Research Article

Using potential distribution models for patterns of species richness, endemism, and phytogeography of palm species in Bolivia

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Abstract

Distribution patterns of palms, particularly species richness along latitudinal and altitudinal gradients in Bolivia, are still unknown. A species distribution model was used to identify areas with potentially high palm species richness and endemism. Two models were used: the environmental niche model and a deductive model. A map of potential palm species richness in Bolivia was prepared using 1 km^2 pixels. Two areas are predicted to concentrate most of the potential palm species richness of Bolivia: the southwestern Amazonian moist forest, and the Yungas Andean forest of Bolivia. The potential distribution of Bolivia's endemic palm species appeared to be associated to the eastern side of the Andes. Most palms have Amazonian phytogeographic influences, followed by Andean. The areas identified with greatest potential species diversity coincided with observed patterns at a continental level. The greatest palm richness of northern and northwestern Bolivia may be related to the climatic conditions of these zones. Bolivia represents the southern and western distribution limit of many palm species in terms of continental phytogeographic patterns.

Keywords: Arecaceae; Bolivia; phytogeography; modelling distribution.

Resumen

Aún se desconocen los patrones de distribución en un contexto geográfico de las palmeras nativas de Bolivia que incluyan el análisis del decremento de la riqueza de especies respecto a la latitud y altitud. Se aplicó el enfoque de modelaje de distribución de especies para identificar áreas con riqueza potencial de palmeras y concentración de las especies endémicas. Se aplicaron dos métodos de modelaje para la distribución de palmeras: el modelo de nicho ambiental y el deductivo. El mapa de riqueza potencial de palmeras bolivianas fue preparado en base al número de especies en cada unidad de muestreo (un pixel de 1 km^2). Se predijeron dos ecorregiones que concentrarían la mayor riqueza de palmeras de Bolivia: el sudoeste del bosque húmedo amazónico y los Yungas, en las laderas orientales de los Andes. La distribución potencial de las palmeras endémicas podría estar asociada a la zona andina oriental del país. La mayor parte de las palmeras estaría influenciada por afinidades amazónicas, seguida por las andinas. Estas áreas con la mayor riqueza de especies de palmeras coinciden con patrones continentales que caracterizan a este grupo de plantas. La mayor riqueza de palmeras al N y NO de Bolivia podría relacionarse a las condiciones climáticas. En Bolivia se representa la distribución más sureña y occidental de muchas especies de palmeras en términos de patrones fitogeográficos continentales.

Palabras clave: Arecaceae; Bolivia; fitogeografía; modelos de distribución.

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Introduction

The Arecaceae family, with 2,450 species worldwide [1], is one of the best-known tropical families of flowering plants [2, 3]. Globally, low temperatures seem to be the main climatic constraint for the distribution of the palm family. Most species are found throughout the tropical and subtropical region, with very little occurrence in temperate areas [2, 4, 5, 6]. According to Pintaud *et al*. [5], the South American continent appears to be one of the main centers of richness and diversity for the family. Eighteen genera are endemic to South America, while other genera show their diversification at the species level: *Geonoma* Willdenow (69 spp.), *Bactris* Jacq. ex Scopoli (61), *Attalea* H.B.K. (56), *Astrocaryum* G. Meyer (39), and *Syagrus* C. Martius (35). Here we examine a total of 87 native palm species that are naturally occurring in Bolivia.

In Bolivia, palm species distribution patterns may depend on altitude [7-9], climate and latitude [9,10], and also topographic and edaphic conditions, but these interactions have not been correlated yet. A few studies have concluded that: a) most of the palm diversity is found at altitudes between 140-500 m (both at the generic, 81%, and specific. 79%, levels) in the west side of the country [8] and b) species diversity decreases with increasing distance from the equator [9]. A preliminary analysis of palm biogeography in Bolivia referred to four main phytogeographic provinces: Amazonian (54% of total species), Cerrado (7%), Gran Chaco (2%), and Andean (29%) [11]. These features (altitudinal, climatic, latitudinal, and others) have not been examined within geographic layers, suggesting the need to identify with greater precision places with suitable ecological characteristics for palm species, especially because of the importance of some species for humans [12,13] and mammals [14,15].

