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REVIEW AND SYNTHESIS | NEOTROPICAL VEGETATION

South American terrestrial biomes as geocomplexes: a geobotanical landscape approach

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Abstract

The classic and current perception of biome in its various meanings is fundamentally based on vegetation types that are considered as discrete or independent and fragmented entities in the landscape. Vegetation units are characterized by their physiognomy, which is based on the dominant life forms and mainly determined by climatic conditions. However, vegetation units are associated and mutually interacting at a landscape level. They are determined by local or regional, climatic, topographic and edaphic gradients within a given territory or geographic area. In this work, we propose a new conceptual and methodological approach aiming to better understand the biome concept in a landscape framework, developing ideas already partially advanced by us. In this sense, we consider the biome as a landscape complex (geocomplex), that spatially includes one to several vegetation geoseries which, in turn, each comprise the following possible geomorphologically linked vegetation series: i) the potential natural climatophilic vegetation (zonal vegetation) and their seral successional stages which occur repeatedly in the landscape; ii) edapho-xerophyllous vegetation (azonal vegetation such as occurs on rocky outcrops or sandy soils); and iii) edapho-hygrophilic vegetation (azonal vegetation such as flooded vegetation on river banks). Based on surveys and field data (more than ca. 300 transects) obtained by the authors in most South American countries from 1990 to the present, 33 South American geocomplex biomes and 16 macrobiomes were identified and synoptically characterized, through graphic general zonation models (phyto-topographic type-profiles) extrapolated from numerous observations along representative bioclimatical, geomorphological and biogeographically stratified transects. Field data and transect-plots are currently being processed to be included into the "GIVD database".

Taxonomic reference: Tropicos.org, Missouri Botanical Garden (https://tropicos.org) [accessed 1 Feb 2023].

In Memoriam: Salvador Rivas-Martínez

Keywords

biome, catena, geocomplex, geoseries, South America, zonation

Introduction

Biomes are large-scale ecosystems, including all the biological diversity found within their boundaries, as well as the ecological and evolutionary processes taking place at the different levels of biological organization, from genes to landscapes. Recent major reviews of the biome concept (Mucina 2018; Faber-Lagendoen et al. 2020; Hunter et al. 2021; Navarro and Molina 2021; Loidi et al. 2022) largely agree on this or a similar definition.

The actual delimitation of biomes, however, has been largely based on zonal vegetation physiognomy as defined by dominant life forms, the regional climate and zonal soils (e.g., Walter and Box 1976; Dinerstein et al. 2017). Recently, functional or ecofunctional traits have been incorporated into the biome definition (e.g., Keith et al. 2020, 2022). The formal delimitation of biomes based on the zonality/azonality framework was largely developed by Walter (1954, 1970, 1976; see Walter and Box 1976; Walter and Breckle 1985–1989). The Walter approach advocates the delimitation of so-called zonobiomes. To this end, zonal and azonal vegetation are treated separately and only zonal vegetation and its relationship to the regional climate is considered in the delimitation of zonobiomes. Azonal vegetation forms other substrate-determined biomes, the so-called pedobiomes (see for example Walter and Box 1976). Furthermore, mountain ecosystems are also excluded from the concept of zonobiomes and are classified as a different class of biomes, the orobiomes. All kinds of biomes (zonobiomes, pedobiomes and orobiomes) are hierarchically arranged and ultimately refer back to biotic communities, which in turn can be subdivided into synusia (Walter and Box 1976).

While a given territory is governed by the presence of a zonobiome, many kinds of biomes may coexist and alternate in the landscape. Mucina (2018) appears to suggest that since the elevational gradients are dependent on regional climatic conditions, orobiomes may be accommodated in a simpler scheme of zonobiomes. However, Mucina (2018) does not totally discard the concept of pedobiomes (he called them azonal biomes) and seems to promote the zonality/azonality framework to define biomes, as becomes clear in his later works (see for example Macintyre and Mucina 2021). One of the problems of the zonality/azonality concept is that some azonal communities may also depend on regional climatic conditions, which complicates the application of that framework. A solution to this problem has been the recognition of intrazonal communities, which in spite of their dependence on substrate conditions, range only within the boundaries of one zonal biome (Mucina et al. 2016). This shifts the conceptual problem to the distinction between azonal and intrazonal communities, which turns out to be scale-dependent (i.e., relative to the spatial scale at which a biome has been defined). While there have been some attempts to discuss the subject of azonality and intrazonality (e.g., Sieben 2019), to our knowledge no in-depth conceptual review of these concepts and their implications has yet been proposed.

Different plant communities in a given geographical area are associated and mutually interactive in the landscape depending on the environmental gradients determined by the climate, topography, geoforms and soils. This spatial association of plant communities has a deep eco-functional meaning, since it expresses recognizable iterative patterns, and the geochemical flows of water and nutrients (Glazovskaya 1963). Each territory has its own hydrogeochemical characteristics, determining the spatial arrangement of zonal and azonal (or intrazonal) plant communities. These sets of spatially arranged vegetation types correspond to territorial vegetation complexes and specifically constitute the biomes (Navarro and Molina 2021). Since this concept differs from the traditional Walterian biome concept (see Mucina 2018), in which the zonal/azonal framework is employed as an initial criterion to distinguish biomes, it might be more appropriate to call them geobiomes or geocomplex biomes.

This idea of biomes as geobiomes has its roots in the classic Russian geographic, edaphic and geochemical landscape schools (e.g., Gerasimov 1946; Perel'man 1960, 1967; Glazovskaya 1963). It is supported by the concept of soil catena or ideal soil toposequence zonation (Milne 1935). The "landscape" aspects of biomes were already dealt with by Sukachev and Dylis (1964), who proposed the concept of biogeocenosis. This was later taken up and developed by Walter (Walter 1970, 1976; Walter and Box 1976; Walter and Breckle 1985, 1989), who also proposed the concept of biogeocoene complexes, indicating that they often coincide with spatially (landscape, catena) and temporally (vegetation dynamics) connected biogeocoenes. For Walter and Box (1976, and other referenced cited above), the hierarchy of units of the biogeosphere is (from more to less inclusive): (a) zonobiome (according to major climatic zones), (b) subzonal biome, (c) biome, (d) biogeocoene complexes, (e) biogeocoenes and (f) synusia. Geobiomes can also be arranged in a similar hierarchical manner, though they differ in that they incorporate the landscape, catenal view, where both orobiomes and pedobiomes (azonal and intrazonal biomes) do not require segregation.

The contributions mentioned above gave rise to the European development of dynamic-catenal phytosociology or landscape phytosociology (e.g., Schmithusen 1959; Tüxen 1979; Géhu and Rivas-Martínez 1981; Rivas-Martínez 2005; Rivas-Martínez et al. 2011b), as well as the development and advances of Landscape Ecology as a formal scientific discipline (e.g., Forman and Godron 1986; Forman 1997). They constitute the basis for the recognition of biomes as geobiomes.

Geocatena (= geoseries, geosigmetum) is defined by Rivas-Martínez (2005) and Rivas-Martínez et al. (2011b) as the complex of vegetation landscapes which include the potential natural climatophilous vegetation and their associated seral communities (zonal vegetation series), as well as the azonal and the intrazonal vegetation series which are spatially contiguous. Vegetation series

(= sigmetum) is here considered as a set of plant communities including both the potential natural vegetation, and the seral plant-communities that replace them because of anthropic or natural impacts. A set of contiguous or adjacent geoseries, existing in the same geographical territory, that share similar characteristics of vegetation types, on the same or topographically related altitudinal levels and in the same biogeographic unit, is called macrogeoseries or macrogeosigmetum by Rivas-Martínez et al. (2011b). We now propose here to consider the latter as geocomplex biomes. As these concepts of geocomplex and geocatena relate several zonal and azonal (or intrazonal) communities in the landscape that replicate several times in each territory, they reflect large-scale ecosystems. They can therefore be regarded as geobiomes as defined in the proposal of Navarro and Molina (2021).

Until now, the integrated application of these concepts to the whole of South America has been scarce or non-existent. This is despite the existence of numerous regional or local works of a floristic or phytosociological nature which cover most of the continent (Cleef 1980, 1981; Cabido et al. 1991, 1994; Duivenvoorden and Lips 1995; Rangel et al. 1997, 2004, 2017; Galán et al. 2004, 2006, 2009, 2011, 2015, 2020; Luebert and Gajardo 2001, 2005; Luebert and Pliscoff 2017; Entrocassi et al. 2020; Minorta-Celys 2020, among others).

In this sense, our main goal is to apply the Geobotanic Landscape Ecology approach to the whole of South America, to provide a new tool for the integrated analysis and understanding of biomes, not only as types of vegetation but also as repetitive geobiophysical entities at large regional or wide local scales.

Landscape biome concept and hierarchical levels

Our proposal develops and extends the concepts defined above to biome level. Hence, we propose the following two biome definitions: Geocatenal biome and Geocomplex biome.

Geocatenal biome (Gcab) is a regional geographic area occupied by the same geoseries (geosigmetum) in a bioclimate and biogeographic unit, on the same ecological belt and geoform. Thus, a Gcab includes both the zonal potential plant formation and the azonal/intrazonal vegetation types associated with it in a repetitive pattern in the landscape. Within the geocatenal components, the zonal series marks the geoseries distribution and geographic extension, as well as its nomenclature. The change in the zonal series also drives the change of the geocatenal biome. When azonal vegetation series are the dominant landscape matrix, then they have to be considered as the geocatenal biome (e.g., extensive wetlands, flooded vegetation, or special substrates such as rock, laterite, serpentine, or sand), as stated in Navarro and Molina (2021).

Geocomplex biome or geobiome (Gcob) is a broad geographic area occupied by the same macrogeoseries (macrogeosigmetum) within a bioclimate, biogeographic and geomorphological unit, and on geographically contiguous altitudinal belts. Thus, a Gcob includes several floristically-structurally and ecologically related geoseries (geosigmetum) that are present as recurrent patterns in the landscape. Moreover, Gcob integrates both dimensions: the horizontal (traditional catenas) and vertical (altitudinal catenas), in a spatial model that can be extrapolated to other areas with analogous conditions. Within the geocomplex components, the spatially dominant geoseries marks the geobiome geographic distribution range and determines its nomenclature. Furthermore, a geocomplex biome (Gcob) may include one or more geocatenal biomes (Gcab). That is, a Gcob is made up of several spatially linked Gcabs.

Above these two conceptual levels, there is the macrobiome level, which is defined both by macrobioclimate and plant formation (Navarro and Molina 2021). This is roughly equivalent to the zonobiome in terms of spatial scale, but it differs conceptually from the latter by including both zonal and azonal (or intrazonal) communities (i.e., it does not use the zonality/azonality framework).

The hierarchical levels of the biome taxonomy and nomenclature that we propose here are updated and revised from Navarro and Molina (2021), to include the landscape ecology approach more adequately into the biome understanding.

The variables or classifiers involved in the delimitation and nomenclature of geocatenal and geocomplex biomes are shown in Table 1, and explicate as follows:

- Macrobioclimate is the first and most important criteria. In this work, the macrobioclimate is used at the beginning of the geobiomes zonation models section and is not repeated in each case.
- Altitudinal belt or ecological belts where the biome occurs. In the same way that geobiomes have a certain geographical extension, they are also typical of a certain ecological belt and are characteristic of specific biogeographic areas.
- Vegetation physiognomy that is dominant in the geographical extension within the boundaries of the geocomplex, with emphasis on life form and foliage phenology (Navarro and Molina 2021).
- Biogeography (region and/or province scale-levels) which is added to the end of the name in [square brackets]. Also including determinant geoforms, soils and lithology.

Moreover, and according to general landform patterns, we distinguish two major geocomplex biome types: A Plains and hills geocomplex biomes (*isogeocomplex*), developed in geoforms such as alluvial plains, pediments, peneplains, plateaus, hills and wide valleys; and B Mountain geocomplex biomes (*orogeocomplex*) in large mountain ranges with abrupt valleys.

Table 1. Hierarchical classification categories proposed for landscape biomes, their defining variables and geographical and biogeographical scale. The symbol '≡' represents some approximate equivalent units.

Defining factors	Geographical scale	Biogeographic scale	BIOME classification
Macrobioclimate Dominant plant formations	Intercontinental and continental	Realm/Sub-realm	MACROBIOME ≡ Zonobiome, Navarro and Molina (2021) ≡ Formation, Faber-Lagendoen et al. (2020)
Altitudinal belts (thermicity) Bioclimate (ombric rhytms)	Continental and sub-continental	Region/Province	GEOCOMPLEX BIOME Macrogeocatenal iterative zonation model ≡ Biome, Navarro and Molina (2021) ≡ Division, Faber-Lagendoen et al. (2020)
Zonal vegetation (Geoform/Soil/Lithology)	Regional and territorial (and sometimes local)	Province/Sector	GEOCATENAL BIOME Geocatenal iterative zonation model ≡ Regional biome, Navarro and Molina (2021) ≡ Macrogroup/Group, Faber-Lagendoen et al. (2020)

In order to clarify the above proposed geocomplex concept, we summarize it as follows:

– The geocomplex biome unites or spatially integrates several geoseries or geocatenes that appear geographically associated or linked in a repetitive way in a physiographical, bioclimatical and biogeographical homogeneous landscape. Thus, a geocomplex is a characteristic and iterative set of catenas or geocatenas.
– The geocomplex biome incorporates several catenas or geocatenas into a single spatial model, as long as these geocatenas are located in the same bioclimatic and biogeographic area.
– The geocomplex biome integrates both the horizontal (traditional catenas) and vertical (altitudinal catenas) dimensions, in a single repetitive spatial model that can be extrapolated to areas with similar climatic conditions within a biogeographical unit.
– The hierarchical key criteria that we propose to define the geocomplex biomes are: 1 - Macrobioclimate, 2 - Bioclimate, 3 - Plant formation, 4 - Altitudinal belt, 5 - Biogeographic unit and geophysical characters (geoforms, lithology, soils).
– In relation to this proposal, we adhere methodologically (with regard to bioclimate and biogeography) to the conceptual and nomenclatural frameworks of Rivas-Martínez (2015) and Rivas-Martínez et al. (2011a, b). These are our interpretation tools, but other classifications may be used within the same conceptual framework.
– The delimitation of a given geocomplex (i.e., setting the points where one geocomplex ends and another begins) is a critical issue. The criteria that we now propose refer to the following spatial discontinuities: a - change of biogeographic unit (region or province); b - significant change in bioclimate; c - important change of geomorphological unit. We also support the main criteria expressed in Zonneveld (1989): geoforms, climate, soils, lithology.

Methodology

The general methodological steps to survey transects and define the geocomplexes are shown in Fig. 1. We follow the classic approximation of integrated surveys and transects to define land-units, as expressed for example in the works of Zonneveld (1989), Duivenvoorden and Lips (1995), Forman (1997) and, recently, in Venezuela, by Guevara (2015) or in Colombia by Minorta-Cely (2020). The sequence of the steps followed can be summarized as follows:

– For each biogeographic province, we delineate preliminary accessible transects in the field.
– Observation and visual analysis of the selected areas in actual or recent satellite Google Earth images (https://earth.google.com/web/).
– Previous study of the bioclimatic, geological, geomorphological and soil characteristics of the different areas proposed for transect implementation.
– Survey of replicated field transects in selected areas that are internally homogeneous with respect to biogeography, landscape geomorphology, lithology and bioclimate.
– Acknowledging that biomes are large-scale units, transects can be several km long. The specific length of each transect depends on regional characteristics and accessibility.
– The transect ends when the biogeographic or bioclimatic conditions or geomorphic characteristics substantially change or there is a clear spatial discontinuity in them.
– Systematic visual analytical comparison between transects to identify repetitive patterns and differentiate distinct types of possible geocomplex biomes.
– Generalized hand drawn schemes of the geobotanical pattern or patterns recorded in the field transect. These drawings do not necessarily have a true or exact horizontal or vertical scale, they only represent in a simplified and idealized schematic way, the repetitive patterns of changes observed in the field. In this sense, these drawings constitute interpretative representational and descriptive models, and not realistic pictures of vegetation or plants, because they graphically explain and "represent a selected part or aspect of the world" (Frigg and Hartman 2020). Symbols of graphic textures below vegetation drawings are represented in all figures where different substrate types (soil and/or rocks) appear, according to widely accepted graphic representations.

Moreover, in a general way, all the figures have a geographical orientation from west to east.
– Finally, selected literature on transect zones is reviewed to adjust or complement the information obtained in the field. This stage is the only one for areas not directly known by field workers. In these cases, the repetitive pattern is deduced or interpreted from the data of the consulted bibliographical sources.

We follow Rivas-Martínez et al. (2011a) for bioclimate classification. The ecological belts that we consider are those of Navarro and Molina (2021) based on Rivas-Martínez et al. (2011a; see Table 2). For vegetation physiognomy, we largely follow Navarro and Molina (2021), as well as the recent advances in the IVC-EcoVeg vegetation classification and its biome derivations (Faber-Lagendoen et al. 2014, 2018, 2020). Vegetation physiognomy in the Neotropics, but for a few azonal or intrazonal exceptions, relate to the bioclimate and ombrotype (see Table 3 in this text, and Table 2 in Navarro and Molina 2021). Biogeographic typology for South America follows Navarro and Ferreira (2007) and Rivas-Martínez et al. (2011b). The biogeographic model of Rivas-Martínez et al. (2011b) has an integrated character, defining biogeographic units not only by types of vegetation or endemic or restricted floristic assemblages (which are chorological models), but mainly by the relationships between the biota distribution with the bioclimate and geophysical characteristics (geoforms or soils). In this sense, this model is particularly useful and accurate in our purpose of identifying and defining integrated geocomplex biomes. In addition, many of the field transects presented in this work were used to corroborate and verify these biogeographic units.

In addition, diverse names from the compilation of Huber and Riina (1997) for Latin America and Caribbean were considered to adjust several determinations of formations, communities and biogeography. For soils types in the description of the units, we follow FAO classification (FAO 2015; Gardi et al. 2015). The conceptual and nomenclatural characterization of flood levels in wetlands follows Cowardin et al. (1979) and FGDC (2013).

Table 2. Equivalence between altitudinal belts and the thermotypes recognized by Rivas-Martínez in Tropical South America.

Altitudinal belts	Thermotypes
Lowland	Infra- and Thermotropical
Montane	Mesotropical (low montane)
	Supratropical (upper montane)
High-montane	Orotropical and low Criorotropical
Subnival	Upper crioro and gelid tropical

Table 3. Relationships between vegetation physiognomy based on leaf phenology and bioclimates and ombrotypes of Rivas-Martínez in the Tropical South America.

Vegetation physiognomy	Bioclimates	Ombrotypes
Evergreen	Pluvial	Hyperhumid to humid
Evergreen seasonal	Pluviseasonal	Humid
Semideciduous		Subhumid
Deciduous	Xeric and desertic	Dry to semiarid and arid

In this work, geocomplex biomes are synoptically characterized, through model zonation profiles (Figs 2 to 42), each one including the following data:

– Biogeography refers to the Biogeographic Region and/or Provinces where the transect has been located.
– Representive locality is a place or geographic area where the unit has been studied in the field by the authors, or where it is cited in the consulted literature. However, representative locality is not necessarily the most "complete" locality among all the analogous ones, but mainly a good specific example that meets the following conditions:
  – It is a locality for which we have specific data collected in a sufficient number of field transects, so that it supports a repetitive spatial pattern.
  – It is an area or locality for which, although we do not personally have transects in the field, they do exist in the literature.

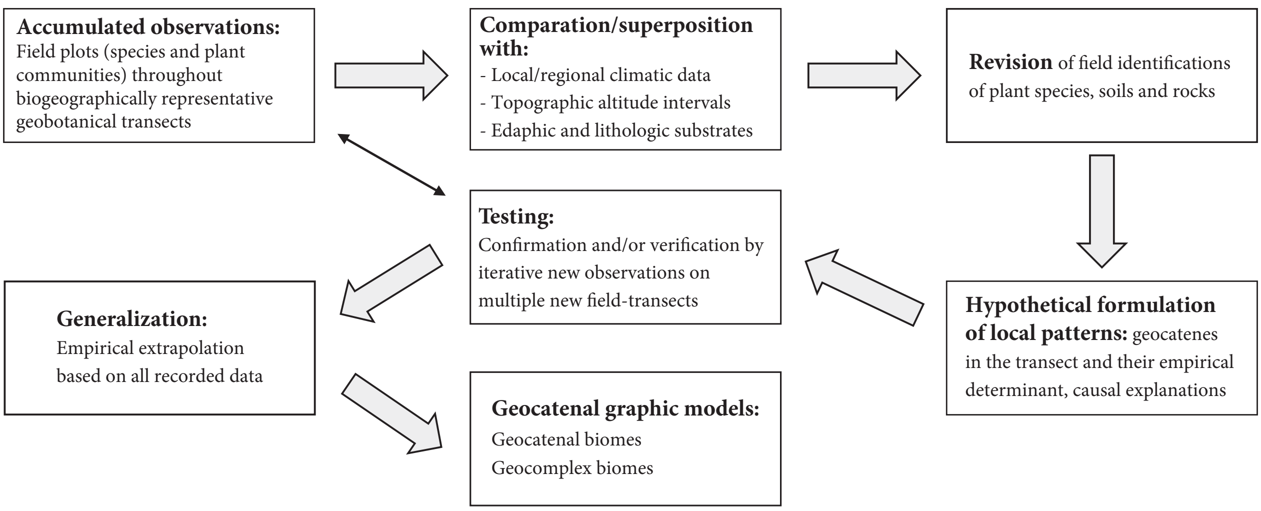

Figure 1. General methodological steps followed in this work (conceptual methodological terms are derived from Pickett et al. 1994).

  - It is a locality that meets our proposed variables to define the geocomplex biome: 1 - Macrobioclimate, 2 - Bioclimate, 3 - Formation plant, 4 - Altitudinal belt, 5 - Biogeographic unit and geophysical characters.
- Altitude: Interval or average altitudinal range obtained from field surveys and/or reported in the literature.
- Average geographical latitude where the transects were made. Since several transects were carried out in each field work area, the latitude data that appears in each figure averages that of all.
- Bioclimate: bioclimate types according to the maps and climate data from Rivas-Martínez et al. (2011a), where the unit naturally occurs. These papers have a large collection of weather stations from around the world with bioclimatic diagnosis and indices calculated for each station.
- Known analogous distribution areas (homoplasic-geobiomes): the South American countries or regions where the existence of the unit or its analogue units are known to occur or have been reported in the literature. We consider biome analogy for those geobiomes (geocomplex biomes and/or geocatenal biomes) that share a similar structure, plant physiognomy and catenal ecological relationships, derived from presumed convergent or parallel evolution in homologous bioclimates, but whose biogeographic origin is independent or different and therefore also its floristic composition. These geographically separated biomes, with putatively different phylogenetic and biogeographic origins, but with analogous characteristics and determinant traits, can be named as "homoplasic-biomes" in the sense of the concept of homoplasy as applied to species in cladistic biogeography and panbiogeography (e.g.: Myers and Giller 1988; Wake et al. 2011).
- IUCN related units: approximate inferred or related affinity to IUCN Global Ecosystem Typology (Keith et al. 2020, 2022). The equivalence with the IUCN approach is only of a general and approximate or indicative nature, because the underlying methodologies, objectives and concepts used are different in both proposals, with only general coincidences. The purpose is to show only the possible relationships with a broader global classification system.
- Selected references: citation of some relevant bibliographic references upon which the proposal of each unit is based, compared, or complemented.
- Phytotopographic or geobotanic profile: represented by a geocomplex biome graphic zonation model profile, raised from the field data (see above), where the distribution of the vegetation types in the geocatena (general plant communities and/or associations) is represented (Figs 2 to 42). The taxonomical nomenclature of characteristic species mentioned in each graphic model captions follows Tropicos.org, Missouri Botanical Garden, (https://tropicos.org, last accessed 01.02.2023). In the legend and captions of each phytotopographic profile, the key environmental and/or geomorphological traits that determine or characterize each type of vegetation are also briefly indicated.
- The syntaxonomic nomenclature of vegetation units refers to general community designations and not necessarily to validate phytosociologically typified associations. However, in examples taken from the literature, the named communities follow the authors who defined them.

Results

Based on the previously outlined concepts and procedures, we propose 33 geocomplex biomes for South America, identified through geocatenal profile zonation models derived from more than 300 representative transect-plots in almost all South American countries (Argentina, Bolivia, Brazil, Chile, Paraguay, Perú, and Venezuela), collected from 1990 to the present. The field data was supplemented with data from the literature for countries without direct field experience of the authors (Colombia and Uruguay) and to corroborate and contrast our data obtained in the field. All transect data and their geolocation are in the process of being included in the recently implemented and published BOVEDA database (Oliveira et al. 2022).

The results obtained are presented below, using graphic zonation models (Figs 2 to 42) that represent the 33 geocomplex biomes identified in South America. These geobotanical models are schematic and do not have an exact horizontal or vertical scale, since the objective is to show the patterns of spatial distribution for the ecosystem sets associated in a repetitive way in the landscape, according to the principles explained in the methods.

The graphic geobotanical catenas have been grouped according to the different macrobioclimates recognized for South America. In each macrobioclimate, the general ordering criteria is mainly altitudinal (from higher to lower elevation) and by the adaptive structural physiognomy of the dominant vegetation (from lower to higher xeromorphy). Likewise, we group the thirty-three geocomplex biomes into sixteen macrobiomes, according to the criteria of macrobioclimate and dominant plant formations. Table 4 summarizes the proposed arrangement and ordering of the geocomplex biomes and macrobiomes, adding their known distribution in the South American biogeographic provinces of Rivas-Martínez et al. (2011b).

Based on the field transects completed and the literature consulted in this regard, we consider that these results likely represent most of the diversity of geocomplex biomes that exist in South America.

Table 4. Macrobiomes, geocomplex biomes and their biogeographical distribution (at the Province level) of South America.

