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Modeling the distribution of meadows in arid and semi-arid Patagonia, Argentina: assessing current distribution and predicting response to climate change

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MODELING THE DISTRIBUTION OF MEADOWS IN ARID AND SEMI-ARID
PATAGONIA, ARGENTINA: ASSESSING CURRENT DISTRIBUTION AND PREDICTING
RESPONSE TO CLIMATE CHANGE

by

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B.S., College of Natural Sciences and Museum Studies, National University of la Plata,
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A Thesis

Submitted in Partial Fulfillment of the Requirements for the
Master of Science

Department of Forestry
in the Graduate School
Southern Illinois University Carbondale
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THESIS APPROVAL

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A Thesis Submitted in Partial
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Master of Science
in the field of Forestry

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AN ABSTRACT OF THE THESIS OF

RAMIRO DANIEL CREGO, for the Master of Science degree in FORESTRY, presented on October 3, 2012, at Southern Illinois University Carbondale.

TITLE: MODELING THE DISTRIBUTION OF MEADOWS IN ARID AND SEMI-ARID PATAGONIA, ARGENTINA: ASSESSING CURRENT DISTRIBUTION AND PREDICTING RESPONSE TO CLIMATE CHANGE

MAJOR PROFESSOR: Dr. Clayton K. Nielsen

Meadows are critical in arid and semi-arid Argentinean Patagonia because of their importance for regional biodiversity. Despite this, little information on the spatial distribution of meadows is available and no analysis of the potential effect of climate change on meadows has been performed, which hampers conservation planning. In this study, I modeled the spatial distribution of meadows and investigated how climate change may affect the current distribution of meadows in arid and semiarid Patagonia by 2050. In addition, I investigated conservation status and areas of desertification vulnerability of those areas predicted to contain meadows. I used high-resolution imagery available in Google Earth software to visually estimate presence and absence of meadows. To model current and future distribution of meadows I used these observations and different socio-environmental predictor variables. I implemented generalized linear, additive, boosting, and random forest models, as the basis for a mean ensemble technique. I predicted future distribution of meadows using four different general circulation models and the A2 SERES scenario. The final ensemble model was an accurate representation of the current distribution of meadows in Patagonia and indicates they are severely under-represented within protected areas. I determined that overall meadow abundance is going to decrease by 2050 given the changes in climate. However, there were two contrasting trends: severe reduction of meadows in northwest Patagonia and Tierra del Fuego Island, and an expansion of suitable areas for meadows in the south and a small section in the northwest. This

first regional map of meadow distribution across Argentinean Patagonia and information on meadows vulnerability to climate change represent key information for planning actions to conserve this critical habitat.

DEDICATION

I want to dedicate this thesis to Hugo Horacio Crego, my uncle. I will never be able to hug you again, but the love for nature that you gave me will remain forever. Also, I want to dedicate this thesis to my family, Papá, Mamá, Faka y Romi. Without you, I would never be able to go anywhere.

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CHAPTER 1

MEADOWS IN PATAGONIA: A BACKGROUND

Arid and semi-arid landscapes

Arid and semi-arid landscapes encompass approximately 41% of Earth's terrestrial surface, and are expanding (Schlesinger et al. 1990; Millenium Ecosystem Assessment 2005). Since more than three decades ago, desertification, understood as "land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors including climate variation and human activities" (ICCD 1994), has been identified as the main environmental problem in these landscapes (Dregne 2002). Biophysical processes are important forces driving natural desertification (Hartley & Chong 2002; Hillel & Rosenzweig 2002), however, agricultural, extractive (e.g., mining) and industrial activities have increased land degradation to unprecedented levels (de Sherbinin 2002). In agricultural landscapes, overgrazing by livestock appears to be one of the most important disturbances, promoting losses in vegetative cover and simplification of vegetation structure, which together exposes soil surfaces to the erosive processes that drive desertification (de Sherbinin 2002; Ares 2003; Paruelo et al. 2008).

Even though wetlands encompass a relatively small portion of arid and semi-arid landscapes, they are the central drivers of many arid-ecosystem processes, such as weathering, soil formation, biological activity and nutrient pools, and distribution of vegetation and associated fauna (Newman et al. 2006). In addition, in arid areas human activities concentrate near wetlands. Such constant human pressure by land use, water withdrawal, pollution, and exotic species introduction trigger desertification processes and loss of biodiversity. Furthermore, current global warming trends may accelerate the desertification process and loss

of wetlands (Sala et al. 2000; Brönmark & Hansson 2002), which will affect even more of the biodiversity associated with them. Consequently, interest in protecting wetlands in arid and semi-arid regions of the world to address such problems has increased recently (Saunders et al. 2002; Brinson & Malvárez 2002; Brönmark & Hansson 2002; Lytle & Poff 2004; Revenga et al. 2005).

Patagonian meadows

About two-thirds of Argentina's continental surface is associated with arid and semi-arid ecosystems (UNESCO 2010). The arid and semi-arid Patagonia region (excluding the subantarctic andino-patagonic forest strip and the seacoast) encompasses >700,000 km² and makes up 28% of the country (Soriano 1983). Approximately 5% of this area is composed of wetlands (Iriondo 1989). Among the different wetlands, azonal meadows are scattered on the landscape. Meadows are small dimension grasslands primarily composed of grasses and reeds, where occurrence is associated with the permanent presence of water near the ground surface (Mazzoni & Vázquez 2004). These wetlands are important habitats in Patagonia, with soils rich in nutrients and organic matter, and act as important water reservoirs (Ayesa et al. 1999; Perotti et al. 2005). In accordance with world desertification trends, meadows in Patagonia appear to be degraded, with numerous threats existing to their continued health and persistence. Overgrazing by livestock is the main cause of meadow degradation, because this activity reduces vegetation cover, encourages evaporation, reduces soil water retention, and therefore, increases fluvial and aeolian erosion patterns (Paruelo & Aguiar 2003; Perotti et al. 2005). Given the aridity of Patagonia, most human settlements occur near rivers where meadows are more abundant. The number of dams are increasing, changing the sedimentation and flow rates on main rivers (Fundación Torcuato Di Tella 2006). Moreover, gas and oil extraction activities often pollute an

enormous amount of both superficial and underground water (i.e., Fiori & Zalba 2000), indirectly affecting the provision of water and its quality on meadows. Furthermore, human activities encourage the introduction of exotic species, which has been identified as another important threat to the biodiversity of meadows in Patagonia (Iglesias & Pérez 1998; Pascual et al. 2002; Perotti et al. 2005). Finally, predicted increases in temperature and decreases in precipitation and river water flows in the area would likely accelerate all degradation processes (Vera et al. 2006; Nuñez et al. 2008; Kitoh et al. 2011).

Previous studies

The first research on meadows in Patagonia began in the late 1950s (Boelke 1957), with research ongoing today. Most research has assessed productivity, fertility, and other agricultural attributes at very specific locations, including assessments of desertification due to livestock overgrazing (Lanciotti et al. 1993). Additionally, during the last 14 years the National Institute of Agricultural Technology (INTA) has started to use remote sensing to assess meadow status in Patagonia. Several projects have been performed in Río Negro province and a Neuquén province covering an area of approximately 27,000 km² (3.35% of arid and semi-arid Patagonia). In these studies, meadow distribution and classification into utility types were performed. Landsat TM images for the years 1985/88/89/2002 were used to conduct supervised classification and visual interpretation, given the Normalized Difference Vegetation Index (NDVI) and band combinations (Bran et al. 1998; Ayesa et al. 1999; López et al. 2005; Gaitán et al. 2009). In addition, Mazzoni & Vázquez (2004) developed a complete map of meadows cover for Santa Cruz province using Landsat TM images for the years 1984/85/86. However, no current and complete assessment of meadows distribution exists for the arid and semi-arid Patagonia, nor does any consider the vulnerability of meadows to future changes in climate.

Climate change

Growing evidence indicates that recent climatic variations are due to an increase of anthropogenic greenhouse gases. Global surface temperatures have already risen 0.74°C since the beginning of the 20th century, with 0.61°C of the increase occurring in the past 30 years (Trenberth et al. 2007), and current models predict at least another increase of 1.1 to 6.4°C for the next century (Meehl et al. 2007). Precipitation patterns have also been altered around the world due to climate change (Trenberth et al. 2007).

Specifically in central and northern Patagonia, Labraga (1994) reported a temperature increase of 0.5 °C at five main weather stations between 1900 and 1980. In addition, Rusticucci and Barrucand (2004) reported an increase in minimum temperature of 0.2 to 0.8 °C per 10 years during the period between 1959 and 1998 for Patagonia, and an increase in maximum temperature of 0.2 to 0.4 °C per 10 years during the same period of time. According to different climate models with different emission scenarios, increases from 1 to 4 °C or 2 to 6 °C are predicted for South America by the year 2100 (Nuñez et al. 2009). In addition, a declining trend in precipitation has been observed in southern Chile and southwest Argentina, and predictions for the Patagonian Andes indicate a decrease in annual mean precipitation (Nuñez et al. 2009).

Patagonia conservation status

Even though the arid and semi-arid Patagonia region encompasses >700,000 km² and represents 28% of the country, protected areas make up only 4.7% of the area, with < 1% of these reserves being IUCN Level I, II, or III protected areas (Burkart et al. 2007). Arid and semi-arid Patagonia is one of the 200 world ecosystems classified as priority for conservation (Olson & Dinerstein 2002) and has a recognized conservation importance by different institutions. BirdLife International selected Southern Patagonia as a high-priority site for

conservation (Stattersfield et al. 1998). In addition, one of the recent biodiversity centers of plants is located in Patagonia (WWF/IUCN 1997).

Given the importance of Patagonia for biodiversity and its lack of protection, a project called “Identification of sites with high values for biodiversity in arid and semi-arid Patagonia” is being developed by the National Park Administration of Argentina in conjunction with the Wildlife Conservation Society (WCS) and The Nature Conservancy. The goal of this project is to prioritize areas for conservation based on a simulation-based optimization approach, using the decision-support software Marxan (Tamone 2010). This software attempts to find a network of conservation areas that reach quantitative objectives for a set of conservation targets for a minimum total cost (see Ball et al. 2009). Input information to Marxan consists of different biodiversity features such as species distributions and land cover data. Given the importance of meadows to the biodiversity of this region and its restricted distribution, a map of meadow distribution is highly important and a derived branch of this conservation project. In addition, meadows distribution could be used as a surrogate to include endemic or restricted range species in the reserve prioritization design. Moreover, studies of how climate change would affect species and community distributions are gaining importance in the field of conservation planning, providing, for instance, information for designing potential corridors (Williams et al. 2005) or assessing the effectiveness of reserve networks (Araujo et al. 2004; Hannah et al. 2005; Lee & Jetz 2008). Estimates of future trends in meadows distribution under climate change will provide important information to allocate properly conservation efforts for the mentioned project.

The need for further research

Land degradation due to anthropogenic activities and climate change is affecting the arid and semi-arid Patagonian landscape. Meadows, which are rare and declining in Patagonia, are important habitat, maintaining high levels of biodiversity and providing high levels of primary productivity and ample water sources relative to the surrounding landscape. Even though local studies have been conducted to map meadows, a current and large-scale study to assess which areas of arid and semi-arid Patagonia contain meadows is needed.

Climate change models forecast an increase of temperature and decrease in precipitation for the region. These environmental alterations may affect vegetation distribution. However, no analysis of the potential affect of climate change on meadows has been performed for Patagonia. Furthermore, knowledge of where degradation processes due to climate change are inevitable would be important to properly focus conservation efforts. Although a project to design a proper reserve network is being conducted in Patagonia (Tamone 2010), meadow distribution and future degradation have not been considered in any analysis.

CHAPTER 2

MODELING MEADOW DISTRIBUTION FOR CONSERVATION ACTION IN ARID AND SEMI-ARID PATAGONIA, ARGENTINA

Introduction

Wetlands include a variety of temperate freshwater systems distributed in major ecoregions of the world (Brinson & Malvárez 2002) and are imperative for providing critical habitat for many species (Bedford et al. 2001). Although wetlands encompass a small portion of arid and semi-arid landscapes, they drive many ecosystem processes, such as weathering, soil formation, biological activity, and nutrient pools (Newman et al. 2006). Worldwide, wetlands are strongly and negatively influenced by anthropogenic activities, because societies commonly settle where wetland areas occur (Brinson & Malvárez 2002).

In Argentina, wetlands make up approximately 5% of arid and semi-arid Patagonia (Iriundo 1989), including lakes, ponds, peatlands (turberas), and meadows (mallines; Modenutti et al. 1998; Brinson & Malvárez 2002). Meadows are grasslands located in low areas, valley rivers, or at sides of hills and are continually irrigated with superficial and underground water (Mazzoni & Vázquez 2004). Consequently, meadows can be small isolated patches on hillsides or form large continuous areas following the drainage system along valleys. In a meadow, generally three main areas can be differentiated: a central area dominated by *Juncus* spp. and *Carex* spp.; an intermediate area dominated by *Festuca pallescens*, *Poa patensis*, and *Distichlis* spp.; and an outermost transition area with the surrounding steppe, normally dominated by *Stipa* spp. and sometimes shrubs like *Senecio filaginoides* (Ciari 2009). Although meadows encompass a small portion of Patagonia, they are important systems in the arid landscape.