In the present study, we examine the potential distribution patterns of palm species in Bolivia for the first time, in order to identify areas with high potential species richness and concentration of endemic species. Given Bolivia's geographic location, ranging from tropical to subtropical latitudes, and the habitat heterogeneity conferred by the Andes, this study contributes important information about the phytogeographic interpretation of palm distribution. Finally, using the distribution models, we assessed the effectiveness of the Bolivian protected area network for the conservation of palm species.

Methods

Study area

Bolivia is a tropical country with an area of 1,098,581 km^2 [16]. It has a wide altitudinal gradient from 72 to 6,204 masl, and a latitudinal southern variation from 9°39' to 22°53'. Bolivia presents a high ecological variability due to geographical, physiographical, and climatic factors [16-21]. Two main factors determine this variability: the Andes mountain chain and Bolivia's tropical and subtropical location both provide conditions of transition and biogeographic confluence [22]. According to Josse *et al*. [23], the phytogeographic units represented in Bolivia are as follows: Andes (mountains: north central moist Andes, and south central dry Andes), Amazonia, and Cerrado (Fg. 1). Only the Andean high plateau at the western side of the country lacks native palms [24,25].

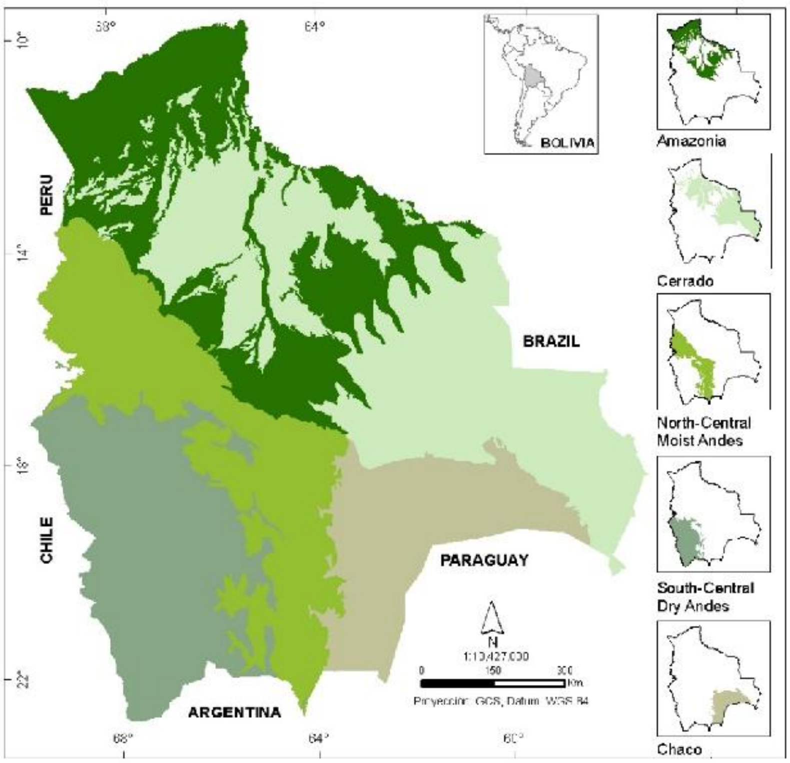

Fig. 1. Map of Bolivia showing the phytogeographic units - based on Josse *et al*.[23] - where native palm species are found,. Each unitis also shown separately.

Species selection and dataset

By reviewing bibliography, published catalogues, species collections, and information available in online databases, a cleaned database of 1,853 georeferenced records was compiled for 87 palm species reported in Bolivia (up until 2010). To build this dataset, we consulted Moraes and Moreno & Moreno [24,25], plant collections of the Herbario Nacional de Bolivia (LPB), the Herbario Nacional Forestal Martín Cárdenas (BOLV), Herbario del Oriente Boliviano (USZ), and data from the Missouri Botanical Garden (www.tropicos.org, May 2013). The dataset includes 87 palm species [24,25]. These data and maps were generated in this study and will be available through the biodiversity information system of the Amazon, an initiative led by Bolivian government to gather biological data at a national scale.

