

## **Mesoscale patterns of plant diversity in Andean South America based on combined checklist and GBIF data**

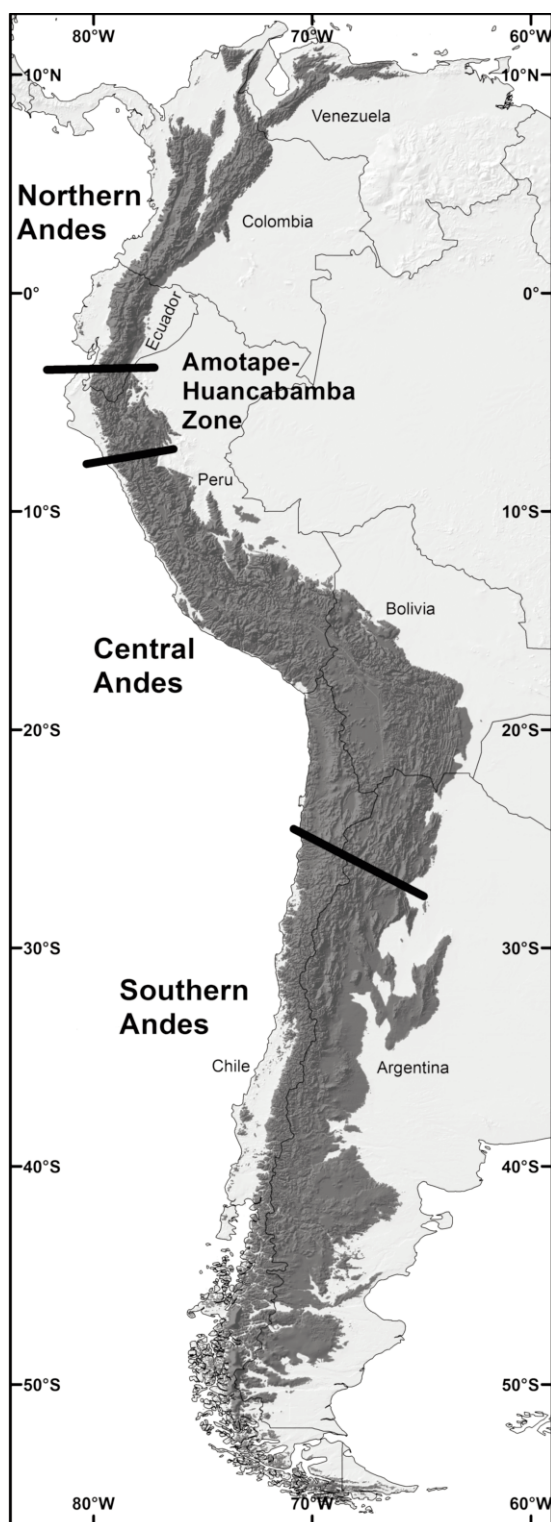
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### **Abstract**

The tropical Andes in South America are a global centre of plant diversity, housing an estimated 50,000 vascular plant species. Unfortunately, our knowledge about the mesoscale patterns of plant diversity within this region is still rudimentary. We use the currently available floristic checklists and a plant distribution dataset downloaded from the GBIF portal to investigate patterns of diversity in general at genus level plus more detailed patterns at species level for trees and epiphytic plants. We confirm extraordinary levels of diversity throughout the tropical Andes, with a displacement towards the eastern slope of the Andes in the Central Andean region. Documented genus and species numbers are particularly high in the northern Andes. The highest levels of generic diversity are reported from Colombia, with up to 2,380 genera per 1° latitudinal band, of which 1,945 are found in the Andes. Ecuador, and especially Peru and Bolivia have slightly lower, but overall similar genus numbers. Across the region, between 71 and 83% of all epiphytic plant species are found in the Andean region, whereas tree diversity is higher in the lowlands. Within the tropical Andes we found no evidence for major biogeographic borders at the genus-level, but a very high number of plant genera reach their southern distribution limit at about 19°S in Bolivia. A more detailed view of mesoscale patterns of diversity is compromised by the very unequal distribution of plant records, which is generally highest in Ecuador and Colombia, much lower in Peru and Bolivia. Seemingly less biodiverse regions there clearly correspond to regions with low numbers of plant records and the same appears to be true for much of the Central and Southern Andes. A correlation of the number species/genera recorded per 1x1° grid cell with the number of records indicates that very few grid cells along the Andes have likely been recorded to near-saturation. The bulk of the grid cells still have less than 5,000 records, which probably captures only a fraction of the plant diversity present. The few well sampled regions in the Central Andes indicate that plant diversity of the humid eastern Andean slopes in Peru and Bolivia is likely similar to that of the Northern Andes. For a more complete understanding of patterns of diversity, it would be required to greatly expand the amount of georeferenced data, mainly by targeted collecting and the systematic evaluation of local and national herbaria in South America.

### **1. Introduction**

The tropical Andes in South America have been identified as a globally outstanding centre of plant diversity and as an overall hotspot of biodiversity (GENTRY 1982, MYERS et al. 2000, BARTHLOTT et al. 2005, CEBALLOS & EHRLICH 2006, JETZ et al. 2009, MUTKE et al. 2011). Alexander von Humboldt some 200 years ago recognised the outstanding diversity of the flora and fauna and illustrated the altitudinal distribution of important plant genera (HUMBOLDT 1806). Even though the Amazonian lowland rainforests are most famous for their extremely high alpha-diversity – especially of trees (VALENCIA et al. 1994) – overall plant diversity at the landscape scale is much higher in the tropical Andes (BRAUN et al. 2002, MUTKE & BARTHLOTT 2005). The Ecuadorian Andes, e.g., harbour twice as many plant species as the Amazonian part of the country (JØRGENSEN & LEÓN-YÁNEZ 1999). Additional-



ly, some plant groups – such as epiphytic plants or shrubs – show higher total diversity in the mid-altitude forests of the Andes (GENTRY 1982, JØRGENSEN & LEÓN-YÁNEZ 1999). This may be linked to the high humidity based on the cloud cover in the case of epiphytic plants, as well as to the high environmental heterogeneity ('Geodiversity', compare BARTHOLOTT et al. 2000, BRAUN et al. 2002) and high dynamics of these forests due to, i.a., frequent land-slides (KESSLER 1999, RICHTER et al. 2009, MUTKE et al. 2014).

