

UNIVERSITY OF CALIFORNIA

Los Angeles

Predicting the Distribution of an Increasingly Vulnerable Ecosystem:

The Past, Present, and Future of the *Polylepis* Woodlands

A dissertation in partial satisfaction of the  
requirements for the degree Doctor of Philosophy  
in Biology

by

Brian Roy Zutta

2009

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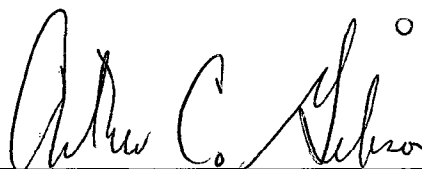
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## ABSTRACT OF THE DISSERTATION

Predicting the Distribution of an Increasingly Vulnerable Ecosystem:

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by

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Professor Philip W. Rundel, Chair

*Polylepis* woodlands are an important and highly threatened ecosystem in the high altitudes of the tropical and subtropical Andes, providing unique habitats for diverse flora and fauna and vital resources for local human communities. Species within this Andean region, a biodiversity hotspot, are predicted to be extremely susceptible to future climate change. In response to increased annual temperatures, *Polylepis* woodlands are predicted to shift their elevational extent, as paleoecological evidence suggests with past climate fluctuations. However, our understanding of *Polylepis* species distribution is severely limited by centuries of woodland fragmentation, beginning with pre-Colombian Andean civilizations and continues to today. This research aimed to predict current *Polylepis*

species and woodland distribution, distribution during the Last Glacial Maximum (LGM), and changes in species distribution resulting from doubled atmospheric CO<sub>2</sub>. Regions of high *Polylepis* species richness were characterized, as well as the extent *Polylepis* woodlands within international and national protected areas throughout the region. Current, LGM, and future distribution as a result of doubled atmospheric CO<sub>2</sub> were predicted for 21 species of *Polylepis* using the Maxent algorithm over South America. Several environmental layers, including climate, optical, and microwave remote sensing data, were used for particular climate scenarios. Range contraction was predicted to occur for most species, from LGM to future climate, as a result of upslope range shifts to smaller land area as a result of increasing annual temperatures. However, the expansion several species ranges were predicted to occur within the Altiplano of Peru and Bolivia as greater land area becomes available. This is contrary to most models of climate change that solely predict contraction in mountain regions. The sites of highest *Polylepis* species richness did not closely match the current location of protected areas, indicating that the expansion and addition of protected areas are necessary to preserve key areas of high altitude tropical ecosystems. Overall, the management of remaining *Polylepis* woodlands must take into account the natural distribution of *Polylepis* species and their response to future climate change to protect this vulnerable ecosystem and the flora, fauna, and human populations that depend on them.

# CHAPTER 1: PREDICTING THE CURRENT DISTRIBUTION OF THE VULNERABLE HIGH-ALTITUDE *POLYLEPIS* WOODLANDS OF THE ANDES

## INTRODUCTION

The *Polylepis* woodlands of the high Andes of South America are an increasingly vulnerable ecosystem. The genus *Polylepis* (Rosaceae) includes approximately 27 species (Mendoza, 2005; Kessler & Schmidt-Lebuhn, 2006); with populations forming highly fragmented evergreen woodlands along the tropical and subtropical Andes. Less than 10% of their original extent is estimated to remain in the high altitude regions of Bolivia and Peru (Fjelds  & Kessler, 1996). Fourteen species are listed as vulnerable, due to a reduction in area of 20% within known areas of occurrence over the last 10 years (IUCN, 2009). Nevertheless, these woodlands contain endemic and endangered species (Servat *et al.*, 2002), serve important geomorphic and hydrologic functions in mist interception and erosion control (Fjelds , 2002; Renison *et al.*, 2004), and provide a vital resource for indigenous communities (Aucca & Ramsay, 2005).

All *Polylepis* species are woody shrubs or trees, some growing to 10 m in height, and share morphological characteristics, which include multilayered red exfoliating bark and small pinnately-lobed leaves. Several species are known for particular ecological characteristics within their distribution along the Andes (Table 1.1). For example, *Polylepis pauta* can dominate upper cloud forests in Ecuador and extend their range to isolated patches in southern Peru (Cierjacks *et al.*, 2008). *Polylepis sericea* is the only species found in Venezuela and has the widest latitudinal distribution of the genus,

reaching to northern Bolivia (Azócar *et al.*, 2007). *Polylepis tarapacana* is known for reaching altitudes up to 5200 m on Volcán Sajama in Bolivia, which may be the highest elevation for woody plants in the world (García-Núñez *et al.*, 2004).

