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# Woody species diversity in temperate Andean forests: the need for new conservation strategies

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## ABSTRACT

Chile has more than half of the temperate forests in the southern hemisphere. These have been included among the most threatened eco-regions in the world, because of the high degree of endemism and presence of monotypic genera. In this study, we develop empirical models to investigate present and future spatial patterns of woody species richness in temperate forests in south-central Chile. Our aims are both to increase understanding of species richness patterns in such forests and to develop recommendations for forest conservation strategies. Our data were obtained at multiple spatial scales, including field sampling, climate, elevation and topography data, and land-cover and spectrally derived variables from satellite sensor imagery. Climatic and land-cover variables most effectively accounted for tree species richness variability, while only weak relationships were found between explanatory variables and shrub species richness. The best models were used to obtain prediction maps of tree species richness for 2050, using data from the Hadley Centre's HadCM3 model. Current protected areas are located far from the areas of highest tree conservation value and our models suggest this trend will continue. We therefore suggest that current conservation strategies are insufficient, a trend likely to be repeated across many other areas. We propose the current network of protected areas should be increased, prioritizing sites of both current and future importance to increase the effectiveness of the national protected areas system. In this way, target sites for conservation can also be chosen to bring other benefits, such as improved water supply to populated areas.

**Key words:** Biodiversity, Hotspot, Natural Protected Areas, Species Richness, Spatial modelling.

## 1. INTRODUCTION

Loss of biodiversity is one of the most serious environmental problems today because of the associated economic, scientific, amenity and ecosystem service losses and the irreversible nature of global extinction (Newton, 2007). Threats to biodiversity remain strong, in large part because of continued increase in the rate of human-mediated destruction and conversion of habitats (May et al., 1995; Nagendra, 2001; Newton, 2007). The need to preserve biodiversity is therefore urgent. One of the main actions to protect biodiversity is to create or expand protected areas (Murphy, 1990; Nagendra, 2001).

Selection of areas for conservation should take into consideration the representation and persistence of key attributes within sets of areas (Araújo, 1999). Species diversity is often used as a target attribute of biological communities to determine areas of high conservation value (De Vries et al., 1999; Luoto et al., 2002; Armenteras et al., 2006; Cayuela et al., 2006a); although it is only one of the important variables, it often correlates with other key measures. In turn, species richness (by which we mean the number of species in a given area), which is both the simplest and most easily interpreted measure of species diversity, tends to correlate strongly with the other measures (Whittaker et al., 2001). Explaining patterns of species richness is, however, a complex challenge because the diversity results from many interacting factors that operate at different spatial and temporal scales (Diamond, 1988; Willis and Whittaker 2002).

At fine scales, a variety of variables typically account for (or at least correlate with) spatial diversity patterns (Whittaker et al., 2001; Field et al., 2009). These fine-scale correlations are usually weaker than those at broad scales (Field et al., 2009). Changes in elevation, slope or exposure can determine the ecological response of individual species and therefore contribute to overall changes in species richness (Luoto et al., 2002). Human activities also influence the shape of geographical patterns of diversity in intensively managed regions (Lawton et al., 1998; Ramírez-Marcial et al., 2001; Cayuela et al., 2006b; Hall et al., 2009).

At broader spatial scales, patterns of species richness are correlated strongly with climatic variables (Currie, 1991; O'Brien, 1998; O'Brien et al., 2000; González-Espinosa et al., 2004, Field et al., 2005). If climate directly or indirectly determines patterns of richness, then when the climatic variables change, richness should change in the manner that spatial correlations between richness and climate would predict (Acevedo and Currie, 2003; Venevsky and Veneskaia, 2003; Field et al., 2005). This might have important consequences for long-term conservation, since prioritization of highly diverse habitats today might not be effective in preserving future hotspots of species richness in the face of climate change.

In this study, we develop empirical models to investigate present and future spatial patterns of woody species richness in temperate forests in south-central Chile. We follow the lead of Cayuela et al. (2006a), who developed a predictive model using a similar approach, which allowed identification of high-priority areas for conservation of tropical forests in areas where the accessibility was limited. Our models include information obtained at multiple spatial scales, including field sampling, climate, topography and land-cover variables. The applied goals of this research are to inform attempts to prioritize the extant forest patches in the region and to provide recommendations for their conservation. This is of paramount importance as these forests are included in the Global 200 initiative launched by the World Wildlife Fund and the World Bank (Dinerstein et al., 1995), which focuses on the most threatened eco-regions in the world. In addition, these forests have been classified as one of the world's biological hotspots, e.g. by Myers et al. (2000), because of their high degree of endemism and presence of monotypic genera (Arroyo et al., 1996; Smith-Ramírez, 2004). The temperate forests of Chile are specifically considered to be vulnerable to impacts of climate change (IPCC, 2001; Pezoa, 2003). Paradoxically, in Chile, at broad scales the amount of land dedicated to conservation is inversely correlated with the number of species and endemism (Armesto et al., 1998). Thus, more than 90% of the 14 million hectares of protected land (CONAF et al., 1999) is concentrated in high latitudes (> 43º), leaving unprotected a large proportion of high-biodiversity areas (Armesto et al., 1998). Here we investigate whether the inverse relationship between amount of conserved land and numbers of species is true at a smaller spatial scale. For all these reasons, establishing guidelines for prioritization of natural protected areas is a crucial step towards biodiversity conservation in this important eco-region.

The specific objectives of this study are: (a) to assess the independent and joint contribution of different groups of variables in describing the variation in woody species richness in the study area, thereby increasing our knowledge and understanding of Chile's temperate Andean forests; (b) to develop a model to estimate present-day, fine-scale woody species richness across the study area; (c) to develop a model to predict the effects of climate change on woody species richness; and (d) to use the models to evaluate the effectiveness of the currently protected areas for maintaining biodiversity both now and in the face of climate change. The models we develop can also be used to inform future modification of the protected area network and to facilitate forest restoration programmes.

## 2. MATERIALS AND METHODS

### *2. 1 Study area*

Our study was conducted in the Maule region of Chile, which lies mainly in the Andean area between 35º and 36º latitude south (Fig. 1). The study area covers approximately 270,000 ha and is between 200 and 3,900 m.a.s.l. The predominant soils are volcanic in origin, with different degrees of development (Schlatter et al., 1997). The predominant climate is of the Mediterranean type, with annual precipitation averaging between 700 and 1,300 mm and concentrated mostly during the winter season, and an average annual temperature of 9ºC (Pezoa, 2003).

The area is characterized by the presence of secondary and old-growth forests (dominated by species like *Nothofagus obliqua*, *N. glauca*, *N. dombeyi* and sclerophyllous species over 2 m high and >50% coverage), shrublands (composed mainly of low-height sclerophyllous species such as *Criptocarya alba*, *Quillaja saponaria* and *Lithraea caustica*), exotic plantations (mainly of *Pinus radiata*), agricultural lands, herbaceous vegetation, grasslands, and other types of land cover such as bare land, urban areas and water bodies (Appendix 1)

(CONAF et al., 1999; Altamirano et al., 2007). The intensification of land use, particularly firewood extraction and selective logging, has caused much deforestation and forest disturbance, which may have a negative impact on biodiversity (Lara et al., 1996, 2003; Olivares, 1999; Echeverría et al., 2006).

The national protected areas system of Chile comprises 96 sites, totalling approximately 14 million hectares and representing 19% of the land (CONAF et al., 1999). The three main types of protected area are National Parks, National Reserves and Natural Monuments. National Reserves are medium-sized areas that are protected with the aim of conserving species, soils and hydrological resources; sustainable natural resource use is allowed. There are two of these reserves in our study area: Altos de Lircay (approx. 12,000 ha) in the north, and Los Bellotos (approx. 400 ha) in the south (Figure 1).

### *2.2 Field sampling and estimation of woody diversity*

The study area was divided into approximately 700 cells, each 2 x 2 km. Of these, 82 were selected via a random sampling scheme stratified by vegetation structure (see below), to contain field plots. One field plot was located in each of these 82 cells so that it was as close to the centre of the plot as possible, given the constraints that it was within the most representative vegetation structure in terms of percentage cover inside the cells, and was accessible. The plots provided good coverage of the main vegetation and soil types, and of the elevational range. In a pilot study, the numbers of species in ten circular plots of 500 $m^2$ and 250 $m^2$ were compared. No significant differences were found (Student's paired t-test, $t= 2.3$, $P= 0.16$), so in order to allow greater replication, 250 $m^2$ (i.e. 9 m radius) was set as the plot size. The 82 plots were sampled in 2005 and 2006. In each, all trees and shrubs with a height greater than 1.4 m were identified to species (see Appendix 1), counted and measured; from this, we calculated basal area. Fisher's alpha index, Shannon's diversity index and species richness (number of species observed) were calculated for each sample. Fisher's alpha and Shannon's indices were, however, highly correlated with species richness ($r = 0.92$, $P < 0.0001$; $r = 0.87$, $P < 0.0001$ respectively). Because of this strong similarity and the ease of interpretability, we only report results for species richness.

