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Biogeographical regionalisation of Colombia: a revised area taxonomy

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Abstract

This study proposes a biogeographical regionalisation of Colombia based on geospatial analyses of plant species turnover and a revised area taxonomy. The spatial patterns of species turnover are calculated for 20,342 plant species in continental Colombia with distributions estimated from 271,568 georeferenced records aggregated to 414 (~50 km) grid cells across Colombia. The proposed biogeographic regions are defined by applying an agglomerative cluster analysis using a matrix of pairwise Simpson's beta (b_{sim}) dissimilarity values. Three main centres of species richness and 25 areas of endemism were identified across Colombia, complementing the definition of regionalisation. Biogeographical regionalisation comprises two dominions (Pacific and Boreal Brazilian), six provinces (Chocó-Darién, Guajira, Magdalena, Paramo, Sabana and Imerí) and thirty-five districts. The revised area taxonomy provides an updated and objective biogeographical classification for Colombia and is the first biogeographic regionalisation exclusively based on the taxic distributional overlap of Colombia´s land plants.

Keywords: Colombia, bioregions, clustering, plants, species turnover, b_{sim}

Introduction

A biogeographical regionalisation is an organized system used to define and categorise geographic areas that represent biotas (Ebach *et al.* 2008, Morrone 2018). Biogeographical regionalisation of Colombia has its beginnings in the 1800´s when Jose Celestino Mútis, Alexander von Humboldt and Francisco José de Caldas began studying Colombia´s flora and its plant geography (González-Orozco *et al.* 2015, Gómez-Gutiérrez 2016). Mútis, Humboldt and Caldas pioneered the identification and classification of tropical vegetation and useful plants into regions in Colombia and other parts of Latin America (Humboldt & Bonpland 1807, Morueta-Holme *et al.* 2015, Ebach 2015). They classified plant regions using detailed cartographical maps and vertical profiles of the Andean mountains (Caldas 1803, Appel 1994).

Since the work of these naturalists in Colombia, different biogeographical classifications have been proposed for Colombia with the most important grouped into four categories: taxonomic and vegetation types (Cuatrecasas 1934, Pérez-Arbeláez 1936, Schultes 1945, Holdridge 1947, Murillo 1951, Espinal & Montenegro 1963, Patiño 1975, Cleef 1981, Guhl 1981-1982, Rangel 1995), structural and functional vegetation units (Hernandez & Sanchez 1992, Van der Hammen 1995), natural regions (Vergara & Velasco 1901, Cortes 1903, Chapman 1917, Instituto Geografico Augustin Codazzi (IGAC)- INDERENA & CONIF 1984, IGAC 1997) and international biogeographical regionalisation of South America (Ryan 1963, Müller 1973, Cabrera & Willink 1973, Udvardy 1975, Beven *et al.* 1984, Hernandez *et al.* 1992a, Dinerstein *et al.* 1995, Olson *et al.* 2001, Morrone 1999, 2002, 2014). Hernandez *et al.* (1992a) conducted a detailed regionalisation of Colombia using vegetation types, landscapes, climate, and biota criteria to establish ninety-nine biogeographic units which was later revised by Morrone (2014).

The aim of this study is to establish an updated and quantifiable biogeographic regionalisation for Colombia based on plant species turnover and revise the natural regions of Colombia. For the purpose of this study I used the Instituto Geográfico Agustín Codazzi's (IGAC) natural regions from 1997, and revised it using geospatial analysis. IGACs classification (IGAC 1997, source of IGACs map: https://bit.ly/3cMfjqV) was established by the Government of Colombia and made responsible for producing the official maps and basic cartography of Colombia. Their natural regions are considered the most recent biogeographical classification in Colombia. IGAC´s classification partitioned

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Colombia into six natural regions: Amazonian, Andean, Caribbean, Orinoquia, Pacific and Insular. This classification delineates natural regional boundaries using thematic layering of topography, ecosystems, vegetation and watersheds. However, this method can produce less accuracy than computer-based regionalisation but was more widely used in the past due to the lack of consistent distributional datasets of species.

Since IGAC established its classification, open access global datasets for the distribution of species have been developed (i.e. Global Biodiversity Information Facility or GBIF). These global data archives are extremely valuable for producing modern and accurate biogeographical regionalisation (Morrone & Crisci 1995, Morrone 1999, González-Orozco *et al*. 2013). Although there has been significant work to create a more accurate and comprehensive regionalisation for the Neotropical region, regionalisation maps in Colombia are underdeveloped.

In addition to updating Colombia's geographical regionalisations, this study also establishes a revised area taxonomy. The definition of area taxonomy, as established by the International Code of Are*a Nome*nclature (ICAN) (Ebach *et al.* 2008), was applied and provided a standardised nomenclature to generate a list of area definitions.

Materials and methods

This study used a diverse set of major land plant groups including non-vascular, vascular and several of the largest angiosperm genera and families in Colombia (see species list and number or records per species in Supplementary material 1). These plant groups and their distributions were extracted from the Botanical Information and Ecology Network (BIEN) version 4.1 database using the RBIEN package (Maitner *et al.* 2018, http://bien.nceas.ucsb.edu/bien/). The BIEN database provides standardised plant observations from herbarium specimens and vegetation plot inventories. A total of 373,162 plant records from Colombia accessed through BIEN were cleaned. Cultivated crops were excluded from the dataset. The records without latitude or longitude and non-accepted scientific names were excluded from the raw dataset. Accepted names and synonyms of species were selected based on the index plantarum database. Of the total 373,162 records that were initially downloaded from BIEN, 271,568 species records were valid after the data was cleaned (the full species distribution dataset is available in Supplementary material 2). They represented the distribution of 20,142 wild native species of plants present in Colombia. They were aggregated into 414 grid cells of approximately 50x50 km (equivalent to 0.5 degrees) and analysed using the BIODIVERSE software version 0.18 (Laffan *et al.* 2010).