Environmental data

In order to prepare prediction maps of the distribution of Bolivian palms, seven climatic variables from the Worldclim project were used [26]: BIO1 = Annual Mean Temperature, BIO10 = Mean Temperature of Warmest Quarter, BIO11 = Mean Temperature of Coldest Quarter, BIO12 = Annual Precipitation, BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, and BIO17 = Precipitation of Driest Quarter. These variables were placed in a grid with a resolution of 30 arcsec (ca. 0.0083 decimal degrees x 0.0083 decimal degrees). The model was run using these seven bioclimatic variables together with a digital elevation model to 90 m (0.81 ha) (DEM, Void-filled seamless SRTM data V1, 2004). The following layers were also employed, MODIS vegetation continuous fields [27]; FAO's soil type classification (www.caf.com/view/index.asp, July 2009); ecological system complexes for South America prepared by The Nature Conservancy [23]; Bolivia's water bodies from the Condor Geographic Information System (www.caf.com/view/index.asp, July 2009); and ecoregions from World Wildlife Fund-WWF [28]. Given the coarse delimitation among units of the classification system defined by Josse *et al.* [23], we considered it as a reference for phytogeographic affinities of palms in Bolivia.

Potential distribution maps

Depending on the total number of records for each species, single-species potential distributions were generated using two approaches. If the species had ten or more independent presence records, separated by at least 1 km, an environmental niche modeling approach was used [29-31]. For species with fewer than 10 records, we applied a deductive approach. Following the procedures of Hernandez [32] and Larrea-Alcázar *et al*. [33], a potential distribution map per species was generated on the basis of each record as a point presence. In order to generate distribution polygons this information was used together with the vegetation series map of Bolivia [21,34], and the altitudinal interval for all points registered for a given species. A joint distribution map was developed when more than two polygons resulted from this process. Maxent is a learning algorithm, based on the concept of maximum entropy, that makes predictions from incomplete information [35,36] and was selected to work with the environmental niche approach. The important features of this approach are that it estimates the most uniform distribution across a given area; that it uses few points to perform its estimations; and that it only needs presence points, unlike other approximations which need absence data as well [29,31].

In order to develop models with Maxent, a 10^{-5} convergence threshold with 1,000 iterations was selected. Eighty percent of the presence records were employed for each species as training points, and the remaining 20%, as testing points. Probabilities of presence values were transformed to presence-absence data, taking the training threshold as a cutting value [36].

Specialists revised the maps obtained with both approaches; in some cases the threshold had to be changed to adjust the species distribution [*sensu* 37]. Isolated cells on the resulting maps were deleted applying the Majority Filter extension of ArcGis (ESRI Inc.). To delete high-altitude overestimation of the presence of each species a 3,500 masl altitude mask layer was applied, as it constitutes the known altitudinal limit of palms in the Neotropics [4].

Patterns of species richness, endemism and conservation
The potential richness map of Bolivian palm species was prepared based on the number of species present on each grid or sampling unit (ca. 30 arcsec). The number of species for each phytogeographic unit below 3,500 masl represented in Bolivia [23] was calculated. Then, the species richness for each ecoregion was obtained through a distribution model and compared with those obtained directly from collection records, using the ratio number of predicted species over the number of collected species, in which values ranged from 0 to 1. A value of zero represents the greatest difference between these two kinds of approaches, and a value of 1 represents the greatest similarity.

The map on endemism richness was prepared using the same criteria used for potential richness, except that in this case just the endemic palm species recorded for Bolivia were considered. Finally, a layer with the boundaries of protected areas at a national level was added to the richness and endemism maps in order to survey the level of conservation of Bolivian palms. All analyses were conducted using ArcGis 10.1 (ESRI Inc.).

