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REVIEW AND SYNTHESIS   INTERNATIONAL VEGETATION CLASSIFICATION

A novel biome concept and classification system based on bioclimate and vegetation – a Neotropical assay

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Abstract

The knowledge of biomes as large-scale ecosystem units has benefited from advances in the ecological and evolutionary sciences. Despite this, a universal biome classification system that also allows a standardized nomenclature has not yet been achieved. We propose a comprehensive and hierarchical classification method and nomenclature to define biomes based on a set of bioclimatic variables and their corresponding vegetation structure and ecological functionality. This method uses three hierarchical biome levels: Zonal biome (Macrobiome), Biome and Regional biome. Biome nomenclature incorporates both bioclimatic and vegetation characterization (i.e. formation). Bioclimate characterization basically includes precipitation rate and thermicity. The description of plant formations encompasses vegetation structure, physiognomy and foliage phenology. Since the available systems tend to underestimate the complexity and diversity of tropical ecosystems, we have tested our approach in the biogeographical area of the Neotropics. Our proposal includes a bioclimatic characterization of the main 16 Neotropical plant formations identified. This method provides a framework that (1) enables biome distribution and changes to be projected from bioclimatic data; (2) allows all biomes to be named according to a globally standardized scheme; and (3) integrates various ecological biome approaches with the contributions of the European and North American vegetation classification systems.

Taxonomic reference: Jørgensen et al. (2014).

Dedication: This work is dedicated to the memory of and in homage to Prof. Dr. Salvador Rivas-Martínez.

Keywords

bioclimatic belts, biogeography, formations, geocatena, Neotropics

Biome: a concept with a universal scope

From the earliest definitions of biome as a climax biotic community over a large geographic area (Clements 1917; Shelford and Olson 1935; Clements and Shelford 1939), to the present day, where recent definitions incorporate ecological, functional and evolutionary advances, the biome remains a key concept in ecology and biogeography (Mucina 2018; Hunter et al. 2021). However, these scientific streams have so far not produced a universal biome classification system that allows a standardized nomenclature based on a set of criteria or quantifiable variables that can explain and causally predict the distribution and global characteristics of biomes (Holdridge 1947, 1967; Box 1981a, 1981b; Bailey 1989a, 2005). This can be explained not only by the polysemic use of the biome concept but also by the considerable overlap between concepts relating to biomes, such as ecoregion, ecosystem, ecological system, biogeoclimatic ecosystem, ecological division, ecozone, formation, and bioregion, among others (Ellenberg and Mueller-Dombois 1967; Holdridge 1967; Whittaker 1970; Bailey 1989a; Dinnerstein et al. 1995; Olson et al. 2001; Josse et al. 2003; Ibisch et al. 2003; Rutherford et al. 2006; Sayre et al. 2008; MacKenzie and Meidinger 2018; Keith et al. 2020).

Assuming ecosystems can be defined as a biotic assemblage of species with an associated abiotic environment, the interactions within and between these complexes, and the physical space in which they operate (Faber-Langendoen et al. 2020), biomes can be considered as large-scale ecosystems. Biome schemes based on ecological concepts have been defined using either vegetation-climate relationships (Holdridge 1947; Olson et al. 2001) or in functional terms (Paruelo et al. 2001; Scheiter et al. 2013; Higgins et al. 2016; Conradi et al. 2020). Other works implicitly link climate to vegetation physiognomy (Whittaker 1970; Walter 1973; Larcher 1975; Bailey 1989a; Box 2016) or vegetation activity to climate restrictions (Larcher 1975; Higgins et al. 2016). All these approaches make little use of comparable ecological factors or fail to use a similar and replicable nomenclatural sequence of criteria. To overcome these limitations, it is necessary that a biome classification contributes to and facilitates the creation of an interpretative and predictive system (Walter 1973; Bailey 1989a; Mucina 2018; Hunter et al. 2021). In our proposal, the biome classification is built on the relationships between both bioclimate and vegetation classifications, understanding bioclimate as a range of climate variables explaining the distribution of a set of biotas and growth forms.

A bioclimate-based approach is eco-functional in nature since the limiting climate variables condition and determine the appearance and structural adaptations of the vegetation, as well as the soil complexes on which it develops; thus, bioclimates behave as ecosystem drivers. The bioclimatic indices enable the objective extrapolation and prediction of existing biomes in different geographically separated locations. Building on our expert knowledge of most Neotropical ecosystems in the field, the aim of this work was to establish a parsimonious and comprehensive biome classification and nomenclature system based on consistent objective and hierarchical criteria. We accomplish this by specifically demonstrating the applicability and representativity of our proposal for tropical biomes (see Tables 1, 2 and Figures 1–5). This proposal is based on hierarchical classifiers for defining biomes, and to some extent follows the vegetation classification of EcoVeg (Faber-Langendoen et al. 2014, 2016, 2018), which is widely used in America, and the Worldwide Bioclimatic Classification System (Rivas-Martínez et al. 2011a) developed in Europe.

Prior assumptions

Our biome approach is founded on six assumptions:

(a) Macrobioclimate is the major factor driving the zonation of biomes, whereby biomes are distributed by global climate zonation into what are known as zonobiomes (Walter 1985). We favour the term macrobioclimate in preference to macroclimate since the bioclimatic approach – linking biota and climate – emphasizes the limiting climate factors that explain the structural and functional differentiation of ecosystems. The role of climate factors (determining zonal biomes) versus other abiotic factors (determining pedobiomes, lithobiomes, hydrobiomes) has been widely discussed (Mucina 2018; Hunter et al. 2021).

(b) Bioclimate is an essential feature in biome definition (Troll 1961; Bailey 1989a, 1989b; Rivas-Martínez et al. 2011a). We consider bioclimate to define the differentiation and zonation of the biomes within each macrobioclimate (Table 1 and Figure 1) by including information on (i) the magnitude and rhythm of rainfall and temperature, (ii) the intensity and duration of the dry season, and (iii) the annual thermicity. Current world bioclimatic maps show a high degree of agreement with biome and ecosystem maps (Rivas-Martínez et al. 2011; Metzger et al. 2012).