The natural extent of *Polylepis* woodlands has been extensively debated as a result of apparent widespread pressure from thousands of years of human populations in the high Andes (Kessler, 2002). These woodlands have been hypothesized to originally have covered the majority of the Andean highlands (Ellenberg, 1979) or alternatively suggested as having ranges limited to specific microclimates (Simpson, 1986). Pollen evidence indicates that their distribution was widespread at high altitudes after the last glacial maximum (Hansen *et al.*, 2003), but palynological analysis have lacked spatial precision (Di Pasquale *et al.*, 2008). Without question, the current distribution of *Polylepis* has been affected by centuries of human activity (Fjeldsø & Kessler, 1996; Chepstow-Lusty *et al.*, 1998; Renison *et al.*, 2006). In many regions, these woodlands face continuous pressure today from such factors as livestock grazing (Teich *et al.*, 2005), fire (Cierjacks *et al.*, 2008), tree cutting, and expansion of roads (Purcell & Brelsford, 2004), all of which have reduced habitat extent and quality (Jameson & Ramsay, 2007). Complicating conservation assessments has been the morphological similarities of many *Polylepis* species that have led many studies to group them as a single woodland type, despite the many habitats types and species represented within the genus (Simpson, 1986; Kessler & Schmidt-Lebuhn, 2006).

Recently available satellite-derived remote sensing data and distribution modeling can contribute insight into the potential extent of *Polylepis* woodlands, as well as other

Andean species with narrow climate regimes, by providing direct measurements of the earth's biophysical characteristics (Kerr & Ostrovsky, 2003). Up to date, passive remote sensing in the optical portion of the electromagnetic spectrum has most commonly provided useful measures of biophysical parameters, such as the Moderate Resolution Imaging Spectroradiometer (MODIS) on board NASA's Aqua and Terra satellites, which provides global measurements of surface reflectance at 250–500 m spatial resolution and frequent revisit times (1–2 days) that improves the quality of data across the Andes where persistent cloud cover is often encountered. Active microwave remote sensing from active space-borne scatterometers are being increasingly applied for monitoring ecological processes including forest biomass and diversity (Saatchi *et al.*, 2007, 2008), and vegetation phenology (Frolking *et al.*, 2006). NASA's QuickSCAT (QSCAT) scatterometer, for example, provides global coverage at 2.25-km spatial and 3-day temporal resolution and is less sensitive to cloud cover and penetrates deeper into the canopy when compared to optical radiation (Long *et al.*, 2001; Saatchi *et al.*, 2007; Buermann *et al.*, 2008).

Our study was designed to accomplish three objectives. The first was to model the potential distribution of individual *Polylepis* species in order to document differences in ecological niches along the length of Andean Cordillera. Environmental layers consisting of climate and remote sensing data were included in the analysis to constrain the potential ecological niche and increase model accuracy. The second objective was to model the potential distribution of each *Polylepis* species and predict *Polylepis* woodland area within each Andean country. Finally, our third objective was to provide quantitative data

to identify key regions of *Polylepis* species richness and the extent of which these areas are protected to support future conservation efforts.

## MATERIALS AND METHODS

### *Data collection*

An extensive review of online herbarium databases and published research was conducted from April 2006 to January 2008, and field surveys by BRZ in March 2003 to obtain georeferenced point localities. The number of points obtained ranged from a pre-set minimum of 20 to more than 100 for 21 species of *Polylepis* (see Appendix 1). Since the points were derived from a variety of sources, quality control was an important step to increase the accuracy of the distribution models. Therefore, points were overlaid on images from Google Earth (version 4.2) to verify the accuracy of each geographic location, based on descriptions from the source (e.g. country, department, elevation, proximity to landmark, etc.) and visibility in high resolution images. Erroneous and duplicate presence records were removed. Records were screened to include georeferenced points obtained from surveys within the last 16 years to ensure a broad time frame overlap between the collection of a verifiable location and the acquisition of remote sensing data.