Species richness (SR) and corrected weighted endemism (CWE) were calculated in BIODIVERSE software version 0.18 (Crisp *et al.* 2001, Laffan *et al.* 2010) for each 50x50 km grid cell. CWE is the degree to which ranges of species found in a grid cell are restricted to that grid cell and SR refers to the number of species per grid cell (Laffan & Crisp 2003). Only the grid cells with scores in the 5 to 95 percentile were used to define the main areas of SR and CWE.

Species turnover, dissimilarity matrix and clustering methods were applied to establish the biogeographical regions (Gonzalez-Orozco *et al*. 2013-2014-2014a, Ebach *et al.* 2015a). We used Simpson's beta dissimilarity (bsim) metric to generate a spatial gridded analysis of species turnover. Simpson's beta was used because it reduces the effect of any species richness imbalance between locations. We used Simpson's beta dissimilarity (b_{sim}) metric to generate a spatial gridded analysis of species turnover. A matrix of Simpson's beta (b_{sim}) species turnover was then generated for all pairwise grid cell combinations (Tuomisto 2010). For the agglomerative cluster analysis, a pairwise distance matrix (b_{sim}) was used to generate a weighted pair-group using arithmetic averages hierarchical cluster in BIODIVERSE software. The outputs of the cluster analysis are a map of biogeographical regions and a dendrogram which shows a representation of the spatial relationship of dissimilarities in species composition among regions. The values shown in the root of each cluster of the dendrogram are the branch lengths of the bioregion's clusters, but they do not represent a phylogenetic tree.

Results

Species richness and endemism

The most species rich regions of plants were found in the Andean region, and centres of endemism scattered across Colombia (Fig. 1). Three main centres of species richness were identified for Colombia (Fig. 1A). Thirty-two grid cells

with the highest species richness scores (1,000-1,294 species per grid cell) were identified of which 17 were located in the main species richness centre (marked 1 in Fig. 1A), which can be found in the northern part of the western and central ranges. Two other species richness centres were found in the high mountain plains of the eastern range and in the southwest of Colombia (marked 2 and 3 in Fig. 1A).

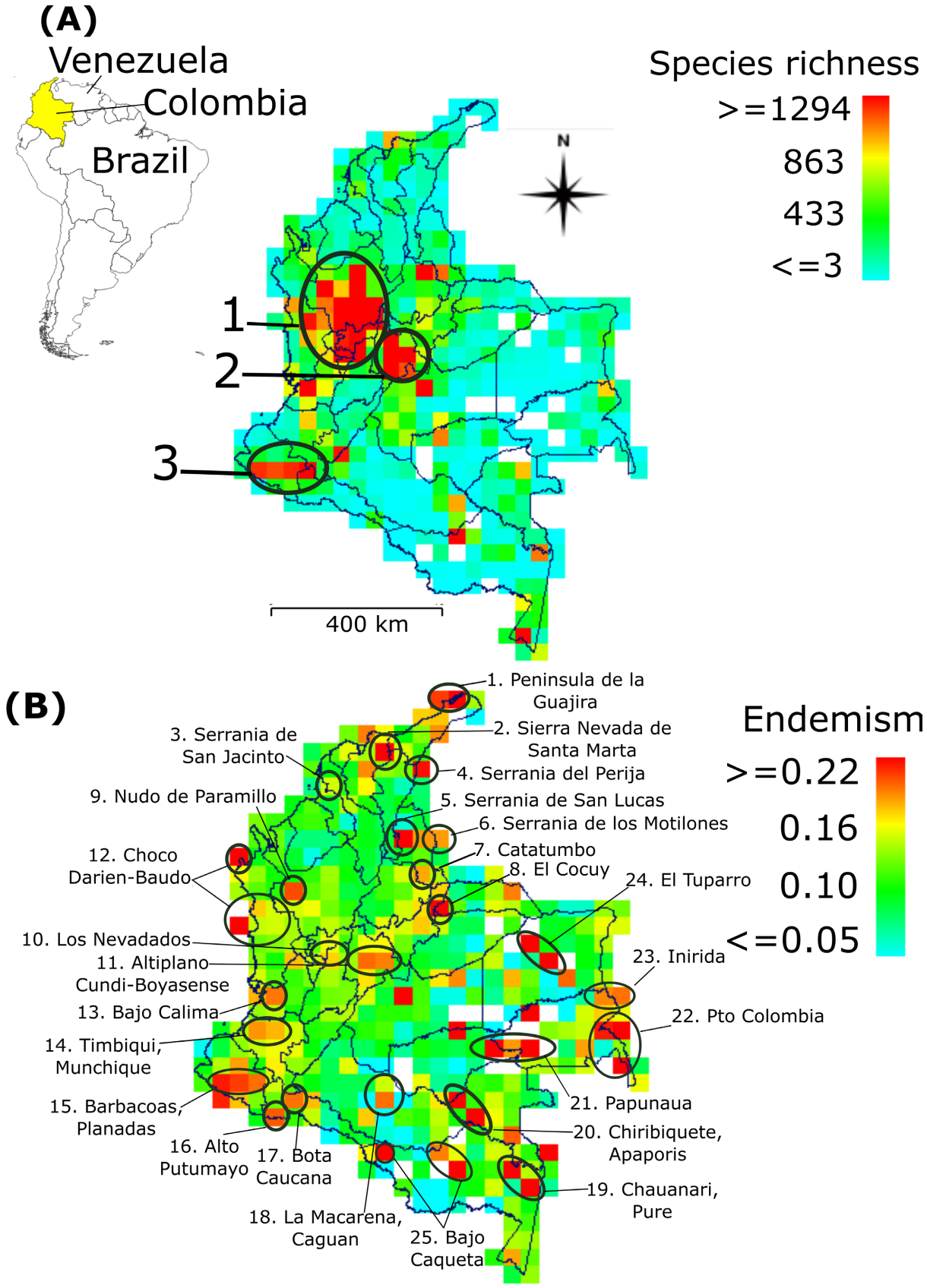

FIGURE 1. Map of South America with Colombia´s three main centres of species richness (A) and 25 areas of endemism (B).

