mammals trapped, per species, during sampling seasons 2015 and 2016.

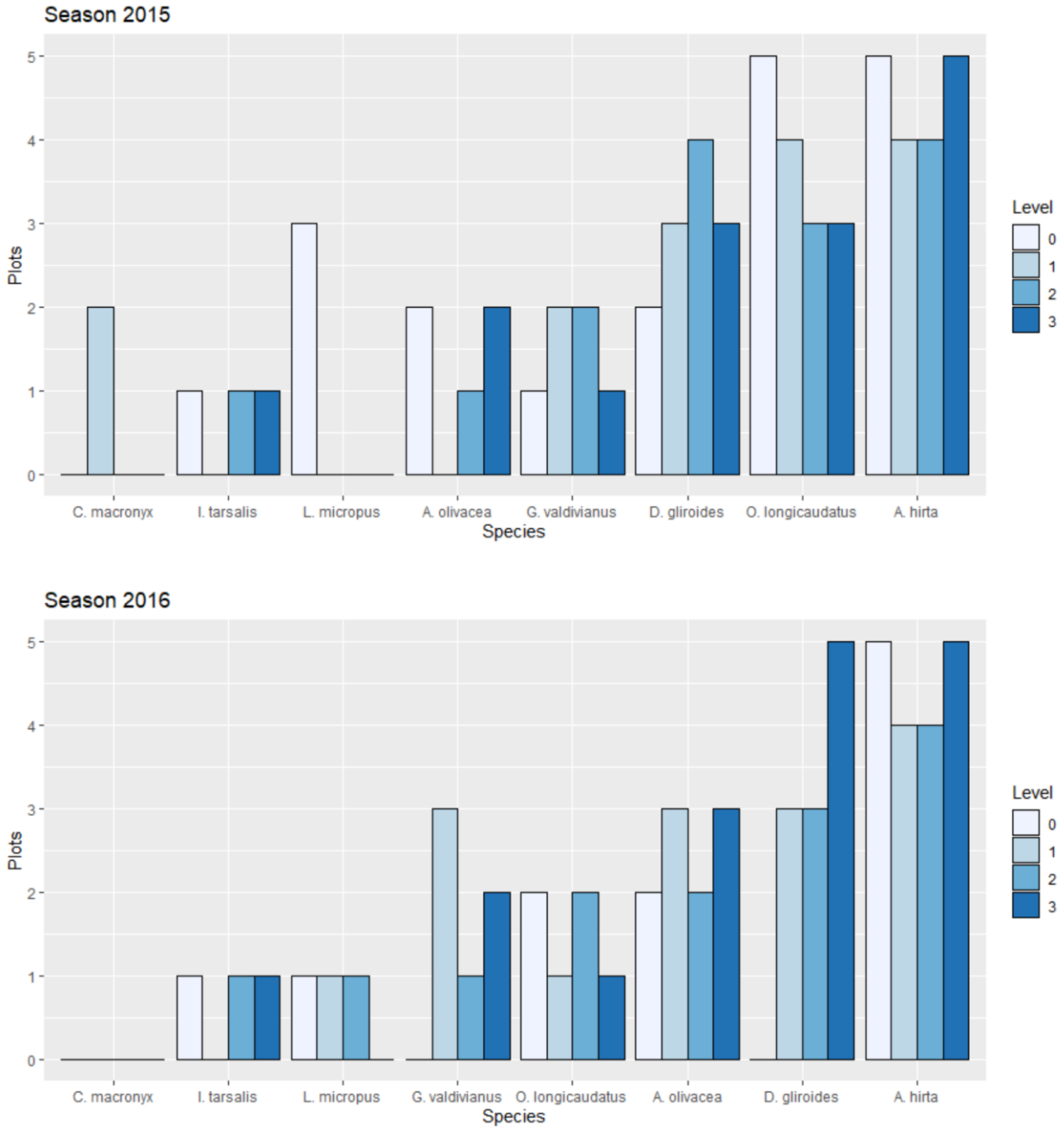


Figure 2.10 Species plot occupancy. Number of plots per level of protection where the species were trapped. Top: Season 2015. Bottom: Season 2016. Level of protection 0: Outside PA, 1: National Reserve, 2: National Park, 3: Strict Nature Reserve.

Species Less Frequently Trapped

Abrothrix olivacea inhabits areas with thick grass, marshes, and forest with sufficient ground cover (Pearson, 1983), preferring microhabitats with vegetation cover from above (Murua et al., 1986). All of our plots had good ground cover; nevertheless, the species was undetected in most of them in 2015 but doubled in occurrence and abundance in 2016 (Fig. 3). This change highlights the importance of long-term studies and also of looking more closely at variables that might affect the occurrence of this species, beyond protection level.

Irenomys tarsalis occupies dense forest with understory dominated by bamboo *Chusquea culeou* (Pearson, 1983). Plots with bamboo as a dominant species had flowered in 2010 (Herrero, 2013). *Chusquea culeou* usually grows vegetatively, but after 50-70 years, it flowers synchronously, produces a massive amount of seeds, then dies. Recovery is slow (Giordano et al., 2009; Marchesini et al., 2009). This could account for our low capture rate (n= 21 in 2015 and n=4 in 2016). Nonetheless, the presence/absence variation among plots between years (Fig. 3) cannot be explained with our current data.

Geouxus valdivianus is the only species whose diet consists solely of invertebrates (Pearson, 1983). Invertebrate abundance across protection levels did not differ (chi-squared= 1.1102, DF 3, p=0.7746 and chi-squared=5.7657, DF=3, p=0.1236, for 2015 and 2016 respectively). The species is widely distributed, although in low abundance.

Loxodontomys micropus is mainly herbivorous and prefers forest with sufficient ground vegetation. (Pearson, 1983). Despite the apparently suitable condition of our plots, we trapped only six individuals in 2015, all outside PAs. A study in Chile in mature and second growth forest reported ten individuals with a trapping effort of 1936 traps/night (Garcia et al., 2013). Further studies are needed to determine the reason for the low abundance we recorded with a total trapping effort of 41,600 traps/night.

Finally, *Chelemys macronyx* has been found mainly in lenga forest (*N. pumilio*) (Garcia et al., 2013). The species has not been detected previously in *N. dombeyi* forest *(*Pearson, 1983). Although we detected the species only in 2015, this study provides novel information regarding habitat preference/suitability for this species. We detected the species in our northernmost samples, in the National Reserve category. This area was still blanketed by volcanic ash (from the June 2011 Cordon Caulle eruption). Research on ash

effect on arthropods has demonstrated its insecticidal action (Buteler et al., 2011). Although *C. macronyx* is omnivorous, invertebrates constitute most of its diet (Sage et al., 2007), so it is interesting that we found them only in that particular area. To increase capture probability, traps must be set near their burrow entrances instead of randomly distributed in a grid as we did (Ojeda R., *personal communication*).

CHAPTER III

EXPLAINING SMALL MAMMAL COMMUNITY VARIATION IN A TEMPERATE FOREST IN NORTHERN PATAGONIA

A version of this chapter will be published by María Daniela Rivarola, Daniel Simberloff, and Juan Manuel Morales.

María Daniela Rivarola conducted a search literature, designed and carried on the fieldwork, analyzed the data and wrote the article. Dan Simberloff revised and edited the article. Juan Manuel Morales designed the models, revised and edited the article.

Abstract

The Anthropocene is characterized by severe landscape modifications, often resulting in habitat loss with detrimental effects on biodiversity. Understanding species distributions and habitat selection is required to assess current and future impacts of such modifications on biodiversity. Small mammal communities inhabiting Patagonian temperate forest have been evaluated both in Chile and Argentina; however, community heterogeneity across a similar habitat remains poorly understood. Furthermore, imperfect species detection biases our understanding of species distributions and habitat associations. Recent advances in occupancy modeling deal with this uncertainty. We studied small mammal communities distributed in the northern portion of Argentinian temperate forest during the austral summers of 2015 and 2016, restricting our study to forests dominated by a southern beech, *Nothofagus dombeyi*, within 500-700 m.a.s.l. We established 20 plots with a total capture effort of 41,600 trap/nights. We proposed eight hierarchical multi-year occupancy models to determine what factors might play an important role in the heterogeneous distribution of these communities. Among such factors we included food and shelter availability, habitat complexity, anthropogenic disturbances, and the existence of protected areas with different levels of protection. We evaluated habitat preferences for seven rodent species and one endemic marsupial. While some of our results support previous studies of habitat selection, we also provide evidence that some habitat characteristics previously assumed to be relevant for species distribution fail to explain the observed heterogeneity.

Introduction

Species distributions across different landscapes have been studied for decades. While it is generally known what kinds of organisms can be found for example in temperate forests, temperate forests around the world harbor completely different sets of species. Furthermore, often species with similar habitat requirements are never found in the same area (Vellend, 2016). The study of natural ecosystems provides a first step toward a full understanding of heterogeneous species distributions and possible consequences of habitat alteration and species loss.

Biodiversity loss has increased greatly in the Anthropocene, and absence of a species from a site with apparently suitable habitat may have resulted from this process, which may have occurred regionally and for reasons not apparent from phenomena occurring at the site itself. An alternative possibility is that subtly different habitat requirements or preferences between species may mean that a superficially suitable habitat for an absent species is not in fact suitable. If anthropogenic activity has created the subtly different habitat, then the puzzling heterogeneous distribution of the species may be an early stage in a change in regional biodiversity. Understanding the causes of surprising distributional gaps is thus of great conservation importance. Research toward this end requires detailed local studies at the community level.

South America has the second highest continental mammal species richness. The conservation status of most of these species is uncertain, but research on threats to its small mammals has revealed that habitat modification (e.g., deforestation) and climate change (i.e., changing rainfall regimes and fire dynamics) are the main factors that will potentially affect species in various ways, altering entire communities (Kelt & Meserve, 2014). Conservation efforts include the creation of protected areas. Currently more than 10,000 sites in Latin America and the Caribbean are under some designated level of protection; nevertheless, only 1283 have been evaluated for management effectiveness (UNEP-WCMC, 2021).

Patagonian Temperate forests throughout Chile and Argentina harbor similar small mammal communities (Meserve et al., 1991). Research on small mammal habitat associations in Patagonia has evaluated variation in communities at different elevations on

both sides of the Andes Mountains (Andrade & Monjeau, 2014; Patterson et al., 1990). Vegetation type has also been studied as a potential determinant of small mammal community variation: comparisons between grassland and shrubland (Lozada et al., 2010; Novillo et al., 2017), grassland and forest (Murua & Gonzalez, 1982), and even between forests with different dominant tree species (Kelt et al., 1994;1999). Patagonian temperate forests have been substantially fragmented since the beginning of the 20th century (Kelt & Meserve, 2014). Effects of forest fragmentation on small mammal species have also been evaluated in both countries (Kelt, 2000; Rodriguez-Cabal et al., 2007).

The aforementioned studies conducted in Chile and Argentina found associations between particular small mammal species and different habitat characteristics. However, the numbers of samples used to evaluate community differences between environments (e.g., different elevations, fragmented vs. intact forest, forest vs. grassland, etc.) were low – in general, two or three plots were sampled for each habitat type. Although this sampling design is appropriate to compare certain attributes of such distinct environments, it assumes that those sampled locations adequately represent small mammal communities inhabiting each habitat type. However, a previous study conducted in Nahuel Huapi National Park, northern Patagonia, could imply otherwise. Dissimilarities between 20 small mammal communities sampled in forest dominated by *Nothofagus dombeyi* and in a narrow elevational range revealed that a small number of sampling locations might affect our understanding of species distributions and habitat preferences at a fine scale (Rivarola et al. 2021). Furthermore, home ranges of most of these small mammals are no bigger than 1 ha (Contreras, 1972; Fonturbel et al., 2012; Pearson, 1983; Rivarola, 2010), which increases the importance of investigating their distributions at a small spatial scale.

Another important factor that might bias our understanding of species distributions is imperfect species detection: the detection probability for a species of interest that is present at a site is usually less than one (Gu & Swihart, 2004; MacKenzie et al., 2002). Factors such as a species' elusive behavior or low population density, inappropriate sampling technique, and an observer's inability to identify a species may contribute to a non-detection of the species in a particular time and location even if it is present (Dorazio et al., 2005). The recent development of occupancy models has accounted for imperfect species detection, improving our estimates of species occurrence and of how it relates to environmental

variables (Dorazio et al., 2005; MacKenzie et al., 2002; Royle & Dorazio, 2008). Despite their high diversity, small mammal communities of Patagonian temperate forests have never been evaluated within this occupancy model framework.

In order to explore small mammal distributions in the northern portion of Patagonian temperate forests, we evaluated communities' similarities and differences in a forest dominated by *Nothofagus dombeyi*. We used hierarchical multi-year occupancy models to assess the effects of a different levels of protection, direct anthropogenic disturbances, food availability, shelter, and patch complexity on small mammal community composition.

Methods

We conducted this study in Nahuel Huapi National Park in the northern part of Argentinian temperate forest (Fig. 3.1). Average monthly temperatures are 3°C for the coldest month (July) and 15°C for the warmest month (January), with frost most nights throughout the year. Average annual precipitation is 1,800 mm, mostly during fall and winter, decreasing from west to east (Cabrera, 1976). Dominant tree species are *Nothofagus dombeyi, N. pumilio, N. antartica*, (Nothofagaceae), and *Austrocedrus chilensis* (Cupressaceae), and the bamboo *Chusquea culeou* (Poaceae) and several species of bushes and smaller trees are present in the understory: *Lomatia hirsuta* (Proteaceae), *Schinus patagonicus* (Anacardiaceae), *Maytenus boaria* (Celastreaceae), *Aristotelia chilensis* (Elaeocarpaceae), *Luma apiculata* (Myrtaceae), and *Azara microphylla* (Salicaceae) (Mermoz & Martin, 1986). *Berberis buxifolia, B. serratodentata* (Berberidaceae)*, Ribes cucullatum* (Grossulariaceae)*, Acaena ovalifolia* (Rosaceae)*, Vicia nigricans* (Fabaceae)*,* and *Fragaria chiloensis* (Rosaceae) are common in the lower strata (Dimitri, 1977)*.* Common nonnative species in NHNP include Douglas fir (*Pseudotsuga menziesii*) (Pinaceae) and *Rosa spp.* (Rosaceae).

In the austral summers of 2015 and 2016, we sampled small mammal communities in 20 plots (60 x 60 m) located at least 1 km apart in areas dominated by the southern beech *N. dombeyi* (coihue) between 500 and 700 m.a.s.l. We used a star design to set four transects

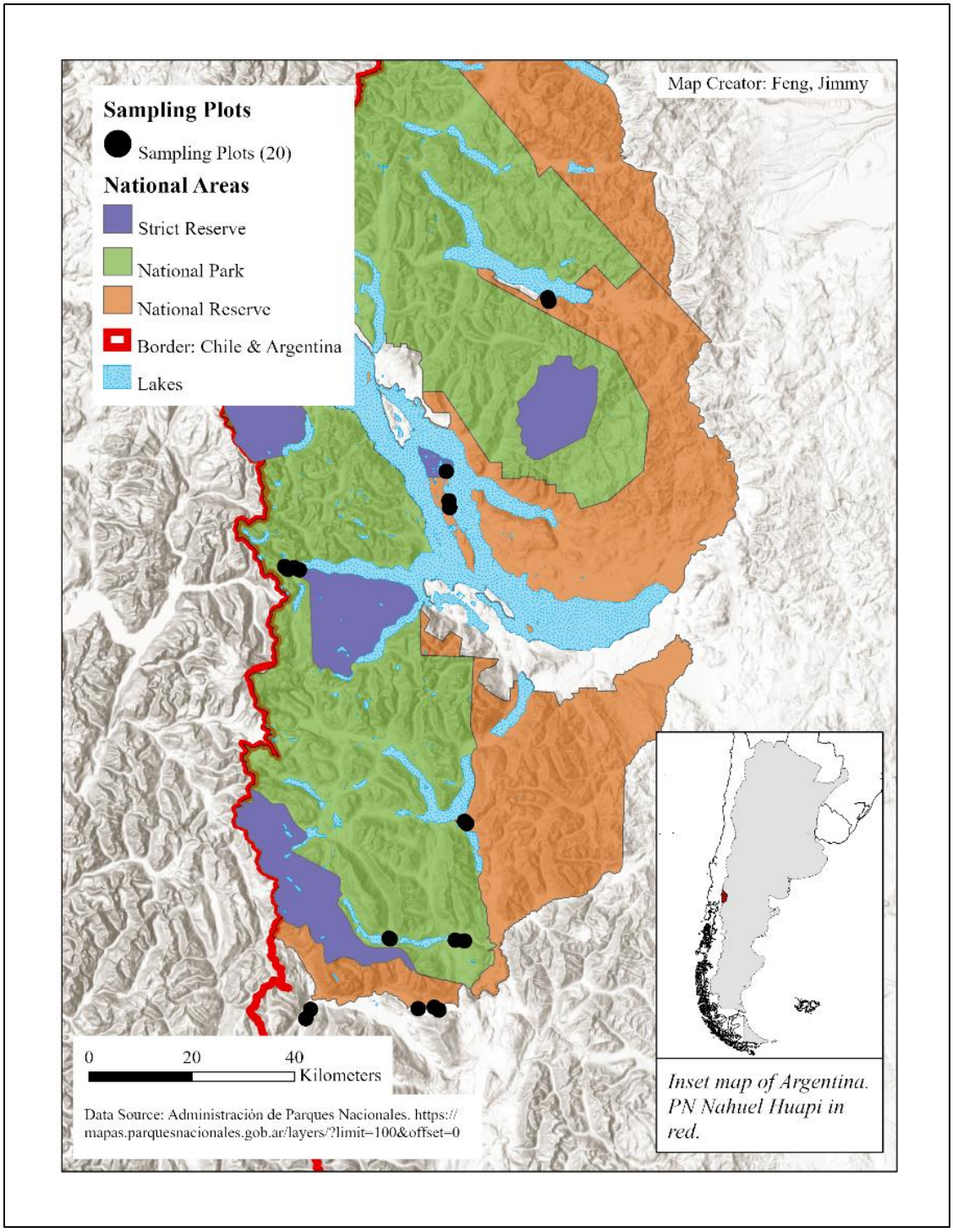


Figure 3.1 Map of Nahuel Huapi National Park. Sampling locations indicated with black dots.

60 m long, converging at their centers. This star or web trap arrangement provides a better estimation of species abundance than do grid-based approaches (Parmenter et al., 2003). We located one trapping station every 10 m along each transect, accounting for a total of 25 trapping stations per plot. A trapping station consisted of a Sherman trap baited with oat and peanut butter on the ground and a Tomahawk trap baited with apple and banana in a branch 1m above the ground. We sampled each plot three times per austral summer 2015 and 2016 on a monthly basis, each time activating each trap for four consecutive days. We checked the traps twice a day, at sunrise and at sunset, and marked trapped rodents with numbered metal ear tags and the marsupial *Dromiciops gliroides* with PIT-tags (model TXP148511B: Biomark, Boise, Idaho; 8.5 x 2.12 mm, 134.2 kHz ISO, 0.067 g) for subsequent identification. We recorded the exact trap location and species for each captured individual and then released them at the trap location.

To measure coleopteran abundance, we set nine pitfall traps per plot, one at the plot center point and one 20 meters from the center along each transect. Each pitfall trap consisted of a plastic container 10 cm in diameter and 15 cm deep half-filled with a solution of water and dishwashing liquid. Each month we combined individuals trapped in the nine traps. We preserved the samples in 70% ethanol, identified organisms to the lowest taxonomic level possible, and recorded their abundances.

We measured microhabitat characteristics at all trapping stations (N=500 stations) once each austral summer in 2015 and 2016. Around each Sherman trap we set a 2 x 2 m square in which we documented ground vegetation diversity and abundance. We used percentage of species cover to indicate abundance. We identified plant species and recorded logs, bare ground, and litter percentage of cover.

We also defined a 2 m diameter vertical cylinder around each Tomahawk trap as a sampling unit. We estimated by eye three variables: a) connectivity, measured as the percentage of available branches that an individual could potentially use to enter the trap without descending to the ground; b) understory cover, measured as the percentage of branches directly above the trap; and c) canopy cover, measured as the percentage of canopy in the highest forest stratum.

