Climate change is becoming an increasing threat to biodiversity. Consequently, methods for delineation, establishment and management of protected areas must consider the species’ future distribution in response to future climate conditions. Biodiversity in high altitude semiarid regions may be particularly threatened by future climate change. In this study we assess the main environmental variables that best explain present day presence of the world’s highest elevation woodlands in the South American Altiplano, and model how climate change may affect the future distribution of this unique ecosystem under different climate change scenarios. These woodlands are dominated by Polylepis tarapacana (Rosaceae), a species that forms unique biological communities with important conservation value. Our results indicate that five environmental variables are responsible for 91% and 90.3% of the present and future Polylepis tarapacana distribution models respectively, and suggest that at the end of the 21st century, there will be a significant reduction (56%) in the potential habitat for this species due to more arid conditions. Since it is predicted that Polylepis tarapacana's potential distribution will be severely reduced in the future, we propose a new network of national protected areas across this species distribution range in order to insure the future conservation of this unique ecosystem. Based on an extensive literature review we identify research topics and recommendations for on-ground conservation and management of Polylepis tarapacana woodlands.

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The Altiplano (or “high plain”) is an area of inland drainage (endorheism) lying in the central Andes, occupying parts of southern Peru, western Bolivia, northern Argentina and Chile with average height of 3750 m. The Altiplano climate is characterized by a reduced seasonality in temperature, but a marked seasonality in precipitation with cool-dry winters and cool-wet summers (Garreaud et al., 2003; Vuille and Bradley, 2000). Annual precipitation in the Altiplano varies between 130 and 450 mm along a northeast-southwest gradient, and is >75% concentrated during the summer months with a uniform pattern of inter-annual variability across the region (Garreaud et al., 2003; Vuille and Keimig, 2004). Precipitation over the Altiplano is highly related to the upper-air circulation with an easterly zonal flow favoring wet conditions and a westerly zonal flow favoring dry conditions (Garreaud et al., 2003). Summer is the warmest season with average temperatures ranging from 9° to 12°C (Christie et al., 2009).

Our target ecosystem is the world’s highest elevation woodlands composed of pure stands of *P. tarapacana* Philippi trees (Rosaceae: Sanguisorbeae). This species grows at elevations between 4000 and 5200 m a.s.l. along the semi-arid highlands of the western section of the Altiplano in the Central Andes of Bolivia, Chile, Argentina, and Peru (16°–23°S; Braun, 1997; Navarro et al., 2010; Renison et al., 2013). *P. tarapacana* is a slow growing tree species (5 mm/year in diameter) that can live for over 700 years (Domic and Capriles, 2009; Morales et al., 2012). It has several morphological and physiological adaptations to the extreme environmental conditions of the Altiplano, including semiarid conditions, high solar radiation, and high daily temperature variations (Azócar et al., 2007; García-Núñez et al., 2004; García-Plazaola et al., 2015; González et al., 2007; Hoch and Körner, 2005; Rada et al., 2001). Presently, *P. tarapacana* is classified by IUCN simultaneously as both Near Threatened and at Lower Risk, indicating the uncertainty about its conservation status. Main threats mentioned include fires, mining and wood collection for fuel, timber and construction (World Conservation Monitoring Centre, 1998; Renison et al., 2013).

**2. Methods**

**2.1. Study area**

The Altiplano Woodlands is a slow growing tree species (5 mm/year in diameter) that can live for over 700 years (Domic and Capriles, 2009; Morales et al., 2012). It has several morphological and physiological adaptations to the extreme environmental conditions of the Altiplano, including semiarid conditions, high solar radiation, and high daily temperature variations (Azócar et al., 2007; García-Núñez et al., 2004; García-Plazaola et al., 2015; González et al., 2007; Hoch and Körner, 2005; Rada et al., 2001). Presently, *P. tarapacana* is classified by IUCN simultaneously as both Near Threatened and at Lower Risk, indicating the uncertainty about its conservation status. Main threats mentioned include fires, mining and wood collection for fuel, timber and construction (World Conservation Monitoring Centre, 1998; Renison et al., 2013).