Even though the exceptional diversity of the tropical Andes has been reported for such a long time (HUMBOLDT 1806, HUMBOLDT 1808, GENTRY 1982, DAVIS et al. 1997, MYERS et al. 2000, KIER et al. 2009, ANTONELLI & SANMARTÍN 2011), we still lack a detailed and spatially explicit understanding of the diversity patterns within this region that spans a range of 32 degrees latitude from c. 11°N close to the Caribbean Coast of Colombia and Venezuela to 20°S in central Bolivia. Many authors divide the overall Andean mountain chain into four major biogeographic regions – the tropical Northern Andes in Colombia, Venezuela, Ecuador, the Amotape-Huancabamba Zones (AHZ) in southern Ecuador and northern-most Peru, the tropical to subtropical Central Andes in Peru, Bolivia, northern Chile and

Fig. 1: Biogeographical subdivision of the South American Andes (regions with  $\geq 500$  m a.s.l. based on U.S. GEOLOGICAL SURVEY 1996) following LUEBERT & WEIGEND

Argentina, and the southern Andes in central to southern Chile and Argentina (compare Fig. 1 and LUEBERT & WEIGEND 2014). However, few explicit data have been published on finer scale patterns of diversity, at least for flowering plants, nor have these biogeographic regions been substantiated with discrete range data.

For the vertebrate fauna, sets of expert opinion based range maps of all known birds, mammals, and amphibians (BIRDLIFE INTERNATIONAL & NATURESERVE 2014, IUCN 2015) allow continental scale mapping and analyses of the diversity patterns (e.g. VEACH et al. 2017) – with possible artefacts based on the interpolated character of the data in less documented regions. These datasets and analyses show that the tropical Andes are important centres of diversity and endemism for vertebrates (HAWKINS et al. 2007, KIER et al. 2009). For plants, the extraordinary diversity of the Andean flora – at least two to three times as species rich as the entire European flora – has prevented more detailed comparative studies in the past (compare as well JØRGENSEN et al. 2011). Especially the highly diverse montane forests are still insufficiently documented (WEIGEND et al. 2005).

The publication of the first complete checklist of the hyper-diverse Colombian flora (BERNAL et al. 2015) complements the work published during the last two decades for most other Latin American Countries and especially all countries of the Tropical Andes (BRAKO & ZARUCCHI 1993, JØRGENSEN & LEÓN-YÁNEZ 1999, JØRGENSEN et al. 2014). The history of the early Peruvian checklist indicates that the documentation of plant diversity is still ongoing and far from completed (ULLOA ULLOA et al. 2004, WEIGEND et al. 2005, BÖHNERT & WEIGEND in review). Nevertheless, these lists provide a best-available-evidence overview on regional plant diversity, the relative and absolute importance of different plant groups and altitudinal gradients in the Andes. They also permit first tentative analyses of diversity patterns along the latitudinal extension of this mountain chain.

However, the taxonomic checklists provide rather crude distribution data on altitudinal distribution and based on political units. In order to obtain a more detailed understanding of the patterns of plant distributions and diversity, georeferenced specimen based data are required. The internet portal of the Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)) allows access to currently more than 700 million occurrence records of plants, animals, and microorganisms. The majority of these refer to animals, but global vascular plant diversity is also documented in ca. 180 million records – some 130 million of these are provided with geographic coordinates. These data sets include, e.g. in central Europe, millions of mostly reliable records based on direct observation, including more than 8 million records of the dataset ‘Flora von Deutschland (Phanerogamen)’ (BUNDESAMT FÜR NATURSCHUTZ & NETZWERK PHYTO-DIVERSITÄT DEUTSCHLAND 2017). In most other regions with less well studied floras, it seems advisable to rely only on records vouchered by herbarium specimens, allowing quality control of the data, especially verification of identity. Several studies, e.g. the study by GOODWIN et al. (2015), demonstrated that herbarium data that has not been revised by taxonomic specialists, has to be treated with extreme caution, especially in the highly diverse tropical floras. We therefore advocate using only vouchered data sets in the tropics. Using these criteria (herbarium specimens & known geographic coordinates) there are still some 28 million relevant records for vascular plants in the GBIF database – although the representation of different regions and data quality are highly uneven (MEYER et al. 2016, GOODWIN et al. 2015). Also, only a fraction of the important regional herbarium collections is currently included in the GBIF portal – though they often hold crucially important material especially in areas with high local endemism (BÖHNERT & WEIGEND in review).

Thus, in order to make optimal use of the large body of data from GBIF, we see two possible shortcuts: 1. Many records are likely wrong at species level, but correct at the genus

level, as indicated by the study by GOODWIN et al. (2015) and our own experience with plant groups included in taxonomic studies of our own institute 2. On the other hand, strict filtering of the large overall dataset might help to narrow the data down to a more reliable subset even at species level (ZIZKA et al. 2017). We would still caution against using these data when the correct identification of all individual records plays a crucial role, e.g., in the context of species conservation. However, at least for a first overview on regional patterns of diversity and distribution, we feel that this is a valid approach (MALDONADO et al. 2015, ENGEMANN et al. 2016, MEYER et al. 2016).