	TROPICAL MACROBIOCLIMATE	
NEOTROPICAL MACROBIOMES	**NEOTROPICAL GEOCOMPLEXES BIOMES**	**BIOGEOGRAPHY (Province level)**
A.1. TROPICAL HIGH MONTANE AND SUBNIVAL MACROBIOME	1. SUBNIVAL AND HIGH MONTANE TROPICAL XEROPHYTIC GEOCOMPLEX (Fig. 2)	Xerophytic Puna
	2. HIGH-MONTANE XEROMORPHIC SHRUBLAND & THICKET GEOCOMPLEX (Fig. 3)	Xerophytic Puna
	3. HIGH-MONTANE HUMID BUNCH-GRASSLAND GEOCOMPLEX (Fig. 4)	Mesophytic Puna
	4. HIGH-MONTANE EVERGREEN PÁRAMO GEOCOMPLEX (Fig. 5)	Colombian-Andean
A.2. TROPICAL MONTANE EVERGREEN & SEASONAL FOREST & WOODLAND MACROBIOME	5. MONTANE EVERGREEN AND SEASONAL ANDEAN FOREST GEOCOMPLEX (Figs 6–8)	Yungas
		Colombian Andean
	6. LOWLAND & MONTANE EVERGREEN PACIFIC FOREST GEOCOMPLEX (Fig. 9)	Colombian Pacific (Chocó-Darién)
	7. LOWLAND & MONTANE EVERGREEN ATLANTIC FOREST GEOCOMPLEX (Fig. 10)	Brazilian Atlantic
	8. LOWLAND & MONTANE EVERGREEN GUYANAN FOREST & SHRUBLAND GEOCOMPLEX (Fig. 11)	Tepuyan
A.3. TROPICAL LOWLAND EVERGREEN FOREST & WOODLAND MACROBIOME	9.LOWLAND SEASONAL EVERGREEN FOREST GEOCOMPLEX (Fig. 12)	Southwestern Amazonian
		Lower Magdalena
	10. LOWLAND EVERGREEN FOREST GEOCOMPLEX (Fig. 13)	West Amazonian
		Lower Magdalena
	11. LOWLAND EVERGREEN GUYANAN FOREST AND SHIELD SAVANNA GEOCOMPLEX (Fig. 14)	Guaviare-Orinoquian
	12. LOWLAND SEASONALLY FLOODED FOREST & SHRUBLAND GEOCOMPLEX "Várzea" (Fig. 15)	Amazonian
		Guyanan
		Lower Magdalena
	13. COASTAL BRAZILIAN RESTINGA GEOCOMPLEX (Fig. 16)	Brazilian Atlantic
A.4. TROPICAL MONTANE SEASONAL AND DECIDUOUS FOREST & WOODLAND MACROBIOME	14. MONTANE EVERGREEN SEASONAL WOODLAND GEOCOMPLEX (Fig. 17)	Mesophytic Puna
		Colombian-Andean
	15. MONTANE EVERGREEN SEASONAL AND DECIDUOUS FOREST & WOODLAND GEOCOMPLEX (Fig. 18)	Bolivian-Tucuman
		Colombian-Andean
		Guajira
A.5. TROPICAL LOWLAND SEASONAL AND DECIDUOUS FOREST & WOODLAND MACROBIOME	16. LOWLAND EVERGREEN SEASONAL AND DECIDUOUS GEOCOMPLEX (Fig. 19)	Brazilian-Atlantic
		Guajira
	17. LOWLAND DECIDUOUS FOREST & SCLEROPHYLOUS WOODLAND GEOCOMPLEX (Fig. 20)	Western Cerrado
		Eastern Cerrado
		Guajira
A.6. TROPICAL DECIDUOUS THORN WOODLAND & SHRUBLAND MACROBIOME	18. LOWLAND DECIDUOUS THORN WOODLAND & SHRUBLAND GEOCOMPLEX (Figs 21–23)	North Chaco
		South Chaco
		Caatinga,
		Guayaquil
		Guajira
		Desertic Peruvian-Equatorian
	19. MONTANE DECIDUOUS THORN WOODLAND & SHRUBLAND GEOCOMPLEX (Fig. 24)	Bolivian-Tucuman
		Guayaquil
		Guajira
		Colombian Andean
		Mesophytic Puna
		Desertic Peruvian-Equatorian
A.7. TROPICAL FOGGY COASTAL HYPERDESERT MACROBIOME	20. FOGGY TROPICAL HYPERDESERT GEOCOMPLEX (Figs 25, 26)	Hyperdesertic Tropical
		Chilean-Arequipan
		Hyperdesertic North Peruvian
A.8. TROPICAL FLOODED SAVANNA MACROBIOME	21. LOWLAND FLOODED SAVANNA AND WOODLAND GEOCOMPLEX (Figs 27–30)	Beni
		Pantanal
		Llanos
	MEDITERRANEAN MACROBIOCLIMATE	
MEDITERRANEAN MACROBIOMES	**MEDITERRANEAN GEOCOMPLEX BIOMES**	**BIOGEOGRAPHY**
B.1. MEDITERRANEAN HIGH-MONTANE MACROBIOME	1. HIGH-MONTANE MEDITERRANEAN GEOCOMPLEX (Fig. 31)	Mediterranean Andean
B.2. MEDITERRANEAN SCLEROPHYLLOUS WOODLAND MACROBIOME	2. LOWLAND & MONTANE EVERGREEN SEASONAL SCLEROPHYLLOUS GEOCOMPLEX (Fig. 32)	Central Chilean
B.3. MEDITERRANEAN SHRUBY-GRASSLAND STEPPE MACROBIOME	3. MONTANE XEROMORPHIC SHRUBBY-GRASSLAND STEPPE GEOCOMPLEX (Fig. 33)	North Patagonian
	4. MONTANE SUBHUMID SHRUBBY-GRASSLAND STEPPE GEOCOMPLEX (Fig. 34)	South Patagonian

B.4. MEDITERRANEAN XEROMORPHIC SHRUBLAND & THICKET MACROBIOME	5. MONTANE XEROMORPHIC SHRUBLAND & THICKET GEOCOMPLEX (Fig. 35)	Argentine Monte
B.5. MEDITERRANEAN OCEANIC HYPER-DESERT MACROBIOME	6. MEDITERRANEAN FOGGY DESERT GEOCOMPLEX (Fig. 36)	Desertic Mediterranean Chilean
	TEMPERATE MACROBIOCLIMATE	
TEMPERATE MACROBIOMES	**TEMPERATE GEOCOMPLEX BIOMES**	**BIOGEOGRAPHY**
C.1. TEMPERATE OCEANIC EVERGREEN & MIXED FOREST MACROBIOME	1. MONTANE TEMPERATE OCEANIC EVERGREEN FOREST GEOCOMPLEX (Fig. 37)	Valdivian
	2. LOWLAND & MONTANE HYPEROCEANIC TEMPERATE FOREST GEOCOMPLEX (Fig. 38)	Valdivian
	3. TEMPERATE HYPEROCEANIC MAGELLANIAN FOREST GEOCOMPLEX (Fig. 39)	Temperate Magellanian
C.2. TEMPERATE GRASSLAND & WOODLAND MACROBIOME	4. TEMPERATE OCEANIC LOWLAND WOODLAND AND GRASSLAND GEOCOMPLEX (Fig. 40)	Mesophytic Pampean
	5. TEMPERATE LOWLAND DRY THORN WOODLAND AND GRASSLAND GEOCOMPLEX (Fig. 41)	Xerophytic Pampean ("Espinal")
	BOREAL CLIMATE	
BOREAL MACROBIOME	**BOREAL GEOCOMPLEX BIOME**	**BIOGEOGRAPHY**
D.1. AUSTROBOREAL HYPEROCEANIC MACROBIOME	1. AUSTROBOREAL WET WOODLAND & PEATBOG GEOCOMPLEX (Fig. 42)	Boreal Austro-Magellanian

A. Tropical (Neotropical) geocomplex biomes

A.1. Subnival and high montane tropical xerophytic geocomplex (Fig. 2) [Biogeography: Tropical South Andean Region, Xerophytic Puna Province]. Representative type locality: Laguna Colorada, Sud Lípez, Potosí, Bolivia, ca. 22°12'S. Altitude: 4400–5150 m. Known analogous distribution areas (homoplasyc geobiomes): W Bolivia, NE Chile, NW Argentina, SW Perú. Bioclime: Oro-criorotropical xeric dry. IUCN related units: "Cool deserts and semi-deserts", "Tropical alpine grasslands and shrublands". Refs.: Cabrera (1976), Ruthsatz and Movia (1975), Luebert and Gajardo (2001, 2005), Josse et al. (2003, 2007), Navarro (1993, 2004, 2005, 2011, 2021), Navarro and Rivas-Martínez (2005), Navarro and Ferreira (2007), Navarro and Maldonado (2002), Galán et al. (2002, 2004, 2009), Sayre et al. (2008), Oyarzábal et al (2018), Navarro and Molina (2019, 2020).

A.2. High-montane xeromorphic shrubland & thicket geocomplex (Fig. 3) [Biogeography: Tropical South Andean Region, Xerophytic Puna Province]. Representative type locality: Coipasa, Oruro, Bolivia, ca. 19°15'S. Altitude: 3650–3800 m. Known analogous distribution areas (homoplasyc geobiomes): SW Bolivia, NE Chile NW Argentina, SW Perú. Bioclime: Orotropical xeric semiarid. IUCN related units: "Cool deserts and semi-deserts", "Thorny deserts and semi-deserts". Refs.: Ruthsatz and Movia (1975), Cabrera (1976), Luebert and Gajardo (2001, 2005), Josse et al. (2003, 2007), Navarro (1993, 2004, 2005, 2011), Navarro and Rivas-Martínez (2005), Navarro and Ferreira (2007), Navarro and Maldonado (2002), Galán et

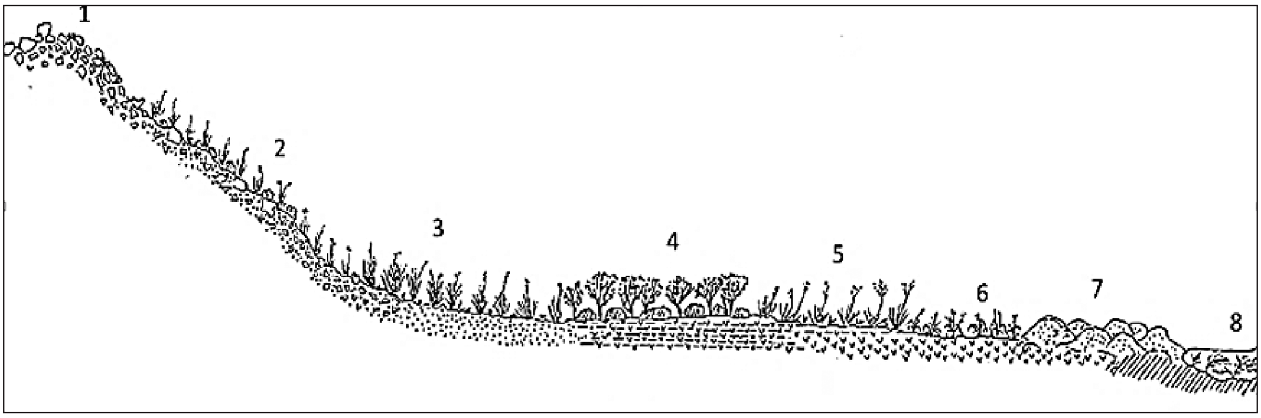

Figure 2. Subnival and high montane tropical xerophytic geocomplex. **1.** Cryomorphic open vegetation: *Nototriche auricoma-Oriastrum sphaeroidalis* community. Strongly-cryoturbed stony soils. **2.** Xeromorphic bunch-grassland: *Senecio puchii-Stipa frigida* community. Cryoturbed high-montane slopes. **3.** Xeromorphic bunch-grassland: *Junellia pappigera-Festuca orthophylla* community. Subnival volcanic sandy-gravel lapilli piedmonts with deep regosols. **4.** Phreatophytic xeromorphic shrubland & thicket: *Frankenia triandra-Parastrephia phylicaeformis* community. Saline plains with shallow seasonal water tables or temporarily ponded. **5.** Saline hygrophitic bunch-grassland: *Xenophyllum incisum-Festuca scirpifolia* community. Damp seasonally ponded saline soils. **6.** Hygrophitic saline meadows and grassland: *Xenophyllum incisum-Deyeuxia curvula* community. Seasonally ponded alluvial plain. **7.** Cushion-like peatbog: *Zameioscirpus atacamensis-Oxychloe andina* community. Saline seasonally flooded peat bog. **8.** High-montane aquatic vegetation: *Lilaeopsis macloviana-Ranunculus uniflorus-Potamogeton filiformis* communities. Graphic interpretation based on our field transect data and cited references.

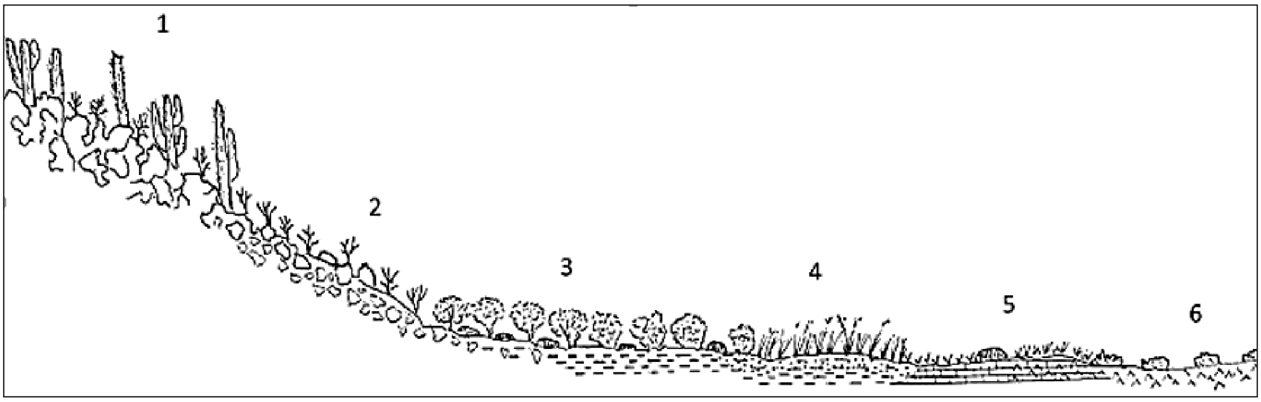

Figure 3. High-montane xeromorphic shrubland & thicket geocomplex. **1.** Xeromorphic succulent shrubland & thicket: *Lycium chanar-Trichocereus atacamensis* community. Altiplano semidesertic vegetation with succulents and cacti on Coipasa Salt Lake karstified lacustrine limestone terraces. **2.** Xeromorphic shrubland & thicket: *Junellia seriphioides-Fabiana densa* community. Altiplano stony hillside with well-drained stony soils. **3.** Phreatophytic xeromorphic shrubland & thicket: *Frankenia triandra-Parastrephia lepidophylla* community. Altiplano proximal and medium glacis sections, on flat calcic loamy-clay soils with sallow phreatic levels. **4.** Phreatophytic bunch-grassland: *Festuca hypsophila* communities. Altiplano distal glacis, on seasonally humid loam-sandy calcic soils with sallow phreatic levels and seasonally ponded. **5.** Gypsic xeromorphic grassland-thicket: *Frankenia triandra-Distichlis humilis* communitiy. Altiplano saline meadows on seasonally ponded silty-gypsic soils. **6.** Saline xeromorphic shrubland & thicket: *Atriplex nitrophiloides-Sarcocornia pulvinata* community. Altiplano saline bassins with seasonally ponded solonetz and solonchaks. Graphic interpretation based on our field transect data and cited references.

al. (2002, 2004, 2009), Sayre et al. (2008), Oyarzábal et al (2018), Navarro and Molina (2019, 2020).

A.3. High-montane humid bunch-grassland geocomplex (Fig. 4) [Biogeography: Tropical South Andean Region, Mesophytic Puna Province] Representative type locality: Nevado Huayna Potosí, La Paz department, Bolivia, western piedmont, ca. 16°17'S. Altitude: 4120 m. Known analogous distribution areas (homoplasyc geobiomes): N Bolivia, W Perú, S Ecuador. Bioclime: Orotropical pluviseasonal humid. IUCN related units: "Tropical alpine grasslands and shrublands". Refs. Luebert and Gajardo (2005), Josse et al. (2003, 2007), Navarro (2004, 2005, 2011), Navarro and Ferreira (2007), Navarro and Maldonado (2002), Sayre et al. (2008), Galán et al. (2004, 2009), Oyarzábal et al (2018).

A.4. High-montane evergreen páramo geocomplex (Fig. 5) [Biogeography: Neogranadian Region, Colombian-Andean Province]. Representative type locality: Páramos del Águila, Las Cruces, Piedras Blancas (Timotes a Mérida, Venezuela), ca. 08°50'N. Altitude: 4020 m. Known analogous distribution áreas (homoplasyc geobiomes): W Venezuela, W Colombia, Ecuador. Bioclime: orotropical pluvial humid-hyperhumid. IUCN related units: "Tropical alpine grasslands and shrublands", "Permanent marshes". Refs.: Cuatrecasas (1968), Goebel (1975), Van der Hammen ed. (1995), Rangel (1997, 2000), Sierrra (1999), Cleef (1981), Luteyn (1999), Sklenár and Ramsay (2001), Van der Hammen et al. (2005), Cleef et al. (2008), Josse et al. (2003, 2007), Costa et al. (2007), Sayre et al. (2008), Pinto and Rangel (2010), Peyre (2015), Peyre et al. (2018), Navarro (2021).

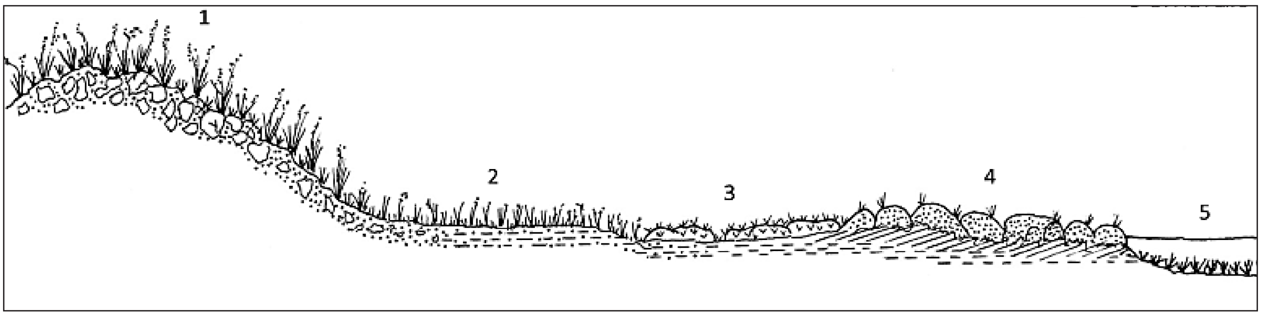

Figure 4. High-montane humid bunch-grassland geocomplex. **1.** High-montane bunch-grassland: *Deyeuxia vicunarum-Festuca orthophylla* communities. Zonal humid Puna vegetation on high-montane stony well-drained hillside soils. **2.** Meadow's grassland: *Deyeuxia rigescens-Festuca humilior* communities. Seasonally ponded or saturated wet Puna flat soils. **3.** Flat-cushion peatbog: *Deyeuxia rigescens-Plantago tubulosa* communities. Seasonally flooded peaty vegetation. **4.** Domed-cushion wet peatbog: *Oxychloe andina-Distichia muscoides* communities. Permanently flooded peaty vegetation. **5.** Puna aquatic vegetation: *Isoetes lechleriana* community. Poorly mineralized acidic stagnant waters. Graphic interpretation based on our field transect data and cited references.

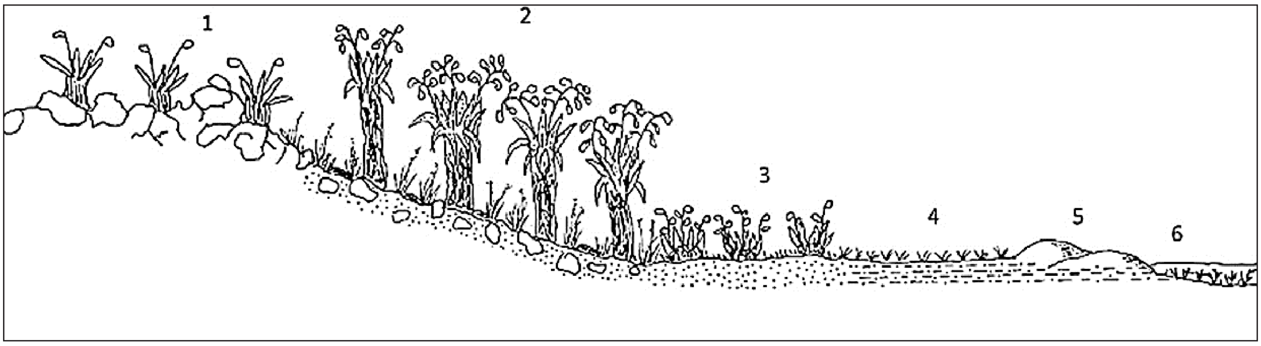

Figure 5. High-montane evergreen páramo geocomplex. **1.** Cauli-rosulate thicket: *Draba interhubera-Espeletia moritziana* community. Stony excessively well drained hillside soils. **2.** Evergreen cauli-rosulate shrubland and bunch-grassland: *Azorella juliani-Coespeletia timotensis* community. Humid well-drained moraine slope soils. **3.** Evergreen cauli-rosulate thicket: *Espeletia alba-Espeletia spicata* community. Wet poorly drained flat soils permanently saturated (umbric gleysol). **4.** Meadow's grassland: *Carex amicta* communities. Swamp soils (dystric anmoor). **5.** Wet domed-cushion peatbog: *Plantago rigida* communities. Permanently flooded peaty soils (dystric histosols). **6.** Páramo aquatic vegetation: *Myriophyllum quitensis-Ranunculus flagelliformis* communities. Poorly mineralized acidic stagnant waters. Graphic interpretation based on our field transect data and cited references.

A.5. Montane evergreen and seasonal andean forest geocomplex (Fig. 6) [Biogeography: Tropical South Andean Region, Yungas Province]. Representive type locality: Cordillera del Ronco, Cochabamba Dept., Bolivia, ca. 17°22'S. Altitude: 1600–4600 m. Known analogous distribution áreas (homoplasyc geobiomes): Tropical Andes in Venezuela, Colombia, Ecuador, Perú, Bolivia. Bioclime: termo to orotropical pluvial hyperhumid-humid. IUCN related units: "Tropical-subtropical montane rainforests". Refs.: Navarro and Maldonado (2002), Josse et al. (2003, 2009), Navarro and Ferreira (2007), Sayre et al. (2008), Navarro (2011), MAE (2012), Fuentes (2016), Galán et al. (2015, 2020).

A.6. Montane evergreen and seasonal andean forest geocomplex (Fig. 7) [Biogeography: Neogranadian region, Colombian Andean Province (central)]. Representative type locality: Cordillera Central Colombia, generalized

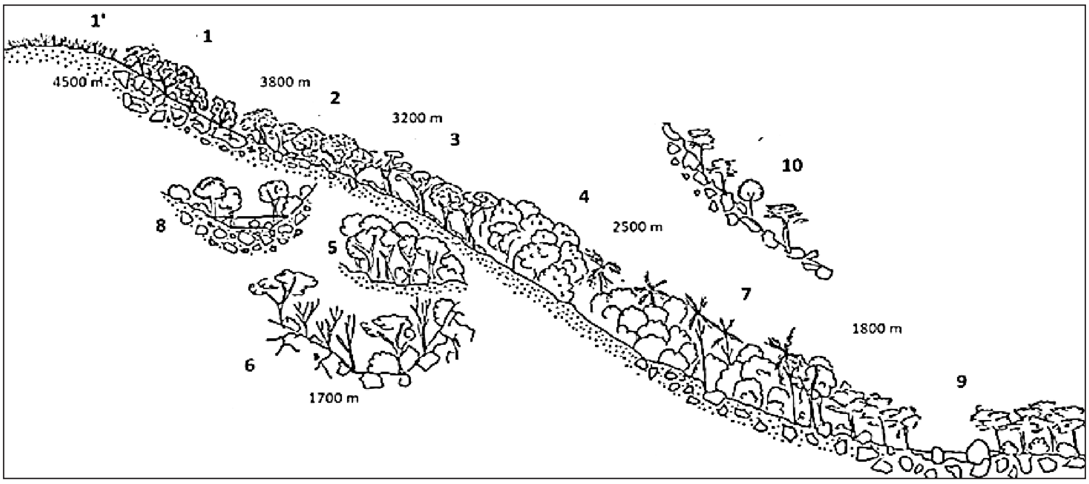

Figure 6. Montane evergreen and seasonal andean forest geocomplex. **1.** Evergreen high-montane woodland: *Gynoxys asterotricha-Polylepis pepei* community. High-montane *Polylepis* Yungas woodland. **1.** High-montane bunch-grassland: *Deyeuxia chrysanta-Festuca steinbachii* community. High-montane Yungas grassland & wet Meadows. **2.** Evergreen upper montane woodland: *Ilex mandonii-Polylepis lanata* community. Upper montane *Polylepis* Yungas forest & woodland. **3.** Evergreen upper montane forest: *Weinmannia bangii-Weinmannia fagaroides* community. Upper montane Yungas forest. **4.** Evergreen montane forest: *Weinmannia cordata-Podocarpus oleifolius* community. Montane Yungas pluvial forest. **5.** Evergreen seasonal montane forest: *Juglans boliviana-Podocarpus oleifolius* community. Montane Yungas pluviseasonal forest on rain-shadow topographic situations. **6.** Deciduous forest and woodland*:* *Samaipaticereus inquisivensis-Schinopsis haenkeana* community. Low-montane Yungas interandean dry forest and woodland. **7.** Evergreen low-montane palm-forest: *Protium aff. altsonii-Dictyocaryum lamarckianum* community. Low-montane Yungas forest. **8.** Montane riverine forest: *Vallea stipularis-Alnus acuminata* community. Intermitently or episodic flooded Yungas streams and riverbanks. Lotic. **9.** Low-montane riverine forest: *Inga adenophylla-Inga marginata* community. Intermitently or episodic flooded Yungas streams and riverbanks. Lotic. **10.** Low-montane erosive successional forest: *Heliocarpus americanus-Inga nobilis* community. Secondary forest on steep hillside landslides. Graphic interpretation based on our field transect data and cited references.

interpretation based on cited literature. Altitude: 700–4000 m. Known analogous distribution áreas (homoplasyc geobiomes): Tropical Andes in Venezuela, Colombia, Ecuador, Perú, Bolivia. Bioclime: infra to orotropical pluvial humid-hyperhumid. IUCN related units: "Tropical-subtropical montane rainforests". Refs.: Cuatrecasas (1958), Cleef (1980), Rangel and Franco (1985), Rangel ed. (1997), Sierra Ed. (1999), Sclenár and Ramsey (2001), Van der Hammen (2003), Cleef et al. (2003), Rodríguez et al. (2006), Josse et al. (2003, 2009), Rodríguez et al. (2006), Rangel and Pinto (2012), Latorre et al. (2014), Josse (2014), Avella (2016), Rangel (2017), Peyre et al. (2018), Galán et al. (2020).