We obtained presence records of *P. tarapacana* through extensive exploration and fieldwork conducted by the authors, scientific publications (Kleier and Lambrinos, 2005; Morales et al., 2004; Renison et al., 2013; Soliz et al., 2009; Zutta, 2009); herbarium collections of the National University of Jujuy (JUA), National University of Salta (MCNS), Miguel Lillo Institute (IL) (Argentina), National Herbarium of Bolivia (LPB; Bolivia) and San Marcos Herbarium (USM, Peru), and online databases from the Missouri Botanical Garden and the Global Biodiversity Information Facility [i.e., Tropicos (www.tropicos.org) and GBIF (www.gbif.org)]. A total of 157 *P. tarapacana* presence records were collected, after removing records that were less than 1 km apart, we retained 116 points that were used to build for SDM of the species.

To develop the present and future SDMs of *P. tarapacana*, we used the maximum entropy algorithm implemented by MaxEnt v3.3K software, which has a predictive performance that has proven to have a good general performance compared to other methods (Elith et al., 2011). Following Phillips et al. (2006), we made 100 partitions by randomly selecting 70% of the *P. tarapacana* presence localities as training data and 30% for testing the spatial accuracy of the resulting models. The area under the ROC (receiver operating characteristic) curve provided a measure of model performance. An Area Under the Curve value for a specific model scenario may range from 0.5 (random) to 1.0 (perfect discrimination). To convert the models with probability values into binary (absence/presence), we used the 10th percentile training presence logistic threshold. This threshold assumes an error...
in 10% of the presence records and therefore excludes the 10% with the lowest probability value. The 10th percentile is commonly used in conservation studies (Abba et al., 2012). For the present model, this value was 0.2429 and approximated well to the distribution of the species based on our knowledge in Argentina (Renison et al., 2013), Bolivia (Navarro et al., 2010) and Chile (personal observations D.C.). As an independent validation of the SDM, after running the model we visited the Altiplano to check the existence of *P. tarapacana* populations in presence areas indicated by the model. Based on currently published research and our knowledge about *P. tarapacana* responses to environmental factors, we selected a set of 11 environmental variables available on the WorldClim database to model its distribution (Hijmans et al., 2005). The spatial resolution of these variables was 30 arc s, approximately 0.85 km². Variables chosen for modeling purposes included: 1. (BIO1) annual mean temperature, 2. (BIO2) annual mean diurnal range (mean of monthly (max temp–min temp)), 3. (BIO3) isothermality (((BIO2/BIO7)*100)), 4. (BIO4) temperature seasonality (standard deviation*100), 5. (BIO7) annual temperature range (max temperature of the warmest month–min temperature of the coldest month), 6. (BIO10) mean temperature of the warmest quarter, 7. (BIO11) mean temperature of the coldest quarter, 8. (BIO12) annual precipitation, 9. (BIO15) precipitation seasonality (coefficient of variation as the standard deviation of the monthly precipitation estimates expressed as a percentage of the annual mean), 10. (BIO16) precipitation of the wettest quarter, and 11. (BIO18) precipitation of the warmest quarter. A Jackknife analysis implemented in the MaxEnt program estimated the relative contribution of those variables. We geographically projected the *P. tarapacana* presence model and divided probabilities of occurrence into the following five categories: values below the threshold value were considered as absent, “low” threshold=0.25, “intermediate” 0.25–0.5, “high” 0.5–0.75, and “very high” >0.75. To calculate the present potential area (km²) of *P. tarapacana* within the existing network of protected areas across it distribution range (Bolivia, Chile, Argentina and Peru), we superimposed the results of the *P. tarapacana* SDM onto a map of the world’s protected areas (IUCN and UNEP-WCMC, 2015).