A total of 25 individual areas of high endemism were identified across the country which were defined as having CWE scores in the 5 to 95 percentiles, equivalent to a CWE score equal to or greater than 22 percent in a single grid cell (Fig. 1B). The Andean region was found to have the largest concentration of high endemism areas (marked 2, 4, 5-11 in Fig. 1B) with a high number of range restricted flora. The Pacific region (marked 12-15 in Fig. 1B) is also an important centre of endemism and is considered one of the world's biodiversity hotspots. Interestingly, the main centre of species richness (Fig. 1A) does not fully coincide with the largest areas of endemism (Fig. 1B).

Spatial patterns of species turnover

Spatial patterns of species turnover are represented in Figure 2. Spatial patterns of turnover represented in Figure 2A were calculated values for all single grid cells. The change in species turnover from red to orange signifies no shared taxa (high dissimilarity), and from blue to yellow, similar species composition (low dissimilarity). White grid cells contain no data. A low degree of shared taxa were located in places with geographic breaks such as the Meta, Caquetá and Vichada rivers, and at the borders between dissimilar floristic regions (i.e. Choco biogeographic region and Serranías of Motilonia-Perijá in northeastern Colombia) (see ovals in Fig. 2A). Figure 2B-D on the other hand, represents species turnover based on a focal grid cell (marked 1 (Fig. 2B), 2 (Fig. 2C) and 3 (Fig. 2D). The rate of change of turnover values (b_{sim}) for geographical distance was 0.5 with the gradient increasing at an average distance of 200 km (Fig. 2B-D). This rapid turnover is indicative of the significant environmental variations in Colombia often as a consequence of changes in elevation. For instance, the rate of spatial turnover coincides with the biogeographical regions as we can see in Figure 2B-D. The rate of turnover change between 0.66 and 0.33 (green and yellow grids) depicts the location of the Andean ranges (Figure 2B); the lowlands in the Caribbean region (Fig. 2C) and the lowlands of the Amazon region (Fig. 2D).

Biogeographical regions of Colombia

The proposed biogeographical regions of Colombia are shown in Figures 3 A-B. A map of IGAC´s regions and sub-regions is shown in figure 3C. The proposed regions recognises Colombia as part of the established neotropical region; its existing two sub-regions, Boreal Brazilian and Pacific (Fig. 3A), and six provinces, Imerí (made up of south and east), Sabána, Páramo, Magdalena, Chocó-Darién and Guajira (Fig. 3B). However, the proposed biogeographical regions recommends the six provinces be divided into 35 sub-levels referred to as districts (Fig. 4). Sub-districts were proposed but only in the case of the Páramo province. Maps 2c, 3c, 4e and 5a in Figure 4 are considered biogeographic breaks due to their dissimilar taxa and high species turnover (Fig. 1A), which suggests a separation of major turnover areas. This deviates from IGAC´s (1997) existing classification which has six regions (here equivalent to provinces) and 50 sub-regions (Fig. 3C). While this proposed new classification´s reduced number of subregions and creates new boundaries, 23 districts closely align with the equivalent sub-regions in IGAC´s classification.

Discussion

This biogeographic regionalisation was developed using computer-based tools to calculate taxic distributional overlap of plants across the different regions of Colombia which differs from IGAC´s classification, which uses cartographic layering of topography, ecosystems, vegetation and watersheds. This computer-based method provides greater spatial accuracy. The biogeographical regions are defined using species turnover which is a precise representation of geographic units with a unique signature of species that are similar to each other. Furthermore, a gridded fine-resolution classification provides greater accuracy compared to thematic layering of extensive geographic areas such as an entire ecosystem or mountain range.

Area taxonomy

Table 1 summarizes the proposed area taxonomy following ICAN´s nomenclature (Ebach *et al.* 2008). Following this, a summary of biogeographical regions of Colombia with a description of each new district and sub-districts is provided and discussed. It includes the name of each region and subregions as well as its original author and any emendations. An emended diagnosis of each of the dominions is also included. This study focuses on native wild terrestrial plants found in continental Colombia and therefore does not include islands or archipelagos.