A.7. Montane evergreen and seasonal andean forest geocomplex (Fig. 8). [Biogeography: Colombian Andean Province, Southern]. Representative type locality: Perú, Cajamarca, Cutervo-Contumazá transect, from Galán et al. (2015). Altitude: 2500–4000 m. Known analogous distribution áreas (homoplasyc geobiomes): Tropical Andes in Venezuela, Colombia, Ecuador, Perú, Bolivia. Predominant Bioclime: termo to orotropical pluviseasonal-pluvial subhumid-humid. IUCN equivalences: "Tropical-subtropical montane rainforests". Refs.: Rangel and Franco (1985), Rangel ed. (1997), Josse et al. (2003, 2009), Costa et al. (2007), Sayre et al. (2008), Galán et al. (2015, 2020).

A.8. Lowland & montane evergreen pacific forest geocomplex (Fig. 9). [Biogeography: Neogranadian Region, Colombian Pacific Province: Chocó-Darién]. Representative type locality: Colombian Chocó western Andean slopes generalized transect, based on Cuatrecasas (1958), Rangel (1997, 2004). Altitude: 0–3000 m. Known analogous distribution areas (homoplasyc geobiomes): W Pacific Colombia, NW Ecuador, SW Panamá. Bioclime: infra to supratropical pluvial ultrahyperhumid. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical flooded forests and peat forests", "Tropical heath forests", "Tropical-subtropical montane rainforest". Refs: Cuatrecasas (1958), Hernández and Sánchez (1992), Rangel ed. (1997, 2004), Josse et al. (2003), Sayre et al. (2008), MAE (2012), Latorre et al. (2014), Avella (2016), Rangel (2017).

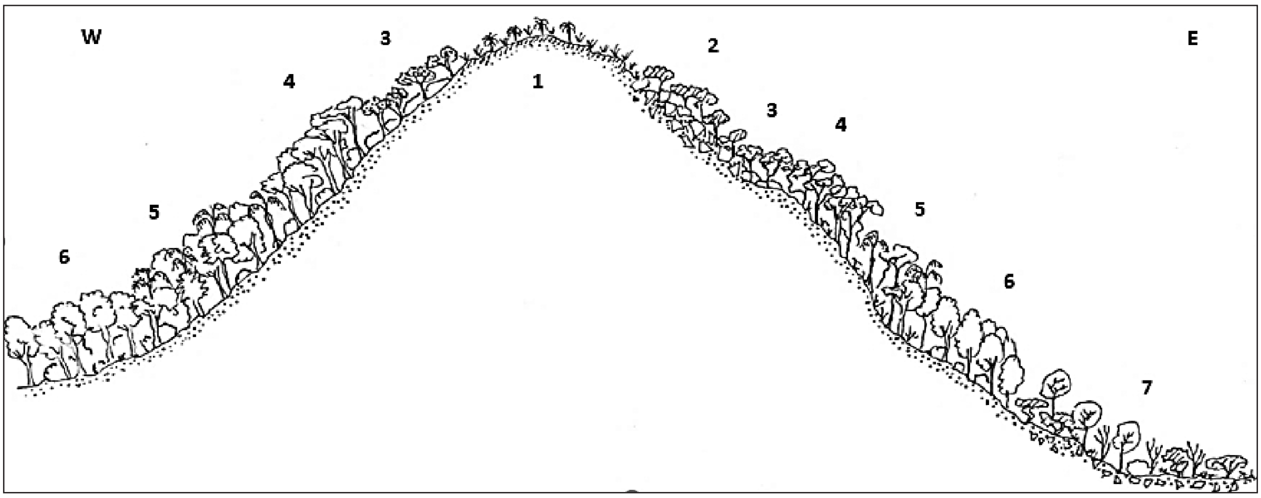

Figure 7. Montane evergreen and seasonal andean forest geocomplex. **1.** Evergreen high-montane caulirosulate Páramo woodland and bunch-grasland: *Espeletia hartwegiana*, *Espeletia sp. pl. Espeletiinae gen. et sp. pl. Deyeuxia effusa*, *Deyeuxia sp. pl.*, *Festuca* sp.pl., *Swalenochloa tessellata*. Orotropical and criorotropical pluvial hyperhumid bioclimatic belt. 4100-4600 m. Permanently saturated to flooded peaty soils. **2.** Evergreen high-montane subsclerophyllous low woodland and shrubland: *Polylepis sericea-Gynoxis tolimensis-Escallonia myrtilloides* communities. Low orotropical pluvial hyperhumid bioclimatic belt. 4000-4300 m. Rocky screes with water saturated humus deep pouchs. **3.** Evergreen upper montane lauroid low-forest: *Weinmannia mariquitae-Weinmannia tomentosa* communities, and *Weinmannia pubescens* communities, with *Weinmannia cochensis*, *W. microphylla*, *W. pinnata*, *W. pubescens*, *Clusia multiflora*, *Clethra fagifolia*, *C. minor*, *Myrsine dependens Qercus humboldtii*, etc. Supratropical pluvial hyperhumid bioclimatic belt, on saturated or ponded moss soils (anmoor, histosols). 3200-4100 m. **4.** Evergreen montane forests: *Brunellia macrophylla-Weinmannia pubescens* communities, with *Podocarpus oleifolius*, *Weinmannia balbisiana*, *W. sorbifolia*, *W. tomentosa*, *Quercus humboldtii*, *Ocotea* sp.pl., *Persea* sp.pl., étc. Mesotropical pluvial hyperhumid bioclimatic level. 2100-3200 m. Exposed outer mountain slopes. **5.** Evergreen low-montane forests: *Freziera tomentosa-Dictyocaryum lamarckianum* communities with *Quercus humboldtii*, *Billia columbiana*, *Prunus myrtifolia*, *Weinmannia pinnata*. Upper termotropical pluvial hyperhumid bioclimatic belt. 1100-2100 m. Exposed outer mountain slopes. **6.** Evergreen seasonal montane forest: *Hyeronima colombiana-Saurauia humboldtiana* communities with *Clethra fagifolia*, *Billia columbiana*, etc. Mesotropical pluviseasonal humid bioclimatic level. 2500–2600 m. Estearn mountain interandean slopes. **7.** Semideciduous basimontane forest: *Bursera tomentosa* communities, wit*: Stenocereus griseus*, *Pithecellobium dulce*, *Ochroma longipes*, *Toxicondendron striatum*, *Hirtella americana*, *Acacia* spp., etc. Upper termotropical pluviseasonal subhumid, and xeric dry bioclimatic level. Intermontane rain shadow slopes and interandean valleys. Graphic simplified and generalized geobotanical interpretation based on above cited references, particularly Rangel and Franco (1985).

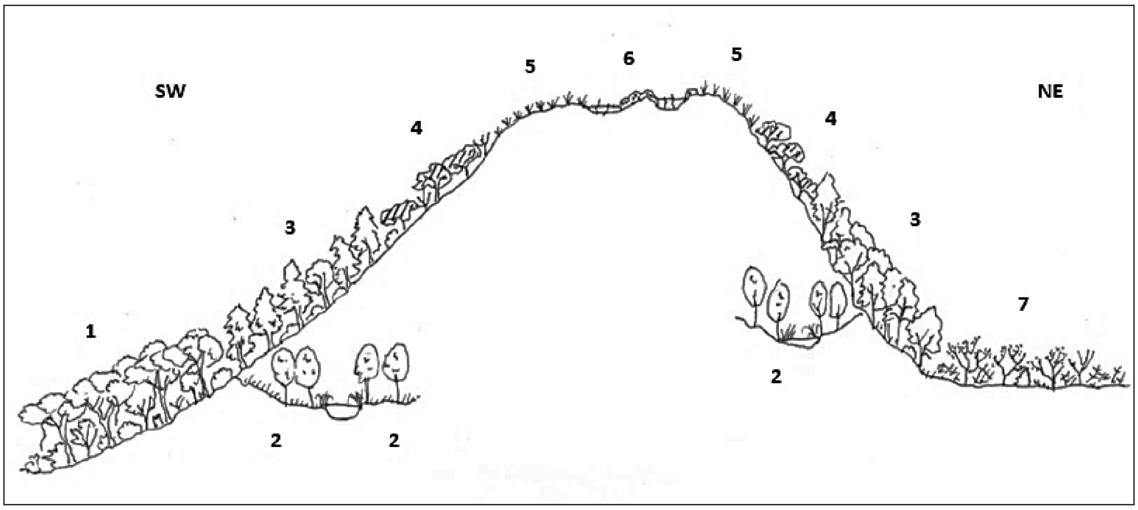

Figure 8. Montane evergreen and seasonal andean forest geocomplex. **1**. Evergreen seasonal basimontane forest: *Cecropia montana-Heliocarpus americanus* community. 1000-1800 m. Upper thermotropical pluviseasonal humid. **2.** Evergreen seasonal to deciduous Andean hygrophyllous forest: *Vallea stipularis-Alnus acuminata* communities. Humid montane valleys and headwaters with hydric or saturated soils. Mesotropical and low supratropical edapho hygrophyllous and riparian vegetation. **3.** Evergreen montane forest: *Axinaea nitida-Podocarpus oleifolius* community. 2500-2600 m. Mesotropical pluvial humid-hyperhumid bioclimatic level. Montane humid lauroid Yungas foresto on exposed mountain slopes and humid high-valleys. **4.** Evergreen sub-sclerophyllous woodland: *Barnadesia dombeyana-Polylepis racemosa* community. 3300-3900 m. Supratropical pluviseasonal humid bioclimatic level. Upper-montane low forest and woodlands on interior mountain slopes. **5.** High-andean bunch-grassland: *Agrostis tolucensis-Paspalum bonplandianum* community. 3800-4000 m. Low orotropical pluvial humid-hyperhumid bioclimatic level. Humic saturated soils of "Herbaceous Páramo". **6.** Mosaic of meadow's grassland, wet domed-cushion Páramo peatbogs (*Plantago rigida* communities), and Páramo aquatic vegetation (*Myriophyllum quitensis-Ranunculus flagelliformis*) communities. 3900-4100 m. Orotropical pluvial hyperhumid. **7.** Semideciduous shrubland and woodland: *Colletia spinosissima-Kageneckia lanceolata* communities. 3180-3300 m. Upper mesotropical pluviseasonal subhumid to upper dry, bioclimatic level. Upper-montane vegetation, in interandean valleys or not exposed mountain slopes, with rain shadow effect. Graphic geobotanical generalized geobotanical interpretation based on Galán et al. (2015) pro part. and Google Earth images.

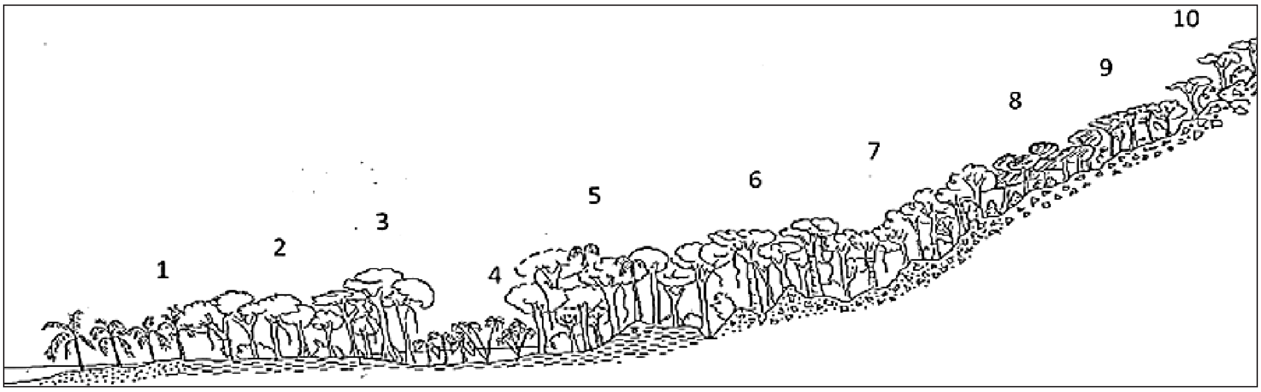

Figure 9. Lowland & montane evergreen pacific forest geocomplex. **1**. Riverine palm-Woodland: *Raphia taedigera* communities. Seasonally flooded sandy-marshy river beaches. **2.** Flooded riverine successional forest: *Chrysobalanus icaco-Erythrina fusca* communiy. **3.** Evergreen mature forest: *Mora megistosperma-Prioria copaifera* communities. Seasonally flooded alluvial floodplain. **4.** Swamp palm-woodland*: Montrichardia arborescens-Mauritiella macroclada* communities. Permanently flooded lowland marshes. **5**. Evergreen lowland Chocó Forest: *Cordia panamensis-Huberodendron patinoi* communities. Lowland alluvial seasonally saturated medium drained soils. **6**. Evergreen lower-hills Chocó forest (100-300 m): *Anacardium excelsum-Cavanillesia platanifolia* communities. **7.** Evergreen medium-hills lowland forest (300-1200 m): *Brosimum utile-Cariniana pyriformis-Dipteryx panamensis* communities. **8.** Evergreen low-montane forest: (1100-1800 m): *Guettarda chiriquensis -Weinmannia balbisiana-Ficus hartwegii* communities. **9.** Evergreen upper montane forest (2400-2800 m): *Quercus humboldtii-Podocarpus oleifolius* communities. **10**. Evergreen high-montane woodland (3500-3700 m): *Miconia gleasoniana-Weinmannia mariquitae* communities. Graphic geobotanical interpretation based on Cuatrecasas (1958), Rangel (1997, 2004).

A.9. Lowland & montane atlantic evergreen forest geocomplex biome (Fig. 10) [Biogeography: Brazilian Atlantic Province, Atlantic sector]. Representative type locality: Generalized transect from Bahía Paraguaná-Serra do Mar-Planalto (Brazil, southern estado do Paraná), 25°–26°S. based on Bolós et al. (1991). Altitude: 0–1400 m. Known analogous distribution areas (homoplasyc geobiomes): E Atlantic Brazil, SE Paraguay, NE Argentina. Bioclime: termo-mesotropical pluvial and pluviseasonal humid. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical-subtropical montane rainforest". Refs.: Rizzini (1979), Bolós et al. (1991), Veloso et al. (1991), Joly et al. (1999), Lorenzi (2008, 2009), Stehman et al. (2009), Felfili et al. Eds (2011), Giaretta et al. (2013), Marques et al. (2015), IBGE (2019).

A.10. Lowland & montane evergreen guyanan forest & shrubland geocomplex (Fig. 11). [Biogeography: Guyanan-Orinoquian Region, Tepuyan Province]. Representive type locality: Cerro Autana tepui area, ca. 04°49'S (Amazonas, Venezuela). Altitude: 95–500 m. Known analogous distribution areas (homoplasyc geobiomes): S. Venezuela, N. Brasil, Guianas. Bioclime: infra-termo (-mesotropical) pluvial humid-hyperhumid. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical flooded forests and peat forests", "Tropical heath forests", "Tropical-subtropical montane rainforest". Refs.: Huber (1988), Huber and Riina (1997), Camaripano-Venero and Castillo (2003), Morales and Castillo (2005), Rangel et al (1995), Rangel ed. (2008), Huber and Oliveira-Miranda (2010), Safont (2015), Usma et al. (2022).

A.11. Lowland seasonal evergreen forest geocomplex (Fig. 12) [Biogeography: Amazonian Region, Southwestern Amazonian Province]. Representative type locality: generalized transect from northern A. Iturralde province (La Paz department) 13°29'S to northern F. Román province (Pando Department) ca. 10°S, Bolivia. Altitude: 200 to 130 m. Known analogous areas (homoplasyc geobiomes): SW Venezuela, SE Colombia, E Ecuador, E Perú, N Brazil, N Bolivia. Bioclime: infratropical pluviseasonal and pluvial humid. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical flooded forests and peat forests", "Tropical heath forests". Refs.: Rizzini (1979), Encarnación (1985, 1993), Salo et al. (1986), Kalliola et al. (1993), Klinge et al. (1995), Junk (1997), Joly et al. (1999), Navarro et al. (2001), Navarro and Maldonado (2002), Morales and Castillo (2005), Encarnación and Zárate (2007), Encarnación et al. (2014), Josse et al. (2003, 2007, 2009), Navarro (2011), Sayre et al. (2008).

A.12. Lowland evergreen forest geocomplex (Fig. 13) [Biogeography: West Amazonian Province, Caquetá-High Vaupés sector, transitional to Guyanan-Orinoquian sector]. Representative type locality: generalized transects based on Duivenboorden and Lips (1995), on the Middle Caquetá-Araracuara area (Colombia). 0°03'S to 0°50'S. Altitude: 200 to 350 m. Known analogous areas (homoplasyc geobiomes): SW Venezuela, SE Colombia,

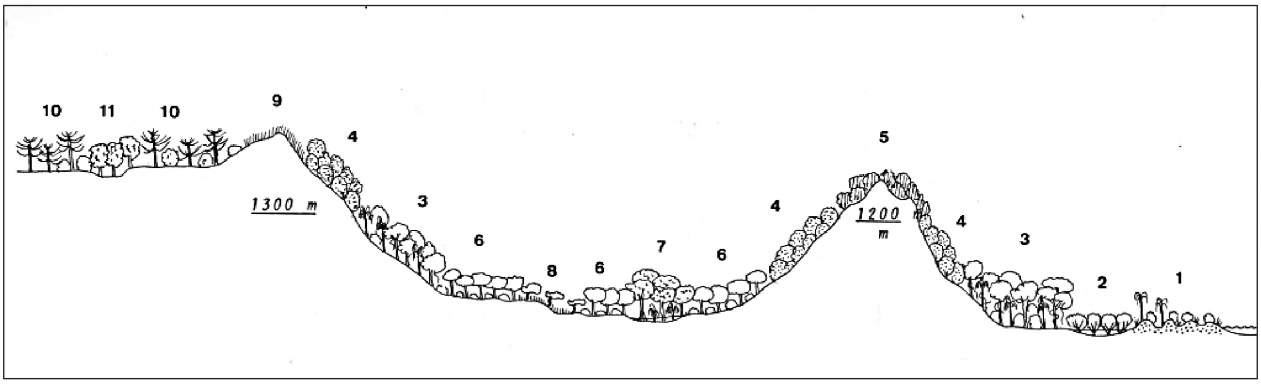

Figure 10. Lowland & montane atlantic evergreen forest geocomplex biome. **1.** Evergreen seasonal coastal shrubland ("restinga"): *Myrcia splendens-Guapira opposita* communities with *Butia capitata*, *Pilosocereus arrabidae*, *Psidium cattleianum*, *Eugenia brasiliensis*, *Pera glabrata*, *Kielmeyera membranacea*, *Spondias macrocarpa*. Sand dunes coastal restinga vegetation. **2.** Mangroves: *Avicennia schaueriana-Rhizophora mangle* communities. **3.** Evergreen lowland forest**:** *Xylopia brasiliensis-Sloanea guianensis* communities, with, *Ocotea puberula*, *Euterpe edulis*, *Attalea dubia*, *Syagrus romanzoffiana*, *Weinmannia paullinifolia*, *Terminalia uleana*. Lowland humid-hyperhumid atlantic forest. **4.** Evergreen low-montane forest: *Oreopanax capitatus-Jacaranda montana-Weinmannia organensis* communities, with *Pyllostylon brasiliense*. **5.** Evergreen montane atlantic woodland: *Clethra uleana-Myrcia obtecta* community. Humid to hyperhumid woodland and shrublands on mountain summits. **6.** Deciduous montane atlantic forest: *Myracrodruon balansae-Schinopsis brasiliensis-Attalea pindobassu* communities. Rain-shadow seasonally dry valleys**. 7.** Evergreen riparian atlantic forest. *Inga tenuis-I. thibaudiana-Cariniana ianeirensis* communities. Seasonally flooded riverine banks and floodplain. **8.** Evergreen seasonal sclerophyllous woodland (Cerrado). *Kielmeyera grandiflora-Callisthene major-Vochysia elliptica* communities. **9.** Montane woodland savanna: *Butia campicola-Berberis glazioviana-Lantana camara*, *Paepalanthus sp. pl.* communities, with *Andropogon bicornis*. Non flooded pyrogenic secondary savannas that replace the forest after the impact of fire and logging. **10.** Evergreen montane Atlantic forest and woodland: *Ocotea puberula-Araucaria angustifolia* communities, with humid grassland: *Leptocoryphium lanatum-Paspalum lineare* community. **11.** Evergreen montane riparian forest: *Podocarpus lambertii* communities. Graphic geobotanical interpretation based on Bolós et al. (1991) and cited references.

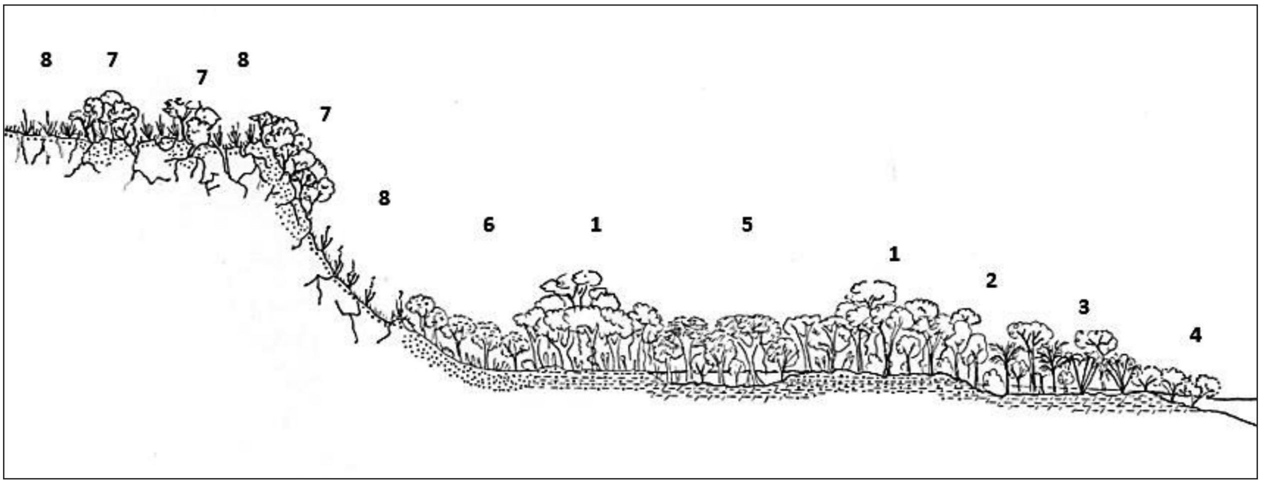

Figure 11. Lowland & montane evergreen guyanan forest & shrubland geocomplex. **1.** Evergreen guyanan-orinoquian forest. *Ruizterania retusa-Chaetocarpus schomburgkianus* communities. Upland plain with seasonally saturated soils. **2.** Flooded riparian forest and woodland ("Igapó"): *Taralea oppositifolia-Aldina latifolia-Malouetia glandulifera* communities. Semipermanently flooded black water stream banks (lotic). **3.** Palm swamp: *Leopoldinia pulchra-Mauritiella aculeata* communities. Permanently flooded black water streams and alluvial ponds (lentic). **4.** Riparian shrubland: *Simaba orinocensis-Coccoloba ovata* communities. Semipermanently flooded by black-water successional vegetation on river and stream banks (lotic). **5.** Flooded forest ("Boyal"): *Malouetia glandulifera-Molongun laxum-Heteropetalum brasiliense* communities. Seasonally flooded alluvial plain. **6.** Seasonal evergreen sclerophyllous woodland ("amazonian caatinga"): *Eperua leucantha-Micropholis maguirei-Caraipa densifolia* communities. Dystrophic podsolized soils on white-sand seasonally ponded paleochannels. **7**. Tepuis evergreen montane woodland and scrubs: *Kunhardtia rhodantha-Brocchinia hechtioides* and *Bonnetia crassa-Podocarpus neblinae* communities. Moderately deep and semipermanently saturated oligotrophic soils of tepuis plateux. **8.** Tepuis evergreen montane forbland & sedge-grasslands: *Stegolepis-Xyris-Eriocaulon-Wurdackia* communities. Shallow poorly drained oligotrophic stony soils of tepuis inselbergs, plateaus and screes. Graphic geobotanical interpretation based on cited references, our own field data (Autana Tepui) and Google Earth images.