The 20 plots surveyed in this study were located in temperate forest dominated by *Nothofagus dombeyi*, but these forests were in different successional stages and subject to

different uses. Tree growth rings of *N. dombeyi* studied in the Puerto Blest area indicated an estimated age of 200 years for a DBH of 120 cm (Pearson & Pearson, 1982). In the austral summer of 2016, we superimposed over each plot a 13 x 13-transect grid, with transects 5 m apart. We defined a node at each point where an N-S transect intersected an E-W transect, resulting in 169 nodes per grid. At each node, we located the nearest tree (within 1 m radius) and measured tree diameter at breast height. If we did not find a tree within a 1 m radius, we recorded zero for that node. We estimated tree density as the number of trees per plot area and we calculated the average tree diameter per plot.

We recorded three indicators of human disturbances at each plot: presence/absence of cattle-grazing, distance to the nearest road (measured in straight-line meters from the plot center to the road), and traffic intensity for each road (low: private or semi-private road, unpaved, one car width; intermediate: open to public, unpaved, two car widths, connecting few destinations; high: paved, two car widths, connecting highly frequented locations).

A limitation in community studies is the uncertainty associated with a report of no detection of a species at a particular time and location (Dorazio et al., 2005). Failure to detect a species implies either the species is not present or the species is present but undetected. The multi-species occupancy model within a Bayesian framework proposed by Dorazio et al. (2005) combines attributes at the community level, such as species richness, with attributes at the species level, such as occurrence. This approach allows variation of detection and occurrence between species and does not assume that each species is present at each location. These models have been expanded to include site-level covariates to estimate their effects on rates of occurrence or detection among sites (Gomez et al., 2018; Kéry & Royle, 2016; Moore et al., 2019). This approach, combining information across multiple sites while introducing covariates, allows us to treat statistical uncertainty in parameter estimates in two-stage analyses: a first stage determining species detectability and a second stage using these estimates as data and relating them to the covariates (Kéry & Royle, 2008). Another advantage of this hierarchical modelling framework is that, because it accounts for species-level effects and habitat-aggregated effects on the community as a whole, it allows a more efficient use of data and better precision in occupancy estimates, especially for infrequently observed species (Zipkin et al., 2009).

To estimate heterogeneity in occurrence and detection of species, we applied the models proposed by Dorazio and Royle (2005). Probability of occurrence of species k at site i and year l is denoted by $\psi_{i,k,l}$, while its detection probability is denoted by $\theta_{i,k,l}$. Occurrence (z) is a hidden variable that we do not observe directly. The occurrence of species is assumed to have a Bernoulli distribution with parameter $\psi_{i,k,l}$

$$z_{i,k,l} \sim \text{Bern}(\psi_{i,k,l})$$

where z is the occurrence of species k= 1, 2, …, 8 at sites i= 1, 2, …, 20 in year $l = 1,2$, and $\psi_{i,k,l}$ is the probability that species k occurs at site i in year l. Detection is conditional on occurrence. It is assumed that if species k occurs at site i and year l ($z_{i,k,l} = 1$), then the number (frequency) of detections will have a binomial distribution with parameters ($J, \theta_{i,k,l}$)

$$p(y_{i,k,l}|z_{i,k,l}, \theta_{i,k,l}) = \left[\binom{J}{y_{i,k,l}} \theta_{i,k,l}^{y_{i,k,l}} (1-\theta_{i,k,l})^{J-y_{i,k,l}}\right]^{z_{i,k,l}}$$

where J is the total number of trapping sessions and $y_{i,k,l}$ is the detection frequency (number of sampling sessions out of J in which the species was detected). If the species is absent ($z_{i,k,l} = 0$), then $y_{i,k,l} = 0$ with probability 1.

By removing $z_{i,k,l}$ from the joint density of the observed number of detections and the indicator of occurrence, we obtained the marginal density of the observed number of detections:

$$p(y_{i,k,l}|\theta_{i,k,l}, \psi_{i,k,l}) = \psi_{i,k,l}\binom{J}{y_{i,k,l}} \theta_{i,k,l}^{y_{i,k,l}} (1-\theta_{i,k,l})^{J-y_{i,k,l}} + (1-\psi_{i,k,l})I(y_{i,j,l} = 0)$$

Where I(.) denotes an indicator function. We modeled no detection ($y_{i,j,l} = 0$) under two possible scenarios, the species is truly absent with probability $(1-\psi_{i,k,l})$ or present but undetected with probability $\psi_{i,k,l}(1-\theta_{i,k,l})^J$. We estimated the detection probability for each species allowing for yearly variation.

We applied multi-species occupancy models accounting for multiple years with known species richness (Brooms et al., 2016), using a Bayesian approach to estimate the effects of level of protection, anthropogenic disturbances, food availability, shelter availability, and environmental complexity on small mammal species. We used models in which occupancy and detection probability varied between years. We fitted eight linear models (logit link) to evaluate the effect that different site-level covariates might have on the

occupancy probabilities for the community as a whole and for each species. We estimated the parameters for every covariate "n" ($\beta n_{[k,l]}$) and the intercept ($\beta 0_{[k,l]}$)for each species and year.

Model 1: Level of Protection. In a previous study, we had evaluated the effect that three different protection categories (from lowest to highest, National Reserve, National Park, Strict Nature Reserve) and lack of protection had on the small mammal community, using raw counts of species (Rivarola et al., 2021). Here we propose a model in which we evaluated the protection effect while accounting for imperfect species detection and including covariates. We modelled the difference in occupancy probability between each protection level and the unprotected area as:

$$\text{logit}(\psi_{[i,k,l]}) = \beta 0_{[k,l]} + \beta 1_{[k,l]} R_{[i,l]} + \beta 2_{[k,l]} P_{[i,l]} + \beta 3_{[k,l]} S_{[i,l]}$$

$R_{[i,l]}$, $P_{[i,l]}$, and $S_{[i,l]}$ are the covariates National Reserve, National Park and Strict Nature Reserve at site i and year l respectively. The latest protection level, Strict Nature Reserve, was established in 1990 and the three categories have remained constant since that time (Rivarola et al., 2021a).

We predicted that a higher protection level would harbor communities with more species.

Model 2: Anthropogenic Effects. We used a model that estimated the effect of cattle grazing, total distance to the nearest road, and road traffic intensity on the small mammal community.

$$\text{logit}(\psi_{[i,k,l]}) = \beta 0_{[k,l]} + \beta 1_{[k,l]} Ca_{[i,l]} + \beta 2_{[k,l]} RD_{[i,l]} + \beta 3_{[k,l]} TI_{[k,l]}$$

The covariate Ca, for cattle, indicates presence/absence of cattle grazing within the sampling plot. Road distance, RD, was measured in straight-line meters from the center of the plot to the nearest road. TI, traffic intensity of that road was classified as 0 (low traffic), 1 (intermediate traffic), or 2 (high traffic).

We predicted that cattle would negatively affect small mammal communities, and similarly for proximity of a road and for high traffic intensity on nearby roads.

Model 3: Food availability. We modeled the effect of cover by herbaceous vegetation, bushes, and trees along with coleopteran abundance on the small mammal community.

$$\text{logit}(\psi_{[i,k,l]}) = \beta 0_{[k,l]} + \beta 1_{[k,l]} H_{[i,l]} + \beta 2_{[k,l]} B_{[i,l]} + \beta 3_{[k,l]} T_{[i,l]} + \beta 4_{[k,l]} Co_{[i,l]}$$

The covariates herbaceous (H), bushes (B) and tree (T) were measured in terms of cover percentage while coleopterans (Co) were recorded as the total number of individuals caught over the sampling season.

Although all the mammals studied here are omnivorous to some extent, vegetation dominates the diet of certain species (Pearson, 1983), and we used vegetation cover and coleopterans abundance as a proxy for food availability. We predicted plots with greater food availability would hold more small mammal species, and each food category (herbaceous, bush, tree, or coleopterans) would affect occupancy probabilities of the various species differently depending on species' food preferences.

Model 4: Shelter. We incorporated habitat features that might function as protection for small mammals against predators, both at ground level and higher up. As predictor variables we used bush (B), tree (T), and log and timber cover (L), understory (U) and canopy cover (CC), and connectivity (Con).

$$\text{logit}(\psi_{[i,k,l]}) = \beta_{0_{[k,l]}} + \beta_{1_{[k,l]}}B_{[i,l]} + \beta_{2_{[k,l]}}T_{[i,l]} + \beta_{3_{[k,l]}}L_{[i,l]} + \beta_{4_{[k,l]}}U_{[i,l]} + \beta_{5_{[k,l]}}CC_{[i,l]} + \beta_{6_{[k,l]}}Con_{[i,l]}$$

We predicted that greater shelter availability in a plot would positively affect small mammals. Ground-dwelling species and arboreal species could respond differently to shelter at different heights.

Model 5: Plot Complexity. We evaluated the effect that patch complexity might have on the small mammal community, measuring complexity as the combination of forest (F), bare ground cover (BG), and vegetation species richness (Rich). We defined forest (F) as the product of tree densities (the number of trees measured along 13 transects 60 m long) and the average diameter at breast height.

$$\text{logit}(\psi_{[i,k,l]}) = \beta_{0_{[k,l]}} + \beta_{1_{[k,l]}}F_{[i,l]} + \beta_{2_{[k,l]}}BG_{[i,l]} + \beta_{3_{[k,l]}}Rich_{[i,l]}$$

We predicted a positive effect of forest and vegetation richness on small mammal species occupancy, and a negative effect of bare ground.

Model 6: Strata Complexity. We grouped the vegetation per stratum - herbaceous, bushes, and trees - and we used their richnesses as an indicator of strata complexity, where HRich, BRich and TRich represent herbaceous, bush, and tree richness respectively.

$$\text{logit}(\psi_{[i,k,l]}) = \beta_{0_{[k,l]}} + \beta_{1_{[k,l]}}HRich_{[i,l]} + \beta_{2_{[k,l]}}BRich_{[i,l]} + \beta_{3_{[k,l]}}TRich_{[i,l]}$$

We predicted that richness of each stratum would affect small mammal species differently.

Model 7: Strata Complexity and Cover. Here we extended model 6 to incorporate not just the stratum richness but also the area occupied by each vegetation type. We obtained a richness-cover index by multiplying herbaceous cover by herbaceous richness (hcr), bush cover by bush richness (bcr), and tree cover by tree richness (tcr).

$$\text{logit}(\psi_{[i,k,l]}) = \beta_{0_{[k,l]}} + \beta_{1_{[k,l]}}\text{hcr}_{[i,l]} + \beta_{2_{[k,l]}}\text{bcr}_{[i,l]} + \beta_{3_{[k,l]}}\text{tcr}_{[i,l]}$$

We predicted that each predictor variable would affect small mammal species differently.

Model 8: Saturated Model. We ran six Principal Component Analyses (PCA). In each PCA we used the predictors proposed for the model (for models 2 to 7). Then, we used the first principal component from each analysis as a regressor for the saturated model. Protect represents the level of protection, PC._An is the first principal component obtained from the PCA evaluating the predictors from the Anthropogenic model; similarly, PC_Fo from the Food model, PC_Sh from the Shelter model, PC_PC from the Plot Complexity Model, PC_SC from the Strata Complexity model, and lastly, PC_SCo from the Strata Complexity and Cover model.

$$\begin{aligned}\text{logit}(\psi_{[i,k,l]}) = {} & \beta_{0_{[k,l]}} + \beta_{1_{[k,l]}}\text{Protec}_{[i,l]} + \beta_{2_{[k,l]}}\text{PC\_An}_{[i,l]} + \beta_{3_{[k,l]}}\text{PC\_Fo}_{[i,l]} + \beta_{4_{[k,l]}}\text{PC\_Sh}_{[i,l]} \\ & + \beta_{5_{[k,l]}}\text{PC\_PC}_{[i,l]} + \beta_{6_{[k,l]}}\text{PC\_SC}_{[i,l]} + \beta_{7_{[k,l]}}\text{PC\_SCo}_{[i,l]}\end{aligned}$$

For each model, the intercept $\beta_{0_{[k,l]}}$ and the parameters denoting covariate effects $\beta_{n_{[k,l]}}$were estimated. Continuous predictor variables were standardized by subtracting the mean and dividing by the standard deviation before being used in the models. We observed the effect of covariates on the community as a whole and on each species. We proposed exploratory models in order to identify site-level variables that could help explain the uneven distribution of species within the same habitat type. We compared models using the Watanabe-Akaike information criterion (Watanabe, 2010) to rank the models in terms of explaining observed occupancy for each species. We made inferences based on 95% Bayesian credible intervals (95% BCI), considering an effect as important when the interval overlapped zero less than 25% (f>0.75), and an effect as strong when the interval does not overlap with zero.

Bayesian methods are the most appropriate for analyzing hierarchical models (Gelman & Hill, 2007). We estimated the posterior distribution of all parameters using Markov Chain Monte Carlo methods implemented in JAGS (Plummer, 2003) interfaced via jagsUI. We used independent weakly informative priors (Normal with mean 0 and standard deviation of 1) for the hyperparameters. We assessed model fit using posterior predictive checks with a Bayesian p-value. The Bayesian p-value was defined as the probability $\Pr\left(D > D^{sim}\right)$, where D^{sim} is the discrepancy measure for the simulated data set. Discrepancy measure was defined as $D = \sum_i (y_i - p_i)^2$, where y_i are the observed values and p_i their expected values. A Bayesian p-value close to 0.5 indicates a good fit while values close to 0 or 1 indicate the model is inadequate (Gelman et al., 1996). We ran five MCMC chains with 50,000 iterations, where 25,000 iterations were discarded (burn-in), thinning by five to reduce autocorrelation. We evaluated chain convergence by looking at $\widehat{R}$ (R-hat), the potential scale reduction factor (Gelman & Rubin, 1992). Successful convergence is based on $\widehat{R} < 1.1$ for all the values estimated.

The 20 plots sampled were not equidistant from one another; some plots were 1 km apart while others were separated by more than 100 km. To evaluate spatial autocorrelation between small mammal richness across the sampled area, we calculated Moran's I on the residuals obtained from each model, for each year individually, with the package "ape" in software R.

Results

We captured a total of 1266 individuals, 735 in summer 2015 and 531 in summer 2016. We identified eight native species in 2015, seven rodent species - *Abrothrix hirta* (Thomas, 1895)*, A. olivacea* (Waterhouse, 1837)*, Oligoryzomys longicaudatus* (Bennett, 1832)*, Geoxus valdivianus* (Philippi, 1858), *Irenomys tarsalis* (Philippi, 1900), *Loxodontomys micropus* (Waterhouse, 1837)*,* and *Chelemys macronyx* (Thomas, 1894) (Cricetidae) - and one marsupial, *Dromiciops gliroides* (Thomas, 1894) (Microbiotheriidae). In 2016, we detected the same species except for *Chelemys macronyx*.

Three species were consistently more abundant, *A. hirta, O. longicaudatus* and *D. gliroides*, accounting for approximately 90 % of the captures in both years (Fig. 3.2). Community capture success measured as the total number captured (including first time capture and re-captures) divided by the trapping effort (the product of the number of traps and the number of trapping sessions) were 10.20% and 9.02% for 2015 and 2016 respectively, with species-specific values ranging from 8.16% (*A. hirta*) to 0 (*C. macronyx*) (Fig. 3.3). Nevertheless, capture success per species varied significantly between different sampling locations (Fig. 3.4).

Our eight exploratory models had Bayesian p-values close to 0.5, which indicates a good general fit to the data. The models had similar Watanabe-Akaike information criterion values (WAIC). WAIC values are used to evaluate how well models explain the data. Specifically, the WAIC difference between models reflects differences in how well the models explain the data. Differences on the order of two provide no greater support for one particular model; if the difference is on the order of ten or more, then the model with the lower WAIC is considered better at explaining our data, without a statement about statistical differences between the models (Gelman et al., 2014). The independent variables proposed for the anthropogenic effect model better explained the variation in the species occurrence probability (lowest WAIC) (Table 3.1).

Each species had highly similar detection probabilities estimated by all the models, with little variation between years 2015 and 2016. Probability of detection in general was low for most of the species ($p < 0.27$), with *A. hirta* the only exception, with mean $p= 0.78$ and $p= 0.81$ for 2015 and 2016 respectively (Table 3.2).

As explained in the methods section, to determine whether the predictors had an important effect on the dependent variables (richness at the community level, or occupancy probability for each particular species), we evaluated the Bayesian credible interval. If BCI did not overlap with zero, then the variable effect would be strong, if BCI overlapped < 25% with zero, then the variable effect would be considered important. Finally, if the BCI overlapped >25% with zero, the variable effect is unclear and should not be used to explain richness or species occupancy probabilities. We identified five predictors with potential effect ($f<0.75$) on the occupancy probability at the community level (Table 3.3). While bare ground cover showed a negative effect on small mammal community richness, the presence

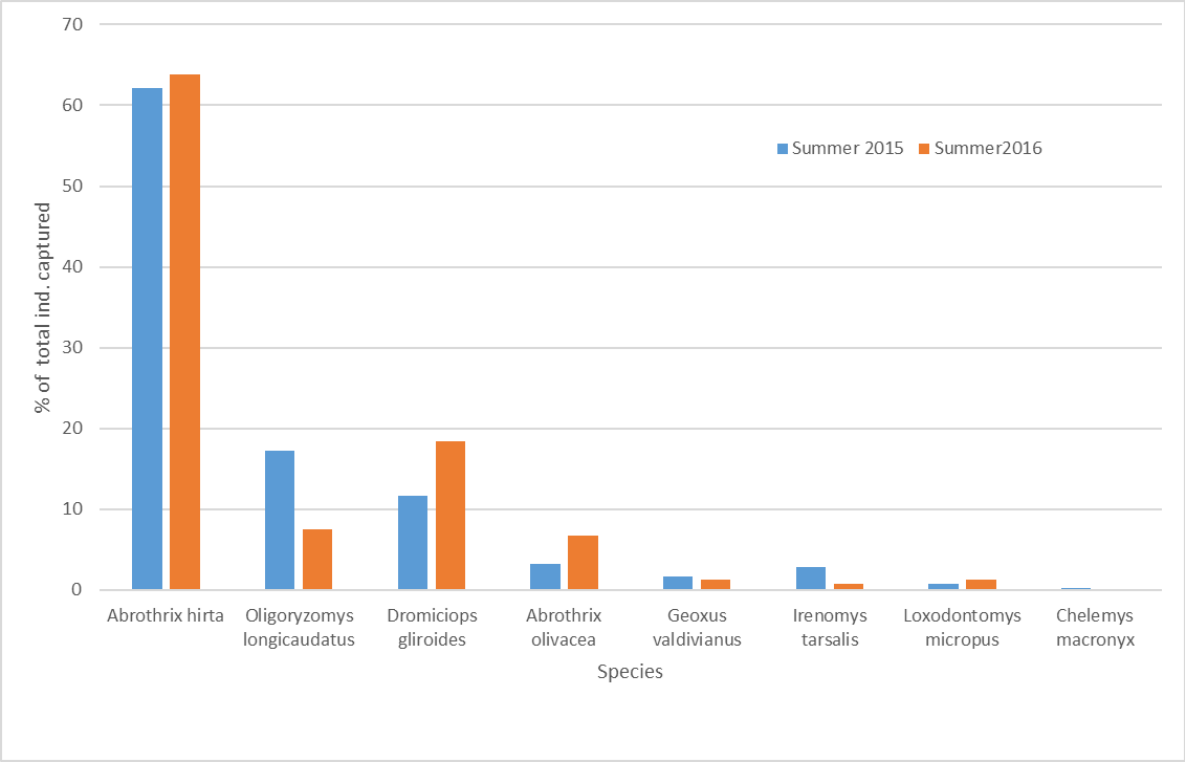


Figure 3.2 Percentage of total individuals captured per species during the summers of 2015 and 2016 in a temperate forest of northern Patagonia.

