

Phytogeographical Patterns of Bolivian Palms

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In this paper the phytogeographical patterns of palms in Bolivia are analyzed with respect to the boundaries of phytogeographical provinces and the present vegetation. Palm communities are characteristic of specific geographical regions. Species related with the Amazon region are 51% of the total palm diversity of the country, followed by the other regions: Andean (31%), Cerrado (14%), and Gran Chaco (2%). Higher species richness is present on humid, well-drained soils over a wide altitudinal range when compared to wet or flooded substrates.

Bolivia has rich biodiversity, with more than 2500 known species of vertebrates and an estimated 18,000 species of vascular plants, both groups placing Bolivia among the most important countries in Latin America for the conservation of biodiversity. This diversity is the result of a juxtaposition of tropical and subtropical climates with mean annual temperatures ranging from 8 to 27°C and mean rainfall of less than 100 to 1800(–6,000) mm (decreasing westwards and southwards) along an altitudinal gradient of 140–6700 m above sea level (although slightly over half of the country lies at 230–900 m). Bolivia includes diverse ecoregions (Moraes & Beck 1992) and is divided into two main zones: highlands to the west (500–6700 m) and lowlands to the east (below 500 m); most of these ecoregions will be mentioned according to the presence

of native palms. A preliminary approach to biogeography of Bolivia recognizes four main phytogeographic provinces: the Amazonian, Cerrado, Gran Chaco, and the Andean region, this last subdivided into the Altiplano, the mid-east, south-east and west cordilleras (based on Moraes & Beck 1992, see figure 1). The Amazon is characterized by a tropical climate (temperatures of 22–27°C and rainfall of 1000–2000 mm per year) with less than five dry months, and the landscape is covered by different types of forests, savannahs, and wetlands. The Cerrado is more related to a prairie landscape and island forests on a hilly relief; the climate is also tropical. The Gran Chaco is mostly dominated by spiny and xerophytic forests and has a very extreme climate: dry and hot during winter (reaching 40°C at noon and dropping to -10°C at night).



1. Phytogeographical provinces of Bolivia based on Moraes & Beck (1992).

Finally, the Andean region shows a distinct chain of mountains and valleys in its eastern slopes and also a high plateau between both "cordilleras." Climatically, there is a north portion with wetter conditions while the south is dry and the vegetation shows a seasonal dynamic during the winter; for example, in the high plateau (or Altiplano) has temperatures 7–11°C (and during winter below 0°C) and rainfall of 300–500 mm, while the montane slopes has ranges of 16–19°C and 1000–1500 mm. The vegetation on the eastern slopes varies from moist forests in the north to dry forests and also a mixture of tropical and temperate forests in the tucumano-boliviano formation towards the north of Argentina. No native palms are found in the western side of

the Andes, nor the high plateau where prairies, deserts and salt lakes are found.

Palms are an important source of fruit, fiber and wood for human communities and are often considered to be a keystone functional group due to their importance to wildlife populations. The distribution patterns of palms are important for the interpretation of their natural history and evolution as well as understanding variation at local and regional scales (Uhl & Dransfield 1987). In addition, they are a useful surrogate for understanding overall patterns of plant diversity because their geographic ranges have been well documented (Henderson 1995, Henderson et al. 1995). Henderson et al. (1995) indicated that for South America as a whole 16% of the species are Andean, and 34% are Amazonian, whereas the Cerrado and Gran Chaco species combined make up 8% of the South American species.

The purpose of this paper is to summarize current knowledge about phytogeographic patterns of native Bolivian palms at the species and community level.

Bolivian palm flora

Eighty palm species, in 28 genera, belonging to four subfamilies are known from Bolivia (Moraes 2004). The most important collection of Bolivian palms is located at the National Herbarium in La Paz (LPB), which has been a general reference for comparative identification. In addition, a database has been compiled from approximately 3500 herbarium collections at LPB and other herbaria, particularly The New York Botanical Garden (NY). Some species are known only from a few limited collections. Some observations are based on less documented sets of specimens

Box 1. Palm genera and species of Bolivia grouped according to phytogeographic provinces; number of species in parentheses.