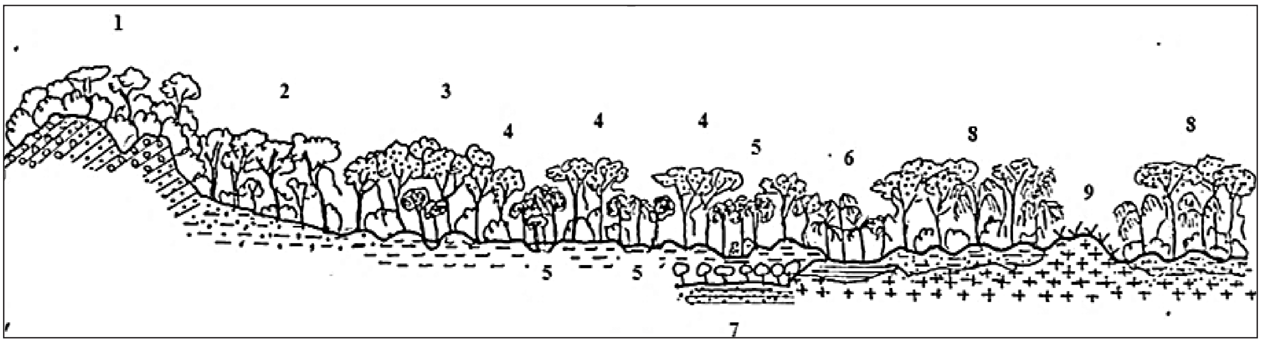

Figure 12. Lowland seasonal evergreen forest geocomplex. **1.** Evergreen seasonal preandean-subandean forest: *Pentaplaris davidsmithii-Quararibea wittii* community. Low mountain ranges of the sub-Andean region. **2.** Evergreen seasonal piedmont forest: *Quararibea wittii-Dypterix odorata* community. Amazonian eastern andean glacis. **3**. Evergreen seasonal hill forest: *Phytelephas macrocarpa-Tachigali vasquezi* community. Western Amazonian preandean hills with sandy soils. **4**. Evergreen seasonal peneplain forest: *Apuleia leiocarpa-Bertholletia excelsa* community. Ondulated lateritic Amazonian peneplains on tertiary materials. **5**. Flooded riparian forest & woodland: *Symphonia globulifera-Cariniana domestica* community. Clear water stream banks (Lotic), semipermanently flooded. **6**. Palm swamp-forest: *Macrolobium acaciifolium-Mauritia flexuosa* community. Black water streams and ponds (lentic) permanently flooded. **7**. Evergreen seasonal sclerophyllous woodland ("Amazonian Caatinga"): *Qualea albiflora-Cariniana domestica* communities. Seasonally ponded in depressed flat paleochannels with sandy quartz sediments and poorly drained oligotrophic-podsolized soils. **8**. Evergreen seasonal precambrian shield forest: *Attalea speciosa-Peltogyne heterophylla* community. Amazonian precambrian shield (gneisitic and granitic).**9.** Saxicolous-fissuricole vegetation: *Monvillea kroenleinii-Cyrtopodium paranaense* community. Precambrian crystalline rocky outcrops. Graphic interpretation based on our own field data, cited references, and Google Earth images.

NE Ecuador, NE Perú. Bioclime: infratropical pluvial humid-hyperhumid. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical flooded forests and peat forests", "Tropical heath forests". Refs.: Rizzini (1979), Encarnación (1985, 1993), Salo et al. (1986), Huber (1988), Klinge et al. (1995), Duivenvoorden and Lips (1995), Junk (1997), Rangel ed. (1997), Joly et al. (1999), Steege et al. (1999), Camaripano-Venero and Castillo (2003), Morales and Castillo (2005), Rangel ed. (2008), Encarnación and Zárate (2007), Josse et al. (2003, 2007, 2009), Romero et al. (2004), Díaz and Rosales (2006), Sayre et al. (2008), Huber and Oliveira-Miranda (2010), Encarnación et al. (2014).

A.13. Lowland evergreen guyanan forest and savanna geocomplex (Fig. 14) (Biogeography: Guyanan-Orinoquian Region, Guaviare-Orinoquian Province) Representative type locality: Lower Meta River (Colombia) to Cinaruco river in Puerto Ayacucho (Venezuela), 6°12'N–5°33'N. Altitude: 70–140 m. Bioclime: infratropical pluviseasonal humid. Known analogous distribution areas (homoplasyc geobiomes): S. Venezuela, SE Colombia, N. Brazil, Guianas. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical flooded forests and peat forests", "Tropical heath forests", "Pyric tussock savannas", "Hummock savannas". Refs.: FAO (1965), Huber (1988), Huber and Riina (1997), Camaripano-Venero and Castillo (2003), Morales and Castillo (2005), Rangel et al (1995), Rangel ed. (2008), Huber and Oliveira-Miranda (2010), Minorta-Cely (2020), Safont (2015), Navarro (2021), Usma et al. (2022).

A.14. Lowland seasonally flooded forest & shrubland geocomplex "Várzea" (Fig. 15) [Biogeography: Amazonian, Guyanan regions]. Representative type locality: generalized transect in lower Beni River, between Riberalta and Cachuela Esperanza, ca 10°40'S (northern Beni/Pando Departments, Bolivia). Altitude: 140–150 m. Known analogous areas (homoplasyc geobiomes): SW Venezuela, SE Colombia, E Ecuador, E Perú, N Brazil, Guianas, N Bolivia. Bioclime: infratropical pluviseasonal humid. IUCN related units: "Tropical-subtropical lowland rainforest", "Tropical flooded forests and peat forests". Refs.: Rizzini (1979), Encarnación (1985), Salo et al. (1986), Huber (1988), Klinge et al. (1995), Duivenboorden and Lips (1995), Junk (1997), Urrrego (1997), Rangel ed. (1997), Joly et al. (1999), Sierra et al. (1999), Morales and Castillo (2005), Rangel ed. (2008), Navarro and Maldonado (2002), Camaripano-Venero and Castillo (2003), Encarnación et al. (2007), Josse et al. (2003, 2007, 2009), Romero et al. (2004), Navarro (2011), Díaz and Rosales (2006), Sayre et al. (2008), Huber and Oliveira-Miranda (2010).

A.15. Coastal brazilian restinga geocomplex (Fig. 16) [Biogeography: Brazilian-Paranean Region, Brazilian Atlantic Province, Atlantic sector]. Representative type locality: Arembepe-Guarajuba (12°40'S) and Cacha Pregos, (13°07'S) transects synthesis, Salvador do Bahia, Brazil.

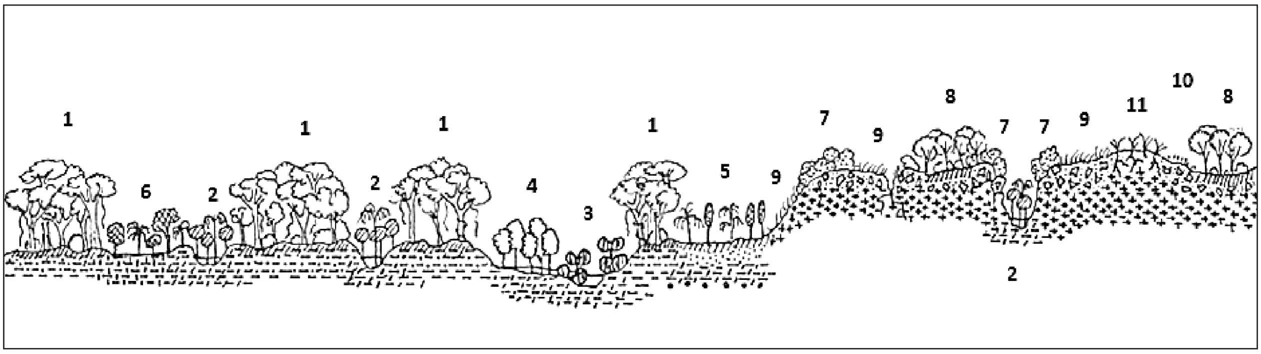

Figure 13. Lowland evergreen forest geocomplex. **1.** Evergreen peneplain forests: *Goupia glabra-Clathrotropis macrocarpa* and *Swartzia schomburgkii-Clathrotropis macrocarpa* communities. Ondulated lateritic Amazonian dissect peneplains on tertiary materials (Miocene). **2.** Flooded riparian forest & woodland: *Didymocistus chrysadenius-Euterpe precatoria* and *Caryocar microcarpum-Macrolobium acaciefolium communities*. Clear water stream flood plain and old meander riverbanks (lotic). **3.** Riparian woodland: *Byrsonima japurensis-Inga punctata* community. Riverine successional clear water stream-banks (lotic). **4.** Flooded riparian forest & woodland: *Acosmium nitens-Amanoa oblongifolia* community. Black water flood plain streams (lotic). **5.** Evergreen seasonal sclerophyllous woodland ("Amazonian Caatinga"): *Mauritia carana-Rhodognaphalopsis brevipes* community. Seasonally ponded flat depressions paleochannels with sandy quartz sediments and poorly drained podsolized-oligotrophic soils. **6.** *Tabebuia insignis-Mauritia flexuosa* community. Dystrophic black-water permanently flooded swamps. **7.** Scleromorphic scrub: *Dimorphandra cuprea-Ilex divaricata* community. Top of sandstone plateaus (Paleozoic Aracuara Formation) with well-drained shallow soils 300-350 m. **8.** *Macairea rufescens-Bonnetia martiana* community. Scleromorphic low forest on top of sandstone plateaus (slightly concave areas) with somewhat deep sandy soils semipermanently saturated. **9.** *Axonopus schultesii-Schoenocephalium martianum* community. Graminoid herbaceous savanna on shallow very acid white-sand saturated soils. **10.** Saxicolous low terophytic open epilithic vegetation: *Xyris wurdackii-Paspalum tillettii* and *Siphanthera hotsmannii-Xyris paraensis communities*. Exposed hard rock with very thin lithic leptosols. **11.** Saxicolous-fissuricole vegetation: *Navia garcia-barrigae* communities. Paleozoic sandstone rocky outcrops. Graphic geobotanical interpretation based on Duivenboorden and Lips (1995) and Google Earth images.

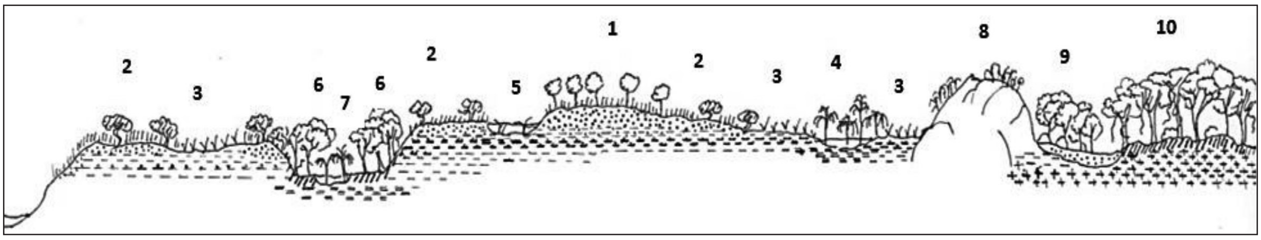

Figure 14. Lowland evergreen guyanan forest and savanna geocomplex. **1.** Evergreen seasonal sclerophyllous woodland-savanna: *Platycarpum orinocense-Vochysia venezuelensis* communities. Moderately deep and medium drained woodland on sandy-lateritic soils **2.** Successional pyrophytic-oligotrophic open woodland-savanna: *Byrsonima crassifolia-Curatella americana* communities with herbaceous savanna: *Axonopus purpusi – Paspalum pectinatum* communities and *Trachypogon plumosus-Schyzachirium sanguineum* communities, with *Thrasya petrosa*, *Trachypogon vestitus*. Pisolitic-lateritic medium-well drained soils, with eolic sandy or loessic cover **3.** Seasonally flooded oligotrophic open herbaceous savanna: *Schizachyrium brevifolium-Trachypogon spicatus* and *Andropogon leucostachyus-Sorghastrum setosum* communities. **4.** Palm-forest: *Euterpe precatoria-Mauritia flexuosa* communities. Lentic streams and topographic depressions permanently flooded by dystrophic black water. **5.** Aquatic vegetation of lakes and swamps. **6.** Flooded evergreen forest: *Lecythis ollaria-Eschweilera tenuifolia-Macrolobium multijugum* communities with *Campsiandra implexicaulis*, *C. macrocarpa*. Evergreen forest on alluvial floodplain of clear water rivers. **7.** Clear water riparian palm-woodland: *Mauritiella armata* communities. **8.** Saxicolous vegetation: *Vellozia tubiflora* communities. Precambrian domed rocky outcrops (inselbergs). **9.** Semideciduous forest: *Vochysia venezuelense-Anadenanthera peregrina* communities with *Caraipa llanorum*, *Hymenaea courbaril*, *Myroxylon balsamum*, etc. Sandy excessively well drained soils on low hillsides and basis of inselberg. **10.** Evergreen western guyanan forest: *Ruizterania retusa-Chaetocarpus schomburgkianus* communities. Deep well-drained lateritic soils above shield crystalline rocks. Graphic geobotanical interpretation based on cited references, our own field data (Cinaruco river to Puerto Ayacucho transect) and Google Earth images.

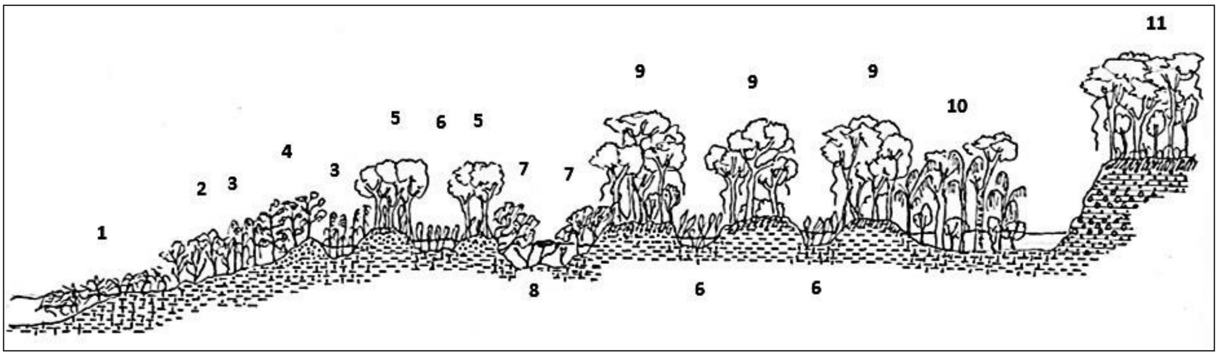

Figure 15. Lowland seasonally flooded forest & shrubland geocomplex "várzea" **A) Recent alluvial floodplain.** Riverine beaches: **1.** Riparian reed-grassland: *Paspalum fasciculatum-Echinochloa polystachia* community. Amazonian white-water riverine successional vegetation on seasonally flooded muddy substrates of the riverside-beaches. **2.** Evergreen seasonal riparian thicket: *Salix humboldtiana-Tessaria integrifolia* community. Amazonian white-water riverine successional vegetation on seasonally flooded muddy substrates of fore-beaches. **3.** Riparian cane-shrubland: *Gynerium sagittatum* communities. Amazonian white-water riverine successional vegetation on seasonally flooded sand-muddy substrates of fore-beaches. **4.** Evergreen seasonal riparian woodland: *Croton draconoides-Cecropia membranacea* community. Seasonally flooded with white-water riverine successional vegetation on back-beaches. Meander floodplain: **5**. Inmature riparian flooded forest: *Guarea guidonia-Ficus insipida* community. Seasonally white-water flooded with sand-muddy substrates and unstable soils of recent point-bars. **6.** White-water Amazonian forbland: *Heliconia marginata* communities. Megaforb helophytic vegetation on seasonally flooded meander plain channels (active, semiactive and inactive). **7.** Amazonian lacustrine custard-apple woodland: *Alchornea castaneifolia-Annona hypoglauca* community. Shores of ox-bow lakes and flooded paleochannel shores. **8.** Amazonian aquatic vegetation: *Nymphaea amazonum-Eicchornia azurea* communities. Ox-bow lakes and ponds. **9.** Mature flooded forest ("Fluvic Várzea forest"): *Manilkara inundata-Pouteria bilocularis* community. Meander floodplain levees and point-bars with white water regular flowing-floods on some stabilized soils. **B) Old alluvial flood plain. 10.** Flood-plain depressions: Backswamp forest ("Stagnic Várzea forest"): *Calycophyllum spruceanum-Hura crepitans* community with *Attalea butyracea*. Old alluvial floodplain with episodic white water stagnant floods. **C) Upland ("Terra firme"). 11**. Evergreen seasonal peneplain forest: *Apuleia leiocarpa-Bertholletia excelsa* community. Zonal mature southwestwen Amazonian Forest of ondulated lateritic upland peneplains on tertiary materials. Graphic geobotanical interpretation based on our own field data in Beni and high Madeira rivers, and Google Earth images.

Altitude: 0–50 m. Known analogous distribution areas (homoplasyc geobiomes): E Atlantic Brazil. Bioclimes: infratropical pluvial and pluviseasonal humid. IUCN related units: “Coastal shrublands and grasslands” “Intertidal forests and shrublands”, “Coastal saltmarshes and reedbeds”, “Sandy Shorelines”, “Muddy shorelines”, “Tropical-subtropical lowland rainforest”. Refs.: Rizzini (1979), Veloso et al. (1991), Navarro (1996), Joly et al. (1999), Andrade (reed. 2007), Lorenzi (2008, 2009), Stehman et al. (2009), Felfili et al. Eds (2011), Silva et al. (2013), Queiroz et al. (2017), IBGE (2019).

A.16. Montane evergreen seasonal woodland geocomplex (Fig. 17) [Biogeography: Tropical South Andean Region, Mesophytic Puna Province]. Representative type locality: Cordillera del Tunari, Cochabamba department, Bolivia, ca. 17°14'S. Altitude: 3620 m. Known analogous distribution áreas (homoplasyc geobiomes): tropical Andes of Argentina, Bolivia, Perú, Ecuador, Colombia, Venezuela. Bioclime: Supratropical pluviseasonal subhumid. IUCN related units: “Tropical-subtropical montane rainforests”. Refs.: Sierra (1999), Josse et al. (2003, 2007), Navarro (2004, 2005, 2011), Navarro and Ferreira (2007), Navarro and Maldonado (2002), Sayre et al. (2008).

A.17. Montane evergreen seasonal and deciduous forest & woodland geocomplex (Fig. 18) [Biogeography: Tropical South Andean region, Bolivian-Tucuman Province]. Representative type locality: Entre Ríos transects synthesis, Tarija department, Bolivia, ca. 21°30'S). Altitude: 1600–4000 m. Known analogous distribution areas (homoplasyc geobiomes): C & S Bolivia, NW & CW Argentina. Bioclime: mesotropical xeric dry and meso-supratropical pluviseasonal subhumid-humid. IUCN related units: “Seasonally dry tropical shrublands”, “Tropical-subtropical dry forests and thickets”. Refs.: Cabido et al. (1991), Navarro et al. (1996), Josse et al. (2003, 2007), Navarro (2004, 2005, 2011), Navarro and Maldonado (2002), Sayre et al. (2008), Josse (2014), Martínez-Carretero et al. (2016), Oyarzábal et al (2018), Entrocassi et al. (2020).

A.18. Lowland evergreen seasonal and deciduous geocomplex (Fig. 19) [Biogeography: Brazilian Atlantic Province, Paraná Sector]. Representive type locality: Caaguazú (Paraguay), ca. 25°26'S. Altitude: 350–600 m. Known analogous distribution areas (homoplasyc geobiomes): E Brazil, E Paraguay. Bioclime: infratropical-termotropical pluviseasonal humid. IUCN related units: “Tropical-subtropical lowland rainforest”, “Tropical-subtropical dry forest and thickets”. Refs.: Rizzini (1979), López et al. (1987), Lorenzi (2008, 2009).

A.19. Lowland deciduous forest & sclerophyllous woodland geocomplex (Fig. 20) [Biogeography: Western Cerrado Province]. Representive type locality: Lomerío transects synthesis, Concepción, Ñuflo de Chávez provincia, Chiquitanía (Santa Cruz, Bolivia), ca. 16°35'S. Altitude: 400–500 m. Known analogous distribution areas (homoplasyc geobiomes): S Venezuela, E Colombia, W Ecuador, E Bolivia, CW Brazil, NE Paraguay. Bioclime: low termotrop-

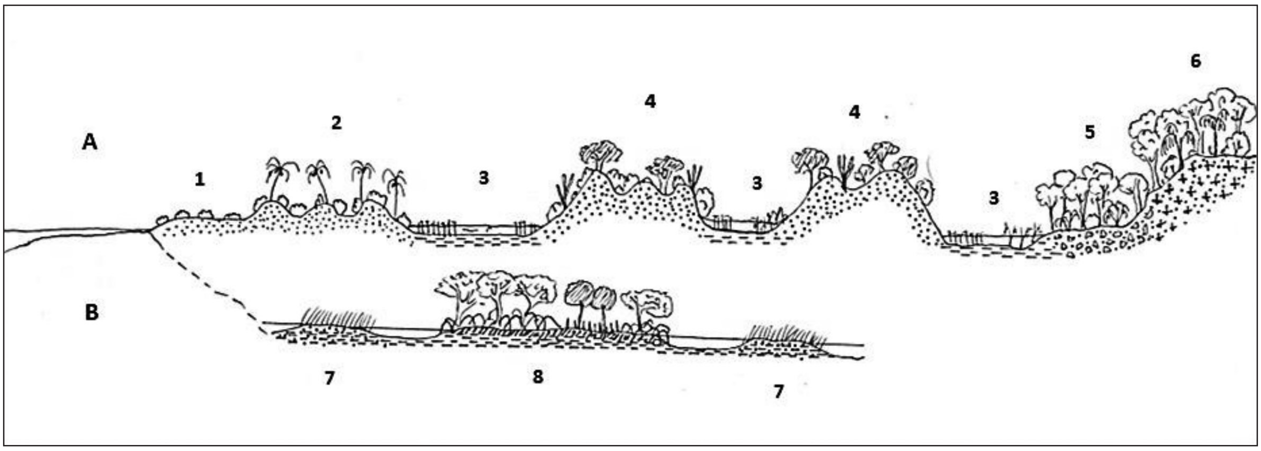

Figure 16. Coastal brazilian restinga geocomplex. **Sand system** (beaches and dune complexes) to Precambrian shield transect: **1.** Pioneer herbaceous sand beaches vegetation: *Sesuvium portulacastrum-Ipomoea pes-caprae* subsp. *brasiliensis* community. Back beach-berm. **2.** Coastal palm woodland: *Ipomoea pes-caprae brasiliensis-Cocos nucifera* communities. Semifixed recent micro-meso dunes with organo-detritic brown sands. **3.** Aquatic vegetation: *Cabomba aquatica-Eleocharis interstincta* communities. Shallow coastal lagoons and interdune depressions with oligotrophic waters. **4.** Evergreen seasonal coastal woodland and shrubland: *Pilosocereus pentaedrophorus-Kielmeyera argentea* communities with *Allagoptera brevicalyx*, *A. arenaria*, *Jacquinia armillaris*, *Manilkara salzmannii*, *Melocactus violaceus*, *Schinus terebinthifolius*, *Clusia* spp., *Protium bahianum*, *Syagrus schizophylla*, etc. Fixed pleistocene meso-macrodunes with white quartz sands. **5.** Evergreen seasonally flooded atlantic forest with *Bactris setosa*. Precambric shield piedmont. **6.** Evergreen Atlantic Forest: *Astronium concinnum-Sloanea eichleri* communities. Brazilian precambric shield, gneiss and quartz (ferralsols, acrisols). **Mud sytem** (estuary mouth): **7.** Coastal reedbed: *Spartina brasiliensis* communities. Estuarine bars with sand-muddy substrates with sulfidic materials (thionic estagnic fluvisols). **8.** Coastal flooded woodland (Mangrove): *Laguncularia racemosa- Rhizophora mangle* communities. Estuarine islands with grey to blackish organo-detrital muds (thionic stagnic fluvisols). Graphic geobotanical interpretation based on cited references, our own 1996 field data (Salvador do Bahia) and Google Earth images.

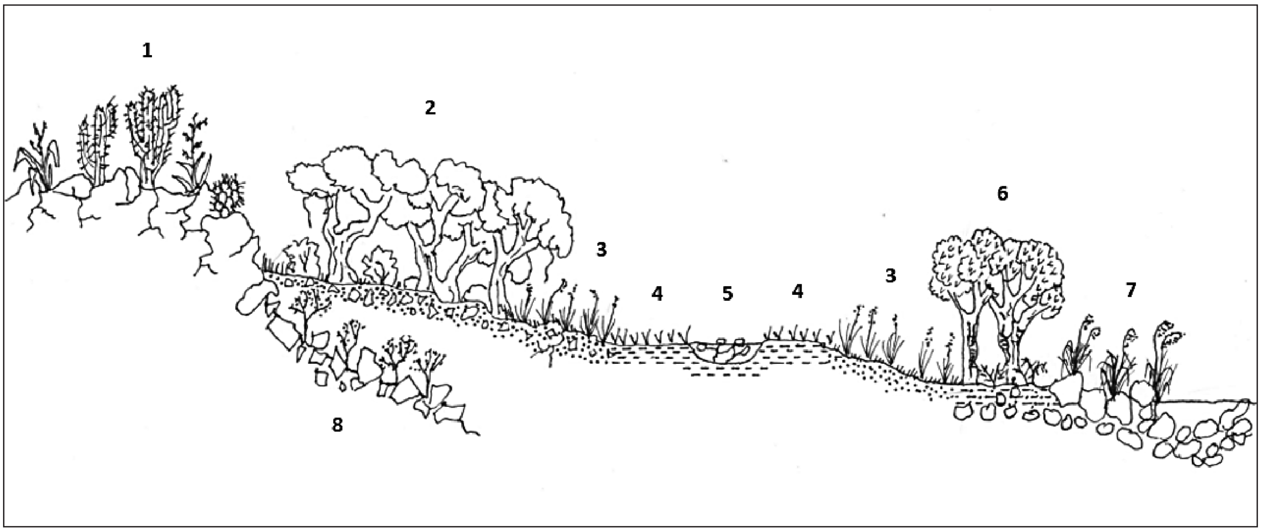

Figure 17. Montane evergreen seasonal woodland geocomplex. **1.** Saxicolous vegetation: *Puya glabrescens-Trichocereus tunariensis* community with *Lobivia maximiliana*. Upper montane rocks & cliffs. **2.** Evergreen seasonal sub-sclerophyllous woodland: *Berberis commutata-Polylepis subtusalbida* community. Zonal upper montane subhumid pluviseasonal vegetation. **3.** Bunch-grassland & thicket: *Baccharis papillosa-Poa asperiflora* community. Upper montane seral/successional vegetation. **4.** Montane swamp reedbed: *Juncus microcephalus* communities. **5.** Montane riverine aquatic vegetation: *Calceolaria aquatica-Mimulus glabratus* community. Flowing water stream vegetation (lotic). **6.** Riparian forest: *Vallea stipularis-Alnus acuminata* community. Seasonally flooded riverine forest (lotic). **7.** Riparian tussock-grassland: *Equisetum bogotense-Cortaderia rudiuscula* community. Lotic successional riverine vegetation with intermittently o episodic flooding. **8.** Scree vegetation: *Senecio clivicola* communities. Upper montaneabrupt hillside rock-scree vegetation. Graphic geobotanical interpretation based on our field transect data and cited references.