Vegetation found in meadows present rates of primary production three to five times higher than the surrounding steppe (Irisarri et al. 2012), which together with the permanent source of water, creates important resources and habitat for native terrestrial species. These grasslands are highly used by guanacos (*Lama guanicoe*), the largest herbivore of Patagonia (Ortega & Franklin 1988; Puig et al. 2008), and by several bird species that use them for feeding, reproduction, and resting (Mazzoni 2000). Furthermore, many studies suggest the importance of meadows for regional biodiversity in general (Iglesias & Pérez 1998; Brinson & Malvárez 2002; Perotti et al. 2005). Nevertheless, because meadows are highly productive and provide permanent access to water, they are prime locations for anthropogenic development. As a consequence, meadows are threatened in Patagonia, with water erosion and overgrazing by livestock the major cause of degradation (Paruelo & Aguiar 2003; Perotti et al. 2005).

Several studies have been conducted in Patagonia across relatively small areas (i.e., 10,000 km²) where meadows were mapped using remote sensing techniques (Bran et al. 1998; Ayesa et al. 1999; Mazzoni & Vázquez 2004; López et al. 2005; Gaitán et al. 2009). Because meadows are rare on the landscape, moderate spatial resolution imagery (i.e., Landsat TM, 30 m spatial resolution) is necessary to identify them in an image classification process. This issue limits the area to map meadows using classification techniques to the size of the image swath (i.e, a mosaic of about 52 Landsat TM images would be necessary to cover Patagonia). However, the recent improvement of Geographic Information Systems (GIS) together with powerful statistical tools has led to development of predictive species distributions models (SDMs), which make it possible to map the broad scale distribution of biological entities and consequently improve management decisions and conservation strategies (see Peterson 2006). Species distribution models are empirical models that relate species occurrence data with

environmental predictor variables such as climate, geology, and topography (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Such modeling techniques have been used broadly to model distributions of individual species, but also entire communities such as grasslands, thereby producing information on spatial patterns in distribution of biodiversity (Ferrier & Guisan 2006).

Much of Patagonia is altogether unprotected from anthropogenic degradation, thus making meadows even more vulnerable to degradation. Only 4.7% of arid and semi-arid Patagonia is protected and <1% is protected by IUCN Level I, II, or III reserves (Burkart et al. 2007). Furthermore, the extent of meadow protection is entirely unknown. In Patagonia, a current and broader-scale study is necessary to truly assess meadows distribution. Given the significance of meadows to regional biodiversity, a current distribution model would be an important data layer to include in future conservation planning projects, and could be also used as a surrogate to account for endemic or restricted range species associated with this environment (Ferrier 2002). In this study I used a SDM approach within the platform BIOMOD (Thuiller et al. 2009) to model the current distribution of meadows in arid and semi-arid Patagonia. I used four modeling techniques, generalized linear models (GLM), generalized additive models (GAM), general boosting models (GBM), and random forests (RF), to generate individual predictive distributions. I then used these predictive distributions as the basis of a mean ensemble method (Marmion et al. 2009) to create our final model. The main aims of this study were to (i) generate a final ensemble distribution model of the distribution of meadows in arid and semi-arid Patagonia; and (ii) investigate conservation status of those areas predicted to contain meadows.

Study area

Arid and semi-arid Patagonia (excluding the subantarctic andino-patagonic forest strip and the seacoast) is >700,000 km² in area and extends from 39° to 55° S and from the Atlantic Ocean to the Andean piedmont in the west. This study area includes two major phytogeographic provinces: Patagonia, a mixed of grass-shrub steppes and semideserts in central and southern Patagonia, and the Monte, composed by shrub steppes in northern Patagonia (León et al. 1998). The climate of the area is cold-temperate. The mean annual temperature ranges from 12° C in the north to 3° C in the south, with absolute minimum temperatures below -20° C (Paruelo et al. 1998). From the Andes to the coast, annual precipitation decreases considerably, with a mean annual precipitation for central Patagonia of 200 mm per year (Paruelo et al. 1998). This combination of low rainfall, high-summer temperatures and strong winds result in high evapotranspiration rates, which is responsible for the dryness of the region (Fernández & Busso 1999).

Material and methods

Presence/absence data for model calibration

Meadows present high spectral contrast with respect to the surrounding steppe, thus they can be easily distinguished from surrounding land cover if satellite imagery is sufficiently high in spatial resolution. During December 2011-January 2012 I used high-spatial-resolution imagery (<4 m) compiled in the Google Earth database (version 6.1, Google Inc., Mountain View, CA, USA) to identify presence of meadows across the study area. Google Earth is one among many Virtual Globe software systems that are being used with growing frequency in many research fields (Sheppard & Cizek 2009). The Google Earth model of the world consists of hundreds of thousands of satellite and aerial images combined from different sources, including non-

commercial satellites (e.g. Landsat, Spot) and commercial satellites (e.g. Digital Globe's QuickBird) and also many providers of aerial photographs. For this reason, I could not determine the year of each image used for assessing meadows presence; however, Google Earth ensures the best image available, which typically included images 1-3 years old (Google Corporation 2012).

I assessed the presence or absence of meadows across the study area by overlaying it with a grid of 1 km² cells and visually assessed a sample of those cells for meadows. I knew *a priori* that they occurred in a small portion of the study region (approximately 5%) and were more likely to be abundant in river valleys and closer to the Andes Mountains. To ensure that my training/validation data set had a sufficient number of presences, I used an equal-stratified sampling strategy; this design ensures more accurate model predictions than the proportional-stratified design (Hirzel & Guisan 2002). I stratified the study area based on elevation (east-west gradient) and distance from rivers given their known influence on potential meadow locations (Bran et al. 1998). I defined three strata for elevation (stratum 1: 0-400 m; stratum 2: 401-800 m; stratum 3: >801 m) and two strata for distance from rivers (stratum 1: 0-2,000 m; stratum 2: >2,001 m). From the study area grid, I randomly selected 167 cells per stratum using the NOAA's Biogeography Branch Sampling Design Tool for ArcGIS (<http://ccma.nos.noaa.gov/products/biogeography/sampling/>, accessed 13 Nov 2011). In total, I randomly selected 1,002 cells, aiming to ensure >100 presences.

High resolution imageries provided by Google Earth make it possible to differentiate meadows, which appear visually as continuous patches of different shades of green, from the surrounding gray and brown steppe. To determine if a meadow was present (1) or absent (0) in a particular 1 km² cell, I first examined the quality of Google Earth imagery within the 1,002 cells

chosen for sampling. Only cells completely covered by high resolution imagery were kept; others were discarded if covered by snow or clouds or unclear. If the cell was covered by $\geq 5\%$ of meadows, I considered meadows to be present, otherwise, I considered that meadows were absent.

I was concerned that my ability to detect meadows when present may be imperfect and, further, that detection ability may vary by image context (e.g., meadow quality, surrounding habitat types, overall wetness of the region). Imperfect detection could result in an inaccurate estimate of presence probability of a feature, such as meadows, which may cause errors in mapping their distribution (Vaughan & Ormerod 2003; Reese et al. 2005). Therefore, I examined my ability to detect meadows when they were present by repeatedly searching a subsample of 20 randomly-selected cells per stratum. I then visually assessed each cell three times (“visits”) for the presence of meadows, with three weeks between each visit, to minimize the chance that recollection from previous visits influenced the probability of detection in subsequent visits. I obtained an overall detection probability of 97.5%; only 2.5% of the time did I fail to detect a meadow in one visit when I detected it in another, indicating that my probability of detection was very high. Based on this high detection probability, I decided it was not necessary to use occupancy models that adjust for probability of detection (MacKenzie et al. 2006) for analysis.

Socio-environmental variables

I initially compiled a set of 30 potential predictor variables I thought likely affect the distribution of meadows, including climate variables; aridity and evapotranspiration indices; physiographic variables such as distance from rivers, Normalized Difference Vegetation Index (NDVI), elevation, slope, and aspect; and human impact variables, such as human population

density, croplands, and pasture lands. I reduced the number of predictor variables based on a cluster analysis using the function `Varclus` within the package `Hmisc` in the R programming language (version: 2.14.0, R Development Core Team 2011), identifying groups of variables that were correlated among themselves but uncorrelated to other clusters. Finally, I arbitrarily selected one variable per cluster based on my understanding of biological influences on meadow occurrence. Cluster analysis has been used similarly in several variable reduction approaches for habitat modeling (Scharine et al. 2011; Anderson et al. 2011).

Cluster analysis resulted in the selection of 11 predictor variables for further modeling. I used five climate variables (maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality) obtained from the WorldClim database, at 30 arc-seconds resolution (Hijmans et al. 2005; available at: <http://www.worldclim.org/download>). Although temperature and precipitation are important determinants of meadow presence, their occurrence is also associated with drainage systems (Buono et al. 2010). Therefore, I also calculated distance to rivers (both permanent and non-permanent) using river shapefiles provided by the Argentinean Geographic National Institute (C. Chehébar, Pers Comm, National Park Administration, San Carlos de Bariloche, Argentina); and I included soil cover information created by the National Institute of Agricultural Technology (INTA), Argentina, selecting soil order classification as the predictor variable (available at: <http://geointa.inta.gov.ar/>). I also used altitude derived from a Digital Elevation Model (DEM) at 30 m resolution. To account for land-use changes driven by human activities in areas suitable for meadows (e.g., degradation by livestock farming, wetlands drainage for agricultural purposes), I included a Human Influence Index (HII) variable produced in conjunction by the WCS and the Center for International Earth Science Information Network

(CIESIN). The HII was calculated from nine global data layers considering population density, human land use and infrastructure (built-up areas, nighttime lights, land use and land cover) and human access (coastlines, roads, railroads and navigable rivers), for the year 2000 (Last of the Wild Data Version 2 2005; available at: <http://sedac.ciesin.columbia.edu/>). Finally, I used a MODIS NDVI image (MYD13A1; 1 km resolution), obtained from Earth Observing System Data and Information System (2009) for 19 Jan 2011, a period in which meadows are obvious on the landscape, hence possess higher NDVI values.

I re-projected each data layer to UTM Zone 19 South. I down-scaled the resolution of altitude layer to match the 30 arc-seconds (equal to 1 x 1 km) resolution of WorldClim, HII and NDVI. I used ArcGIS 9.3 (ESRI, Redlands, California, USA) for most geospatial operations. For NDVI data we used the Modis Reprojection Tool 4.1 (https://lpdaac.usgs.gov/tools/modis_reprojection_tool_swath, accessed 17 Jan 2012) to mosaic original images and re-project them to the UTM Zone 19 South.

BIOMOD ensemble forecasting framework

I predicted the current distribution of meadows throughout the study area using BIOMOD (Thuiller et al. 2009), which works in the R programming language (version: 2.14.0, R Development Core Team, 2011). I used four modeling techniques used frequently in the literature that perform accurately compared to other modeling techniques (Segurado & Araújo 2004; Araújo et al. 2005; Elith et al. 2006; Cutler et al. 2007; Marmion et al. 2009):

1. Generalized Linear Models (GLM; McCullagh & Nelder 1989) are extensions of the linear (regression) model, but provide more flexibility and can handle different error distributions in the response variable and non-constant variance functions. I ran GLMs with a binomial variance and a logistic link function, and fit them using linear, quadratic

and polynomial terms (second and third order). I used a stepwise procedure with Akaike's Information Criterion (AIC) to select the most parsimonious models (Akaike 1973).

2. Generalized Additive Models (GAM; Hastie & Tibshirani 1990) are similar to GLM but are more flexible because they do not require fitting a parametric response function to the predictor variable. Instead, GAMs use smoothing functions to locally fit a subsection of data. Thus, the algorithm fits a smooth curve to each predictor variable and then combines the results additively. I ran GAMs with a binomial variance and a logistic link function, and I used cubic-smooth splines with a degree of smoothness of ≤ 4 degrees of freedom for each variable. Here I also used AIC for model selection.
3. Generalized Boosting Models (GBM), also known as Boosted Regression Trees (BRT), seek to fit a large number of relatively simple models whose predictors are then combined to give more robust estimates of the response of the species' distribution to the set of predictor variables. The algorithm used in BIOMOD is a boosting regression tree, where each simple model consists of a classification tree (Friedman 2001). Each tree is built by repeatedly splitting the data into two homogeneous groups, defined by a simple rule based on a single explanatory variable. The GBM uses an iterative method for developing a final model, where trees are progressively incorporated into the model at the time that re-weighting the data accentuates cases poorly predicted by previous trees. As a result, an additive regression model in which individual terms are simple trees is obtained. Boosting differs from other multi-model techniques in that it is a sequential, forward stage-wise procedure. I ran GBM using a maximum number of 5,000 trees and five lambda fold-cross-validation to progressively grow models.

4. The Random Forests model (RF; Cutler et al. 2007) is an extension of classification tree analysis. Instead of producing a single classification tree, it produces many trees, a “forest”, and then combines all the predictions into one. At each node of the tree, a selected group of random variables are used, and the best split from these random variables is used to split the node. The number of random variables selected is held constant during the forest growing and each tree is grown to the largest extent possible. I ran RF with 500 trees.