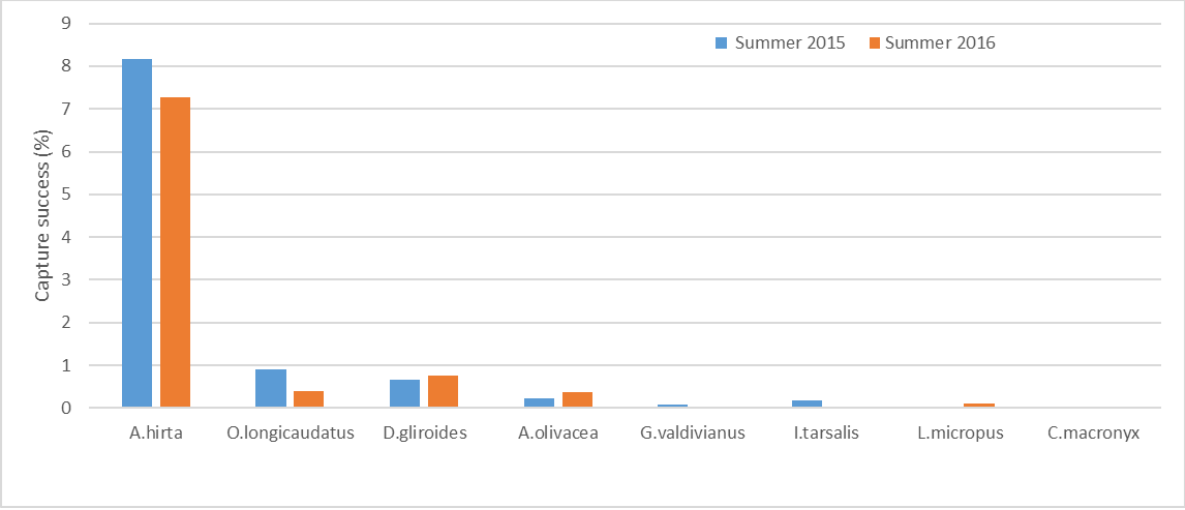
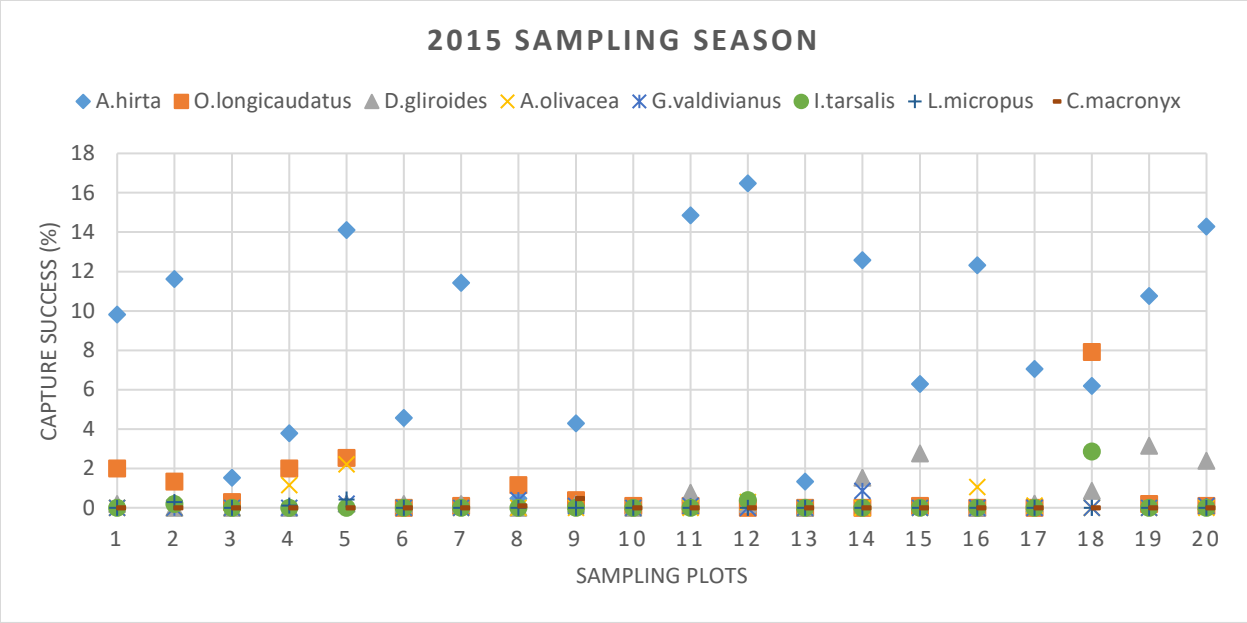


Figure 3.3 Small mammal capture success during sampling seasons 2015 and 2016.



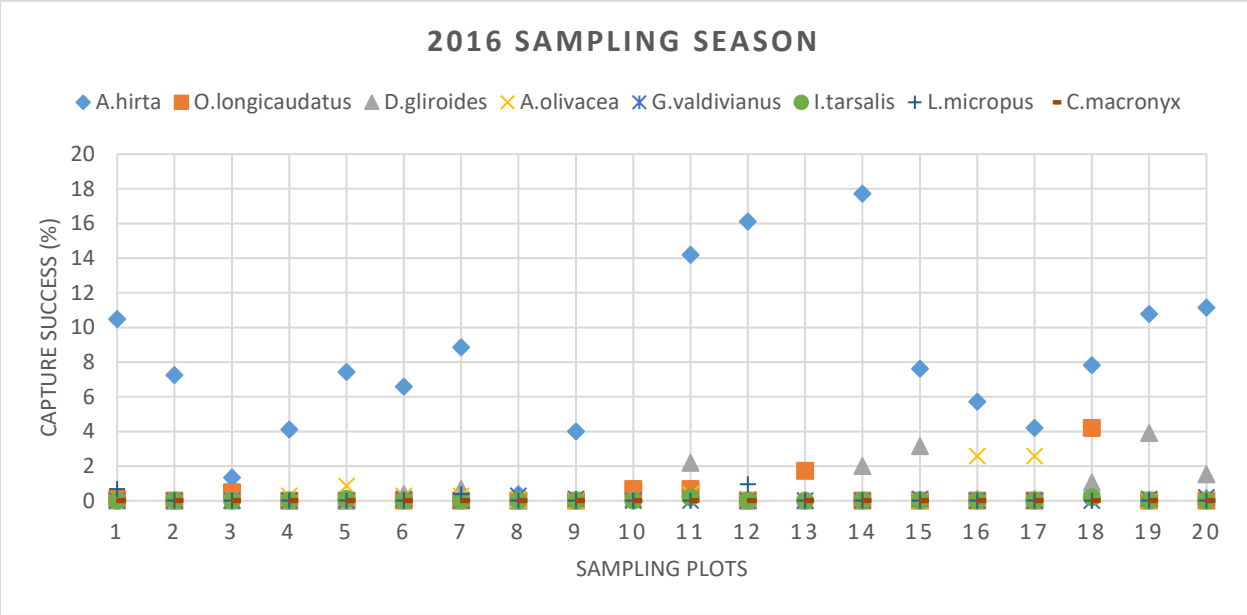


Figure 3.4 Species-specific capture success at each sampling location. For example, 10% of the traps at location 1 caught A. hirta, both years.

Table 3.1 Exploratory models predicting occupancy probability of small mammals in a temperate forest of northern Patagonia, organized from lowest to highest WAIC.

Model	Deviance	WAIC	ΔWAIC	P-value
Anthropogenic effect	797.85	1119.66		0.508
Food availability	800.27	1131.95	12.29	0.506
Saturated model	801.68	1131.99	12.33	0.515
Strata complexity and cover	798.19	1139.66	20	0.512
Plot complexity	798.62	1153.17	33.51	0.514
Level of protection	795.77	1153.45	33.79	0.509
Shelter	805.39	1153.75	34.09	0.510
Strata complexity	797.41	1157.95	38.29	0.511

Table 3.2 Estimated detection probabilities per species for each model.

Species	**Models**						
	AE	FA	SCC	PC	LP	SA	SC
Abrothrix hirta	0.78±0.02	0.78±0.02	0.78±0.02	0.78±0.02	0.78±0.02	0.78±0.02	0.78±0.02
	0.81±0.02	0.81±0.02	0.81±0.02	0.81±0.02	0.81±0.02	0.81±0.02	0.81±0.02
Oligoryzomys longicaudatus	0.22±0.02	0.22±0.02	0.22±0.02	0.22±0.02	0.22±0.02	0.22±0.02	0.22±0.02
	0.25±0.03	0.25±0.03	0.25±0.03	0.25±0.03	0.25±0.03	0.25±0.03	0.25±0.03
Dromiciops gliroides	0.25±0.02	0.25±0.02	0.25±0.02	0.24±0.02	0.25±0.02	0.25±0.02	0.25±0.02
	0.27±0.03	0.27±0.03	0.27±0.03	0.27±0.03	0.27±0.03	0.27±0.03	0.27±0.03
Abrothrix olivacea	0.20±0.03	0.20±0.03	0.20±0.03	0.20±0.03	0.20±0.03	0.20±0.03	0.20±0.03
	0.21±0.03	0.21±0.03	0.21±0.03	0.21±0.03	0.21±0.03	0.21±0.03	0.21±0.03
Irenomys tarsalis	0.21±0.05	0.21±0.05	0.21±0.05	0.21±0.05	0.21±0.05	0.21±0.05	0.21±0.05
	0.09±0.04	0.08±0.04	0.08±0.04	0.08±0.04	0.08±0.04	0.08±0.04	0.08±0.04
Geoxus validivianus	0.11±0.03	0.11±0.03	0.10±0.03	0.11±0.03	0.11±0.03	0.10±0.03	0.11±0.03
	0.06±0.02	0.06±0.02	0.06±0.02	0.06±0.02	0.06±0.02	0.06±0.02	0.06±0.02
Loxodontomys micropus	0.12±0.05	0.12±0.05	0.13±0.04	0.12±0.05	0.13±0.04	0.11±0.04	0.12±0.05
	0.23±0.05	0.23±0.05	0.23±0.05	0.23±0.05	0.23±0.05	0.24±0.05	0.23±0.05
Chelemys macronix	0.15±0.05	0.14±0.05	0.14±0.05	0.14±0.05	0.14±0.05	0.14±0.06	0.15±0.05
	0.20±0.16	0.17±0.15	0.17±0.16	0.18±0.16	0.18±0.16	0.16±0.15	0.18±0.16

AE: Anthropogenic Effect, FA: Food Availability, SCC: Strata Complexity and Cover, PC: Plot Complexity, LP: Level of Protection, SA: Shelter Availability, SC: Strata Complexity. Detection probabilities are expressed as mean ± SD. Top 2015, bottom 2016.

of cattle, higher understory cover, and more canopy cover had a positive effect on the communities studied. Furthermore, the variability captured by the first PC with the Anthropogenic model and the Strata Complexity and Cover model had a positive effect at the community level, while those variables from the Shelter and the Strata Complexity model negatively affected the communities (Table 3). The first principal component for each model explained less than 55% of the total variability among the predictors (Appendix 1). Based on this saturated model, larger values of PC_Ah were associated with smaller values of road distance, while larger values of PC_ SCo were associated with higher values of bush cover multiplied by bush richness in 2015, and lower values of connectivity in 2016. The negative effect of Shelter was dominated by logs cover in 2015 and by connectivity in 2016. Loadings for these two predictors were negative. Similarly, bush cover had a negative loading and was the predictor accounting for most of the variability of the PC_SC. (Appendix 1).

Four species had higher occurrence probabilities in environments shared with cattle in 2015 (*A. hirta, A*. *olivacea, C. macronyx*, and *G. valdivianus*, with more than 75% of the interval having the same sign as the mean effect), whereas there was no effect of cattle on the other species (Fig. 5, Appendix 2). However, this effect remained only for *A. hirta* (f=0.833) and *A. olivacea* (f=0.971) during 2016 (Fig. 5, Appendix 2). *Abrothrix hirta, D. gliroides*, and *G. valdivianus* presented a consistent higher occurrence probability in plots farther from roads (Fig. 5, Appendix 2), while *O. longicaudatus, I. tarsalis, C. macronix,* and *L. micropus* behaved in the opposite way (Fig. 5, Appendix 2). The model did not predict a relation between occurrence of *A. olivacea* and road distance (Fig. 5, Appendix 2). Roads with higher traffic intensity increased the occurrence probability of *A. hirta* and *G. valdivianus* and reduced it for *I. tarsalis* (Fig. 5, Appendix 2); nevertheless, the model did not provide evidence for traffic effects on *A. olivacea* and *L. micropus* (Fig. 5, Appendix 2).

Herbaceous cover seems to be a weak predictor of occupancy probabilities for the rodent species (Fig. 6, Appendix 2). However, it had a consistent negative effect on the occurrence probability of the arboreal *D. gliroides* (Fig 6., Appendix 2). Similarly, bush cover and coleopteran abundance had a consistent positive effect only on *A. hirta* (Fig. 6, Appendix 2). Finally, the model did not provide clear evidence regarding tree cover effects (Fig. 6, Appendix 2).

Table 3.3 Models indicating predictor's effects on the community as a whole. Coefficients expressed in the logit scale. The percentage of the BCI interval with same sign as the mean is indicated in the "f" column, f>75% in bold.

Model	Predictor	$\hat{\beta}$		95% BCI		f
		Mean	SD	2.5%	97.5%	
Anthropogenic effect	Cattle	0.429	0.479	-0.519	1.378	**0.820**
	Road dist.	-0.083	0.441	-0.980	0.783	0.576
	Road traffic	0.182	0.357	-0.510	0.918	0.700
Food availability	Herbaceous	0.046	0.353	-0.708	0.703	0.571
	Bush	0.083	0.362	-0.638	0.816	0.596
	Tree	0.093	0.274	-0.446	0.640	0.634
	Coleopterans	0.094	0.328	-0.565	0.739	0.621
Saturated model	Protection	-0.047	0.391	-0.845	0.710	0.544
	PC_An	0.288	0.418	-0.552	1.110	**0.765**
	PC_Fo	-0.149	0.363	-0.867	0.558	0.660
	PC_Sh	-0.577	0.372	-1.321	0.158	**0.944**
	PC_PC	-0.130	0.349	-0.817	0.567	0.654
	PC_SC	-0.433	0.379	-1.177	0.318	**0.876**
	PC_SCo	0.690	0.393	-0.090	1.464	**0.961**
Strata complexity and cover	hcr	-0.173	0.419	-1.062	0.612	0.660
	bcr	0.203	0.317	-0.422	0.840	0.747
	tcr	0.041	0.255	-0.471	0.537	0.572
Plot complexity	Forest	0.024	0.275	-0.524	0.561	0.539
	Bare ground	-0.227	0.323	-0.869	0.410	**0.768**
	Richness	0.149	0.352	-0.543	0.861	0.678
Level of protection	R-O	-0.045	0.476	-0.999	0.895	0.537
	P-O	-0.166	0.446	-1.056	0.714	0.651
	S-O	0.079	0.524	-0.968	1.111	0.566
Shelter	Bush	0.075	0.408	-0.702	0.918	0.565
	Log	-0.259	0.380	-1.012	0.495	**0.757**
	Tree	-0.046	0.317	-0.681	0.570	0.557
	Understory	0.351	0.375	-0.392	1.059	**0.824**
	Canopy	0.587	0.384	-0.165	1.351	**0.940**
	Connectivity	-0.166	0.446	-1.035	0.729	0.652
Strata complexity	Herb rich	0.050	0.370	-0.701	0.784	0.565
	Bush rich	0.122	0.275	-0.422	0.668	0.677
	Tree rich	-0.033	0.257	-0.541	0.486	0.560

hcr: herbaceous cover * richness, bcr: bush cover * richness, tcr: tree cover * richness, Forest: tree density * average dbh, Richness: total vegetation richnesss, R-O: National Reserve-Outside, N-O: National Park-Outside, S-O: Strict Nature Reserve-Outside, Herb rich: herbaceous richness, Bush rich: bush richness, Tree rich: tree richness.

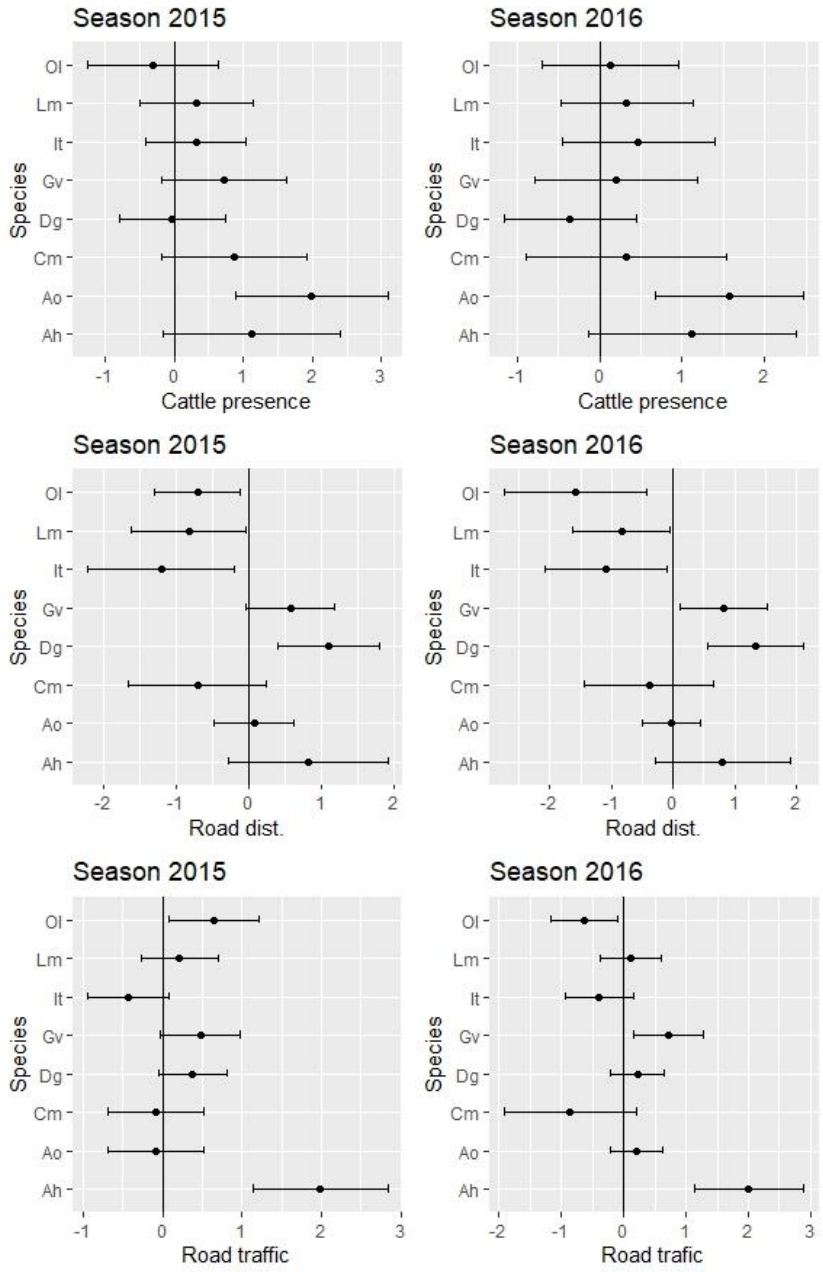


Figure 3.5 Cattle (top), Road distance (center) and Road traffic intensity (bottom) coefficients in the logit scale ($\hat{\beta} \pm SD, 95\%\ BCI$) on logit occupancy (logit ($\widehat{psi}$)) of each small mammal species by year for the Anthropogenic model. Ah. Abrothrix hirta, Ao. Abrothrix olivacea, Cm. Chelemys macronyx, Dg. Dromiciops gliroides, Gv. Geoxus valdivianus, It. Irenomys tarsalis, Lm. Loxodontomys micropus, Ol. Oligoryzomys longicaudatus.