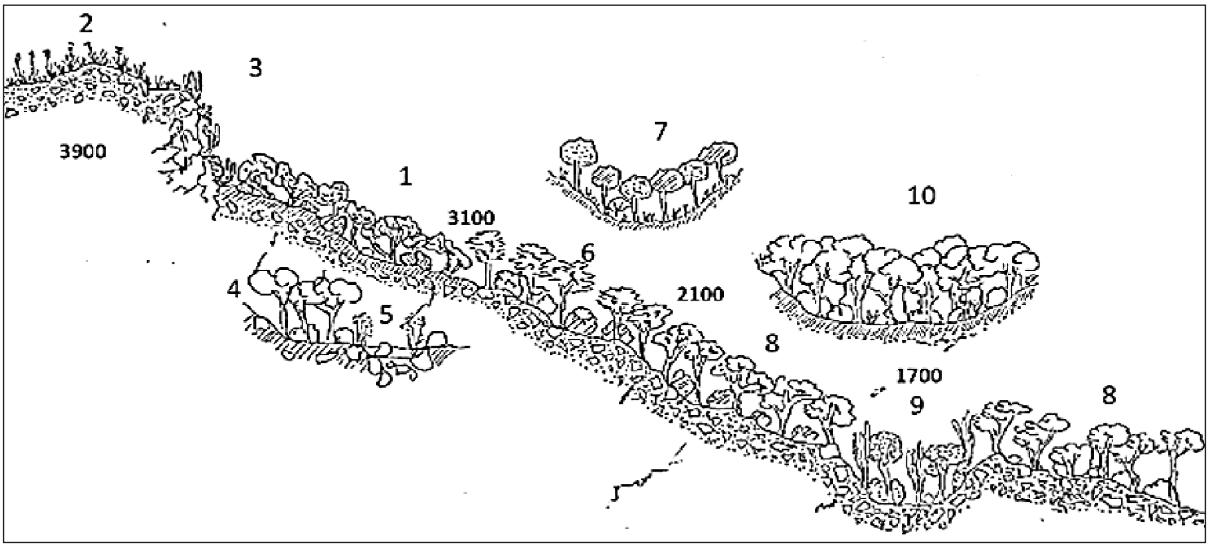

Figure 18. Montane evergreen seasonal and deciduous forest & woodland geocomplex. **1.** Evergreen seasonal woodland: *Escallonia hypoglauca-Polylepis crista-gallii* community. Zonal high-montane humid pluviseasonal vegetation. **2.** Bunch-grasslands & thickets: *Aristida mandoniana-Festuca hieronymi* communities. 3200-4000 m. High-montane seral/successional communities **3.** Saxicolous vegetation: *Rebutia fiebrigii-Cleistocactus straussii* communities. 3200-3800 m. High-montane cliffs and rocks vegetation. **4.** Flooded deciduous forest: *Vallesia glabra-Alnus acuminata* community. Seasonally or intermitently flooded riverine forest (lotic). **5.** Riparian tussock-grassland: *Cortaderia rudiuscula* communities. Lotic successional riverine vegetation with seasonal to episodic flooding. **6.** Evergreen seasonal forest: *Prunus tucumanensis-Podocarpus parlatorei* community. Zonal montane humid pluviseasonal forest and woodland. **7.** Evergreen seasonal woodland (Sahuintal): *Myrcianthes callicoma-Myrcianthes pseudomato* community. Intrazonal wet basin headwater vegetation. **8.** Deciduous forest: *Parapiptadenia excelsa-Tipuana tipu* community. Zonal montane pluviseasonal subhumid vegetation. **9.** Deciduous thorn woodland and shrubland: *Trichocereus terscheckii-Schinopsis haenkeana* community. Zonal rain-shadow interandean valleys dry vegetation. **10.** Evergreen seasonal forest: *Phoebe porphyria-Juglans australis* community. Zonal low-montane humid pluviseasonal vegetation. Graphic geobotanical interpretation based on our numerous field transect data (from 1990 to 2020) and cited references.

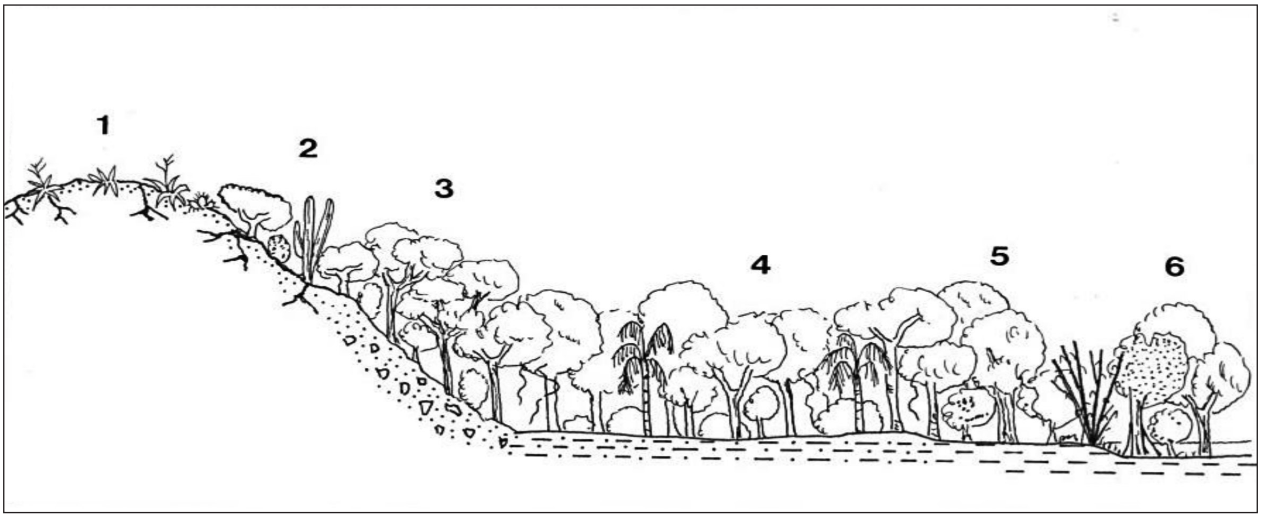

Figure 19. Lowland evergreen seasonal and deciduous geocomplex. **1.** Tropical lowland saxicolous outcrop vegetation: *Notocactus*, *Frailea*, *Dyckia*, *Tillandsia* communities. Precambric rock outcrops. **2.** Seasonally dry deciduous woodland: *Tabebuia pulcherrima-Protium heptaphyllum* community. Excesively well-drained stony leptosols. **3**. Evergreen seasonal forest: *Tabebuia impetiginosa-Anadenanthera colubrina* community. Well-drained deep sandy-stony soils. **4.** Evergreen Atlantic forest: *Piptadenia rigida-Balfourodendron riedelianum* community, with *Peltophorum dubium*, *Apuleia leiocarpa*, *Cedrela fissilis*. Zonal deep soils. **5.** Flooded Forest: *Nectandra angustifolia-Luehea divaricata* community. Seasonally flooded alluvial plain. **6.** Flooded riparian forest: *Guadua angustifolia-Copaifera langsdorfii* community. Riverine banks and alluvial plain. Lotic. Graphic geobotanical interpretation based on cited references, our own field data (Asunción-Caaguazú transect) and Google Earth images.

ical pluviseasonal subhumid. IUCN related units: "Tropical-subtropical dry forest and thickets", "Seasonally dry tropical shrublands", "Pyric tussock savannas", "Hummock savannas". Refs.: Rizzini (1979), Veloso et al. (1991), Ribeiro and Teles (1998), Rodal and Sampaio (2002), Silva and Abdón (1998), Joly et al. (1999), Giulietti et al. (2003), Josse et al. (2003, 2007), Aguirre-Mendoza et al. (2006), Sayre et al. (2008), Lorenzi (2008, 2009), Navarro (2011), Navarro and Maldonado (2002), Aymard and González (2013).

A.20. Lowland deciduous thorn woodland & shrubland geocomplex (Fig. 21) [Biogeography: Chaco Region, North Chaco Province]. Representative Type locality: Southeastern Bañados de Izozog to Parapetí River transects synthesis, Santa Cruz, Bolivia, ca. 19°S. Altitude: 350–420 m. Known analogous distribution áreas (homoplasyc geobiomes): S Bolivia, N Paraguay, N Argentina, SW Brazil (Chaco), NE Brazil (Caatinga), N Venezuela and Colombia (Guajira), W Ecuador (Guayaquil province), NW Perú (Tumbes). Bioclime: termotropical xeric dry and semiarid. IUCN related units: "Seasonally dry tropical shrublands", "Thorny deserts and semi-deserts". Refs.: López (1984), López et al. (1987), Cabido et al. (1994), Josse and Balslev (1994), Mereles and Degen (1994, 1998), Rodal and Sampaio (2002), Giulietti et al. (2003), Josse et al. (2003, 2007), Sayre et al. (2008), Navarro (2004, 2005, 2011), Navarro and Maldonado (2002), Navarro et al. (2006) Aguirre-Mendoza et al. (2006), Martínez-Carretero et al. (2016).

A.21. Lowland deciduous thorn woodland & shrubland geocomplex (Fig. 22) [Biogeography: Brazilean-Paranense Region, Caatinga Province]. Representative Type locality: Sr. Bonfim-Capim Grosso- Juazeiro-Curaçá transects synthesis, Bahia, Brazil, ca. 12°15'S. Altitude: 350–420 m. Known analogous distribution áreas (homoplasyc geobiomes): S Bolivia, N Paraguay, N Argentina, SW Brazil (Chaco), NE Brazil (Caatinga), N Venezuela and Colombia (Guajira), SW Ecuador (Guayaquil province), NW Perú (Tumbes). Bioclime: infratropical xeric dry and semiarid. IUCN related units: "Seasonally dry tropical shrublands", "Thorny deserts and semi-deserts". Refs.: Veloso et al. (1991), Josse and Balslev (1994), Rodal and Sampaio (2002), Giulietti et al. (2003), Josse et al. (2003, 2007), Sayre et al. (2008), Lorenzi (2008, 2009), Felfili et al. (2011), IBGE (2019).

A.22. Lowland deciduous thorn woodland & shrubland geocomplex (Fig. 23) [Biogeography: Guayaquil province]. Representative Type locality: Puerto López to Agua Blanca transect, Manabí, Ecuador, ca. 01°35'S. Altitude: 35–50 m. Known analogous distribution áreas (homoplasyc geobiomes): S Bolivia, N Paraguay, N Argentina, SW Brazil (Chaco), NE Brazil (Caatinga), N Venezuela and Colombia (Guajira), SW Ecuador, NW Perú (Tumbes). Bioclimes: infratropical xeric dry and semiarid. IUCN related units: "Seasonally dry tropical shrublands", "Thorny deserts and semi-deserts". Refs.: Josse and Balslev (1994), Sierra et al. (1999), Josse et al. (2003, 2007), Sayre et al. (2008), MAE (2012), Aguirre-Mendoza et al. (2006a, b, 2012).

A.23. Montane deciduous thorn woodland & shrubland geocomplex (Fig. 24) [Biogeography: Tropical South Andean region, Bolivian-Tucuman Province]. Representative type locality: Aiquile-Pasorapa transects synthesis, Cochabamba department, Bolivia, ca. 18°17'S. Altitude: 1300–2400 m. Known analogous distribution

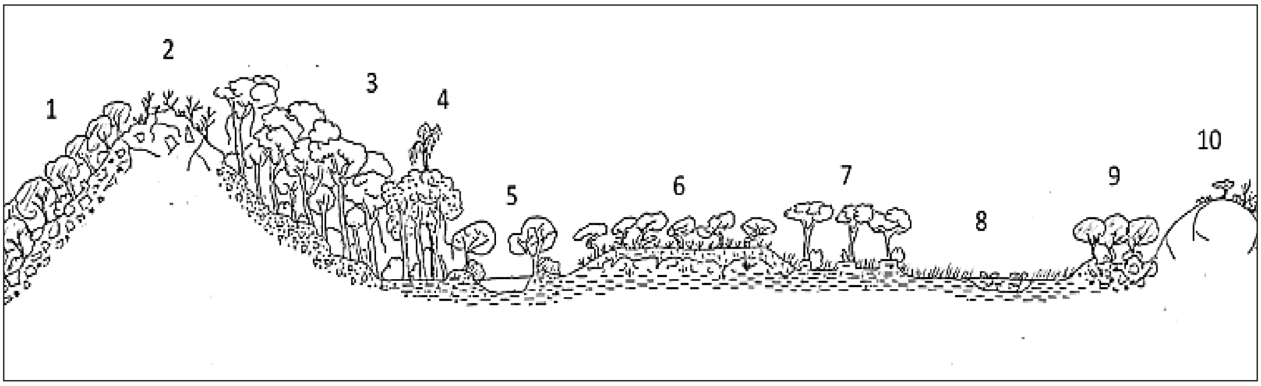

Figure 20. Lowland deciduous forest & sclerophyllous woodland geocomplex. **1.** Deciduous woodland: *Machaerium acutifolium-Myracruodruon urundeuva* community ("Cerradão). Low forest on hillsides stony soils (ferric regosols). **2** Non flooded savanna ("Cerrado rupestre", "Campo rupestre"). Edaphoxerophyllous communities on mountaintops with rocky soils (lithic and ferric regosols). **3.** Deciduous Forest: *Machaerium scleroxylon-Schinopsis brasiliensis* community. Tall dry deciduous to semideciduous fores. Deep well drained soils (ferralsols, cambisols). **4.** Evergreen seasonal flooded forest: *Cariniana ianeirensis-Vitex cymosa* community. Poorly drained floodable soils on valley bottom (fluvisols, gleysols). **5**. Evergreen seasonal riparian forest: *Lonchocarpus pluvialis-Inga nobilis* community. Seasonally flooded (fluvisols) with flowing waters (lotic). Fluvisols. **6**. Evergreen seasonal sclerophyllous woodland-savanna ("Cerrado"): *Salvertia convalliodora-Caryocar brasiliense* community, with *Priogymnanthus hasslerianus*. Dystrophic lateritic well-drained soils (plinthosols, ferralsols, acrisols). **7**. Flooded open arboreal savanna: *Genipa americana-Tabebuia heptaphylla* community. Hummocky dystrophic seasonally ponded soils (estagnosols). **8.** Flooded herbaceous savanna*: Schizachyrium microstachyum-Sorghastrum setosum* community on oligotrophic stagnosols; and associated aquatic/ hidrophylic vegetation. **9.** Evergreen seasonal sclerophyllous woodland on poorly drained soils: *Tabebuia heptaphylla-Callisthene fasciculata* community. **10.** Inselberg saxicolous vegetation: *Sapium argutum-Commiphora leptophloeos* community. Leptic regosols on cristaline precambric rocks (gneiss and granites). Graphic geobotanical interpretation based on cited references, our own field data (Concepción to San Antonio de Lomerío transects) and Google Earth images.

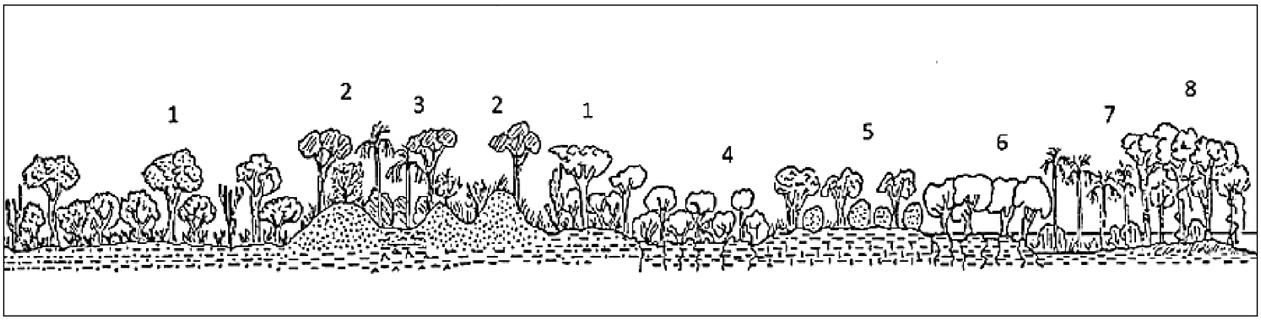

Figure 21. Lowland deciduous thorn woodland & shrubland geocomplex. **1.** Deciduous thorn-woodland and shrubland: *Senegalia emilioana-Schinopsis quebracho-colorado* community. Zonal medium drained clay-silty soils (regosols and luvisols). **2.** Deciduous woodland on deep sandy soils: *Senegalia emilioana-Schinopsis cornuta* community. Sand dunes and eolic surfaces (arenosols). **3.** Flooded palm-woodland: *Prosopis ruscifolia-Copernicia alba* community. Interdune temporarily ponded depressions (clay solonchaks). **4.** Xeromorphic shrubland: *Aspidosperma triternatum-Bulnesia sarmientoi* community. Poorly drained clay soils with strong gilgai microrelief (eutric vertisols). **5.** Phreatophyllous thorn-woodland: *Vallesia glabra-Prosopis chilensis* community. Alluvial clay silty soils with shallow water table (gleyic luvisols). **6.** Seasonally flooded thorn-woodland: *Coccoloba guaranitica-Geoffroea spinosa* community. Seasonally ponded with stagnant waters (gilgai vertisols and stagnosols). **7.** Palm-woodland: *Triplaris gardneriana-Copernicia alba* community. Seasonally flooded with mesotrophic flowing waters (sodic humic eutric vertisols and fluvisols). **8.** Riverine forest: *Crataeva tapia-Albizia inundata* community. Seasonally flooded with mesotrophic flowing waters (gleyic humic eutric fluvisols). Graphic geobotanical interpretation based on cited references, our own numerous field data (1993 to 1998), and Google Earth images.

areas (homoplasyc geobiomes): C and S Bolivia, NW and CW Argentina. Bioclime: termo-mesotropical xeric semiarid-dry. IUCN related units: "Seasonally dry tropical shrublands", "Tropical-subtropical dry forests and thickets". Refs.: Cabido et al. (1991), Navarro et al. (1996), Josse et al. (2003, 2007), Sayre et al. (2008), Navarro (2004, 2005, 2011), Navarro and Maldonado (2002), Navarro (2011), Martínez-Carretero et al. (2016), Entrocassi et al. (2020).

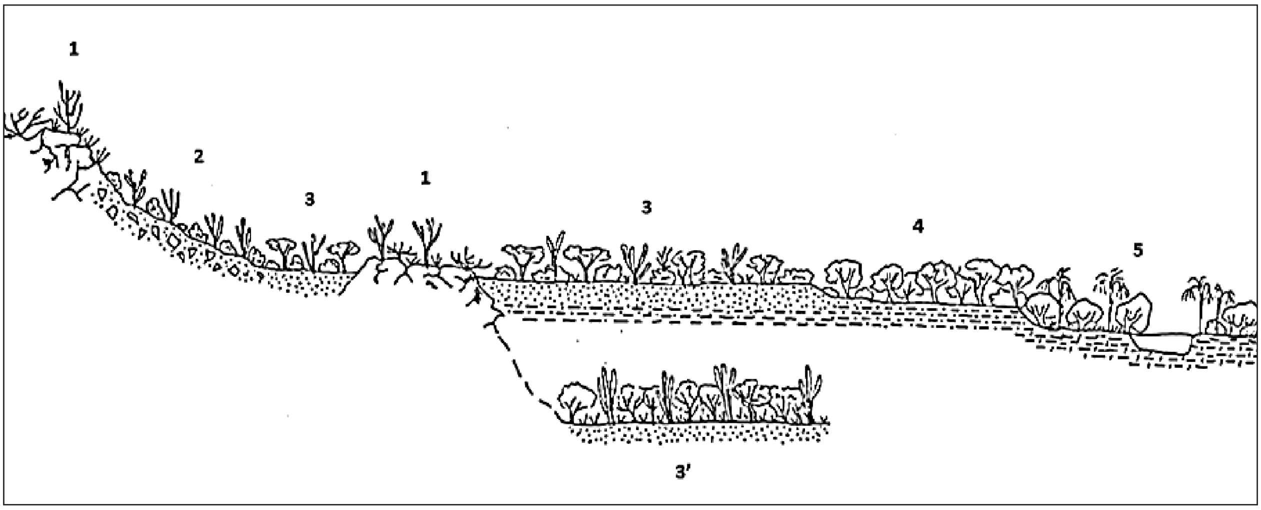

Figure 22. Lowland deciduous thorn woodland & shrubland geocomplex. **1.** Saxicolous vegetation*: Zehntnerella squamulosa* community. Gneiss rock outcrops **2.** Deciduous succulent thorn-woodland: *Pilosocereus pachycladus-Mimosa tenuiflora* community, with *Melocactus zehntneri*, *Senegalia bahiensis*, *Syagrus coronata*, *Cereus jamacaru*, *Pilosocereus gounelleii*, etc. Hillsides with stony (quartz and gneiss) squeletic regosols. **3.** Deciduous succulent thorn-woodland and shrubland*: Espostoopsis dybowskii-Caesalpinia laxiflora* community, with *Pilosocereus pentaedrophorus*, *P. pachycladus*, *Leocereus bahiensis*, *Commiphora leptophloeos*, *Opuntia inamoena*, etc. (in Juazeiro region). Extensive glacis and plains with sandy-loamy soils (arenic regosols and luvisols). **3'** Deciduous succulent thorn-woodland and shrubland: *Pilosocereus catingicola-Caesalpinia pyramidalis* community, with *Syagrus coronata*, *Cnidoscolus phyllacanthus*, *Pseudobombax simplicifolium*, etc. (in Senhor de Bonfim-Riacho Jacuípe region). Extensive glacis and plains with sandy-loamy soils (arenic regosols and luvisols). **4.** Phreatophyllous thorn-woodland: *Parkinsonia aculeata-Prosopis juliflora* community. Clay-silty soils with shallow water table (gleyic luvisols). **5.** Flooded palm-woodland: *Geoffroea spinosa-Copernicia prunifera* community with *Acacia piauhyensis*, *Ruprechtia laxiflora*, *Zizyphus joazeiro*. Seasonally flooded alluvial plains of São Francisco River (sodic humic vertisols and fluvisols). Graphic geobotanical interpretation based on our own field transect data in Bahia (1996) and cited references.

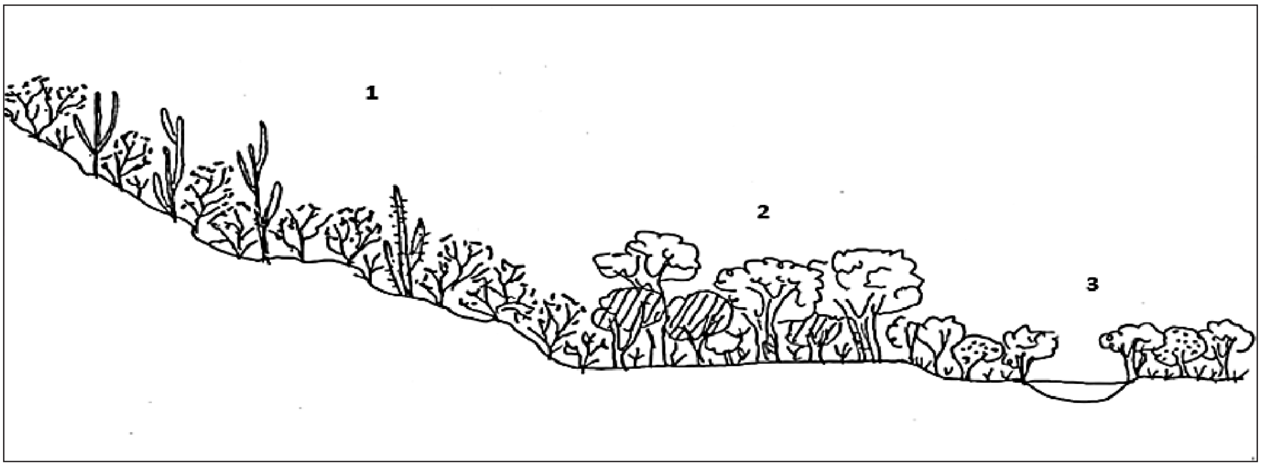

Figure 23. Lowland deciduous thorn woodland & shrubland geocomplex. **1.** Deciduous succulent thorn-woodland: *Pilosocereus tweeddianus-Cordia lutea* community, with *Armatocereus cartwrightianus*, *Caesalpinia corymbosa*, *Bursera graveolens*, *Jacquinia pubescens*, *Capparis* spp., etc. Coastal limestone hillsides (clay-stony vertisols). **2.** Phreatophyllous thorn-woodland: *Tecoma castaneifolia-Prosopis juliflora* community. Glacis and plains, with clay-silty soilS. Shallow water tables (gleyic luvisols). **3.** Riparian flooded shrubland and woodland: *Muntingia calabura-Pluchea absinthioides* community. Seasonally flooded alluvial plains of intermitent streams. Graphic geobotanical interpretation based on our own field transect data (2010) and cited references.