(c) The easiest and most intuitive way to identify, describe and classify biomes is through vegetation (Figure 1). The type of vegetation involved in biome definition must be the potential natural vegetation or climax, since it is in balance with the prevailing climate and soil conditions (Tüxen 1956; Loidi et al. 2010; Mucina 2010; Loidi and Fernández-González 2012; Zhao et al. 2019). It should be noted that the potential natural vegetation is sometimes difficult to identify, since it may have been removed by human activities or only be represented by remnants in a matrix of different substitution stages (Figure 2C). Vegetation-based biome maps are currently available, both globally (Bailey 1989b; Olson et al. 2011; Keith et al. 2020) and regionally for several countries (e.g., Neotropical vegetation maps). For reasons of scale, these maps mostly interpret and map the potential natural vegetation and have been taken into account for this proposal. Derived successional stages should be considered as being subsumed in the potential natural vegetation, which is the concept of sigmetum or vegetation series (Tüxen 1979; Géhu and Rivas-Martínez 1981; Rivas-Martínez 2005). The vegetation series or sigmetum expresses the whole set of plant communities or stages that can be found in related geographic spaces as a result of the succession process, which includes both the representative association of the climax stage, and the initial or subserial associations that can replace it (e.g. Figure 2C). It also comprises the disclimax cases created by vegetation dominated by exotics that cannot evolve towards the potential natural vegetation (e.g. Figure 3A).

(d) We assumed that the biome refers to the landscape matrix, that is to say, the dominant and more continuous or connected ecosystem (Forman and

Godron 1986) in a landscape mosaic. Thus, each type of dominant or zonal vegetation – potential natural vegetation or climax vegetation – also includes the azonal vegetation with which it is repeatedly associated in the landscape, such as xeric vegetation on rocky outcrops or sandy soils, or wetland vegetation on flooded soils. Therefore, the biome is not restricted to a single structural type of vegetation, but encompasses different structural types that are functionally and geomorphologically associated and connected in the landscape in a repetitive way. Following the concept of the association geocomplex, geocatena or vegetation geoseries (geosigmetum concept: Schmithusen 1959; Tüxen 1979; Rivas-Martínez 2005; Rivas-Martínez et al. 2011b; Choisnet et al. 2019), each biome consists of a specific geoseries that occupies a regional area with the same bioclimate and biogeography, or of a group of homologous geoseries (macrogeoseries) whose zonal (climatophilous) series share analogous physiognomic-structural characteristics. We thus consider macrogeoseries as an accessory spatial qualifier for biomes, and geoseries for regional biomes (Table 1).

(e) Other abiotic factors such as lithology and hydrology are important, but usually play a role at finer scales within biomes, e.g. as regional biomes (Tables 1 and 2). However, when azonal vegetation is the dominant landscape matrix, we consider it as a biome in its own right (e.g. extensive wetlands – Figure 2D – or vast special substrates such as rocks, serpentine or sands). Such landscapes are considered as azonal biomes (Walter 1973; Navarro et al. 2010) since they are not directly determined by the macroclimate but by the hydrology.

(f) The physiognomy and structure of the potential natural vegetation are adequate descriptors of biomes (Loidi et al. 2010; Mucina 2010) since they represent a global biological response to past and present climate conditions. Biomes based primarily on floristic composition should not be considered at the global level, mainly due to the scale of application of the concept. Similarly, fauna is not directly addressed, as it is regarded as dependent and adapted to the vegetation-climate complex: in general, we assume that each type of vegetation contains characteristic fauna ensembles.

(g) Anthropogenic cultural systems (or anthromes) are considered here a secondary biome because, although these biomes are human-altered, they currently occupy large areas (Faber-Langendoen et al. 2014; Ellis 2015, 2020) and are also influenced by the bioclimate and altitudinal zonation (Table 2; Figure 3A–D).

Hierarchical classifiers for defining biomes

We propose that biome classification should be based on the typology of a hierarchical system in which, as a first step, the macrobiome (zonobiome) is defined through the macrobioclimate and plant formation characteristics, and in a second step, the biome is defined through the altitudinal belt and characterization of the bioclimate.

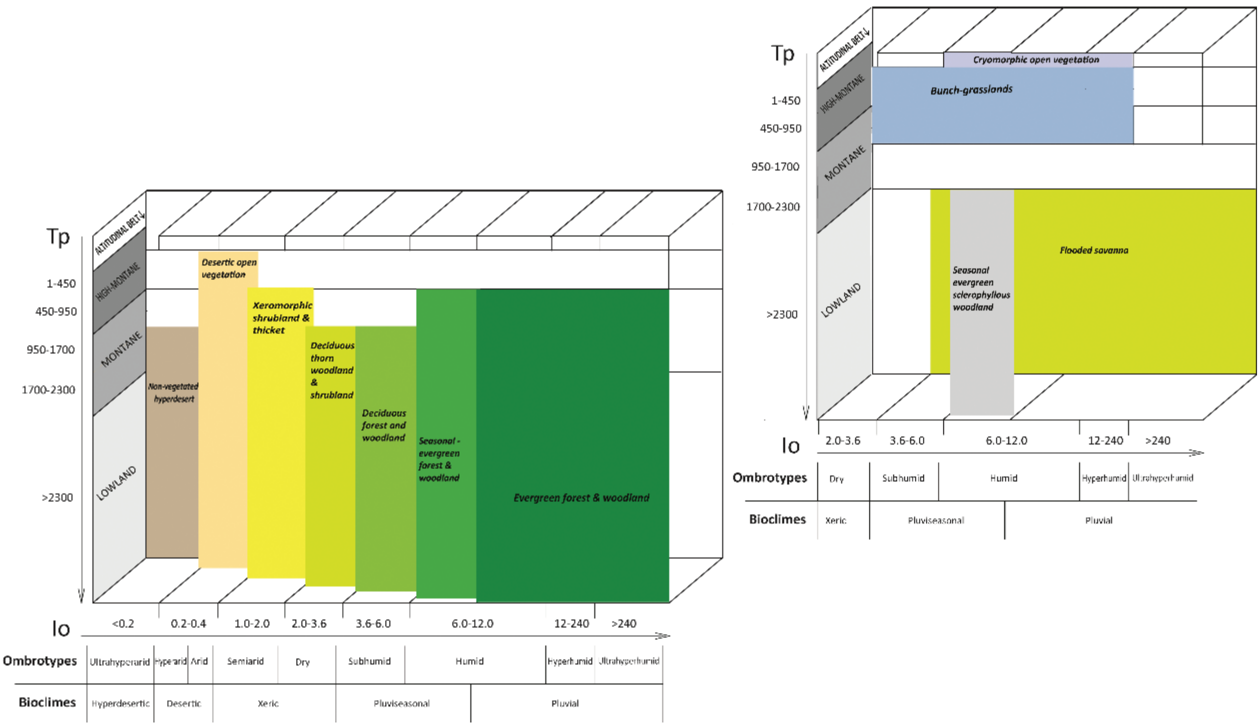

Figure 1. Whittaker-style diagram showing neotropical biomes distribution in relation to Rivas-Martínez values of positive temperature (Tp) and ombrothermic index (Io).