The present paper explores which meaningful subsets of data can be extracted from the large GBIF distribution dataset. In order to minimize problems with misidentifications (see above) and taxonomic uncertainties, our analyses of the overall plant diversity focus at the genus level. Andean mountain forests are the focus of a more detailed analysis of plant diversity, especially in trees and epiphytic plants. We combine the recently available taxonomic standardized national checklists of the tropical Andean countries with the GBIF data to study plant diversity across the entire latitudinal and altitudinal range of the tropical Andes. The main questions that we want to address with these data are:

- 1) Which patterns of biodiversity can be recognized in the different biogeographic sub-regions of the Andes and at a mesoscale?

Table 1: Reported numbers of native species of trees and epiphytic plants in the tropical Andes according to the national checklists.

Country	Overall Andean Plant diversity	Trees & Treelets	Epiphytic Plants <sup>1</sup>	Source
<b>Colombia</b> (country: 1.14 million km <sup>2</sup> Andean Region: 290,000 km <sup>2</sup> )	17,407 taxa  (country total: 26,749 sp.)	3,127 species in 620 genera  (country total: 7,585 sp.)	3,377 species in 266 genera  (country total: 4,298 sp.)	Catálogo de plantas y líquenes de Colombia (BERNAL et al. 2015, online database)
<b>Ecuador</b> (country*: 0.26 million km <sup>2</sup> Andean Region: 115,000 km <sup>2</sup> )	9,849 taxa  (country total: 15,306 sp.)	1,390 species in 360 genera  (country total: 3,064 sp.)	2,958 species in 259 genera  (country total: 3,960 sp.)	Catalogue of Vascular Plants of Ecuador (JØRGENSEN & LEÓN-YÁNEZ 1999, online database)
<b>Peru</b> (country: 1.28 million km <sup>2</sup> Andean Region: 648,000 km <sup>2</sup> )	11,465 taxa  (country total: 17,143 sp.)	1,851 species in 529 genera  (country total: 3,814 sp.)	961 species in 184 genera  (country total: 1,357 sp.)	Catalogue of the Flowering Plants and Gymnosperms of Peru (BRAKO & ZARUCCHI 1993, online database)
<b>Bolivia</b> (country: 1.09 million km <sup>2</sup> Andean Region: 428,000 km <sup>2</sup> )	9,222 taxa  (country total: 14,508 sp.)	1,391 species in 460 genera  (country total: 2,642 sp.)	1,459 species in 238 genera  (country total: 1,768 sp.)	Catálogo de las Plantas Vasculares de Bolivia (JØRGENSEN et al. 2014, online database)
<b>Tropical Andes of all 4 countries</b>	Probably ≥50,000 taxa <sup>2</sup>	5,835 species in 915 genera	7,109 species in 453 genera	

\*excl. Galapagos Islands; 1 obligate & facultative epiphytic species, excl. species listed only as hemiepiphytes; 2 according to JØRGENSEN et al. (2011), the combined documented species number of Ecuador, Peru, and Bolivia is 36,192, compare as well MYERS et al. (2000)

- 2) Are the patterns observed linked to differences in collection intensity rather than representing differences in diversity and distribution?
- 3) Which altitudinal and latitudinal gradients can be retrieved from the data set for the entire Andean region?

## 2. Material and Methods

We use two sets of floristic data for our analyses. Distribution records were queried in March 2017 from the GBIF data portal (GBIF.org 2017). This dataset covers 2,424,740 records of vascular plants based on herbarium specimens in all Andean countries (northern Venezuela to southern Chile and Argentina). After excluding all records with no data regarding the exact locality and the elevation, the trimmed dataset includes 1,698,285 records. 645,777 of these fall in the Andean region shown in Fig. 1, representing 3,846 genera, corresponding to 174 genera of pteridophytes, 24 genera of gymnosperms, and 3,647 genera of angiosperms. The final data selection includes original datasets from more than 140 data providers – the most important data providers representing >90% of the final dataset are: Missouri Botanical Garden, Herbario Nacional Colombiano, Universidad de Antioquia (Colombia), Aarhus University (Denmark), Instituto Humboldt (Colombia), the Smithsonian Institution, and The New York Botanical Gardens. Analyses of the overall GBIF-dataset are carried out at genus level only.

The second dataset combines taxonomic reference lists for two important plant groups in Andean forests: 1) all Andean tree species and 2) all Andean species of epiphytic plants listed in the national checklists of Colombia, Ecuador, Peru, and Bolivia (See Tab. 1 for references). We included only native species documented in the Andean regions of the respective countries. Native versus non-native species are differentiated in all sources apart from the online version of the Peru Checklist. The classification of the growth form for the species is not 100% congruent between the lists. We included all species listed *inter alia* as trees ('Arbol'), treelets ('Arbolito'), and 'palmas solitarias'. Species listed only as shrubs, but not as trees are excluded. Similarly, we queried all plants that are listed *inter alia* as epiphyte ('epifita'), but excluded species that are only listed as hemi-epiphytes. These specifications are required, because, e.g., our query from the Colombian checklist included species with up to six different habits listed. We added the Checklist of Panama (D'ARCY 1987) and Costa Rica (INBIO 2005) to our database in order to identify Andean taxa ranging into (southern) Central America for our analysis of range limits. We did not try to further standardize names by translating possible synonyms between the four country lists. However, as three of the four checklists are coordinated by Missouri Botanical gardens, we assume taxonomy to be largely standardized. This reference list of species of trees and epiphytic plants was then used to filter the GBIF-dataset for these two plant groups for separate analysis for their ranges and distribution patterns.