A.24. Foggy tropical hyperdesert geocomplex (Fig. 25) [Biogeography: Hyperdesertic Tropical Pacific Region, Hyperdesertic Tropical Chilean-Arequipan Province]. Representative type locality: Tacna to Tarata transect, Perú, ca. 17°48'S. Altitude: 0–2700 m. Known analogous distribution areas (homoplasyc geobiomes): W Perú, NW Chile. Bioclime: Thermotropical and low mesotropical hyperdesertic hyperarid-arid. IUCN related units: "Hyper-arid

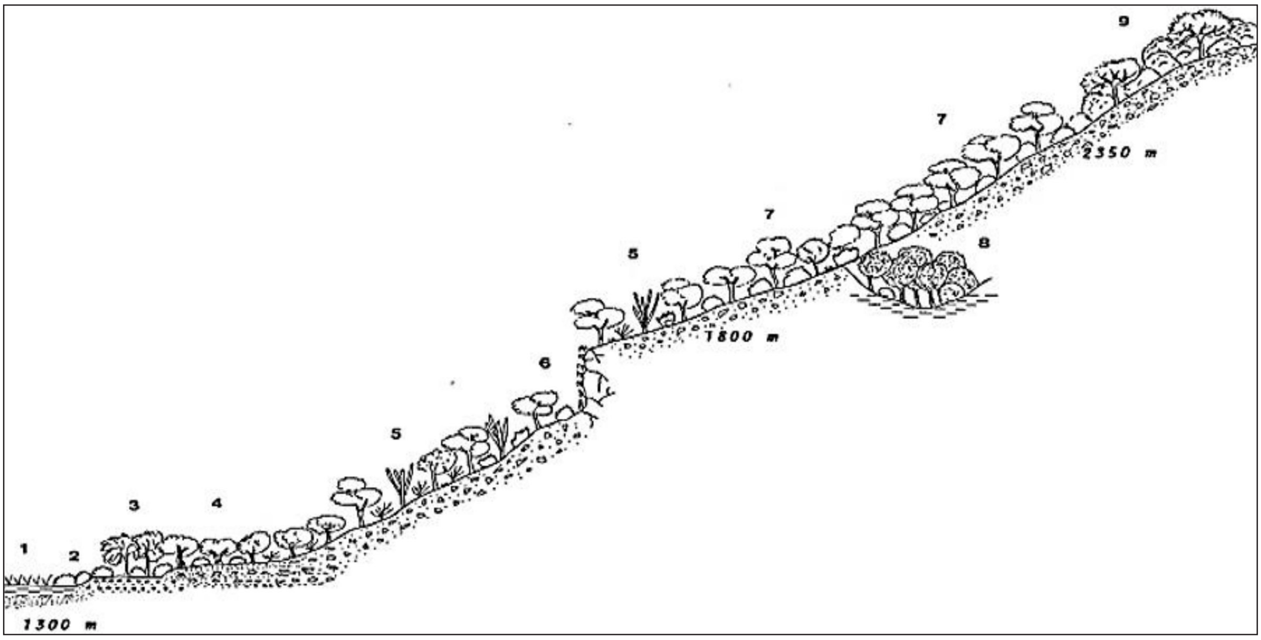

Figure 24. Montane deciduous thorn woodland & shrubland geocomplex. **1.** Riparian pioneer thicket*: Equisetum bogotensis-Tessaria absynthioides* community. Pioneer successional riverine vegetation with intermitently to episodic irregular flooding **2.** Intermitently flooded riverine successional shrubland: *Baccharis salicifolia* communities. **3.** Riparian forest: *Pisoniella arborescens-Salix humboldtiana* community. Montane interandean seasonally flooded riverine forest. **4.** Phreatophyllous thorn-woodland: *Acacia visco-Prosopis alba* community. Alluvial floodplain with shallow water tables. **5.** Deciduous thorn woodland & shrubland: *Neocardenasia herzogiana-Schinopsis haenkeana* community (1400-1900 m) and *Espostoa guentherii-Loxopterygium grisebachi* (< 1400 m) community. Interandean low-montane dry and semiarid zonal vegetation. **6.** Saxicolous vegetation: *Barbaceniopsis boliviana-Deuterocohnia longipetala* community. Interandean montane azonal saxicolous vegetation. **7.** Deciduous thorn woodland: *Cardenasiodendron brachypterum-Schinopsis haenkeana* community. Interandean montane dry zonal vegetation. **8.** Evergreen seasonal riparian woodland: *Pisonia ambigua-Myroxylon peruiferum* community. Interandean montane stream vegetation with irregular or episodic flooding. **9.** Deciduous forest and woodland: *Jacaranda mimosifolia-Tipuana tipu* community. Interandean montane dry and lower subhumid zonal vegetation. Graphic geobotanical interpretation based on our numerous field transect data (from 1990 to 2020) and cited references.

deserts". Refs.: Rundel et al. (1991), Gajardo (1994), Marquet et al. (1998), Luebert and Gajardo (2005), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006), Pinto et al. (2006), Pinto and Luebert (2009), Galán et al. (2002, 2004, 2009, 2011), Navarro (2021).

A.25. Foggy tropical hyperdesert geocomplex (Fig. 26) [Biogeography: Hyperdesertic Tropical Pacific Region, Hyperdesertic Tropical Chilean-Arequipan Province]. Representative type locality: Southern Iquique to Pampa del Tamarugal transects synthesis, Chile, ca. 20°18'S. Altitude: 0–800 m. Known analogous distribution areas (homoplasyc geobiomes): NW Chile, SW Perú. Bioclime: upper thermotropical to low mesotropical hyperdesertic hyperarid. IUCN related units: "Hyper-arid deserts". Refs.: Rundel et al. (1991), Navarro and Rivas-Martínez (1994b), Gajardo (1994), Marquet et al. (1998), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006), Pinto et al. (2006), Pinto and Luebert (2009), Galán et al. (2002, 2004, 2009, 2011), Navarro (2021), Amigo et al. (2022a, b).

A.26. Lowland flooded savanna and woodland geocomplex (Fig. 27) [Biogeography: Brazilean-Paranean Region, Beni Province]. Representive type locality: Northeastern Trinidad, Beni, Bolivia. ca. 14°25'S. Altitude: 150 m. Known analogous distribution areas (homoplasyc geobiomes): E Bolivia, SW Venezuela, E Colombia. Bioclime: infratropical pluviseasonal humid. IUCN related units: "Pyric tussock savannas", "Hummock savannas", "Permanent marshes", "Seasonal floodplain marshes", "Tropical flooded forests and peat forests". Refs.: Navarro and Maldonado (2002), Josse et al. (2003, 2009), Boixadera et al. (2003), Pouilly et al. (2004), Sayre et al. (2008), Navarro (2011), Navarro et al. (2013), Aymard and González (2013).

A.27. Lowland flooded savanna and woodland geocomplex (Fig. 28) [Biogeography: Brazilean-Paranean Region, Pantanal Province]. Representive type locality: San Matías and Otuquis Pantanal transect synthesis, Eastern Santa Cruz department, Bolivia, ca. 16°56'S. Altitude: 110–120 m. Known analogous distribution areas (homoplasyc geobiomes): C-W Brazil, SE Bolivia; NE Paraguay, NE Argentina. Bioclime: infratropical and termotropical pluviseasonal subhumid. IUCN related units: "Pyric tussock savannas", "Hummock savannas", "Permanent marshes", "Seasonal floodplain marshes". Refs.: Rizzini (1979), Veloso et al. (1991), Pott and Pott (1997), Silva and Abdon (1998), Joly et al. (1999), Josse et al. (2003, 2007), Navarro (2011), IBGE (2019).

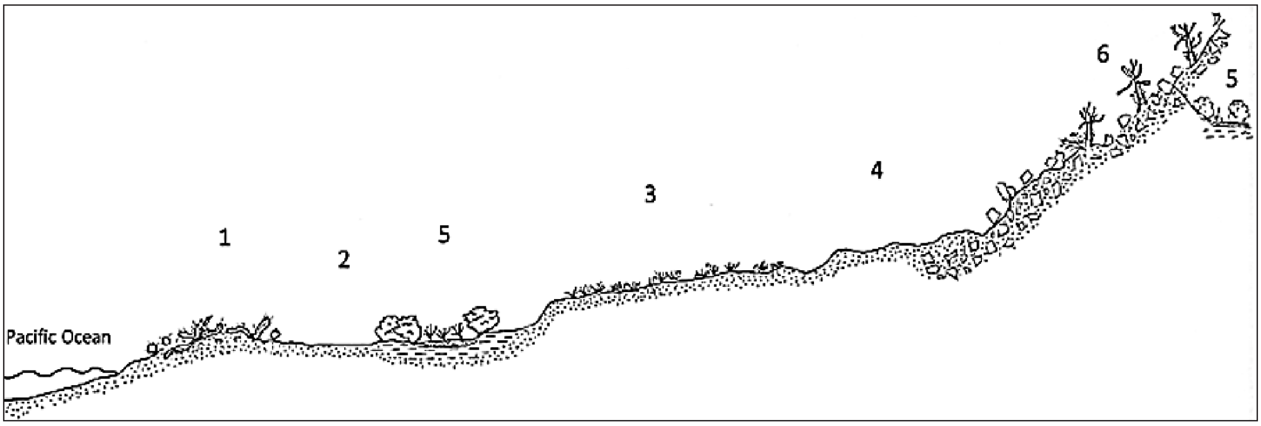

Figure 25. Foggy tropical hyperdesert geocomplex. **1.** Foggy coastal hyperdesert: *Eryosice islayensis-Haageocereus* australis community. Cacti disperse communities on coastal sandy microdunes "lomas". **2.** Not vegetated coastal hyperdesert. Bare sandy eolic coastal surfaces. **3.** Foggy coastal hyperdesert: *Tillandsia werdermannii* community. Piedmont glacis with sandy eolic cover. **4.** Not vegetated interior hyperdesert. Low-montane piedmont glacis and pediments with sandy eolic cover. **5.** Flooded woodland and shrubland: *Solanum chilense-Tecoma fulva* community. Seasonal allochtonous streams riparian desert vegetation. **6.** Desert open vegetation: *Haageocereus platinospinus-Browningia candelaris* community. Rocky soils of low-montane hillside slopes. Graphic geobotanical interpretation based on our field transect data (1993) and cited references.

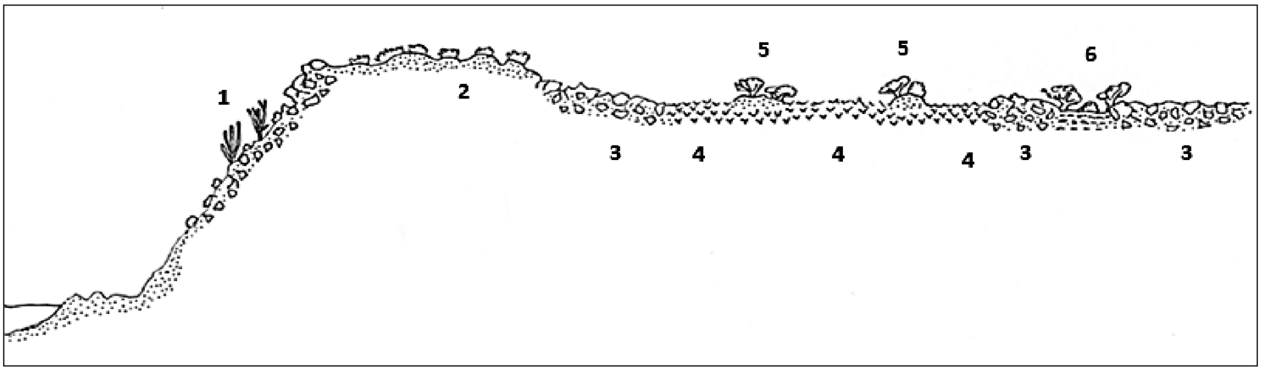

Figure 26. Foggy tropical hyperdesert geocomplex. **1.** Foggy coastal hyperdesert: *Ephedra breana-Eulychnia iquiquensis* community. Xeromorphic shrubland and thicket with cacti and succulents. Relictic on abrupt coastal cliffs and screes with *Eulychnia* population partially death. Windswept sands covering rocky substrates. Moderate to strong incidence of seasonal coastal fogs. **2.** Foggy tillandsia hyperdesert: *Tillandsia landbeckii* community. Sandy mesodunes with persistent seasonal fogs. **3.** Not vegetated hyperdesert. Bare desertic rocky pavement in sandy matrix. **4.** Not vegetated hyperdesert. Salt flats without vascular vegetation ("Salar Grande"). **5.** Deciduous thorn shrubland: Phreatophyllous disperse *Prosopis tamarugo* shrubs on salar microdunes. **6.** Deciduous thorn woodland and shrubland: *Caesalpinia aphylla-Prosopis tamarugo* community. Open phreatophyllous saline vegetation in anastomosed silt channels with seasonal ephemeral drainage. Pampa del Tamarugal, Salar de Pintados. Graphic geobotanical interpretation based on our field transect data (1995) and cited references.

A.28. Lowland flooded savanna and woodland geocomplex (Fig. 29) [Biogeography: Neogranadian Region, Llanos Province, Llanos of Apure]. Representive type locality: Venezuela, Barinas, El Frío transect, Llanos de Apure, ca. 07°52'S. Altitude: 130 m. Known analogous distribution areas (homoplasyc geobiomes): E Bolivia, SW Venezuela, E Colombia. Bioclime: infratropical pluviseasonal humid. IUCN related units: "Pyric tussock savannas", "Hummock savannas", "Permanent marshes", "Seasonal floodplain marshes", "Tropical flooded forests and peat forests". Refs.: Castroviejo and López (1985), Rangel ed. (1997), Josse et al. (2003, 2009), Romero et al. (2004), Galán et al. (2006), Sayre et al. (2008), Huber and Oliveira-Miranda (2010), Aymard and González (2013), Guevara (2015), Minorta-Cely (2020).

A.29. Lowland flooded savanna and woodland geocomplex (Fig. 30) [Biogeography: Neogranadian Region, Llanos Province, Llanos of Meta-Capanaparo)]. Bioclimate: infratropical pluviseasonal humid. Representive type locality: Colombia, Río Arauca-Casanare-Meta, ca. 6°12'N–5°30'N. Interpretation based mainly on Rangel and Minorta-Cely (2014), Minorta-Cely (2020). Altitude: 130–300 m. Known analogous distribution areas (homoplasyc geobiomes): E Bolivia, SW Venezuela, E Colombia.

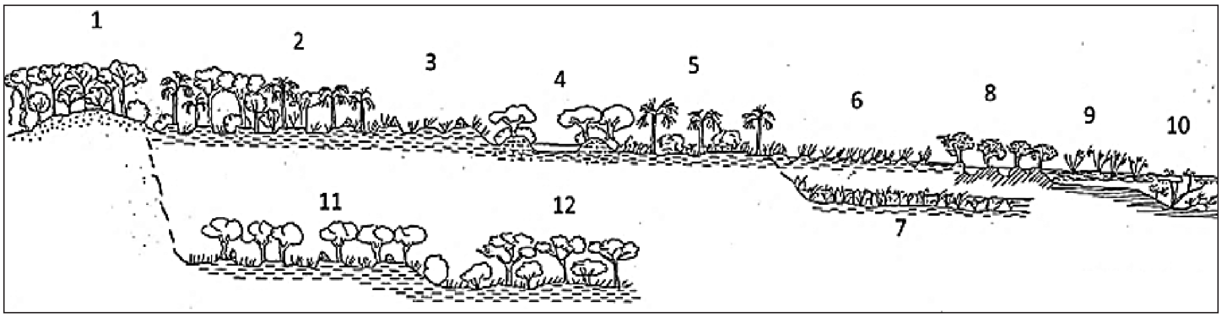

Figure 27. Lowland flooded savanna and woodland geocomplex. **1.** Deciduous phreatophyllous forest: *Swartzia jorori-Anadenanthera colubrina* community. Shallow water tables, on upland fluvial paleo-levées (sandy-loamy gleysols). **2.** Palm woodland: *Piptadenia robusta-Copernicia alba* community. Temporarily ponded sodium-alkaline soils with gilgai microrelief on semi-elevations (planosols, vertisols). **3.** Ponded herbaceous savanna: *Paspalum plicatulum-Paspalum virgatum* community. Mesotrophic soils on temporarily ponded topographic semi-elevations. **4.** Flooded riparian forest: *Croton sampatik-Albizia inundata* community. Seasonally flooded savanna streams levees (fluvic). **5.** Flooded open Palm savanna: *Combretum laxum-Copernicia alba* community. Mesotrophic soils (planosols, gleysols). Seasonally flooded alluvial plain. **6.** Semipermanently ponded herbaceous hummocky savanna: *Arundinella hispida-Hypogynium virgatum* community. Ancient alluvial floodplain topographic depressions with oligotrophic soils. **7.** Seasonally flooded herbaceous savanna: *Paspalum fasciculatum* community. Recent alluvial floodplain with flowing white waters. **8.** Swamp woodland: *Ludwigia peruviana-Tabebuia insignis* community. Ancient alluvial floodplain, in lakes and ponds with deep histic hydromorphic soils (tropical saprimoor). **9.** Marshland: *Rhabdadenia pohlii-Cyperus giganteus*. "Junquillo" sedge-marsh communities in swamps and lakes with semi-floating hydromorphic soils (tropical fibrimor). **10.** Aquatic Beni vegetation: *Cabomba furcata-Nymphaea amazonum* communities. **11.** Temporarily ponded woodland: *Tabebuia heptaphylla-Callisthene fasciculata* community. Precambric shield lateritic pedeplain of Beni transitional to Cerrado in semi-elevations. Termite-mound oligotrophic soils (stagnosols, gleysols). **12.** Seasonally flooded woodland: *Byrsonima orbignyana-Tabebuia heptaphylla* community. North Beni lateritic pedeplain transitional to Cerrado in oligotrophic soils (gleysols). Graphic geobotanical interpretation based on cited references, our own field data (Trinidad-San Ramón del Beni transects) and Google Earth images.

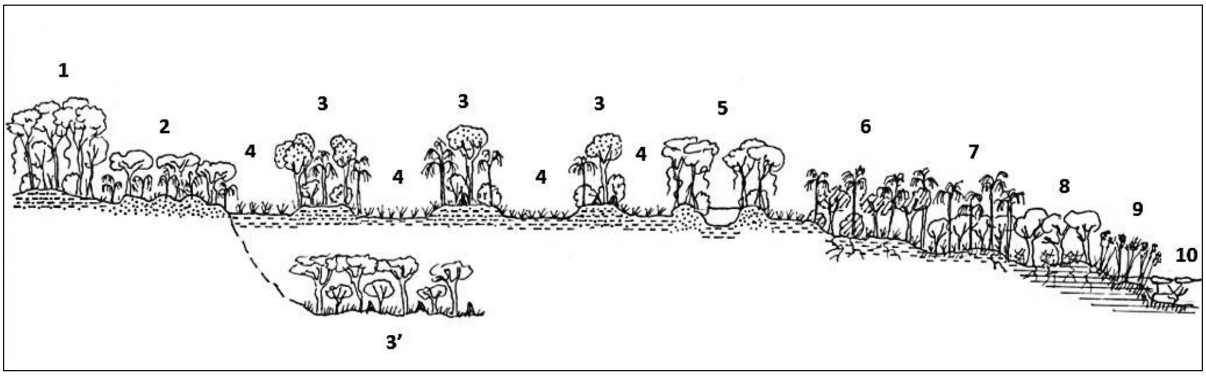

Figure 28. Lowland flooded savanna and woodland geocomplex. **1.** Deciduous woodland: *Schinopsis brasiliensis-Lonchocarpus nudiflorens* community. Drought deciduous to semideciduous Chiquitano forest on poorly drained soils of semi-upland areas with shallow phreatic levels (gleyic luvisols). **2.** Seasonal evergreen sclerophyllous woodland: *Attalea eichleri-Hymenaea stigonocarpa* community. Precambric shield pediment with deep sand-eolic cover (arenic ferralsols). **3**. Palm woodland: *Copernicia alba-Tabebuia heptaphylla* community. Seasonally ponded alluvial plain semi elevations on eutric-calcic vertisols and gleyic stagnosols with strong gilgai microrelief and termite mounds. **3.** Flooded woodland on oligotrophic semi elevations (paleolevées): *Muellera fluvialis-Tabebuia aurea* community. Seasonally ponded dystric planosols. **4.** Seasonally flooded herbaceous savanna: *Cyperus surinamensis-Panicum laxum* community. Alluvial seasonally flooded flat depressions. **5.** Riverine seasonally flooded forest: *Ficus obtusifolia-Sapindus saponaria* community. Fluvial riverbanks and recent levées (eutric fluvisols). **6.** Seasonally flooded palm-woodland: *Microlobius foetidus-Copernicia alba* community. Slightly to low flooded alluvial veretic soils (calcic vertisols). **7.** Flooded palm-savanna: *Triplaris gardneriana-Copernicia alba* community. Highly flooded sodic alluvial soils (calcic solonetzs). **8.** Ponded woodland: *Zygia pithecollobioides-Geoffroea spinosa* community. Very poorly drained to seasonally ponded alluvial vertic soils (calcic gleyic vertisols) on fluvial paleo channels. **9.** Semipermanently flooded sedge-marsh: *Rhabdadenia pohlii-Cyperus giganteus* community. Pantanal "Junquillo" communities in swamps and lakes with semi-floating hydromorphic soils (tropical fibrimoor). **10.** Pantanal aquatic vegetation. Graphic geobotanical interpretation based on cited references, our own field data (San Matías and Otuquis Bolivian Pantanal), and Google Earth images.

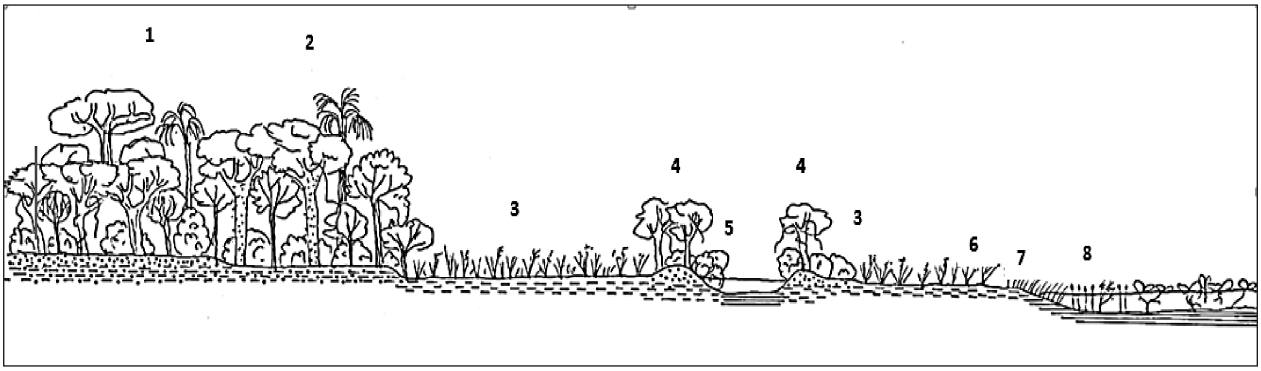

Figure 29. Lowland flooded savanna and woodland geocomplex. **1.** Evergreen seasonal forest: *Pterocarpus rohrii-Ceiba pentandra* communities with *Vitex appunii*, *Sterculia apetala*, etc. Flat semi-elevations ("bancos") with sandy-silty soils and shallow phreatic level. **2.** Evergreen seasonal flooded forest: *Pisonia macranthocarpa-Hura crepitans* community, with *Copernicia tectorum*, *Albizia caribaensis*, etc. Levées semi-elevations ("bancos"). **3.** Flooded tall-herbaceous savanna: *Andropogon virgatum-Panicum junceum* communities, with *Imperata contracta*. Ancient alluvial floodplain topographic depressions with seasonally flooded soils. **4.** Flooded riparian forest: *Copaifera officinalis-Vitex apuhnii* community. Savanna streams levées ("caños"). **5.** Flooded shrubland: *Coccoloba obtusifolia* community. Successional vegetation on riparian stream banks. **6.** Flooded low-herbaceous savanna: *Paspalum orbiculatum* communities. Lakes and ponds margins. **7.** Aquatic emergent vegetation: *Oxycarium cubensis-Eleocharis interstincta* communities. Helophytic vegetation on shallow water. **8.** Aquatic floating vegetation: *Eichhornia heterosperma-Eichhornia azurea* communities, with *Eichhornia crassipes*, *Limnobium laevigatum*, *Nymphaea spp.*, etc. Graphic geobotanical interpretation based on cited references, our own field data (Barinas-San Fernando de Apure) and Google Earth images.

Bioclime: infratropical pluviseasonal humid. IUCN related units: "Pyric tussock savannas", "Hummock savannas", "Permanent marshes", "Seasonal floodplain marshes", "Tropical flooded forests and peat forests". Refs.: FAO (1965), Huber and Riina (1997), Camaripano-Venero and Castillo (2003), Morales and Castillo (2005), Rangel et al (1995), Rangel ed. (1997, 2008), Huber and Oliveira-Miranda (2010), Rangel and Minorta-Cely (2014), Minorta-Cely (2020), Usma et al. (2022).

B. Mediterranean (Austromediterranean) geocomplex biomes

B.1. High-montane mediterranean geocomplex (Fig. 31) [Biogeography: Mesomediterranean-Patagonian Region, Mediterranean Andean Province]. Representative type locality: Santiago-Farallones-La Cumbre transect, central Chile, ca. 32°52'S. Altitude: 2600 to 2900 m. Known analogous distribution areas (homoplasyc geobiomes): C Chile, CW Argentina. Bioclime: supra-oromeditherranean pluviseasonal subhumid. IUCN related units: "Seasonally dry temperate heaths and shrublands". Refs: Gajardo (1994), Ramírez et al. (2004), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006, 2017, 2022), Amigo and Flores-Toro (2012), Oyarzábal et al (2018), Navarro (2021) Amigo et al. (2022a, b).

B.2. Lowland & montane evergreen seasonal sclerophyllous geocomplex (Fig. 32) [Biogeography: Mesomediterranean-Patagonian Region, Central Chilean Province]. Representative type locality: Viña del Mar-Santiago-La Cumbre transects synthesis, Chile, ca. 33°13'S. Altitude: 0–1800 m. Known analogous distribution areas (homoplasyc geobiomes): C Chile. Bioclime: thermomediterranean to upper mesomeditherranean xeric dry and pluviseasonal subhumid. IUCN related units: "Temperate pyric sclerophyll forests and woodlands". Refs: Villaseñor and Serey (1981), Gajardo (1994), Ramírez et al. (2004), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006, 2006b, 2022), Amigo and Flores-Toro (2012), Navarro (2021), Amigo et al. (2022a, b).

