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Authors: Pacheco, Silvia, Malizia, Lucio R. , and Cayuela, L.

Research Article

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Silvia Pacheco[1], Lucio R. Malizia[1,2], and L. Cayuela[3]

[1] Fundación ProYungas, Argentina. Avenida Aconquija 2423, (4107) Yerba Buena, Tucumán, Argentina. Tel/Fax: 54-381-4253728. pacheco@proyungas.org.ar
[2] Facultad de Ciencias Agrarias, Universidad Nacional de Jujuy, Alberdi 47, (4600) San Salvador de Jujuy, Jujuy, Argentina.
[3] Ecolab, Centro Andaluz de Medio Ambiente, Universidad de Granada-Junta de Andalucía, Av. del Mediterráneo s/n, E-18006 Granada, España

Abstract

Premontane forest in northern Argentina and southern Bolivia represents a conservation priority due to its biological values, role of connectivity among different forest types, and precious timber resources. Premontane forest distribution has fluctuated in correspondence to habitat use and changes in climatic conditions. The objective of this study was to determine current and future distributions of premontane forest and of six distinctive tree species in response to climate change, and to relate distribution changes to the current system of protected areas. Using the Maxent program, we developed species distribution models at the community and species levels. We used future climate scenarios available at WorldClim, in its original version and calibrated with local data. Future models determined a retraction of premontane forest of about 40% and a general tendency of this environment to migrate toward higher altitudes. Future distribution of individual species showed a similar response although concentrated at some particular areas, suggesting a shift in tree species composition of premontane forest in the future. The Yungas Biosphere Reserve represents a stable protection area for premontane forest.

Key Words: Subtropical forests, climate change, species distribution models.

Resumen

La selva pedemontana del norte de Argentina y sur de Bolivia representa un ambiente prioritario de conservación debido a sus valores biológicos, a su posición estratégica de conectividad y a sus recursos forestales de alto valor. Su superficie ha sufrido fluctuaciones debido a una larga historia de aprovechamiento y a cambios en las condiciones climáticas. El objetivo de este trabajo fue determinar la distribución actual y futura de este ambiente y de seis de sus especies típicas en respuesta al cambio climático, y relacionar estos cambios con el sistema actual de áreas protegidas. Para esto, desarrollamos modelos de distribución de especies, a nivel comunitario y de especies individuales, usando el programa Maxent. Usamos los escenarios climáticos futuros disponibles en WorldClim, en su versión original y calibrada con datos locales. Los modelos futuros determinan una reducción cercana al 40% de la selva pedemontana y una tendencia general de este ambiente a migrar a alturas mayores. La distribución futura de las especies individuales tiene una respuesta similar, si bien quedan concentradas en ciertas áreas, por lo que la composición futura de la selva pedemontana podría variar respecto a la actual. La Reserva de Biosfera de las Yungas se presenta como un área estable de protección de este ambiente.

Palabras clave: bosques subtropicales, cambio climático, modelos de distribución de especies

Introduction

The lowest altitudinal vegetation level of subtropical Andean forests in northern Argentina (Yungas) is known as premontane forest ("Selva pedemontana de palo blanco y palo amarillo") and covers flat areas and low hills between 400 m and 700 m above sea level (asl) [1]. Premontane forest plays a key ecological role due to its high biological diversity, the presence of high-value timber resources, its strategic position connecting two forested eco-regions (Yungas and Chaco), and because it acts as shelter for migratory species located at higher altitudinal levels [2-3]. From a social perspective, it presents a substantial industrial development and contains some of the largest cities of the region. Land-use history of premontane forest is mainly associated with timber use [4] and transformation into agricultural lands. These impacts led to the degradation of most of the remaining premontane forest areas and largely confined this habitat to steeper and less accessible areas [5-6]. Nowadays, premontane forest is considered a conservation priority for Argentina [3].

Climate variations can seriously affect the distribution of premontane forest, as it has in the past [7]. The current distribution of premontane forest is the relict of an environment with a wider distribution in South America [7]. Understanding forest spatial dynamics in relation to climate change would allow us to identify long-term stable areas and areas of retraction or expansion. This is essential for analyzing the impact of changes of forest distribution on regional biodiversity, and for making decisions aiming to strengthen the regional system of protected areas and planning long-term forest and agricultural production systems.

Species distribution models are used to predict changes in species distribution ranges in response to climate or other attributes. Many of these models are based on occurrence data and environmental maps [8-9]. They have been used, in general, for conservation purposes [10], in the study of spatial patterns of diversity [11], and for predicting climate change effects [12-15].

In climate change studies, distribution models determine whether particular areas harbor suitable or unsuitable conditions for the occurrence of the species and communities analyzed. The area of distribution at a community level can be obtained by combining distribution models of individual taxa or by modelling the community as a whole [16-17]. However, no inferences can be drawn on the occupation of areas by different species, because models lack information on biotic interactions, species physiological adaptations to climate change, and dispersal ability, among other things [18-19].