We use the GTOPO30 digital elevation model for our maps and the analyses related to altitudinal diversity patterns (U.S. GEOLOGICAL SURVEY 1996).

Data processing and querying was mainly done in MS Access 2010 and R Version 3.4.0, using the RStudio 1.0.143 user interface. Spatial analyses and map production was done in ESRI ArcMap 10.4.

## 3. Results and Discussion

*Patterns of biodiversity.* According to the country checklists summarized in Tab. 1, each of



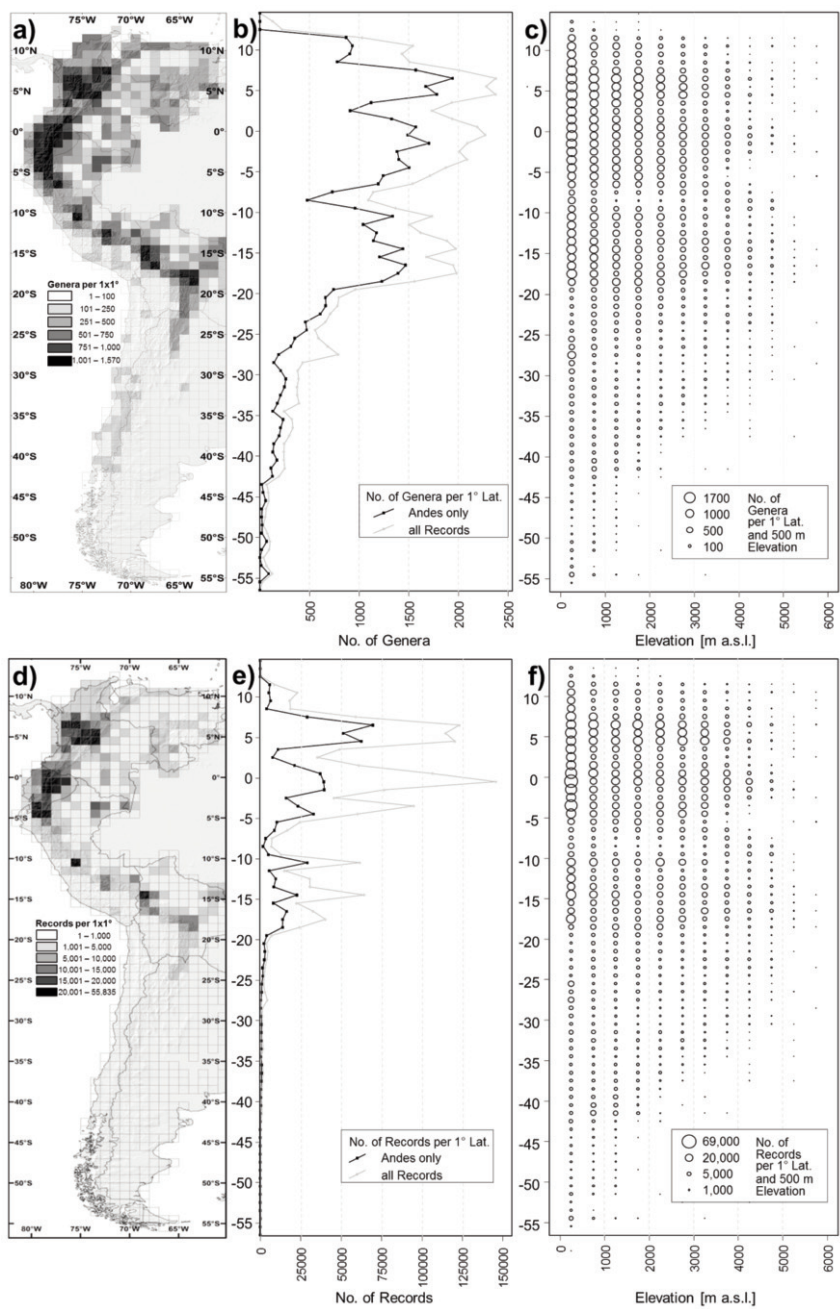


Fig. 2: Latitudinal and altitudinal patterns of plant diversity in the Andean countries as documented in the GBIF dataset (version March 2017): a) numbers of documented genera of vascular plants per 1° Grid cell, b) numbers of documented genera of vascular plants per 1° latitudinal band: grey line refers to all records in the Andean countries as shown in map 2a, black line refers only to records within the Andean region shown in Fig 1, c) number of documented genera of vascular plants per 1° latitudinal band and 500 m elevational zone, d) numbers of records (documented herbarium specimen) of vascular plants per 1° grid cell, e) number of records per 1° latitudinal band, f) number of records per 1° latitudinal band and 500 m elevational zone.

the four countries has overall plant species and genus numbers considerably higher than the plant diversity documented, e.g., in the entire Flora Europaea (TUTIN et al. 1964-1980, TUTIN et al. 1993). Ecuador, Peru, and Bolivia harbour both comparable overall species numbers and numbers of tree species at the country level and in their Andean regions. However, the documented diversity of epiphytic plants in Ecuador is two to three times higher compared to Peru and Bolivia. It represents a considerable proportion of both the overall flora of Ecuador (ca. 25%) and the Andean flora of Ecuador (ca. 30%). In all four country checklists, between 71 and 83% of all epiphytic plant species occur in the Andean region. The percentage of Andean species is lower for trees (41-53%), for which diversity is higher in the lowlands of the Amazon and the Chocó regions.