Phytogeographic trends
In order to describe the phytogeographical affinity of palms in Bolivia more accurately,a list of present species distribution was adjusted based on current knowledge of sites with a high number of species per genera, and also information about their probable dispersal routes. The number of species was registered for five phytogeographic zones below 3,500 masl in Bolivia –Cerrado, Amazonian, Andes (with two divisions: North Central moist and South Central dry), and Chaco [23]. These trends were also described using published palm distribution data from regional [4], Amazonian [38], Andean [39,40], as well as Bolivian studies [9-11,41,42]. Additionally, this information was supplemented with unpublished recent information from the database of the national herbarium in La Paz. We considered total species richness per phytogeographic zone, as well as exclusive species or those widely occurring in more than one zone.

Results

For the 87 palm species occurring in Bolivia, a total of 1,853 valid distribution records were obtained. Fifty-nine species had more than 10 records, allowing us to model their potential distribution with the Maxent program. For the remaining 29 species, the deductive method was employed.

The average number of records obtained per species was 21 (min: 1, max: 137). Five species were recorded only once and their potential distribution was estimated using the deductive method. The species with the greatest number of records was *Geonoma deversa* (Poit.) Kunth (socalled jatata palm). All the final models obtained with Maxent had an AUC greater than 0.9, except for *Syagrus comosa* C. Martius, which only reached a value of 0.717. The models of two species were somewhat inconsistent as expected by the program, having obtained a value of 1.00; therefore those models were had to be redone using the deductive method.

Similarities between predicted and collected species

The phytogeographic unit with the largest number of species with a verified distribution based on presence points was the Amazon with 68 species, followed by the north central moist Andes with 54 and the Cerrado with 45 (Table 1). In the Chaco, eleven species were present and in the South central dry Andes, just one species was registered. In the potential distribution map, the Amazon unit presented the highest number of species (78), representing 89% of all species at a national level; followed by the Cerrado (75), and then the north central moist Andes (67) (Table 1). Again, the Chaco and the South central dry Andes hosted lower potential numbers of palms with only 37 and 21 species respectively. According to the distribution models, the ratio between the observed and expected species was high for the phytogeographic units with the greatest number of species (0.87 for the Amazon), and progressively lower as the number of recorded species and those predicted by the models declined (0.05 for the South central dry Andes).

Table 1. Presence of palm species recorded and estimated by Maxent for each of the phytogeographic units of Bolivia. The ratio recorded species /estimated species shows, indirectly, the degree of taxonomic knowledge for the group in each unit. The environment describes the landscape main environmental features and its location inside the country.

Phytogeographic units [24]	Recorded (R)	Estimated by Maxent (E)	Ratio (R/E)	Environment
Amazonia	68	69	0.98	Humid north
North central moist Andes	54	60	0.90	Humid west
Cerrado	45	48	0.93	Humid east
South central dry Andes	1	1	1.00	Dry central and south
Chaco	11	13	0.84	Dry south

Potential richness, endemism and conservation

Two areas were predicted to concentrate most of the potential palm species richness of Bolivia. The first area corresponds to the northeastern zone of the country (Amazon) and the second to the central western zone (Central moist Andes). Although the north east of the country (in the area surrounding Riberalta) shows grids with the greatest number of species (31 to 38 species per grid), the central-western zone exhibits the greatest number of grids with high values of potential richness. However, most of the palm distribution area in the country (almost 90%) had grids containing fewer than 16 species (Fig. 2). In the humid Andean mountains, two patches of high richness were found: one to the west (close to the Peruvian border) and another in the central region of the country.

The potential distribution map of Bolivia's endemic palm species shows a predominant association with the eastern side of the Andes. Only in the central part of the country were small areas that could potentially harbor two endemic palm species. The rest of the distribution area of endemic species to Bolivia shows pixels with only one species (Fig. 3).