The general objective of this study was to determine the future distribution of premontane forest in northwestern Argentina and southern Bolivia under a climate-change scenario and to analyze the consequences of potential changes for conservation purposes. The specific objectives were: (1) to determine present and future distribution ranges of premontane forest, (2) to determine future

distributions of selected species, and (3) to analyze how these changes may affect present conservation strategies of premontane forest.

Methods

Study site

This work was carried out in premontane forest areas of northern Argentina, which occupy wide stretches of the Orán and San Martín departments in the Salta province, and Ledesma and Santa Bárbara departments in the Jujuy province. Within Yungas, this forest type has the highest percentage of exclusive tree species [20], of which over 70% are deciduous, making it one of the most seasonal forest systems in South America [7,21]. Among the distinctive and more abundant premontane-forest tree species, we can mention palo blanco (*Calycophyllum multiflorum,* Rubiaceae*)*, palo amarillo (*Phyllostylon rhamnoides,* Ulmaceae*)*, lapacho rosado (*Tabebuia impetiginosa,* Bignoniaceae), cedro orán (*Cedrela balansae,* Meliaceae), roble criollo (*Amburana cearensis,* Leguminosae), and urundel (*Astronium urundeuva,* Anacardiaceae) [1]. Precipitation varies between 800 mm and 1000 mm per year, concentrated in the summer (November-March) [22]. Mean annual temperature is 18-20ºC; in the summer temperatures can exceed 40ºC [23].

We defined three geographic areas covered by premontane forest: (1) the Orán-Ledesma sector is located on the west side of the San Francisco and Bermejo rivers and is almost entirely included within the Yungas Biosphere Reserve (RBYungas); (2) the San Martín sector is located in the San Martín department in Salta province, mainly on the west side of National Highway 34; (3) the Santa Bárbara sector is located mainly in the Jujuy province and is related to the Santa Bárbara, Maíz Gordo, and Centinela mountain ranges (Fig. 1).
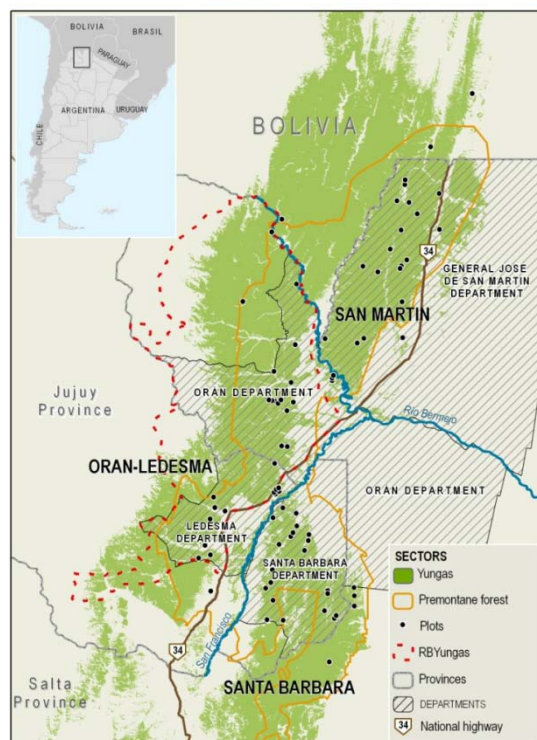

Fig. 1. Location of the study area. Orán-Ledesma, San Martín and Santa Bárbara sectors and presence locations used in the distribution models are presented. Yungas limits were obtained by digital classification of an SACC satellite image.

Species distribution models

We used a geographic information system (GIS) and species distribution models (SDM) to obtain the distribution of premontane forest and of selected tree species under current climatic conditions and a scenario of climate change.

Premontane forest presence data used in the distribution models were obtained from 19 permanent plots from the Subtropical Network of 1-ha Permanent Plots of Fundación ProYungas [24] and from 50 rapid assessments at 0.1 ha circular plots (17.84 m radius). In each plot, we recorded the number of individuals of all tree species with >10 cm diameter at breast height (1.3 m). We considered as presence locations of premontane forest those plots including at least three distinctive species (see study site). By using three or more species, we were able to obtain enough sample points to cover all the latitudinal and altitudinal range of premontane forest. In this way, we were certain to be sampling in premontane forest, and not in marginal areas with isolated species. Sample plots were large enough to efficiently sample the most distinctive species as required. We worked with a total of 69 plots distributed across the study area (Fig. 1).