Documented genus and species numbers per latitudinal band in the GBIF dataset (Fig. 2b, 3) are highest in central Colombia with up to 2,380 genera per 1° latitudinal band and up to 1,945 of these in the Andes. Overall, however, genus numbers are comparable throughout the northern Andes in Colombia, Ecuador, and northern Peru between 5°S and 8°N with >2,000 genera per 1° latitude (>1,400 in the Andes). In the central Andes of Peru and Bolivia, these numbers are on average 20-25% lower (1,500-2,000 genera per 1° latitude, 1,000-1,500 in the Andean part). Patterns in trees and epiphytic plants per 1° latitude in the Andes (Fig. 3) are quite similar, but the differences between the northern and the central Andes are even more pronounced. Whereas the tree species numbers per 1° latitude reach 1,500 to 2,400 species in the northern Andes (5°S—8°N), the values are in the range of 1,000 and 1,600 species in the central Andes and thus roughly one third lower. A parallel, but even more pronounced, trend is found in epiphytic plants (Fig. 3), where documented species numbers in the northern Andes (except a very distinctive local minimum at 2-4°N) are more than twice as high (1,000 – 1,700 species compared to 240 – 770 species in the central Andes).

Looking at these mesoscale latitudinal patterns (Fig. 2b, 3), there is a clear minimum of

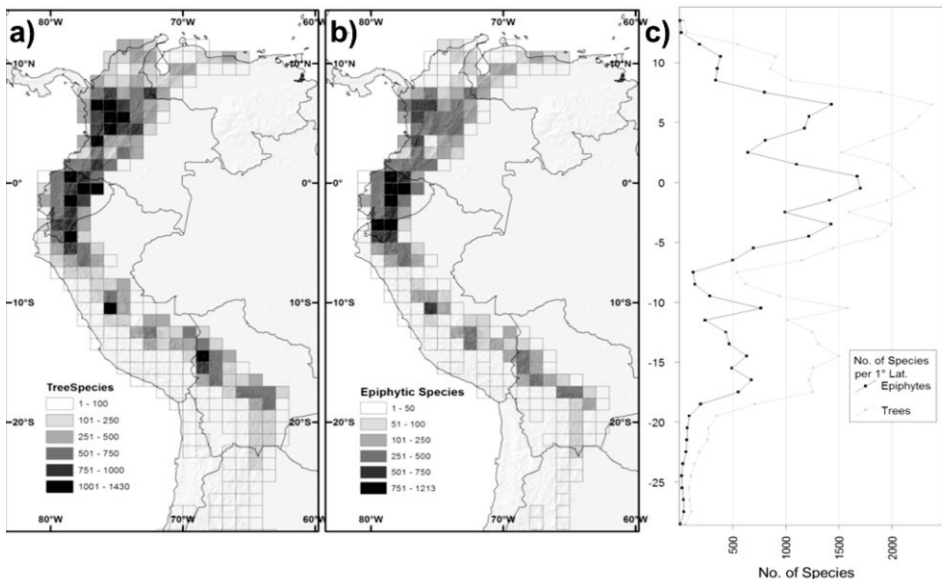


Fig. 3: Latitudinal patterns of documented species richness of trees and epiphytic plants in the tropical Andes based on a query of the GBIF distribution data using species lists in the national checklists of Colombia, Ecuador, Peru, and Bolivia. a) Species richness of Andean trees and treelets in 1x1° Grid cells; b) Species richness of Andean epiphytic plants (obligate and facultative epiphytes), c) species numbers of trees and treelets and of epiphytic plants per 1° latitudinal band

documented plant diversity between 7° and 10°S. This corresponds to an extremely low number of GBIF records from these latitudes across all altitudinal belts (Fig. 2d-f). A similar, but not as pronounced local minimum in the number of collection and the number of documented genera and species is found in southern Colombia (ca. 3°N) and to some degree also in southern Ecuador (ca. 3°S). Interestingly, the low collection numbers corresponding to the low documented plant diversity between 7° to 10°S continue northwards to 5°S. Nevertheless, genus numbers between 5° and 7°S are comparable to those of the remaining part of the northern Andean average and species numbers are at least two to four times higher compared to the neighbouring minimum.-

The documented tree flora of Colombia is around twice as high as for all three other countries (Tab. 1) and Peru and Bolivia have lower reported species numbers across all groups. Interestingly, the Ecuadorian tree flora appears comparable to that of Peru and Bolivia despite of the much smaller country area. The mapped data underscore the extremely high genus number in Colombia, followed by Ecuador, then Peru and Bolivia (Fig. 2a). Overall records and Andean records are essentially parallel graphs, i.e., the latitudinal bands (1 degree) with the highest recorded genus numbers overall are also the ones with the highest recorded Andean genus numbers (Fig. 2b): Figure 2c further shows that the number of genera recorded appears to be relatively parallel across altitudes in the individual latitudinal band. Similar overall patterns are again found at species level looking at Andean trees and epiphytic plants (Fig. 3), however the differences between latitudinal bands appear to be even more extreme. One minor deviation in details is that for epiphytic plants, Ecuador harbours a slightly higher diversity than Colombia.

The mesoscale (1x1° grid) patterns of the GBIF dataset (Fig. 2a) retrieve recorded genus numbers of 500 - 1,570 per 1x1° grid (c. 110x110 km) throughout the northern Andes – including both the western slopes and the eastern slopes. In the central Andes, high genus numbers (Fig. 2a) and species numbers (Fig. 3a, b) are restricted to the more humid eastern slopes of Peru and Bolivia, including the subtropical eastern slopes in S Bolivia and N Argentina. Moderate documented genus numbers between 100 and 250 genera per 1x1° grid cell in the southern Andes are restricted to the western slopes of the Mediterranean climate region in central Chile. Extremely low genus and species numbers are documented in the dry corridor of northern Chile, SW Bolivia, and NW Argentina.