Amazonian taxa

Astrocaryum (4), *Attalea* (3), *Bactris* (10), *Chamaedorea* (2), *Chelyocarpus chuco*, *Desmoncus* (3), *Euterpe precatória*, *Geonoma* (8), *Iriartella stenocarpa*, *Mauritia flexuosa*, *Mauritiella armata*, *Oenocarpus* (3), *Phytelephas macrocarpa*, *Socratea exorrhiza*, *Wendlandiella gracilis*

Andean taxa

Aiphanes horrida, *Bactris* (2), *Ceroxylon* (3), *Chamaedorea* (2), *Dictyocaryum lamarckianum*, *Geonoma* (6), *Hyospathe elegans*, *Iriartea deltoidea*, *Oenocarpus mapora*, *Parajubaea* (2), *Prestoea acuminata*, *Socratea salazarii*, *Syagrus* (2), *Wettinia augusta*

Cerrado taxa

Acrocomia aculeata, *Allagoptera leucocalyx*, *Astrocaryum* (2), *Attalea* (2), *Bactris glaucescens*, *Syagrus* (4)

Gran Chaco taxa

Acrocomia aculeata, *Copernicia alba*, *Trithrinax schizophylla*

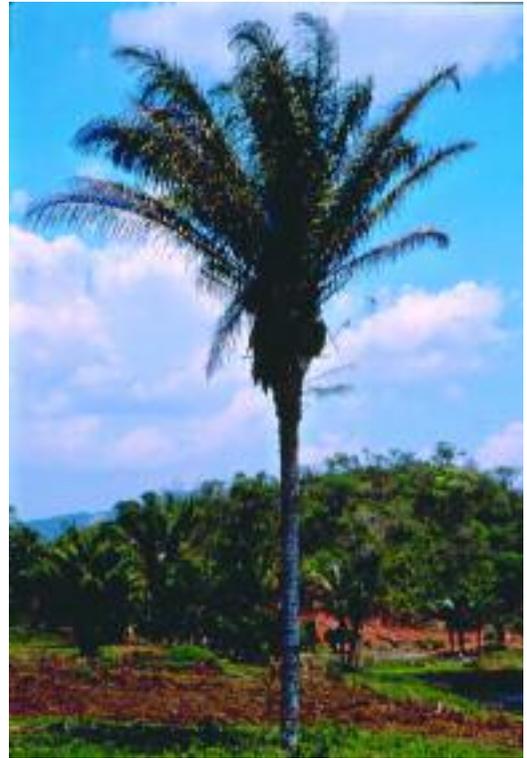
that inadequately document variation recently described for species with two or more subspecies known to occur in the Amazon region. Some genera, such as *Astrocaryum* and *Geonoma*, are represented by incomplete material making identification uncertain (e.g. flowers for *Astrocaryum* are often lacking).

Phytogeographic patterns

Native palms of Bolivia have been analysed with respect to their occurrence in one or more of the four phytogeographic provinces of Bolivia (Box 1 & Fig. 1). Some species have distributions that span more than one phytogeographic province showing intermediate affinities. These include Cerrado-Amazonian species in the north-east of Bolivia, Andean-Amazonian species along the Andean foothills, Gran Chaco-Andean species in several valleys of the eastern Cordillera, and Andean-Cerrado from foothills in the west towards the eastern plain of the country (Boxes 2 & 3). Several Amazonian species reach their southern limit in Bolivia, while some Andean taxa reach their southernmost limit near the border with Argentina. Both the Cerrado and Gran Chaco provinces have their westernmost limits in the north-central region of the Bolivian lowlands and Andean foothills.