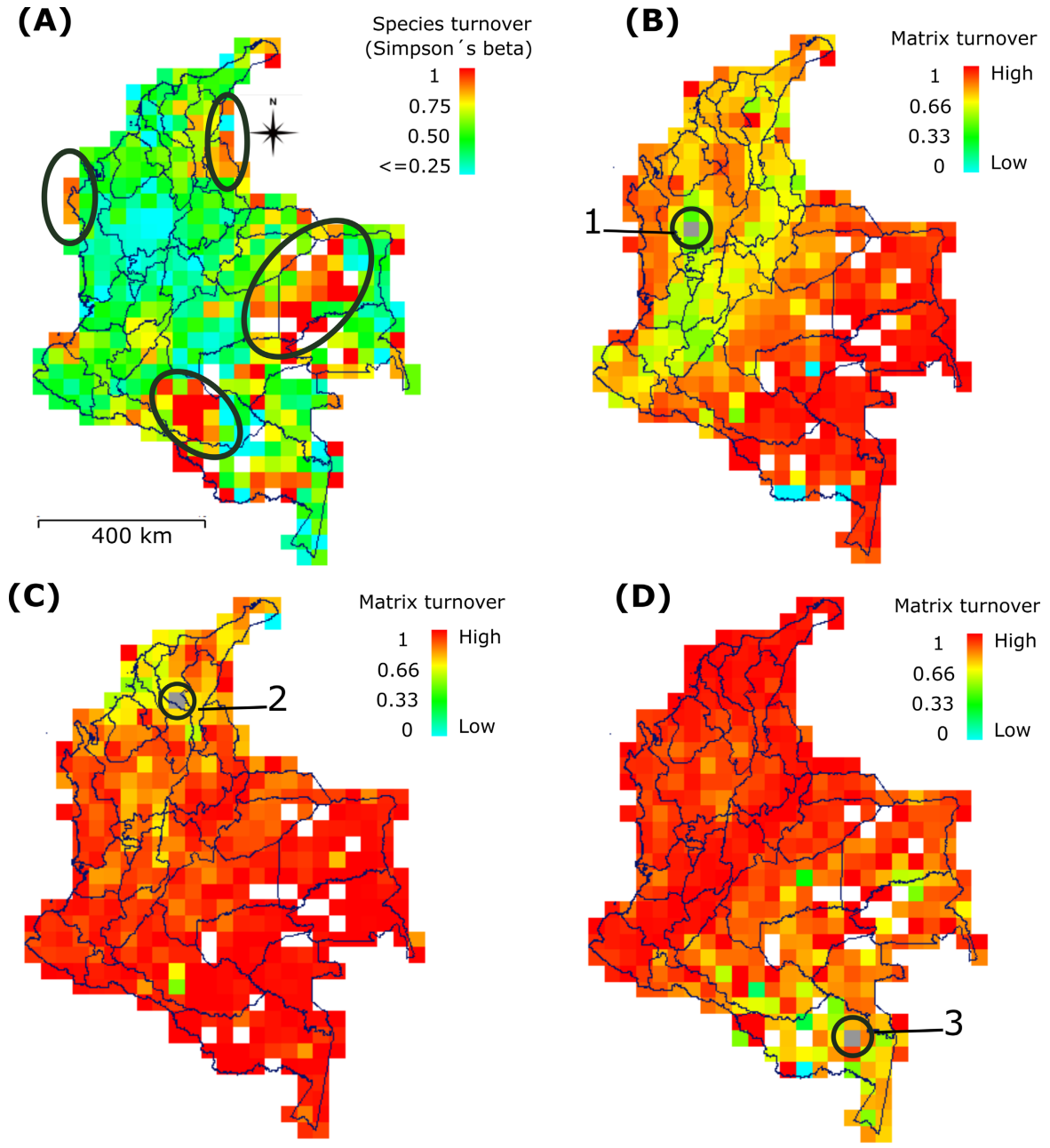

FIGURE 2. Map of Colombia showing plant species turnover: (A) red grid cells show no shared taxa (high dissimilarity); blue and green grid cells show a high level of shared taxa (low dissimilarity); (B-D) plants species turnover relative to a focal grid cell (circled grid cell).

TABLE 1. A list of the biogeographical regions of Colombia with their area taxonomy classification.

Region	Sub-region	Dominion	Province	Districts
Neotropical				
	Brazilian			
		Pacific		
			Guajira- Cabrera & Willink 1973	(1a-c)
			Magdalena- Müller 1973	(2a-d)
			Chocó-Darién- Ryan 1963	(3a-d)
			Páramo- Cabrera 1957	(4a-e: 4b1-5; 4d1-2; 4c1-4)
		Boreal Brazilian	Imerí- Beven *et al.* 1984	(5a-e: south) (5f-h: east)
			Sábana- Orfila 1941	(6a-c)

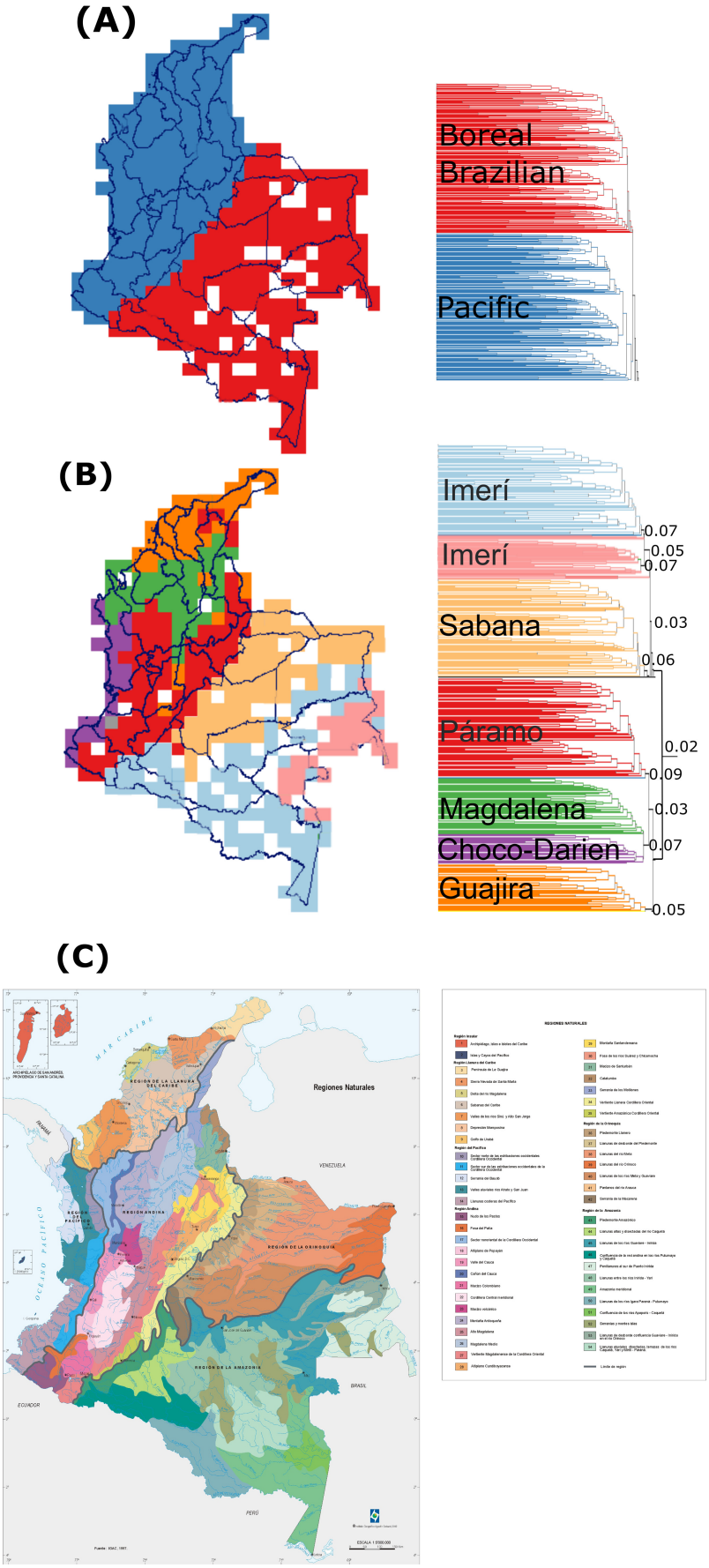

FIGURE 3. Biogeographic regionalisation of Colombia with two subregions (A), and six provinces with the corresponding branch lengths in the cladogram (B). IGAC´s (1997) classification of the natural regions of Colombia (C). IGAC´s (1997) map is freely available at http://www2.igac.gov.co/.