In addition, we selected six distinctive species found exclusively in premontane forest to model their distribution ranges within this forest type. The species were roble criollo (*Amburana cearensis*), urundel (*Astronium urundeuva*), palo blanco (*Calycophyllum multiflorum*), cedro orán (*Cedrela balansae*), palo amarillo (*Phyllostylon rhamnoides*), and lapacho rosado (*Tabebuia impetiginosa*). We used permanent and circular plots and 61 other field surveys conducted by Fundación ProYungas in the study area as presence locations. This resulted in 29 presence points for roble criollo, 69 for urundel, 103 for palo blanco, 130 for cedro orán, 110 for palo amarillo. and 65 for lapacho rosado.

Climate variables

Selection of appropriate future climate-change scenarios is critical because this in turn will determine species distributions [25]. Global scenarios available in WorldClim (http://www.worldclim.org/download) for northern Argentina predict an increase in temperature and precipitation for the study area. Comparing current WorldClim and local precipitation data, we observe that mean annual precipitation values from WorldClim are underestimated. Mean annual precipitation from local data is significantly higher than from WorldClim data (1041 mm ± 240 SE and 871 mm ±121 SE, respectively; F = 3.16; p<0.0001). Mean annual temperature did not vary between data sources (F = 1.25; p=0.159), with a mean around 20°C. Therefore, we worked with two sets of environmental variables, the WorldClim original version (current variables and CCM3 future scenario) and a calibrated version using Bianchi's local precipitation model [23] to adjust the mean annual precipitation data. These sets of variables were called original and calibrated models, respectively.

WorldClim current climate variables have an approximate resolution of 0.86 km^2 in the study area and represent annual and seasonal trends as well as temperature and precipitation extreme values for the period between 1950 and 2000 [26]. This database has been used in the development of distribution models for different functional groups in northwestern Argentina [27-29, 4]. Future projections of these climate variables are based on the *National Center for Atmospheric Research* (NCAR) *Community Climate Model* (CCM3), for an atmospheric CO_2 duplication condition [30]. This situation is predicted to occur before the end of this century [31]. The CCM3 scenario can be considered as an extreme scenario by assuming a duplication of greenhouse-gas emissions, but is roughly equivalent to the average of the current IPCC scenarios [32, 33]. From the available WorldClim climate variables, we selected those with less auto-correlation (Pearson correlation less than 0.7) and with greater biological significance. The

variables used were: mean annual precipitation, precipitation of driest month, temperature seasonality, and maximum temperature of warmest month.

For the calibrated set of variables, we used the same variables as in the original set, but current mean annual precipitation was replaced by the local one determined by Bianchi et al. [23]. Future mean annual precipitation was generated by adding current local precipitation to the differences between the predicted precipitation by WorldClim CCM3 model and current precipitation by WorldClim.

Distribution models

Distribution models were developed using Maxent [34-35]. This program works well with few presence data, does not require absence data, combines continuous and categorical variables, provides the contribution of each variable to the model, controls the excessive adjustment of distributions and the output is a continuous occurrence probability. To obtain a better fit and a measure of the model dispersion, we performed 100 runs using Maxent standard parameters. Thirty percent of presence data was used for internal validation and the remaining data were used for model construction. The overall efficiency evaluation of the model was made by the ROC operator, from which the indicator of the area under the curve (AUC) is derived [36-37]. A value above 0.75 is considered adequate in studies oriented to management and conservation [38]. Contribution of each variable to model construction was evaluated with the Jackknife test, implemented by the program. Finally, we selected a threshold to elaborate a binary classification of presence-absence data. No single procedure is used to select this threshold [39]. In this study, we used the Equal Test Sensitivity and the Specificity Logistic threshold, offered by Maxent. Pixels with a value higher than this threshold were considered presence data, meaning that they harbored the appropriate climate conditions for the species. Each grid of actual and future distributions for premontane forest and for each distinctive species was reclassified as a function of the selected threshold.

Maxent generates distribution models based on current variables and then projects the relationship of these variables with the distribution, using variables of future scenarios. Therefore, each model used in this study has a current and future distribution version of premontane forest.

Spatial analysis

Quantification of current and future premontane forest areas and of stable, expansion and retraction areas was analyzed with ArcGis 9.3 and the Spatial Analyst extension (ESRI, Redlands, CA). Stable areas are those which currently correspond to premontane forest and will continue as premontane forest in the future. Expansion areas are those that do not correspond to premontane forest in the present but, due to climate change, will be colonized by distinctive species of this environment. Retraction areas are those that currently support premontane forest and that will shift to other vegetation types in the future.

To determine the current distribution of premontane forest, we first produced a potential distribution map with Maxent and then subtracted those transformed areas identified by visual interpretation of Landsat images (path 230-231, row 75-77, year 2008) and corroborated with field visits. This subtraction of transformed areas was done only to calculate the current real distribution of premontane forest. For comparisons between current and future distributions, both for premontane forest and for distinctive species, the entire distribution was considered, without subtracting the transformed areas. Distribution maps of individual species were overlapped to that of premontane forest to assess which distinctive species will continue in the future to be an important component of premontane forest. Considering the edges of the presence-absence binary map of the current distribution of premontane forest, we

calculated current temperature and precipitation values and compared them with those under future climate scenarios. In this way, we were able to establish changes in future climatic conditions within the area currently occupied by premontane forest. To calculate forest altitudinal shifts along mountain ranges, we determined average elevation range (m asl) of premontane forest based on current and future distributions. Finally, taking into account official cartography of national and provincial protected areas of the region, we determined the current and future area of premontane forest included in each protected area.