Accuracy assessment of individual models

Proper measures of model accuracy may use independent data different from the dataset used to build the model. However, because it is difficult to obtain independent locations, I implemented a data partitioning approach on training and validation data sets (Fielding & Bell 1997). Araújo et al. (2005) have shown that models’ predictive accuracy obtained from a splitting strategy provides a generally good assessment compared to model validation using independent data. I split the data set into a 75% training data set and 25% validation data set. The size of the split was determined using: $[1 + (p - 1)^{1/2}]^{-1}$, where p is the number of predictor variables (Fielding & Bell 1997). I used a cross-validation procedure to assess model accuracy. For each modeling technique I ran 10 iterations, each time with a different random split of the data for training and validation. This ensures more robust estimates of the prediction performance and an assessment of the sensitivity of the models to the initial conditions (Thuiller 2009).

To assess prediction accuracy, I used area under the curve (AUC) of the receiver-operating characteristic (ROC) plot (Fielding and Bell 1997). AUC is not dependent on a threshold value to convert continuous model outputs in presence/absence data, and AUC values

range from 0.5 (model predicted no better than random) to 1 (perfect predictions). I interpreted AUC accuracy values following Swets (1988): excellent $AUC > 0.9$, good $0.9 > AUC > 0.8$, fair $0.8 > AUC > 0.7$, poor $0.7 > AUC > 0.6$ and fail $0.6 > AUC > 0.5$. It is important to highlight that AUC is criticized as an accuracy assessment (see Lobo et al. 2008). Thus, I also calculated sensitivity and specificity of my predictions, using the threshold that maximized the percentage of presence and absence cells correctly predicted for ROC curves to transform probability values into presence/absence format. If AUC values for models were >0.7 , then I used the whole data set for calculating sensitivity and specificity (W. Thuiller Pers Comm, Laboratory of Alpine Ecology, University Joseph Fourier, Grenoble, France). Sensitivity measures the percentage of cells correctly predicted as having meadows present and specificity measures the percentage of cells correctly predicted as having meadows absent (Fielding & Bell 1997).

Combining models

Because different models may produce different results for the same data set (Segurado & Araújo 2004), modelers have increasingly used ensemble (also known as consensus) model techniques which improve prediction accuracy over single models (Araújo & New 2006; Marmion et al. 2009). I used a mean ensemble approach, which is the mean value of the outputs of all single runs, which has been shown to perform better than other ensemble techniques (Marmion et al. 2009). I first extrapolated each of the 40 individual models (10 using each technique) to the entire study area, obtaining 40 distribution models. Subsequently, I calculated the mean ensemble model as the mean presence-probability value among the 40 individual models created. I then transformed the final ensemble model in a binary presence/absence format using a threshold calculated as the mean value of all threshold values obtained for the

individual models. To measure the accuracy of the ensemble approach, I calculated the AUC using the original calibration data set.

As additional accuracy measures, I randomly selected 100 predicted presences and 100 predicted absences (a separate set of observations than those used to train the model) from the final ensemble model. Implementing the same method used previously to obtain the meadows presence/absence data, I visually assessed every cell in Google Earth and calculated AUC, sensitivity, and specificity of the ensemble model based on those 200 cells. Finally, I also measured sensitivity of the final ensemble model using an independent dataset comprised of 23 known field locations of meadows located at the west-central portion of the study area (L. Epele, Laboratory of Ecological and Animal Systematic Research, Esequel, Chubut, Argentina). I located the cells on the final ensemble map that corresponded to those 23 locations and investigated whether predictions were presences or absences, and calculated the percentage of cells correctly predicted as having meadows present.

Protection status

Using ArcGIS 9.3 (ESRI, Redlands, California, USA) and based on the final presence/absence ensemble model, I calculated the percentage of cells containing meadows that were included within any existing protected area. I considered first all existent protected areas, and second, only those protected areas assigned IUCN level I, II or III status, which included National Parks, Provincial Parks, Province Natural Monuments, Natural Reserves, and Natural and Cultural Reserves. IUCN level I, II or III are the only reserves that ensure strict and effective protection to the area. The layer of Patagonian-protected areas was provided by the National Park Administration, Argentina (C. Chehébar, Pers Comm, National Park Administration, San Carlos de Bariloche, Argentina).

Results

I determined the presence or absence of meadows in 976 of the 1,002 cells intended for sampling; the other 26 cells were covered by clouds, snow, or the image was unclear. Meadows were present in 146 cells (15% prevalence; Table 2.1).

Accuracy of the 40 final models was excellent, good, and fair, 37.5%, 55% and 7.5% of the time, respectively (Table 2.2). Sensitivity and specificity values of all models were >80% and different runs were consistent, as represented by low standard deviations (Table 2.3).

Accuracy of the final ensemble model predicting cells covered by $\geq 5\%$ of meadows was excellent (AUC = 0.97). Area under the curve, sensitivity, and specificity measured over 100 predicted presences and 100 absences selected from the final ensemble model and examined in Google Earth were 0.88, 93% and 75%, respectively. Sensitivity of the final ensemble model based on independent field locations was 78.3%. However, one field location predicted as an absence by the final ensemble model was a small meadow that covered $< 5\%$ of a 1 km² cell when viewed in Google Earth. Eliminating this cell from the analysis, as it was considered as an absence, would increase sensitivity to 81.8%.

Among the 11 predictor variables, maximum temperature of the warmest month, precipitation of the wettest month, NDVI, distance to permanent rivers and distance to both permanent and non-permanent rivers were consistently selected by the four modeling techniques (Table 2.4), indicating their overall importance to the distribution of meadows. General boosting models and RF produced the most complex single models, selecting all 12 variables in each run, whereas GLM and GAM produced more simple single models selecting, on average, 7.2 and 6.1 explanatory variables, respectively.

A total of 11.5% (90,889 km²) of all 1 km² cells were predicted by the final ensemble model to be covered by $\geq 5\%$ of meadows in arid and semi arid Patagonia (Figure 2.1). Meadows were more clustered in the western portion of the study area and along rivers and occurred only on the Patagonia phytogeographic Province, and not the Monte Province. In the southern region, meadows also were located near the Atlantic coast following major rivers. Meadows also were highly abundant on Tierra del Fuego Island. From all cells predicted to be covered by $\geq 5\%$ of meadows, only 2.74% were included in any kind of protected area, and just 0.14% were located in any IUCN level I, II or III protected area (Figure 2.1).

Discussion

Land managers require information on the spatial distribution of natural entities to ensure their conservation. This study represents the first attempt to determine the distribution of meadows across arid and semi-arid Patagonia at a broad scale. I found that Google Earth was a useful tool for studying the distribution of meadows and could be valuable for assessing community-level distributions elsewhere. Furthermore, I obtained highly accurate models of the distribution of meadows in arid and semi-arid Patagonia, with high AUC, specificity, and sensitivity values. Such accuracy was improved by the final ensemble model, which also had high values of AUC, sensitivity, and specificity measured for 200 cells randomly selected from the final ensemble model and examined in Google Earth, and high sensitivity based on independent field locations. I also found that a vast majority of meadows are currently unprotected. The final ensemble model provided an accurate representation of meadow occurrence and will be a vital piece of information to improve the conservation network in arid and semi-arid Patagonia.

When modeling the distribution of natural entities, the main source of prediction error is the “noise” associated with species occurrence data and predictor variables (Vaughan & Ormerod 2003; Reese et al. 2005). When possible, both presence and absence records are preferable (Brotons et al. 2004), but presence-only data can also be useful (Elith et al. 2006). In my case, existing field observations were not available for Patagonia and collection of presence/absence information in the field was prohibitively costly. Therefore, I used Google Earth to obtain presence/absence data based on high resolution imagery, which led to accurate models of meadows at a low cost. Using Google Earth also allowed me to develop an environmental stratification with a random sampling design to enable more accurate predictions (Hirzel & Guisan 2002; Vaughan & Ormerod 2003; Reese et al. 2005). Google Earth is a novel technology that is increasingly being implemented in different fields (Sheppard & Cizek 2009). I contend that Google Earth could be used for modeling the distribution of vegetation communities that are homogeneous in their physiognomy and can be visually identified via high resolution imagery.

Because the use of only AUC as accuracy measures on SDMs has been criticized (Lobo et al. 2008), I additionally performed two analyses of sensitivity and specificity to test the accuracy of the final ensemble model. I found a general consensus among the different accuracy measures, supporting the robustness of the model. Although the model exhibited high levels of sensitivity, I found that sensitivity assessed using independent field locations was low (78%), perhaps due to relatively few field data, compared to sensitivity measured using Google Earth (93%). However, meadows present high interannual and spatial primary-production variation (Buono et al. 2010; Irisarri et al. 2012), and because I could not control the timing of images from Google Earth, it was harder to identify meadows presences on images taken during the

winter months of low vegetative productivity. Hence, it was possible to miss presences if I confused meadows with the surrounding steppe. This issue could explain the lower sensitivity of the field data. Despite this, the ensemble model was able to correctly predict the presence of most of the known existing meadows; only four or five cells were misclassified. In addition, the sensitivity value obtained for the ensemble model using field points was in the range of those values obtained for the individual GLM and GAM models.

The final ensemble model predicted presences of meadows better than absences when evaluating accuracy using Google Earth for 200 cells selected from the final ensemble model. When I visually examined the 25% of the cells indicated as false presences (predicted as a presence but determined as absence when using Google Earth), I noted four possible reasons for these inaccuracies. First, many of the false presences may have been confused with agricultural areas, as they mainly occurred in the eastern zone of the study region and near rivers. Many of these areas likely corresponded to agricultural fields along river valleys that often produce high NDVI values similar to those produced by meadows. Although most of these agricultural areas were excluded in the model by the HII layer that represents human impact, this predictor layer was 12 years old and may not have captured many current agricultural areas. Second, the southern extreme of the study area, Tierra del Fuego Island, was predicted to have a high density of meadows. Peatlands, another type of wetlands characterized by the accumulation of organic matter and closely related to meadows (Roig & Roig 2004), are widespread in the Magallanic Tundra Complex (Brinson & Malvárez 2002; Malvárez et al. 2004). I likely could not differentiate peatlands from meadows, or both wetlands occur simultaneously, resulting in a high presence rate in that area. Third, cells with <5% of meadow cover, when examined closely, were often surrounded by other cells covered with $\geq 5\%$ of meadows. This error originates from the

intrinsic spatial error of different predictor variables. Finally, some cells may have been “on the edge” of the threshold value in terms of probability (moderate or low) of containing meadows. It was inherently more difficult to accurately predict presence or absence in this threshold edge value. Understanding these sources of error, I was not surprised to get a lower AUC value measured for the 200 cells analyzed via Google Earth in our final ensemble model (0.88) compared to the AUC value obtained from the total calibration data (0.97).

Meadows are mostly unprotected in arid and semi-arid Patagonia, with only 0.14% of the cells predicted to be covered by $\geq 5\%$ of meadows currently included in any IUCN level I, II or III protected area. In northwestern Patagonia, two Provincial Parks, El Tromen and Domuyo; the National Park Laguna Blanca; and the Natural Provincial Monument Cañada Molina had meadows present. In addition, studies conducted by INTA described different classes of meadows for Patagonia at smaller scales based on their quality conditions (Bran et al. 1998; Ayesa et al. 1999; López et al. 2005; Gaitán et al. 2009). Specifically, Bran et al. (1998) and Ayesa et al. (1999) stated that 80% of meadows in northwest Patagonia were degraded. In this large-scale study, I could not differentiate meadow conditions, however, it is likely that a significant percentage of the meadows are degraded, making the need for conservation efforts even more critical.

Systematic conservation planning is the practice of locating, configuring, implementing, and maintaining areas with the aim of promoting the persistence of biodiversity (Margules & Pressey 2000), and SDMs are a powerful tool to provide the spatial information needed to conduct a conservation strategy (Peterson 2006). Given the small proportion of arid and semi-arid Patagonia that is currently protected, a multi-agency project to improve the conservation reserve network is currently underway, including collaborators such as WCS, The Nature

Conservancy (TNC) and the National Park Administration of Argentina. This project intends to prioritize and eventually create areas for conservation based on a simulation-based optimization approach, using decision-support software Marxan. This software attempts to find a network of conservation areas that reach quantitative objectives for a set of conservation targets for a minimum total cost (see Ball et al. 2009). Given the importance of meadows to the biodiversity of arid and semi-arid Patagonia, their restricted distribution and the potential of meadows to be used as a surrogate to include endemic or restricted range species, my final regional map will be an important data layer for planning future conservation areas, ensuring protection for meadows and associated Patagonian biodiversity.

CHAPTER 3

PREDICTING CLIMATE-CHANGE IMPACTS ON MEADOWS DISTRIBUTION IN ARID AND SEMI-ARID PATAGONIA, ARGENTINA

Introduction

Climate change has created a growing concern within the scientific community about how resultant environmental alterations are going to impact ecosystems. It is well accepted in biogeography science that climate has a strong top-down effect on natural distributions of species. Paleontological evidence (i.e., Davis & Shaw 2001; Davies et al. 2009) as well as current observed trends (i.e., McCarty 2001; Gian-reto et al. 2002; Parmesan 2006; Thuiller 2007; Thomas 2010) showed that climate influences the change of species' range. With the wide acceptance of global warming and rapid environmental change, the demand for accurate predictions of its effects has increased, especially in the field of conservation biology (Botkin et al. 2007). In addition, with this accepted influence and real impacts on biodiversity, climate change has become a central issue in worldwide conservation planning (McCarty 2001; Olson & Lindsay 2009).