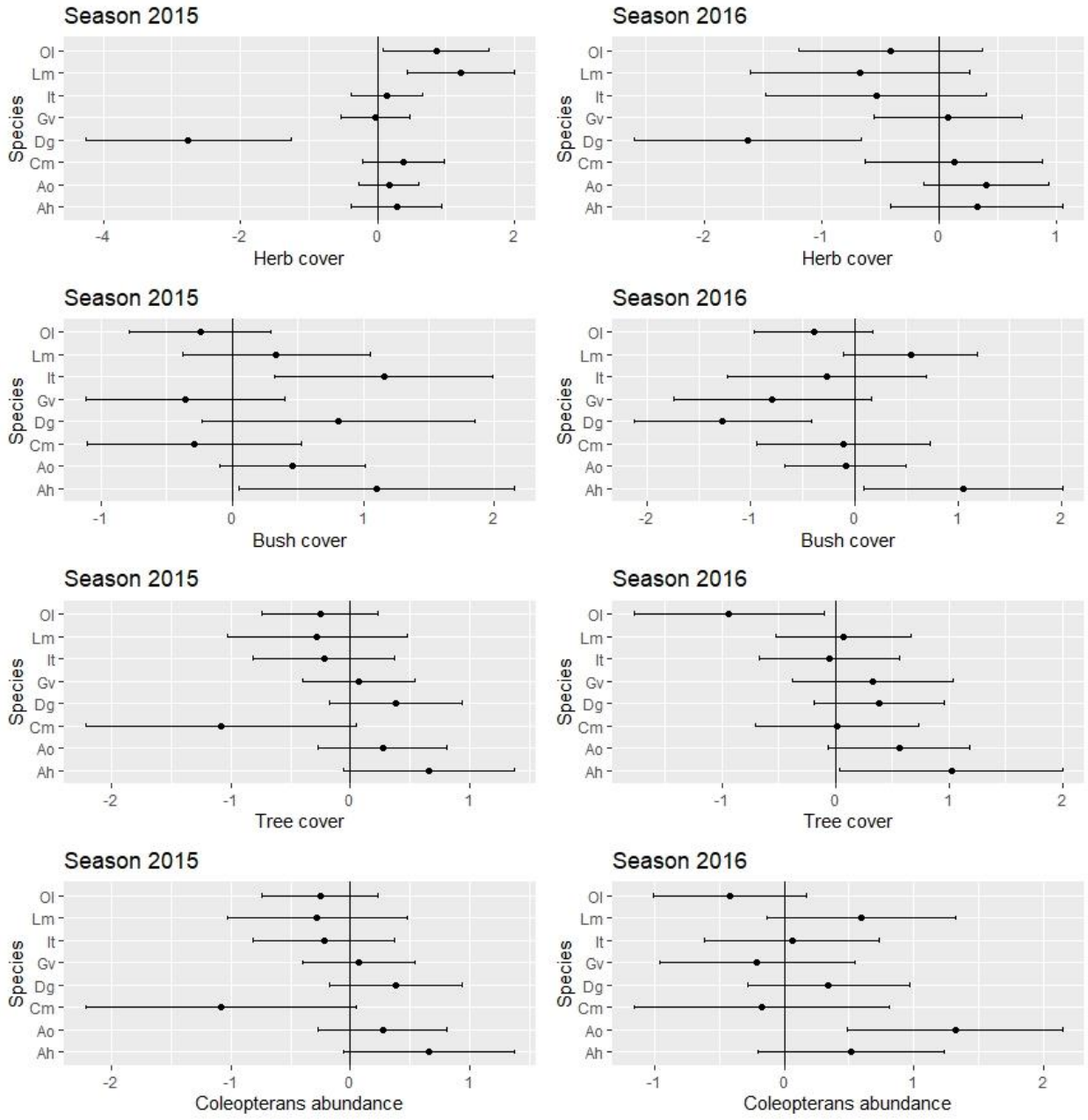


Figure 3.6 Herbaceous cover (top), Bush cover (2nd), Tree cover (3rd), and Coleopteran's abundance (bottom) coefficients in the logit scale $\left(\hat{\beta} \pm SD, 95\%\ BCI\right)$ *on logit occupancy* $\left(logit\ (\widehat{psi})\right)$ *of each small mammal species by year for the Food Availability Model. Ah. Abrothrix hirta, Ao. Abrothrix olivacea, Cm. Chelemys macronyx, Dg. Dromiciops gliroides, Gv. Geoxus valdivianus, It. Irenomys tarsalis, Lm. Loxodontomys micropus, Ol. Oligoryzomys longicaudatus.*

The model "Strata complexity and cover" used as predictors the products of strata richness (herbaceous, bush, and tree) and their cover. The herbaceous stratum had a negative effect on the occurrence probability of the arboreal *D. gliroides* (mean±SD: -1.977±1.012, f=0.997 in 2015, and -1.721±1.248, f=0.945 in 2016) and the fossorial *G. valdivianus* (mean±SD: -1.019±0.875, f=0.918 in 2015, and -0.874±1.043, f=0.827 in 2016), while it did not provide clear evidence for the other species (Appendix 2). The only consistent pattern for the bush stratum was the positive response of *A. hirta* and *L. micropus* (Appendix 2). The tree stratum measured at this level did not have a consistent effect (Appendix 2).

Geoxus valdivianus' occurrence probability was higher in response to the forest predictor for the Plot Complexity Model (mean±SD: 0.395±0.513, f=0.788 in 2015, and 0.426±0.589, f=0.782 in 2016) and lower in plots with higher vegetation richness (mean±SD: -0.777±0.656, f=0.909 in 2015, and -0.773±0.929, f=0.832 in 2016). By contrast, *A. hirta* responded positively to vegetation richness (mean±SD: 1.786±1.178, f=0.977 in 2015, and 1.443±1.097, f=0.938 in 2016). Bare ground had a consistent negative effect on *A. olivacea, I. tarsalis* and *L. micropus* occurrence. We found no consistent response for the remaining species (Appendix 2).

We used the model "Levels of protection" to compare differences in occurrence probabilities between each level of protection within NHNP (National Reserve < National Park < Strict Nature Reserve) and the unprotected neighboring area (outside). Surprisingly, two species responded negatively to the protection system; *I. tarsalis* presented a lower occupancy probability within the National Reserve protection level than in the unprotected area both years (mean±SD: -1.036±1.237, f=0.819 in 2015, and -0.990±1.269, f=0.801 in 2016), while *L. micropus* occurrence probability was lower at each level of protection than in the unprotected area in 2015, while in 2016 the only difference was between the highest level of protection and the unprotected area (Appendix 2). On the contrary, *D. gliroides* was more likely to occur within the two highest protection categories, National Park and Strict Nature Reserve, and at least for the 2016 sampling season it also had higher occupancy probability within the National Reserve (Appendix 2). Although present in almost every plot, *A. hirta* had a higher occupancy probability within the Strict Nature Reserve (Appendix 2).

The "Shelter model" used as predictors environmental variables that could shelter both arboreal (*D. gliroides, I. tarsalis*, and *O. longicaudatus*) and ground-dwelling species. The ground-dwelling *A. hirta* had a higher occurrence probability in plots with more bush cover, while protection from above (canopy cover) appears to be more important for *D. gliroides, A. olivacea, G. valdivianus* and *L. micropus*. *Abrothrix olivacea* and *I. tarsalis* had higher occurrence probability in plots with higher understory cover. Log cover negatively affected occurrence probability of *I. tarsalis* and *L. micropus.* Finally, connectivity did not affect most of the species occurrence probabilities with the sole exception of the ground-dwelling *A. olivacea*, which had a lower occurrence probability in plots with higher connectivity measured 1m above the ground (Appendix 2).

Finally, our "Strata complexity model" evaluated vegetation richness divided into herbaceous, bush, and tree strata. None of the variables analyzed in the model had an effect at the community level. Herbaceous richness positively affected the occurrence probability of *A. hirta* and *O. longicaudatus* while having the opposite effect on *D. gliroides* and *G. valdivianus*. The predictor variables bush and tree richness either had no effect on the species or the sign of the effect switched between years (Appendix 2).

There was no spatial autocorrelation between community richness for most of the analyses, with the only exceptions the model Level of Protection for the season 2015 and the model Strata Complexity for the season 2016 (Appendix 3).

Discussion

The total diversity of species found in the present study agrees with that documented in previous studies conducted in NHNP (Christie, 1984; Pearson, 1995), except for the endemic marsupial *Rhyncholestes raphanurus.* However, this marsupial is distributed almost entirely in Chile with only two records in Argentina (Martin, 2011).

The overall trap success was comparable to those reported for La Picada (Chile) for elevations between 505 m.a.s.l (7.2%) and 715 m.a.s.l. (8.0%) (Patterson et al., 1989); however, trap success for an eight-year study regarding small mammal communities in NHNP was almost double the one reported here (Pearson, 1995). This difference might be

due to seasonal variation in small mammal abundance, since our study was conducted in summer while Pearson (1995) sampled in fall and spring. Nevertheless, demographic trends of small mammals in temperate rainforest of southern Chile show an increasing number of individuals captured throughout the summer with peaks in fall (Meserve et al., 1991; Meserve et al., 1999), emphasizing the importance of multi-season studies. Furthermore, the El Niño Southern Oscillation (ENSO) event has been linked to variation in small mammal abundances, with varying effect at different latitudes in Chile. Small mammal densities of certain species were higher in central and northern Chile during ENSO events followed by rapid decline during a La Niña event (Iriarte et al., 1989; Meserve et al., 2003; Milstead et al., 2007), while this pattern was not as clear for small mammals inhabiting Patagonian rainforests (Meserve et al., 1999). The Oceanic Index Niño (ONI) recorded during the austral summer was above the 0.5°C threshold for both 2015 and 2016, indicating the occurrence of an ENSO, but while ONI for summer 2015 was 0.6°C (weak ENSO), the index increased to 2.5°C during austral summer 2016 (very strong ENSO) (National Weather Service – Climate Prediction Center). The 27% decline in captures reported for 2016 could suggest a negative effect of a very strong ENSO on small mammal communities in Argentinian Temperate Forests; nevertheless, multi-year studies are needed to evaluate these fluctuations over time.

Pearson (1995) reported a higher species trap success for all the rodents; on the contrary, our overall trap success for the marsupial *D. gliroides* was higher. The low abundance of *D. gliroides* reported by Pearson (1995) might be due to a sampling artifact, as it has been demonstrated that *D. gliroides* abundance is underestimated by Sherman traps (Fonturbel & Jimenez, 2009). Furthermore, *D. gliroides* is active from late spring to early fall, falling into a winter torpor during the coolest months (Franco et al., 2011). In our study, we included both Sherman and Tomahawk traps at each sampling location to avoid such a sampling artifact. Nevertheless, both our average marsupial trap success and our trap success per plot (ranging from 0% to 3.90%) were markedly lower than those reported in a seven-year study conducted in Llao Llao Municipal Park in the vicinity of NHNP (trap success ranged from 5.63% to 21%) (Balazote Oliver et al., 2017). The variability per plot of relative abundance found in the current study and the high abundance of *D. gliroides* in the small area sampled by Balazote et al. (2017) support our view that the species has a patchy distribution

and that small-scale analyses with multiple sampling locations, such as the one proposed here, are needed to understand what causes such an uneven distribution.

The use of hierarchical models allows us to assess the community-level response to the predictor variables and to make inferences about the effects on each observed species. The advantage of using hierarchical models to conduct composite analyses of community response resides in the effective use of all the data, including data on rare or infrequent species, instead of data only from the most common and abundant species (Russell et al., 2009; Zipkin et al., 2009). The scale of analysis influences our understanding of ecological processes, so the scale selected must reflect the processes being studied (Morris, 1987). We evaluated community responses at a macrohabitat level, based on the fact that macrohabitat areas are similar in size to species home ranges and constitute distinguishable units within the same habitat type (*N. dombeyi* dominant temperate forest in our study) (Morris 1987). Furthermore, by using 20 sampling units of equal dimensions and conducting the small mammal captures almost simultaneously across the 20 plots, we eliminated scale-dependent effects while minimizing temporal effects (Whittaker et al., 2001).

In a previous study we specifically evaluated the effectiveness of the NHNP protection system in conserving its small mammal community, concluding that these different levels of protection afforded only minor protection to most of the species, with the only exception being substantial protection of the marsupial *D. gliroides* (Rivarola et al. 2021). The new approach in this study confirms the importance of the protection system in conserving this endemic marsupial.

Results from our Anthropogenic model suggest that cattle presence positively affects several small mammals. Occupancy probability of *Abrothrix hirta, A. olivacea, Geoxus valdivianus*, and *Chelemys macronyx* were higher in areas with livestock, although these results need to be carefully considered, since browsing intensity was not evaluated. A synthesis of cattle grazing effects on natural environments worldwide concluded that positive, negative, and neutral effects reported are related to the specific attribute measured (Mazzini et al., 2018). Small mammal diversity indexes were greater on ungrazed than on grazed areas in a protected area in Oregon (US) where domestic livestock and native elk coexisted (Moser & Witmer, 2000). Livestock can negatively affect small mammals indirectly

by modifying vegetation characteristics (Mazzini et al., 2018). A study conducted in Patagonian temperate forest found that degraded environment has both negative and positive effects on arboreal small mammal species: while *Dromiciops gliroides* was more abundant in low-degradation patches, the opportunistic *Oligoryzomys longicaudatus* was more abundant in degraded areas (Fonturbel, 2011). We did not find a clear response by these arboreal species to the presence or absence of cattle. Importantly, with the exception of one plot outside the protected area (plot A3), none of the plots surveyed in the current study where cattle were present could be considered "degraded", suggesting that browsing intensity may be low. In Nahuel Huapi National Park high browsing intensity produces herb-dominated communities with reduction of woody plants (Veblen et al., 1992). We evaluated these variables under other proposed models. Only two species were captured in plot A3, the opportunistic *O. longicaudatus* and the dominant *A. hirta*, in low abundance both years. Livestock were present in four plots in the unprotected area, while the fifth plot (A2) was established in an area fenced since 1999 to facilitate forest restoration. Small mammal abundance and diversity in plot A2 were higher than in the neighboring plots in 2015; however, in 2016, only one species was trapped in this plot. Finally, studies on cattle in Patagonian temperate forest found that they feed on native woody species including *N. dombeyi*, with detrimental effects on native forest (Vila & Borrelli, 2011).

Roads alter natural landscapes with a wide array of implications for wildlife conservation (Forman & Alexander, 1998). Roadways negatively affect small mammal communities in forest areas by movement inhibition and road mortality, while traffic intensity alone does not explain reduced small mammal movement (Oxley et al., 1974). We did not find a clear effect of road distance and traffic intensity at the community level. On the contrary, our study indicates that *A. hirta, D. gliroides,* and *G. valdivianus* occupancy probabilities are higher in areas near roads while *O. longicaudatus, I. tarsalis*, and *L. micropus* responded in an opposite manner. Traffic intensity positively affected *A. hirta* and *G. valdivianus* occupancy probabilities. To interpret these results further, it is important to take into account species behavior and activity patterns. For instance, *D. gliroides* and *O. longicaudatus* are almost entirely nocturnal, and we did not discriminate between car road use at different times throughout the day. While translocation studies of small mammals have revealed that roads can reduce the probability of successful return, small mammal

densities where not affected by road proximity or traffic intensity (McGregor et al., 2008). Road edge effect has been correlated with higher abundance of opportunistic species (Goosem, 2002). In our study, only three plots were at the edge of a road; however, these roads were narrow (one car wide) and unpaved, traffic was less than one car per day, and canopy almost entirely covered the road. These features diminished the edge effect. While macrohabitat is related to individual home range, microhabitats are smaller sub-units quantified by variables able to influence the time and energy allocated per individual of different species (Morris 1987). To secure a good determination of plot quality, we measured 100 microhabitats per plot, plus a grid of 169 nodes to characterize the forest. Analyses conducted at the microhabitat level provide evidence regarding habitat use rather than habitat selection (Morris, 1992). We conducted our analyses at the macrohabitat level, and quality of macrohabitats results from their combinations of microhabitats.

It has been proposed that microhabitats are enhanced in complex landscapes, and that more microhabitats would provide more refuges and food allowing the coexistence of more small mammal species (Novillo et al., 2017). Our results suggest that this pattern is not evident within the same habitat type, as the community responses in evaluations of food availability, shelter availability, and plot complexity were inconclusive (no effect or switching effect between years). None of the models proposed seemed to explain well the heterogeneity among the 20 community samples studied; nevertheless, some variables provided useful information regarding individual species habitat selection.

The dominant species *Abrothrix hirta* preferred areas with high vegetation diversity, particularly herbaceous vegetation and shrubs; furthermore, shrub cover increased its occurrence probability, a pattern also reported in Chile (Kelt et al., 1999) and in its ecotonal distribution in Argentina (Lozada et al., 2010). It is an omnivorous species reported as highly insectivorous in shrubland (Pearson, 1983). We observed higher occupancy probability correlated with arthropod abundance, suggesting that beetles are an important part of their diet also in forested areas, at least during the summer season.

Bare ground cover negatively correlated with *A. olivacea* occupancy probability. This association with ground cover has been found in temperate forests in Chile (Murua & Gonzalez, 1982) and Argentina (Pearson, 1983). However, another study conducted in temperate forest in Chile suggests that the species prefers habitat with more bare ground

cover and more species of trees, and less bush and herbaceous cover (Kelt et al., 1994; Kelt et al., 1999). We did not find an association with tree diversity. However, canopy and understory cover were important habitat variables associated with the presence of the species, which agrees with selection of habitats that facilitate avoidance of predation from above, as has been previously suggested (Murua & Gonzalez, 1982).

Oligoryzomys longicaudatus has been described as an irrupting species, with high abundances followed by almost complete disappearance (Meserve et al., 1991; Murua et al., 1986), a situation observed in our study where 127 specimens were captured in 15 plots in 2015 versus only 40 individuals identified in six plots in 2016. Our results regarding habitat selection are inconclusive; habitat characteristics associated with higher occurrence probability in 2015 were not important in 2016 or switched effects toward a negative correlation. The species' absence from nine previously occupied plots might have affected the statistical power of our models and hidden the effect of variables. Herbaceous richness was associated with higher occurrence probability both years. Although this variable alone does not necessarily imply shelter, habitat selection that favors protection from horizontal viewing has been suggested for this species (Kelt et al., 1994).

The nocturnal and scansorial marsupial *Dromiciops gliroides* (Pearson, 1983) was among the most abundant and widely distributed species in our study (third most abundant in 2015 and present in 13 plots, and second most abundant in 2016 and present in 11 plots). Studies conducted with camera traps in Chile (Franco et al., 2011) and Argentina (Di Virgilio et al., 2014) concluded that it is the most common species in the arboreal stratum in old-growth *Nothofagu*s forests. Based on our models, tree cover and canopy cover were related to higher occurrence probability. The species has been associated with environments with dense understory dominated by bamboo (Fonturbel et al., 2012; Rodriguez-Cabal & Branch, 2011), but we did not find this pattern. Its wide distribution among our sampling locations provides further evidence that the species might be able to thrive or at least persist in more habitats than previously thought (Fonturbel, 2011; Rodriguez-Cabal et al., 2007), as suggested by its presence in pine-dominated forest (Uribe et al., 2017). Nevertheless, more than 60% of the individuals captured in our study resided in the vicinity of Puerto Blest, a remote area accessed only by boat, with a high daily load of tourists (diurnal use only), low

number of permanent residents, and total absence of domestic animals, particularly cats, which are known to prey on *D. gliroides* (Di Virgilio et al., 2014).

The semifossorial *Geoxus valdivianus* is a small mole-like rodent with enlarged forefoot claws for digging (Patterson et al., 1990; Pearson, 1983). In Argentina it inhabits pure or mixed *Nothofagus* forests as well as marsh and meadow but does not extend into the steppe (Pearson, 1983). It eats small animals (annelids, arthropods, mollusks) (Pearson, 1983) and fungi (Patterson et al., 1990). We found no relation between arthropod abundance and occupancy probability. We found this species in six plots both years, but only three plots where the species was identified in 2015 remained occupied in 2016. Furthermore, at each site we usually trapped only a single individual, making this an uncommon species (Meserve et al., 1991). Two of these sites were heavily covered by volcanic ash from a volcanic eruption in June of 2011, suggesting the volcanic fine particulate material would not affect the persistence of this species. It has been associated with habitats with loose soil (Kelt et al., 1994) and many fallen trees and substantial bare ground (Meserve et al., 1991). In our study, occupancy probability was unrelated to bare ground cover and log cover. Finally, herbaceous cover and herbaceous richness negatively correlated with occupancy probability, indirectly supporting the pattern of preference for areas with more bare ground.