### *2.3 Explanatory variables*

To model species richness we focused on six climatic variables, two topographic variables and three land-cover variables (Table 1). We initially obtained 19 climatic variables from the WorldClim database (www.worldclim.org). WorldClim is a set of global climate layers (climate grids) with a spatial resolution of 1 x 1 km (Hijmans et al., 2005). This set includes 19 temperature, rainfall and bioclimatic variables. The bioclimatic variables were derived from the monthly temperature and rainfall values in order to be more biologically meaningful, and represent annual trends in seasonality and extreme or limiting environmental factors (Hijmans et al., 2005). We carefully examined the correlation matrix to determine the degree of collinearity and redundancy between these climatic variables (and the other explanatory variables), as well as their correlations with species richness. We additionally performed a hierarchical cluster analysis of these variables in order to identify groupings of correlated explanatory variables. To achieve this, we used the 'Hmisc' library (Harrel et al., 2009) of the R environment (R Development Core Team, 2009), defining a threshold of Spearman's $\varrho = 0.6$. We combined this information with theoretical considerations to select climatic variables for further analysis that would minimise multicollinearity, while being expected to account best for species richness, as recommended by Carsten F. Dormann (pers. comm.). Multicollinearity tends both to promote statistical artefacts (resulting in false model accuracy) and to cause unstable parameter estimates, which are particular problems when making predictions of future diversity. Thus we chose the following climatic variables for the regression analyses (Table 1): minimum temperature of the coldest month ($T_{min}$), temperature seasonality ($T_{seas}$), mean annual precipitation ($P_{an}$), mean precipitation of the driest month ($P_{min}$) and precipitation seasonality ($P_{seas}$). Mean annual temperature was strongly correlated with $T_{min}$ ($r = 0.98$); we chose $T_{min}$ because it is very similar to minimum monthly potential evapotranspiration calculated by the Thornthwaite method, which previous empirical and theoretical work has shown to be a good predictor of woody species richness (e.g. Field et al., 2005). In our dataset, $T_{min}$ correlated more strongly with species richness than $T_{mean}$, supporting our reasoning. $P_{min}$ is appropriate in climates where precipitation is lowest during the summer months, as in our study area, because it represents a strong constraint on growth.

Elevation was derived from a digital elevation model, with a spatial resolution of 90 x 90 m, based on the Shuttle Radar Topography Mission (SRTM). The SRTM data are available from the Global Land Cover Facility (GLCF) website (http://www.landcover.org). It was classed as a climate proxy for several reasons. Elevation is a powerful and very precise determinant of small-scale climatic variation, particularly temperature; this is because of the close association between temperature and elevation that results from the effects of the adiabatic lapse rate. The relationship between elevation and precipitation is less strong, more indirect and more complex. In this study, elevation, with its resolution of 90 x 90 m, is much more precisely measured than the WorldClim variables (resolution 1 x 1 km), so it can be expected to model climate (particularly temperature) well for the field plots. Given the scale of the field plots and the nature of the study area, elevation was also a poor topographic measure, indicating nothing about topographic heterogeneity, nor about aspect. This reasoning is backed up by the fact that, in our dataset, elevation was not correlated with topographic variables ($r = 0.035$ and -0.044 for slope and aspect respectively), but was almost perfectly inversely correlated with

$T_{min}$ and mean annual temperature ($r$ = -0.95 and -0.94) despite the difference in resolution. The correlation between elevation and precipitation was moderate ($r$ = -0.55 for $P_{an}$; $r$ = -0.71 between 1/elevation and $P_{min}$).

The topographic variables used were aspect and slope (Table 1). Aspect was measured as degrees from north. These variables were derived from the digital elevation model.

We performed image analysis on remotely sensed imagery, acquired in March 2003 by the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER), to identify different forest types in relation to their degree of disturbance and to calculate different vegetation indices. We georeferenced the image using 43 control points derived from vector maps of roads and rivers, obtained from the Native Vegetation Survey (CONAF et al., 1999), resulting in an estimated error of less than one pixel. We atmospherically corrected the image using the dark pixel subtraction method and features such as water bodies (Mather, 1999).

We performed a supervised land cover classification (Aplin, 2004) of the image using the maximum likelihood algorithm (Lillesand et al., 2004). Four different types of vegetation structure (VST) were identified in relation to human disturbance: open shrubland (VST1), dense shrubland (VST2), arborescent shrubland (VST3) and forest (VST4), which includes old-growth forest, secondary forest and an intermediate condition(Altamirano et al., 2010). Other land cover types were excluded from the analyses and predictions reported herein. Training sites were selected using different sources of information such as vegetation maps, aerial photographs from 2003 and field visits conducted between 2004 and 2006. The overall accuracy of the supervised classification was 92%. The lowest accuracy was obtained for shrubland and secondary forests; this was because of spectral confusion between these two classes. The pre-processing and classification of remotely sensed data were performed using the ERDAS Imagine 8.4® software (ERDAS 1999).

In addition, we calculated two spectral indices: the normalised difference vegetation index (NDVI) and the normalised difference infrared index (NDII). The NDVI was calculated as the difference between the near-infrared and red reflectances divided by their sum, which represents a measure of vegetation productivity (Turner et al., 2003; Aplin, 2005). The NDII was calculated as the difference between the near-infrared and mid-infrared reflectances divided by their sum, which is related to the hydric stress (Bannari et al., 1995; Gao, 1996). We did not use spectral bands from the ASTER image because they were both highly correlated with, and less interpretable than, NDVI and NDII ($|r| > 0.85$, $P < 0.001$).

### *2.4 Statistical analyses*

To inform subsequent analysis, we used variance partitioning to explore the independent and joint contribution of all available explanatory variables, including all 19 WorldClim variables and elevation ('climatic' category), the spectral bands from the ASTER image and derived land-cover variables ('land cover') and slope and aspect ('topographic') in accounting for spatial variation in woody species richness. The partition of the variance is derived from partial redundancy analyses (RDA) and was used to determine the proportions that could be attributed to the single and combined effects of explanatory variables (Legendre and Legendre, 1998), using adjusted $R^2$ ratios (Peres-Neto et al., 2006). These analyses were computed using the 'vegan' library (Oksanen et al., 2008) of the R environment (R Development Core Team, 2009).

The results of the variance partitioning informed the selection of variables for modelling, in which we used multiple regression to develop models to predict woody species richness in the study area. Most regression analysis was performed with the S-PLUS 6.0 software (Insightful Corporation, 2001); spatial analysis was conducted using SAM (Rangel et al., 2006). Before performing multiple regression, we examined the correlation matrix and the hierarchical cluster analysis. We noted explanatory variables that were highly correlated ($|r| > 0.6$) and the clusters of such correlated variables, which might therefore lead to problems associated with multicollinearity. We used the same mix of theoretical and statistical considerations as described above for selection of WorldClim variables, to determine which of all the explanatory variables could be combined in any one model. We also calculated the variance inflation factor (VIF) for all terms in all multiple regression models, to quantify any remaining multicollinearity, using a maximum allowable level of VIF of 4. In addition, we examined the correlations between species richness and all selected explanatory variables (Table 1). Further, because relationships between species richness and environmental variables are often curvilinear (Austin, 1980) and interactive (Francis and Currie, 2003), we included quadratic and cubic terms in the models, as well as some interactions expected from previous research (e.g. between temperature and water variables).

Our modelling procedure was step-wise and manual (Murtaugh, 2009), using a combination of model building and model simplification. We produced the first model by building from the null model (the mean), adding terms in order of explanatory power, defined as the change in residual sum of squares resulting from the addition of individual terms to the current model. Model building finished when no more terms were both significant and reduced AIC (Akaike Information Criterion) (Venables and Ripley, 2002; Anderson and Burnham, 1999). We then used a similar procedure, but with different starting variables (chosen according to variable type and variance accounted for) and different orders of addition. We also produced a series of models by simplifying from various maximal models (Crawley, 2002). It was necessary to simplify from more than one maximal model because the sample size of 82 did not support highly complex models. We compared all models obtained statistically using P-values, AIC and the proportion of variation accounted for ($R^2$). We also used 'Model Selection and Multi-model Inference' in SAM to rank over 16,000 possible models by AICc and AIC-weights and to calculate the 'importance' of each variable across all the models. This combination of model fitting approaches allowed confidence in the robustness of the results. Selection of the 'best' models was based on both theoretical criteria (plausibility, generality, simplicity, parsimony) and statistical strength (O'Brien et al., 2000).

We used Moran's I to evaluate the spatial autocorrelation of the residuals of the fitted models. Finding no residual spatial autocorrelation means that we can assume the significance values to be reliable, and that we do not need to introduce the further uncertainties (coefficient instability) associated with spatial regression (Bini et al., 2009). We checked the model residuals for normality using histograms and the Kolmogorov–Smirnov test. We assessed homoscedasticity via residual plots, and we mapped model residuals to examine their spatial patterning. To validate the predictive power of the models, we used a bootstrap approach for each model. This method generates new samples with replacement from the original sample, allowing a quantification of the error introduced by data uncertainty as well as model estimation procedure (Quinn and Keough, 2003).