The Amazonian taxa

Species whose diversification is centered in the Amazonian, actually fall into two distinct groups: species that occur throughout the neotropics and species restricted to Amazonia. Although data are scarce, fifteen genera and 41 species are in these categories (Box 2). Three species are widespread throughout the Neotropics: *Astrocaryum murumuru*, *Attalea*



2. The *motacú* palm (*Attalea phalerata*) a widespread species in the lowlands and Andean foothills.

phalerata (Fig. 2), and *Desmoncus polyacanthos*. Those species that cross into an Amazonian-Andean transition zone are *Chamaedorea angustisecta*, *Geonoma deversa* and *Socratea exorrhiza* (Box 2). Four species that occur in the Amazonian province as their natural occurrence or possibly due to human intervention are presently found in boundaries of Cerrado-Amazonian landscapes, e.g. *Astrocaryum jauari* and *Oenocarpus distichus*.

Box 2. Palms centered in the Amazon with restricted and widespread distribution.

Amazonian centered species origin with a distribution beyond Amazonia (widespread)

Astrocaryum murumuru, *Attalea phalerata*, *A. butyracea*, *Bactris major*, *B. maraja*, *Desmoncus polyacanthos*, *D. mitis*, *Mauritia flexuosa*

Amazonian centered species origin widely distributed within Amazonia (restricted)

Astrocaryum aculeatum, *A. gynacanthum*, *A. jauari*, *Attalea maripa*, *Bactris acanthocarpa*, *B. brongniartii*, *B. chaveziae*, *B. concinna*, *B. elegans*, *B. hirta*, *B. riparia*, *B. simplicifrons*, *Chamaedorea pauciflora*, *Chelyocarpus chuco*, *Geonoma laxiflora*, *G. leptospadix*, *G. maxima*, *Oenocarpus balickii*, *Wendlandiella gracilis*

Palms in both Andean and Amazonian landscapes

Aiphanes horrida, *Astrocaryum murumuru*, *Bactris gasipaes*, *Chamaedorea angustisecta*, *Geonoma deversa*, *G. interrupta*, *G. macrostachys*, *G. stricta*, *Hyospathe elegans*, *Iriartea deltoidea*, *Iriartella stenocarpa*, *Oenocarpus bataua*, *O. mapora*, *Phytelephas macrocarpa*, *Socratea exorrhiza*, *Wettinia augusta*

Palms in both Amazonian and Cerrado landscapes

Astrocaryum jauari, *Desmoncus orthacanthos*, *Mauritiella armata*, *Oenocarpus distichus*

Box 3. Palms centered in the Andes with restricted and widespread distribution.**Andean centered taxa with a restricted distribution**

Bactris faucium, *Ceroxylon parvifrons*, *C. parvum*, *C. vogelianum*, *Chamaedorea linearis*, *Geonoma brongniartii*, *G. densa*, *G. jussieuana*, *G. macrostachys*, *G. orbignyana*, *G. undata*, *G. weberbaueri*, *Parajubaea sunkha*, *P. torallyi*, *Syagrus yungasensis*

Andean centered taxa with a widespread distribution

Aiphanes horrida, *Chamaedorea angustisecta*, *Dictyocaryum lamarckianum*, *Oenocarpus bataua*, *Syagrus sancona*

Palms in both Andean and Amazonian landscapes (see Box 2)**Palms in both Andean and Cerrado landscapes**