Conducting experimental research to determine how biodiversity will respond to climate change at the regional or global scale is difficult or even unviable (Woodward 1987). Thus, the use of model simulations appears to be the most efficient and feasible method for these studies (Thuiller 2007). Several models, known as Species Distribution Models (SDMs), were developed with the capability of assessing distributions and predicting climate-induced range shifts under different global change scenarios at the single-species level (Guisan & Thuiller

2005) and community level (Ferrier & Guisan 2006). The main challenge when modeling species distribution is the variability in model outputs given by different modeling techniques (Segurado & Araújo 2004; Lawler et al. 2006) and differences in climate change models and scenarios (Pearson & Dawson 2003; Thuiller 2004; Lawler et al. 2009). As a result, modelers are increasingly using ensemble (also known as consensus) modeling techniques which improve prediction accuracy over single models (Araújo & New 2006; Marmion et al. 2009). By combining different modeling techniques with different climate-change models, more robust predictions can be made with an appropriate interpretation of results (Araújo & New 2006; Buisson et al. 2010). However, the complexities of natural systems limit the scope of modeling results, as predictive errors are inevitable. For example, although it is well known that spatial and time lags are a common phenomenon affecting species distributions (Pearson & Dawson 2003; Guisan & Thuiller 2005; Lawler et al. 2006), most SDMs do not account for such lags. When modeling at the community level, it is also falsely assumed that species interactions will not change over time (Ferrier & Guisan 2006). Notwithstanding these limitations, when an appropriate set of environmental predictor variables that account for natural and human effects are used, SDMs can provide a useful approximation to understand how species distributions may respond to climate change. Predictions of SDMs should be considered a first approximation of potential future impact on distributions and not an accurate simulation of future range shifts (Pearson & Dawson 2003; Lawler et al. 2006). Such information is crucial in developing countries, where threats to natural landscapes are imminent and where monetary resources are limited for conservation planning.

Arid and semi-arid Patagonia encompasses >700,000 km² of steppe-like plains in Argentina. This arid landscape is irregularly interrupted by wetlands, covering approximately

5% of the total area (Iriondo 1989), counting lakes, ponds, peatlands (turberas), and meadows (mallines; Brinson and Malvárez 2002; Modenutti et al. 1998). Specifically, meadows are grasslands whose structure and composition differ along their distribution, but in general three main areas can be distinguished: a center dominated by *Juncus* spp. and *Carex* spp.; an intermediate area dominated by *Festuca pallescens*, *Poa patensis* and *Distichlis* spp.; and an outermost transition area of steppe, normally dominated by *Stipa* spp. and sometimes shrubs like *Senecio filaginoides* (Ciari 2009). Meadows occur in low areas where superficial or underground water continually irrigates them, mainly along river valleys or hill sides (Mazzoni & Vázquez 2004), and are three to five times more productive than the surrounding steppe (Irisarri et al. 2012). These characteristics make meadows important ecosystems for the biodiversity of this arid region. Meadows are nesting, feeding and resting areas for birds (Mazzoni 2000) important source of grass for guanacos (*Lama guanicoe*; Ortega and Franklin 1988, Puig et al. 2008), and many studies suggest meadows' importance to regional biodiversity in general (Iglesias & Pérez 1998; Hauenstein 2002; Brinson & Malvárez 2002; Perotti et al. 2005). However, this habitat is under high anthropogenic pressures that cause degradation, such as livestock overgrazing (Paruelo & Aguiar 2003; Perotti et al. 2005). Furthermore, climate change may accelerate such degradation processes (Brinson & Malvárez 2002) by increases in temperature and changes in precipitation regimes.

In Patagonia, climate has a strong influence on the distribution of vegetation, mainly through precipitation patterns. Relative abundance of grasses and shrubs is related to precipitation gradients (Bertiller et al. 1995; Jobbágy et al. 1996). It was suggested that temperature and mainly precipitation influence productivity of meadows (Buono et al. 2010; Irisarri et al. 2012). In addition, Bertiller et al. (1995) showed that the cover of *Festuca*

pallescens, an important grass of steppes but also encountered in meadows, increased with water availability, and depends on clay content of the upper soil and soil depth, which are variables related to water balance. The climate of Patagonia has already changed, with increases of minimum and maximum temperatures (Rusticucci & Barrucand 2004) and decreases of precipitation with a resultant decrease of river water flows (Fundación Torcuato Di Tella 2006). Changes in temperature and precipitation regimes may accentuate this trend. Southern Argentina might experience increases from 0.5 to 2.5 °C for the period 2081-2090 (Nuñez et al. 2008), and decreases in precipitation especially on the Andes side (Vera et al. 2006; Kitoh et al. 2011).

In Chapter 2 I assessed the current distribution of meadows; however, no analysis of the potential effect of climate change on meadows has been performed for Patagonia. Furthermore, to mitigate climate change effects, long-term actions (i.e., reducing emission of greenhouse gases) as well as short-term actions are needed (Botkin et al. 2007). The most important short-term action is to design a proper system of natural reserves to protect threatened areas from human activities and target conservation activities to mitigate potential climate-change impacts. Only a small portion of meadow distribution is currently under protection in Patagonia (see Chapter 1). Therefore, information about how the distribution of meadows will respond to climate change is important to properly focus conservation efforts. The objectives of this Chapter were (i) to investigate how climate change might affect the current distribution of meadows in arid and semiarid Patagonia by 2050 and (ii) investigate change trends and areas of desertification vulnerability using climate-change models. I refer to the term “change” as the difference in meadow distribution between the selected climatic statistics in the climate change scenarios and the reference distribution simulation during 2012.

Study area

Arid and semi-arid Patagonia (excluding the subantarctic andino-patagonic forest strip and the seacoast) covers an area $>700,000 \text{ km}^2$ and extends from 39° to 55° S and from the Atlantic Ocean to the Andean piedmont in the west. The region includes two major phytogeographic Provinces: Patagonia, a mixed of grass-shrub steppes and semideserts in central and southern Patagonia, and the Monte, composed by shrub steppes in northern Patagonia (León et al. 1998). The climate is cold-temperate. The mean annual temperature ranges from 12° C in the north to 3° C in the south, with absolute minimum temperatures below -20° C (Paruelo et al. 1998). Annual precipitation decreases dramatically in a west-east direction, being the mean annual precipitation for central Patagonia of 200 mm per year (Paruelo et al. 1998).

Materials and methods

Meadows presence/absence data

Meadows present high spectral contrast with respect to the surrounding steppe, thus they can be easily distinguished from surrounding land cover if satellite imagery is sufficiently high in spatial resolution. During December 2011-January 2012 I used high-spatial-resolution imagery ($<4 \text{ m}$) compiled in the Google Earth database (version 6.1, Google Inc., Mountain View, CA, USA) to identify presence of meadows across the study area. Google Earth is one among many Virtual Globe software systems that are being used with growing frequency in many research fields (Sheppard & Cizek 2009). The Google Earth model of the world consists of hundreds of thousands of satellite and aerial images combined from different sources, including non-commercial satellites (e.g. Landsat, Spot) and commercial satellites (e.g. Digital Globe's QuickBird) and also many providers of aerial photographs. For this reason, I could not determine the year of each image used for assessing meadows presence; however, Google Earth

ensures the best image available, which typically included images 1-3 years old (Google Corporation 2012).

I assessed the presence or absence of meadows across the study area by overlaying it with a grid of 1 km² cells and visually assessed a sample of those cells for meadows. I knew *a priori* that meadows occurred in a small portion of the study region (approximately 5%) and were more likely to be abundant in river valleys and closer to the Andes Mountains. To ensure that my training/validation data set had a sufficient number of presences, I used an equal-stratified sampling strategy; this design ensures more accurate model predictions than the proportional-stratified design (Hirzel & Guisan 2002). I stratified the study area based on elevation (east-west gradient) and distance from rivers given their known influence on potential meadow locations (Bran et al. 1998). I defined three strata for elevation (stratum 1: 0-400 m; stratum 2: 401-800 m; stratum 3: >801 m) and two strata for distance from rivers (stratum 1: 0-2,000 m; stratum 2: >2,001 m). From the study area grid, I randomly selected 167 cells per stratum using the NOAA's Biogeography Branch Sampling Design Tool for ArcGIS (<http://ccma.nos.noaa.gov/products/biogeography/sampling/>, accessed 13 Nov 2011). In total, I randomly selected 1,002 cells, aiming to ensure >100 presences.

High resolution imageries provided by Google Earth make it possible to differentiate meadows, which appear visually as continuous patches of different shades of green, from the surrounding gray and brown steppe. To determine if a meadow was present (1) or absent (0) in a particular 1 km² cell, I first examined the quality of Google Earth imagery within the 1,002 cells chosen for sampling. Only cells completely covered by high resolution imagery were kept; others were discarded if covered by snow or clouds or unclear. If the cell was covered by $\geq 5\%$

of meadows, I considered meadows to be present, otherwise, I considered that meadows were absent.

I was concerned that my ability to detect meadows when present may be imperfect and, further, that detection ability may vary by image context (e.g., meadow quality, surrounding habitat types, overall wetness of the region). Imperfect detection could result in an inaccurate estimate of presence probability of a feature, such as meadows, which may cause errors in mapping their distribution (Vaughan & Ormerod 2003; Reese et al. 2005). Therefore, I examined my ability to detect meadows when they were present by repeatedly searching a subsample of 20 randomly-selected cells per stratum. I then visually assessed each cell three times (“visits”) for the presence of meadows, with three weeks between each visit, to minimize the chance that recollection from previous visits influenced the probability of detection in subsequent visits. I obtained an overall detection probability of 97.5%; only 2.5% of the time did I fail to detect a meadow in one visit when I detected it in another, indicating that my probability of detection was very high. Based on this high detection probability, I decided it was not necessary to use occupancy models that adjust for probability of detection (MacKenzie et al. 2006) for analysis.

Climate data

I used the following seven climatic variables to evaluate climate change impact on meadows distribution: maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of the wettest month, precipitation of the driest month and precipitation seasonality. I selected extreme variables rather than means because they represented better the ranges of conditions where species can occur (Zimmermann et al. 2009), hence climate change on those

extremes will have more impact on meadow distribution. I simulated future meadow distributions using the same climate variables for the period of time 2040-2069 (2050 hereafter), from four General Circulation Models (GCMs) derived from IPCC (2007) Special Report Emission Scenarios (SRES). The GCMs were CGCM3.1(T47), MK3.0, HadCM3 and MIROC3.2(hires). I selected those four GCMs to capture existing variability among the different model predictions (Pearson & Dawson 2003; Thuiller 2004; Lawler et al. 2009), and because those models have been used in other climate-change studies in South America (Marini et al. 2010; Kitoh et al. 2011). I used the A2 SRES scenario, which assumes that global carbon emissions will continue unconstrained given by an economy still dependent on fossil-fuel consumption (Nakicenovic et al. 2000). Furthermore, this scenario is preferable because the current actual trajectory of emissions (1990 to present) corresponds to a high emission scenario (Nakicenovic et al. 2000), and it is unlikely that such emission rate will change in the near future. All data were obtained from the WorldClim database, at a 30 arc-seconds resolution (Hijmans et al. 2005; available at: <http://www.worldclim.org/download>). I obtained future climate-data resolution at a resolution of 30 arc-seconds (1 x 1 km), which was statistically downscaled by the Delta Method (Ramirez-Villegas and Jarvis 2010).

Because meadows are rare on the landscape, relatively small cell sizes are needed to predict their presence or absence. In addition, climate change that occurs in small areas may have high impact on species locations, and fine-resolution grids are necessary to account for this in ecological models (Zhang 2005). When SDMs are used in conservation planning under future climate scenarios, high-resolution data sets are also needed to account for change in small regions (Kremen et al. 2008), especially because 75% of globally recognized protected parks and reserves are 300 km^2 in area (WDPA 2006). This creates a problem when modeling future

climate scenarios, because GCMs are often created with coarse resolutions (100 or 200 km), and downscaling such resolution incorporates uncertainties (Ramirez-Villegas & Jarvis 2010).

However, given my goal of a first broad-ensemble assessment of climate change impacts on meadows, and given the impossibility of using bigger cell sizes for presence/absence data, I decided to use downscaled-climate models, and considered these limitations acceptable.

Environmental data

Including static variables in SDMs when assessing climate-change effects on species distributions has been shown to improve or not affect model outputs (Stanton et al. 2011). Authors suggested excluding static variables highly correlated with climate variables but that have indirect effects on the species distribution, such as altitude. However, they suggested to include static variables that interact with climate, such as soil, even under the unrealistic assumption that such variables will not change with time (Stanton et al. 2011). Consequently, I selected three static variables used in Chapter 1, assuming they will remain constant over time. Because of the importance of river and soil characteristics to the presence of meadows (Mazzoni & Vázquez 2004), I included the variables distance to permanent rivers which I calculated using river shapefiles provided by the Argentinean Geographic National Institute (C. Chehébar Pers Comm, National Park Administration, San Carlos de Bariloche, Argentina). In addition, I used a soil cover layer created by the National Institute of Agricultural Technology (INTA), Argentina, selecting soil order classification as the predictor variable (Available at: <http://geointa.inta.gov.ar/>). Finally, I included a Human Influence Index (HII) variable to account for land-use changes driven by human activities in areas suitable for meadows (e.g., degradation by livestock farming, wetland drainage for agricultural purposes). This layer was produced by the WCS and CIESIN. The HII was calculated from nine global data layers

considering population density, human land use and infrastructure (built-up areas, nighttime lights, land use and land cover) and human access (coastlines, roads, railroads and navigable rivers) for the year 2000 (Last of the Wild Data Version 2 2005; available at: <http://sedac.ciesin.columbia.edu/>). Although those characteristics will change over time, it is necessary to account for human impact effects, understanding that predictions would be conservative given the increasing pressure of human activities on the landscape. Each layer was re-projected to UTM Zone 19 South. I used ArcGIS 9.3 (ESRI, Redlands, California, USA) for most geospatial operations.