Results

Current distribution of the premontane forest

Current distribution models of premontane forest have a high overall accuracy. The Test AUC value for the model developed from original climate variables is 0.94 (±0.013), while from calibrated climate variables it is 0.95 (±0.013). Current distribution maps of premontane forest for both climate models show similar spatial patterns, representing good current distribution models from which we can generate distribution hypotheses under climate change scenarios. Based on fieldwork and expert knowledge, the distribution map generated through the calibrated model is slightly better, even if it only entails a 3% difference in the total forest area. The difference between both models is mainly due to an exaggeration in the original model of the distribution of premontane forest in the north of the Orán-Ledesma sector; this erroneously includes part of Baritú National Park, which corresponds to montane forest, another altitudinal level of Yungas (Fig. 2). In contrast, the calibrated model expands the distribution towards the south in the Santa Bárbara sector, which fits better with what is observed in the field, even though it establishes a premontane forest area within El Rey National Park, which may correspond to a transition zone between premontane and montane forests. In both models, 10% of the original forested area has been transformed into agricultural lands, mainly in flat areas below 5% of slope, in the Orán-Ledesma sector.
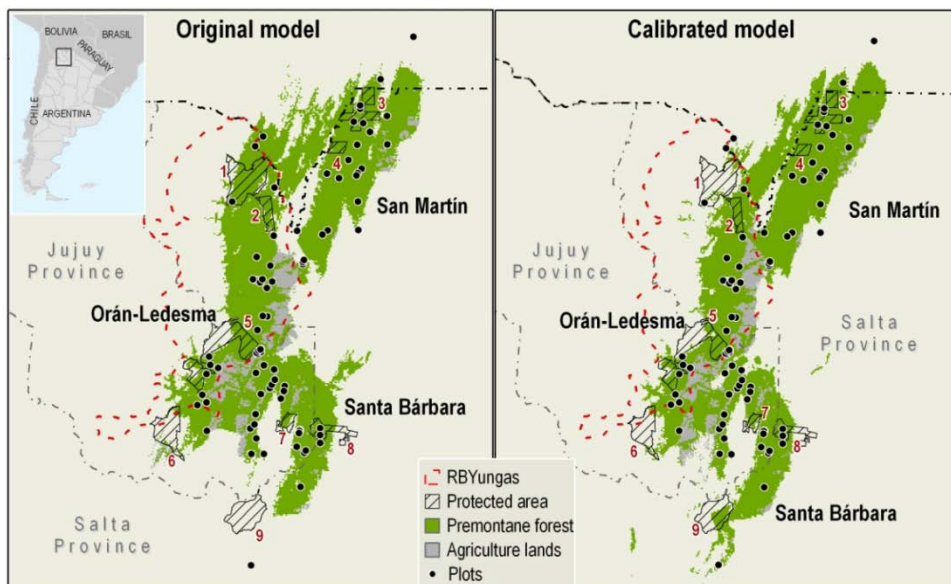

Fig.2. Distribution of current premontane forest in northwestern Argentina based on original and calibrated climate models. References for protected areas: 1) Baritú, 2) Pintascayo, 3) Acambuco, 4) Piarfon, 5) Calilegua, 6) Serranías del Zapla, 7) Lancitas, 8) Pizarro, 9) El Rey.

Future premontane forest distribution

Distribution models under climate change scenarios (original and calibrated) predict a future coverage of 37% and 47%, respectively, of the current predicted forest area. Approximately 30% of this area corresponds to stable areas of the original forest and the remaining percentage corresponds to areas that could potentially expand due to future climate conditions (Table 1).

Table 1. Current and future areas of premontane forest obtained from original and calibrated climate models. Ref: PF: premontane forest.

	Original model (km²)	Calibrated model (km²)
Current PF	20411	19843
Future PF	7508 (36.7% current PF)	9327 (47% current PF)
- Future stable area	5574 (27% current PF)	6766 (34% current PF)
- Future retraction area	14837	13076
- Future expansion area	1934	2561

Using original and calibrated variables, distribution models predict a future retraction in the area occupied by premontane forest and a tendency to migrate towards higher altitudes. Both models agree on a forest retraction in the San Martín sector and its permanence in the Orán-Ledesma sector (particularly in the original model). In addition, both models show the permanence of premontane forest in the Santa Bárbara sector, while the calibrated model shows a greater expansion zone of the forest in this sector (Fig. 3).