Syagrus sancona, *S. yungasensis*

Palms in both Andean and Gran Chaco landscapes

Acrocomia aculeata, *Trithrinax schizophylla*

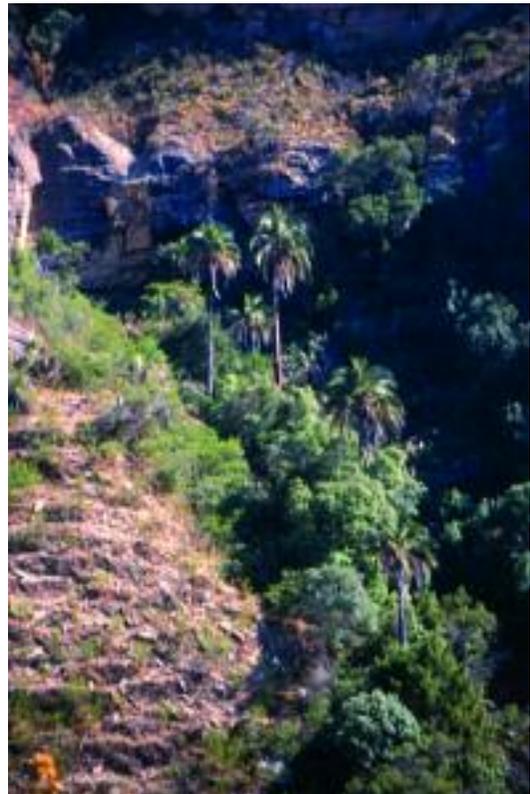
Geonoma brevispatha has a disjunct distribution in the Cerrado and in the Andean foothills. Some riparian species expand their distribution along rivers, such as *Bactris glaucescens* (Fig. 3), *B. major*, *B. riparia* and *Syagrus sancona*.

The Andean taxa

Henderson (1995) listed 21 genera and 87 species in the Andes, and this is updated to 24 genera and 110 species (Borchsenius & Moraes

2006). In Bolivia, 25 species belong to the Andean province (Box 1). Some species such as *Ceroxylon vogelianum*, *Dictyocaryum lamarckianum*, and *Geonoma jussieuana* are clearly centered in the Andes (Box 3), whereas *Syagrus sancona* and *S. cardenasii* appear to be transitional between the Andean and the Cerrado. *Aiphanes horrida*, *Hyospathe elegans* and *Iriartea deltoidea* are part of transitional Andean-Amazonian ecosystems. The moist

3 (left). *Bactris glaucescens* that grows in clumps in riverine forests along Amazonian rivers. 4 (right). Three stands of *Parajubaea torallyi* are centered in dry sandstone valleys up to 3400 m elevation.





5 (left). A representative of the Cerrado genus *Allagoptera*, *A. leucocalyx* shows a spicate infructescence and a very short aerial stem up to 10 cm high. 6 (right). *Trithrinax schizophylla* with its characteristic stiff and palmate leaves is found in dry and spiny forests.

interandean valleys of Bolivia include a relatively high palm diversity, whereas the dry to moist valleys (in the center and south of the country) contain fewer species in total and more endemic species (Moraes 1999a).

In addition, five species are endemic to Bolivia (Box 4), most of them of Andean origin and restricted to interandean valleys of the Cordillera Oriental. Both species of the genus *Parajubaea* – *P. sunkha* and *P. torallyi* – are centered in the so called “interandean” valleys and both are endemic to Bolivia (Front Cover & Fig. 4).

The Cerrado taxa

The Cerrado includes the regions of central and NE Brazil and adjacent areas of Bolivia and Paraguay, which are characterized by a strong seasonal climate. It has five palm genera (Henderson 1995). Eleven Bolivian species have a largely Cerrado distribution corresponding to the Brazil Shield which is typified by highly weathered soils with limited fertility (Box 1). These species reach their westernmost limit in Bolivia and are extensively adapted to open vegetation types.

Palm species transitional to Amazonia and belong to savannas and other open vegetation types are *Allagoptera leucocalyx* (Fig. 5), *Astrocaryum huaimi* and *Bactris glaucescens*, while *Syagrus cardenasii* is also found in the Andes.

The Gran Chaco taxa

The Gran Chaco or Chaco-Pampean province is a semi-arid scrub land with scattered grasslands that are usually associated with sand dunes; in Bolivia three species have distributions that are largely restricted to this phytogeographic province (Box 1). The transitional Chaco-Andean palm taxa include *Acrocomia aculeata*, and the transitions between Chaco and the Amazon include *Copernicia alba*. *Trithrinax schizophylla* (Fig. 6) is found between Cerrado and Gran Chaco boundaries.