Modeling procedure

To investigate potential climate-change effects on the distribution of areas that contain meadows, I used SDM techniques under the platform BIOMOD (Thuiller et al. 2009). I used four modeling techniques, generalized linear models (GLM), generalized additive models (GAM), general boosting models (GBM), and random forest (RF), to generate individual predictive distributions as the basis of a final mean consensus method (Araújo & New 2006; Marmion et al. 2009). Such modeling techniques were shown to function accurately compared to other modeling techniques (Segurado and Araújo 2004, Araújo et al. 2005, Elith et al. 2006, Cutler et al. 2007, Marmion et al. 2009) and performed well when modeling current distribution of meadows in Chapter 2. I ran GLMs and GAMs with a binomial variance and logistic link function. I fit GLMs using linear, quadratic, and polynomial terms (second and third order) and GAMs using cubic-smooth splines with a degree of smoothness of ≤ 4 degrees of freedom for each variable. In both methods, I used a stepwise procedure to select the most parsimonious models using Akaike's Information Criterion (AIC; Akaike 1973). I ran GBMs using a

maximum number of 5,000 trees and 5 lambda fold-cross-validation to progressively grow models. Finally, I ran RF with 500 trees.

Model evaluation

I used a data partitioning approach on training and validation data sets for measuring models accuracy (Fielding & Bell 1997). I used a 70% random sample of the observed data to calibrate models and the remaining 30% for model validation. The size of the split was determined using the formula: $[1 + (p - 1)^{1/2}]^{-1}$, where p is the number of predictor variables (Fielding & Bell 1997). To ensure robust estimations and assess sensitivity of the models to initial conditions, I used a cross-validation procedure, running 10 iterations per model, each time with a different random split of the data for training and validation (Thuiller 2009). I used the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot for assessing model accuracy (Fielding and Bell 1997). The AUC score varies between 0.5 (model predicted not better than random) and 1 (model predicted perfect). I interpreted AUC accuracy values following Swets (1988): excellent $AUC > 0.9$, good $0.9 > AUC > 0.8$, fair $0.8 > AUC > 0.7$, poor $0.7 > AUC > 0.6$, and fail $0.6 > AUC > 0.5$. As another measure of accuracy, if AUC values were >0.7 , then I also estimated sensitivity (percentage of presence correctly predicted) and specificity (percentage of absence correctly predicted) using the whole data set (W. Thuiller Pers Comm, Laboratory of Alpine Ecology, University Joseph Fourier, Grenoble, France). To transform probability values into presence/absence format I used the threshold that maximized the percentage of presence and absence cells correctly predicted for ROC curves.

Ensemble forecasting

To build the final model of current distribution of meadows, I used a mean ensemble approach, where the output model is calculated as the mean value of the outputs of all single

runs, and has been shown to perform well compared to other ensemble techniques (Marmion et al. 2009). To estimate the current meadow distribution of the entire study area and predict the future distribution under each GCM, I used the model trained with the presence/absence data to project the 40 individual models (10 using each technique) to the entire study area. Afterward, I calculated the mean ensemble model as the mean presence-probability value among the 40 individual models created. I then transformed the final ensemble model in a binary presence/absence format using a threshold calculated as the mean value of the threshold values obtained for the individual models. Overall, I produced one ensemble model projection for the year 2012 and four ensemble models for each of the four GCMs. I then combined those four models from the GCMs into a final mean ensemble model for the year 2050. To project future meadow distributions I assumed that the plant species that compose meadows would be able to disperse into any new geographic range.

To investigate the source of variation of the different predictions used in the ensemble forecast, I calculated uncertainty maps. I computed the standard deviation per cell within each global circulation model using the 40 single predictions coming from the 40 training models (the four techniques and 10 iterations). I also computed the standard deviation among the predictions for the four GCMs.

Predicting future distribution of species can be problematic when future climatic variables fall outside the range under which the model was trained. This is because the observed distribution does not provide information about how species might respond to the novel conditions, thus, such forecasting has been considered by several authors as ecologically and statistically invalid (Fitzpatrick & Hargrove 2009). In this study, all future variables presented values outside the training-value range (Table 3.1). In order to indicate the areas where my

model projections present limitations and may not be reliable (Fitzpatrick & Hargrove 2009), I created a map showing the total number of variables (seven variables x four GCMs) per cell that fall outside the training-value range. I assumed that areas were reliable if <10 variables were outside the training-value range. Because similarity among variables from different GCMs, a maximum of 10 variables means that no more than two variables per model were outside the training-value range.

Vulnerability analysis

I analyzed changes in meadows distribution by contrasting the final ensemble model of current meadow distribution (2012) versus the final mean ensemble model for year 2050. To investigate shifts in meadow distribution, I first overlaid a grid over the study area with a cell size of 50 x 50 km. I used a large-cell resolution aiming to obtain a broad assessment and to account for potential error in the final model given the high resolution of the climate change models. I calculated meadow abundance given the percentage of 1 km² cells with meadows present within each 50 x 50 km cell. I then compared the change of meadow abundance per cell and defined five categories: 1- Areas without meadows: cells that did not encompass more than 10% of meadow presences neither for present distribution nor future distribution; 2- Areas with little or no change: cells between 10% increase or 10% decrease of meadow abundance; 3- Areas with expansions: cells with an increase >10% of meadows abundance; 4- Areas with reductions: cells with a reduction of 10% - 50% of meadow abundance; and 5- Areas of severe reductions: cells with >50% reduction of meadow abundance. Cells that covered unreliable areas for predictions based on previous analyses were excluded.

I used a layer of Patagonian-protected areas provided by the National Park Administration, Argentina (C. Chehébar, Pers Comm, National Park Administration, San Carlos

de Bariloche, Argentina) to describe viability of meadows currently under protection under climate change effects. I considered only those protected areas assigned IUCN level I-II-III, which included National Parks, Provincial Parks, Province Natural Monuments, Natural Reserves and Natural and Cultural Reserves, because they are the only reserves that ensure strict and effective protection to the area.

Results

From the 1,002 cells selected for sampling, 26 cells were discarded because they were covered by clouds, snow, or the image was unclear. I determined 830 absences and 146 presences that I used for training models. Overall, models agreed between observations and current predictions of meadows distribution; however, GBM and RF models performed consistently better than GLM and GAM models (Table 3.2). Based on AUC values, RF, GBM and GAM models on average performed good and GLM models fair. Based on sensitivity and specificity values RF performed better, followed by GBM, GAM and GLM models (Table 3.2). All runs were consistent indicating low sensitivity to training datasets. The final current ensemble model improved accuracy considerably over single models (AUC = 0.95) measured on the total calibration dataset. This model also exhibited high sensitivity (93%) and specificity (82%) values measured on the calibration dataset. The four ensemble models of the GCMs presented a similar general pattern in meadows distribution. The uncertainty maps showed that the variation among different model techniques was higher than the variation among the four different GCMs (Figure 3.1). This indicates less consensus among modeling techniques regarding presence probability, but more consensus among the different GCMs. The variation among GCMs was higher in the southern region of the study area. Areas without meadows present were generally not reliable for climate change predictions, however, prediction of

meadow reductions in a wide area in the central-east region of the study area were also not reliable (Figure 3.2).

The final ensemble model for 2012 predicted that 11.43% of all 1 km² cells were covered by $\geq 5\%$ of meadows in arid and semi arid Patagonia. Meadows were clustered along the western portion of the region and followed major river systems, especially in the south. The same general pattern was observed on the predicted distribution for 2050 under the A2 SRES scenario. Overall meadow distribution was predicted to be reduced by 7.85% by the year 2050 based on the GCMs ensemble map (Figure 3.3). Predicted suitable cells for meadows decreased from 90,633 in 2012 to 83,519 in 2050. However two different major trends were observed: meadows contracted in central and northern Patagonia while southern regions would become more suitable for meadows (Figure 3.3). There was a predicted reduction of 34,950 cells (38.56%) mostly in the north-central region and also on Tierra del Fuego Island. In contrast, there was a predicted expansion of 27,836 suitable cells (30.71%) for meadows, mostly located in the south region, but also in a small portion of northwestern Patagonia.

Based on the broad vulnerability analysis and discarding areas with low reliability, northwestern Patagonia and Tierra del Fuego Island are likely to face reductions of meadow abundance; meadows are likely to expand in the southwest; and the central area region represents a transition zone from reductions in the north to expansions in the south (Figure 3.3). Of the 15 IUCN I-II-III category protected areas that constitute the effective reserve network of arid and semi-arid Patagonia, 11 (73.3%) are located in areas where meadows were not predicted to be present neither currently nor for the year 2050 (Figure 3.3). Of the other 4 reserves, Domuyo and El Tromen Provincial Parks are located in areas where meadows will not be affected by climate change. Laguna Blanca National Park and the Natural Provincial Monument Cañada

Molina will likely become ineffective at protecting meadows as they are located in an areas were meadows abundance would decrease (Figure 3.4), however predictions over the area of the Natural Provincial Monument Cañada Molina are unreliable.

Discussion

The mean ensemble technique allowed me to obtain a reliable model of the current distribution of meadows in arid and semi-arid Patagonia on the basis of four different modeling techniques. GBMs and RFs performed consistently better than GLM and GAMs, however, all models presented AUC values over 0.75. By averaging projections of these different regression and machine learning techniques, the robustness of model predictions increased and model accuracy was considerably improved (Araújo & New 2006; Buisson et al. 2010). In addition, the ensemble projection of the four different GCMs allowed me to obtain a broad general forecast pattern of meadow distribution for the next half century. On the basis of the projected distribution of meadows, and an understanding of the forecasting limitations in some areas of the study region, I determined that overall meadow abundance is going to decrease by the middle of the century given the changes in climate. However, there are two contrasting trends, severe reductions of meadows in northwest Patagonia and Tierra del Fuego Island, and an expansion of suitable areas for meadows in the south and a small portion of the northwest. Such information on meadow vulnerability to climate change will be important information for conservation planning.

Aiming to increase the understanding of potential climate-change effects on meadows in arid and semi-arid Patagonia, I modeled their distribution using mainly climatic predictor variables. However, I also included three static predictor variables, soil, distance to permanent rivers and HII. The inclusion of static variables in SDMs to investigate climate-change effects

was shown to improve model performances or do not interfere in the predictive performance of future distributions (Stanton et al. 2011). In this study, the exclusion of an important predictor variable, such as the Normalized Difference Vegetation Index (NDVI), resulted in a reduction in the ability of models to accurately predict the current distribution as compared to findings reported in Chapter 1. However, while NDVI measured during the growing season is useful for predicting the current distribution of meadows in places where ground data observation do not exist, I choose to exclude NDVI in predictions of the future distribution. High NDVI values are a useful characteristic of meadows as an indication of their presence, rather than a variable that may contribute to or “cause” their presence, as soil characteristics or water presence make an area suitable to establish wetland vegetation. Thus, to include NDVI in future predictions would be highly unrealistic and would likely affect the interpretation of future distributions. Soil, distance to permanent rivers and HII were important static predictor variables to consider. Given that changes in soil mostly occur over long periods of time, it was possible to assume stability for the next half century. Distance to permanent rivers was more problematic, because stream flow and riverbeds are more variable (Newman et al. 2006). Nevertheless, given the association between meadows and river valleys, it was necessary to incorporate that variable in models under the false assumption of stability in time. In addition, meadows will not expand in areas where climate becomes favorable if there is no permanent water, therefore, a distance to permanent rivers variable would have limited the expansion of suitable areas for meadows under the assumption of free dispersion capacity.

Besides the lower performance of single models when compared to findings in Chapter 1, the ensemble model improved significantly model accuracy, resulting in an AUC value (0.95), closer to the value of the ensemble model in Chapter 1 (0.97). In addition, the number of cells

containing meadows in arid and semi-arid Patagonia for 2012 was only 0.2% lower than the number of cells with meadows reported in Chapter 1. Furthermore, the distribution pattern was similar between the two analyses, reaffirming that the ensemble models provided a reliable representation of the current distribution. However, my study suffered the same methodology limitations of other SDM studies (Pearson & Dawson 2003; Guisan & Thuiller 2005; Araújo & New 2006; Araújo & Guisan 2006; Thuiller et al. 2008). Among them, I assumed that vegetative species interactions with other species and with the environment will remain similar over time, that the species will not adapt or acclimate to climate change and that they can disperse without limitations (Pearson & Dawson 2003). However, it was my goal to generate a general understanding of future trends of meadows distribution and not a detailed forecasting at a high resolution (Pearson & Dawson 2003; Lawler et al. 2006). In addition, I accounted for those areas where predictions were not reliable, because future climate variables are outside the values used during the model training.