### *Environmental data*

Environmental variables ranged from ground-based interpolated climate surfaces to satellite detected land features such as topography, vegetation density, and moisture

(Table 1.2). Bioclimatic metrics, as typically used in distribution modeling, were obtained from Worldclim (version 1.4; Hijmans *et al.*, 2005). These metrics are derived from climate records, which were compiled from several weather station networks, restricted to a 50-year period (1950–2000), and interpolated to produce climate surfaces for global land areas available at a 1-km spatial resolution (Hijmans *et al.*, 2005). Eleven temperature and eight precipitation metrics were used, representing annual means, seasonality, and extreme or limiting environmental factors.

Optical remote sensing data were obtained from the MODIS 8-day LAI product (Myneni *et al.*, 2002) over a 5-year period (2000–2004). Monthly composites of each year were produced by averaging the 8-day LAI product. The 5 years of data were then averaged to create monthly LAI fields to reduce both the effects of persistent cloud cover encountered over the many regions of the Andes and natural interannual variability (Buermann *et al.*, 2008). Five metrics of LAI, which provide spatial information on net primary productivity and vegetation seasonality, were generated from these monthly fields: annual maximum, minimum, mean, standard deviation, and range (difference of maximum from minimum). The percentage of tree canopy cover from the MODIS VCF land cover product (Hansen *et al.*, 2002) was also used in this study. We obtained the tree canopy cover product based on multi-temporal composites of MODIS data from 2001, and aggregated it from its native 500 m pixel resolution to 1 km. Validation efforts have shown that the VCF product can successfully differentiate open, closed and fragmented forest canopy types (Hansen *et al.*, 2002).



Microwave QSCAT data was available in 3-day composites at 2.25-km resolution (Long *et al.*, 2001). Average monthly composites, for 2001, were produced and re-aggregated (through nearest neighbor) to a 1-km spatial resolution. For this study, four metrics were computed including annual mean and standard deviation at horizontal and vertical polarizations of radar backscatter (Buermann *et al.*, 2008). Elevation data was obtained from the Shuttle Radar Topography Mission (SRTM) digital elevation data at 90-m resolution. Mean elevation and the standard deviation of elevation, a measure of surface ruggedness, were included and aggregated to the 1-km target spatial resolution.

After data reduction to minimize covariance and facilitate the interpretation of the predicted species distribution (see Buermann *et al.*, 2008), a total of 18 environmental layers were used for this analysis. Covariance within the sets of climate and remote sensing layers was estimated using cross-correlation matrixes based on *Polylepis* point localities and 1000 random points drawn from South America. Frequency of use in distribution modeling, greatest variation within the study area, and quality of data also determined which layers were included in the analysis. The final subset of 11 bioclimatic layers included annual mean temperature, mean diurnal temperature range, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, and precipitation of coldest quarter. The subset of five remote sensing layers included LAI annual maximum, LAI annual range, the horizontal polarization of QSCAT annual mean and QSCAT

standard deviation (seasonality), and percentage of tree cover. The two topography layers from SRTM (mean elevation and standard deviation) were also included.

### *Species distribution modeling*

The species distribution model algorithm Maxent (version 3.2.1) was used for the current study. Maxent is a modeling technique that uses a species known presence together with predictor variables to model distribution over the study area (Phillips *et al.*, 2006). Recent updates on the Maxent modeling technique have improved model performance over previous versions (Phillips & Dudík, 2008).

Several characteristics make Maxent especially suitable for distributional modeling regarding *Polylepis* species. Maxent can run on presence-only point occurrences. Since *Polylepis* woodlands are highly fragmented, presence-only points are more reliable than points that represent absences, which may incorrectly reflect anthropogenic activity rather than environmental limits. In addition, Maxent performs well with relatively few point localities (Wisz *et al.*, 2008). This algorithm property is extremely beneficial for the present study as available presence localities for several species of *Polylepis* may be limited by the fragmentation of woodlands, the restricted distribution of endemics species, and limited availability of high-quality presence data in several countries.

We used Maxent default settings for regularization and selecting feature classes for all model runs (Phillips & Dudík, 2008) and the jackknife option, which estimates the importance of individual environmental data layers. Maxent (version 3.2.1) models

produce a logistic output format, as an image, with pixel values from 0 to 1 that represent an estimate of relative probability of presence (Phillips & Dudík, 2008). Pixels with logistic value close to 1 are the sites most suitable for a species (Phillips & Dudík, 2008). In this study, pixels with values at or above 0.5 are identified as areas with a greater probability of presence, than lower thresholds, as they are predicted to contain typical bioclimatic conditions of a species' ecological niche. Pixels with values at or above 0.75 are areas near optimal environmental conditions for the species.