NEOTROPICAL región- Sclater 1858

Neotropical region- Morrone 2014

BRAZILIAN subregión- Blyth 1871

PACIFIC dominion- Clarke 1892 (Fig. 3A)

Emended diagnosis. The area covers the western half of the country between 0˚-12˚N and 71-77˚W. The dominion neighboring areas are: the Caribbean Ocean to the north, the Pacific Ocean to the west, northern Ecuador to the south and the eastern plains and Amazon foothills to the east (Fig. 3A). The Pacific dominion is sub-divided into four provinces: Guajira, Magdalena, Chocó-Darién and Páramo. Guajira is the most dissimilar from other clusters in the Pacific dominion. Magdalena province is more similar to the Chocó-Darién. The Páramo province is the largest and most complex province and is an independent cluster (Fig. 3B). The Páramo was previously classified by Morrone (1999) as part of the South American transition zone, but the new classification proposes to shift the Paramo transition zone to the Pacific dominion due to its similarities with this region of Colombia.

Remarks. The Pacific dominion has never been classified before as a single biogeographical area. According to IGAC (1997), western Colombia composes of the Caribbean, Pacific and Andean regions (islands of the Caribbean and Pacific oceans included). The new classification identifies the Andean cluster which includes the western, central, and eastern Andean ranges. The Andean cluster is independent but has many floristic similarities to the Chocó-Darién and Magdalena provinces. None of the previous classifications have identified these similarities between the two provinces.

Provinces included. Guajira Cabrera & Willink 1973, Magdalena Müller 1973, Chocó-Darién Ryan 1963, Páramo Cabrera 1957.

GUAJIRA province- Cabrera & Willink 1973 (Fig. 3B).

Santa Marta centre- Müller 1973
Venezuelan Dry Forest province- Udvardy 1975
Northern Andes- Dinerstein *et al.* 1995
Región de la llanura del Caribe- IGAC 1997
Barranquilla province- Morrone 1999
Maracaibo province- Morrone 2002
Guajira province- Morrone 2014

Districts. This province is recognized by IGAC (1997) as a single biogeographic region, but the new classification splits it in two provinces: Guajira and Magdalena (maps 1 and 2 in Fig. 4). Guajira is the area at the top end of Colombia between 12˚N-71˚E and 8˚N-76˚W. Guajira is a single cluster independent from its neighbours. Guajira is sub-divided into three districts (1a-c in Fig. 4). District 1a is the area northeast of the Sierra Nevada de Santa Marta extending to Punta Gallina, which is known as Península de La Guajira. The areas west of Sierra Nevada de Santa Marta and Magdalena river, represents a geographical barrier, and are parts of the departments of Cordoba, Sucre, Bolivar, and Cesar. This area is composed of district 1b, which is part of the western side of the Magdalena river mouth and plains. Further down, district 1c is part of the Sinú and San Jorge river valleys. This district includes not only the coastal areas of Sincelejo and Montería but also to the south limits of this province in the wetlands known as Depresión Momposina.

According to IGAC (1997), there are 7 sub-regions in the Llanura del Caribe region: 1. Península de La Guajira, 2. Sierra Nevada de Santa Marta, 3. Delta del río Magdalena, 4. Sabanas del Caribe, 5. Valles de los ríos Sinú y Alto San Jorge, 6. Depresión Momposina, 7. Golfo de Urabá. The new classification also recognises IGAC´s sub-regions 1,3,5,6 and 7 as part of the Llanura del Caribe because they are similar to the Guajira districts in this biogeographical regionalisation.

Remarks. According to IGAC (1997), Sierra Nevada de Santa Marta is part of the Caribbean region. Here, Sierra Nevada de Santa Marta is a cluster under the Andean sub-region. Golfo de Urabá is not part of this sub-region as presented by IGAC (1997).

MAGDALENA province- Müller 1973 (Fig. 3B).

Guajira province- Cabrera & Willink 1973
Barranquilla centre- Müller 1973
Colombian coastal province- Udvardy 1975
Colombian province- Rivas-Martínez & Navarro 1994
Northern Andes bioregion- Dinerstein *et al.* 1995
Región de la llanura del Caribe- IGAC 1997
Maracaibo province- Morrone 1999
Santa Marta province- Morrone 2002
Magdalena province- Morrone 2014

Districts. This province is located in the area between 7˚N-73˚E and 5˚N-77˚W. Magdalena is sub-divided into four districts (2a-d in Fig. 4). District 2a is the area known as Golfo de Urabá in the most northwestern part of Antioquia department. District 2b is located in western slopes on the tip of the western range connecting the Pacific and the northern inter-Andean foothills. District 2c is in the northeast of the Magdalena province where there is a geographical break between the eastern Andes range and the Magdalena valley separating floristic elements that converge at the tip of the eastern range. District 2c is made of the lower Magdalena and Cauca river valleys, with both rivers creating a geographic barrier with the Serranía de San Lucas between those rivers. The Magdalena valley south of the Bolivar department form the district 2d which follow the inter-Andean valleys between the central and eastern ranges.

According to IGAC (1997), there are 7 sub-regions as part of the Llanura del Caribe region: 1. Península de La Guajira, 2. Sierra Nevada de Santa Marta, 3. Delta del río Magdalena, 4. Sabanas del Caribe, 5. Valles de los ríos Sinú y Alto San Jorge, 6. Depresión Momposina, 7. Golfo de Urabá. The new classification also recognises IGAC´s sub-regions 1, 3, 5, 6 and 7 as part of the Llanura del Caribe region because they are similar to the Magdalena districts in this biogeographical regionalisation.