To generate the future *P. tarapacana* SDM we utilized projections to the year 2070 of the previously mentioned environmental variables available on the WorldClim database (Hijmans et al., 2005), which are calculated from future climate projections of General Circulation Models (GCM) of the Coupled Model Intercomparison Project Phase 5 (CMIP5). Based on work conducted by Seiler et al. (2013), which evaluated the hindcast skill of different GCMs to predict the Altiplano’s climate, we selected the three best available GCMs (MIROC-ESM, IPSL-CM5A-LR, and HadGEM2-ES); each one was run under two different greenhouse gas concentration trajectories (RCP 8.5 and RCP 6.0 [Representative Concentration Pathways]). The RCP 8.5 assumes that global greenhouse gas concentration trajectories will continue to rise throughout the XXI century, and will stabilize in the year 2100. The RCP 6.0 assumes that global greenhouse gas concentration trajectories will peak around 2060 and then decline to stabilize around 2080 at levels higher than those of present day (Meinshausen et al., 2011). As in McCollum et al. (2014) we assume that the RCP 8.5 would be the most likely scenario if no measures are taken to avoid the effects of climate change, and that the RCP 6.0 would be a less dramatic scenario assuming some reductions in emissions do occur.

Finally, to assess the effects that future climate change will have on the presence of *P. tarapacana* in the present network of national protected areas, we generated an average SDM according to the mean environmental variables considered in the three selected GCMs (Pierce et al., 2009; Seager et al., 2007; Velásquez-Tibatá et al., 2013) for both the RCP 6.0 and the 8.5 scenarios. We calculated the mean of threshold of different future models to apply to the consensus model, which was 0.2465 (RCP 6.0) and 0.2624 (RCP 8.5). According to these results, we propose a network of priority protected areas for *P. tarapacana*'s conservation under a future scenario of climate change.

### 3. Results

#### 3.1. Distribution models

The Jackknife analysis showed that five environmental variables explained 91% and 90.3% of *P. tarapacana* presence in the present and the average future models respectively. These variables included mean diurnal range (mean of monthly (max temp–min temp)) (bio2), precipitation seasonality (bio15), mean temperature of the coldest quarter (bio11), mean temperature of the warmest quarter (bio10), and precipitation of the wettest quarter (bio16) (Fig. 2).

With respect to the in situ validation of the SDM carried out by visiting some *P. tarapacana* presence areas indicated by the model, we confirmed the species presence in all the 14 visited localities (blue dots in Fig. 4). The present model is concordant with our knowledge about the species’ current distribution and predicts that *P. tarapacana* will occur most frequently in habitats with high mean diurnal range of temperatures and strong variation in precipitation seasonality (Fig. 3).

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**Fig. 2.** Contribution of the environmental variables determining the potential *P. tarapacana* distribution for present and future climate (RCP 6.0 - Average Model) across the Altiplano.
Fig. 3. Partial dependence plots showing the marginal response of *P. tarapacana* to the two most important variables (i.e., for constant values of the other variables). The percentage of variable importance is indicated below each graph. The y-axes indicate logistic output.

Fig. 4. Digital elevation model of the study area in the Altiplano, Central Andes. Present potential distribution model of *Polylepis tarapacana*, occurrence probabilities are represented as: absence (<0.24), low (0.24–0.25), intermediate (0.25–0.5), high (0.5–0.75), very high (>0.75). Red dots indicate the *P. tarapacana* presence records used to develop the Species Distribution Models (N = 116), and the blue dots indicate confirmed presence records predicted by the model. The diagonal red (light blue) arrow indicate the direction of the tropospheric westerly (easterly) winds which determine the prevalence of dry (wet) conditions over the study region.
Presence records and species distribution models show that this species is present in Chile, Argentina, Bolivia and marginally in Peru, the latter country with only one presence record and approximately 35 km² of potential distribution predicted by a model with good general performance (AUC > 0.9). The main areas of potential presence are situated along the northern and southern limits of its range, with a fragmented distribution in the center of its distribution area. The principal area of potential presence of *P. tarapacana* is located in the humid northern part of its distribution along the border of Chile and Bolivia and with lower probabilities of occurrence in a semicircular area between Bolivia and Argentina, along the southeastern limit of its distribution. The present *P. tarapacana* potential distribution model covers approximately 52,349 km² and is congruent with our knowledge about this species’ distribution, with the exception of an area suggested by the model as of low probability presence for which we have no records of present day populations in the limit between Bolivia and Argentina and west towards the Atacama Desert.