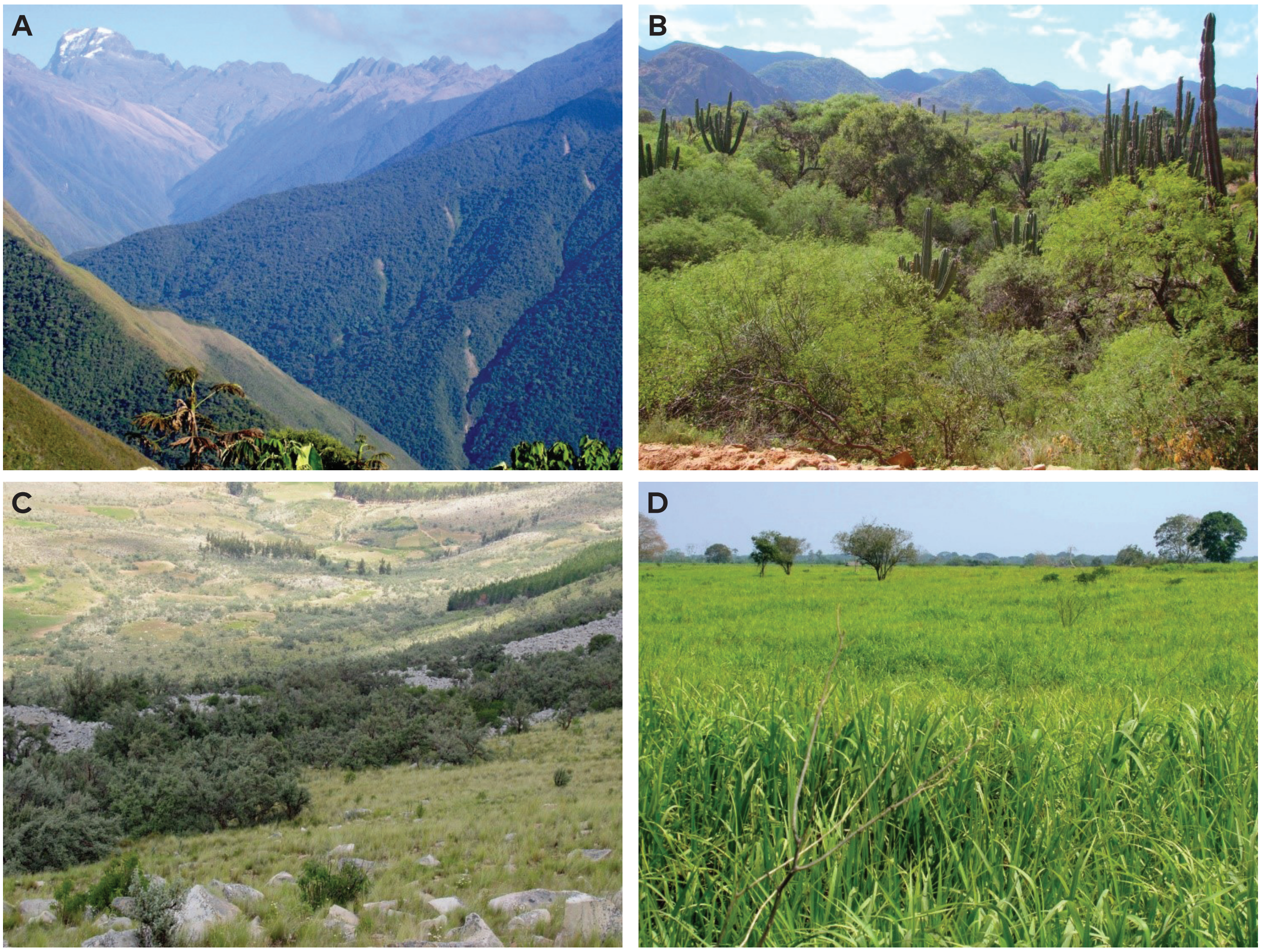

Figure 2. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Belt zonation in the north-eastern Bolivian Andes showing two main altitudinal belts, montane, and high-montane (Cordillera Real, La Paz, 1900 m to 5100 m); **B.** Tropical montane deciduous thorn woodland and shrubland, *Neocardenasia herzogiana-Schinopsis haenkeana* community (Interandean dry valleys, Cochabamba, 1890 m); **C.** Remnants of Tropical montane evergreen seasonal sclerophyllous woodland of *Polylepis subtusalbida* community in a matrix of seral stages, mainly bunch-grasslands (pajonal) of *Festuca dolichophylla*, and scattered plantations of *Eucalyptus* (Cordillera Tiraque, Cochabamba, 3670 m); **D.** Tropical lowland flooded savanna, *Paspalum fasciculatum* community (Llanos del Beni, 148 m). (Photos: Gonzalo Navarro).

Here we follow the Rivas-Martínez bioclimatic system (Rivas-Martínez et al. 2011a), which hierarchically differentiates the macrobioclimate at higher scales, and within this, several bioclimates differentiated by specific ranges of bioclimatic indices. A biome regionalization, with consideration of floristic composition, can also be defined when a biogeographic typology is included, as biogeographic sectorization is mainly based on the regional distribution of plant species and communities. Our procedure also emphasises the importance of using the same nomenclatural sequence to define biomes, and implicitly or explicitly includes bioclimatic characteristics. It is also important to note that our approach is actualistic, in the sense that it seeks to explain the current adaptive occurrence of biomes, which may vary depending on the diverse and complex incidence of climate change around the world. This is the case of various relict vegetation types that do not correspond directly to the current climate, which implies a degree of uncertainty in the causal relationships between climate and vegetation. A good illustration of this phenomenon are vegetation types that are currently in separate or disjunct zones with respect to their main continuous areas of distribution. For example, in South America, climatic fluctuations during the Quaternary (drier climates oscillating along the north-south direction) can explain the isolated and disjunct areas of Gran Chaco vegetation currently located much further north, within the Beni, Chiquitanía or Pantanal (Navarro and Maldonado 2002; Navarro 2011).