The Chilean climbing mouse *Irenomys tarsalis* is distributed between 39.5° and 45° S and is endemic to *Nothofagus* forests in Chile and Argentina (Chébez et al., 2014). It has been suggested that low captures of this species using ground traps might be due to a trap artifact since the species is mainly arboreal (Patterson et al., 1990). However, we recorded more captures in Sherman traps set on the ground than in Tomahawk traps placed 1 m above ground both years (25 out 36 captures in 2015, and 3 out of 5 captures in 2016). We found that understory cover, measured as percent of area aboveground where the animal can move and access the trap without descending to the ground, was positively correlated with its occupancy probability, as expected by its movement patterns.

Loxodontomys micropus is a large mouse with an extensive latitudinal distribution from northern Mendoza to Santa Cruz in Argentina, and from Ñuble to the Strait of Magellan in Chile. It is mostly associated with forests, with some records in humid grasslands in the steppe (Teta et al., 2009). It prefers shrubby habitats (Patterson et al., 1990) and forest with abundant ground cover (Pearson, 1983). Accordingly, we found higher occupancy

probability linked to bush cover, bush diversity, and canopy cover. We captured few individuals both years, distributed in three plots, although only one plot remained occupied between years.

Finally, *Chelemys macronix* has been described as a moderately abundant species inhabiting both forest and steppe (Chébez et al., 2014). Nevertheless, we captured only two specimens in 2015 in the vicinity of Traful Lake in the two northernmost plots. This result is unexpected given the high trapping effort and large area sampled. Further studies are needed to elucidate its low prevalence.

Most research on small mammal microhabitat selection in Patagonia compared different habitat types. To the best of our knowledge, this is the first study that examined small mammal heterogeneity within the same habitat, providing evidence that a reduced number of sampling locations per habitat could limit our understanding of species distributions and their habitat preferences.

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Appendices
Appendix 1

Table 3.4 PCA results, values for the first PC from each model (2015)

Year	Model	PC	Cumulative prop. PC1	Variables	Load
2015	Anthropogenic	PC_An	0.47	Cattle	0.58
				Road dist.	-0.75
				Traffic	-0.32
	Food availability	PC_Fo	0.37	herb	0.59
				Bush	0.11
				Tree	-0.56
				coleoptera	-0.58
	Shelter	PC_Sh	0.38	Bush	0.16
				Tree	0.25
				Logs	-0.6
				Understory	0.16
				Canopy	-0.55
				Connectivity	-0.46
	Plot Complexity	PC_PC	0.47	Forest*	-0.59
				Bare ground	0.71
				Vegetation richness	-0.38
	Strata Complexity	PC_SC	0.51	Herb richness	-0.61
				Bush richness	-0.67
				Tree richness	-0.43
	Strata Complexity and Cover	PC_SCo	0.50	Herb_cov_richn	0.60
				Bush_cov_richn	0.65
				Tree_cov_richn	-0.47

Table 3.5 PCA results, values for the first PC from each model (2016)

Year	Model	PC	Cumulative prop. PC1	Variables	Load
2016	Anthropogenic	PC_An	0.47	Cattle	0.58
				Road dist.	-0.75
				Traffic	-0.32
	Food availability	PC_Fo	0.48	herb	0.30
				Bush	-0.51
				Tree	0.52
				coleoptera	-0.61
	Shelter	PC_Sh	0.38	Bush	-0.31
				Tree	0.17
				Logs	0.33
				Understory	-0.57
				Canopy	-0.30
				Connectivity	-0.59
	Plot Complexity	PC_PC	0.55	Forest*	-0.40
				Bare ground	0.68
				Vegetation richness	0.61
	Strata Complexity	PC_SC	0.44	Herb richness	-0.70
				Bush richness	-0.71
				Tree richness	0.02
	Strata Complexity and Cover	PC_SCo	0.53	Herb_cov_richn	-0.69
				Bush_cov_richn	-0.72
				Tree_cov_richn	0.13

Appendix 2

Brackets indicate species and year as follow:

[1,1] Abrothrix hirta, 2015
[2,1] Abrothrix olivacea, 2015
[3,1] Chelemys macronix, 2015
[4,1] Dromiciops gliroides, 2015
[5,1] Geoxus valdivianus, 2015
[6,1] Irenomys tarsalis, 2015
[7,1] Loxodontomys micropus, 2015
[8,1] Oligoryzomys longicaudatus, 2015

[1,1] Abrothrix hirta, 2016
[2,1] Abrothrix olivacea, 2016
[3,1] Chelemys macronix, 2016
[4,1] Dromiciops gliroides, 2016
[5,1] Geoxus valdivianus, 2016
[6,1] Irenomys tarsalis, 2016
[7,1] Loxodontomys micropus, 2016
[8,1] Oligoryzomys longicaudatus, 2016

co.lpsi: intercept
co.beta: refers to the effect of such predictor (number) at the community level.
For example, co.beta1 = cattle
beta: refers to the effect of such predictor (number) for one species and one year.
For example, beta1[1,1] for the Anthropogenic model expresses coefficient for the pred
ictor “cattle”, species A. hirta, in 2015.

Anthropogenic Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
    beta1[k,l]*cattle[i,l] +
    beta2[k,l]*road[i,l] +
    beta3[k,l]*traffic[i,l]
JAGS output for model 'OcMod_anthrop.bug', generated by jagsUI.
Estimates based on 5 chains of 50000 iterations,
adaptation = 100 iterations (sufficient),
burn-in = 25000 iterations and thin rate = 5,
yielding 25000 total samples from the joint posterior.
```

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
co.lpsi	-1.414	0.741	-2.910	-1.399	-0.002	FALSE	0.975	1.001	3439
co.beta1	0.429	0.479	-0.519	0.432	1.378	TRUE	0.820	1.001	3392
co.beta2	-0.083	0.441	-0.980	-0.079	0.783	TRUE	0.576	1.000	7727
co.beta3	0.182	0.357	-0.510	0.173	0.918	TRUE	0.700	1.001	5640

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta1[1,1]	1.123	1.279	-0.977	0.970	4.124	TRUE	0.836	1.001	2540
beta1[2,1]	1.985	1.102	0.178	1.872	4.508	FALSE	0.987	1.000	23356
beta1[3,1]	0.874	1.051	-0.999	0.790	3.233	TRUE	0.816	1.000	16848
beta1[4,1]	-0.025	0.760	-1.583	-0.003	1.431	TRUE	0.501	1.000	25000
beta1[5,1]	0.718	0.899	-0.897	0.656	2.671	TRUE	0.801	1.001	3971
beta1[6,1]	0.023	0.914	-1.960	0.079	1.704	TRUE	0.536	1.000	25000
beta1[7,1]	0.320	0.812	-1.326	0.330	1.919	TRUE	0.670	1.000	17695
beta1[8,1]	-0.305	0.941	-2.472	-0.208	1.267	TRUE	0.600	1.001	2862
beta1[1,2]	1.119	1.259	-0.986	0.977	3.996	TRUE	0.833	1.001	3098
beta1[2,2]	1.578	0.899	-0.054	1.526	3.476	TRUE	0.971	1.000	20974
beta1[3,2]	0.321	1.215	-2.346	0.384	2.643	TRUE	0.651	1.001	3698
beta1[4,2]	-0.356	0.799	-2.091	-0.296	1.054	TRUE	0.653	1.000	17451
beta1[5,2]	0.203	0.988	-1.847	0.230	2.094	TRUE	0.608	1.000	10005
beta1[6,2]	0.470	0.928	-1.310	0.436	2.437	TRUE	0.707	1.000	25000
beta1[7,2]	0.332	0.808	-1.313	0.339	1.947	TRUE	0.675	1.000	13551
beta1[8,2]	0.129	0.833	-1.552	0.141	1.788	TRUE	0.572	1.001	4226
---									
beta2[1,1]	0.809	1.094	-0.910	0.646	3.422	TRUE	0.776	1.000	11966
beta2[2,1]	0.068	0.545	-1.023	0.067	1.163	TRUE	0.554	1.000	20252
beta2[3,1]	-0.713	0.951	-2.935	-0.587	0.820	TRUE	0.778	1.000	16352
beta2[4,1]	1.095	0.704	-0.086	1.030	2.678	TRUE	0.962	1.000	12987
beta2[5,1]	0.566	0.608	-0.500	0.523	1.913	TRUE	0.846	1.001	3036
beta2[6,1]	-1.211	1.004	-3.605	-1.070	0.333	TRUE	0.920	1.002	1298
beta2[7,1]	-0.833	0.792	-2.651	-0.734	0.440	TRUE	0.878	1.001	3549
beta2[8,1]	-0.713	0.591	-1.967	-0.687	0.375	TRUE	0.899	1.001	4568
beta2[1,2]	0.807	1.098	-0.933	0.650	3.442	TRUE	0.773	1.001	3412
beta2[2,2]	-0.024	0.479	-1.012	-0.014	0.904	TRUE	0.512	1.000	17630
beta2[3,2]	-0.383	1.049	-2.643	-0.323	1.587	TRUE	0.644	1.002	2233
beta2[4,2]	1.349	0.776	0.092	1.257	3.131	FALSE	0.984	1.000	8097
beta2[5,2]	0.829	0.710	-0.339	0.751	2.474	TRUE	0.908	1.001	25000
beta2[6,2]	-1.094	0.988	-3.406	-0.967	0.471	TRUE	0.896	1.003	1204
beta2[7,2]	-0.837	0.785	-2.652	-0.742	0.430	TRUE	0.879	1.001	2409
beta2[8,2]	-1.586	1.154	-4.515	-1.341	-0.007	FALSE	0.976	1.004	953
---									
beta3[1,1]	1.986	0.846	0.575	1.896	3.908	FALSE	0.999	1.003	1413
beta3[2,1]	-0.259	0.501	-1.329	-0.223	0.634	TRUE	0.685	1.000	5774
beta3[3,1]	-0.086	0.602	-1.292	-0.082	1.113	TRUE	0.555	1.000	25000
beta3[4,1]	0.381	0.432	-0.434	0.367	1.270	TRUE	0.819	1.000	16550
beta3[5,1]	0.479	0.503	-0.423	0.447	1.574	TRUE	0.840	1.002	1840
beta3[6,1]	-0.425	0.512	-1.508	-0.397	0.511	TRUE	0.797	1.001	3956
beta3[7,1]	0.217	0.486	-0.687	0.194	1.250	TRUE	0.668	1.001	4236
beta3[8,1]	0.641	0.569	-0.423	0.620	1.829	TRUE	0.880	1.001	3465

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta3[1,2]	2.009	0.880	0.555	1.911	4.007	FALSE	0.998	1.002	2761
beta3[2,2]	0.206	0.427	-0.632	0.200	1.065	TRUE	0.691	1.001	4392
beta3[3,2]	-0.851	1.057	-3.516	-0.669	0.715	TRUE	0.805	1.004	1100
beta3[4,2]	0.229	0.428	-0.631	0.232	1.063	TRUE	0.712	1.000	11811
beta3[5,2]	0.712	0.557	-0.218	0.659	1.946	TRUE	0.924	1.002	1715
beta3[6,2]	-0.388	0.550	-1.522	-0.365	0.638	TRUE	0.766	1.000	5387
beta3[7,2]	0.116	0.480	-0.823	0.108	1.089	TRUE	0.594	1.001	4306
beta3[8,2]	-0.627	0.540	-1.774	-0.597	0.353	TRUE	0.886	1.001	2784

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 92.5 and DIC = 890.115
DIC is an estimate of expected predictive error (lower is better).

Food Availability Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
    beta1[k,l]*herb[i,l] +
    beta2[k,l]*bush[i,l] +
    beta3[k,l]*tree[i,l] +
    beta4[k,l]*coleop[i,l]
```

JAGS output for model 'oc_food_avail.bug', generated by jagsUI.
Estimates based on 5 chains of 50000 iterations,
adaptation = 100 iterations (sufficient),
burn-in = 25000 iterations and thin rate = 5,
yielding 25000 total samples from the joint posterior.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
co.lpsi	-0.636	0.648	-1.930	-0.641	0.666	TRUE	0.844	1.000	25000
co.beta1	0.046	0.353	-0.708	0.059	0.703	TRUE	0.571	1.000	5821
co.beta2	0.083	0.362	-0.638	0.080	0.816	TRUE	0.596	1.000	17049
co.beta3	0.093	0.274	-0.446	0.089	0.640	TRUE	0.634	1.001	3794
co.beta4	0.094	0.328	-0.565	0.095	0.739	TRUE	0.621	1.001	3003
beta1[1,1]	0.283	0.661	-0.906	0.228	1.766	TRUE	0.665	1.000	25000
beta1[2,1]	0.168	0.436	-0.705	0.169	1.035	TRUE	0.664	1.000	19874
beta1[3,1]	0.376	0.599	-0.766	0.353	1.611	TRUE	0.747	1.000	13676
beta1[4,1]	-2.760	1.495	-6.496	-2.470	-0.691	FALSE	0.999	1.002	2059

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta1[5,1]	-0.034	0.504	-1.070	-0.019	0.953	TRUE	0.517	1.000	22877
beta1[6,1]	0.141	0.515	-0.898	0.142	1.167	TRUE	0.619	1.000	6238
beta1[7,1]	1.220	0.786	-0.014	1.135	3.000	TRUE	0.973	1.001	11203
beta1[8,1]	0.855	0.781	-0.298	0.720	2.732	TRUE	0.902	1.001	3936
beta1[1,2]	0.326	0.734	-0.969	0.258	2.012	TRUE	0.673	1.000	7549
beta1[2,2]	0.404	0.534	-0.527	0.353	1.608	TRUE	0.785	1.000	10744
beta1[3,2]	0.129	0.755	-1.538	0.159	1.563	TRUE	0.602	1.000	8807
beta1[4,2]	-1.628	0.971	-3.824	-1.526	-0.005	FALSE	0.975	1.001	5409
beta1[5,2]	0.080	0.630	-1.148	0.071	1.427	TRUE	0.555	1.001	7292
beta1[6,2]	-0.536	0.943	-2.858	-0.344	0.806	TRUE	0.706	1.001	5964
beta1[7,2]	-0.669	0.935	-2.830	-0.545	0.807	TRUE	0.752	1.001	4172
beta1[8,2]	-0.412	0.782	-2.245	-0.294	0.815	TRUE	0.672	1.001	3356
---									
beta2[1,1]	1.101	1.055	-0.464	0.914	3.608	TRUE	0.884	1.001	8366
beta2[2,1]	0.460	0.556	-0.482	0.409	1.724	TRUE	0.808	1.000	25000
beta2[3,1]	-0.290	0.817	-2.200	-0.193	1.083	TRUE	0.613	1.001	5209
beta2[4,1]	0.807	1.041	-0.817	0.658	3.187	TRUE	0.769	1.000	8918
beta2[5,1]	-0.357	0.762	-1.905	-0.323	1.149	TRUE	0.707	1.001	6157
beta2[6,1]	1.157	0.834	-0.126	1.036	3.155	TRUE	0.956	1.000	9955
beta2[7,1]	0.335	0.716	-1.040	0.309	1.864	TRUE	0.710	1.000	6733
beta2[8,1]	-0.244	0.540	-1.384	-0.215	0.726	TRUE	0.682	1.000	25000
beta2[1,2]	1.055	0.962	-0.401	0.908	3.306	TRUE	0.897	1.000	13066
beta2[2,2]	-0.082	0.585	-1.351	-0.042	0.983	TRUE	0.531	1.000	12886
beta2[3,2]	-0.105	0.837	-1.875	-0.079	1.520	TRUE	0.544	1.001	5663
beta2[4,2]	-1.269	0.857	-3.159	-1.183	0.154	TRUE	0.955	1.000	25000
beta2[5,2]	-0.790	0.956	-3.105	-0.642	0.691	TRUE	0.820	1.002	2071
beta2[6,2]	-0.264	0.956	-2.335	-0.194	1.491	TRUE	0.595	1.000	7276
beta2[7,2]	0.546	0.646	-0.566	0.484	1.985	TRUE	0.814	1.000	15128
beta2[8,2]	-0.391	0.574	-1.678	-0.342	0.616	TRUE	0.752	1.001	4096
---									
beta3[1,1]	-0.449	0.642	-1.854	-0.391	0.659	TRUE	0.747	1.000	15796
beta3[2,1]	-0.327	0.502	-1.424	-0.277	0.536	TRUE	0.735	1.000	23286
beta3[3,1]	0.121	0.564	-0.992	0.112	1.292	TRUE	0.593	1.000	19217
beta3[4,1]	0.078	0.427	-0.799	0.086	0.902	TRUE	0.586	1.000	17305
beta3[5,1]	0.008	0.440	-0.892	0.019	0.866	TRUE	0.516	1.001	4498
beta3[6,1]	0.040	0.480	-0.940	0.046	0.999	TRUE	0.542	1.000	6190
beta3[7,1]	0.123	0.529	-0.932	0.115	1.210	TRUE	0.600	1.000	8586
beta3[8,1]	0.664	0.539	-0.277	0.624	1.827	TRUE	0.905	1.000	5398
beta3[1,2]	1.025	0.984	-0.411	0.840	3.369	TRUE	0.884	1.000	25000
beta3[2,2]	0.561	0.625	-0.438	0.476	1.970	TRUE	0.823	1.000	6553
beta3[3,2]	0.019	0.719	-1.565	0.054	1.387	TRUE	0.540	1.001	2680
beta3[4,2]	0.382	0.574	-0.577	0.307	1.743	TRUE	0.753	1.001	3268

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta3[5,2]	0.330	0.706	-0.766	0.221	2.078	TRUE	0.684	1.001	4896
beta3[6,2]	-0.048	0.619	-1.416	-0.012	1.107	TRUE	0.509	1.000	24835
beta3[7,2]	0.072	0.591	-1.179	0.083	1.238	TRUE	0.567	1.000	13306
beta3[8,2]	-0.963	0.838	-2.842	-0.878	0.389	TRUE	0.885	1.000	7783
---									
beta4[1,1]	0.658	0.717	-0.451	0.541	2.379	TRUE	0.847	1.000	11420
beta4[2,1]	0.268	0.542	-0.806	0.265	1.350	TRUE	0.706	1.001	7885
beta4[3,1]	-1.084	1.130	-3.775	-0.860	0.524	TRUE	0.849	1.002	2213
beta4[4,1]	0.382	0.555	-0.566	0.328	1.637	TRUE	0.756	1.001	4151
beta4[5,1]	0.066	0.468	-0.875	0.069	0.989	TRUE	0.566	1.001	5407
beta4[6,1]	-0.219	0.592	-1.599	-0.153	0.766	TRUE	0.618	1.001	5583
beta4[7,1]	-0.227	0.755	-2.018	-0.121	0.969	TRUE	0.580	1.001	5482
beta4[8,1]	-0.255	0.486	-1.256	-0.246	0.675	TRUE	0.703	1.000	11420
beta4[1,2]	0.517	0.714	-0.748	0.444	2.136	TRUE	0.778	1.001	5585
beta4[2,2]	1.321	0.831	-0.003	1.227	3.165	TRUE	0.975	1.000	9458
beta4[3,2]	-0.172	0.985	-2.266	-0.136	1.772	TRUE	0.570	1.001	4093
beta4[4,2]	0.342	0.627	-0.823	0.298	1.705	TRUE	0.716	1.000	11496
beta4[5,2]	-0.207	0.750	-1.947	-0.117	1.069	TRUE	0.581	1.002	3528
beta4[6,2]	0.062	0.672	-1.274	0.051	1.502	TRUE	0.537	1.001	3306
beta4[7,2]	0.595	0.731	-0.647	0.505	2.269	TRUE	0.803	1.000	8417
beta4[8,2]	-0.420	0.588	-1.736	-0.361	0.589	TRUE	0.766	1.000	15888

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 103 and DIC = 903.316
DIC is an estimate of expected predictive error (lower is better).