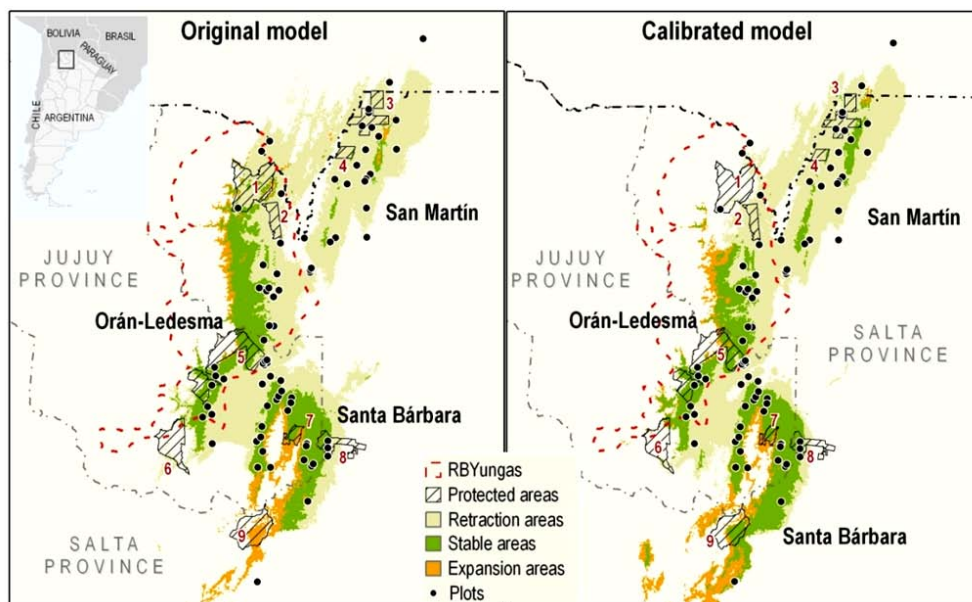Fig. 3. Potential future distribution of premontane forest using original and calibrated climate models. Retraction and stable areas correspond to the current premontane forest area. Expansion and stable areas correspond to the future premontane forest area. References for protected areas: 1) Baritú, 2) Pintascayo, 3) Acambuco, 4) Piarfon, 5) Calilegua, 6) Serranías del Zapla, 7) Lancitas, 8) Pizarro, 9) El Rey.

The original and calibrated climate models show an increase in temperature and precipitation for the area that is currently occupied by premontane forest. Temperature increase is *ca.* 1ºC in mean annual temperature and in maximum temperature of warmest month, while mean annual precipitation increases 80 mm (Table 2). These climate changes would cause an upward migration of premontane forest of about 268 m asl in the original model and of about 260 m asl in the calibrated one.

Table 2. Values of climate variables of premontane forest for current conditions and future projections based on the original and calibrated models. Temperature values are the same for the original and calibrated models.

Environmental variables	Current	Original model	Change
Mean annual precipitation (mm)	905 (±136)	982 (±158)	77
Mean annual temperature (°C)	20.7 (±1.1)	21.9 (±1.6)	1.2
Maximun temperature of warmest month (°C)	31.8 (±1.8)	33.3 (±1.9)	1.5
	Current	**Calibrated model**	**Change**
Mean annual precipitation (mm)	1071 (±262)	1146 (±277)	75

Distribution of distinctive premontane forest species

Overall, the six distinctive species of premontane forest analyzed have individually similar current and future distribution patterns compared with premontane forest as a whole. In the future modeled distributions, we observe a marked retraction in the San Martín sector, and stable and expansion areas in Orán-Ledesma and Santa Bárbara sectors. However, several differences emerge among the modeled distributions of the individual species. Palo blanco and palo amarillo, the most distinctive premontane-forest species, suffer a clear retraction of their distribution southward in the Orán-Ledesma and Santa Bárbara sectors. On the other hand, lapacho rosado and cedro orán maintained a more widespread distribution in all three sectors (Fig. 4).

Table 3. Current and future distribution areas of distinctive premontane forest species using the calibrated climate model.

	Roble	Urundel	Palo blanco	Cedro orán	Palo amarillo	Lapacho rosado
Current area (km²)	16478	17553	14126	17093	15575	19362
Future area (km²)	6667 (40.5%)	8436 (48%)	6185 (43.8%)	8480 (49.6%)	7219 (46.3%)	9375 (48.4%)
- Future stable area	(60%)	(51.6%)	(46%)	(55.3%)	(63.8%)	(75%)
- Future expansion area	(40%)	(48.4%)	(54%)	(44.7%)	(44.9%)	(25%)
% stable area in relation to current area	24.2	24.8	20.1	27.4	25.5	36.6