We used the resulting regression models to predict current species richness values for parts of the study area where there were no field plots. This was done for every pixel in the ASTER imagery and involved using the coefficients from the models and substituting the applicable values for the explanatory variables, to calculate predicted current species richness.

### *2.5 Climate change scenario*

We used the coefficients derived from modelling current woody species richness to predict future species richness across the study area, using climatic data obtained for a climate-change scenario. Climate scenarios are guesses of future climates, based on assumptions about future emissions of greenhouse gases and other pollutants, and obtained via general circulation models, such as CCCMA, HadCM3 and CSIRO. We used projected climate data for 2050, from the Hadley Centre's climate model (HadCM3 Worldclim implementation) under the low (B2a) CO2 emissions scenarios (Zhang and Nearing, 2005), obtained from WorldClim. We used scenario B2a because it emphasizes more regionalized solutions to economic, social, and environmental sustainability (Zhang and Nearing, 2005).

### *2.6 Conservation value*

To analyse conservation value we produced categorized maps of the predicted current woody species richness into three levels: high (> 8 species), medium (5–8 species) and low (< 5 species). When examining tree species richness, we used > 6, 4–6 and < 4 species respectively. This was done for all pixels of the ASTER image (with a spatial resolution of 15 m) that had land cover in one of the categories VST1, VST2, VST3 and VST4. Pixels classified as other categories were excluded from further consideration. Predicted future species richness was categorized using the same criteria and results were compared in terms of: (1) forest area occupied by each conservation value category now and in 2050; (2) overall forest area that will change to a different conservation value category by 2050; and (3) forest area in current natural protected areas assigned to different conservation value categories now and in 2050.

## 3. RESULTS

We recorded 67 woody species (28 trees and 39 shrubs) in the field plots (Appendix 1), with a mean (± S.D.) number of species per plot of 8.3 (± 3.1), ranging from 2 to 16. We found significantly lower mean tree and overall (tree + shrub) species richness in VST1 (open shrubland) than in the other three categories (ANOVA, $P = 0.006$ and 0.017 respectively), but no differences between VST2 (dense shrubland), VST3 (arborescent shrubland) and VST4 (forest). Therefore for regression modelling we re-categorized the forest structure variable into two categories: VST1 and closed canopy (VST2, VST3 and VST4 combined) because this is more robust and parsimonious (Crawley, 2002). Interestingly, there was no significant difference between VST categories in either tree or shrub abundance.

The strongest single-variable correlates of both tree and overall species richness in the 82 field plots were $T_{min}$, $P_{min}$ and ELEV (Table 1). None of the explanatory variables in Table 1 correlated with shrub species richness at the 1% significance level. At the 5% level only NDVI and NDII were significant, both correlating weakly and negatively with shrub species richness (Table 1); this effect was driven by the open shrubland ($r = -0.50$ for both NDVI and NDII) and was not significant for the denser woody vegetation categories. The difference in shrub diversity between the different VST categories was also not significant. Basal area of woody plants correlated negatively with shrub species richness ($r = –0.31$, $P = 0.005$) and band 5 of the ASTER image correlated positively ($r = 0.36$, $P = 0.0009$). Band 5 and basal area represented the strongest statistical model, with neither NDVI nor NDII significantly improving it, but this model only accounted for 18% of the variation, had non-normal residuals and contained potential circularity. Overall, then, we were unable to produce a satisfactory model of shrub species richness, which also did not correlate significantly with tree species richness (Table 1). Models of overall woody species richness were all qualitatively identical to, but quantitatively weaker than, those for tree species richness; they were driven by the tree species richness pattern, with shrub species richness effectively adding noise. We therefore focus on reporting the results for tree species richness.

Minimum temperature ($T_{min}$) correlated positively and ELEV negatively with tree species richness, both consistent with greater energy allowing more species. The correlation between tree species richness and $P_{min}$, however, was negative, both singly and when included in multiple-regression models. Both log and inverse transformations of ELEV improved the linearity of its association with tree species richness, 1/ELEV the more so, which also improved the normality of regression residuals compared with models using ln(ELEV). Using 1/ELEV made the relationship with tree species richness positive and increased the strength of the bivariate correlation to $r = 0.66$.

In variance partitioning, topographic, climatic, and land-cover variables accounted for 2%, 52% and 7%, respectively, of the adjusted variance of woody species richness (Fig. 2). Overlap between the categories in variance accounted for was minimal (Fig. 2), supporting our contention that elevation acts as a climatic, not topographic, variable in our dataset.

### *3.1 Predictive models of species richness*

$T_{min}$ correlated strongly with 1/ELEV (r = 0.91), so only one of the two variables could be used in the same regression model. We developed models independently using both variables. In all cases, as with simple correlation, 1/ELEV gave a closer fit with woody species richness (Model 1, Table 2a). However, for predicting species richness for the year 2050 we preferred models featuring $T_{min}$ instead of 1/ELEV (model 2a and b). Temperature has a direct physiological effect on species performance, while elevation is a surrogate variable for a mixture of influences, but driven by temperature (Guisan and Zimmermann, 2000; Pausas and Austin, 2001), so temperature is preferred on theoretical grounds. Most of the effect of elevation is related to temperature and precipitation, and with climatic changes over the next 40 years, the regression coefficients derived from current conditions for elevation are not applicable to prediction for 2050. Therefore for prediction of future species richness, and for comparison of the conservation value of protected areas now and in the future, we used the best models that were based on $T_{min}$ (Models 2a and 2b; Table 2b,c). VST was considered appropriate for 2050 because its main determinant is human activity (disturbance); its inclusion in Model 2a,b assumes no change in the disturbance regime during the first half of the 21st century.

The 'best' regression models (Models 1 and 2a,b) were selected on the grounds of theoretical plausibility, simplicity and statistical strength (secondary to the other two). These best models included two alternative models based on $T_{min}$: Model 2a and Model 2b (Table 2). These were statistically indistinguishable and both were ecologically plausible. The strongest effects are the same in both models, and in a reduced model with only VST and $T_{min}$. The first is a strong increase in tree species richness with increased $T_{min}$, of approximately 1 species per 1°C. The second is approximately 1.5 fewer species in open shrubland than the other vegetation types. Thus the core of the models is the same; they differ in the final variable included, which in each case only accounts for an additional 4% of the variance (approx.). In Model 2a this is $T_{seas}$, with a decrease of approximately 6 tree species for every 1°C increase in seasonality (measured as the standard deviation; Table 1); this is ecologically plausible. In Model 2b the third variable is $P_{min}$, with a decrease of approximately 1 tree species for every 3 mm increase in driest-month precipitation. Exploring this negative effect further (see also Table 1), we found a negative correlation (r = –0.40) between $P_{min}$ and overall tree abundance, suggesting a competition or crowding effect, coupled with a more individuals effect (positive correlation, r = 0.54, between tree abundance and tree species richness). However, using data for basal area and average tree diameter for all plots in the dataset, we found no correlation between either variable and $P_{min}$. Nor did either basal area or average tree diameter correlate with tree species richness. So, while $P_{min}$ could be measuring a competition effect, we are far from certain that it does indeed do so, or whether it is measuring another biologically meaningful effect such as inhibition of seed germination or seedling survival (Donoso, 1994), or whether the apparent effect is due to correlation with other important biological influences. Because $P_{min}$ and $T_{seas}$ are positively correlated (r = 0.58) and neither is even close to significant when the other is in the model, Models 2a and 2b are straight alternatives and we are unable satisfactorily to reject one in favour of the other. Therefore our predictive modelling was based on average predictions from the two models, hereafter referred to collectively as Model 2. This averaging of predictions, a form of ensemble forecasting (Araújo and New, 2007), should also increase the robustness of the predictions.

All models presented in Table 2 are statistically significant ($P < 0.0001$) and all rely on few explanatory variables, reducing the likelihood of artefact, which is particularly important when predicting future species richness. All the models met assumptions of homoscedasticity and normality of residuals. For all the models, Moran's I values for residuals were not significant for any of the short distance classes (Fig. 3), indicating no inflation of degrees of freedom resulting from spatial autocorrelation, and the absence of intrinsic autocorrelation that could disturb the Type I error rates and the coefficient estimates. In other words, the regression models have accounted for the spatial autocorrelation present in the species richness data. This also means that our predictive model is of the type considered the best for predicting responses to climate change by Algar et al. (2009): they concluded that the most accurate predictions of shifts in species diversity in response to climate change are obtained via the single best richness–environment regression model, after accounting for the effects of spatial autocorrelation. Further, our model has the advantage that the spatial autocorrelation is accounted for via ordinary least-squares regression, so that there is no chance of real effects being 'corrected for' while removing spatial autocorrelation in spatial regressions.