Strata Complexity and Cover Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
    beta1[k,l]*hcr[i,l] +
    beta2[k,l]*bcr[i,l] +
    beta3[k,l]*tcr[i,l]
```

hcr: herbaceous cover richness= total_herb* herb_richness
bcr: bush cover richness= total_bush * bush_richness
tcr: tree cover richness = tree_cover * tree_richness

JAGS output for model 'OcMod_StrataComplexity_AND_Cover.bug', generated by jagsUI.
Estimates based on 5 chains of 50000 iterations,
adaptation = 100 iterations (sufficient),
burn-in = 25000 iterations and thin rate = 5,
yielding 25000 total samples from the joint posterior.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
co.lpsi	-0.683	0.617	-1.884	-0.691	0.563	TRUE	0.871	1.000	23493
co.beta1	-0.173	0.419	-1.062	-0.159	0.612	TRUE	0.660	1.000	14728
co.beta2	0.203	0.317	-0.422	0.197	0.840	TRUE	0.747	1.001	5997
co.beta3	0.041	0.255	-0.471	0.046	0.537	TRUE	0.572	1.000	18865
beta1[1,1]	0.717	1.043	-0.807	0.521	3.270	TRUE	0.746	1.002	2061
beta1[2,1]	0.254	0.443	-0.576	0.236	1.193	TRUE	0.722	1.000	10564
beta1[3,1]	-0.596	0.870	-2.683	-0.456	0.757	TRUE	0.754	1.000	9653
beta1[4,1]	-1.977	1.012	-4.362	-1.835	-0.433	FALSE	0.997	1.003	1731
beta1[5,1]	-1.019	0.875	-3.102	-0.882	0.290	TRUE	0.918	1.000	25000
beta1[6,1]	-0.049	0.507	-1.087	-0.037	0.926	TRUE	0.533	1.000	7845
beta1[7,1]	1.383	0.876	0.046	1.254	3.475	FALSE	0.980	1.001	11810
beta1[8,1]	0.796	0.836	-0.387	0.630	2.891	TRUE	0.866	1.003	3090
beta1[1,2]	0.449	1.026	-1.239	0.307	2.900	TRUE	0.649	1.001	6948
beta1[2,2]	0.246	0.563	-0.810	0.220	1.459	TRUE	0.673	1.000	25000
beta1[3,2]	-0.305	0.957	-2.313	-0.253	1.492	TRUE	0.638	1.001	5270
beta1[4,2]	-1.721	1.248	-4.574	-1.570	0.347	TRUE	0.945	1.001	3585
beta1[5,2]	-0.874	1.043	-3.270	-0.748	0.923	TRUE	0.827	1.000	10945
beta1[6,2]	-0.322	0.844	-2.292	-0.234	1.154	TRUE	0.647	1.001	5399
beta1[7,2]	-0.838	1.084	-3.385	-0.689	0.836	TRUE	0.780	1.000	25000
beta1[8,2]	-0.212	0.792	-2.067	-0.126	1.139	TRUE	0.581	1.000	10843
---									
beta2[1,1]	0.940	0.872	-0.359	0.779	3.064	TRUE	0.901	1.001	3430
beta2[2,1]	0.297	0.461	-0.572	0.277	1.283	TRUE	0.751	1.000	25000
beta2[3,1]	0.004	0.648	-1.464	0.053	1.168	TRUE	0.538	1.001	4244
beta2[4,1]	1.281	0.950	-0.272	1.179	3.411	TRUE	0.935	1.000	24134
beta2[5,1]	0.173	0.721	-1.061	0.092	1.939	TRUE	0.567	1.000	25000
beta2[6,1]	1.237	0.842	-0.060	1.118	3.216	TRUE	0.966	1.001	5079
beta2[7,1]	0.405	0.648	-0.874	0.388	1.775	TRUE	0.768	1.001	7226
beta2[8,1]	0.006	0.520	-0.991	-0.004	1.092	TRUE	0.496	1.000	8238
beta2[1,2]	0.788	0.758	-0.398	0.670	2.592	TRUE	0.884	1.000	5696
beta2[2,2]	0.099	0.422	-0.786	0.112	0.901	TRUE	0.616	1.000	25000
beta2[3,2]	0.109	0.686	-1.350	0.132	1.424	TRUE	0.592	1.001	12279
beta2[4,2]	-1.146	0.784	-2.876	-1.068	0.178	TRUE	0.949	1.000	11416
beta2[5,2]	-0.535	0.892	-2.742	-0.387	0.812	TRUE	0.731	1.002	2392
beta2[6,2]	-0.313	0.854	-2.247	-0.214	1.149	TRUE	0.615	1.000	6474
beta2[7,2]	0.548	0.527	-0.403	0.507	1.707	TRUE	0.868	1.000	9901

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta2[8,2]	-0.187	0.492	-1.274	-0.147	0.683	TRUE	0.632	1.000	8408
---									
beta3[1,1]	0.095	0.511	-0.905	0.084	1.179	TRUE	0.574	1.000	13840
beta3[2,1]	-0.323	0.497	-1.507	-0.252	0.470	TRUE	0.733	1.000	17256
beta3[3,1]	0.241	0.574	-0.791	0.206	1.493	TRUE	0.673	1.001	13926
beta3[4,1]	0.357	0.472	-0.443	0.306	1.443	TRUE	0.785	1.000	11236
beta3[5,1]	-0.302	0.512	-1.461	-0.247	0.569	TRUE	0.717	1.000	12993
beta3[6,1]	0.018	0.526	-1.039	0.016	1.065	TRUE	0.513	1.000	25000
beta3[7,1]	-0.129	0.556	-1.381	-0.086	0.872	TRUE	0.570	1.000	8927
beta3[8,1]	0.400	0.506	-0.438	0.334	1.564	TRUE	0.794	1.000	8591
beta3[1,2]	0.495	0.658	-0.495	0.373	2.104	TRUE	0.788	1.000	10206
beta3[2,2]	0.084	0.402	-0.680	0.068	0.936	TRUE	0.577	1.000	25000
beta3[3,2]	0.067	0.666	-1.379	0.088	1.381	TRUE	0.569	1.000	17882
beta3[4,2]	0.231	0.447	-0.611	0.211	1.184	TRUE	0.702	1.000	14906
beta3[5,2]	0.290	0.572	-0.675	0.225	1.623	TRUE	0.690	1.000	8715
beta3[6,2]	-0.616	0.792	-2.560	-0.460	0.521	TRUE	0.791	1.000	13418
beta3[7,2]	-0.130	0.520	-1.313	-0.086	0.792	TRUE	0.580	1.001	4785
beta3[8,2]	-0.216	0.477	-1.292	-0.162	0.595	TRUE	0.652	1.000	9695

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 92.2 and DIC = 890.385
DIC is an estimate of expected predictive error (lower is better)

Plot complexity Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
    beta1[k,l]*forest[i,l] +
    beta2[k,l]*bareg[i,l] +
    beta3[k,l]*richness[i,l]
```

Forest= product between tree density and average DBH
Richness= number of plant species around the Sherman traps

JAGS output for model 'OcMod_PlotComplexity.bug', generated by jagsUI.
Estimates based on 5 chains of 50000 iterations,
adaptation = 100 iterations (sufficient),

```
burn-in = 25000 iterations and thin rate = 5,
yielding 25000 total samples from the joint posterior.

                 mean     sd    2.5%     50%   97.5% overlap0     f  Rhat n.eff
co.lpsi        -0.596  0.635  -1.828  -0.605   0.695      TRUE 0.834 1.000 12968
co.beta1        0.024  0.275  -0.524   0.027   0.561      TRUE 0.539 1.001  2277
co.beta2       -0.227  0.323  -0.869  -0.223   0.410      TRUE 0.768 1.000 25000
co.beta3        0.149  0.352  -0.543   0.147   0.861      TRUE 0.678 1.000  6888

beta1[1,1]      0.352  0.588  -0.739   0.307   1.656      TRUE 0.736 1.000  7732
beta1[2,1]     -0.186  0.430  -1.107  -0.156   0.597      TRUE 0.657 1.000  8435
beta1[3,1]     -0.506  0.701  -2.084  -0.422   0.635      TRUE 0.767 1.000 25000
beta1[4,1]      0.804  0.568  -0.148   0.749   2.057      TRUE 0.943 1.001  5047
beta1[5,1]      0.395  0.513  -0.519   0.353   1.535      TRUE 0.788 1.000 25000
beta1[6,1]     -0.531  0.557  -1.765  -0.476   0.404      TRUE 0.840 1.000  7646
beta1[7,1]     -0.326  0.555  -1.532  -0.280   0.661      TRUE 0.720 1.000  7092
beta1[8,1]     -0.074  0.421  -0.967  -0.062   0.733      TRUE 0.566 1.000 15510

beta1[1,2]      0.374  0.559  -0.620   0.325   1.616      TRUE 0.753 1.000  5985
beta1[2,2]      0.094  0.421  -0.703   0.078   0.981      TRUE 0.582 1.000 11203
beta1[3,2]     -0.102  0.727  -1.577  -0.097   1.408      TRUE 0.567 1.001 15647
beta1[4,2]      0.000  0.481  -1.018   0.025   0.903      TRUE 0.478 1.000 18466
beta1[5,2]      0.426  0.589  -0.604   0.368   1.739      TRUE 0.782 1.001 10287
beta1[6,2]     -0.138  0.558  -1.261  -0.135   0.992      TRUE 0.610 1.000  9596
beta1[7,2]     -0.075  0.518  -1.119  -0.072   0.982      TRUE 0.562 1.001  3844
beta1[8,2]      0.008  0.401  -0.788   0.004   0.826      TRUE 0.505 1.000 12189

---
beta2[1,1]      0.110  0.660  -1.034   0.040   1.607      TRUE 0.528 1.001  3943
beta2[2,1]     -0.676  0.582  -1.967  -0.627   0.346      TRUE 0.899 1.001  3772
beta2[3,1]      0.460  0.775  -0.852   0.383   2.164      TRUE 0.712 1.001  8038
beta2[4,1]      0.081  0.538  -0.850   0.028   1.290      TRUE 0.523 1.000 23635
beta2[5,1]     -0.170  0.576  -1.333  -0.175   0.991      TRUE 0.638 1.001  7161
beta2[6,1]     -0.493  0.667  -1.968  -0.444   0.727      TRUE 0.786 1.000 21389
beta2[7,1]     -0.568  0.705  -2.189  -0.493   0.679      TRUE 0.814 1.001  3936
beta2[8,1]      0.036  0.501  -0.926   0.018   1.086      TRUE 0.515 1.000  7212

beta2[1,2]      0.032  0.643  -1.109  -0.019   1.470      TRUE 0.486 1.001  8755
beta2[2,2]     -0.773  0.525  -1.943  -0.725   0.106      TRUE 0.954 1.000  5688
beta2[3,2]     -0.145  0.813  -1.884  -0.123   1.359      TRUE 0.574 1.001  8894
beta2[4,2]     -0.414  0.487  -1.496  -0.376   0.463      TRUE 0.813 1.000 22629
beta2[5,2]     -0.040  0.649  -1.227  -0.082   1.416      TRUE 0.563 1.000 14060
beta2[6,2]     -1.002  0.888  -3.201  -0.831   0.273      TRUE 0.922 1.001  8386
beta2[7,2]     -0.732  0.700  -2.419  -0.626   0.364      TRUE 0.884 1.001  6908
beta2[8,2]      0.255  0.462  -0.568   0.220   1.255      TRUE 0.697 1.000  8320

---
                 mean     sd    2.5%     50%   97.5% overlap0     f  Rhat n.eff
```

beta3[1,1]	1.786	1.178	0.021	1.612	4.533	FALSE	0.977	1.004	1162
beta3[2,1]	0.186	0.407	-0.609	0.178	1.026	TRUE	0.681	1.000	25000
beta3[3,1]	-0.569	0.847	-2.571	-0.435	0.751	TRUE	0.740	1.001	3516
beta3[4,1]	-0.035	0.444	-0.884	-0.047	0.871	TRUE	0.545	1.000	14287
beta3[5,1]	-0.777	0.656	-2.261	-0.710	0.297	TRUE	0.909	1.001	3053
beta3[6,1]	0.267	0.468	-0.654	0.262	1.204	TRUE	0.724	1.000	9620
beta3[7,1]	0.923	0.624	-0.101	0.853	2.329	TRUE	0.960	1.000	25000
beta3[8,1]	0.633	0.548	-0.260	0.573	1.834	TRUE	0.905	1.003	2416
beta3[1,2]	1.443	1.097	-0.309	1.301	3.957	TRUE	0.938	1.003	1394
beta3[2,2]	0.108	0.513	-0.955	0.112	1.136	TRUE	0.600	1.000	25000
beta3[3,2]	0.019	0.908	-1.833	0.027	1.864	TRUE	0.515	1.001	6196
beta3[4,2]	-0.686	0.703	-2.313	-0.592	0.425	TRUE	0.854	1.000	15164
beta3[5,2]	-0.773	0.929	-2.934	-0.650	0.715	TRUE	0.832	1.001	25000
beta3[6,2]	0.178	0.665	-1.191	0.178	1.529	TRUE	0.630	1.000	17804
beta3[7,2]	0.183	0.689	-1.350	0.229	1.440	TRUE	0.641	1.000	7513
beta3[8,2]	0.221	0.571	-1.013	0.244	1.305	TRUE	0.683	1.001	4224

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 93.9 and DIC = 892.518
DIC is an estimate of expected predictive error (lower is better).

Level of protection Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
     beta1[k,l]*prot1[i,l] +
     beta2[k,l]*prot2[i,l] +
     beta3[k,l]*prot3[i,l]
```

prot1: difference in occupancy probability between National Reserve and Outside the PA
prot2: difference in occupancy probability between National Park and Outside the PA
prot3: difference in occupancy probability between Strict Nature Reserve and Outside t
he PA

JAGS output for model 'OcMod_Level_of_proteccion.bug', generated by jagsUI.
Estimates based on 5 chains of 50000 iterations,
adaptation = 100 iterations (sufficient),
burn-in = 25000 iterations and thin rate = 5,
yielding 25000 total samples from the joint posterior.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
co.lpsi	-0.561	0.569	-1.678	-0.561	0.579	TRUE	0.846	1.000	5440
co.beta1	-0.045	0.476	-0.999	-0.041	0.895	TRUE	0.537	1.002	1419
co.beta2	-0.166	0.446	-1.056	-0.169	0.714	TRUE	0.651	1.003	978
co.beta3	0.079	0.524	-0.968	0.078	1.111	TRUE	0.566	1.002	1318
beta1[1,1]	-0.261	0.888	-2.086	-0.243	1.479	TRUE	0.621	1.001	5859
beta1[2,1]	-0.957	1.173	-3.791	-0.769	0.837	TRUE	0.808	1.001	3497
beta1[3,1]	1.073	1.164	-0.838	0.945	3.659	TRUE	0.828	1.001	5062
beta1[4,1]	0.415	0.825	-1.153	0.386	2.124	TRUE	0.690	1.001	2758
beta1[5,1]	0.510	0.924	-1.193	0.453	2.452	TRUE	0.714	1.001	3940
beta1[6,1]	-1.036	1.237	-3.966	-0.838	0.857	TRUE	0.819	1.002	2847
beta1[7,1]	-0.816	1.104	-3.401	-0.659	0.945	TRUE	0.776	1.000	7399
beta1[8,1]	0.071	0.851	-1.506	0.026	1.951	TRUE	0.514	1.001	5286
beta1[1,2]	-0.252	0.886	-2.085	-0.228	1.472	TRUE	0.615	1.000	6555
beta1[2,2]	0.224	0.859	-1.354	0.175	2.044	TRUE	0.589	1.001	4868
beta1[3,2]	-0.013	1.277	-2.883	0.060	2.406	TRUE	0.477	1.001	3580
beta1[4,2]	0.815	0.897	-0.716	0.739	2.776	TRUE	0.822	1.002	2038
beta1[5,2]	0.956	1.068	-0.750	0.828	3.416	TRUE	0.830	1.001	3067
beta1[6,2]	-0.990	1.269	-3.996	-0.801	0.990	TRUE	0.801	1.002	3000
beta1[7,2]	-0.340	0.926	-2.323	-0.283	1.391	TRUE	0.639	1.001	4927
beta1[8,2]	-0.420	0.844	-2.298	-0.352	1.071	TRUE	0.682	1.000	6267
---									
beta2[1,1]	-0.295	0.840	-2.018	-0.278	1.358	TRUE	0.647	1.001	4085
beta2[2,1]	-0.352	0.760	-1.994	-0.314	1.054	TRUE	0.680	1.001	3145
beta2[3,1]	-0.595	1.088	-3.125	-0.464	1.233	TRUE	0.711	1.001	2784
beta2[4,1]	0.617	0.870	-0.827	0.526	2.576	TRUE	0.753	1.001	3984
beta2[5,1]	0.121	0.811	-1.396	0.079	1.838	TRUE	0.543	1.001	3288
beta2[6,1]	-0.102	0.806	-1.760	-0.100	1.505	TRUE	0.556	1.001	2395
beta2[7,1]	-0.804	1.085	-3.425	-0.634	0.861	TRUE	0.791	1.001	4130
beta2[8,1]	-0.323	0.757	-1.913	-0.295	1.105	TRUE	0.671	1.001	3235
beta2[1,2]	-0.301	0.834	-2.025	-0.286	1.364	TRUE	0.649	1.001	4983
beta2[2,2]	-0.209	0.721	-1.695	-0.202	1.229	TRUE	0.622	1.001	2658
beta2[3,2]	-0.509	1.115	-3.093	-0.387	1.441	TRUE	0.681	1.001	3312
beta2[4,2]	0.347	0.791	-1.102	0.299	2.044	TRUE	0.659	1.000	6458
beta2[5,2]	-0.122	0.856	-1.874	-0.116	1.595	TRUE	0.563	1.002	2497
beta2[6,2]	-0.049	0.839	-1.733	-0.067	1.708	TRUE	0.535	1.001	6021
beta2[7,2]	-0.318	0.858	-2.148	-0.289	1.332	TRUE	0.648	1.001	3732
beta2[8,2]	-0.127	0.740	-1.580	-0.138	1.404	TRUE	0.583	1.001	2212
---									
beta3[1,1]	1.037	1.326	-1.083	0.856	4.194	TRUE	0.798	1.002	2217
beta3[2,1]	0.347	0.796	-1.234	0.342	1.920	TRUE	0.675	1.001	5955
	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff

```
beta3[3,1]      -0.721  1.344  -3.834  -0.545   1.468     TRUE 0.689 1.001 10538
beta3[4,1]       1.357  1.067  -0.495   1.272   3.682     TRUE 0.918 1.002  1937
beta3[5,1]      -0.051  0.922  -1.965  -0.023   1.726     TRUE 0.512 1.001  5676
beta3[6,1]       0.029  0.907  -1.844   0.054   1.784     TRUE 0.526 1.001  4099
beta3[7,1]      -1.310  1.363  -4.488  -1.129   0.799     TRUE 0.852 1.001 12880
beta3[8,1]      -0.442  0.854  -2.201  -0.417   1.189     TRUE 0.698 1.001  2676

beta3[1,2]       1.042  1.325  -1.087   0.856   4.193     TRUE 0.799 1.001  2700
beta3[2,2]       0.472  0.794  -1.022   0.440   2.132     TRUE 0.729 1.000  9864
beta3[3,2]      -0.630  1.360  -3.743  -0.468   1.703     TRUE 0.663 1.001  5877
beta3[4,2]       1.938  1.257  -0.116   1.796   4.793     TRUE 0.966 1.001  4873
beta3[5,2]       0.403  0.998  -1.398   0.333   2.544     TRUE 0.652 1.001  4799
beta3[6,2]       0.090  0.947  -1.813   0.096   1.968     TRUE 0.546 1.000 12661
beta3[7,2]      -1.315  1.374  -4.490  -1.124   0.807     TRUE 0.850 1.001 18689
beta3[8,2]      -0.574  0.873  -2.461  -0.518   0.994     TRUE 0.744 1.001  2712