In conclusion, there are 15 genera in the Amazonian province, 14 in the Andes, whereas the Cerrado has five, and the Gran Chaco three. The palm species of the Amazon make up 51% of the Bolivian species, the Andean 31%, the Cerrado 14%, and the Chaco 2%. The remaining few taxa are mixed in more



7. *Bactris riparia*, whose stands are closely related with rivers and flooded zones in the lowlands.

than one phytogeographic province. In addition, when the palms that grow in the lowlands of Bolivia are analyzed according to their phytogeographic affinities, the trends are different: 63% of Bolivian palm species belong to genera whose distribution is centered in the Amazon, 16% are Andean, whereas 24% were mixed from the Cerrado and/or Gran Chaco (Moraes 1999b).

Along the Andean foothills an important exchange of palm species occurs with the Amazon phytogeographical province (Box 2). Palms of the Cerrado are found in Bolivia only on Precambrian substrates in the eastern region of the country and there are included main diversity of the genus *Syagrus* in the country: *Syagrus petraea*, *S. comosa* and *S.*

oleracea, while *S. cardenasii*, *S. sancona* and *S. yungasensis* show extensive ranges towards the Andes. *Syagrus sancona* is adapted both to flooded and riparian forests and to seasonally inundated forest islands with a wide distribution on the alluvial plain. Both genera of the Butiinae, *Syagrus* and *Allagoptera* (Moraes 1996a & b), are diversified in central Brazil, with few species reaching the interandean valleys and the Amazon plain, respectively.

Palms in different vegetation types and altitudinal gradients

Native palm species of Bolivia are found in savannas (alluvial, seasonally flooded and on well-drained soils), marshes (riparian or alluvial) and forests (evergreen to deciduous in the lowlands montane or riparian habitats)

Box 4. Endemic palm species of Bolivia, their origin and present distribution in vegetation types.

<i>Bactris faucium</i>	Andes: Interandean humid montane forests (central to NW Bolivia)
<i>Parajubaea sunkha</i>	Andes: Dry interandean valleys on rich soils (south valleys in central Bolivia)
<i>Parajubaea torallyi</i>	Andes: Dry interandean valleys on sandstone (central Bolivia)
<i>Syagrus cardenasii</i>	Cerrado: Alluvial plain in eastern lowlands also on low interandean foothills) (central – SE Bolivia)
<i>Syagrus yungasensis</i>	Andes: Dry interandean valleys towards NW of the country



8. Amazonian vegetable ivory, *Phytelephas macrocarpa*, showing male inflorescences on a very short trunk.

(Moraes 1996c). Also they are distributed along an altitudinal gradient at 140–3400 m. No palm species grow in the west where a xeric and reduced vegetation cover dominates the highland landscape.

Some species show remarkable environmental adaptability, such as *Bactris gasipaes*, *Iriarte deltoidea*, *Oenocarpus bataua* and *O. mapora*, which grow in wet montane forests up to 1000 m elevation and also are found in the lowlands at 200 m. Near 900 m in the Yungas forests of these Andean moist slopes, *Euterpe precatoria* sometimes is found growing together with *Dictyocaryum lamarckianum*; while in the Amazon lowlands the former usually is most commonly associated with *Socratea exorrhiza* and occasionally with some species of *Bactris*. Canopy and subcanopy palms in montane forests are *Syagrus sancona*, *Euterpe precatoria*, *Aiphanes horrida*, *Dictyocaryum lamarckianum*, *Ceroxylon vogelianum*, *Prestoea acuminata*, *Socratea exorrhiza*, *S. salazarii*, *Geonoma weberbaueri* and *Wettinia augusta*. In the understory palms are represented by *Chamaedorea linearis*, *Geonoma orbignyana* and *Bactris faucium*. On the piedmont of the Andean mountains and in interandean valleys, several species of palms have been used as a main reference for vegetation description, such as *Socratea exorrhiza*, *Astrocaryum murumuru* and *Bactris major*.