We therefore adopt, for regional biome characterization, both the classical biogeographical approach largely based on climate and vegetation alone (De Candolle 1855; Engler 1879–1882; Drude 1890; Schimper 1898; Schmithüsen 1959), and other integrated proposals (Cabrera and Willink 1973; Rivas-Martínez et al. 2011b), one of whose main bases is phytochorionomy (Takhtajan 1986), which recognizes different scales

Figure 3. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Tropical lowland permanent livestock anthrome (Bolivia, Santa Cruz, 440 m); **B.** Tropical lowland pluvial exotic cultural anthrome, oil palm crops of *Elaeis guineensis* (Ecuador, Esmeraldas, 60 m); **C.** Tropical montane pluviseasonal subhumid traditional cultural anthrome (Bolivian Andes, Cochabamba, 3600 m); **D.** Tropical montane urban anthrome (Bolivian Andes, Cochabamba, 2600 m); **E.** Tropical high-montane Andean mining anthrome (Bolivia, Potosí, Cerro Rico, 4300 m); **F.** Tropical high-montane pluviseasonal subhumid traditional cultural anthrome (Bolivian Andes, Cochabamba, 3800 m). (Photos: Gonzalo Navarro).

of biogeographic units, namely: region, province and sector (Good 1974). Additionally, biogeophysical and landscape qualifiers are considered when specifying biomes at regional scales.

Defining macrobiomes and biomes

In our proposal, the macrobiome (= zonobiome) is defined by the macrobioclimate and the potential vegetation structure (plant formation), as shown in Table 1 for the Neotropics (columns 1 and 2). Most of the current biome terminology initially refers to some type of macroclimate and ecosystem aspect, whether physiognomic or structural, that can be related to plant formation. This is unsurprising, since macroclimate plays a fundamental role in the structure and functioning of ecosystems and thus in the evolutionary-adaptive groups of associated flora and fauna. In this context, "evolutionary" refers to biotic assemblages that have evolved adaptively and differentially in each biome, depending on the different climatic conditions. Major macrobioclimates can be summarized in a few types such as Tropical, Mediterranean (included by certain authors in Temperate), Temperate, Boreal and Polar (Rivas-Martinez et al. 2011a). We do not consider the desert bioclimate (according with Rivas-Martínez et al. 2011) to be a single bioclimate since it is present in areas with differing macrobioclimates and consequent different floristic assemblages (e.g., deserts occur under different Mediterranean, Tropical and Temperate macrobioclimates). Ecosystem aspects such as vegetation structure and foliage phenology – including the morphology and persistence of plant leaves – photosynthetic rates, the formation and dynamics of humus types, rates of biogeochemical cycles and others, are primarily conditioned by the macrobioclimate (Troll 1961; Holdridge 1967; Whittaker 1970; Larcher 1975; Walter and Box 1976; Box 1981a,b; Bailey 2004; Mucina 2018). Major natural formations worldwide can also be summarized in a few broad types, namely forest, woodland, savanna, shrubland, tundra, grassland, and steppe (Ellenberg and Mueller-Dombois 1967). We propose a detailed characterization and definition of Neotropic plant formations in Table 2.

Biome relates ecosystems to climate through bioclimate. Different bioclimate zones can be defined within each macrobioclimate when biome zonation is related to ranges in thermicity (bioclimatic belts) and rainfall/temperature ratios (ombrotypes) along both altitudinal and latitudinal gradients (Table 1; Figure 1). In addition, the numerical calculation of bioclimatic indices (e.g. Rivas-Martínez et al. 2011a) from extensive and updated global climate data (e.g. Fick and Hijmans 2017) confers a robust possibility of prediction and extrapolation. Thus, bioclimate classifies aspects of vegetation structure and phenology more precisely than macrobioclimate. In our proposal, the biome is primarily defined by the bioclimate, the altitudinal belt and the plant formation.

Likewise, the regional biome incorporates additional qualifiers referring to the biogeographic distribution (centres of origin and evolution of the flora) and landscape qualifier (geoseries). Our proposal to some extent overlaps with the International Vegetation Classification (IVC; Faber-Langendoen et al. 2020). Thus, macrobiome, biome and regional biome, as defined here, are roughly equivalent to the formation, division and macrogroup levels of the IVC.

Table 1. Successive application of the five main criteria proposed (macrobioclimate, formation, altitudinal belt, bioclimate, biogeography) and additional qualifiers to identify and name the three levels of scale proposed for the Neotropics biomes.

Zonobiome		Biome Landscape additional qualifier: macrogeoseries		Regional Biome Landscape additional qualifier: geoseries
1. Macrobioclimate	2. Formation	3. Altitudinal belt (thermicity)	4. Bioclimate (ombric rhytms)	5. Biogeography (Biogeographic region)
Tropical	1. Cryomorphic open vegetation 2. Bunch-Grassland 3. Evergreen forest 4. Evergreen seasonal forest & woodland 5. Evergreen seasonal sclerophyllous woodland 6. Deciduous forest and woodland 7. Deciduous thorn woodland and shrubland 8. Xeromorphic shrubland & thicket (semidesert) 9. Desert open vegetation 10. Non vegetated hyperdesert 11. Foggy coastal hyperdesert 12. Flooded forest and woodland 13. Mangroves 14. Flooded savanna 15. Non flooded savanna 16. Anthropic and cultural vegetation	High-montane (3,900–5,200 m)	Pluvial	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN
			Pluviseasonal	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN
		Montane (1,000–3,900 m)	Pluvial	NEOGRANADIAN (Colombian-Venezolan) GUYANAN-ORINOQUIAN TROPICAL SOUTH ANDEAN AMAZONIAN BRAZILIAN-PARANEAN
			Pluviseasonal	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN AMAZONIAN BRAZILIAN-PARANEAN
			Xeric	NEOGRANADIAN (Colombian-Venezolan) TROPICAL SOUTH ANDEAN
			Desertic	TROPICAL SOUTH ANDEAN
			Hyperdesertic	HYPERDESERTIC TROPICAL PACIFIC
		Lowland (< 1,000 m)	Pluvial	NEOGRANADIAN (Colombian-Venezolan) GUYANAN-ORINOQUIAN AMAZONIAN BRAZILIAN-PARANEAN
			Pluviseasonal	NEOGRANADIAN (Colombian-Venezolan) GUYANAN-ORINOQUIAN AMAZONIAN BRAZILIAN-PARANEAN
			Xeric	NEOGRANADIAN (Colombian-Venezolan) BRAZILIAN-PARANEAN CHACOAN
			Desertic	HYPERDESERTIC TROPICAL PACIFIC
			Hyperdesertic	HYPERDESERTIC TROPICAL PACIFIC