My predictions indicate that meadow distribution in arid and semi-arid Patagonia will decline by 7.85% by the year 2050 and shift mainly toward the south. Reductions in meadows will be greatest in the central and northern regions and Tierra del Fuego Island. The predicted reduction of meadows goes in accordance with the predicted reduction of precipitation. While the surface air temperature is predicted to increase more or less constantly in the entire region (Nuñez et al. 2009), significant decreases in annual precipitation are predicted to occur in northwest Patagonia (Nuñez et al. 2009), especially during the summer (i.e., the growing season) that may lead to the reduction of meadows in the area. It is important to note that a fraction of these predictions were, in my opinion, not reliable. In Tierra del Fuego, surface air temperature is predicted to increase more than the rest of Patagonia and annual precipitation is predicted to

decrease (Nuñez et al. 2009), these factors may explain the strong predicted reduction of meadows. Conversely, southern regions will become more suitable for meadows. The combination of predicted increases of surface air temperature with no changes in annual or seasonal precipitation (Nuñez et al. 2009) may benefit the establishment of new meadows. As well, there is a small portion of northern Patagonia that may experience increases in suitable areas for meadows; nevertheless, half of these predicted areas were not reliable. The increase of suitable areas could be responding to an increase of precipitation on the Chilean side of the Andes (Nuñez et al. 2009). It is important to notice that climate models for Patagonia have overestimated precipitation, likely due to insufficient observation network (Kitoh et al. 2011). This potential error makes our predictions conservative given the importance of precipitation for meadows.

Water plays a key role in meadow formation and persistence and from the predictions of this study, precipitation changes are going to be important drivers of future changes in meadow distribution. Vegetation in arid environments has a limited ability to respond to changes in precipitation (Paruelo et al. 1999), nevertheless, meadows in arid and semi-arid Patagonia present a vegetation structure that corresponds to humid environments. Therefore, meadows can respond to variation in precipitation (Buono et al. 2010). This supports the predictions of decreasing meadows where precipitation may diminish and increasing suitable areas where precipitation may increase. However, in Patagonia there are three sources of water for meadows: precipitation, deep percolation from steppes, and high mountain snowmelt. I could not include variables for the last two sources as they were not available, therefore, it will be important to model such variables and include them in future research to improve the accuracy of climate change predictions.

Protected areas are important to shield biodiversity from the impact of human activities and to mitigate potential climate-change effects (Botkin et al. 2007). Such protection needs are even higher in developing countries, where poverty increases the pressure to exploit natural resources and convert natural areas, such as wetlands, into agricultural use (Brinson & Malvárez 2002). In the Argentinean Patagonia, human pressure on meadows is high, mainly due to livestock production which results in severe degradation (Paruelo & Aguiar 2003; Perotti et al. 2005). Under these threats, the current network of IUCN I-II-III reserves results inappropriate for protecting meadows. Only a small portion of arid and semi-arid Patagonia is effectively protected (Burkart et al. 2007) and only a small portion of meadows occur inside such protected areas (Chapter 1). On the basis of my results, in the long term, one of the four reserves containing meadows is likely going to become ineffective because of climate change.

Conservation planning is an effective tool to develop or improve existing reserve networks (Margules & Pressey 2000). However, in the practice, protected areas are often created opportunistically, without any specific biodiversity objectives (Margules & Pressey 2000). Moreover, opportunistic procedures of reserve design may be more costly than the use of systematic procedures based on model information (Pressey & Cowling 2001). Despite the inherent uncertainty that limits the use of SDMs (Thuiller 2004), they provide important spatial and forecasting information to incorporate in conservation planning (Thuiller 2007). In addition, the use of ensemble approaches reduce significantly the amount of uncertainty coming from different GCMs, and with that, the likelihood of making wrong conservation decisions (Araújo & New 2006).

For the aim of improving protection of meadows in arid and semi-arid Patagonia and create new protected areas, my broad map of vulnerability analysis to climate change will be

important information to incorporate into conservation decisions (Groves et al. 2012). This map provides broad information on trends of climate change on meadows, and thereby areas of potential degradation and potential climatic refugia (Groves et al. 2012). Central and southern Patagonia appear to be important areas to prioritize for the creation of new reserves with the goal of protecting meadows, as they would likely not be affected or even favored by climate change. These are areas to consider more important (i.e., give more weight) at the time of performing a conservation planning analysis. However, it is important for further studies to investigate climate impact on other Patagonian species to include in such conservation planning project. Nevertheless, under the limited information available on climate change effects of species for the region, meadows appear as important habitat for several species (Ortega & Franklin 1988; Mazzoni 2000; Brinson & Malvárez 2002; Perotti et al. 2005; Puig et al. 2008), thus meadows could act as surrogate for improve protection to those species (Ferrier 2002). In addition, in those areas where meadow abundance would be reduced, management actions should be taken to mitigate potential desertification trends. Because livestock is the main cause of meadow degradation, future management plans for reducing livestock impact should be considered (e.g., reduce animal charge, alter grazing patterns, or even exclude livestock from certain regions). If negative effects of climate change and livestock production are combined, the results could exacerbate the degradation process already occurring in meadows.

This is the first attempt to study meadow distribution response to climate change. The use of the ensemble technique provided final models to assess climate-change effects on meadows with less uncertainty and more accuracy than single models and single GCMs. I identified a broad area of Patagonia that is likely going to face severe reduction in meadow abundance. This is not only going to affect the biodiversity associated with meadows but also,

the economy of those areas that rely on agricultural activities. My study is also important given the lack of information on climate change impacts on biodiversity in the Southern Hemisphere (IPCC 2007). Although this information should not be considered alone at the time of planning future conservation actions, it is likely that climate change will have a deep impact on Patagonian meadows. On the basis of this study and given the low representation of meadows in reserves, the need of improving the conservation network in arid and semi-arid Patagonia is imperative to ensure long-term protection of meadows and the associated biodiversity that relies on this habitat.

Table 2.1. Summary of the equal-stratified sampling results for modeling current (2012) meadows distribution in arid and semi-arid Patagonia.

Stratum	Dist. from river (m)	Altitude (m)	Cells sampled	Cells discarded	Number of presences
1	0-2000	0-400	167	4	31
2	0-2000	400-800	167	9	47
3	0-2000	>800	167	4	40
4	>2000	0-400	167	4	1
5	>2000	400-800	167	2	10
6	>2000	>800	167	3	18

Table 2.2. Performance of 40 single-model runs (10 runs per model) predicting current (2012) meadows distribution in arid and semi-arid Patagonia, based on three different accuracy categories of area under the curve (AUC).

Model performance	Modeling technique			
	GAM	GBM	GLM	RF
Excellent	40%	50%	20%	40%
Good	50%	50%	70%	50%
Fair	10%	0%	10%	10%

GAM, general additive models; GBM, general boosting models; GLM, general linear models; RF, random forests; excellent $AUC > 0.9$; good $0.9 > AUC > 0.8$; fair $0.8 > AUC > 0.7$.

Table 2.3. Mean (\pm SD) sensitivity and specificity across 10 repetitions for each of four different modeling techniques, and mean (\pm SD) area under the curve (AUC) for such models for predicting current (2012) meadows distribution in arid and semi-arid Patagonia. Sensitivity and specificity were calculated for the whole data set, whereas AUC was calculated on 25% validation data (different from the 75% used for model training).

Model	Sensitivity (%)	Specificity (%)	AUC
GAM	81.84 \pm 0.68	81.71 \pm 0.60	0.88 \pm 0.04
GBM	88.30 \pm 1.13	88.29 \pm 1.09	0.88 \pm 0.04
GLM	81.09 \pm 1.17	81.06 \pm 1.24	0.87 \pm 0.04
RF	93.81 \pm 1.62	93.84 \pm 1.59	0.87 \pm 0.05

GAM, general additive models; GBM, general boosting models; GLM, general linear models; RF, random forests; sensitivity: percentage of presence correctly predicted; specificity: percentage of absence correctly predicted.

Table 2.4. Frequency of the predictor variables selected in the four different modeling techniques for predicting current (2012) meadows distribution in arid and semi-arid Patagonia.

Variables	GLM	GAM	GBM	RF	Mean	SD
Max temp of warmest month	10	10	10	10	10	0.0
Min temp of coldest month	0	0	10	10	5	5.8
Precipitation of wettest month	10	10	10	10	10	0.0
Precipitation of driest month	1	0	10	10	5.25	5.5
Precipitation seasonality	7	1	10	10	7	4.2
NDVI	10	10	10	10	10	0.0
Altitude	4	0	10	10	6	4.9
Distance to permanent rivers	10	10	10	10	10	0.0
Distance to all rivers (permanent and non-permanent)	10	9	10	10	9.75	0.5
Human influence index	5	3	10	10	7	3.6
Soil	6	7	10	10	8.25	2.1

GAM, general additive models; GBM, general boosting models; GLM, general linear models; RF, random forests.

Table 3.1. Minimum (Min), mean (Me), and maximum (Max) values of the climate variables used for modeling current (2012) and future (2050) meadows distribution in arid and semi-arid Patagonia. Values correspond to variables used for model training and for four General Circulation Models (CGCM3.1(T47), HadCM3, MIROC3.2(hires), and MK3.0).

	Training data			CGCM3.1(T47)			HadCM3			MIROC3.2(hires)			MK3.0		
	Min	Me	Max	Min	Me	Max	Min	Me	Max	Min	Me	Max	Min	Me	Max
Max T of the warmest month	11.2	23.8	33.0	0.0	27.3	36.6	0.0	27.3	36.7	0.0	27.9	36.6	0.0	26.5	34.3
Min T of the coldest month	10.0	-2.0	3.0	16.2	-0.3	4.5	16.3	-0.2	4.6	15.5	0.5	5.4	16.7	-0.9	4.0
Mean T of wettest quarter	-3.5	7.0	22.0	10.5	7.1	25.0	10.5	10.2	26.0	-9.2	9.7	26.3	10.9	12.4	25.1
Mean T of driest quarter	3.3	11.7	21.5	-0.1	15.7	25.9	-2.0	13.1	25.9	-5.2	12.9	24.8	-3.5	11.5	21.7
Prec. of the wettest month	15.0	40.0	164.0	0.0	35.7	194.0	0.0	35.6	181.0	0.0	36.3	175.0	0.0	56.2	183.0
Prec. of the driest month	4.0	11.2	45.0	0.0	3.6	61.4	0.0	8.5	57.0	0.0	2.2	58.0	0.0	2.8	54.0
Prec. seasonality	12.0	35.4	76.0	0.0	59.0	109.0	0.0	40.0	82.0	0.0	68.3	130.0	0.0	71.4	109.0

Table 3.2. Area under the curve (AUC), sensitivity and specificity statistics for four modeling techniques with ten repetitions for each one (me = mean, min = minimum, max = maximum) used for calculating a mean ensemble model for projecting current (2012) and future (2050) meadows distribution in arid and semi-arid Patagonia. AUC was calculated on 30% validation data (different from the 70% used for model training), while sensitivity and specificity were calculated for the whole data set (training + validation).

	AUC			Sensitivity (%)			Specificity (%)		
	Me	Min	Max	Mean	Me	Max	Me	Min	Max
GAM	0.81	0.78	0.84	73.13	71.43	74.15	73.23	71.41	74.55
GBM	0.85	0.82	0.89	84.69	82.99	85.71	84.62	82.75	85.89
GLM	0.78	0.76	0.81	72.38	70.75	73.47	72.41	70.69	73.22
RF	0.86	0.84	0.89	92.04	90.48	93.88	92.09	90.47	93.85

GAM, general additive models; GBM, general boosting models; GLM, general linear models; RF, random forests; sensitivity: percentage of presence correctly predicted; specificity: percentage of absence correctly predicted.

Figure 2.1. Predicted distribution map for current meadows (2012) and IUCN level I, II, and III protected areas for arid and semi-arid Patagonia. Map (a) shows probability of each cell to be covered by $\geq 5\%$ of meadows, whereas map (b) shows meadows presence (cell covered by $\geq 5\%$ of meadows) or absence (cell cover by $\leq 5\%$ of meadows). Map B also shows current IUCN level I, II, and III protected areas.