All *P. tarapacana* future distribution models under the two greenhouse gas concentration trajectories (RCP 8.5 and RCP 6.0) showed a significant decrease in the potential distribution of *P. tarapacana* (Fig. 5). The minor reductions were under RCP 6.0, ranging from −41.6% (−21,801 km²) for the MIROC-ESM to −67.7% (−35,431 km²) for the IPSL-CM5A-LR models. For the RCP 8.5, the minor reduction of the potential distribution of *P. tarapacana* was −70.8% (−37,054 km²) for the HadGEM2-ES model, and the most severe reduction was 97.0% (−50,782 km²) for the MIROC-ESM model. All models exhibited a good general AUC performance (Table 1).

At present, the principal protected areas of *P. tarapacana* are located in Bolivia, Chile and Argentina, consisting of 8.1% (4133 km²), 10.1% (5112 km²) and 3.3% (1663 km²), respectively, of the total actual potential distribution, while according to the RCP 6.0 future projection, the current protected areas will contain 13.6% (3885 km²), 17.8% (5095 km²), and 3.6% (1015 km²), respectively, of the total future distribution (Table 2). The RCP 8.5 scenario suggests extreme reductions in the distribution of this species and therefore no new areas for conservation could be identified. Based on the RCP 6.0 average model, we suggest three priority conservation areas. The first two priority areas are already well represented in protected areas situated along the northern edge of...
its distribution along the border of Chile and Bolivia, and in the south between Argentina and Bolivia. A third suggested priority area is located in the middle between the two previously mentioned areas (Fig. 6), where at present no protected area exists. Establishing protected areas between the northern and the southern distribution blocks would reduce isolation of the latitudinal extremes of this species’ distribution range, and given the presumed long distance pollen transport for this Polylepis species, this would ensure gene flow between populations (Schmidt-Lebuhn et al., 2006). The current system of protected areas protects 21.4% (10,908 km²) of the present and 35% (9994 km²) of the future potential species distribution, and our proposed system of priority areas would protect 49% of its future distribution (14,112 km²; Table 2) and 27.7% of current distribution.

4. Discussion

Future reduction of the potential distribution of P. tarapacana would be a consequence of warmer and drier conditions predicted by climate models in Central Andes, as indicated by a lower mean diurnal range of temperatures due to an increment of minimum daily temperatures with respect to maximum daily temperatures (Collins et al., 2013), and a reduction in precipitation seasonality as a consequence of the reduced rainfall in the summer (Minvielle and Garreaud, 2011; Neukom et al., 2015; Thibeault et al., 2010). The fact that MaxEnt model uses certain climatic factors to describe the current distribution of Polylepis does not mean that these fully determine the distribution of the species (i.e. a causality effect);
needed. resilience and adaptation to future environmental conditions more stress (Hamann and Wang, 2006). To further comprehend the species’ P. tarapacana HAdGEM2-ES, IPSL-CM5A-LR) models, negative values indicate retraction from 0.5 (random) to 1.0 (perfect discrimination).

tative Concentration Pathways of greenhouse gasses (RCP 8.0 and RPC 6.5). AUC ranges difference with present surfaces (km²) between present and future (MIROC-ESM, HAdGEM2-ES, IPSL-CM5A-LR) models, negative values indicate retraction of P. tarapacana woodlands. The results of each future climate model are from two Representative