Remarks. Magdalena province acts as a transitional zone between the Guajira and the most northern parts of the central, eastern, and western Pacific Andean regions. The region most similar to the Magdalena province is the Chocó-Darién province which is part of the hyper-humid Pacific region (Fig. 3B). The new classification includes district 2b-d in the Pacific region however there are greater similarities with the Magdalena province. According to IGAC (1997), Magdalena province is part of the Andean region, however this study found no evidence to support this classification.

CHOCÓ-DARIÉN province- Ryan 1963 (Fig. 3B).

Pacific province- Cabrera & Willink 1973
Colombian coastal province- Udvardy 1975
Northern Andes- Dinerstein *et al.* 1995
Región Pacífica- IGAC 1997
Chocó province- Morrone 1999, 2002
Chocó-Darién province- Morrone 2014

Districts. This province is located in the areas of coastal and alluvial plains on the Pacific region between 1-7˚N and 77-78˚W. Chocó-Darién province is sub-divided into four districts following a north-south pattern (3a-d in Fig. 4). District 3a is the area of Serranía del Baudó covering the northern and central coastal plains of Choco. The alluvial plains of the Atrato and San Juan Rivers and the coastal areas of Valle del Cauca make up district 3b. To the south, district 3c is identified as a geographical break between Cauca and Nariño departments. In the most southern extreme of this province, is district 3d which covers the coastal valleys of Nariño.

According to IGAC (1997), there are 5 subregions in the Pacific region: 1. Sector norte de las estribaciones occidentales de la Cordillera Occidental, 2. Sector sur de las estribaciones occidentales de la Cordillera Occidental, 3. Serranía del Baudó, 4. Valles aluviales ríos Atrato y San Juan, 5. Llanuras costeras del Pacífico. The new classification also recognises sub-regions 3,4 and 5 as part of the Pacific regions because they are similar to the Chocó-Darién districts in this biogeographical regionalisation.

Remarks. The closest geographically related floristic region to Chocó-Darién province is the Magdalena province (Fig. 3B). The southwestern coastal areas of the departments of Valle del Cauca, Cauca and Nariño are classified as

part of the Chocó-Darién province which extends to the borders with Ecuador in Nariño. According to IGAC (1997), the Pacific region includes the western slopes of the western range. Here, no evidence was found to support that claim. On the contrary, the Pacific region´s western slopes were clustered in the Paramo province in the Andean region.

PÁRAMO province- Cabrera 1957 (Fig. 3B).

Altoandean province- Cabrera & Willink 1973
Cauca province- Müller 1973
Northern Andean province- Udvardy 1975
Colombian Montane province- Udvardy 1975
Roraima-Trombetas province- Rivas-Martínez & Navarro 1994
Northern Andes- Dinerstein *et al.* 1995
Región Andina- IGAC 1997
Magdalena province- Morrone 1999
Cauca province- Morrone 1999
Paramo norandino- Morrone 1999
Magdalena province- Morrone 2002
Cauca province- Morrone 2002
Cauca province- Morrone 2014
Paramo province- Morrone 2014
Magdalena province- Morrone 2014

Districts/sub-districts. This province is located in the Andean ranges between 0-10˚N and 72-76˚W with elevations above 1,000 masl. The Paramo province is sub-divided into five districts and eleven sub-districts (4a-e in Fig. 4). District 4a is the Catatumbo region. Districts 4b-c correspond to areas of high elevations such as Paramo ecosystems along the Andean ranges in the departments of Santander, Boyacá, Cundinamarca, Huila, Cauca and Nariño. District 4b is sub-divided into five areas that represent different sections of the slopes around the western, central and eastern ranges. For instance, district 4b1 is part of the most northern section of the western slopes in the western range. The eastern slopes of the western range facing the Magdalena valley in the northeast of Antioquia department are representative of district 4b2. On the southern contiguous region, we find districts 4b1 and 4b3 which are part of the Pacific foothills of Valle del Cauca and Choco. District 4b5 covers the foothills of Valle del Cauca, Cauca and Nariño. The slopes of the eastern ranges of Meta department are grouped into a separate cluster from the western range (4b4). Sierra Nevada de Santa Marta, Serranía del Perijá and Motilones are part of the most northern section of district 4c1–3. The southern section of district 4c3 is part of the western slopes of the eastern range facing the Magdalena river in the inter-Andean valleys. The central part of district 4c3 represents the highlands of Cundinamarca and Boyacá. The northern part of district 4c3 represents the mountainous areas of Santander and the Santurbán region. The Valleys of the Cauca river are shown in district 4d1, following a north-south pattern from Valle del Cauca all the way to Quindío. The middle elevations of the coffee region all the way to the high elevations of the volcanic region shared by Caldas, Quindío and Risaralda are depicted in the district 4d2. In between the northern part of 4d2 and 4e is the district of the upper Magdalena valley. District 4e acts as a geographic break where three Andean ranges converge into the Macizo Colombiano.

According to IGAC (1997), there are 21 sub-regions in the Andina region: 1. Nudo de los pastos, 2. Fosa del Patía, 3. Región nororiental de la cordillera Occidental, 4. Altiplano de Popayán, 5. Valle del río Cauca, 6. Cañón del río Cauca, 7. Macizo Colombiano, 8. Cordillera Central meridional, 9. Macizo volcánico, 10. Montaña Antioqueña, 11. Alto Magdalena, 12. Magdalena Medio, 13. Vertiente Magdalenense de la Cordillerra Oriental, 14. Altiplano Cundiboyacense, 15. Montaña Santandereana, 16. Fosa de los ríos Suárez y Chicamocha, 17. Macizo de Santurbán, 18. Catatumbo, 19. Serranía de los Motilones, 20. Vertiente llanera de la cordillera Oriental, 21. Vertiente Amazónica de la cordillera Oriental. The new classification also recognises IGAC´s sub-regions 4, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 17, 18, 19, 20 and 21 as part of the Andean region because they are similar to the Páramo districts in this biogeographical regionalisation.