B.3. Montane xeromorphic shrubby-grassland steppe geocomplex (Fig. 33) [Biogeography: Middle Chilean and Patagonian Region, North Patagonian Province]. Representative type locality: Southern Mendoza, San Rafael transect, Argentina, ca. 34°32'S. Altitude: 1360–1400 m. Known analogous distribution areas (homoplasyc geobiomes): CW Argentina. Bioclime: supramediterranean xeric semiarid. IUCN related units: "Semi-desert steppes". Refs.: Roig (1972), Cabrera (1976), Boelcke et al. (1985), Roig et al. (1996), León et al. (1998), Collantes et al. (1999), Josse et al. (2003, 2007), Sayre et al. (2008), Roig et al. (2009), Martínez-Carretero et al. (2016), Oyarzábal et al. (2018), Navarro (2021).

B.4. Montane subhumid shrubby-grassland steppe geocomplex biome (Fig. 34) [Biogeography: Middle Chilean and Patagonian Region, South Patagonian Province]. Representative type locality: Southern Argentina transect from Andes to Atlantic Ocean, ca. 51°30'S. Altitude: 0–300 m. Known analogous distribution areas (homoplasyc geobiomes): S Argentina. Bioclime: Supramediterranean xeric dry and pluviseasonal subhumid. IUCN related units: "Temperate subhumid grasslands". Refs.: Cabrera (1976), Roig et al. (1985), Boelcke et al. (1985), Hildebrand-Vogel et al. (1990), León et al. 1998, Collantes

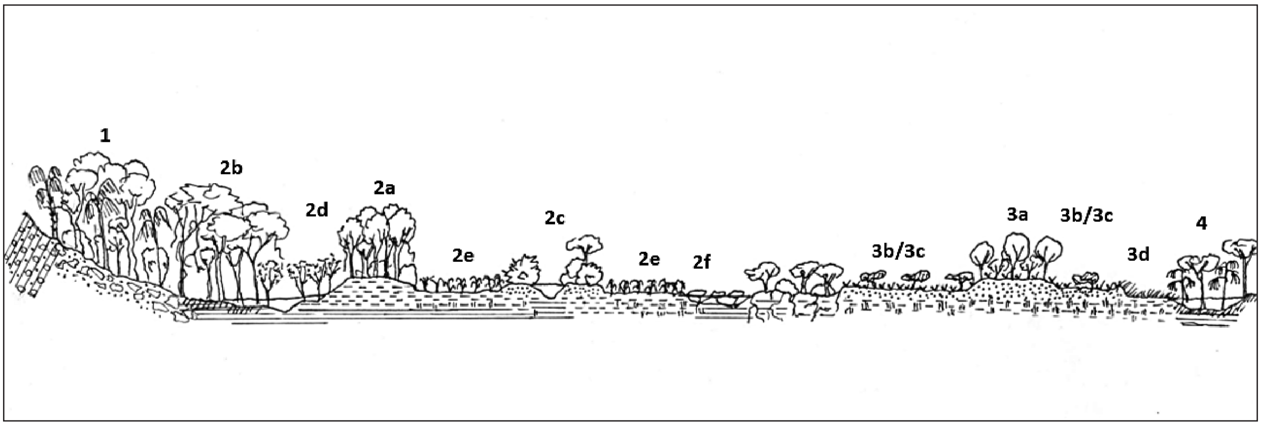

Figure 30. Lowland flooded savanna and woodland geocomplex**. 1.** Andean distal piedmont: alluvial fans and glacis: Evergreen seasonal degraded/successional forest *Spondias mombim-Attalea butyracea* communities with *Copaifera pubiflora*. **2.** Alluvial polycyclic floodplain vegetation mosaic: **2a**- Evergreen seasonally ponded forest: *Ocotea cernua-Vitex orinocensis* communities. Semi-upland low flat elevations, levees ("bancos") with shallow phreatic levels; **2b**- Evergreen flooded forest: *Ceiba pentandra-Luehea seemanii* communities with, *Brosimum lactescens*, *Genipa americana*, *Pseudolmedia laevigata*, *Virola surinamensis*, *Vochysia ferruginea*. Alluvial white-water flood plain; **2c**- Seasonally flooded riparian woodland: *Coccoloba ovata-Piranhea trifoliata* and *Symmeria paniculata-Leptobalanus apetalus* (riparian) communities. Clear and black water flood-plain savanna stream (lotic); **2d**- *Coccoloba mollis-Tessaria integrifolia* communities. Riparian white-water successional woodland; **2e**- Tall herbaceous-flooded savanna: *Hymenachne amplexicaulis-Paspalum repens* communities. Ancient white-water alluvial floodplain depressions with seasonally flooded soils ("bajíos"); **2f**- Swamps and lagoons aquatic vegetation ("esteros"); **2g**- Evergreen woodland and shrublans ("zurales"): *Garcinia madruno-Jacaranda obtusifolia* communities, with *Swartzia pittieri*. Floodplain vertisols with gilgai microrelief.**3-** Old alluvial flood plain with eolic sandy-loessic coberture: **3a.** Evergreen seasonal woodlands and low forest: *Protium guianensis-Caraipa llanorum* communities with *Attalea maripa*, *Eschweilera parvifolia*. Well to medium drained lateritic soils of old alluvial plain with sandy-loess coberture and often sallows phreatic levels; **3b**- Successional pyrophytic-oligotrophic open woodland-savanna: *Byrsonima crassifolia-Curatella americana* communities; **3c**- Oligotrophic herbaceous savanna: *Axonopus purpusi – Paspalum pectinatum* and *Trachypogon plumosus-Schyzachirium sanguineum* communities, with *Thrasya petrosa*, *Trachypogon vestitus*. Pisolitic-lateritic medium-well drained soils, with eolic sandy or loessic cover; **3d.** Seasonally flooded oligotrophic open herbaceous savanna: *Schizachyrium brevifolium-Trachypogon spicatus* communities with *Andropogon leucostachyus*, *Rhynchospora corymbosa*, *Rhynchanthera bracteata*, *Sacciolepis angustissima*, *Sorghastrum setosum*. **4.** Depressional swamp-palm forest: *Xylopia calophylla-Mauritia flexuosa* communities. Stagnic dystrophic black waters with thic acid humus bottom layers. Graphic geobotanical interpretation based on cited references, and Google Earth images.

et al. (1999), Barrera et al. (2000), Promis et al. (2008), Oyarzábal et al (2018).

B.5. Montane xeromorphic shrubland & thicket geocomplex (Fig. 35) [Biogeography: Middle Chilean-Patagonian Region, Argentine Monte Province]. Representative type locality: west Sierra Pie de Palo transect, San Juan, Argentina, ca. 31°24'S. Altitude 600–650 m. Analogous known distribution areas (homoplasyc geobiomes): CW Argentina. Bioclime: meso-supra mediterranean desertic arid and xeric semiarid. IUCN related units: "Thorny deserts and semi-deserts". Refs.: Roig (1972), Roig et al. (1996, 2009), Martínez-Carretero et al. (2016), Navarro (2021), Oyarzábal et al (2018).

B.6. Mediterranean foggy desert geocomplex (Fig. 36) [Biogeography: Middle Chilean-Patagonian Region, Desertic Mediterranean Chilean Province]. Representative type locality: Vallenar-Caldera-Copiapo transects synthesis, Chile, ca. 27°12'S. Altitude: 0–980 m. Known analogous distribution areas (homoplasyc geobiomes): C Chile. Bioclime: termomediterranean and lower mesomediterranean hyperdesertic oceanic. IUCN equivalences: "Hyper-arid deserts". Refs.: Rundel et al. (1991), Gajardo (1994), Navarro and Rivas-Martínez (1994 b), Marquet et al. (1998), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006), Pinto et al. (2006), Pinto and Luebert (2009), Galán et al. (2002, 2004, 2009, 2011), Navarro (2021), Amigo et al. (2022a, b).

C. Temperate (Austrotemperate) geocomplex biomes

C.1. Montane temperate oceanic evergreen forest geocomplex (Fig. 37) [Biogeography: Valdivian-Magellanian Region, Valdivian Province]. Representative type locality: El Bolsón a Bariloche transect, Río Negro, CWArgentina, ca. 41°40'S. Altitude: 400–900 m. Known analogous distribution areas (homoplasyc geobiomes): CW Argentina, CE Chile. Bioclime: mesotemperate and supratemperate pluviseasonal humid. IUCN related units: "Warm temperate laurophyll forests". Refs.: Gajardo (1994), Navarro et al (1994d), Donoso (1995), Amigo and Ramírez (1998),

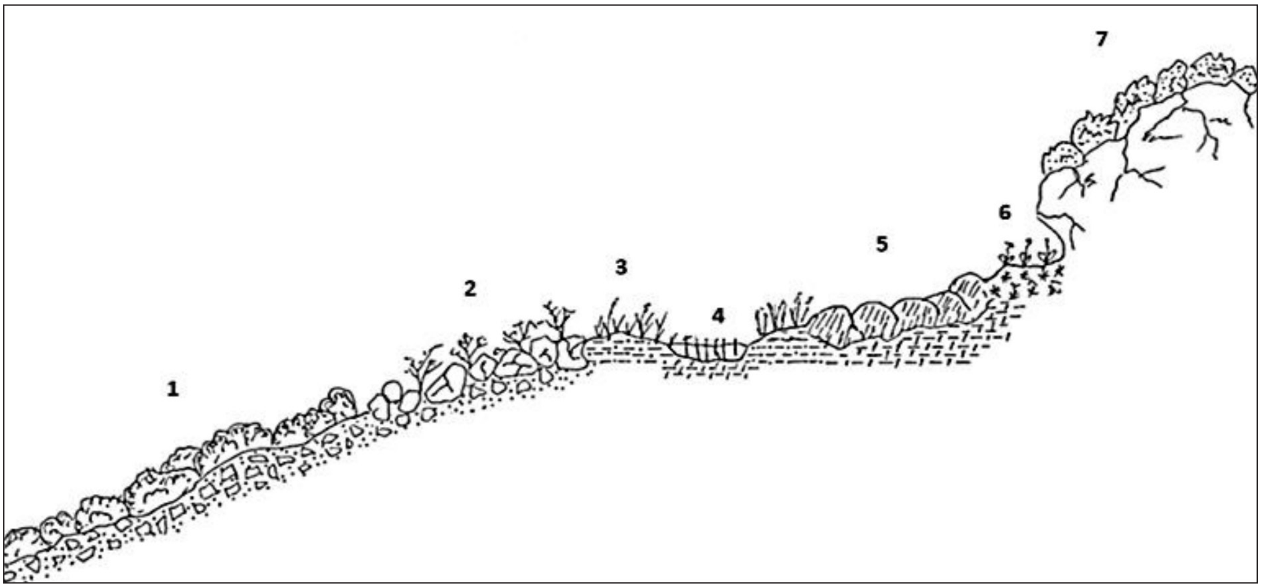

Figure 31. High-montane mediterranean geocomplex. **1.** High-montane pulvinate thorn shrubland & thicket: *Nardophyllum lanatum-Anarthrophyllum cumingii* community, with *Nassauvia heterophylla*, *Junellia spathulata*, *Berberis empetrifolia*, etc. High-montane mediterranean zonal vegetation on well-drained stony soils (skeletic umbrisols). **2.** High-montane scree vegetation: *Senecio glaber-Nicotiana corymbosa* community. Skeletic regosols. **3.** High-montane meadows: *Colobanthus quitensis-Carex gayana* community. Seasonally wet to flooded soils. **4.** Aquatic vegetation: *Juncus-Eleocharis* communities. Shallow high-montane ponds and streams. **5.** Cushion-like peatbog: *Caltha sagittata-Patosia clandestina* community. Permanently flooded or ponded peaty soils. **6.** Chionophile subnival vegetation: *Calceolaria biflora* communities. Semi-permanent snowy niches cavities or depressions. **7.** High-montane transition to subnival pulvinate shrubland & thicket: *Anarthrophyllum gayanum-Laretia acaulis* community, with *Triglochin alatum*, *Poa holciformis*, *Haplopappus scrobiculatus*, *Chuquiraga oppositifolia*. Well drained stony soils (skeletic umbrisols), associated to cryomorphic open vegetation: *Chaetanthera euphrasioides* community on leptic cryosols. Graphic interpretation based on our field transect data and cited references.

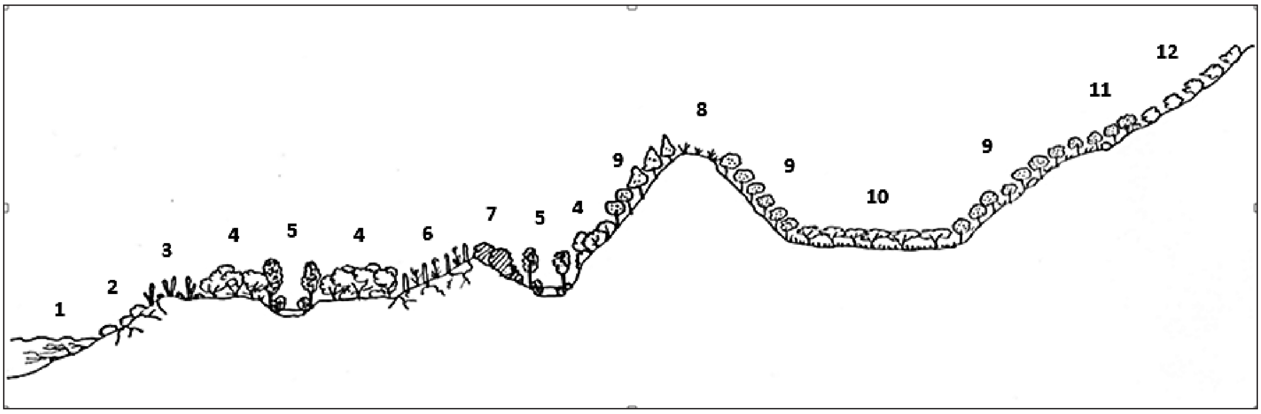

Figure 32. Lowland & montane evergreen seasonal sclerophyllous geocomplex. **1.** Benthonic macro algal coastal vegetation: *Lessonia trabeculata-Durvillea antarctica* communities. **2.** Saxicolous aero-halophile vegetation*: Calandrinia grandiflora-Nolana crassulifolia* community. **3.** Saxicolous coastal vegetation: *Neoporteria subgibbosa-Trichocereus littoralis* community**. 4.** Evergreen sclerophyllous woodland: *Peumus boldus-Cryptocarya alba* community. Lowland zonal climacic association to ca. 650 m altitude. **5.** Riparian forest and woodland: *Persea lingue-Crinodendron patagua* communities. Lowland riverbanks vegetation, seasonally flooded. **6.** Saxicolous lowland vegetation: *Puya chilensis-Trichocereus chilensis* community. Rocks and cliffs. **7.** Lowland dry sclerophyllous woodland: *Quillaja saponaria-Cryptocarya alba* communities. On stony north-exposed hillsides. **8.** Montane saxicolous vegetation: *Puya coerulea* communities**. 9.** Montane evergreen sclerophyllous woodland: *Kageneckia oblonga-Quillaja saponaria* communities. **10.** Secondary dry deciduous thorn woodland: *Lithraea caustica-Acacia caven* community. In dry rain shadow inner flat valleys with somewhat shallow phreatic levels. **11.** Upper montane evergreen sclerophyllous dry woodland: *Quillaja saponaria-Lithraea caustica* communities, and montane saxicolous shrubland & thicket: *Puya coerulea-Trichocereus chiloensis* community. **12.** Upper montane evergreen sclerophyllous subhumid woodland: *Talguenea quinquenervia-Kageneckia angustifolia* communities. Graphic interpretation based on our field transect data and cited references.

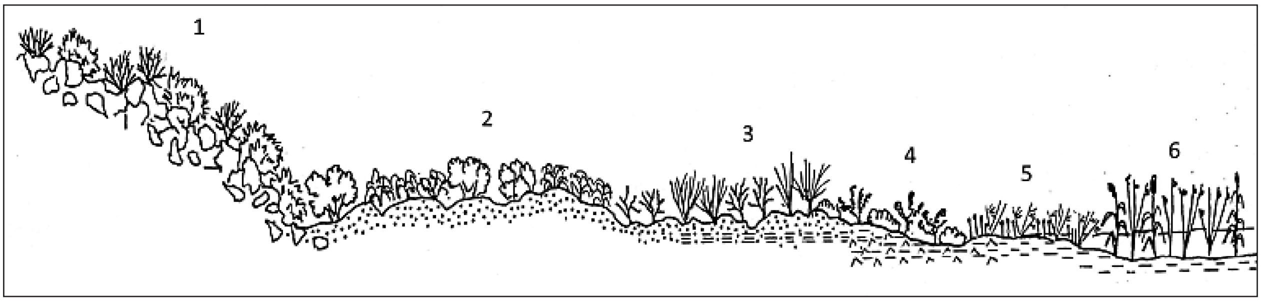

Figure 33. Montane xeromorphic shrubby-grassland steppe geocomplex. **1.** Xeromorphic shrubby-grassland steppe: *Colliguaja integerrima-Neosparton aphyllum* community. Hillsides with stony excessively well drained soils. **2.** Xeromorphic shrubby steppe (on sandy soils): *Styllingia patagonica-Cassia arnottiana* community. Micro-mesodunes with eolic sandy soils. **3.** Phreatophytic xeromorphic shrubby steppe: *Hyalis argentea-Neosparton ephedroides* community. Ephemeral ravines and depressions with shallow seasonal water table. **4.** Saline shrubland: *Sarcocornia neei-Heterostachys ritteriana* community. Seasonally ponded saline soils. **5.** Swamp reedbed: *Eleocharis albibracteata-Juncus balticus* community. Seasonally ponded marshes. **6.** Flooded sedge-marsh: *Typha subulata-Schoenoplectus californicus* community. Lakes and ponds margins. Graphic interpretation based on our field transect data and cited references.

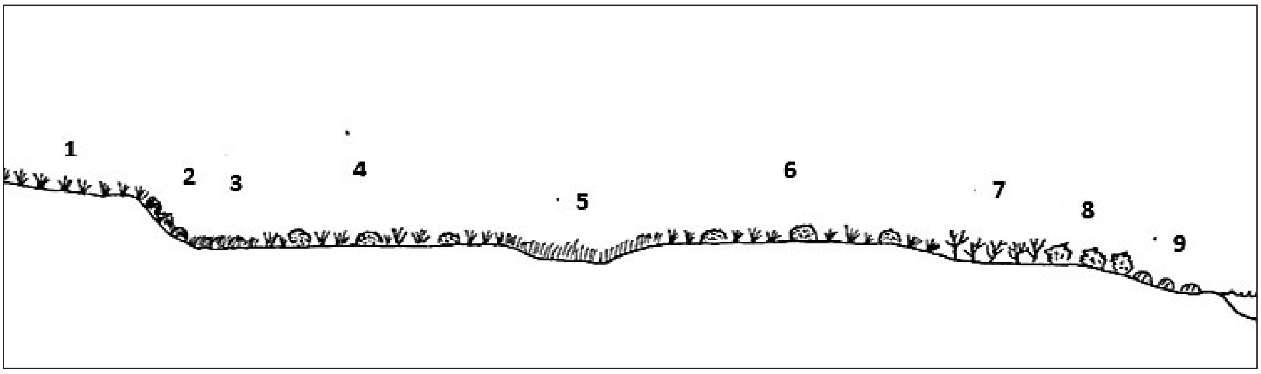

Figure 34. Montane subhumid shrubby-grassland steppe geocomplex biome**. 1.** Humid shrubby-grassland steppe: *Gamochaeta nivalis-Festuca gracillima* community. Oriental Andean piedmont on humic well-drained soils (umbrisols). **2.** Criomorphic open thicket: *Oreopolus glacialis-Empetrum rubrum* community. Hillside oriental Andean piedmont, with geliturbated soils. **3.** Wet bunch-grassland: *Festuca pallescens* community and peatland bogs: *Caltha sagittata* communities. **4.** Dry shrubby-grassland steppe: *Verbena ameghinoi-Festuca gracillima* community. **5.** Festuca pallescens flooded grasslands and *Carex subantarctica-Eriachaenium magellanicum* community. Lacustrine litoral aquatic vegetation. **6.** Halo-hygrophilous shrubland: *Lepidophyllum cupressiformis* communities. **7.** Saline coastal wetland shrubland and thicket*: Frankenia chubutensis-Atriplex macrostyla* community. **8.** Saline coastal wetland prostrate thicket: *Salicornia ambigua-Suaeda argentinensis* community. Graphic geobotanical interpretation based on Roig et al. (In Boelcke et al. 1985).

Ramírez et al. (2004, 2014), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006, 2006b, 2022), Amigo and Rodríguez-Guitián (2011), Oyarzábal et al (2018), Navarro (2021), Amigo et al. (2022a, b).

C.2. Lowland & montane hyperoceanic temperate forest geocomplex (Fig. 38) [Biogeography: Valdivian-Magellanian Region, Valdivian Province]. Representative type locality: Osorno-Antillanca transects synthesis, Valdivia, Chile, ca. 40°41'S. Altitude: 0–1200 m. Known analogous distribution areas (homoplasyc geobiomes): S Chile, SW Argentina. Bioclime: oceanic mesotemperate-supratemperate hyperhumid-humid. IUCN related units: "Oceanic cool temperate rainforests", "Boreal and temperate high montane forests and woodlands". Refs**.:** Gajardo (1994), Donoso (1995), Amigo and Ramírez (1998), Ramírez et al. (2004, 2014), Josse et al. (2003, 2007), Sayre et al. (2008), Luebert and Pliscoff (2006a, 2006b, 2022), Amigo and Rodríguez-Guitián (2011), Navarro (2021), Amigo et al. (2022a, b).

C.3. Temperate hyperoceanic magellanian forest geocomplex (Fig. 39) [Biogeography: Valdivian-Magellanian Region, Temperate Magellanian Province]. Representative type locality: Argentina-Chile transects synthesis, ca. 51°30'S. Altitude: 0–200 m. Known analogous distribution areas (homoplasyc geobiomes): S Chile, S Argentina. Bioclime: meso-suprathemperate hyperoceanic hyperhumid-humid. IUCN related units: "Oceanic cool temperate rainforests". Refs.: Boelcke et al. (1985), Hildebrand-Vogel et al. (1990), Gajardo 1994; León et al. 1998; Amigo and Ramírez 1998; Collantes et al. (1999), Barrera et al. (2000), Promis et al. (2008), Luebert and Pliscoff (2006, 2022), Amigo and Rodríguez-Guitián (2011), Amigo et al. (2022a, b).

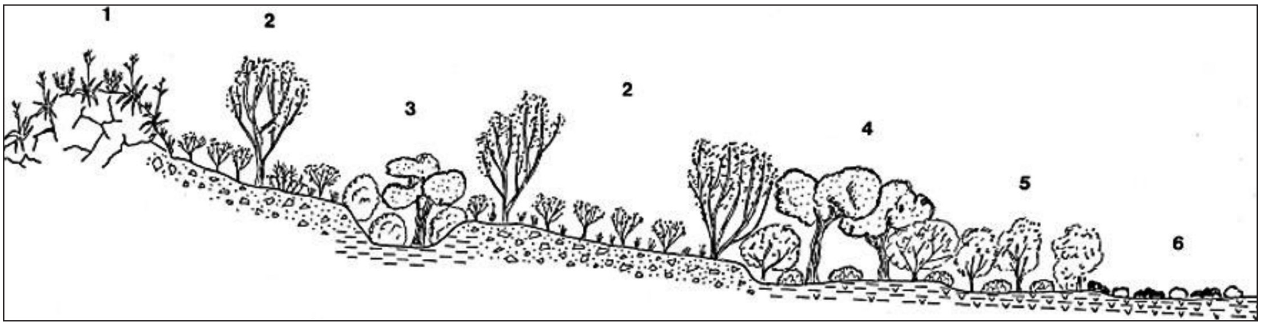

Figure 35. Montane xeromorphic shrubland & thicket geocomplex. **1.** Monte saxicolous vegetation: *Tephrocactus halophilus-Deuterocohnia longipetala* community. Rock outcrops, and screes. **2.** Monte xeromorphic shrubland & thicket: *Bulnesia retama-Larrea cuneifolia* community. Zonal vegetation on sandy-stony hillsides with well-drained soils. **3.** Phreatophyllous xeromorphic shrubland & thicket: *Trichomaria usillo-Larrea divaricate-Prosopis flexuosa* communities. On flat temporal streambeds and topographic depressions with shallow water table. **4.** Deciduous thorn woodland & shrubland: *Cyclolepis genistoides-Prosopis flexuosa* community. Sub-halophile phreatophytic vegetation. **5.** Deciduous thorn woodland & shrubland: *Allenrolfea vaginata-Prosopis strombulifera* community. Saline wet shrubland temporarily ponded. **6.** Saline wetland thicket: *Plectrocarpa tetracantha-Sarcocornia neei* community. Halophyllous seasonally flooded thorn and succulent thicket. Graphic geobotanical interpretation based on our field transect data and cited references.

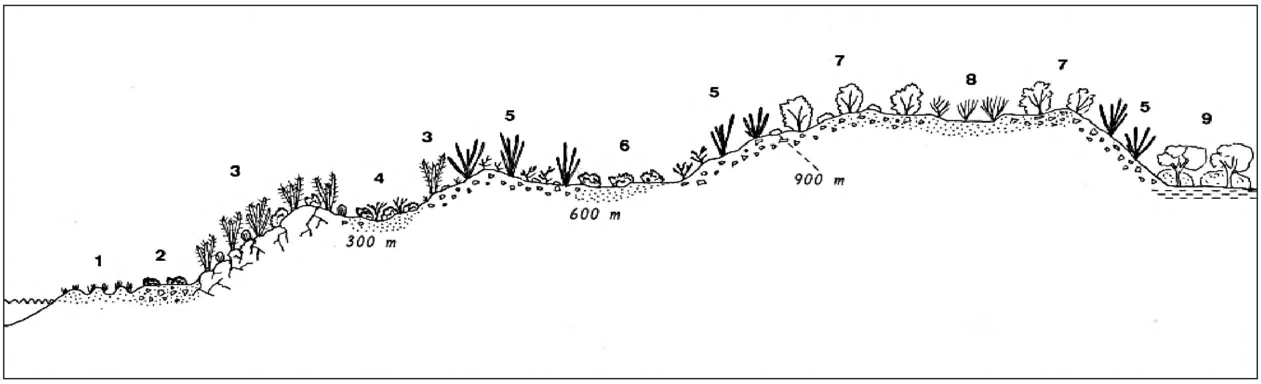

Figure 36. Mediterranean foggy desert geocomplex. **1.** Xeromorphic shrubland & thicket: *Nolana divaricata-Tetragonia maritima* community. Succulent aero-halophile vegetation on coastal beach sand dunes. **2.** Xeromorphic scrub: *Skytanthus acutus* communities. Deep coastal soils. **3.** Foggy coastal hyperdesert: *Copiapoa cinerea-Eulychnia breviflora tenuis* community. Xeromorphic shrubland and thicket with cacti and succulents on granitic boulder stony soils. **4.** Phreatophilic coastal scrub: *Gypothamnium pinifolium* communities. Topographic depressions with shallow temporal water tables **5.** Desert open succulent shrubland: *Caesalpinia angulicaulis-Eulychnia acida elata* community. **6.** Open phreatophile-xeromorphic shrubland: *Skythanthus acutus-Balsamocarpon brevifolium* communities. Temporal ravines with shallow seasonal water tables. **7.** Open xeromorphic shrubland: *Krameria cistoidea-Bulnesia chilensis* communities. Desert zonal vegetation. **8.** Desert open ravine shrublands: *Atriplex atacamensis-Adesmia argentea* community (on temporary arroyo beds) and *Nolana sedifolia-Skytanthus acutus* community (on recent low fluvial terraces). **9.** Thorn woodland and shrubland: *Geoffroea decorticans-Schinus molle* community. Phreatophylle riparian on temporarily flooded allochthonous streams (arroyos). Graphic geobotanical interpretation based on our field transect data and cited references.