*Collection intensity versus diversity.* The general patterns outlined indicate that latitudinal bands are relatively uniform in diversity, but a closer look at Figures 2a-c reveals striking mesoscale irregularities – some neighbouring latitudinal bands show stark differences in documented genus and species numbers, which are counterintuitive from a biogeographical perspective. There are clear “lows” in diversity in southern Colombia and southern Ecuador. Figures 2d-f provide a break-down of collection intensity by giving the number of records per 1x1° grid cell (Fig. 2d), 1°-latitudinal band (Fig. 2e) and per altitudinal band (Fig. 2f). The graphics are strikingly parallel to the figures 2a-c. The current patterns of recorded biodiversity are thus evidently strongly influenced by different collection intensities. This is particularly evident when looking more closely at the Central Andes: Here, there are only three regions with over 10,000 records per grid cell (Fig. 2d) representing the PN Yanachaga-Chemillén (Peru), Cuzco (Peru) and the department La Paz (Bolivia). The diversity map clearly retrieves these regions as the most diverse along the Central Andes. The records are thus very unevenly distributed along much of the Andes. The obvious question to ask is how many of the grid cells can be considered as “saturated” with regards to records, i.e., in which grid cells are additional records increasingly unlikely to add genera or species to the inventory. The correlation between the number of genera or species recorded per 1x1° grid cell versus the number of records from



that grid cell is graphically represented in Figure 4. Looking at documented genus numbers across the regions (Fig. 4a), there is an extremely close correlation to the number of records especially for those grid cells with less than 5,000 records – the  $R^2$  for the Log10-transformed numbers of records and documented genera is 0.98! Above 5,000 records per grid cell, the correlation between number of records and number of recorded taxa becomes weaker and the record to genus ratio shows a higher scatter, indicating real differences in diversity rather than differences based on record number. However, genus numbers still increase dramatically with the number of records up to at least 30,000 records per grid cell. For those better sampled grid cells with at least 5,000 records the  $R^2$  for the log-transformed data still is 0.66. Even in those better collected grid cells, there are no obvious differences between the regions regarding genus numbers for a given number of records. Overall, only 4% of all grid cells reach the collection density of 1 specimen per km<sup>2</sup> (c. 12,000 records per 1x1° grid cell close to the Equator) that has been proposed by CAMPBELL (1989) as a threshold indicating well collected areas (compare as well JØRGENSEN et al. 2011). But even for those better sampled regions Fig. 4a does not indicate any sign of real saturation. The vast majority of grid cells (c. 92 %),

especially in the central and southern Andes, but also in the Amotape-Hunacabamba Zone is well below ca. 5,000 records per grid cell. Probably, only a fraction of the genera actually present in any given grid cell has been recorded – indicating that the threshold of collections indicating well sampled regions that has been proposed by CAMPBELL (1989) might be much too low for the tropical Andes. The situation is even worse with regards to the percentage of species documented by current data sets. The number of tree genera recorded indeed seems to increase little in grid cells with more than c. 5,000 records (Fig. 4b), but the number of

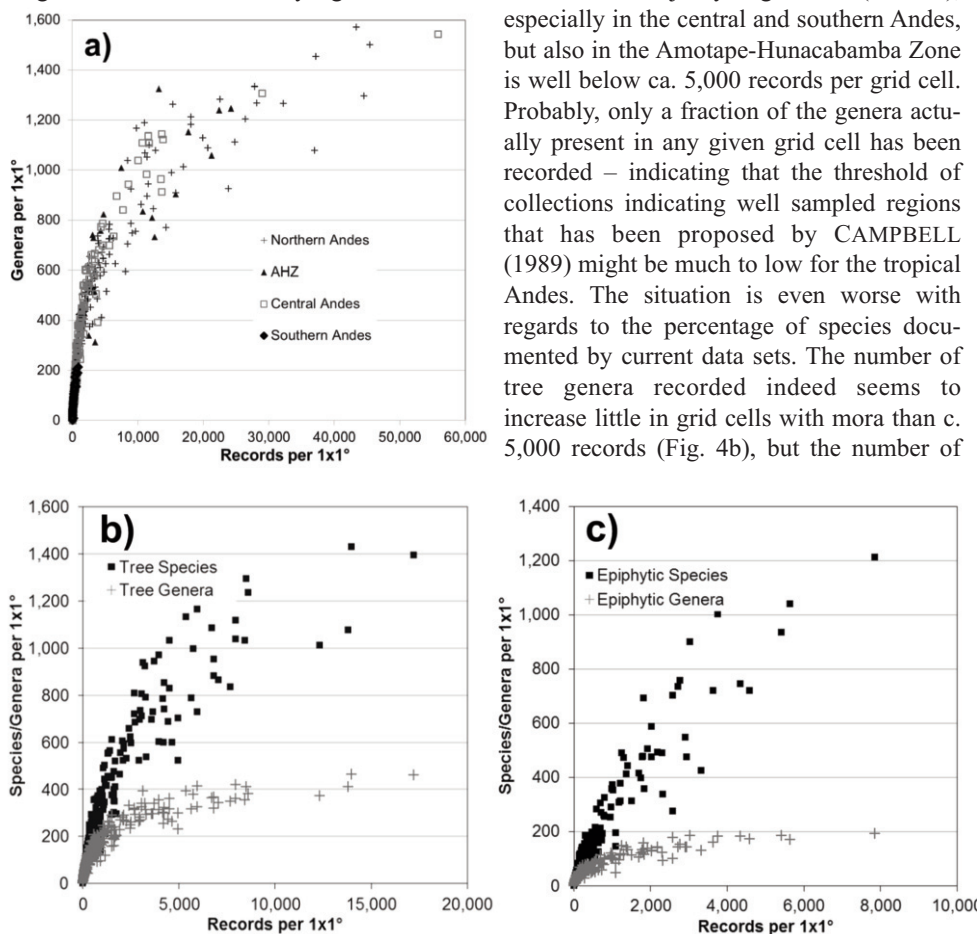


Fig. 4: Numbers of documented taxa of vascular plants plotted against the number of records per 1x1° grid cell based on the GBIF dataset. a) total genus numbers for all vascular plants – only grid cells within the Andean region as shown in Fig 1; b) species and genus numbers of trees and treelets; c) species and genus numbers of epiphytic plants extracted from the GBIF dataset based species lists in the national checklists of Colombia, Ecuador, Peru, and Bolivia