Remarks. We found that elevation has an important influence on the formation of the Andean biogeographical regions of Colombia. The districts mapped here represent the main Andean ecosystems: Páramos (high mountains), mid-elevations (Andean ranges slopes) and low inter-Andean valleys (district 4 in Fig. 4). These independently mapped floristic areas clearly follow an elevational trend**.** The high mountain sub-districts mapped here are in accordance

with previous biogeographical studies (Jiménez-Rivillas *et al.* 2018). The eastern, western and northern limits of this province were different to any other previous classification because they mapped lower limits starting at 1,000 meters above sea level (masl), for example in the eastern limits, the South American transition zone identified by Morrone (2014) was found clustered into the Pacific dominion. Therefore, it is transferred to the Pacific dominion.

BOREAL BRAZILIAN dominion- Clarke 1892 (Fig. 3A)

Emended diagnosis. This Boreal Brazilian dominion is located between 7˚N-4˚S and 73-76˚W. The limits on the western side are demarcated by the slopes of the eastern range under 1,000 masl. The neighbouring regions to this dominion are: Orinoco plains of Venezuela to the north and the Amazon region of Ecuador, Peru, and Brazil to the east. Boreal Brazilian is sub-divided in the Amazonian or Imerí and the Orinoquia or Sabana provinces. The Sabana province is an independent geographic region with shorter branches in the dendrogram (Fig. 3B). The Boreal Brazilian dominion is sub-divided into eleven districts.

Remarks. According to IGAC (1997), the Boreal Brazilian dominion is composed of the Orinoquia and Amazonian regions. This dominion has never been classified before as a single biogeographical unit for plants in Colombia.

Provinces included. Sabana Orfila 1941 and Imerí Beven *et al.* 1984.

IMERÍ province- Beven *et al.* 1984 (Fig. 3B).

Amazonian province- Cabrera & Willink 1973
Amazonian province- Udvardy 1975
Imerí province- Beven *et al.* 1984
Amazonia bioregion- Dinerstein *et al.* 1995
Región de la Amazonia- IGAC 1997
Napo province- Morrone 1999
Imerí province- Morrone 2014

Districts. Two areas within this province were found as different clusters: south (5a-e in Fig. 4) and east (5f-h in Fig. 4). The southern area of Imerí province is between 4˚N-4˚S and 72-76˚W. This area is sub-divided into eight districts. The most western districts 5c-d are on the slopes and foothills of the eastern ranges including the upper plains of Caquetá river. District 5c is made up of the eastern range slopes, and district 5b of the foothills. These two are the most dissimilar to the other Amazon districts. The transitional zone between Meta and Guaviare is represented by district 5a, and the most southern Amazon areas, districts 5d-e. The southern area of the Imerí province (5a-e in Fig. 4) forms one cluster defined by the boundaries of the Caquetá-Apaporis and Guaviare rivers. District 5d is located north of Caquetá river with more similarity to the Guaviare region. District 5e is located located in the lower Caquetá river in the direction to Leticia, in the Amazon department. The eastern area of the Imerí province (5f-h in Fig. 4) is between 1˚N-2˚N and 69-70˚W in Guanía and Vaupes departments bordering with Brazil. The eastern area of Imerí is sub-divided into three districts. The Inírida river plains are in district 5f, which is most dissimilar to the Río negro peninsula to the south of district 5h. Further east connecting the Inírida plains with the Vaupes and Apaporis valleys is the stretch of alluvial forests found in district 5g. These eastern Amazon districts (5f-h) form a separate floristic cluster dissimilar to the Vichada and Guaviare neighboring regions.

According to IGAC (1997), there are 12 sub-regions part of the Amazonia region: 1. Piedemonte Amazónico, 2. Llanuras altas y disectadas del río Caquetá, 3. Llanuras de los ríos Guaviare e Inírida, 4. Confluencia de la red andina en los ríos Putumayo y Caquetá, 5. Penillanuras al sur de Puerto Inírida, 6. Llanuras entre los ríos Inírida y Yarí, 7. Amazonía meridional, 8. Llanuras de los ríos Igara, Paraná y Putumayo, 9. Confluencia de los ríos Apaporis y Caquetá, 10. Serranías, montes e islas, 11. Llanuras de desborde (Confluencia Guaviare – Inírida en el río Orinoco), 12. Llanuras aluviales disectadas (Terrazas de los ríos Caquetá, Yarí y Marití – Paraná). The new classification also recognises IGAC´s IGAC´s sub-regions 1, 4, 5, 7 and 9 as part of the Amazonia region because they are similar to the areas south of the Imerí districts.

Remarks. According to IGAC (1997), the Amazon region is composed of 12 sub-regions. This new classification does not include as many districts as IGAC´s classification. This is because new boundaries were identified along the transitional zone between the southern part of the savannas and the most northern Amazon limits. The unique characteristics found in this area have resulted in the formation of a new intermixed district. Spatial patterns of species turnover support this observation and show high values of species turnover concentrated all along the transitional

savannas-Amazonian zone supporting the formation of a new district (Fig. 2A-D). These boundaries have been mentioned previously in the literature but have not gone as far as supporting the formation of a separate district. According to IGAC (1997), these areas are referred to the Llanuras de los Ríos Guaviare-Apaporis. The Amazon foothills of Meta were mapped as part of the slopes of the Andean eastern range, and not as part of the Amazon region as suggested by IGAC (1997). The upper Caquetá and Bajo Caguán rivers are an area of high species turnover suggesting a geographic break (Fig. 2A). This region appears to connect the Serranía de la Macarena and Chiribiquete National Park with the Caquetá-Caguán river plains. This is considered a transitional zone between the most eastern and western districts. According to IGAC (1997), the eastern section of Imerí, is known as the Perillanuras del Río Inírida and llanuras del río Guaviare. The new classification differs from IGAC´s classification because the east area of Imerí form an independent floristic cluster dissimilar to the districts located to the west. Figure 1A shows these areas having high species turnover indicating dissimilar floras from the western Amazonian districts.