### *3.2 Predicted species richness*

Present-day woody species richness was predicted for the whole study area using Model 1 (Fig. 4a) and Model 2 (Fig. 4b). Model 2 predicted slightly higher species richness on average than Model 1, but the spatial patterns were very similar. The areas of higher predicted richness at this scale (250 m$^2$) are concentrated mainly in the western locations of the study area and in valleys, at lower elevation and higher temperatures. These areas are dominated by shrubland and arborescent vegetation. The two protected areas in the study area have relatively low levels of predicted current species richness (Fig. 4a,b).

Our map predictions for 2050 (Fig. 5a) suggest that the higher ground in the east of the study area will increase in tree species richness, while the lower ground in the west will decrease. Thus the species-richness gradient across the study area is expected to persist but weaken (compare Fig. 5a with Fig. 4b) with climate change. Overall, of the 1296 km$^2$ for which we made predictions, a net loss of species was predicted for 490 km$^2$ (38%) and a net gain for 698 km$^2$ (54%), the remainder staying approximately constant. Using our categories for conservation value, 58% of the pixels (each 225 m$^2$) were predicted by Model 2 to have present-day woody species richness in the low category (0–3 species), with 31% having more than six species (Fig. 6a). Of all the pixels, 34% were predicted to change from low to medium conservation value, while 16% were predicted to change from high to medium (Fig. 6a).

Only 29.0 km² of the land currently designated as protected areas is covered by woody vegetation, as judged by our analysis of the ASTER image. All of this area is currently in the low conservation priority (value) category, according to Model 2. Our map predictions suggest that 8.6 km² (30%) of the protected area will improve to the medium category by 2050, the rest remaining 'low' (Fig. 6b).

## 4. DISCUSSION

We found that the highest tree species richness occurs in low and medium elevation areas, with the highest minimum temperatures, and where there is relatively dense woody vegetation cover. The protected areas within the study area contain very low tree species richness and our modelling suggests that the areas of highest tree conservation value are far from the currently protected areas. Our predictions for changed climate indicate reduced tree diversity where it is currently high and increased diversity where it is currently low. The currently protected areas may therefore slightly increase in tree conservation value over the next 40 years, but will still be relatively low in diversity. Meanwhile, the areas of greatest species richness are predicted to suffer losses, thereby degrading in conservation value. The resulting predominance of areas of relatively average conservation value suggests a need for the conservation of greater areas of forest. Greater connectivity of patches of woody vegetation may also be important. Although the protected areas may be important for species other than woody plants, their continued low value for tree species conservation is of great conservation concern because Chile has more than half of the temperate forests in the southern hemisphere (Donoso, 1994), because of the uniqueness of these forests (Smith-Ramírez, 2004), and because of the high levels of threat to these forests (Dinerstein et al., 1995).

These concerns about tree conservation that arise from our species richness modelling are backed up by our field observations of threatened species within our study plots. We recorded four threatened species, all of which are trees: *Nothofagus glauca, Austrocedrus chilensis*, *Beilschmiedia berteroana* and *Cytronella mucronata*. These species have a restricted distribution and highly specific habitats (Hechenleitner et al., 2005). Migration capabilities for these species under climate change may well be limited. *N. glauca* (by far the most common of the four in our field plots) is restricted largely to the Maule region and is found mainly in intermediate elevation sites (Hechenleitner et al., 2005), so may not be much affected by climate change. However, *B. berteroana* may be negatively affected by climate change because its habitat is coincident with sites where species richness is expected to decrease. To aggravate the problem, only 8 sub-populations of this species have been identified in the country (Hechenleitner et al., 2005). The other two threatened species have wider distributions and may therefore be less vulnerable to climate change. An additional consideration is that many mountain plants reproduce vegetatively and grow slowly; consequently they are likely to take a long time to disperse into new, climatically suitable areas (Trivedi et al., 2008).

There are continuing threats to temperate Andean forests and their biodiversity, such as hydroelectric-power projects and the rapid growth of the exotic plantations industry (Lara et al., 2003). In recent years, exotic plantations have expanded specifically in the south-central temperate forests of Chile (Echeverría et al., 2006) because of the growth of the pulp and wood industry (Lara et al., 2003). These developments may facilitate the establishment and invasion of alien species, which may also be enhanced by predicted rises in the frequency of natural disturbances (e.g. forest fires), and ultimately reduce the cover of native vegetation (Pickering et al., 2008). Studies in Chile have shown that alien species are moving into native forests in national parks in mountain areas (Pauchard and Alaback, 2004). Given these various forms of disturbance in the study area, our results suggest that protected areas are important for conservation: we found that the most disturbed areas of woody vegetation have the lowest tree species richness, with no accompanying increase in shrub species richness. This suggests that one way of improving conservation is to minimize disturbance.

Our predictions, by necessity, assumed no change in protection/disturbance regime (land-cover type). Nonetheless, our coefficients for the disturbance variable (VST) can be used to explore future scenarios in which disturbance regimes do change in prescribed ways. Our assumption of no increase in disturbance may be optimistic, unless the protected area network is modified, or unless parts of the landscape not in protected areas are managed for woody plant conservation. We consider that both strategies should be implemented. New protected areas should be created, and because our prediction maps indicate that current high-priority sites are coincident with high-priority sites in 2050, we suggest that sites that have high tree species richness now should be targeted for national protection. In the study area, these sites include river valleys, and so this should help to ensure reliable supplies of clean water downstream. Such targeting is important: Babcock et al. (1997) demonstrated that enrolling land into a conservation programme on the basis of the lowest cost of purchasing land (as has been the case for many of Chile's protected areas) is a far less efficient use of taxpayers' money than targeting land on the basis of the cost–benefit ratio of that land. The application of newer approaches to protected area design could help stakeholders find designs that simultaneously maximize ecological, societal and industrial goals (Gonzales et al., 2003). Planning tools such as Sites (Davis et al., 1999) and Marxan (Game and Grantham, 2008) represent good examples. Of high relevance to areas not formally protected, in 2008 Chile passed a new law that supports native forest management and biodiversity conservation. This law gives economic incentives to landowners to engage in biodiversity conservation. Again, the law can target high-priority conservation sites, as indicated by our prediction maps, for improved effectiveness (Macmillan et al., 1998). Subsidies to encourage landowners to manage their land in ways that increase the provision of non-market benefits may also be appropriate (Van der Horst, 2007).

Our research represents a starting-point, but more work is needed to inform conservation in the temperate Andean forests. First, our model should be seen as a tool, for addressing urgent conservation issues, that should be assessed, discussed and evaluated further. Also, we have not investigated individual species' requirements; for example, species-specific conservation measures for endemic and threatened species, including ex situ conservation, may be required. Woody species may have differential abilities to cope with climate change (Parolo and Rossi, 2008), and habitat connectivity may be important in enabling some to migrate. Species usually differ in their habitat requirements and habitat mosaics may be appropriate in meeting each species' needs (Drechsler et al., 2007). In this context, important future challenges for biodiversity conservation research are to investigate beta diversity and determine how much habitat heterogeneity is needed to maintain species diversity at coarser scales than in our study. Furthermore, we used climatic and topographic data that are widely used for this sort of analysis (WorldClim and SRTM). However, some environmental data sets may be less useful in some areas (i.e. rugged, remote and steep terrain) and scales (Peterson and Nakazawa, 2008). Therefore, further corroboration and testing of other source information will be necessary.

Our study adds to knowledge and understanding of species richness patterns and their correlates. Tree species richness correlated most strongly with temperature-related variables (elevation and minimum temperature), which is common at broad scales but less common at the finer scale of our study (Field et al., 2009). This may be because we sampled quite a large altitudinal range, and fits with the findings of Bhattarai & Vetaas (2003). The closer match, in terms of scale of measurement, between elevation and species richness, compared with climatic variables, probably explains the stronger correlation of species richness with elevation. The relatively small amount of variation accounted for by $P_{min}$ and $T_{seas}$ is probably due, in large part, to the fact that both vary little in the data for our study plots (Table 1). Despite their coarse scale of measurement, climatic variables performed well in accounting for tree species richness patterns, relative to the fine-resolution variables such as slope, aspect and NDVI. This supports the contention (Cayuela et al., 2006a) that broad-scale patterns (e.g. Hawkins et al., 2003; Field et al., 2005) can be replicated across altitudinal gradients at finer spatial scales. In addition, there was a positive correlation ($r = 0.54$) between tree abundance and tree species richness in our field plots; adding tree abundance to any of the final tree species richness models led to about a 5% increase in variation accounted for. This suggests a 'more individuals' effect, whereby more individuals tend to be associated with more species (Srivastava & Lawton, 1998; Currie et al., 2004). However, this was of little use for modelling because our best model of tree abundance contained only $T_{min}$ and only accounted for 26% of the variation.