Biome nomenclature

Some examples are provided to aid the understanding of the nomenclatural procedure in our approach (see also Figures 1–5). The first step defines the macrobiome or zonobiome (Table 1). For instance, the name of the Tropical evergreen forest macrobiome (Table 2, formation type 3, columns 1 and 2) – also broadly known as the Tropical evergreen rainforest biome – refers to both the macrobioclimate (Tropical) and the formation (evergreen forest).

The second step defines the biome, which takes into account the altitudinal belt and the bioclimate. An example is the Tropical lowland pluvial evergreen forest biome (Table 1, formation type, column 1, 2, 3, 4). In this definition "lowland" corresponds to the altitudinal belt and pluvial to bioclimate. It is worth noting that in most biome classifications, the formation name is often linked to an adjective denoting the dominant leaf morphology or phenology, e.g., "sclerophyllous woodland and shrubland", or "evergreen broadleaf forest", whereas other times it is related to the growth form, e.g., "prostrate dwarf-shrub tundra". In our proposal each plant formation (Table 2) is defined by their physiognomy (e.g., forest, woodland, shrubland) and the phenology of the foliage of the dominant stratum (e.g., evergreen, semi-deciduous), since these are the elements most closely related with both the bioclimate and the key soil factors and adaptive history of each biogeographic region. In some cases, we consider it properly justified to introduce complementary specific qualifiers in the formation's name. This additional nomenclature is related to key geobiophysical variables such as hydrological factors (e.g., flooded forest).

Biogeographical qualifiers (at the biogeographic region or province level) can more accurately specify the regional biome (Table 1) and can be entered in brackets after the main biome name: e.g., Tropical lowland evergreen forest biome [Amazonian]. We do not consider it useful or practical to formally use local or regional names to denominate the biomes, such as the "South American Cerrado", or the "South African Fynbos". Nevertheless, due to the long tradition of their use in certain biomes, it may be useful to point out equivalences between regional names and plant formations (see Table 2).

Table 2. Physiognomic-structural characterization of the 16 plant formations recognized for the Neotropics and their correspondence with bioclimates, altitudinal belts and dominant major soil groups. This correspondence emphasizes the simultaneous use of structural and eco-functional criteria in the proposed methodology for the classification of biomes. Soil types follow Gardi et al. (2015).

Formation	Structure and foliage phenology	Bioclimate	Altitudinal belt/ Geographical distribution	Soils
1. Cryomorphic open vegetation	Dwarf caespitose grasslands and open or sparse low perennial subfruticose herbs on cryoturbed high montane Andean soils	Humid Pluviseasonal and Pluvial	Subnival > 4600 m	**Cryosols,** Leptosols, Regosols
2. Bunch-Grassland	Mountain tropical tall to medium-high graminoid grasslands that grow forming somewhat separate tillers or tufts with dense rooting (*Puna*, *Páramo*, *Pajonal*). Including swamp-grasslands and peat-bogs.	Humid Pluvial and Pluviseasonal	Upper Montane and High Montane belts / Tropical Andean, High Guyanas	**Umbrisols, Regosols, Histosols, Gleysols,** Leptosols
3. Evergreen forest	Tall or medium-high forests and woodlands with perennial foliage (*Rainforest*, *Selva*). It presents a complex and very diverse vertical structure: emergent strata, canopy, sub-canopy, shrub layers, herbaceous layers, lianas and epiphytes	Humid to Hyperhumid Pluvial and Humid Pluviseasonal	Lowland, Montane and Upper Montane belts / Amazonian, Tropical Andean (N. & C.), Atlantic Brazil, Guyanean	**Ferralsols, Acrisols, Ultisols,** Umbrisols
4. Evergreen seasonal forest and woodland	Tall to medium or low-high forests and woodlands with foliage which is partially lost continuously, although with a maximum loss in dry season, but simultaneously regenerates it in moderately short time so the foliage looks green all year. (*Seasonal rainforest*, *Seasonal Andean Polylepis woodland*)	Humid to subhumid Pluviseasonal	Lowland, Montane and Upper Montane belts / Amazonian, Tropical Andean, Venezuelan, Atlantic and central Brazil, Guyanean	**Ferralsols,** Acrisols, Umbrisols
5. Evergreen seasonal sclerophyllous-woodland	Dense to open low woodlands with notoriously sclerophyllous or chartaceous perennial to semi-persistent foliage (*Cerrado* –on poor and acidic soils developed on laterite substrates–, Amazonian *Campinarana* –on white quartzitic sands–). The Cerrado is a successional complex (vegetation series) whose climax vegetation is sclerophyllous woodland. It includes: *Cerradão* (dense woodland), *Cerrado* (open woodland), *Campo Cerrado* (bush savanna) and *Campo limpo* (herbaceous savanna)	Humid to subhumid Pluviseasonal	Lowland belt / Central Brazil, E Bolivia, NE Paraguay (*Cerrado*); and Central-Southern Amazonia (*Amazonian Campinarana*)	**Ferralsols, Plinthosols,** Planosols, Tropical Podzols
6. Deciduous forest and woodland	Medium-high forests and woodlands with foliage which is fully or almost fully lost (deciduous to semideciduous) during the dry season (*Seasonally dry forests & woodlands*). Generally, with abundant vines and climbers	Subhumid Pluviseasonal and Dry Xeric	Lowland and Montane belts / Venezuelan, Tropical Andean, Central and NE Brazil, Northern Chaco	**Ferralsols, Cambisols,** Luvisols
7. Deciduous thorn woodland and shrubland	Dense intricate to open low woodlands and shrublands with wholly or almost *deciduous*, predominantly microfoliate leaves and/or many thorns on branches and stems, as well as cacti (*Guajira*, Brazilian *Caatinga*, *Chaco*)	Dry Xeric	Lowland and Montane belts / Venezuelan, N. Colombian, NE Brazil, Tropical Andean, Gran Chaco (Bolivia, Argentina, Paraguay)	**Luvisols, Cambisols** Solonetzs, Vertisols
8. Xeromorphic shrubland and thicket (semidesert)	Semi-dense to open and sparse, low xeromorphic shrublands and thickets with predominantly microfoliate and/or resinous leaves and often with many cacti and other succulent plants (*Guajira*, *Caatinga*, *Chaco*, Central-Southern Dry *Puna*: Andean *Altiplano*)	Semiarid Xeric (semidesertic)	Lowland, Montane and Upper Montane belts / Venezuelan, N. Colombian, NE Brazil, Central-Southern Tropical Andean, Gran Chaco (Bolivia, Argentina, Paraguay)	**Regosols,** Leptosols, Luvisols