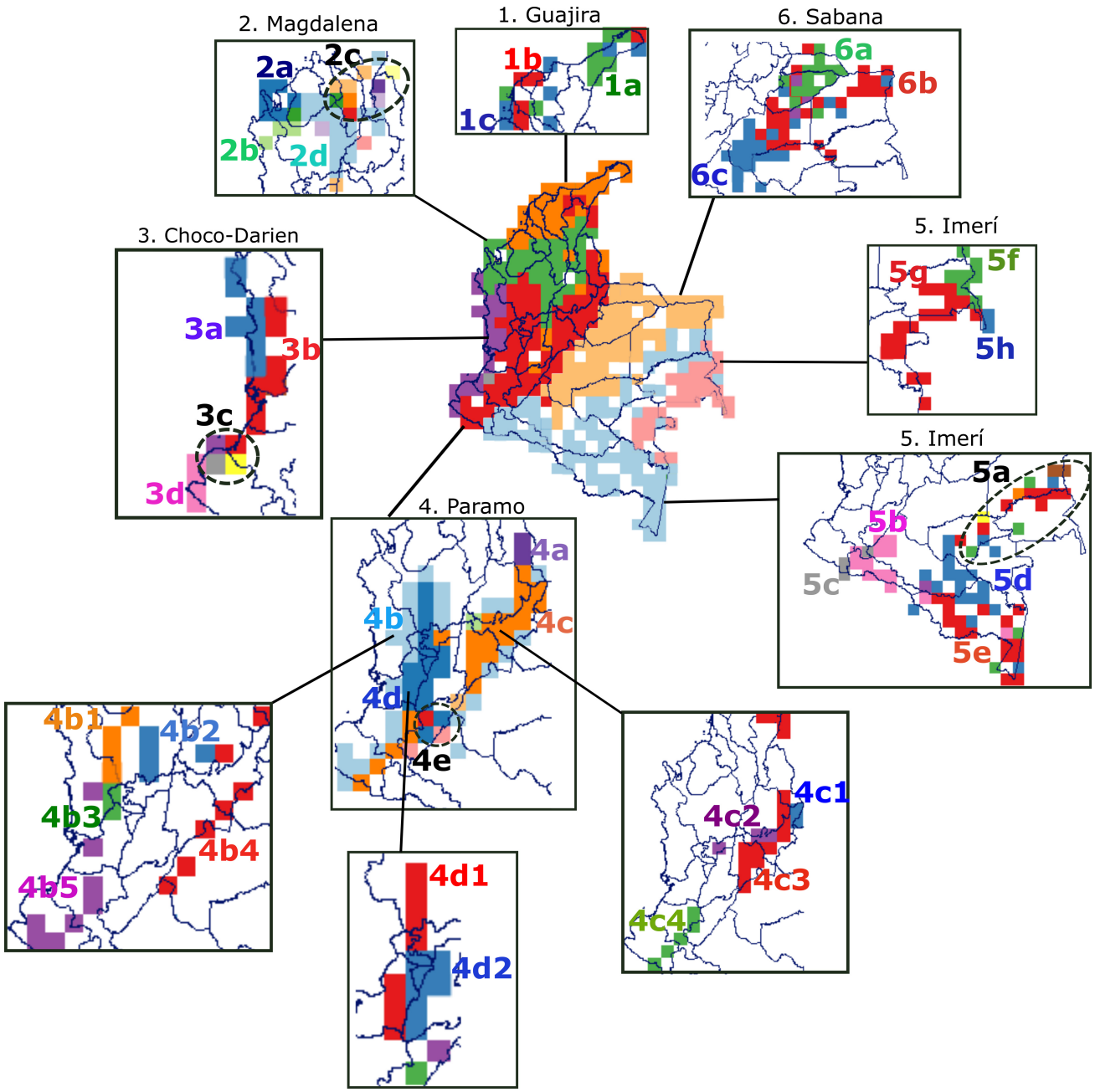

FIGURE 4. Biogeographical districts (maps 1 to 6) and sub-districts (sub-divisions 1 to 5 in district 4) of Colombia.

SABANA province- Orfila 1941 (Fig. 3B)

Sabana province- Cabrera & Willink 1973
Llanos province- Udvardy 1975
Llanos province- Rivas-Martínez & Navarro 1994
Orinoco- Dinerstein *et al.* 1995
Región de la Orinoquia- IGAC 1997
Llanos Venezolanos- Morrone 1999
Llanos province- Morrone 2002
Sabana province- Morrone 2014

Districts. This province is located between 1˚N-6˚N and 67-74˚W and includes Arauca, Casanare, Meta and Vichada departments (Fig. 2B). The Sabana province is divided into three districts (6a-c in Fig. 4): flooding savannas (6a), non-flooding savannas (6b) and the transition zone into the Amazon composed of the Serranía de la Macarena and San Jose del Guaviare borders (6c). The Meta river acts as a geographic barrier separating the flooding from the non-flooding savannas. Flooding savannas are north of the Meta river in the central and eastern parts of the departments of Arauca and Casanare. A cluster composed of the non-flooding savannas and transitional Amazonian zone is found there, which is dissimilar to the rest of the districts. Non-flooding savannas are found in the Vichada and Meta departments. The foothills of the eastern ranges below 900 metres above sea level are part of the non-flooding savannas. The district 6c is unique because it acts as a geographic barrier, mainly occupy by the region of the Serranía de la Macarena.

According to IGAC (1997), there are 5 subregions as part of the Orinoquia region: 1. Piedemonte Llanero, 2. Llanuras de desborde del piemonte, 3. Llanuras del río Orinoco, 4. Llanuras del río Guaviare, 5. Llanuras del río Meta, 6. Pantanos del río Arauca, 7. Serranía de la Macarena. The new classification also recognises IGAC´s sub-regions 1, 2, 6 and 7 as part of the Orinoquia region because they are similar to the Sabana districts in this biogeographical regionalisation.

Remarks. According to IGAC (1997), this area is sub-divided into five sub-regions. The new classification differs from IGAC´s classification because it classifies regions according to flooding and non-flooding savannas whereas IGAC does not differentiate between the two in the Llanuras del río Meta and Guaviare regions.

Data Availability

In supplementary material 1, a species list with the number of records per taxa is provided. Species range maps in this list can be downloaded through the R package BIEN (Maitner *et al.* 2018). See http://bien.nceas.ucsb.edu/bien/. The complete spatial dataset for all species used in this study can be found in supplementary material 2.

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