Our best tree species richness model accounts for approximately 50% of the variance, which is quite typical for this scale (Field et al., 2009). Small-grain species richness is hard to predict, as it depends on so many interacting factors and chance events (Diamond, 1988; Whittaker et al., 2001; Willis and Whittaker 2002), and small-grained studies typically account for less than 50% of the variation in species richness, even at geographic extents spanning hundreds of km (Field et al., 2009). Not surprisingly, therefore, even our best models left much of the variation unaccounted for, suggesting that other, unmeasured factors also influence woody species richness in the study area. Hydrological, soil factors and biotic interactions might account for some of the residual variation. This is particularly relevant to shrub species richness, which did not correlate strongly with any of our measured variables, and which we could not model well enough to allow prediction. The strongest correlation with shrub species richness was a negative one with basal area, suggesting that shading by trees may reduce shrub diversity. This accords with the recent findings by Oberle et al. (2009) that understorey plant species richness in field plots of similar size to ours correlates much less with regional productivity-related variables than does tree species richness, and that canopy density partly controls shrub species richness at this scale.

Overall, our research contributes to understanding of globally important temperate Andean forests, and represents a step towards targeting conservation of the forests more effectively.

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**APPENDIX 1.** List of tree species and shrubs sampled in the study area. Nomenclature follows the Index Kewensis, except for those cases in which no record was found, for which the Gray Herbarium Card Index (http://www.ipni.org) was used.

| Species | Family |
|---|---|

| | |
|---|---|
| Trees | |
| *Acacia caven* (Molina) Molina | Leguminosae |
| *Aextoxicon punctatum* Ruiz & Pav. | Aextoxicaceae |
| *Austrocedrus chilensis* (D.Don ) Pic.Serm. & M.P.Bizzarri | Cupressaceae |
| *Beilschmiedia berteroana* (Gay) Kosterm. | Lauraceae |
| *Crinodendron patagua* Molina | Elaeocarpaceae |
| *Cryptocarya alba* (Molina) Looser | Lauraceae |
| *Citronella mucronata* (Ruiz & Pav.) D.Don | Icacinaceae |
| *Dasyphyllum diacanthoides* (Less.) Cabrera | Asteraceae |
| *Drimys winteri* J.R.Forst. & G.Forst. | Winteraceae |
| *Embothrium coccineum* J.R.Forst. & G.Forst. | Proteaceae |
| *Gevuina avellana* Molina | Proteaceae |
| *Kageneckia oblonga* Ruiz & Pav. | Rosaceae |
| *Laureliopsis philippiana* (Looser) Schodde | Monimiaceae |
| *Laurelia sempervirens* (Ruiz & Pav.) Tul. | Monimiaceae |
| *Lithraea caustica* Hook. & Arn. | Anacardiaceae |
| *Lomatia dentata* R.Br. | Proteaceae |
| *Lomatia hirsuta* (Lam.) Diels | Proteaceae |
| *Luma apiculata* (DC.) Burret | Myrtaceae |
| *Luma chequen* F.Phil. | Myrtaceae |
| *Maytenus boaria* Molina | Celastraceae |
| *Nothofagus alpina* (Poepp. & Endl.) Oerst. | Fagaceae |
| *Nothofagus dombeyi* (Mirb.) Oerst. | Fagaceae |
| *Nothofagus glauca* (R.Phil) Krasser | Fagaceae |
| *Nothofagus obliqua* (Mirb.) Oerst. | Fagaceae |
| *Nothofagus pumilio* (Poepp. & Endl.) Krasser | Fagaceae |
| *Persea lingue* (Miers ex Bertero) Nees | Lauraceae |
| *Peumus boldus* Molina | Monimiaceae |
| *Quillaja saponaria* Molina | Rosaceae |
| Shrubs | |
| *Acrisione denticulata* (Hook. & Arn.) B.Nord. | Asteraceae |
| *Aristotelia chilensis* Stuntz | Elaeocarpaceae |
| *Azara celastrina* D. Don | Flacourtiaceae |
| *Azara dentata* Ruiz & Pav. | Flacourtiaceae |

| | |
|---|---|
| *Azara petiolaris* (D.Don) I.M.Johnst. | Flacourtiaceae |
| *Azara serrata* Ruiz & Pav. | Flacourtiaceae |
| *Baccharis concava* Pers. | Asteraceae |
| *Baccharis linearis* (Ruiz & Pav.) Pers. | Asteraceae |
| *Baccharis salicifolia* (Ruiz & Pav.) Pers. | Asteraceae |
| *Berberis chilensis* Gill. | Berberidaceae |
| *Berberis grevilleana* Gill. | Berberidaceae |
| *Berberis microphylla* G.Forst. | Berberidaceae |
| *Buddleja globosa* C.Hope | Buddlejaceae |
| *Cestrum parqui* L'Hér. | Solanaceae |
| *Colletia spinosissima* J.F.Gmel. | Rhamnaceae |
| *Collihuaja sp 1* | Euphorbiaceae |
| *Discaria chacaye* (G.Don) Tortosa | Rhamnaceae |
| *Ephedra chilensis* C.Presl | Ephedraceae |
| *Undetermined sp1* | Escalloniaceae |
| *Fabiana imbricata* Ruiz & Pav. | Solanaceae |
| *Gochnatia foliolosa* D.Don ex Hook. & Arn. | Asteraceae |
| *Maytenus magellanica* Hook.f. | Celastraceae |
| *Mutisia spinosa* Hook. & Arn. | Asteraceae |
| *Myoschilos oblongum* Ruiz & Pav. | Santalaceae |
| *Myrceugenia ovata* O.Berg | Myrtaceae |
| *Pernettia mucronata* Gaudich. ex G.Don | Ericaceae |
| *Podanthus mitiqui* Lindl. | Asteraceae |
| *Proustia cuneifolia* D.Don | Asteraceae |
| *Undetermined sp 2* | Rhamnaceae |
| *Ribes cucullatum* Hook. & Arn. | Grossulariaceae |
| *Ribes magellanicum* Poir. | Grossulariaceae |
| *Schinus montanus* Engl. | Anacardiaceae |
| *Schinus patagonicus* (Phil.) I.M.Johnst. ex Cabrera | Anacardiaceae |
| *Senna sp 1* | Fabaceae |
| *Schinus polygamus* (Cav.) Cabrera & I.M.Johnst. | Anacardiaceae |
| *Undetermined sp 3* | Solanaceae |
| *Sophora macrocarpa* Sm. | Leguminosae |

| | |
|---|---|
| *Undetermined sp 4* | *Undetermined* |
| *Undetermined sp 5* | *Undetermined* |

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## FIGURE CAPTIONS

Figure 1. Map of the study area in the Andean range.

Figure 2. Venn diagram of the partition of the variation of tree species richness for climatic, topographic and land-cover variables. Table 1 shows which of the key variables were included in each category; other WorldClim data were included as 'climatic' and other variables derived from ASTER imagery were included as 'land cover'. The rectangle represents the total variance of tree species richness while each circle represents a given group of explanatory variables. The adjusted $R^2$ (expressed as % of the variance in tree species richness) is presented for each part of the Venn diagram. Intersections between circles represent the fraction of the variance of tree species richness jointly accounted for; if missing this fraction does not differ significantly from 0.

Figure 3. Correlograms for tree species richness, fitted values and residuals of the 'best' regression models: (a) Model 1, (b) Model 2a, (c) Model 2b. Equal distance classes; only classes with $n > 100$ shown. See Table 2 for model specifications ($n=82$ cells).

Figure 4. Map of predicted current woody species richness in 225 $m^2$ pixels. A. current tree species richness according to Model 1; B. current tree species richness according to Model 2 (average of predictions from Models 2a and 2b); C. current conservation priority (value) category, as defined by tree species richness predicted by Model 2 (low = <4, medium = 4–6, high = >6). No colour means no prediction because the pixel is not currently classed as any of the land-cover types in our analyses. See Table 2 for model specifications.

Figure 5. Map of predicted tree species richness in 2050, in 225 $m^2$ pixels. A. tree species richness in 2050 according to Model 2 (average of predictions from Models 2a and 2b); B. change in tree species richness from now to 2050, according to Model 2; C. uncertainty for 2050 tree species richness predictions (absolute difference between the predictions of Models 2a and 2b); D. conservation priority (value) category in 2050, as defined by species richness predicted by Model 2 (low = <4, medium = 4–6, high = >6). No colour means no prediction because the pixel is not currently classed as any of the land-cover types in our analyses. See Table 2 for model specifications.

Figure 6. Current forest area by conservation priority (value) category (horizontal axis labels), and how these conservation priorities will change in the year 2050 (shading), according to Model 2 (average of predictions from Models 2a and 2b). A) in the study area. B) in the current protected areas. See Table 2 for model specifications.