#### *Model building and spatial accuracy*

The final subset of eleven bioclimatic and five remote sensing layers with all available point localities were used to build the species distribution models. Following Phillips *et al.* (2006), we made 10 partitions by randomly selecting 70% of the presence localities as training data and 30% for testing the spatial accuracy of the resulting models. The area under the receiver operating characteristic (ROC) curve (AUC) provided a measure of model performance. An AUC value for a specific model scenario may range from 0.5 (random) to 1.0 (perfect discrimination). To test if the AUC of a prediction was significantly better than random, a ties-corrected one-tailed Mann-Whitney *U*-test (AccuROC; Vida, 1993) was used. AUC data are presented as means  $\pm$  S.E. ( $n = 10$  partitions).

### *Woodland conservation and species richness*

Potential *Polylepis* woodland extent was identified by overlaying pixels with values at or above 0.5 from the 21 distribution models. Potential woodland area per country was then estimated from these values. National and internationally protected areas in 2007 (WDPA, 2007) were overlaid on the potential woodland extent to identify gaps in conservation.

Areas of species richness were identified by summing modeled species distributions produced from all available environmental layers and point localities as performed in Gap analysis (Csuti, 1996) and biodiversity studies (Hurlbert & Jetz, 2007; Loarie *et al.*, 2008). Only pixels with value at or above a 0.5 logistic output were used. Forty random points in areas predicted to contain greater than 10 species were taken to evaluate the environmental information that correlated with high *Polylepis* species richness.

## RESULTS

### *Potential species distribution*

Predicted distributions of 21 species of *Polylepis* modeled using all environmental layers showed expected limited ranges of occurrence along the Andes, but these ranges were generally larger than the known distribution from herbarium records using predicted area near optimal conditions ( $\geq 0.75$  logistic threshold) (Fig. 1.1). *Polylepis australis*, thought to be endemic to northern Argentina, had an estimated distributional area occurring 94% in Argentina and 6% in Bolivia (Table 1.3). Five species known to occur

only as far north as Ecuador, specifically *P. incana* (Fig. 1.1e), *P. lanuginosa* (Fig. 1.1h), *P. pauta* (Fig. 1.1k), *P. reticulata* (Fig. 1.1n) and *P. weberbaueri* (Fig. 1.1u), were predicted to have a small area of distribution of less than 2000 km<sup>2</sup> within the Cordillera de Mérida, Venezuela (Table 1.3). Similarly, Colombia had six modeled species distributions that included species not known to naturally occur within the country, namely *P. incana* in southern Colombia (Fig. 1e), *P. lanuginosa*, *P. reticulata* (Fig. 1n), and *P. weberbaueri* (Fig. 1u) in northern and central Colombia (Fig. 1h), and *P. pauta* in southern Colombia (Fig. 1k).

The number of predicted *Polylepis* species per country was generally closer to recorded values for countries south of Colombia, using areas identified with optimal conditions ( $\geq 0.75$  logistic threshold). Ecuador has six previously recorded species, which were modeled with distributions greater than 4,000 km<sup>2</sup> (Table 1.3). Although not known in Ecuador, *P. tomentella* was also modeled as potentially occurring with a relatively small distributional area of about 381 km<sup>2</sup>. This may indicate an overprediction since there is no apparent continuous distribution to its modeled range in southern Peru. Argentina and Chile were modeled with five and two predicted species with distribution areas greater than 100 km<sup>2</sup>, respectively, which reflects the current number of observed species in these countries. The relatively high number of species modeled in Bolivia, (18) and Peru (20) reflects the high number of species observed and recently described in these regions of the Andes.

### *Model evaluation*

The AUC values were statically significant ( $P > 0.001$ , Mann-Whitney  $U$ -Test) for all *Polylepis* species distribution predictions, indicating that all model scenarios and data partitions were significantly better than random. The average AUC value, based on 10 random partitions, for models using all environmental layers was  $0.996 \pm 0.003$ . The importance of each environmental variable in a Maxent distribution model can be estimated using the training gains, when each variable is used in isolation and excluded from the set of variables, in the form of a jackknife test of variable importance. Mean elevation contained the most useful information in isolation and temperature seasonality was identified as the environmental layer with the most information not shared with any other variable for 17 and 11 species of *Polylepis*, respectively.