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 85.1 and DIC = 881.047
DIC is an estimate of expected predictive error (lower is better).
```

Shelter Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
    beta1[k,l]*bush[i,l] +
    beta2[k,l]*logs[i,l] +
    beta3[k,l]*tree[i,l] +
    beta4[k,l]*uncov[i,l] +
    beta5[k,l]*canopy[i,l] +
    beta6[k,l]*connect[i,l]

 JAGS output for model 'OcMod_Shelter.bug', generated by jagsUI.
 Estimates based on 5 chains of 50000 iterations,
 adaptation = 100 iterations (sufficient),
 burn-in = 25000 iterations and thin rate = 5,
 yielding 25000 total samples from the joint posterior.

                   mean     sd    2.5%     50%   97.5% overlap0     f  Rhat n.eff
 co.lpsi         -0.653  0.667  -1.976  -0.654   0.660     TRUE 0.845 1.000 25000
                   mean     sd    2.5%     50%   97.5% overlap0     f  Rhat n.eff
```

```
co.betalpsi1     0.075  0.408  -0.702   0.061   0.918      TRUE 0.565 1.003  1075
co.betalpsi2    -0.259  0.380  -1.012  -0.256   0.495      TRUE 0.757 1.000  6475
co.betalpsi3    -0.046  0.317  -0.681  -0.044   0.570      TRUE 0.557 1.001  2534
co.betalpsi4     0.351  0.375  -0.392   0.356   1.059      TRUE 0.824 1.002  1530
co.betalpsi5     0.587  0.384  -0.165   0.587   1.351      TRUE 0.940 1.001  2573
co.betalpsi6    -0.166  0.446  -1.035  -0.175   0.729      TRUE 0.652 1.003  1680

beta1[1,1]       1.342  1.193  -0.456   1.164   4.180      TRUE 0.901 1.001  2928
beta1[2,1]       0.469  0.622  -0.583   0.406   1.896      TRUE 0.778 1.001  4724
beta1[3,1]      -0.470  0.857  -2.424  -0.371   0.998      TRUE 0.714 1.001 21416
beta1[4,1]       0.589  0.753  -0.648   0.506   2.285      TRUE 0.779 1.000  9019
beta1[5,1]      -0.354  0.862  -2.135  -0.329   1.392      TRUE 0.687 1.001 16860
beta1[6,1]       0.913  0.905  -0.501   0.788   3.009      TRUE 0.864 1.001  3254
beta1[7,1]       0.550  1.125  -1.182   0.340   3.358      TRUE 0.670 1.005   881
beta1[8,1]      -0.332  0.648  -1.608  -0.329   0.942      TRUE 0.724 1.000 25000

beta1[1,2]       1.250  1.081  -0.421   1.099   3.787      TRUE 0.904 1.000  7964
beta1[2,2]       0.301  0.554  -0.722   0.273   1.475      TRUE 0.704 1.000  6416
beta1[3,2]      -0.207  0.906  -2.126  -0.169   1.520      TRUE 0.590 1.000 20353
beta1[4,2]      -0.923  0.843  -2.868  -0.805   0.413      TRUE 0.886 1.001  6641
beta1[5,2]      -0.570  0.922  -2.704  -0.467   1.037      TRUE 0.743 1.001 25000
beta1[6,2]      -0.625  1.147  -3.251  -0.483   1.302      TRUE 0.707 1.001  8911
beta1[7,2]       0.708  0.799  -0.565   0.599   2.544      TRUE 0.824 1.003  1155
beta1[8,2]      -0.767  0.679  -2.331  -0.696   0.347      TRUE 0.893 1.000 14942

---
beta2[1,1]       0.010  0.774  -1.400  -0.044   1.713      TRUE 0.474 1.001  3796
beta2[2,1]      -0.143  0.608  -1.292  -0.171   1.169      TRUE 0.619 1.000 21845
beta2[3,1]      -0.357  0.786  -2.017  -0.335   1.175      TRUE 0.691 1.001  4923
beta2[4,1]       0.500  0.648  -0.633   0.450   1.908      TRUE 0.776 1.000 25000
beta2[5,1]       0.341  0.861  -1.144   0.244   2.301      TRUE 0.639 1.001  2588
beta2[6,1]      -1.276  0.919  -3.365  -1.170   0.195      TRUE 0.949 1.000 16922
beta2[7,1]      -1.462  0.981  -3.691  -1.335   0.092      TRUE 0.964 1.001  8643
beta2[8,1]      -0.534  0.670  -2.051  -0.478   0.653      TRUE 0.803 1.001  5969

beta2[1,2]      -0.347  0.674  -1.807  -0.308   0.904      TRUE 0.700 1.000 10670
beta2[2,2]      -0.397  0.507  -1.452  -0.382   0.558      TRUE 0.787 1.000  7760
beta2[3,2]      -0.254  0.838  -1.976  -0.254   1.424      TRUE 0.637 1.001  3401
beta2[4,2]       0.344  0.563  -0.698   0.319   1.516      TRUE 0.722 1.000 10858
beta2[5,2]       0.434  0.804  -0.955   0.357   2.219      TRUE 0.693 1.001  6830
beta2[6,2]      -0.698  0.861  -2.565  -0.641   0.883      TRUE 0.812 1.001  9814
beta2[7,2]      -0.981  0.813  -2.743  -0.919   0.458      TRUE 0.904 1.001  4648
beta2[8,2]      -0.268  0.523  -1.310  -0.262   0.758      TRUE 0.705 1.000 23100

---
beta3[1,1]      -0.645  0.713  -2.200  -0.585   0.582      TRUE 0.821 1.001  4035
                  mean     sd    2.5%     50%   97.5% overlap0     f  Rhat n.eff
```

beta3[2,1]	-0.374	0.509	-1.506	-0.328	0.511	TRUE	0.769	1.000	7006
beta3[3,1]	-0.043	0.599	-1.255	-0.040	1.163	TRUE	0.532	1.001	5328
beta3[4,1]	0.385	0.484	-0.466	0.348	1.451	TRUE	0.789	1.000	7135
beta3[5,1]	0.193	0.656	-1.008	0.148	1.647	TRUE	0.612	1.000	21208
beta3[6,1]	-0.244	0.572	-1.476	-0.213	0.837	TRUE	0.668	1.000	14258
beta3[7,1]	-0.297	0.608	-1.598	-0.266	0.833	TRUE	0.694	1.000	6692
beta3[8,1]	0.390	0.569	-0.604	0.345	1.628	TRUE	0.748	1.001	6017
beta3[1,2]	0.989	1.023	-0.539	0.832	3.397	TRUE	0.848	1.001	16841
beta3[2,2]	0.284	0.601	-0.704	0.215	1.670	TRUE	0.659	1.000	11854
beta3[3,2]	-0.112	0.783	-1.834	-0.086	1.423	TRUE	0.556	1.001	6586
beta3[4,2]	0.205	0.531	-0.825	0.187	1.330	TRUE	0.657	1.001	3223
beta3[5,2]	0.290	0.773	-1.032	0.209	2.102	TRUE	0.640	1.000	20491
beta3[6,2]	-0.340	0.733	-2.024	-0.272	0.980	TRUE	0.689	1.000	8004
beta3[7,2]	-0.475	0.719	-2.143	-0.388	0.723	TRUE	0.750	1.000	12908
beta3[8,2]	-1.142	0.841	-3.001	-1.064	0.234	TRUE	0.933	1.000	9840
---									
beta4[1,1]	0.277	0.630	-1.001	0.288	1.526	TRUE	0.686	1.001	2473
beta4[2,1]	0.516	0.594	-0.628	0.507	1.743	TRUE	0.819	1.001	2769
beta4[3,1]	-0.552	1.021	-3.056	-0.378	0.953	TRUE	0.678	1.001	7262
beta4[4,1]	0.233	0.530	-0.859	0.243	1.244	TRUE	0.688	1.000	6687
beta4[5,1]	-0.239	0.819	-2.128	-0.144	1.107	TRUE	0.581	1.000	8730
beta4[6,1]	0.683	0.663	-0.532	0.641	2.122	TRUE	0.867	1.001	6131
beta4[7,1]	0.393	0.699	-0.981	0.383	1.850	TRUE	0.735	1.002	2433
beta4[8,1]	0.671	0.725	-0.567	0.598	2.335	TRUE	0.842	1.000	17042
beta4[1,2]	0.355	0.763	-1.167	0.351	1.965	TRUE	0.706	1.001	5828
beta4[2,2]	0.920	0.838	-0.395	0.799	2.895	TRUE	0.899	1.000	18905
beta4[3,2]	0.535	1.109	-1.438	0.424	3.100	TRUE	0.700	1.002	3033
beta4[4,2]	0.451	0.666	-0.803	0.416	1.912	TRUE	0.770	1.000	8516
beta4[5,2]	0.560	0.913	-1.073	0.477	2.655	TRUE	0.747	1.000	14218
beta4[6,2]	0.640	0.870	-0.931	0.577	2.596	TRUE	0.800	1.000	16965
beta4[7,2]	0.598	0.791	-0.814	0.533	2.388	TRUE	0.795	1.001	2534
beta4[8,2]	-0.211	0.858	-2.222	-0.088	1.153	TRUE	0.545	1.000	11884
---									
beta5[1,1]	0.631	0.751	-0.794	0.597	2.280	TRUE	0.818	1.000	6824
beta5[2,1]	1.077	0.650	-0.036	1.012	2.527	TRUE	0.970	1.001	4191
beta5[3,1]	0.342	0.781	-1.311	0.378	1.832	TRUE	0.699	1.001	2910
beta5[4,1]	0.805	0.590	-0.283	0.773	2.074	TRUE	0.929	1.000	5490
beta5[5,1]	1.489	0.971	0.027	1.347	3.774	FALSE	0.977	1.003	2071
beta5[6,1]	0.336	0.744	-1.296	0.382	1.705	TRUE	0.708	1.001	2874
beta5[7,1]	0.840	0.890	-0.938	0.824	2.641	TRUE	0.846	1.001	3738
beta5[8,1]	-0.324	0.696	-1.809	-0.288	0.961	TRUE	0.672	1.001	4821
	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff

```
beta5[1,2]       0.308  0.631  -0.997   0.332   1.521     TRUE 0.705 1.001  6244
beta5[2,2]       0.738  0.502  -0.210   0.724   1.775     TRUE 0.937 1.000  5785
beta5[3,2]       0.442  0.830  -1.231   0.453   2.122     TRUE 0.731 1.000 11094
beta5[4,2]       0.630  0.505  -0.347   0.616   1.655     TRUE 0.902 1.000  5725
beta5[5,2]       1.292  0.830  -0.098   1.200   3.194     TRUE 0.965 1.001  3710
beta5[6,2]       0.665  0.718  -0.664   0.633   2.182     TRUE 0.847 1.001  5289
beta5[7,2]       1.660  0.891   0.215   1.550   3.693    FALSE 0.991 1.001  3397
beta5[8,2]      -0.453  0.595  -1.698  -0.423   0.613     TRUE 0.773 1.000  7524

---
beta6[1,1]       0.239  0.961  -1.372   0.120   2.493     TRUE 0.559 1.000 17255
beta6[2,1]      -1.016  0.831  -2.782  -0.961   0.524     TRUE 0.905 1.002  1439
beta6[3,1]       0.007  0.871  -1.739  -0.013   1.825     TRUE 0.494 1.002  2226
beta6[4,1]      -0.116  0.666  -1.433  -0.131   1.244     TRUE 0.583 1.001  6325
beta6[5,1]       0.235  0.846  -1.267   0.162   2.105     TRUE 0.587 1.001  3837
beta6[6,1]      -0.395  0.869  -2.318  -0.352   1.227     TRUE 0.679 1.001  5281
beta6[7,1]      -0.443  0.847  -2.286  -0.392   1.112     TRUE 0.704 1.003  1690
beta6[8,1]       0.434  0.826  -1.004   0.353   2.273     TRUE 0.686 1.001  3399

beta6[1,2]      -0.452  0.884  -2.392  -0.396   1.178     TRUE 0.698 1.001  4210
beta6[2,2]      -1.465  0.934  -3.531  -1.383   0.099     TRUE 0.965 1.001  2294
beta6[3,2]       0.289  1.060  -1.549   0.172   2.776     TRUE 0.582 1.001  5070
beta6[4,2]      -0.110  0.669  -1.426  -0.125   1.259     TRUE 0.579 1.001  5496
beta6[5,2]      -0.224  0.895  -2.172  -0.190   1.493     TRUE 0.603 1.000 25000
beta6[6,2]      -0.055  0.888  -1.751  -0.086   1.871     TRUE 0.546 1.000 17510
beta6[7,2]      -0.242  0.860  -1.995  -0.248   1.513     TRUE 0.629 1.002  3607
beta6[8,2]       0.141  0.772  -1.342   0.105   1.756     TRUE 0.561 1.002  2049

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 113.6 and DIC = 919.177
DIC is an estimate of expected predictive error (lower is better).
```

Strata complexity

```
logit(psi[i,k,l]) <- lpsi[k,l] +
    beta1[k,l]*hrichness[i,l] +
    beta2[k,l]*brichness[i,l] +
    beta3[k,l]*trichness[i,l]

hrichness: Herbaceous richness
```

brichness: Bush richness
trichness: Tree richness

JAGS output for model 'OcMod_StrataComplexity.bug', generated by jagsUI.
Estimates based on 5 chains of 50000 iterations,
adaptation = 100 iterations (sufficient),
burn-in = 25000 iterations and thin rate = 5,
yielding 25000 total samples from the joint posterior.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
co.lpsi	-0.662	0.632	-1.898	-0.671	0.623	TRUE	0.860	1.000	7684
co.beta1	0.050	0.370	-0.701	0.055	0.784	TRUE	0.565	1.000	16672
co.beta2	0.122	0.275	-0.422	0.124	0.668	TRUE	0.677	1.003	1068
co.beta3	-0.033	0.257	-0.541	-0.038	0.486	TRUE	0.560	1.002	2768
beta1[1,1]	1.383	1.006	-0.170	1.241	3.691	TRUE	0.952	1.000	12380
beta1[2,1]	0.315	0.429	-0.491	0.300	1.211	TRUE	0.773	1.000	25000
beta1[3,1]	-1.230	1.071	-3.793	-1.058	0.360	TRUE	0.908	1.002	2577
beta1[4,1]	-0.404	0.450	-1.335	-0.387	0.445	TRUE	0.821	1.000	25000
beta1[5,1]	-1.125	0.740	-2.881	-1.034	0.050	TRUE	0.968	1.001	8208
beta1[6,1]	0.198	0.486	-0.782	0.198	1.154	TRUE	0.670	1.000	13911
beta1[7,1]	0.849	0.654	-0.205	0.771	2.357	TRUE	0.936	1.000	25000
beta1[8,1]	0.569	0.520	-0.317	0.517	1.726	TRUE	0.878	1.001	3823
beta1[1,2]	1.085	0.928	-0.462	0.991	3.167	TRUE	0.900	1.000	12970
beta1[2,2]	0.106	0.495	-0.925	0.121	1.060	TRUE	0.604	1.000	25000
beta1[3,2]	-0.293	1.023	-2.424	-0.273	1.762	TRUE	0.624	1.000	14202
beta1[4,2]	-0.571	0.588	-1.883	-0.524	0.449	TRUE	0.849	1.000	25000
beta1[5,2]	-1.006	0.844	-2.908	-0.920	0.448	TRUE	0.910	1.001	6411
beta1[6,2]	0.237	0.680	-1.042	0.209	1.704	TRUE	0.647	1.001	12050
beta1[7,2]	0.071	0.705	-1.494	0.123	1.346	TRUE	0.578	1.000	10093
beta1[8,2]	0.353	0.520	-0.653	0.341	1.415	TRUE	0.760	1.000	11943
---									
beta2[1,1]	0.379	0.607	-0.704	0.324	1.768	TRUE	0.746	1.000	11927
beta2[2,1]	-0.078	0.455	-1.023	-0.065	0.813	TRUE	0.563	1.001	5721
beta2[3,1]	0.107	0.592	-1.125	0.107	1.299	TRUE	0.587	1.001	4550
beta2[4,1]	0.600	0.581	-0.424	0.557	1.839	TRUE	0.857	1.000	6876
beta2[5,1]	0.579	0.592	-0.394	0.504	1.936	TRUE	0.855	1.001	6050
beta2[6,1]	0.254	0.516	-0.726	0.230	1.370	TRUE	0.700	1.001	3140
beta2[7,1]	0.622	0.677	-0.463	0.521	2.192	TRUE	0.843	1.000	21295
beta2[8,1]	0.322	0.474	-0.517	0.290	1.359	TRUE	0.757	1.001	9804
beta2[1,2]	0.325	0.550	-0.733	0.292	1.509	TRUE	0.735	1.000	10723
beta2[2,2]	-0.296	0.458	-1.293	-0.258	0.508	TRUE	0.735	1.000	7823
	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta2[3,2]	0.246	0.699	-1.079	0.203	1.818	TRUE	0.647	1.000	9339
beta2[4,2]	-0.966	0.718	-2.539	-0.905	0.236	TRUE	0.927	1.001	4842

```
beta2[5,2]      -0.182  0.721  -1.954  -0.070   0.938     TRUE 0.552 1.001 10226
beta2[6,2]       0.035  0.549  -1.139   0.060   1.090     TRUE 0.551 1.000  6330
beta2[7,2]      -0.044  0.554  -1.225  -0.011   0.996     TRUE 0.509 1.000  9607
beta2[8,2]       0.005  0.438  -0.914   0.026   0.823     TRUE 0.525 1.001  4709

---
beta3[1,1]       0.399  0.655  -0.672   0.308   1.921     TRUE 0.722 1.000 18745
beta3[2,1]      -0.142  0.397  -0.985  -0.128   0.623     TRUE 0.641 1.001  3865
beta3[3,1]       0.382  0.665  -0.730   0.298   1.929     TRUE 0.712 1.002  1945
beta3[4,1]       0.164  0.421  -0.593   0.137   1.070     TRUE 0.643 1.000 19262
beta3[5,1]      -0.597  0.609  -1.992  -0.509   0.366     TRUE 0.859 1.000 25000
beta3[6,1]       0.114  0.543  -0.888   0.078   1.296     TRUE 0.564 1.001  6111
beta3[7,1]      -0.264  0.489  -1.338  -0.226   0.613     TRUE 0.707 1.000 13166
beta3[8,1]      -0.090  0.428  -0.987  -0.079   0.742     TRUE 0.584 1.001  4706

beta3[1,2]       0.173  0.568  -0.894   0.134   1.408     TRUE 0.610 1.000 25000
beta3[2,2]      -0.110  0.395  -0.931  -0.101   0.671     TRUE 0.616 1.001  7036
beta3[3,2]       0.104  0.729  -1.410   0.093   1.562     TRUE 0.565 1.000 12078
beta3[4,2]       0.092  0.444  -0.778   0.081   1.014     TRUE 0.580 1.000 14583
beta3[5,2]       0.098  0.599  -1.019   0.056   1.413     TRUE 0.543 1.000 25000
beta3[6,2]      -0.945  0.919  -3.176  -0.773   0.359     TRUE 0.883 1.000 25000
beta3[7,2]      -0.113  0.487  -1.138  -0.102   0.843     TRUE 0.595 1.000  7553
beta3[8,2]      -0.010  0.405  -0.826  -0.015   0.812     TRUE 0.516 1.001  4567


Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.

overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

DIC info: (pD = var(deviance)/2)
pD = 86.6 and DIC = 884.033
DIC is an estimate of expected predictive error (lower is better).
```

Saturated Model

```
logit(psi[i,k,l]) <- lpsi[k,l] +
      betalpsi1[k,l]*protec[i,l] +
      betalpsi2[k,l]*PC_An[i,l] +
      betalpsi3[k,l]*PC_Fo[i,l] +
      betalpsi4[k,l]*PC_Sh[i,l] +
      betalpsi5[k,l]*PC_PC[i,l] +
      betalpsi6[k,l]*PC_SC[i,l] +
      betalpsi7[k,l]*PC_SCo[i,l]
```

protec: level of protection
PC_An: 1st PC from predictors used in Anthropogenic Model
PC_Fo: 1st PC from predictors used in Food Availability Model
PC_Sh: 1st PC from predictors used in Shelter Model
PC_PC: 1st PC from predictors used in Plot Complexity Model
PC_SC: 1st PC from predictors used in Strata Complexity Model
PC_SCO: 1st PC from predictors used in Strata Complexity and Cover Model

JAGS output for model 'modelo_PCA.bug', generated by jagsUI. Estimates based on 5 chai
ns of 50000 iterations, adaptation = 100 iterations (sufficient), burn-in = 25000 iter
ations and thin rate = 5, yielding 25000 total samples from the joint posterior.