Table 1. Climatic, topographic and land-cover variables used to model the spatial variation in woody species richness in the study area. Values given are for the 82 field plots. (Code = abbreviation used, St dev = standard deviation, r(WSR) = Pearson's correlation coefficient for the relationship with woody species richness, r(TSR) = correlation with tree species richness, r(SSR) = correlation with shrub species richness, CV = coefficient of variation.)

| Variable and unit of measurement | Code | Mean | St dev | Min | Max | r (WSR) | r (TSR) | r (SSR) |
|---|---|---|---|---|---|---|---|---|
| *Response variable* | | | | | | | | |
| Woody species richness | n.a. | 8.3 | 3.1 | 2 | 16 | n.a. | 0.83 *** | 0.63 *** |
| Tree species richness | n.a. | 5.0 | 2.4 | 0 | 11 | 0.83 *** | n.a. | 0.10 n.s. |
| Shrub species richness | n.a. | 3.3 | 1.7 | 0 | 8 | 0.63 *** | 0.10 n.s. | n.a. |
| *Climatic variables* | | | | | | | | |
| Elevation (m) – untransformed | ELEV | 674 | 292 | 288 | 1603 | –0.50 *** | –0.63 *** | –0.03 n.s. |
| Minimum temperature of coldest month (ºC) | $T_{min}$ | 0.31 | 1.29 | –3.0 | 2.2 | 0.50 *** | 0.60 *** | 0.05 n.s. |
| Temperature seasonality (st dev) | $T_{seas}$ | 4.54 | 0.09 | 4.39 | 4.74 | –0.28 * | –0.42 *** | 0.09 n.s. |
| Annual precipitation (mm) | $P_{an}$ | 1080 | 76 | 853 | 1260 | 0.22 * | 0.40 *** | –0.16 n.s. |
| Precipitation of driest month (mm) | $P_{min}$ | 15.8 | 1.6 | 11 | 18 | –0.47 *** | –0.53 *** | –0.11 n.s. |
| Precipitation seasonality (CV x 100) | $P_{seas}$ | 83.9 | 1.9 | 78 | 88 | 0.33 ** | 0.44 *** | –0.02 n.s. |
| *Topographic variables* | | | | | | | | |
| Aspect (degrees from north) | ASPE | 83.2 | 55.7 | 1 | 180 | 0.02 n.s. | 0.17 n.s. | –0.21 n.s. |
| Slope (degrees) | SLOP | 14.2 | 8.5 | 1 | 38 | –0.18 n.s. | –0.11 n.s. | –0.17 n.s. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Land-cover variables* | | | | | | | | |
| Normalised difference vegetation index | NDVI | 0.678 | 0.196 | 0.056 | 1.000 | –0.13 n.s. | 0.01 n.s. | –0.26 * |
| Normalised difference infrared index | NDII | 0.719 | 0.064 | 0.455 | 0.825 | –0.23 * | –0.11 n.s. | –0.26 * |
| Vegetation structure[1] | VST | n.a | n.a. | 1 | 4 | n.a. | n.a. | n.a. |

[1] Categorical data: 4 categories (1 = open shrubland, 2 = dense shrubland, 3 = arborescent shrubland, 4 = forest)

*P < 0.05, ** P < 0.01, *** P < 0.001, n.s. = not significant

n.a. = correlation is not applicable.

Table 2. 'Best' models for predicting spatial variation in tree species richness in the study area: (a) Model 1 – model for predicting current species richness (best model using all available variables); (b) Model 2a – model for predicting future species richness and for comparison of predictions; (c) Model 2b – alternative model for predicting future species richness and for comparison of predictions. D.f. = degrees of freedom; VIF = variance inflation factor; $R^2$ = proportion of the variance accounted for (tested by deletion from the model); AICc = Akaike Information Criterion; RMSE (root mean square error) = square root of the error variance. All predictions are for plots of 250 m². See Table 1 for full variable names and units.

| Model | Coefficient | D.f. | VIF | t-value | p | $R^2$ | AICc |
|---|---|---|---|---|---|---|---|
| Null Model | | 81 | | | | | 383.5 |
| | | | | | | | |
| (a) Model 1 (RMSE: 3.0) | | | | | | | |
| Intercept | –0.34 | | | –0.53 | 0.597 | | |
| 1/ELEV(in km) | 2.35 | 1 | 1.00 | 8.07 | 0.000 | 0.41 | 376.7 |
| VST | 1.59 | 1 | 1.00 | 3.33 | 0.001 | 0.07 | 338.2 |
| Overall model | | 2 | | | 0.000 | 0.50 | 329.6 |
| | | | | | | | |
| (b) Model 2a (RMSE: 3.3) | | | | | | | |
| Intercept | 30.18 | | | 2.79 | 0.007 | | |
| VST | 1.54 | 1 | 1.01 | 3.09 | 0.003 | 0.07 | 344.5 |
| $T_{min}$ | 0.93 | 1 | 1.21 | 5.40 | 0.000 | 0.20 | 361.0 |
| $T_{seas}$ | –5.88 | 1 | 1.20 | –2.47 | 0.017 | 0.04 | 341.2 |
| Overall model | | 3 | | | 0.000 | 0.47 | 337.3 |
| | | | | | | | |
| (c) Model 2b (RMSE: 3.3) | | | | | | | |
| Intercept | 9.51 | | | 2.90 | 0.005 | | |
| VST | 1.51 | 1 | 1.01 | 3.02 | 0.003 | 0.06 | 344.8 |
| $T_{min}$ | 0.81 | 1 | 1.66 | 3.98 | 0.000 | 0.11 | 350.9 |
| $P_{min}$ | –0.38 | 1 | 1.65 | –2.31 | 0.024 | 0.04 | 341.2 |
| Overall model | | 3 | | | 0.000 | 0.46 | 338.0 |

Figure 1

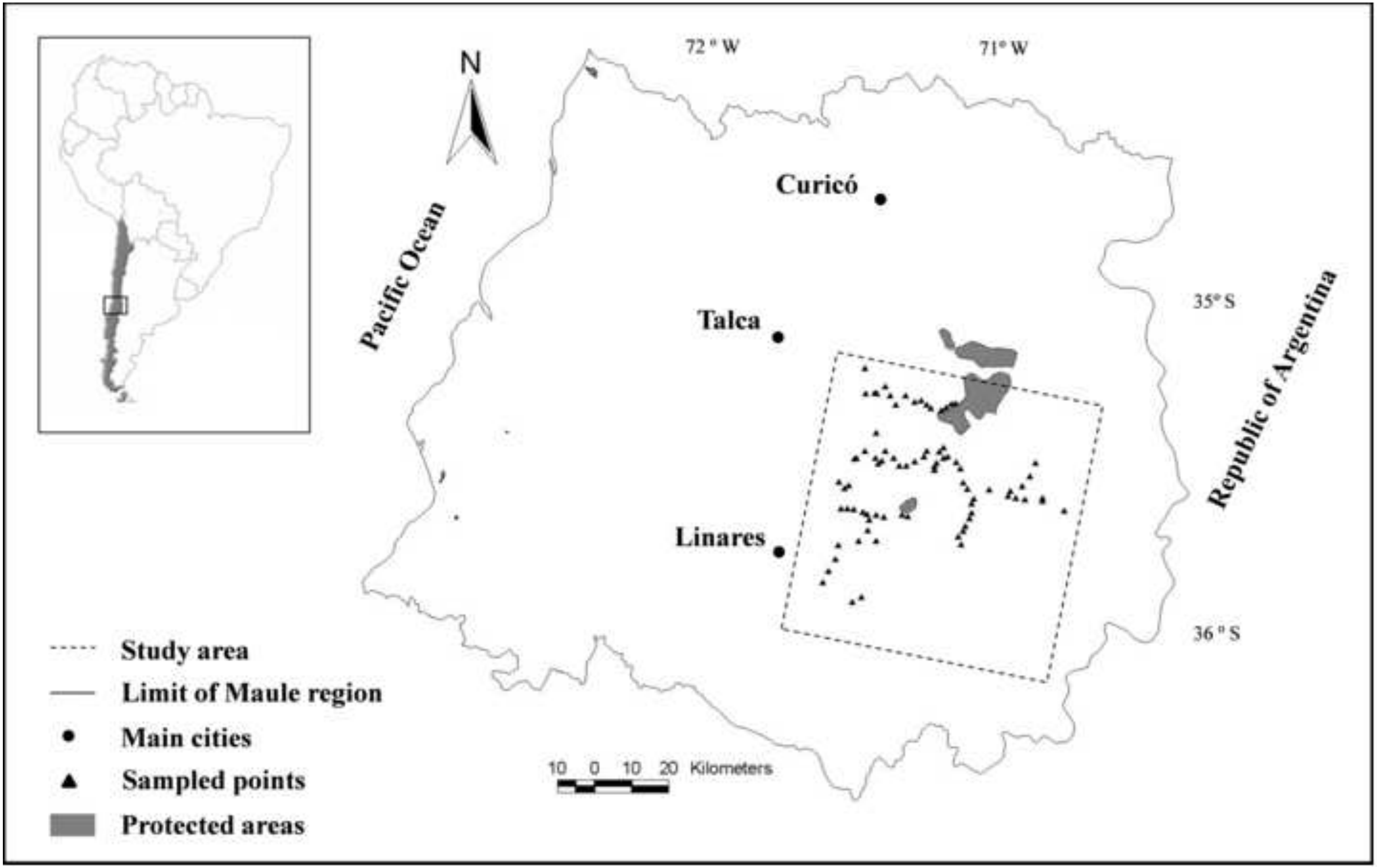

N
72 ° W
71° W
Pacific Ocean
Curicó
Talca
Linares
35° S
36 ° S
Republic of Argentina
10 0 10 20 Kilometers
Study area
Limit of Maule region
Main cities
Sampled points
Protected areas