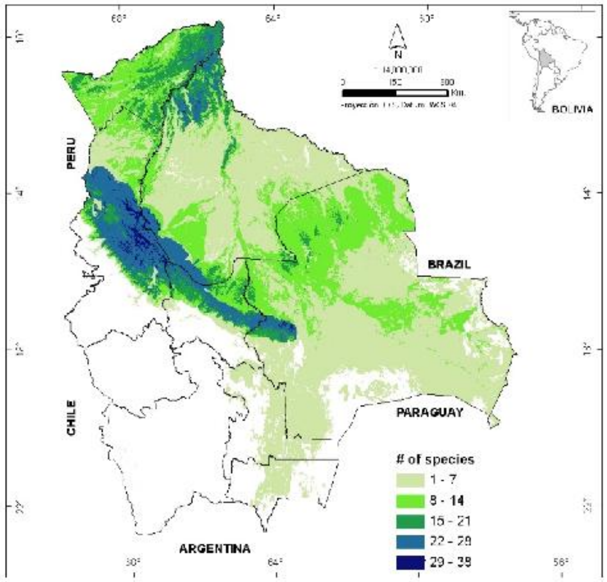

Fig. 2. Map of potential species richness of Bolivian palms. The potential richness is composed of single maps produced by inductive (MaxEnt) and deductive methods.

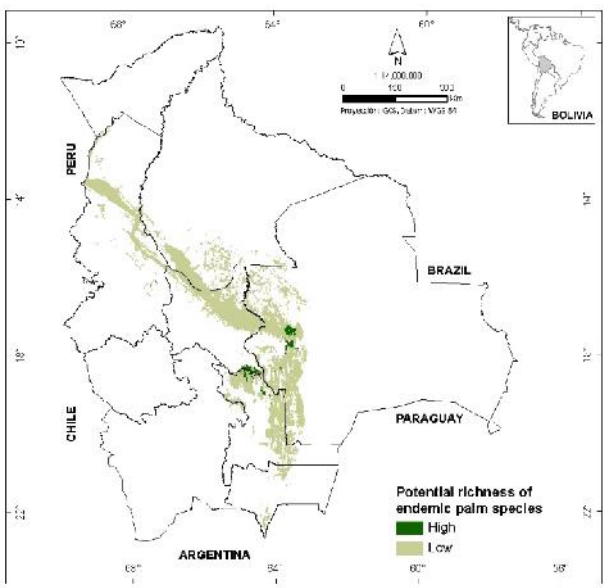

Fig. 3. Map of areas of concentration of Bolivia's endemic palm species and silhouettesof 22 conservation units of the national system of protected areas. Dark sites are the places where two species were present; the remaining distribution area corresponds to the presence of a single species.

The protected area network analysis for potential richness (Fig. 2) represents approximately 35% of the grids containing more than 17 species. The west of Bolivia bears an extensive area conserving palm species, whilst other areas of high palm diversity located in the north are covered partially by only one protected area. In the case of endemic species, 28% of the potential area with endemic species was included within a protected area; *Bactris faucium* C. Martius (marayaú palm) has a wider extension and was present in more than one protected area (Fig. 3). On the other hand, two species were not present in the Bolivian protected area network (*Parajubaea sunkha* Moraes -sunkha palm- and *Syagrus yungasensis* Moraes- coquito palm).

Phytogeographic trends

For these 87 palms, the phytogeographic zone with more species (70) was the Amazon, but only 22 species were exclusively found there; the remnant are distributed within 2-3 zones. Forty-eight Andean palms (38 under moist regimes and 10 under drier regimes) have 10 exclusive species (eight under moist regimes and two under dry). The Cerrado is represented by 32 palms (three exclusive) and the Chaco by seven (none exclusive). The Cerrado and Amazon have the highest number of widespread species, with 15 and 14, respectively; only two palms are found in four units: *Acrocomia totai* (totai palm) and *Copernicia alba* (palma blanca palm) (Table 2). A total of 35 species exclusively belong to one phytogeographic unit, and the Amazon bears the highest number of these palms of restricted distribution (22) (table 3).

Table 2. Widespread palms that are found in more than two phytogeographic units of Bolivia. Presence: 1, absence: 0.

	Cerrado	Amazonia	NC-moist Andes	Chaco	SC-dry Andes
Acrocomia totai	1	1	0	1	1
Allagoptera leucocalyx	1	1	0	1	0
Astrocaryum gratum	0	1	1	0	1
Attalea princeps	1	1	1	0	0
Bactris concinna	1	1	1	0	0
Bactris gasipaes	1	1	1	0	0
Bactris major	1	1	0	1	0
Copernicia alba	1	1	0	1	1
Euterpe precatoria	1	1	1	0	0
Geonoma occidentalis	1	1	1	0	0
Geonoma densa	0	1	1	0	1
Mauritia flexuosa	1	1	1	0	0
Socratea exorrhiza	1	1	1	0	0
Syagrus cardenasii	1	0	0	1	1
Syagrus sancona	1	1	1	0	0
Trithrinax schizophylla	1	0	0	1	1
Total	15	14	10	6	5

Table 3. Restricted distribution of Bolivian palms that exclusively belong to one unit.