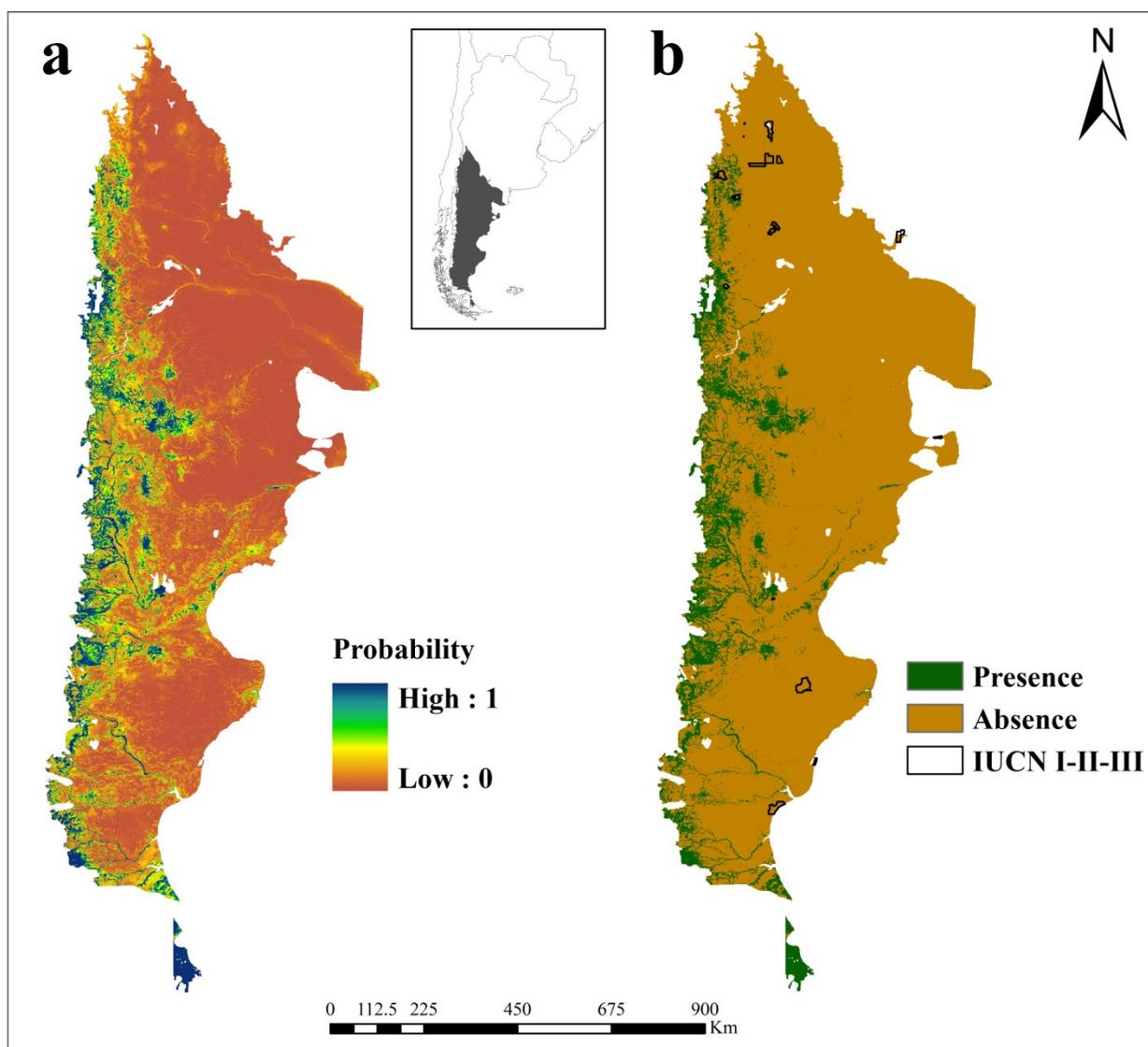


Figure 3.1. Map of prediction reliability for simulating future (2050) meadows distribution in arid and semi-arid Patagonia. This map shows the total number of variables (seven variables x four General Circulation Models) per cell which values fall outside the training-value range. Browns represent reliable predicting areas and blues represent unreliable predicting areas.

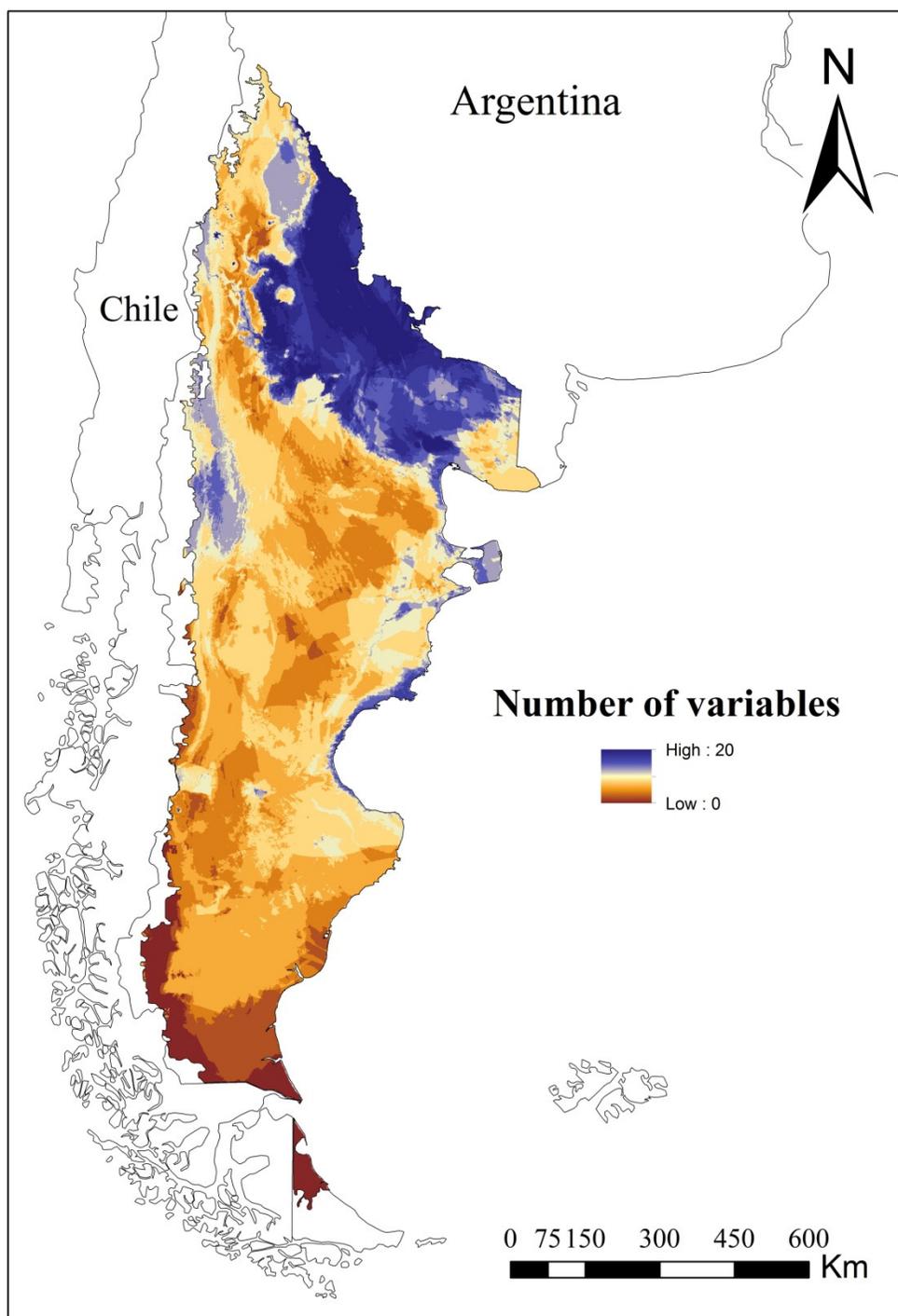
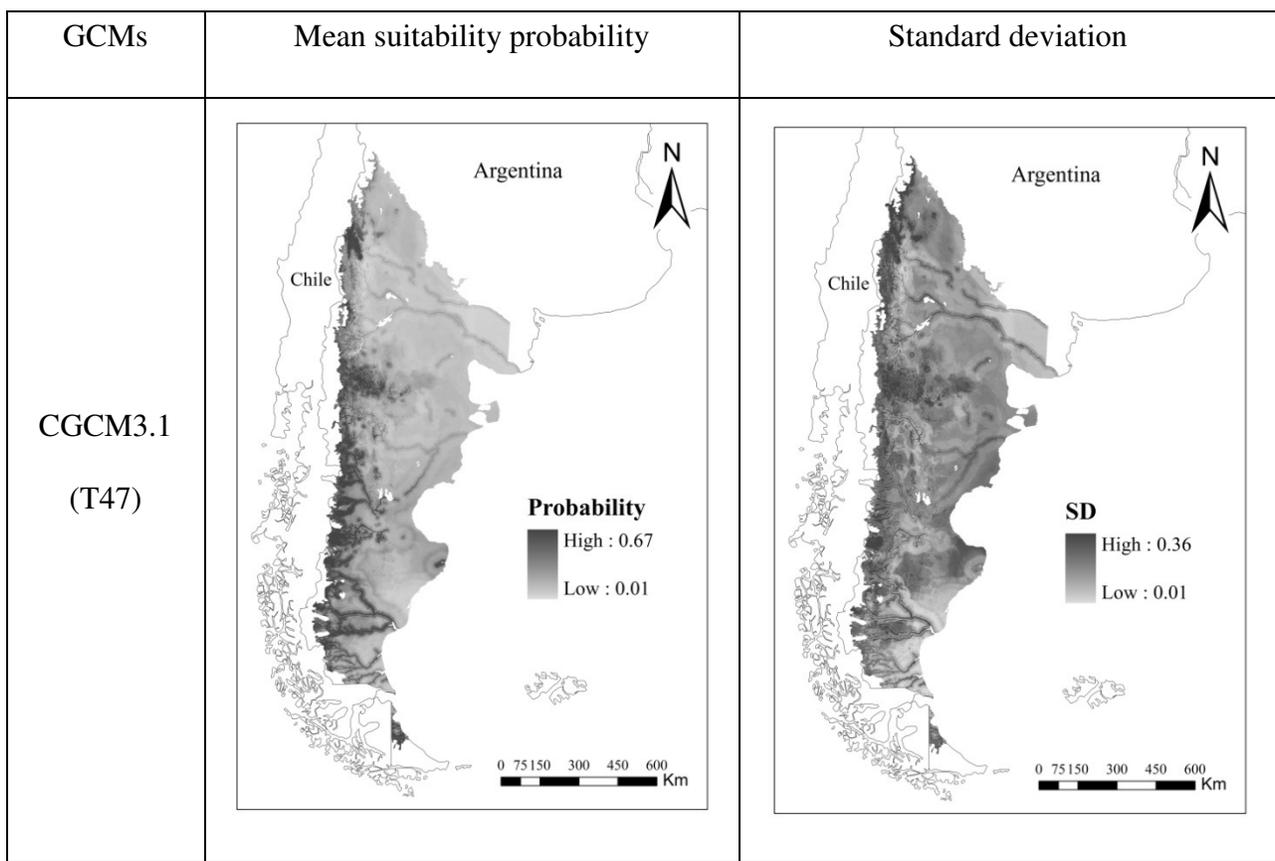
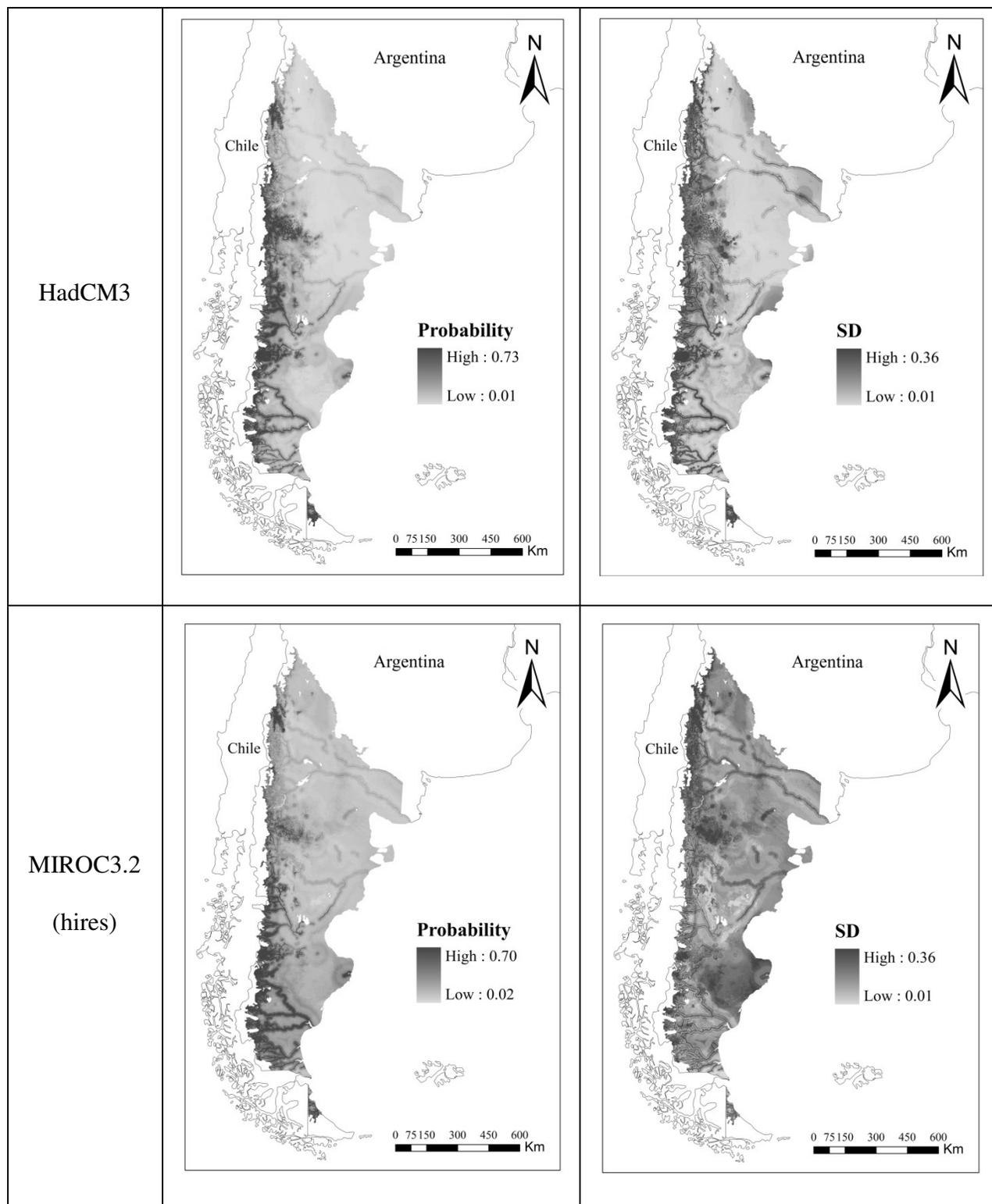


Figure 3.2. Maps of mean predicted suitability probabilities and standard deviations obtained in the ensemble forecast framework for modeling current (2012) and future (2050) meadows distribution in arid and semi-arid Patagonia. The first 8 maps show mean predicted probabilities and standard deviations among the 4 single models and 10 repetitions per model for each of the 4 different General Circulation Models (GCMs). The last 2 maps show mean predicted probabilities and standard deviations among the 4 ensemble GCMs.