Mean elevation contributed the most to the production all species models when using all environmental layers, followed by climate variables, in particular temperature seasonality. However, a greater contribution relative to climate layers was given with the standard deviation of radar backscatter, for *P. incarum*, and percent tree cover, for *P. lanata* and *P. pacensis*.

### *Woodland distribution*

The potential *Polylepis* woodland area for each country, using a  $\geq 0.5$  logistic threshold, was highest in Peru with a potential area above 290,000 km<sup>2</sup> and Bolivia, with a potential area above 230,000 km<sup>2</sup> (Table 1.4). Argentina was third with a potential area of 76,000 km<sup>2</sup>, followed by 45,000 km<sup>2</sup> in Ecuador, 31,000 km<sup>2</sup> in Colombia, and about

29,500 km<sup>2</sup> in Chile. Venezuela had the least amount of potential woodland distribution with an approximate area of 5600 km<sup>2</sup> centered on the Cordillera de Mérida.

#### *Predicted species richness*

Summing the predicted distribution of 21 species of *Polylepis*, species richness peaked at the high elevation range of the eastern Andes of southern Peru and Bolivia (Fig. 1.2a, d). The distribution models projected a peak of 12 species of *Polylepis* within 75 and 11 km<sup>2</sup> in Peru and Bolivia, respectively (Table 1.4). Also, a much smaller region of the Cordillera Blanca of Peru (Fig. 1.3c) contained high potential concentration of 11 species in the western side of the mountain range. Although potentially containing fewer species, Ecuador peaked at seven species and contained the third highest area for 5–6 species, behind Bolivia and Peru (Table 1.4). Although the predicted richness in Argentina peaked at five species, the total potential woodland area was 69% greater than in Ecuador. Colombia had a potential richness of six species in a total area of about 31,000 km<sup>2</sup>, while Chile had a maximum potential richness of three species within 29,000 km<sup>2</sup>. Venezuela had a predicted richness of seven species, but total potential woodland was restricted to 5,682 km<sup>2</sup>, only 20% of Chile, which had the second least amount of potential woodland.

Areas with the potential of high *Polylepis* species richness had an average elevation of  $3520 \pm 30$  m and standard deviation of topography of  $98 \pm 2$  m. Climate averages indicated an annual mean temperature of  $10.9 \pm 0.2^{\circ}\text{C}$ , a mean diurnal range of  $17.7 \pm 0.1^{\circ}\text{C}$ , and an annual precipitation of  $646 \pm 7.2$  mm. Remote sensing data

indicated a tree cover of  $16.8 \pm 1.0\%$ , a 5 year maximum LAI of  $10.9 \pm 0.2$ , a 5 year LAI range of  $6.4 \pm 0.2$ , and a QSCAT annual mean of  $-10.01 \pm 0.05$  dB.

### *Protected areas*

Our models indicated that in 2007, 172 existing national and international protected areas could potentially support *Polylepis* woodlands (Fig. 1.3). Peru was estimated to contain the most protected woodlands with approximately 30,200 km<sup>2</sup>, which represented only 10.3% of Peru's total predicted *Polylepis* woodland area, using a  $\geq 0.5$  logistic threshold. Similarly, Bolivia's protected areas could potentially contain 26,800 km<sup>2</sup> of *Polylepis* woodlands, representing 11.5% of their total predicted woodland area. Colombia and Ecuador's protected areas could potentially hold 6,000 and 7,200 km<sup>2</sup> of *Polylepis* woodlands, which represent 19.1 and 16.1% of the total, predicted woodland area within their borders, respectively. The southernmost predicted distribution of *Polylepis* in Argentina and Chile were modeled to cover 3,200 km<sup>2</sup> or 4.2% and 6,000 km<sup>2</sup> or 20.3% within their protected areas, respectively. Although Venezuela had among the smallest predicted woodland area within their national and international protected areas, 3,800 km<sup>2</sup>, 66.4% of the total predicted woodland would be protected by existing reserves.

## DISCUSSION

The production of spatially accurate models for the distribution of *Polylepis* species, using climate and remote sensing layers, demonstrated the useful information