Phytogeographic unit	Restricted palm species
Amazonia (22)	*Attalea blepharopus, Astrocaryum jauari, A. gynacanthum, Bactris maraja, B. hirta, Chamaedorea pauciflora, Chelyocarpus chuco, Desmoncus mitis, D. polyacanthos, Iriartella stenocarpa, Oenocarpus balickii, O. mapora, Geonoma deversa, G. interrupta, G. laxiflora, G. leptospadix, G. macrostachys, G. pohliana, G. maxima, G. stricta, Phytelephas macrocarpa, P. tenuicaulis.*
North Central moist Andes (8)	*Bactris faucium, Ceroxylon parvifrons, C. pityrophyllum, Dictyocaryum lamarckianum, Euterpe longevaginata, Geonoma megalospatha, G. undata, Syagrus yungasensis*
Cerrado (3)	*Attalea eichleri, Astrocaryum campestre, Syagrus comosa, S. oleracea, S. petraea*
South Central dry Andes (2)	*Parajubaea sunkha, P. torallyi*

Discussion

Bolivia's palm species richness (87 species) is moderate compared with that of other South American countries [11,42]. The country is ranked sixth among 13 countries of this region. This is due to the fact that in the American continent, a greater part of the diversity of this family is found closer to the equator [2,9,42,44]. Among limiting factors for palm distribution, latitude, altitude, climatic conditions, and historical events have shaped present-day distribution patterns [2,4,11,45,46]; Moraes [11] pointed out that the higher palm species richness of Bolivia occurs on humid, well-drained soils over a wide altitudinal range compared to wet or flooded substrates. Except for the niche approach explained by climate used by Svenning *et al*. [46], all the other factors were considered during the modeling phase of the present study. Moreover, our work corroborates Blach-Overgaard *et al.*[47]who found that although climate is the only strong environmental control of palm species distributions in Africa at large scales, non-climatic variables are needed for accurate estimations of the distribution area of this keystone group.

Areas identified with greatest species diversity coincide with observed patterns at a continental [2, 9] and national level [11,44,48]. Other studies [11,44,48] show that Bolivia's northwestern, central and northern regions may have the greatest palm species richness. On the other hand, palms exhibit a richness pattern different from those of other plant groups in Bolivia [49]; unlike studies finding Bolivia's Yungas region (Central moist Andes) the most diverse for bromeliads, tree legumes, orchids, grasses, and Solanaceae, our results show that the Amazonian forest is similar to the Central moist Andes in terms of palm species richness. At landscape and broader scales, the distribution of palm species is driven by climate, soil, topography, vegetation, and dispersal, the last being poorly studied [50].

Palm richness of mentioned regions in Bolivia may be related to the climatic conditions of these zones. The northern area belongs to Amazonia and the Central moist Andes in Bolivia [23] and encompasses humid regimes towards the center of the country – in the Chapare region – with more than 6 meters of annual rainfall. These areas are characterized by high humidity (with vapor pressure levels of up to 27 hectapascals) and warm temperatures (between 22 and 27ºC) that make them favorable sites for the establishment of many palm species [2]. We include two additional remarks on the Riberalta site, the northern-east in Bolivia: it includes both Amazonian and Cerrado phytogeographic palm elements and contains many species with restricted ranges for the country; most of the species under the deductive method had records in that area.

On the other hand, the forests of the Andes in Bolivia have many palm species and their influence is even larger. Compared to Peru, from 0 to 1,000 masl the Andean region concentrates 18 genera and 45 species while for Bolivia decreases to 12 genera and 26 species [4]. According to Bjorholm *et al*. [51], in the American continent there are two areas with high palm species richness: 1) northern Peru and southern Colombia with elements of Andean, Colombian Chocó, Amazonian, and Pleistocenic refugia [52],characterized by their high diversity ; and 2) the Manaus region, in the Center of the Brazilian Amazonia, characterized by climatic stability with high humidity and temperature values that ensure the establishment of palms.