tree species still increases strongly well beyond 10,000 records per grid cell and shows no sign of saturation even in grid cells with more than 30,000 records. In epiphytic plant species (Fig. 4c), the situation is similar with regards to genera – the number of genera recorded seems to even out roughly at 5,000 records per grid cell, the number of species still rises sharply without indications of evening out. These interpretations are, of course, based on the implicit assumption that diversity is actually similar across the region under study, which is certainly not the case. However, the presence of two grid cells from the Central Andes in the upper right of Figure 4a indicates that at least the eastern slope of the Central Andes may have similar actual diversity to the northern Andes, and the same is likely true for the Amotape-Huancabamba Zone. The vast majority of the grid cells in the Central Andes have less than 5,000 records – almost one order of magnitude less than many grid cells in the Northern Andes. Individual latitudinal bands in the Northern and Central Andes differ by a factor 10 to 20 in the overall number of records. This strongly compromises a detailed understanding of mesoscale patterns of biodiversity, especially since there is a clear correlation between the overall number of records and the number of taxa reported – with few grid cells apparently coming close to saturation (compare Figure 4). One might test these patterns with more sophisticated indicators of sampling completeness as proposed by YANG et al. (2013) and used, e.g., by ENGEMANN et al (2015) to confirm the still much too low number of records to represent real diversity patterns of the Flora of Ecuador. However, it would be more important to prioritize the digitization of at least the most important national and regional herbaria in the Central Andes especially in Peru, which are completely missing in the GBIF dataset. As shown, e.g., in BÖHNERT & WEIGEND (in review), these collections can significantly improve our knowledge of the Andean plant diversity. The herbarium USM at the Universidad Nacional Mayor de San Marcos in Lima houses around 500,000 plant specimens, mainly from Andean Peru. This represents a vast amount of data, when considering that the entire Andean dataset we use here comprises "only" c. 645,000 records.

*Mesoscale altitudinal and latitudinal gradients.* The above data clearly indicate that the analysis is still fraught with artefacts based on the highly unequal documentation of biodiversity along the Andes. However, in spite of these limitations, some general conclusions can already be drawn, e.g. on altitudinal patterns. Based on the GBIF dataset altitudinal diversity gradients of overall genus number reveal the highest genus numbers in the lowland below 500 m a.s.l. (Fig. 2c) ranging from almost 1,700 genera per 1° latitude in Colombia and Ecuador to c. 1,300 in central Bolivia. Numbers at mid-altitudes are roughly uniform between 500 m and about 3,000 to 3,500 m a.s.l. (Fig. 2c) and only decline markedly at higher elevations. Only in the Andean depression of the Amotape-Huancabamba Zone (AHZ) in S Ecuador and N Peru, the genus number already drops at lower elevations (between 2,500 and 3,000 m a.s.l.). Tree species richness again shows highest values in the lowland and decreasing documented species richness from North to South. As previously demonstrated by, e.g., JØRGENSEN et al. (2011) with national checklists data, the numbers of epiphytic species show a mid-altitude maximum around 2,000 m a.s.l. – however, at least in our GBIF dataset both the number of genera documented and the number of species documented again show a close correlation to collection density along the elevational gradient.

Looking at diversity patterns at the northern and southern end of the tropical Andes, a strong decline of documented genus and species numbers north of c. 8°N and south of c. 19°S is obvious. In the case of the northern end, this decline corresponds to the northern end of the Cordilleras Central and Occidental in Colombia. The southern rapid declines in genus numbers (Fig. 2a-c) and species numbers (Fig 3) occur at the latitude of the 'Andean knee' in Central Bolivia. However, even though the genus and species richness in all altitudinal zones and

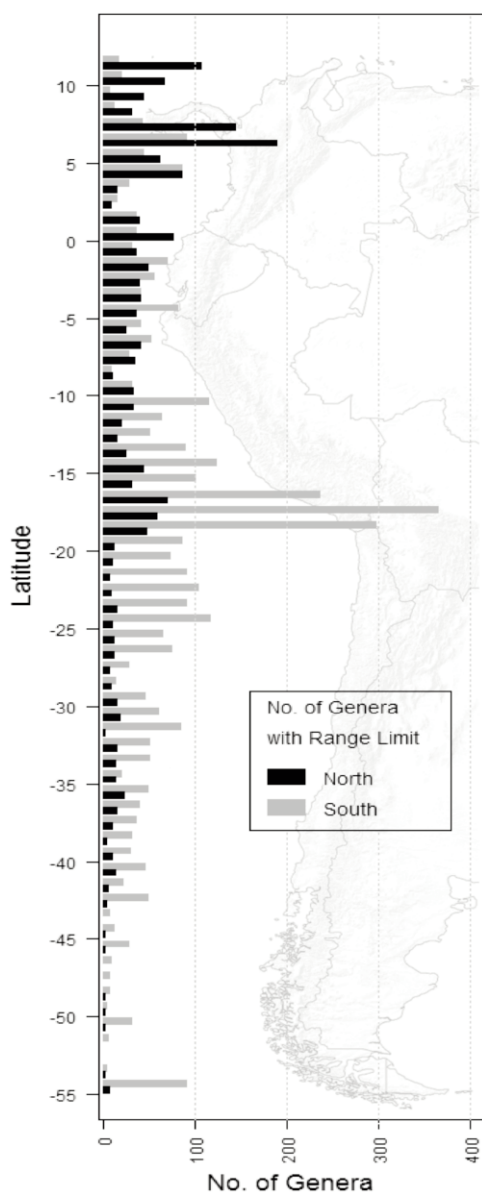


Fig. 5: Number of genera with their southern range limits (grey) or their northern range limits (black) at a given 1° latitudinal band based on the GBIF dataset. For the analysis of the northern range limits, all genera occurring as well in Panama and Costa Rica are excluded. The limit is always defined as the southernmost/northernmost latitudinal band from which the genus is reported.