Table 1

<table>
<thead>
<tr>
<th>Model</th>
<th>RCP</th>
<th>AUC</th>
<th>Surface (km²)</th>
<th>Difference with present km² (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present</td>
<td>0.978</td>
<td>52,349</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MIROC-ESM</td>
<td>0.976</td>
<td>8928</td>
<td>-43,421 (-82.9)</td>
<td></td>
</tr>
<tr>
<td>HAdGEM2-ES</td>
<td>0.975</td>
<td>29,631</td>
<td>-22,718 (-43.4)</td>
<td></td>
</tr>
<tr>
<td>IPSL-CM5A-LR</td>
<td>0.965</td>
<td>30,548</td>
<td>-21,801 (-41.6)</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>0.976</td>
<td>28,608</td>
<td>-23,741 (-45.46)</td>
<td></td>
</tr>
<tr>
<td>MIROC-ESM</td>
<td>0.976</td>
<td>373</td>
<td>-51,976 (-98.3)</td>
<td></td>
</tr>
<tr>
<td>HAdGEM2-ES</td>
<td>0.976</td>
<td>15,295</td>
<td>-37,054 (-70.8)</td>
<td></td>
</tr>
<tr>
<td>IPSL-CM5A-LR</td>
<td>0.976</td>
<td>1567</td>
<td>-50,782 (-97.0)</td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td>0.977</td>
<td>1911</td>
<td>-50,438 (-96.3)</td>
<td></td>
</tr>
</tbody>
</table>

nevertheless, our results are consistent with the current ecological knowledge available for P. tarapacana.

All future distribution models showed a significant decrease in the potential distribution range of P. tarapacana, especially towards the southern and driest portion of its current distribution (Garreau et al., 2003). The current lower limit of annual precipitation (bio12) according to the present model is 111 mm, similar to the 100 mm limit proposed by Kessler (1995). The northern and southern limits of P. tarapacana would practically remain unchanged; from 23.407°S in the present to 23.059°S in the future and 17.919°S to 17.597°S in the future.

At present, during the P. tarapacana growing season the lower altitudinal limit of the species distribution exhibits more arid microclimatic conditions than the upper limit (García-Plazaola et al., 2015), generated by higher temperatures (15%) and vapor pressure deficit (19%). Considering that these microenvironmental conditions determine diurnal march of stomatal opening and carbon assimilation by P. tarapacana (García-Plazaola et al., 2015), we expect that under the future scenario of more arid conditions the lowest elevation populations will be the most negatively affected, while it is very likely that higher mountain altitudes will be occupied by P. tarapacana, areas that will constitute a refuge for the species. Interestingly, recent studies of the genetic diversity of the species across its distribution range suggest that during warmer periods of the Pleistocene P. tarapacana populations were restricted to higher elevations and that during cooler periods they migrate to lower altitudes (Peng et al., 2015). Moreover, it remains unknown if P. tarapacana has the potential to respond positively to increments of atmospheric CO₂, as has been described in other species under drought stress (Hamann and Wang, 2006). To further comprehend the species’ resilience and adaptation to future environmental conditions more studies related to its genetics, migration capability, and physiology are needed.

Table 2

<table>
<thead>
<tr>
<th>Country</th>
<th>Potential habitat distribution of Polylepis tarapacana</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Present</td>
</tr>
<tr>
<td></td>
<td>Total surface km²</td>
</tr>
<tr>
<td>Peru</td>
<td>85</td>
</tr>
<tr>
<td>Bolivia</td>
<td>27,652.2</td>
</tr>
<tr>
<td>Chile</td>
<td>15,015.3</td>
</tr>
<tr>
<td>Argentina</td>
<td>8106.5</td>
</tr>
<tr>
<td>Total</td>
<td>50,859</td>
</tr>
</tbody>
</table>

Our models show a northern and southern main nucleus of potential distribution of P. tarapacana separated by a patchy distribution in the middle. If the species’ population would be separated in the future, this could have important genetic consequences despite that P. tarapacana presently exhibits a high gene flow within and between populations (Peng et al., 2015). Given the current high gene flow of P. tarapacana (Schmidt-Lebuhn et al., 2006) and the long distance wind dispersal capacity of the pollen of Polylepis (Liu et al., 2005), it is reasonable to signal the Alto del Loa as a priority corridor area, and thus increases future connectivity between the northern and southern proposed nuclei (Fig. 6).

MaxEnt software accounts for some pitfalls, for example, it does not estimate the probability of occurrence directly, but rather the environmental suitability for the species that can be mapped in a geographic space (Royle et al., 2012). Other software such as MaxLike has been shown to outperform MaxEnt in some cases (Fitzpatrick et al., 2013). Nevertheless, MaxEnt is by far the most widely-used and it has a good general performance (Elith et al., 2006). By using presence records from its entire range and testing for collinearity among bioclimatic variables, we improved the scientific rigor of MaxEnt analysis.