Formation	Structure and foliage phenology	Bioclimate	Altitudinal belt/ Geographical distribution	Soils
9. Desert open vegetation	Low and sparse extremely xeromorphic thickets with therophytes and several succulents. In ecological situations such as temporary streams, the desert may include linear dense to sparse formations of woody phreatophytes. (*Atacama Puna*, *Argentina Monte*, *Central Chilean Desert*, *Peruvian montane desert*)	Arid Desertic	Lowland, Montane, Upper Montane and High montane belts. Southern Tropical Andean	**Regosols,** Leptosols
10. Non vegetated hyperdesert	Mountainous reliefs and plains devoid of superior vegetation, except for some populations of extreme xeromorphic or phreatophytic plants that can grow dispersedly in beds of ravines or occasional streams. In ecological situations such as seasonal streams and rivers, the desert may include linear dense to sparse formations of riparian shrubby or arboreal vegetation. (Atacama Desert, Peruvian Desert)	Hyperarid Desertic	Lowland and Montane. Pacific coastal and hilly deserts in extreme south-western Ecuador, western Perú and north-central western Chile	**Regosols, Leptosols**
11. Foggy coastal hyperdesert	Succulent xeromorphic vegetation foggy-dependent on coastal areas of the Pacific Chilean-Peruvian Hyperdesert, locally named as "Lomas": *Tillandsia* Lomas and Succulent *Eulychnia* Lomas. (Atacama Desert, Peruvian Desert)	Hyperarid Desertic	Lowland. Coastal Pacific areas from northern Perú to central Chile	**Arenosols, Leptosols**
12. Flooded forest and woodland	Tall or medium-high dense and diverse forests and woodlands with perennial or semi-perennial foliage, that are flooded seasonally or permanently due to rainfall or river overflow (*Várzea*, *Igapó*, *Bañados chaqueños*)	Pluvial, Pluviseasonal and Xeric	Lowland and Montane belts / Widely distributed	**Gleysols, Fluvisols,** Stagnosols, Vertisols
13. Mangroves	Low or medium high forest & woodland with coastal distribution and affected by both, tidal sea water and fresh water from the mouth of rivers. Typically, on substrates with acidic iron sulfates (jarosite and natrojarosite)	Pluvial, Pluviseasonal and Xeric	Coastal lowlands	**Fluvisols tidalic thionic,** Planosols thionic
14. Flooded savanna	Tropical tall-grasslands (graminoid and cyperoid) with or without open coverage of palms, shrubs and trees patches, that are flooded seasonally (for 4 to 7 months on average), or permanently, due to rainfall and/or river overflow (*Venezuelan-Colombian Llanos*, *Beni – Llanos de Moxos–*, *Gran Pantanal*)	Pluvial and Pluviseasonal	Lowland belt / S. Venezuela, E. Colombia, E. Bolivia, SW Brazil	**Planosols,** Stagnosols, Gelysols
15. Non flooded savanna	Tropical grasslands on well-drained soils. With or without open coverage of palms, shrubs and trees patches. Often as secondary formation. Only represents the potential natural vegetation on unfavorable substrates and soils	Pluviseasonal	Widely distributed in the Neotropical lowlands and montane belts	Ferralsols, Acrisols, Cambisols, Luvisols, Fluvisols, Regosols, Leptosols
16. Anthropic and Cultural Vegetation (Anthromes)	Landscapes largely dominated by vegetation types cultivated or strongly conditioned by man, including agricultural biomes (woody and or herbaceous crops, cultivated pastures, as well as irrigated or rain-fed agriculture). Livestock extensive areas, and the natural seral vegetation that colonizes substrates of anthropogenic origin in urban-industrial ecosystems, such as streets, roadsides, parks and gardens, urban wastelands, mining and industrial waste, dumps and abandoned or fallow crops	Pluvial, Pluviseasonal, Xeric, Desertic, Hyperdesertic	Widely distributed in the Neotropical lowlands, montane, upper montane and high- montane belts	Anthrosols, Technosols, Regosols, Fluvisols, Vertisols, Chernozems

Application to the Neotropics

We used the Neotropical region for the initial development and testing of our proposal. This application is primarily based on the vegetation classification work and maps of Navarro and Maldonado (2002), Navarro and Ferreira (2007), and Navarro (2011). The Neotropics extends southward from southern North America to Central America and north-central South America. We follow the criteria of Rivas-Martínez (1997) and Rivas-Martínez et al. (1999, 2011b), who recognize the Neotropical-Austro-American kingdom, and within it, the Neotropical sub-kingdom whose northern limit is located towards 33°N latitude in southwestern USA (California, Texas, Arizona) and towards 27°S in southeast Texas and Florida. Tropical (warm) deserts are included in this concept. In South America, the border with the Austro-American sub-kingdom runs approximately along the 30°S latitude line in northern Uruguay, southern Paraguay, northern Argentina and northern Chile.