Most Bolivian palms are adapted to the lowlands and include more than 80% of genera and species [8,10]. According to Moraes [11,48], this richness is not homogeneous. More than half of the palm species (62.5%) are found between 500 and 1,800 masl along the NW limit of Madidi national park, within the Amazonian ecological system; three other sites in northern, central and eastern Bolivia show medium richness with up to 37 species; and six zones in the south and open landscapes of the NEhave up to 14 species. Our model supports these patterns: most Bolivian palms would be expected to be distributed below 500, since most of them have their origin in the Amazonian lowlands [2,11]. In a study of richness patterns along an altitudinal gradient of the Yungas montane forest [7] in central Bolivia, those at intermediate altitude (approximately 1,500 masl) showed the greatest richness of palms for the ecoregion [53]. Our data confirm this pattern for the northwestern part of the country, where the highest number of species of the Yungas forests (central moist Andes system) is predicted at intermediate altitudes within that ecoregion.

Low richness of palms in eastern and southern Bolivia can be explained by Salm *et al*. [44]. Although these authors present a map of palm species richness for Brazil, their data can be applied to the lowlands of north and eastern Bolivia, as both countries share two phytogeographic units (Amazon and Cerrado). These authors found that the Cerrado region and the Madeira – Tapajós moist forest (in the Amazon that connects with E. Bolivia) have the lowest number of palms (5-13 species). Our results thus highlight the importance of the humid forests in the Bolivian Amazon, as opposed to the Cerrado on the Precambrian shield, which shows a low to moderate richness for the group.

The geographic region occupied by Bolivia represents the southern and western limit of many palm species. For example, Moraes [42] cited 16 palm genera with southern distributional limits in Bolivia. The presence of species like *Copernicia alba* Morong ex Morong & Britton and *Trithrinax schizophylla* Drude (sao palm), in the composition of plant communities of Bolivia's subtropical zones distinguishes and characterizes this zone [4], which encounters seasonal flooding and extreme dry conditions, both limiting factors, especially for the second species [10].

On the other hand, it is known that as species reach their distributional limits, they decline in abundance and their distribution becomes discontinuous [54,55]. Apparently, many species that are found in Bolivia follow that pattern, since they have relatively small distribution areas within the country. This explains why the northern region exhibits low population values, although they have a wide distribution at a continental level.

Comparisons between potential and real distribution confirmed that most species fit into trends predicted along with climatic variables. However, some species were outliers to this trend, such as several species of *Geonoma* and *Ceroxylon* that are mostly adapted to humid conditions and showed predicted presence in the Cerrado or Chaco (less humid and dry, respectively), or *Trithrinax schizophylla* Drude that is found naturally in dry forests and was predicted to occur in the humid conditions of the Amazon and Yungas.

Henderson [38] pointed out some recurring endemicity patterns that show a continental trend in four geological provinces: the Guayana and Brazilian shields, the Amazon basin, and the central Andes. The five endemic species of Bolivia are characteristic of montane forests which are humid and dry. Moraes [56] recognized three types of valleys: moister forests in the north, central dry and deciduous forests, and southern dryer vegetation with a higher percentage of endemic palms. Only *Bactris faucium* C. Martius is present in the areas with greater potential richness of Bolivian palms, and it is the only endemic palm occurring in the southwestern Amazonian moist forest [28]. The remaining four species show various degrees of adaptation to dry habitats (11,24). Both *B. faucium* and *Syagrus cardenasii* Glassman (corocito palm) could be considered widely distributed palms, while the other three species have limited distributions and can be considered rare (*Parajubea sunkha*, *P.torallyi* (C. Martius) Burret, and *Syagrus yungasensis*).