Flooded alluvial plains in the lowlands host different palms in island forests (among trees: *Attalea phalerata*, *Syagrus sancona* and *Astrocaryum murumuru*; also a common climber: *Desmoncus polyacanthos*), savannas with dense stands of *Copernicia alba*, *Acrocomia aculeata* and *Attalea phalerata*, and marshes with *Mauritia flexuosa*, *Mauritiella armata* and different species of *Bactris*. A group of species are found in the forest understory like *Geonoma deversa*, *G. brongniartii*, *G. macrostachys*, *Bactris maraja*, *Chamaedorea angustisecta*, *Ch. pinnatifrons* and *Hyospathe elegans*. Finally, in the upland savannas and rock outcrops of the Precambrian Shield, dwarf palms such as *Allagoptera leucocalyx*, *Syagrus petraea*, *Attalea eichleri* and *Astrocaryum campestre* are common.

Most species are found between 140 and 500 m mainly along the Andean piedmont and on Tertiary undulating plains in northern Bolivia meeting Amazonian landscapes. Fewer than half of the Bolivian palm species occur between 500 and 1800 m in the mountain forests and piedmont on the eastern slopes of the Andes, where *Iriarte deltoidea* is the most abundant species (see Table 1 for other sites). In contrast, only one species – *Syagrus cardenasii* – is present in the southern part of the country in the Andes between 900 and 2200 m (Tab. 1), while only *Trithrinax*

schizophylla is found in an extensive area of dry shrubs in the south along a gradient of 400–1100 m. These trends of palm richness (summarized in Tab. 1 according to palm richness) fit into the four climatic zones in which moist conditions host a higher number of species than drier valleys: 1) NW–NE with moist to perhumid conditions throughout the year and with high palm diversity, 2) W–SW with dry conditions with no native palms, 3) SE with extreme seasonality and with few palms, and 4) Center–E with seasonally moist conditions throughout the year with medium palm diversity.

Palm species richness is relatively high in upland evergreen forests and savannahs. Only few species grow on rich riparian soils, such as *Attalea butyracea*, *Bactris riparia* (Fig. 7) and *Chelyocarpus chuco*, whereas *Mauritia flexuosa* and *Mauritiella armata* are adapted to permanent marshes with organic soils. *Allagoptera leucocalyx* and *Geonoma deversa* are most common in well-drained, sandy soils. Species adapted to seasonally flooded soils are *Copernicia alba* and *Trithrinax schizophylla*. Colluvial soils host palms such as *Parajubaea*, *Ceroxylon* and *Prestoea* in different physiographic zones of Bolivia.

Mixed palm communities occur in different types of landscapes, and the communities are characteristic to a variety of ecological conditions. *Attalea phalerata*, *Oenocarpus bataua*, *Iriartea deltoidea* and *Astrocaryum murumuru* grow together in the lowlands at 200–1000 m altitude. In fragmented forests on alluvial plains, *Copernicia alba*, *Acrocomia aculeata* and *Attalea phalerata* occur in northern Bolivia. *Syagrus sancona*, *Attalea phalerata*, *Desmoncus polyacanthos* and *Astrocaryum murumuru* are found in savannas with forest islands. Flooded and riparian forests are characterized by *Bactris riparia*, *B. major*, *Syagrus sancona* and *Attalea phalerata*. *Euterpe precatoria*, *Bactris major*, *B. maraja* and *Socratea exorrhiza* are part of seasonally flooded forests in the lowlands and near the Andean foothills; these forests are mostly dominated by few palm species.