All this area, from the lowlands to the high mountains, has a Tropical macrobioclimate (Rivas-Martínez et al. 2011a) and is possibly one of the most biodiverse areas in the world. The Americas, with over 125,000 species, represent 33% of the estimated number of vascular plants worldwide. Specifically, South America is home to 6% more vascular plants than the whole of Africa, which has an area twice its size (Antonelli and Sanmartín 2011; Ulloa et al. 2017). It is worth noting that the main feature of the Tropical macrobioclimate is that, if there is a seasonal difference in rainfall throughout the year, then the wettest and warmest periods coincide (Troll 1961; Bailey 1989). This phenomenon is constant in both the lowlands and the mountains. It is also important to highlight that in the tropical mountains the value of the daily thermal range exceeds the value of the annual thermal range (Troll 1961). These two main factors together condition the structure, composition, differentiation and functioning of tropical biomes and set them apart (Rivas-Martínez et al. 2011a) from other biomes in adjacent extratropical macrobioclimates with opposing annual rainfall and temperature rhythms (Mediterranean macrobioclimate with summer hot dryness), or which do not follow differentiated or pronounced annual rainfall patterns (Temperate oceanic bioclimate). As noted above, in our proposal and based on Rivas-Martínez et al. (2011a), the desert bioclimate is not a single bioclimate since it is present in areas with differing macrobioclimates and consequent different floristic assemblages.

All the possible tropical ecological altitudinal levels (= bioclimatic belts or thermotypes) occur in the Neotropics. Bioclimatic belts are nomenclaturally and numerically delimited by thermicity values (Rivas-Martínez et al. 2011a). These altitudinal levels use terms widely adopted in Latin America (Josse et al. 2009) for the tropical Andes (Venezuela south to Northern Argentina and Chile), and include, in an operative, parsimonious and simplified way, three main altitudinal belts: Lowland, Montane, and High-montane (High Andean). The lowland belt (0–1,000 m) occupies the lowland plains, foothills and lower areas of the neotropical mountain ranges, and corresponds to infratropical and thermotropical Rivas-Martínez thermotypes. The montane belt (1,000–3,900 m) is widely distributed in zones with intermediate to medium high altitudes in the Andes, and in the mountain ranges of southern Venezuela, Tepuís and north and south-eastern Brazil, and corresponds to mesotropical and supratropical Rivas-Martínez thermotypes. The high-montane belt (>3,900 m) occurs mainly in the Andes, and corresponds to Rivas-Martínez's orotropical, cryorotropical and gelid thermotypes.

All the tropical bioclimates are recognized in the Neotropics (Rivas-Martínez et al. 2011a, 2011b). They include the following bioclimates: Pluvial, Pluviseasonal, Xeric, Desertic and Hyperdesertic (Table 2). The great climate diversity of the Neotropics also comprises the whole variation of ombrotypes, from the ultra-hyper-arid to the ultra-hyper-humid. Both the bioclimate and ombrotype show a close correlation with the structure of the Neotropical plant formations, and a close relationship can also be seen between most formations and the large groups of zonal soils recognized in the FAO world classification system (Chesworth et al. 2008; Gardi et al. 2015; see Table 2).

Sixteen plant formations are identified in the Neotropics (Table 2), and serve as the cornerstone of the biomes we recognize in this biogeographical region. Four of these formations correspond exclusively to the lowland belt, four to the lowland and montane belts, one to the high-montane belt, while the others are distributed in more than two ecological belts. The tropical cryomorphic open-vegetation occurs in a humid climate in the high-montane belt (Figure 4A). Andean mountains are also characterized by a tropical bunch-grassland which consists of graminoid grasslands growing in pluviseasonal-pluvial bioclimates in the high-montane belt (Figure 4B).

The tropical pluvial and/or pluviseasonal evergreen forest extends from the lowland to the high-montane belt under a humid to hyperhumid climate (Figure 4C). The tropical evergreen seasonal forest corresponds to the distinctive forests and woodlands whose foliage is partially and continuously lost and regenerating. It occurs in humid to subhumid climates from the lowland to high-montane belt (Figure 4D). The tropical lowland seasonal-evergreen sclerophyllous-woodland consists of woodland with perennial or semi-persistent foliage developing under a subhumid to humid climate in the lowland belt (Figure 4E, F). The tropical pluviseasonal and xeric dry-deciduous forest and woodland occur in a subhumid to dry climate from the Lowland to the Montane belt.

In the Neotropics, drier biomes are found from the lowland to the high-montane belt under an ultra-hyper-arid to dry climate. Specifically, the tropical xeric dry-deciduous thorn woodland and shrubland extends under a dry climate in the lowland and montane belts (Figure 5A). The tropical xeric shrubland and thicket occurs under a semiarid climate (semidesert) from the lowland to the high-montane belt (Figure 5B; Table 1, 2). Tropical desertic open vegetation consists mainly of xeromorphic thickets occurring under an arid climate from the lowland to the high-montane belt (Figure 5C). The tropical hyperdesertic non-vegetated is found under a hyperarid to ultra-hyperarid climate from the lowland to the montane belt (Figure 5D). The tropical foggy coastal hyperdesert, characterized by fog-dependent succulent xeromorphic vegetation, is found on coastal areas of the Pacific. Biomes on wet soils are typically restricted to azonal conditions. Specifically, the tropical flooded forest and woodland is widely distributed on seasonally or permanently flooded soils (Figure 5E). The mangroves formation is restricted to tropical coastal tidal and deltaic environments. The tropical flooded savanna is widely distributed (Figure 2D), whereas the tropical non-flooded savanna extends throughout the neotropical lowland and montane belts. Azonal tropical anthropic and cultural vegetation is widely distributed in the Neotropics (Figure 3). This anthrome is found in rural and urban industrial ecosystems characterized by the anthropic influence. They include such diverse systems as crops, groves, pastures, cities, mines, quarries and dumps.