	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
co.lpsi	-0.842	0.775	-2.396	-0.840	0.701	TRUE	0.867	1.000	25000
co.beta1	-0.047	0.391	-0.845	-0.041	0.710	TRUE	0.544	1.002	1786
co.beta2	0.288	0.418	-0.552	0.290	1.110	TRUE	0.765	1.001	5401
co.beta3	-0.149	0.363	-0.867	-0.148	0.558	TRUE	0.660	1.001	4541
co.beta4	-0.577	0.372	-1.321	-0.571	0.158	TRUE	0.944	1.000	5721
co.beta5	-0.130	0.349	-0.817	-0.130	0.567	TRUE	0.654	1.001	3296
co.beta6	-0.433	0.379	-1.177	-0.439	0.318	TRUE	0.876	1.001	4891
co.beta7	0.690	0.393	-0.090	0.691	1.464	TRUE	0.961	1.001	3827
beta1[1,1]	0.026	0.745	-1.481	0.020	1.537	TRUE	0.511	1.002	1490
beta1[2,1]	0.203	0.520	-0.808	0.192	1.263	TRUE	0.657	1.001	4133
beta1[3,1]	-0.343	0.831	-2.199	-0.271	1.145	TRUE	0.645	1.000	5946
beta1[4,1]	0.326	0.627	-0.894	0.315	1.605	TRUE	0.702	1.001	4408
beta1[5,1]	-0.407	0.789	-2.094	-0.360	1.066	TRUE	0.704	1.001	2513
beta1[6,1]	0.688	0.713	-0.546	0.621	2.280	TRUE	0.846	1.000	6006
beta1[7,1]	-1.503	0.975	-3.672	-1.418	0.102	TRUE	0.963	1.001	10992
beta1[8,1]	-0.667	0.648	-2.104	-0.613	0.442	TRUE	0.862	1.000	12915
beta1[1,2]	0.301	0.755	-1.059	0.238	1.982	TRUE	0.645	1.002	1669
beta1[2,2]	0.178	0.547	-0.890	0.167	1.299	TRUE	0.633	1.001	4642
beta1[3,2]	-0.109	0.907	-2.001	-0.086	1.685	TRUE	0.546	1.001	5217
beta1[4,2]	1.273	0.945	-0.185	1.141	3.486	TRUE	0.948	1.000	12190
beta1[5,2]	0.078	0.861	-1.490	0.019	2.043	TRUE	0.510	1.001	2956
beta1[6,2]	0.372	0.711	-0.996	0.347	1.842	TRUE	0.707	1.001	2145
beta1[7,2]	-1.260	0.992	-3.492	-1.165	0.404	TRUE	0.922	1.001	5755
beta1[8,2]	-0.328	0.574	-1.482	-0.316	0.791	TRUE	0.722	1.000	25000
beta2[1,1]	-0.401	0.786	-2.130	-0.336	1.001	TRUE	0.686	1.000	9890
beta2[2,1]	1.542	0.836	0.225	1.437	3.480	FALSE	0.991	1.000	8263
beta2[3,1]	0.993	1.073	-0.739	0.834	3.534	TRUE	0.850	1.008	577
beta2[4,1]	-0.640	0.746	-2.265	-0.583	0.682	TRUE	0.808	1.001	3441
beta2[5,1]	0.356	0.859	-1.132	0.276	2.304	TRUE	0.646	1.001	7953
beta2[6,1]	0.835	0.851	-0.728	0.781	2.656	TRUE	0.853	1.001	3164
beta2[7,1]	0.436	0.798	-1.093	0.407	2.153	TRUE	0.723	1.000	23171
	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta2[8,1]	0.187	0.595	-1.041	0.209	1.307	TRUE	0.641	1.001	4057
beta2[1,2]	-0.638	0.808	-2.491	-0.550	0.694	TRUE	0.784	1.001	4950

beta2[2,2]	0.990	0.588	-0.093	0.958	2.237	TRUE	0.965	1.001	3422
beta2[3,2]	0.474	1.019	-1.473	0.441	2.647	TRUE	0.695	1.004	1873
beta2[4,2]	-0.992	0.832	-2.899	-0.888	0.362	TRUE	0.908	1.001	3597
beta2[5,2]	-0.872	0.979	-3.074	-0.764	0.751	TRUE	0.821	1.001	3569
beta2[6,2]	1.300	0.977	-0.214	1.158	3.657	TRUE	0.948	1.002	2550
beta2[7,2]	0.512	0.723	-0.789	0.462	2.097	TRUE	0.767	1.000	6241
beta2[8,2]	1.033	0.799	-0.180	0.905	2.926	TRUE	0.943	1.001	5717
beta3[1,1]	-0.184	0.610	-1.459	-0.172	1.007	TRUE	0.625	1.001	5546
beta3[2,1]	-0.007	0.578	-1.166	-0.020	1.173	TRUE	0.516	1.000	9627
beta3[3,1]	0.523	0.916	-0.941	0.382	2.677	TRUE	0.701	1.002	2672
beta3[4,1]	-2.523	1.435	-5.729	-2.360	-0.224	FALSE	0.989	1.001	5462
beta3[5,1]	-0.291	0.713	-1.765	-0.262	1.087	TRUE	0.659	1.000	11303
beta3[6,1]	-0.081	0.682	-1.438	-0.095	1.347	TRUE	0.563	1.001	2485
beta3[7,1]	-0.029	0.945	-1.765	-0.108	2.062	TRUE	0.554	1.001	2459
beta3[8,1]	-0.247	0.574	-1.398	-0.244	0.918	TRUE	0.681	1.001	3729
beta3[1,2]	-0.128	0.614	-1.409	-0.118	1.067	TRUE	0.587	1.001	3460
beta3[2,2]	0.042	0.522	-0.981	0.032	1.120	TRUE	0.526	1.000	6137
beta3[3,2]	0.088	0.870	-1.587	0.053	1.958	TRUE	0.528	1.002	2398
beta3[4,2]	0.282	0.771	-1.185	0.266	1.857	TRUE	0.639	1.001	2813
beta3[5,2]	1.007	1.136	-0.744	0.833	3.609	TRUE	0.820	1.000	12382
beta3[6,2]	-0.165	0.758	-1.852	-0.132	1.265	TRUE	0.586	1.002	2621
beta3[7,2]	-1.092	0.818	-2.947	-0.996	0.239	TRUE	0.937	1.001	4950
beta3[8,2]	-0.537	0.591	-1.843	-0.480	0.459	TRUE	0.841	1.002	1806
beta4[1,1]	-0.871	0.732	-2.529	-0.806	0.427	TRUE	0.908	1.001	5240
beta4[2,1]	-0.935	0.617	-2.329	-0.866	0.106	TRUE	0.959	1.001	4547
beta4[3,1]	-0.740	0.799	-2.436	-0.702	0.815	TRUE	0.850	1.000	16337
beta4[4,1]	-0.578	0.572	-1.750	-0.565	0.537	TRUE	0.857	1.000	6494
beta4[5,1]	-2.096	1.290	-5.265	-1.849	-0.313	FALSE	0.994	1.001	7507
beta4[6,1]	0.844	1.118	-0.924	0.711	3.382	TRUE	0.759	1.001	2618
beta4[7,1]	-0.605	0.793	-2.162	-0.625	1.085	TRUE	0.805	1.001	6838
beta4[8,1]	0.199	0.627	-0.944	0.172	1.510	TRUE	0.614	1.000	16058
beta4[1,2]	-0.789	0.637	-2.156	-0.759	0.395	TRUE	0.907	1.001	3130
beta4[2,2]	-0.563	0.495	-1.552	-0.563	0.420	TRUE	0.880	1.000	7048
beta4[3,2]	-0.516	0.864	-2.252	-0.520	1.280	TRUE	0.761	1.001	6005
beta4[4,2]	-0.588	0.604	-1.863	-0.572	0.573	TRUE	0.854	1.000	6498
beta4[5,2]	-1.171	1.008	-3.495	-1.081	0.635	TRUE	0.910	1.001	10016
beta4[6,2]	-1.077	0.989	-3.327	-0.952	0.527	TRUE	0.897	1.001	5157
beta4[7,2]	-1.125	0.781	-2.895	-1.036	0.184	TRUE	0.952	1.001	5032
beta4[8,2]	0.370	0.579	-0.666	0.339	1.604	TRUE	0.729	1.000	8124
beta5[1,1]	-0.106	0.630	-1.387	-0.113	1.179	TRUE	0.577	1.000	20344
beta5[2,1]	-0.362	0.600	-1.638	-0.340	0.785	TRUE	0.735	1.000	6332
beta5[3,1]	1.295	1.068	-0.384	1.175	3.661	TRUE	0.911	1.000	12691
beta5[4,1]	-0.042	0.540	-1.078	-0.057	1.081	TRUE	0.543	1.000	25000
beta5[5,1]	0.027	0.610	-1.141	0.002	1.338	TRUE	0.501	1.000	14818
beta5[6,1]	0.120	0.696	-1.189	0.070	1.619	TRUE	0.546	1.000	10151
	mean	sd	2.5%	50%	97.5%	overlap0	f	Rhat	n.eff
beta5[7,1]	-0.391	0.734	-2.034	-0.328	0.924	TRUE	0.707	1.000	19786
beta5[8,1]	-0.175	0.535	-1.290	-0.164	0.865	TRUE	0.634	1.001	4883

beta5[1,2]	0.068	0.715	-1.260	0.018	1.661	TRUE	0.511	1.001	6052
beta5[2,2]	-0.919	0.749	-2.637	-0.816	0.272	TRUE	0.923	1.000	16336
beta5[3,2]	0.007	1.065	-2.269	0.039	2.109	TRUE	0.518	1.001	2819
beta5[4,2]	-0.091	0.620	-1.351	-0.097	1.175	TRUE	0.571	1.000	21582
beta5[5,2]	-0.362	0.810	-2.229	-0.277	1.063	TRUE	0.675	1.001	2384
beta5[6,2]	-0.553	0.820	-2.472	-0.440	0.816	TRUE	0.756	1.000	8049
beta5[7,2]	-0.480	0.735	-2.148	-0.406	0.812	TRUE	0.749	1.000	25000
beta5[8,2]	0.057	0.562	-0.966	0.024	1.278	TRUE	0.520	1.000	11073
beta6[1,1]	-1.451	0.967	-3.639	-1.327	0.123	TRUE	0.962	1.002	2366
beta6[2,1]	-0.286	0.535	-1.314	-0.298	0.814	TRUE	0.719	1.000	22548
beta6[3,1]	-0.054	0.799	-1.478	-0.116	1.709	TRUE	0.568	1.000	11346
beta6[4,1]	-0.841	0.713	-2.436	-0.771	0.395	TRUE	0.901	1.001	5697
beta6[5,1]	0.410	0.822	-1.016	0.345	2.180	TRUE	0.677	1.001	3011
beta6[6,1]	-0.617	0.647	-1.970	-0.600	0.641	TRUE	0.846	1.001	3617
beta6[7,1]	-0.853	0.779	-2.618	-0.781	0.511	TRUE	0.889	1.002	1529
beta6[8,1]	-0.623	0.587	-1.912	-0.585	0.409	TRUE	0.875	1.001	3256
beta6[1,2]	-1.601	1.050	-4.001	-1.455	0.077	TRUE	0.968	1.003	1344
beta6[2,2]	-0.357	0.606	-1.581	-0.367	0.881	TRUE	0.743	1.000	9224
beta6[3,2]	-0.214	0.898	-1.997	-0.244	1.671	TRUE	0.625	1.001	3394
beta6[4,2]	0.012	0.867	-1.449	-0.099	1.990	TRUE	0.449	1.001	4531
beta6[5,2]	0.453	1.001	-1.208	0.336	2.729	TRUE	0.654	1.002	2070
beta6[6,2]	-0.808	0.807	-2.599	-0.738	0.648	TRUE	0.873	1.001	8057
beta6[7,2]	-0.376	0.734	-1.764	-0.404	1.204	TRUE	0.723	1.000	8207
beta6[8,2]	-0.409	0.625	-1.617	-0.424	0.896	TRUE	0.766	1.000	6983
beta7[1,1]	0.862	0.791	-0.560	0.803	2.638	TRUE	0.884	1.001	6467
beta7[2,1]	0.959	0.661	-0.191	0.900	2.434	TRUE	0.947	1.000	8959
beta7[3,1]	-0.083	0.985	-2.389	0.059	1.510	TRUE	0.475	1.001	2470
beta7[4,1]	0.514	0.781	-1.112	0.548	2.031	TRUE	0.764	1.000	8662
beta7[5,1]	0.452	0.763	-1.193	0.497	1.868	TRUE	0.760	1.001	5448
beta7[6,1]	1.043	0.737	-0.280	0.980	2.659	TRUE	0.941	1.002	2171
beta7[7,1]	1.226	0.809	-0.141	1.127	3.076	TRUE	0.961	1.003	1070
beta7[8,1]	0.153	0.707	-1.361	0.200	1.420	TRUE	0.614	1.000	10245
beta7[1,2]	0.269	0.930	-1.942	0.392	1.791	TRUE	0.682	1.001	2763
beta7[2,2]	0.219	0.658	-1.222	0.274	1.363	TRUE	0.663	1.000	6837
beta7[3,2]	0.567	0.967	-1.334	0.547	2.621	TRUE	0.751	1.002	1567
beta7[4,2]	1.843	1.320	0.011	1.557	5.156	FALSE	0.976	1.002	2152
beta7[5,2]	1.008	1.000	-0.674	0.886	3.368	TRUE	0.889	1.001	25000
beta7[6,2]	1.137	0.903	-0.413	1.041	3.222	TRUE	0.934	1.002	1263
beta7[7,2]	0.979	0.725	-0.356	0.938	2.562	TRUE	0.928	1.004	929
beta7[8,2]	1.044	0.779	-0.217	0.943	2.864	TRUE	0.942	1.001	2557

Successful convergence based on Rhat values (all < 1.1).
Rhat is the potential scale reduction factor (at convergence, Rhat=1).
For each parameter, n.eff is a crude measure of effective sample size.
overlap0 checks if 0 falls in the parameter's 95% credible interval.
f is the proportion of the posterior with the same sign as the mean;
i.e., our confidence that the parameter is positive or negative.

```
DIC info: (pD = var(deviance)/2)
pD = 104.9 and DIC = 906.56
DIC is an estimate of expected predictive error (lower is better).
```

Appendix 3

Table 3.6 Moran's I results.

Model	2015	2016
Level of Protection	$observed [1] 0.4033439 $expected [1] -0.05263158 $sd [1] 0.1944259 $p.value [1] 0.01901484	$observed [1] -0.1090975 $expected [1] -0.05263158 $sd [1] 0.1710963 $p.value [1] 0.7413815
Anthropogenic effects	$observed [1] -0.06572317 $expected [1] -0.05263158 $sd [1] 0.1980007 $p.value [1] 0.9472831	$observed [1] -0.007431069 $expected [1] -0.05263158 $sd [1] 0.1726363 $p.value [1] 0.7934563
Food availability	$observed [1] -0.05257602 $expected [1] -0.05263158 $sd [1] 0.01193508 $p.value [1] 0.9962856	$observed [1] -0.02751336 $expected [1] -0.05263158 $sd [1] 0.172085 $p.value [1] 0.8839498
Shelter	$observed [1] 0.1174161 $expected [1] -0.05263158 $sd [1] 0.1841433 $p.value [1] 0.3557713	$observed [1] -0.07883622 $expected [1] -0.05263158 $sd [1] 0.1684389 $p.value [1] 0.8763692
Plot Complexity	$observed [1] 0.2486263 $expected [1] -0.05263158 $sd [1] 0.1965864 $p.value [1] 0.1254127	$observed [1] -0.01258011 $expected [1] -0.05263158 $sd [1] 0.1714985 $p.value [1] 0.8153434

Table 3.6 Continued

Model	2015	2016
Strata Complexity	$observed [1] -0.1090053 $expected [1] -0.05263158 $sd [1] 0.1538649 $p.value [1] 0.7140783	$observed [1] 0.8439326 $expected [1] -0.05263158 $sd [1] 0.1538601 $p.value [1] 5.638549e-09
Strata Complexity and Cover	$observed [1] -0.06860322 $expected [1] -0.05263158 $sd [1] 0.158528 $p.value [1] 0.9197492	$observed [1] -0.08399629 $expected [1] -0.05263158 $sd [1] 0.1719252 $p.value [1] 0.8552435
Saturated model - PCA	$observed [1] -0.0539426 $expected [1] -0.05263158 $sd [1] 0.01184008 $p.value [1] 0.9118327	$observed [1] -0.06561918 $expected [1] -0.05263158 $sd [1] 0.1754665 $p.value [1] 0.9409964

If $p<0.05$ there is spatial autocorrelation
If $p>0.05$ THERE IS NOT SPATIAL AUTOCORRELATION

CONCLUSIONS

An effective management of PAs is essential to conserve natural ecosystems. Their biodiversity assets and ecological services go beyond the limits of a PA, and constitute a country's national capital, supporting national sustainable development and human well-being (Bovarnick et al., 2010). Our main conclusions are as follow:

- ✓ Canopy photosynthetic activity measured as Normalized Difference Vegetation Index is higher in the highest level of protection, Strict Natural Reserve. However, it is unclear if this difference in NDVI is due to the protection category or to the higher rate of precipitation recorded in SNR.
- ✓ Further studies are needed to understand if the overall greening process across the area reflects better forest conditions (more leaves produced per plant, bigger leaves, growth of natural forests), or if native forest has been increasingly replaced by non-native species, or if forests had increasing amounts of bamboo-dominated understory.
- ✓ Negative changes in NDVI during the period 2000-2020 was low, and they were similar inside NHNP and in adjacent unprotected areas, hindering the attempt to determine if this change was due to a global impact such as climate change, or if, on the contrary, protection measures inside the PAs were not sufficiently effective.
- ✓ While the use of remote sensing provides an excellent opportunity for studies at a large scale over long periods of time, ground truth data remain crucial and must be included in the analysis in order to arrive at meaningful conclusions and appropriate interpretations.
- ✓ A combination of remote sensing analysis with ground truth data allows detection of the species (*Nothofagus pumilio*) that has been most affected by environmental degradation, supporting previous studies.
- ✓ Strict Natural Reserve are at higher risk of degradation owing to wildfires, a situation that is exacerbated by climate change.
- ✓ While there was no clear evidence of the effect that NHNP has on the native small mammal community as a whole, higher abundance and richness were reported in

Strict Natural Reserve and National Park, suggesting that direct human interaction negatively affects this fauna.

- ✓ A keystone species, the marsupial Dromiciops gliroides, manifested higher abundance in Strict Natural Reserve and National Park, implying that these categories are important in its conservation.
- ✓ Presence and abundance of small mammal species varies significantly at a small spatial scale.
- ✓ A higher number of replicates is needed to enable better understanding of small mammal distributions and habitat preferences.
- ✓ Long-term monitoring studies are needed to understand small mammal population dynamics, because periodic effects such as the El Niño Southern Oscillation (ENSO) and La Niña event differentially affect different species inhabiting southern latitudes.
- ✓ The use of hierarchical models allows the assessment of both community and species-specific responses to environmental variables. Furthermore, the effective use of all available data in this method permits assessment of the responses to protection level and particular habitat features of less frequently observed species, rather than responses of only the abundant and common ones.
- ✓ Effects of direct anthropogenic disturbances (livestock, road distance, and road traffic intensity) vary between different species in the small mammal community.
- ✓ Similarly, the natural conditions evaluated, such as vegetation diversity, understory cover, canopy cover, and arthropod abundance, were differentially associated with the abundance of the different small mammal species.
- ✓ This research provides a wealth of information regarding habitat preferences and distribution of small mammal species in the temperate forests of northern Patagonia. While some of our findings support those of previous studies, other do not.

VITA

María Daniela Rivarola was born in Ayacucho, Buenos Aires province, Argentina. She obtained her degree in Biological Sciences at Universidad Nacional del Comahue, located in Bariloche, northern Patagonia, Argentina, where she developed a strong love and bond with the native forest and its fauna. Daniela won a scholarship funded by the European Union to conduct undergraduate studies during eight months in Sweden (Swedish University of Agricultural Sciences, Umeå- SLU). She has participated in several studies monitoring small mammal populations and communities both in Argentina and Chile. Daniela has presented her research in national and international conferences along with scientific publications in high impact journals. Currently, she resides with her husband and two daughters in Denver, Colorado, where she has accepted a tenure-track assistant professor position at Regis University.