Certain species form a continuous and dense population such as on landscapes in northern Amazonian Bolivia (*Astrocaryum murumuru*, *Geonoma deversa* and *Mauritia flexuosa*), the Cerrado landscape (*Attalea speciosa*) and the Gran Chaco (*Copernicia alba*). *Oenocarpus bataua* and *Phytelephas macrocarpa* (Fig. 8) also share this pattern and are presently distributed

Table 1. Palm species diversity registered in different sites of Bolivia.

Sites	Altitude (m)	# Palm species	References
W Pando, NW Bolivia	280	26 (33%)	Alverson et al. 2000*
E Pando, NE Bolivia	140	30 (38%)	Alverson et al. 2003**
S Iturrealde (N La Paz), W Bolivia	500–1800	51 (64%)	Moraes et al. 1995b
Alto Madidi (N La Paz), W Bolivia	200–700	21 (26%)	Parker & Bailey 1991***
E Tamayo (E La Paz), W Bolivia	350–700	11 (14%)	Moraes unpubl. data
C Cochabamba, C Bolivia	500–2200	20 (25%)	Kessler 2000
Chapare, Cochabamba, C Bolivia	360–700	9 (11%)	Moraes 1998a
W S. Cruz, C Bolivia	350–2000	25 (32%)	Nee unpubl. data
NE Velasco (E S. Cruz), E Bolivia	200–900	27 (34%)	Killeen & Schulenberg 1998
SE Velasco (SE S. Cruz), E Bolivia	170–400	4 (5%)	Parker et al. 1993
S–C Chuquisaca, C Bolivia	900–2200	1 (1.3%)	Schulenberg & Awbrey 1997
C Tarija, C–S Bolivia	350–800	3 (4%)	Moraes 1998b

* One new record for the country.
 ** Three new records.
 *** Two new records.

in disjunct spots (along the Andean piedmont and also in Amazonian forests of northern Bolivia). Finally, *Parajubaea torallyii* and *P. sunkha* in inter-Andean valleys have dense populations.

Conclusions

Palm species distribution and diversity in Bolivia are related to a continental scale phytogeographic patterns, as well as local and regional features such as climate, elevation, soil properties, and vegetation types. Twenty-eight genera and 80 palm species are known to occur in Bolivia, but the distribution and abundance of many taxa are still poorly known and some are poorly documented. The inventory by Henderson et al. (1995) produced a total of 67 genera and 550 species of South American palms. Bolivia thus contributes 42% at the generic level, but has only 14.5% of all these species.

Most of the genera occurring in the Andes are more species-rich in the lowlands and only three genera (*Ceroxylon*, *Wettinia* and *Aiphanes*) are more diversified in the Andes (Moraes et al. 1995a). A preliminary analysis of palm diversity and its distribution patterns demonstrate general features showing trends that largely correspond to Amazonian, Andean, Cerrado, and Gran Chaco phyto-geographic provinces. There is a high palm richness at the boundary between Amazonian and Andean landscapes (at less than 1,000 m) that decreases to the south. Cerrado and Amazonian taxa are mixed together in the east of the country with moderate levels of species diversity.

Two phytogeographic regions contribute the majority of the actual diversity and geography of native palms of Bolivia, namely the Amazonian and Andean provinces. The Cerrado and Gran Chaco provinces contribute to the palm flora of Bolivia to a lesser degree. Restricted and widespread geographic patterns for certain palms have potential implications for understanding the conservation at both local and regional scales.

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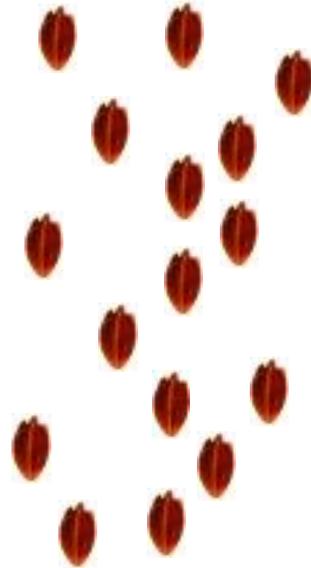
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