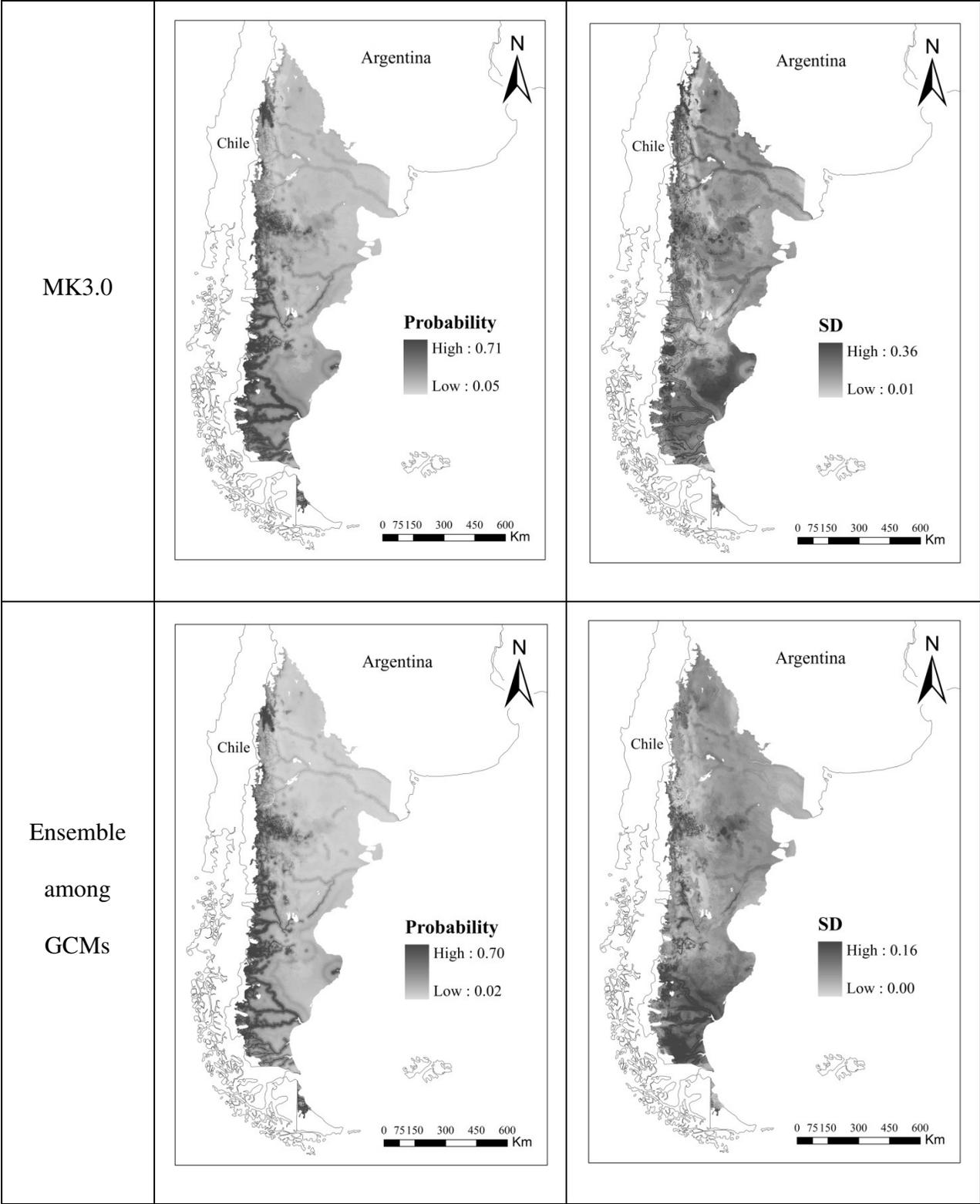


Figure 3.3. Predicted distribution map for current (2012) and future (2050) meadows and IUCN level I, II, and III protected areas for arid and semi-arid Patagonia. This map shows the distribution of cells (1 km²) that were predicted to maintain a cover $\geq 5\%$ of meadows (green), cells that were predicted to maintain a cover $< 5\%$ of meadows (orange), cells that were predicted to lose cover $\geq 5\%$ of meadows (red), and cells that were predicted to increase cover $\geq 5\%$ of meadows by the year 2050.

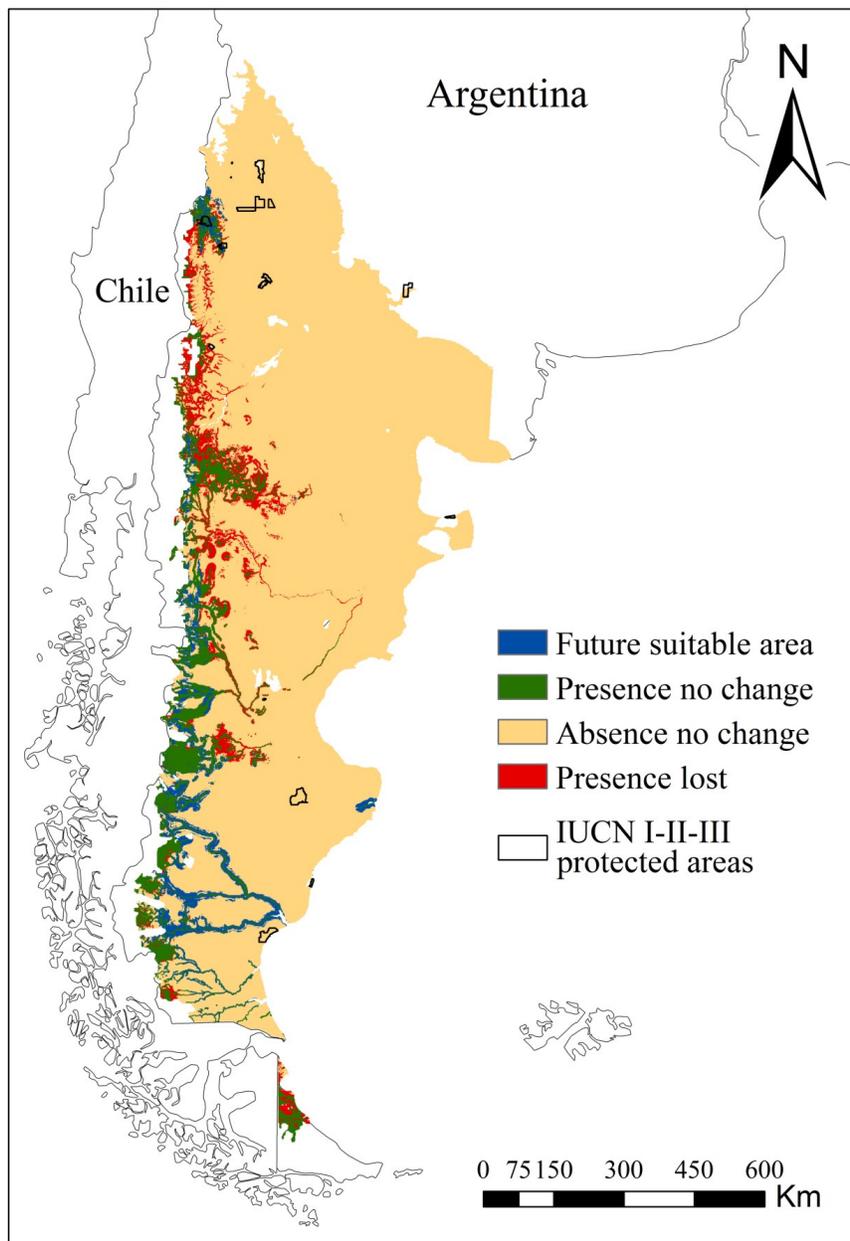
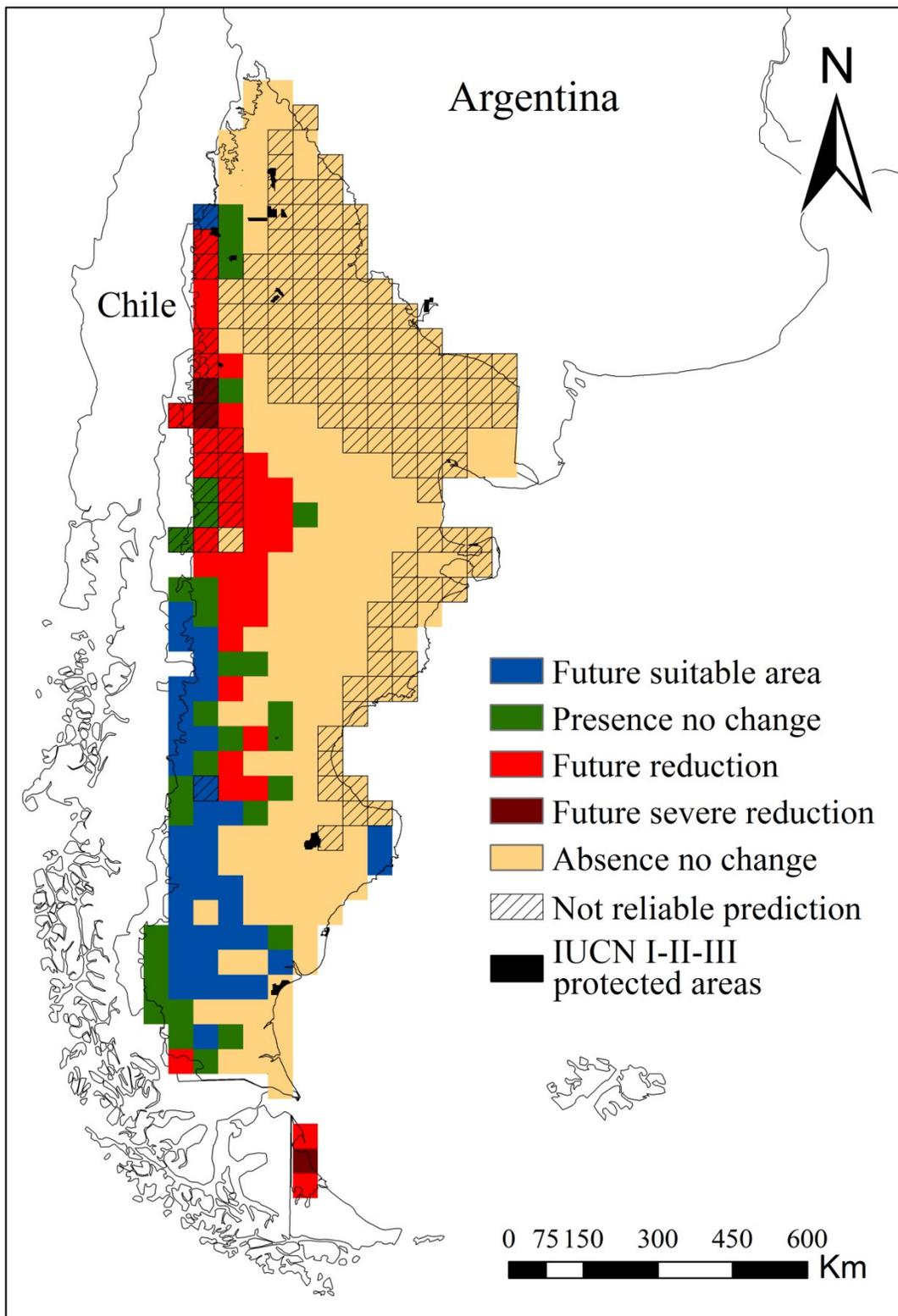


Figure 3.4. Map of vulnerability to climate change for meadows abundance in arid and semi-arid Patagonia on the basis of predictions of distribution change by the year 2050. This map shows areas that were reliable predicted to change (hatch cells are not reliable predictions): do not encompass more than 10% of meadow presences neither for present distribution nor future distribution (orange); present little or no change of meadows abundance: cells between 10% increase or 10% decrease of meadow abundance (green); increase abundance: cells with an increase >10% of meadows abundance (blue); reduce abundance: cells with a reduction of 10% - 50% of meadow abundance (light red); reduce severely abundance: cells with >50% reduction of meadow abundance (dark red). Abundance was calculated as the percentage of 1 km² cells with meadows predicted to be present within a 50 x 50 km cell.



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