In general, all species will cover in the future between 40% and 50% of the original forest area. However, this future area corresponds mainly to expansion areas i.e., few are stable areas. The most affected species by retraction of the original distributions are palo blanco, roble criollo, and urundel, maintaining less than 25% of the original area. The other species maintain between 25% and 36% of the original area (Table 3).
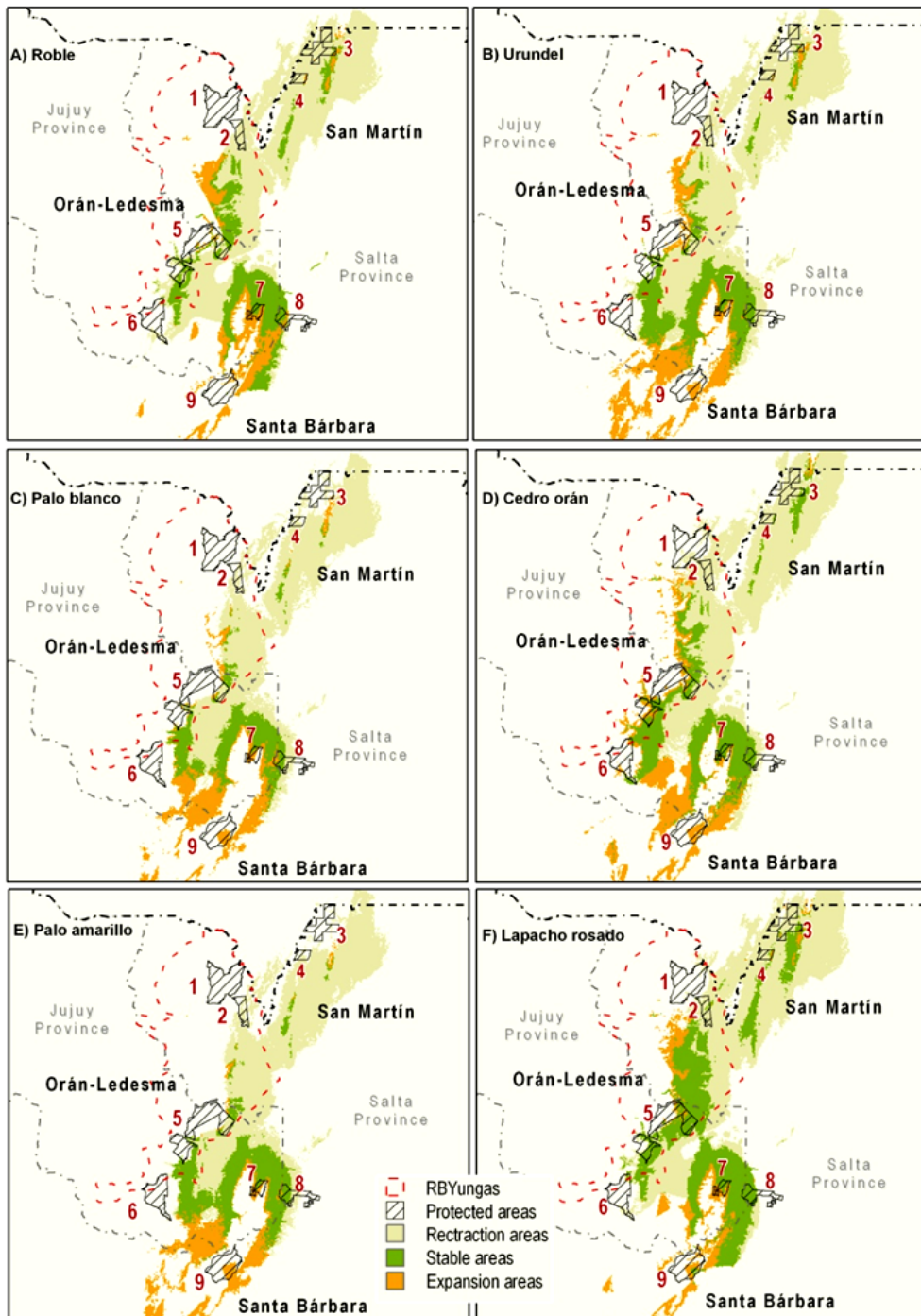

Fig. 4. Current and future distribution of distinctive premontane forest species using the calibrated climate model. For each species, current distribution corresponds to the sum of retraction and stable areas, and the future distribution corresponds to the sum of stable and expansion areas. References for protected areas: 1) Baritú, 2) Pintascayo, 3) Acambuco, 4) Piarfon, 5) Calilegua, 6) Serranías del Zapla, 7) Lancitas, 8) Pizarro, 9) El Rey. A) Roble (*Amburana cearensis*), B) Urundel (*Astronium urundeuva*), C) Palo blanco (*Calycophyllum multiflorum*), D) Cedro orán (*Cedrela balansae*), E) Palo amarillo (*Phyllostylon rhamnoides*), F) Lapacho rosado (*Tabebuia impetiginosa*).