Figure 2

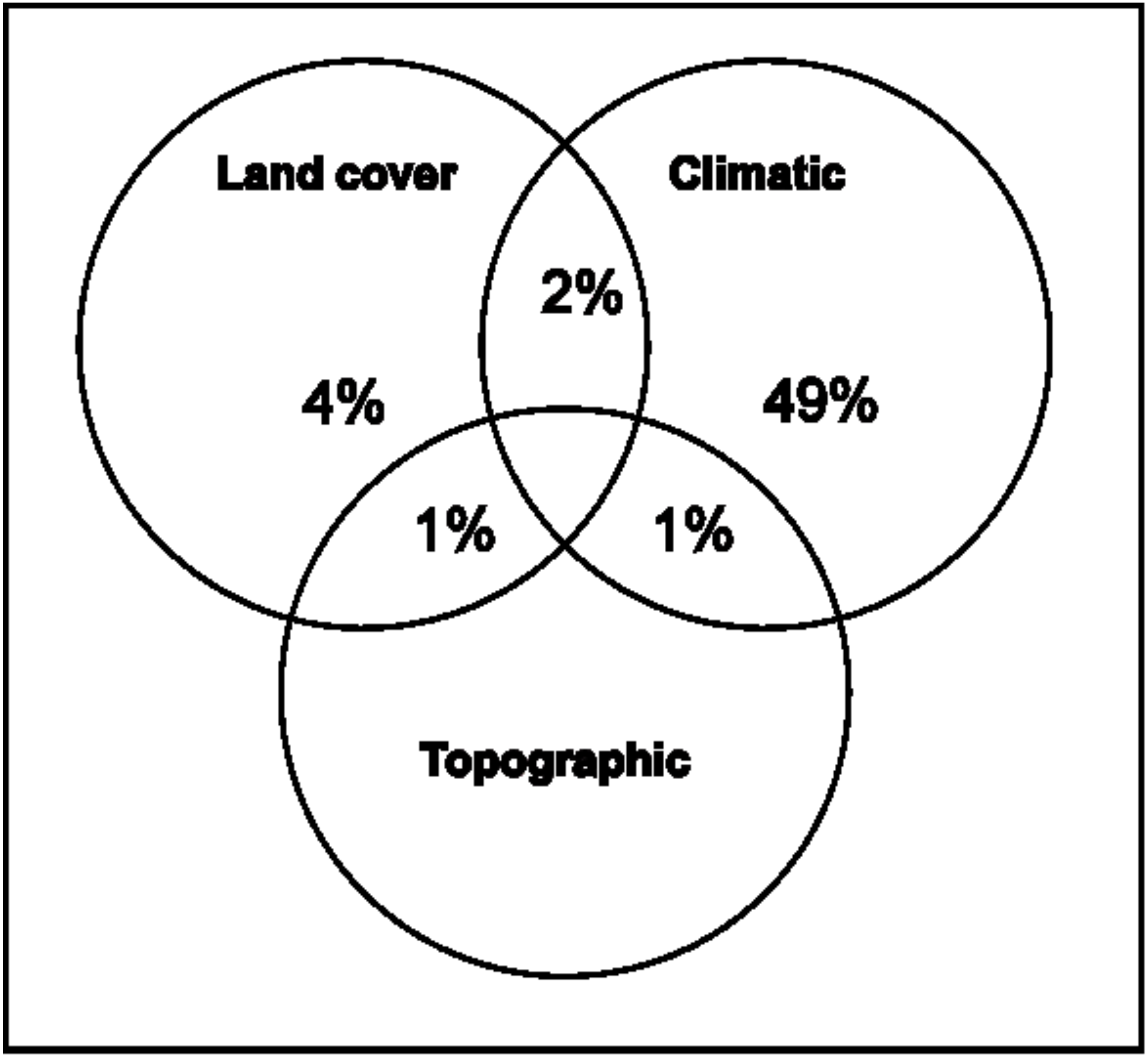
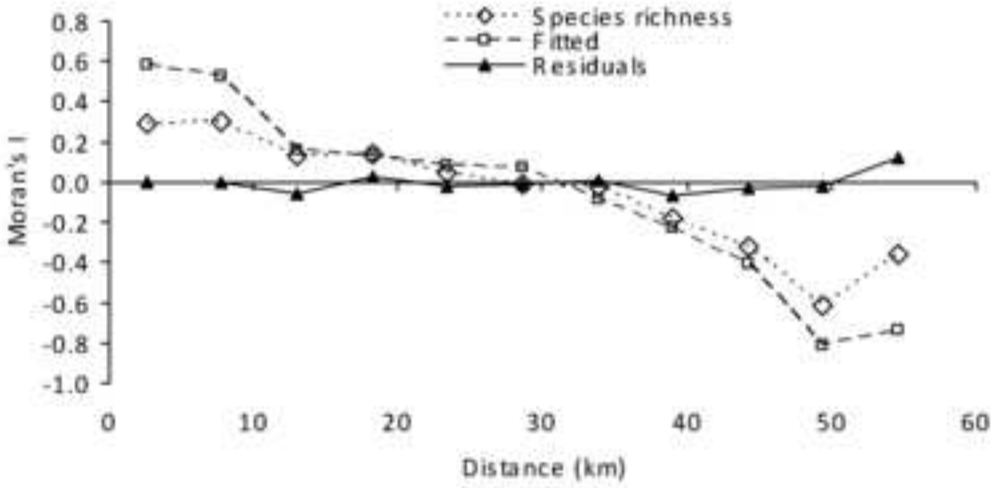
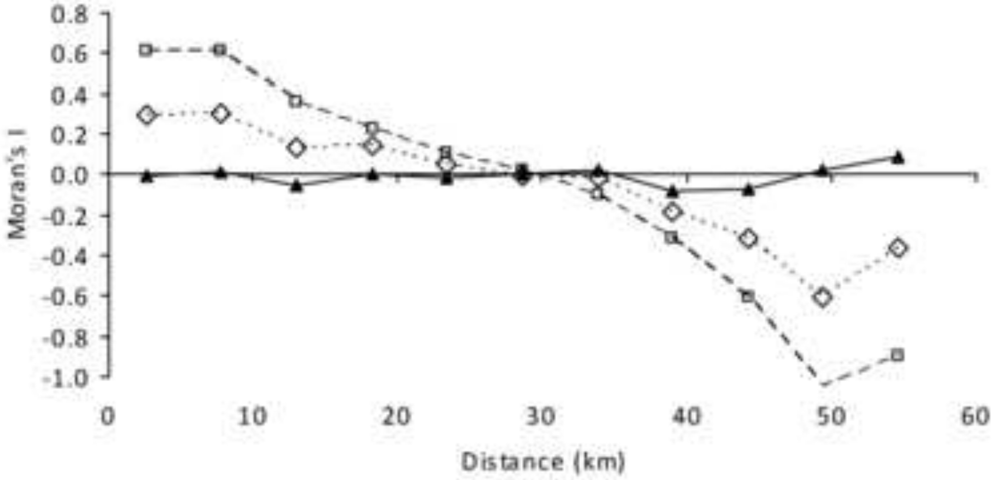