Our results corroborate previous phytogeographical trends reported by other publications [9-11,42,56]. On average, the contribution of Bolivia to the palm genera richness of the Neotropical phytogeographic region is of 29%; displaying three patterns of influences, 1) northern Neotropics related to the Andes with reduced number of palms, 2) central Neotropics related to the Amazon with high number of palms, and 3) central South America related to the Cerrado with intermediate numbers [44]. For example, only three exclusive Cerrado palms were registered for Bolivia (*Attalea*: 1 sp., *Syagrus*: 2 spp.). Henderson [38] remarked that Brazilian shield palms are fewer and mostly belong to two genera (*Syagrus* and *Attalea*). The least represented phytogeographic zone in Bolivia is the Chaco (7 spp.) and has no exclusive species.

Historical dispersal of palms in the continent was also helped by human occupation, based on the economic importance of certain species such as *Bactris gasipaes* (chima or tembe palm), *Socratea exorrhiza* (pachiuba palm), *Oenocarpus bataua* (majo palm), and *Syagrus sancona* (sumuque palm) [38]. These species were registered in three phytogeographic zones in our analysis for Bolivia.

The western Amazon has a higher number of species, with 63% of taxa included within Amazonian boundaries [10,41]. Most Amazonian palms in Bolivia, at their southernmost distribution limit, show a widespread distribution along other phytogeographic zones, such as the Cerrado and Andes. Finally, the Andes are enriched by a high number of palms due to topographic reliefs and historic uplifts that resulted in modelled fragmented scenarios for their establishment [38]. The predominance of 79% of palm species in the Bolivian northern central Andes over the southern dry Andes may also be derived from historical geological and climatic events. Two exclusive palms of the southern dry Andes in Bolivia were probably influenced by southern Gondwanic tracks [4,9].

Implications for conservation

The application of this model to potential native palms in Bolivia is useful for conservation purposes because phytogeographic units do not show a transitional gradient from one landscape to the next, and this feature provides an enhanced viewpoint. Fortunately, the model can also be supported by real but scarce information based on georeferenced data (from scientific material). Moreover, no palm species has distribution patterns that are comprehensively understood. The richness trend supported by the distribution model for Bolivian palms is fundamental to identifying larger spatial areas of greatest importance for conservation planning and decision-making. Thus the western limit of the central moist Andes in Bolivia would be of particular conservation importance for palms because of their species richness and are included in a large complex of national protected areas that in total represent 20% of Bolivia (see Fig. 3), namely Madidi, Apolobamba and indigenous lands (for example,Tacanas and Lecos ethnic groups) [57,58]. As local human communities in Bolivia are already involved in discussionsabout conservation and management of biological resources in protected areas and indigenous lands, both areas may ensure the conservation of palms by regulating their use and protecting their environment under general and specific management plans. In the north of Bolivia, within the Amazon basin, the conservation scenario is less encouraging because only one protected area is present, the Manuripi Amazonian Wildlife National Reserve [57,58], with fewer options to protect all Amazonian species. Because many rare species at a national level are also found in this area, it is also necessary to promote palm conservation outside protected areas and to attend conservation vulnerabilities that need to be documented under a landscape ecology perspective. This would provide a way forward to reconcile two seemingly opposing visions, the landscape ecology and protected areas. In this sense, palms would be a prime example.

The current national protected areas network is inadequate to conserve all the endemic palm species. Three species – *Bactris faucium, Parajubaea torallyi* and *P. sunkha*- are partially protected (just a quarter of their potential distribution) but the remaining two endemic species are devoid of any level of protection and are under threat from overexploitation and loss of habitat. We suggest additional conservation strategies are needed, such as local municipal protected areas to complement protected areas managed by the central government. In Bolivia there is already the precedent of a protected area (ANMI El Palmar) created mainly to conserve populations of *Parajubaea torallyi* [57,59], a palm species with a vulnerable conservation status according to the Red Book of Andean Bolivian plant species [60].

Considering that climatic variables - especially related to water regimes – concentrate palm diversity in two areas of the Andean region of Bolivia, future climatic changes will threaten these populations with increased temperatures and drier conditions. A particular concern is the retreat of glaciers and their water melt reservoirs in the high Andean mountains of Bolivia due to atmospheric warming [61], since they provide 20% of the Andean and Amazonian watershed flow.

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