Besides designating a new protected area, existing protected areas should have effective management plans (Bonham et al., 2008; Bruner, 2001), such as the management plan of Sajama National Park that has a specific chapter for the conservation and management of P. tarapacana (BID et al., 1997) and the Chilean national reserves where logging of the species is forbidden and controlled. Management plans should contemplate tourism, restriction of grazing and fire use, and regularization of firewood extraction, involving social actors including local governments, mining companies, ONG’s and local communities. The tripartite area between Argentina, Bolivia and Chile is of special conservation interest as it is also a key area for the conservation of the endangered Andean cat (Marino et al., 2010), flamingos (Caziani et al., 1999), vicuñas (Arzamendia et al., 2006), and several bird species. This is also the area where P. tarapacana exhibits the highest genetic diversity in this area (Peng et al., 2015). The remoteness of this area could facilitate its conservation, but also makes management and implementation more difficult. In Bolivia, main conservation efforts should be focused in the northern extreme by setting a larger single protected area. In Peru, the species has a distribution which is so restricted that probably conservation efforts would not have a significant impact at a global scale, but it is up to the country its national heritage.

The potential P. tarapacana distribution does not necessarily mean real presence or future disappearance of the species. Nevertheless, niche modeling is a very useful method for species distribution projections. After running the SMD, all the visited P. tarapacana presence areas presented populations of the species, corroborating the good predictive power and the usefulness of the model. It is also a valuable tool to estimate future biodiversity representation in protected areas and set up measurable conservation goals. Moreover, results of habitat loss do not necessarily mean extinction but certainly increase the local extinction risk (Alarcón and Cavieres, 2015). The Convention on Biological
Diversity recommended a minimum representation level of ecosystems and species habitat under protection between 10% and 12% (Burgess et al., 2005; Tear et al., 2005), or 17% for terrestrial ecosystems (Molainer et al., 2013). According to our results, the current network of protected areas achieves this recommended area (21%) and in the future will include 35% of the species distribution, and with our proposed areas; this would increase to 49%. However, this is not due to an increase in protection, but to the reduction in future potential habitat that take place outside protected areas, what could be called “a blessing in disguise” (Fig. 6).

P. tarapacana woodlands represent the world’s highest elevation woodlands that protect watershed and offer habitat for unique biogeographical communities (Kessler, 2006; Yallico, 1992). Presently, the Polylepis woodlands are threatened by logging, grazing, fire and in some areas by large-scale mining (Renison et al., 2013; Segovia et al., 2012). Consumption of large water volumes is the most important environmental challenge of mining activities (Kirschbaum et al., 2012; Mighenetara et al., 2009; Navarro et al., 2008) since groundwater has a very slow rate of natural recovery (Strahler and Strahler, 1989). A relatively new threat for the species is the infection with the Lepthosphaeriapolylepidis fungus, which may become more severe under future climate conditions (Coca-Morante and Oteng-Amaako, 2012). Our results demonstrate that climate change would severely and negatively impact P. tarapacana distribution and may become the main factor threatening the future conservation of these ecosystems.

Presently, water stress is increasing tree mortality at global scale (Allen et al., 2010). An increment in the number of meteorological stations in the Altiplano region would help improve climate data utilized in P. tarapacana distribution models and thus the reliability of SDM. The presented future P. tarapacana distribution models suggest important changes over the present century, a relative short timescale compared to the lifespan of the species. The present study represents the first effort to assess how climate change may affect the future distribution and conservation of P. tarapacana, the world’s highest elevation woodlands in the South American Altiplano.

Acknowledgments

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Elith, J., Graham, H.C., Anderson, P.R., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R., H 2011. A relative new threat for the species is the infection with the Lepthosphaeriapolylepidis fungus, which may become more severe under future climate conditions (Coca-Morante and Oteng-Amaako, 2012). Our results demonstrate that climate change would severely and negatively impact P. tarapacana distribution and may become the main factor threatening the future conservation of these ecosystems.

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Acknowledgments

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