Figure 3

(a) Model 1



(b) Model 2a



(c) Model 2b

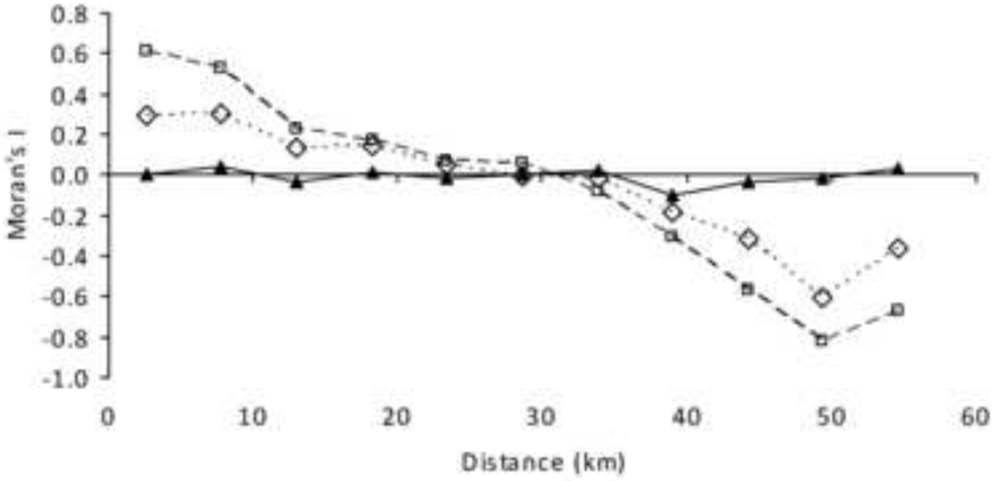


**Figure 4**

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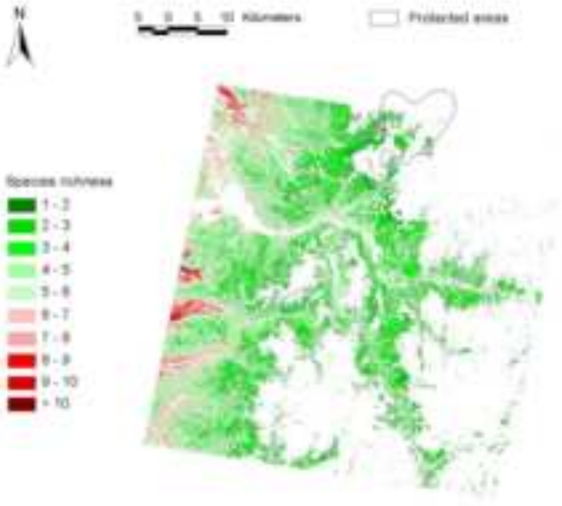
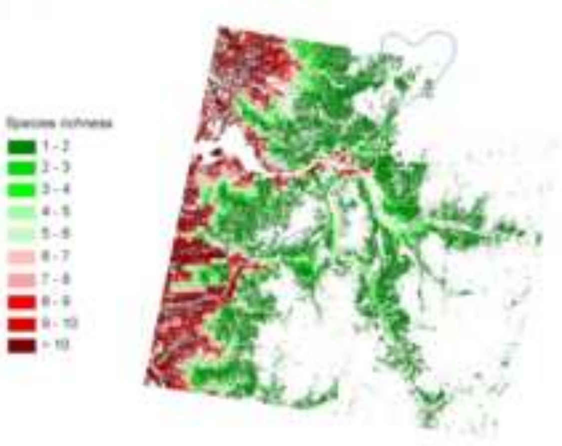
A.

Predicted current species richness (according to Model 1)



B.

Predicted current species richness (according to Model 2)



C.

Current conservation priority (according to Model 2)

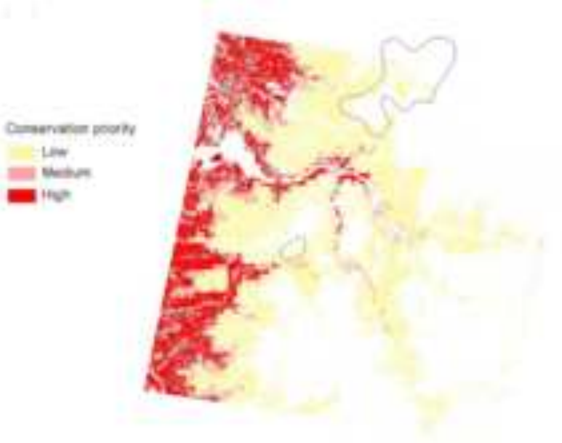


Figure 5

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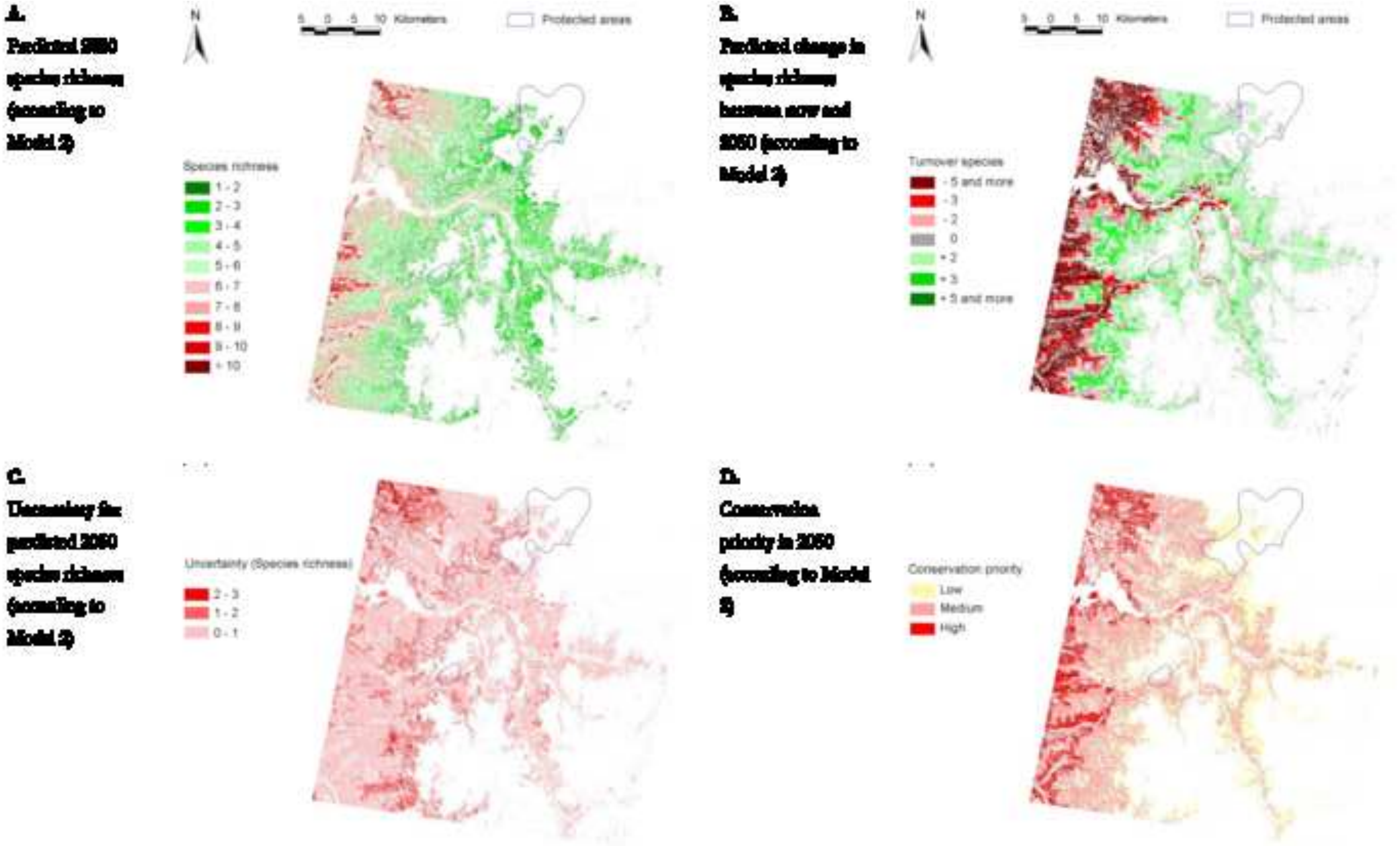

A. Predicted 2050 species richness (according to Model 2)

B. Predicted change in species richness between now and 2050 (according to Model 2)

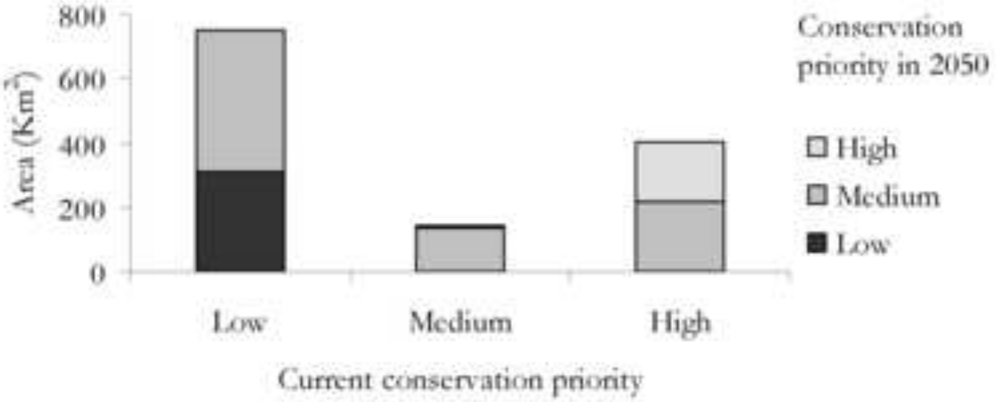
C. Uncertainty for predicted 2050 species richness (according to Model 2)

D. Conservation priority in 2050 (according to Model 2)

Figure 6

A.

Whole study area.



B.

Protected areas within the study area.