C.4. Temperate oceanic lowland woodland and grassland geocomplex (Fig. 40) [Biogeography: Pampean Region, Mesophytic Pampa Province]. Representative type locality: Samborombón-San Clemente del Tuyú transects synthesis, E Buenos Aires province, Argentina, ca. 36°05'S. Altitude: 20–65 m. Known analogous distribution areas (homoplasyc geobiomes): Central Eastern Argentina. Bioclime: oceanic thermo temperate pluviseasonal humid-subhumid. IUCN related units: "Temperate subhumid grasslands", "Temperate woodlands". Refs.: Cabrera (1976), Burkart et al. (1998, 1999), Josse et al. (2003, 2007), Sayre et al. (2008), Matteuci (2012), Martínez-Carretero et al. (2016), Oyarzábal et al. (2018), Navarro (2021).

C.5. Temperate lowland dry thorn woodland and grassland geocomplex (Fig. 41) [Biogeography: Pampean Region, Xerophytic Pampean Province ("Espinal")]. Representative type locality: General Achá to Santa Rosa transect, La Pampa province, Argentina, ca. 36°33'S. Altitude: 510 m. Known analogous distribution areas (homoplasyc

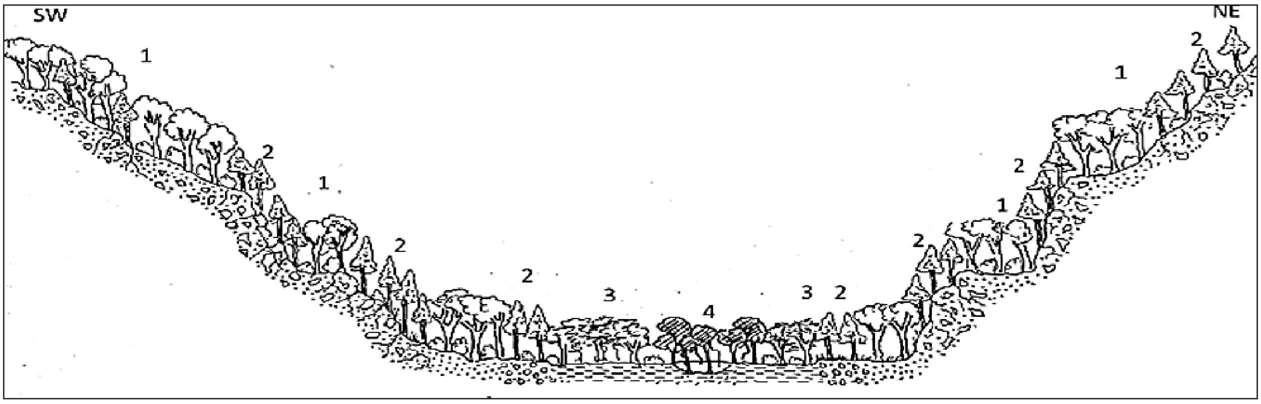

Figure 37. Montane temperate oceanic evergreen forest geocomplex. **1.** Evergren mixed forest: *Austrocedrus chilensis-Nothofagus dombeyii* community. Mountain well to medium drained hillside soils. **2.** Evergreen coniferous forest: *Lomatia hirsuta-Austrocedrus chilensis* community. Mountain hillsides and fluvial terraces on stony hyper-drained soils. **3.** Flooded deciduous woodland: *Laureliopsis philippiana-Nothofagus antarctica* community. Seasonally to permanently saturated or ponded flat alluvial bottom valley. **4.** Evergreen riparian forest: *Boquila trifoliata-Myrceugenia exsucca* community. Permanently flooded riverbeds. Lotic. Graphic geobotanical interpretation based on our field transect data and cited references.

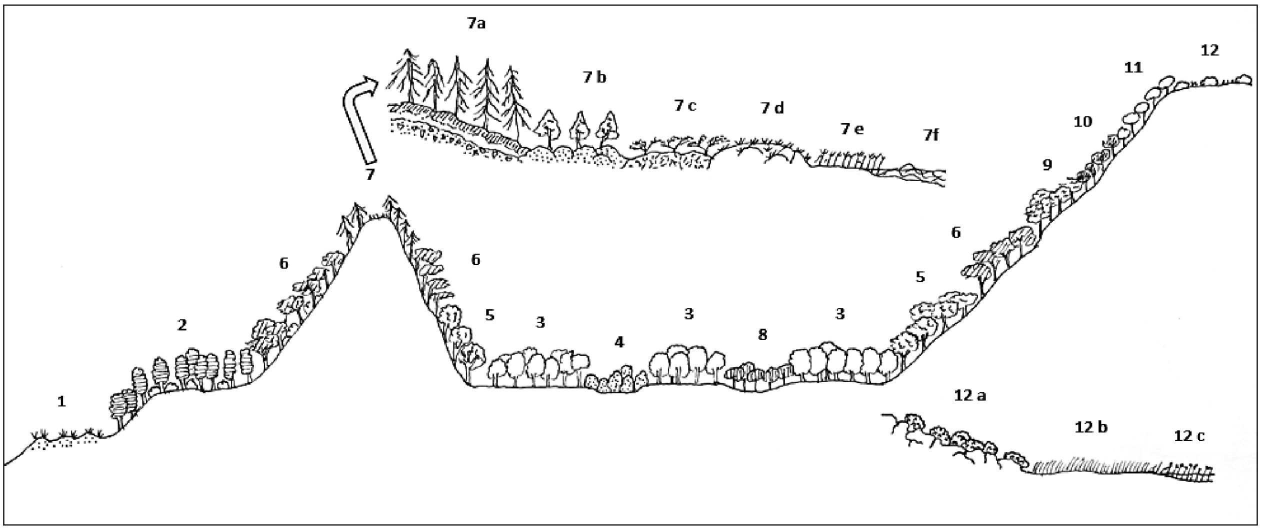

Figure 38. Lowland & montane hyperoceanic temperate forest geocomplex. **1.** Coastal thicket: *Ambrosia chamissonis* communities. Psammophilous vegetation on coastal sand dunes. **2.** Lowland evergreen Valdivian Forest: *Lapageria rosea-Aextoxicon punctatum* community**. 3.** Lowland cold deciduous Valdivian Forest: *Persea lingue-Nothofagus obliqua* community, with *Nothofagus alpina*. **4.** Flooded Forest & woodland: *Temu divaricata-Myrceugenia exsucca* community. **5.** Montane evergreen humid Valdivian Forest: *Nothofagus dombeyi-Eucryphia cordifolia* community. **6.** Montane evergreen hyperhumid zonal forest: *Laurelia sempervirens-Weinmannia trichosperma* community. **7.** Montane cold deciduous humid forest: *Nothofagus nitida* communities in mosaic with: **7a.** Edapho-xerophilous coniferous forest: *Fitzroya cupressoides* community, on sandy-stony podsoil soils. **7b.** Coniferous domed peat bog: *Pilgerodendron uviferum-Gaimardia australis* community. **7c.** *Sphagnum magellanicum* peat bog with *Dacrydium fonckii*. **7d**. Subantarctic domed peat bog: *Oreobolus obtusangulus-Donatia fascicularis* community. **7e.** Helophytic vegetation: *Marsippospermum* community. **7f.** Aquatic vegetation: *Scirpus inundatus* communities. **8.** Flooded cold deciduous woodland: *Notohofagus antarctica* communities. On marshy wet soils. **9.** Upper Montane evergreen hyperhumid Valdivian Forest: *Chrysosplenium valdivianum-Nothofagus dombeyi* community. **10.** Upper montane cold deciduous hyperhumid Valdivian woodland: *Nothofagus pumilio* communities. **11.** High-montane cold deciduous hyperhumid Valdivian woodland: *Nothofagus antarctica* community. **12.** High-montane pulvinate thorn shrubland & thicket: **12a** *Adesmia longipes-Empetrum rubrum* community; in mosaic with: **12b** Meadows: *Elymus andinus-Hierochloe juncifolia* community; **12c** Helophytic vegetation: *Carex spp*. Communities. Graphic geobotanical interpretation based on our field transect data and cited references.

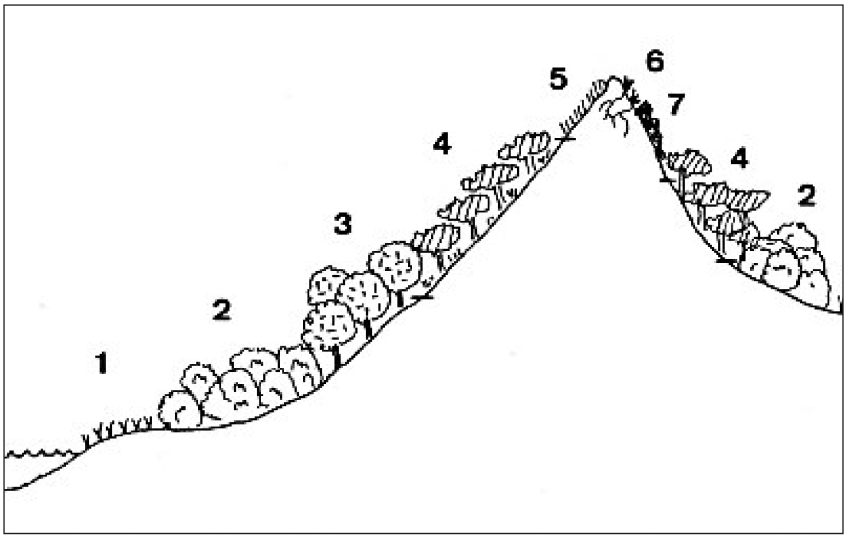

Figure 39. Temperate hyperoceanic magellanian forest geocomplex. **1.** Coastal pioneer herbaceous vegetation: *Apium australe-Senecio smithii* communities. **2.** Evergreen coastal-flooded woodland: *Nothofagus antharctica* community; and moss peatland: *Sphagnum magellanicum* communities. **3.** Evergreen hyperoceanic woodland: *Nothofagus betuloides* communities. **4.** Cold deciduous hyperoceanic montane woodland: *Nothofagus pumilio* communities. **5.** High-montane hyperoceanic grassland: *Bolax gummifera-Festuca gracillima* community and alpine cryomorphic open vegetation: *Adesmia parviflora-Perezia megalantha* community. **6.** Saxicolous temperate alpine vegetation: *Leucheria hannii-Nassauvia lagascae* community. **7.** High-montane pulvinate thorn shrubland & thicket: *Adesmia parviflora-Empetrum rubrum* community. Graphic geobotanical interpretation based on Roig et al. (in Boelcke et al. 1985).

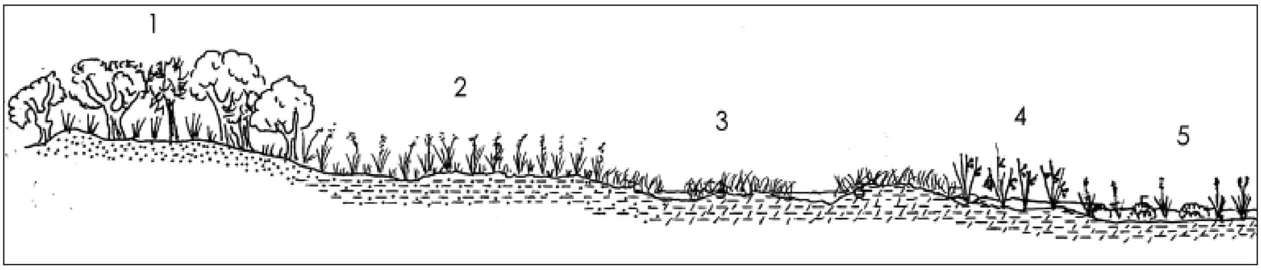

Figure 40. Temperate oceanic lowland woodland and grassland geocomplex. **1.** Thorn woodland & shrubland: *Celtis tala-Geoffroea decorticans-Jodina rhombifolia* communities. Remanents of Pampa zonal potential natural vegetation, on well-drained sandy soils ("LOMA"). **2.** Not flooded Pampa grassland: *Piptochaetium montevidense-Nassella neesiana* communities. Medium-drained mesophytic soils (Gleyic Chernozems) ("SEMILOMA"). **3.** Flooded Pampa grasslands: *Danthonia montevidensis-Paspalum vaginatum* communities. Wet hygrophytic soils (Stagnic chernozems) ("BAJO"). **4.** Reedbed marshland: *Schoenoplectus californicus* communities. **5.** Saline grassland & thicket: *Spartina densiflora-Sarcocornia neei* communities. Halophyllous lacustrine and palustrine vegetation of estuarine coastal marshes. Graphic geobotanical interpretation based on our field transect data and cited references.

geobiomes): CE Argentina. Bioclime: thermo-temperate xeric dry. IUCN related units: "Seasonally dry temperate heaths and shrublands" "Temperate subhumid grasslands". Refs.: Navarro et al. (1994d), Josse et al. (2003, 2007), Sayre et al. (2008), Lewis et al. (1985, 2009), Matteuci (2012), Martínez-Carretero et al. (2016), Oyarzábal et al. (2018), Navarro (2021).

D. Boreal (Austroboreal) geocomplex biomes

D.1. Austroboreal wet woodland & peatbog geocomplex (Fig. 42) [Biogeography: Valdivian-Magellanian Region, Boreal Austromagellanian Province]. Representative type locality: Isla Navarino, southern Chile, ca. 55°12'S. Altitude: 0–800 m. Known analogous distribution areas (homoplasyc geobiomes): S Chile, S Argentina. Bioclime: meso-supraboreal hyperoceanic humid-hyperhumid. IUCN related units: "Oceanic cool temperate rainforests", "Cool temperate heathlands". Refs.: Pisano (1983), Hildebrand-Vogel et al. (1990), Gajardo (1994), Donoso (1995), Collantes et al. (1999), Barrera et al. (2000), Luebert and Pliscoff (2006, 2022), Promis et al. (2008), Amigo and Rodríguez-Guitián (2011), Ramírez et al. (2004, 2014); Rivas-Martínez et al. (2015), Molina et al. (2016), Amigo et al. (2022a, b).

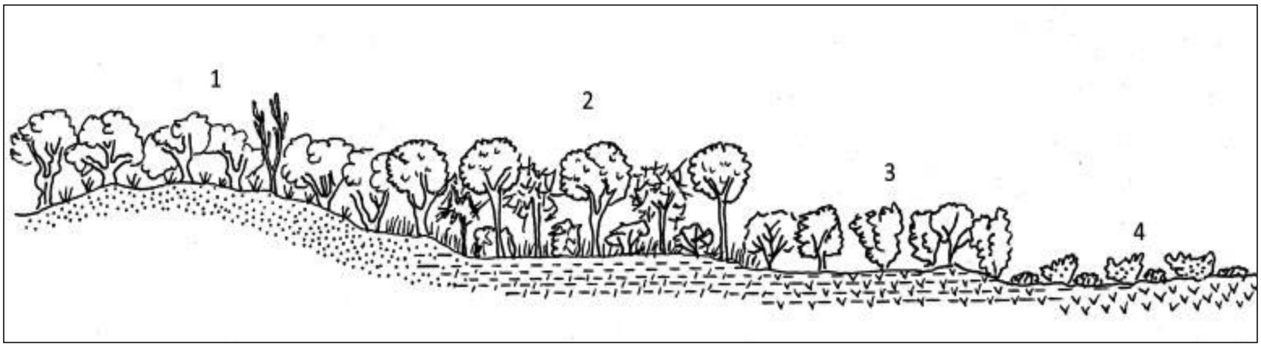

Figure 41. Temperate lowland dry thorn woodland and grassland geocomplex. **1.** Deciduous thorn woodland & shrubland**:** *Celtis tala-Geoffroea decorticans* communities. Hillsides well-drained sandy soils (Arenic Luvisols). **2.** Phreatophytic deciduous thorn woodland & shrubland: *Jodina rhombifolia-Prosopis caldenia* communities. Flat alluvial soils with shallow water table (gleyic regosols). **3.** Saline phreatophile shrubland: *Cyclolepis genistoides-Plectrocarpa tetracantha* community. Halophyllous vegetation on seasonally saturated to temporarily ponded soils with fluctuating shallow water tables (gleyic solonchak and sololonetz). **4.** Salt flats wetland thicket: *Sarcocornia neei-Heterostachys ritteriana* community. Saline seasonally ponded-depressional soils (stagnic solonetz). Graphic geobotanical interpretation based on our field transect data and cited references.

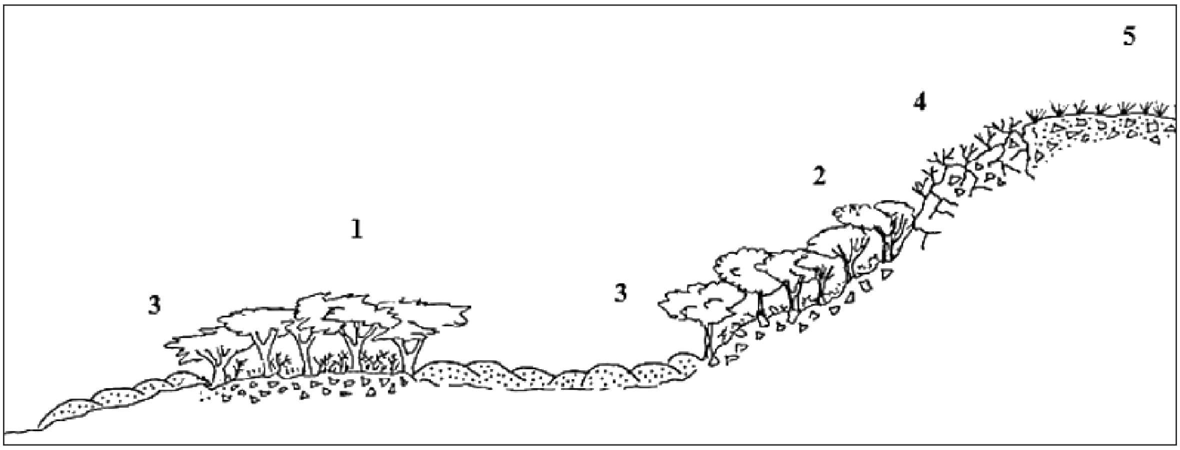

Figure 42. Austroboreal wet woodland & peatbog geocomplex **1.** Mixed evergreen and deciduous coastal wet forest: *Nothofagus betuloides-Nothofagus pumilio* community and *Nothofagus antharctica-Nothofagus betuloides* community (in the most southern and western locations). Mesoboreal bioclimatic level (0–300 m) on coastal well-drained dystric soils. **2.** Deciduous montane wet woodland and shrubland: *Maytenus disticha-Nothofagus pumilio* community. Supraboreal bioclimatic level (300–600 m) on hillside well-drained dystric soils. **3.** Domed-cushion antartic peatbog: *Astelia pumila-Donatia fascicularis* community. Azonal oligotrophic histic soils on wet topographic depressions. **4.** Pulvinate-cushion shrubland & thicket: *Bolax bovei-Bolax gummifera-Abrotanella marginata* communities. Oroboreal bioclimatic level (> 600 m). On high-montane steep slopes with rocky substrates. **5.** Bunch-grassland boreal antartic steppe: *Poa flabellata-Deschampsia laxa* community. Graphic geobotanical interpretation based on Molina et al. (2016).

Discussion

The geobotanic landscape approach that we propose here to conceptualize the biome has not been explicitly contemplated by any previous author, especially with regard to integrating the contributions of European dynamic-catenal geobotanical phytosociology into the idea of biome.

It is necessary to highlight that our work is not floristic-phytosociological, since already in South America there are detailed regional or local works of this type, particularly in countries such as Colombia, Chile, Brazil or Argentina (see following paragraph). However, there is a lack of synthesis and integration that combines these important contributions in a series of spatial and altitudinal models that are generalized, comprehensive and comparative, and allow a global interpretative and predictive vision of the South American diversity. What we present in this work aims to contribute to achieve this goal.

Some related works have been carried out in several south American countries such as Colombia (e.g., Cleef 1980, 1981; Duivenvoorden and Lips 1995; Rangel et al. 1997, 2004, 2017; Minorta-Celys 2020), in Peru by Galán and collaborators (2004, 2006, 2009, 2011, 2015, 2020) or in Chile by Luebert and Gajardo (2001, 2005) or Luebert and Pliscoff (2017). However, their works are fundamentally floristic-phytosociological, defining plant associations or communities in the sense of the Braun-Blanquet methodology, but they do not contemplate a spatial-geographical integration on a landscape scale, except for some local phytotopographic profiles made by some of these authors, such as Galán et al (op cit.). Similarly, nor do they try to apply the geobotanical concepts of geocatena (geosigmetum) and sets of geocatenas for the understanding of repetitive sets of vegetation units in the landscape. Luebert and Pliscoff (2017) constructed longitudinal profiles of the Chilean vegetation types, stratified from north to south throughout the country. These vegetation profiles are also related to the work we present, but they differ in that, with few exceptions, they represent several chained or successive complexes along more than one bioclimate, physiography and biogeography. Likewise, these authors do not formalize or conceptually define criteria to spatially define and delimit the geocomplexes and do not explicitly relate their results to the bioma concept. Another proposal in South America that is somewhat related to ours is the extensive work by Morello et al. (2012) on the ecoregions and ecosystem complexes of Argentina, where the characteristic ecosystem patterns of each large natural area considered an ecoregion are described in detail. We agree with these authors in the idea that these repetitive sets of ecosystems are typical or differential of their ecoregions, but their approach is fundamentally descriptive and they do not formalize a conceptual framework for it. Additionally, interpretative graphic models are not formulated either, but rather the various environmental factors that coincide with the ecosystem complexes (geology, soils, etc.) are described as separate elements for each of them. Nor is there an explicit relationship of these complexes with the biome concept.

In general, we stated that the analogies between representative geocomplex biomes of each biogeographic region are very notable for the different types of ecosystems present in the geocomplex; while the floristic homologies are much smaller and only partial, depending on each group of biogeographic provinces, in relation to the centers of origin and dispersion of the flora.

The number of geocomplex biomes identified in South America shows a pattern of decline from the tropical to boreal macrobioclimate, and from north to south. This corresponds to the classic global latitudinal patterns of species diversity recognized by different authors, and also for South America (i.e., Cingolani et al. 2010; Antonelli and Sanmartín 2011; Qian and Son 2013); patterns that generally are related to global thermal and humidity gradients.

Moreover, our proposal for geocomplex biomes for South America, although coinciding in some respects with the IUCN proposal (Keith et al. 2020, 2022), differs substantially from it in several key conceptual aspects. For example, IUCN has a heterogeneous nomenclature and conceptual basis, particularly with no consistency or homogeneity in the IUCN GFS names assigned and their delimitation factors. Also, IUCN present detailed principles designed for a global ecosystem typology, but lack an objective, consistent and explicit protocol or keys to properly define, delimit and name the units. It is a difficult system to standardize and repeat, as the units and their mapping are based mainly on expert opinion. Furthermore, some relevant Neotropical biomes are not represented, e.g., the extensive woodlands and wooded or arboreal savannas of the Cerrado, and they do not explicitly follow any bioclimatic system. Furthermore, the IUCN proposal does not contemplate an explicit or conceptual landscape ecological approach.

Our framework can be applied using perhaps others classifications of bioclimate and biogeography, for example using Köppen's climatic system (Köppen 1936; Beck et al. 2018) and Morrone's biogeographic regionalization (Morrone 2001, 2006, 2014). To what extent employing the cited (but somewhat related) bioclimatic and biogeographic classification systems might impact the delimitation of gecomplexes remains to be seen and exceeds the scope of the present contribution.

Conclusions and main contributions

The successive application of biogeophysical criteria based mainly on the bioclimate, geomorphology, soils and vegetation, makes it possible to objectively differentiate the biomes considered from an integrated perspective at landscape scales.

In this sense, our work proposes a new and comprehensive approach to the biome concept based on the integration of dynamic-catenal geobotany and landscape ecology concepts, within a bioclimatic, geophysic and biogeographic homogeneous framework. The definition and identification of the geocomplex biome (geobiome) is based on observable or measurable criteria and variables, as a group of repetitively associated geocatenes related and interacting in the landscape. Further, our work provides for the first time thirty-three standardized ecosystem zonation models for all South America which graphically show the geocomplex biomes identified and characterized for the continent, grouped consistently into sixteen neotropical macrobiomes. However, there remains a need for additional surveys in areas that are poorly known or difficult to access, which may lead to an increase in the number of existing geocomplex biomes, as well as to specifications and adjustments of those already proposed. We expect that this approach will make geocomplex biomes a better and more precise basis for the development of integrated and holistic conservation strategies, much needed in a continent subjected to strong increasing threats and pressures.

Author contributions

G.N. designed the survey, provided the core data information and produced the figures, F.L. and J.A.M. contributed substantially to the conceptual writing and took part in shaping and adequacy of the proposal.

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