The sum of the current distribution of the six distinctive premontane forest species reaches 54% of the current distribution of premontane forest as a whole. However, considering the future distribution of this environment, the future distribution of the six species would only occupy 35% of premontane forest, mainly concentrated in the Santa Bárbara sector (Fig. 5).
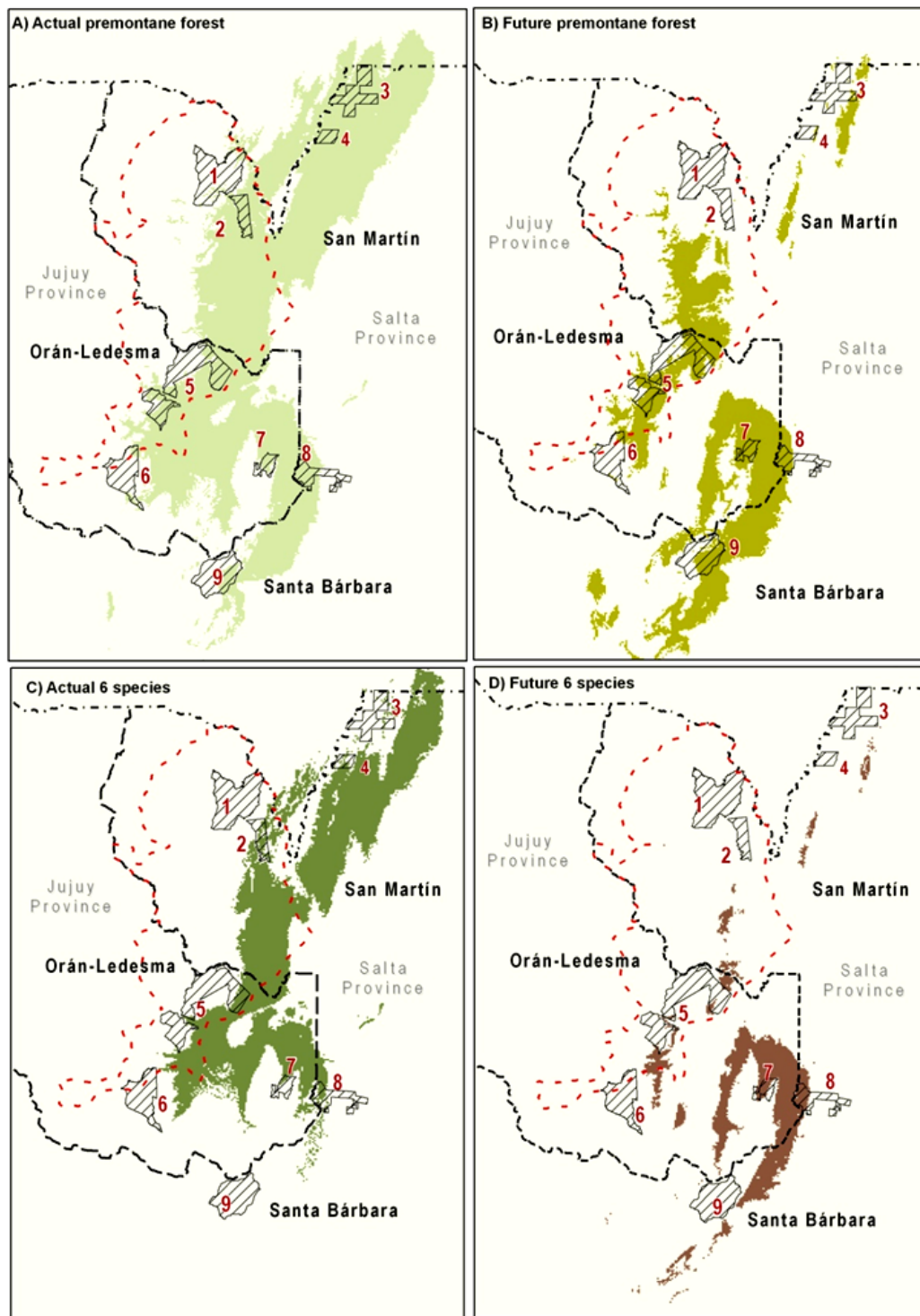

Fig. 5. Current and future distribution models of premontane forest (A and B), in relation to the distribution of six distinctive premontane forest species (C and D) using the calibrated climate model.

Protected-areas system

According to the models developed with original and calibrated climate variables, 9.5% and 8%, respectively, of current premontane forest is located within a protected area (Table 4). This difference is due to the misplacement of premontane forest within the Baritú National Park, as mentioned before. The protected areas that currently include a portion of premontane forest are Acambuco, Piarfon, Pintascayo, and Pizarro in Salta province, and Calilegua in Jujuy province (Fig. 3).