especially in higher altitudes drop sharply at about 19°S, there is only a gradual decline in the upper limit of plant life documented in GBIF with increasing southern latitude (Fig. 2c). High elevation plant records in the Andes between 30° and 35°S still reach more than 4,000 m a.s.l., but genus numbers drop sharply above c. 1,500 m. South of 38°S, the upper limit is roughly at 2,500 m a.s.l., dropping to below 1,000 m south of ca. 44°S – with few unverified records at higher elevations even at these latitudes.

The sharp decline in documented plant diversity south of the ‘Andean knee’ in central Bolivia corresponds with high numbers of plant genera having their southern distribution limit in this region according to the GBIF data. Figure 5 summarizes the southern and northern distribution limits of individual genera as their southernmost respectively northernmost records. The number of southern genus distribution limits per 1° latitudinal band is always around or well below 100 genera throughout the tropical Andes including the Amotape-Huancabamba Zone and only increase in the central Andes south of c. 10°S. Between 16–19°S latitude, these numbers reach more than 200 and up to 365 genera. Another c. 600 genera have their southern distribution limit in southern Bolivia and northern Argentina between 20–27°S. The same is true for northern genus distribution limits which as well show values below 100 genera per 1° latitudinal band throughout the tropical Andes. The only region with high numbers of genera reaching their northern distribution limit is at about 6–8°N corresponding with the northern end of the Cordilleras Central and Occidental in Colombia. However, about 2039 genera out of the 3846 documented in our Andean GBIF dataset are also reported from southern Central America and are thus not shown with

their northern distribution limit in Fig. 5. There is also an elevated number of genera reaching their northern distribution limit at the southern end of the tropical Andes between 16–19°S. At

genus level, there thus seems to be surprising floristic continuity along the tropical Andes, with none of the biogeographic units proposed highlighted by increased taxonomic turnover. Conversely, the northern and southern ends of the tropical Andes are quite well delimited.

#### 4. Conclusion

Based on the data and analysis here presented several conclusions can be drawn. Overall, the flora of the Andes is still dramatically under documented. Especially the Central and Southern Andes are massively under collected and individual grid cells with a higher collection number (e.g., near Cuzco and La Paz) clearly demonstrate that the apparent drop in diversity especially on the eastern slope of the Andes is largely, if not completely an artefact of poor taxon records. Similar collection gaps are found also in Ecuador and Colombia, here seemingly interrupting what is likely a perfectly continuous centre of diversity. The species data on epiphytic plants and trees underscore that the effect that is here demonstrated mainly based on genus-level data is even more dramatic at species level. The graph correlating collection number with species number in epiphytic plants leads to the conclusion that in grid cells with less than 1,000 records less than 10% of the epiphytic plants actually present have likely been documented.

In spite of these serious limitations, some conclusions on diversity can be clearly drawn: there are exorbitant levels of diversity at genus level, but also in tree and epiphyte species in the Northern Andes. These high levels of diversity extend – probably quite continuously – down the western slope of the Andes to the Amotape-Huancabamba Zone and on the eastern slope down to the “Andean knee” in Bolivia. Diversity levels are high from the lowest elevations to elevations well above 3,000 m a.s.l.

The high reported diversity of epiphytic plants in Ecuador might be surprising, with the country having a much smaller area size compared to Peru and Bolivia. On the other hand, diverse humid mountain forests originally covered both slopes and parts of the inner Andean valleys in the Andes of Ecuador, whereas these forests are restricted to a sometimes relatively narrow band on the eastern slopes of the Peruvian and Bolivian Andes, the so-called Yungas. Also, this region of Ecuador has the highest number of specimen based records of any region along the entire extent of the Andes. Taking into consideration the correlation of the number of epiphytic species recorded with the absolute number of records (Fig. 4c), this could easily explain the extremely high numbers of epiphytes reported from this region as a result of high record density – and conversely dramatic underreporting in most of the remaining parts of the Andes.

The various evident collection gaps, e.g., between 7° and 10°S in N Peru at the northern End of the Central Andes render a detailed understanding of actual regional diversity levels problematic. The low collection numbers in this region may correlate to the fact that the area size per 1° latitudinal band both of the overall country area in our dataset, as well as of the diverse humid forests (both lowland and Andean) is lower compared to all other parts of the regions (compare Fig. 1,2a). On the other hand, the very low number of southern and northern distribution limits in this region (Fig. 5) clearly argues against a major biographic boundary anywhere in the Northern or Central Andes.

Overall, the data here provided indicate that our understanding of plant diversity at genus level in the South American Andes is still highly incomplete and shows a very strong collection bias. Our understanding of diversity levels at a species and landscape level can be at best called rudimentary. For most grid cells, especially in the Central Andes, record number per grid cell would likely have to be increased by a factor of at least 10 to 50 to remotely reflect

the actual diversity present. With the degree and speed of deforestation in most of Andean South America, the chance of fully recording natural diversity patterns is long gone. A systematic evaluation of herbarium records, including local herbaria, and large-scale novel collections may, however, permit at least a tentative record of plant diversity.

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