Taking into account the original model, the current system of protected areas would include 4.7% of total future premontane forest. The calibrated model suggests that 5% of future premontane forest would be maintained within the protected system. In the original and calibrated models, 70% and 80%, respectively, of this area corresponds to stable forest (Table 4). According to both models, premontane forest would disappear from Acambuco, Piarfon, and Pintascayo, and would remain stable in Calilegua, Pizarro, Lancitas, and Yungas Biosphere Reserve. According to the calibrated model, premontane forest would also remain stable in El Rey, but, as previously mentioned, this area does not harbor a typical premontane environment (Fig. 3).

Discussion

Retraction of plant communities in response to climate change has previously been reported in several studies. In temperate forests in Mexico, the distribution of oaks and pines is showing a retraction, depending on the climatic affinity of each species [40]. Most *Polylepis* species along Andean mountains in South America are also suffering a retraction of their distribution [41]. Our results indicate that changes of climate conditions would affect the distribution of premontane forest and a group of distinctive species along the Andes, representing to our knowledge the first study of the kind for a forested subtropical environment.

Current premontane forest distribution models generated from original and calibrated climate variables could both be considered good distribution maps to make predictions concerning climate change. While there are some differences among them, these represent just 3% of the total distribution area. As a main difference, the current model based on original data extends premontane forest distribution to Baritú National Park in the northern part of the Orán-Ledesma sector. Furthermore, both models, original and calibrated, predict the distribution of premontane forest between the Orán-Ledesma and Santa Bárbara sectors. This is a transition area between premontane and Chaco forests that has been entirely transformed into agricultural land, making it hard to distinguish the boundaries of these two vegetation units. Thus, it is hard to evaluate the extent to which the models make an accurate assessment of the past distribution in the area.

The distribution models coincide with the stable areas being inside the Orán-Ledesma sector, mainly within the Yungas Biosphere Reserve; the maintenance of premontane forest in the Santa Bárbara sector; and the retraction of large premontane areas in the San Martín sector. According to both models, expansion areas are partly located in the Orán-Ledesma sector and to a larger extent in the Santa Bárbara sector.

Distribution models, developed with original and calibrated climate variables, agree on the general pattern of future retraction and upward migration of premontane forest along the Andes, which is probably due to a general increase in temperature. These upward areas are currently covered with montane forest, which constitutes the immediate vegetation level above premontane forest. This upward shift of premontane forest might be a general response of all Yungas vegetation belts, so that a general increase in the altitudinal levels could be expected along the Andes.

The six distinctive species analyzed have a current distribution pattern similar to that of premontane forest as a whole. However, several differences are observed in the future individual distributions of these species. Therefore, future species composition of premontane forest could vary from the current one. The Santa Bárbara sector and some areas of the Orán-Ledesma sector might host the six distinctive species. In contrast, other future distribution areas may not contain two of the most characteristic species of this environment: palo blanco (*Callycophylum multiflorum)* and palo amarillo (*Phylostyllon rhamnoides).* On the other hand, lapacho rosado (*Tabebuia impetiginosa)* maintains more area in the San Martín sector than any other species analyzed. Based on this, we might expect that species composition of future premontane forest would be different from the current one in each sector, depending on each species' response. The southern area of the current distribution of premontane forest will probably harbor a composition similar to that of the current one. In contrast, the northern area of the Orán-Ledesma sector, and mainly the San Martín sector, will disappear or be composed of a combination of premontane and Chaco species tolerant of higher temperatures.

The hypotheses of the future species composition of premontane forest assume that the species are capable to accompany the displacement of those climatic conditions favorable for each species, without taking into account dispersal limitations, adaptations, and biotic interactions, among other factors. Since hypothetical future distributions mainly imply retraction from current areas and expansion over contiguous areas, dispersal limitation and geographic barriers do not appear as a main limitation to the future potential distribution of the selected species.

Implications for conservation

We observe a significant retraction of 40-50% of premontane forest inside protected areas in both climate change models. Moreover, part of the area represented by these percentages corresponds to areas of possible future expansion, making even more vulnerable the conservation role of protected areas. Overall, protected areas of the Orán-Ledesma and Santa Bárbara sectors are more likely to maintain premontane forested areas, while the San Martín sector does not present stable premontane forest within protected areas under any climate change scenario.

The results presented here question the long-term viability of those systems of protected areas that have been designed to conserve particular habitat types and that might be severely affected by climate change. Far from making an argument against protected areas, we propose considering the re-design of more dynamic systems, largely integrated with the non-protected landscape and focusing on regional functionality. In the particular case of northwestern Argentina, there is still the opportunity to design and implement a combined strategy between protected and non-protected forest areas that could cope with the potential effects of climate change. However, this opportunity loses degrees of freedom as more habitat is transformed outside a regional land use-planning strategy and as more forests are degraded by being made subject to non-sustainable uses.

Acknowledgements

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