Discussion

In general, publications referring to biomes or related concepts can be grouped into biogeographic, ecoregional, ecological and functional approaches (Table 3). Biogeographic classifications and maps are diverse and mainly based on the distribution patterns of plants and/or animal species (Cabrera and Willink 1973; Udvardy 1975; Takhtajan 1986; Morrone 2001); and on integrated criteria that include the bioclimate, plant communities and geophysical factors (Rivas-Martínez et al. 2011b). The nomenclature of these biogeographic units is heterogeneous and their cartographic delimitation is difficult to replicate as it is mainly based on expert knowledge. Our proposal considers the higher scale biogeographic levels such as region and province as complementary criteria in the delimitation of biomes and regional biomes. EcoVeg (Faber-Langendoen et al. 2014) implicitly uses biogeographic region and biogeographic province at the division and macrogroup levels of their classification respectively. NatureServe (Josse et al. 2003) also includes the biogeographic province level in the characterization of ecological systems.

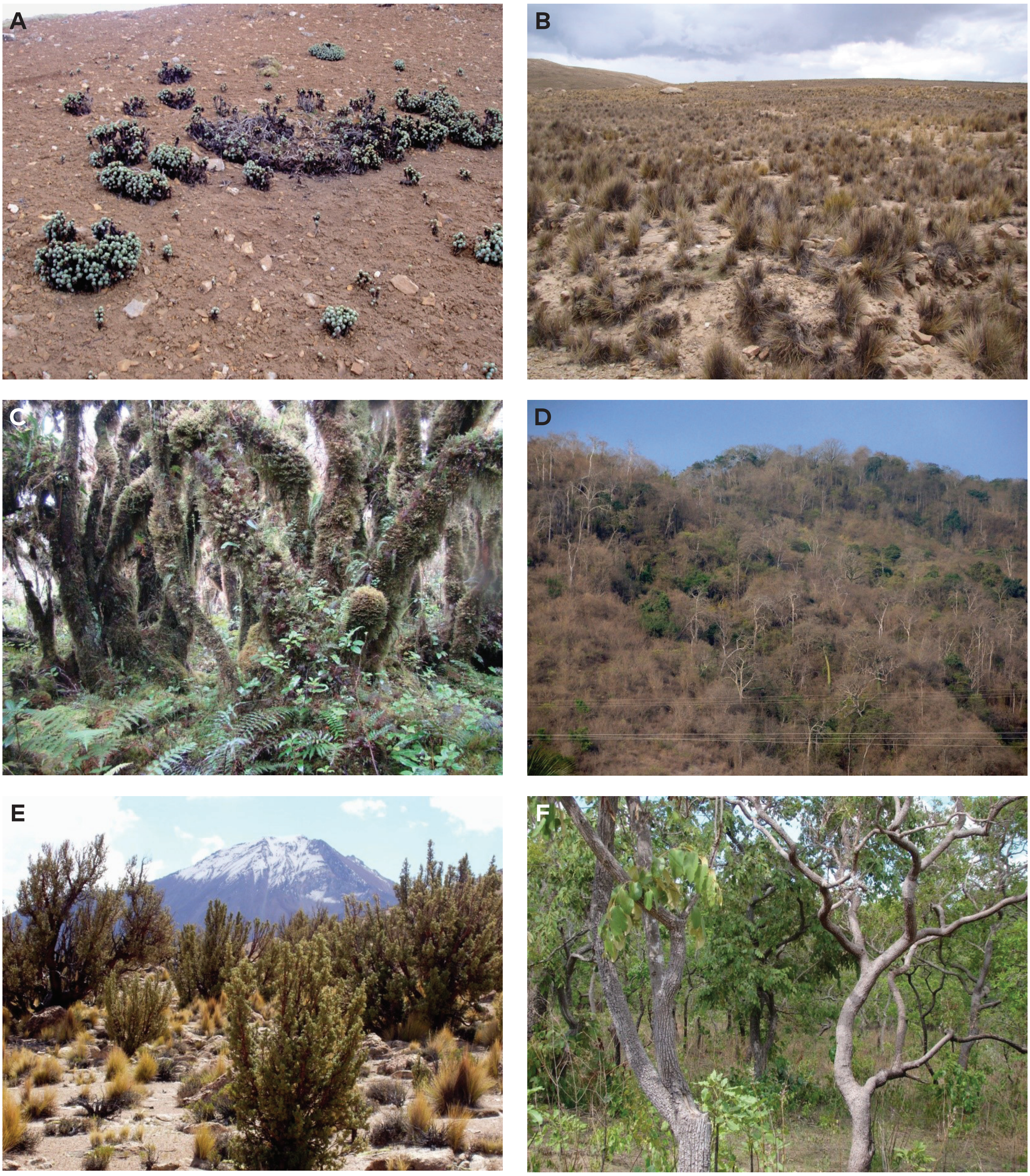

Figure 4. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Tropical high-montane cryomorphic open vegetation with *Xenophyllum dactilophyllum* (Bolivia, La Paz, Cordillera Real, 4900 m); **B.** Tropical high-montane seasonal bunch-grassland of *Festuca orthophylla* (Cordillera de Morococala, 4100 m); **C.** Tropical montane and high-montane evergreen woodland, *Weinmannia fagaroides* community (Andean Yungas, Bolivia, Cochabamba, 3000 m); **D.** Tropical lowland deciduous forest and woodland (Coastal central Ecuador, 220 m); **E.** Tropical high montane evergreen seasonal sclerophyllous-woodland of *Polylepis tarapacana* (Bolivian Andes, western Oruro, 4400 m); **F.** Tropical lowland evergreen seasonal sclerophyllous-woodland (Bolivian Cerrado, Santa Cruz, Chiquitanía, 460 m). (Photos: Gonzalo Navarro).

Ecoregional approaches (Bailey 1996a, 1996b; Olson et al. 2001; Dinnerstein et al. 2005, 2017) have produced world maps that are widely used; however, the cartographic delimitation of ecoregions is also fundamentally based on expert knowledge and is difficult to replicate (Table 3). Furthermore, the ecoregion concept and its nomenclature are not yet consistently defined and there are several overlaps between criteria such as vegetation, biogeography,

Figure 5. Representative examples of biomes from South America, showing their classification and nomenclature according to the proposal of this work. **A.** Tropical lowland deciduous thorn-woodland and shrubland (central coastal Ecuador, 120 m); **B.** Tropical high montane xeromorphic shrubland and thicket, *Trichocereus atacamensis-Fabiana densa* community (Oruro, Bolivia 3700 m); **C.** Tropical high-montane desert with *Acantholippia punensis-Atriplex imbricata* community (northern piedmont of Ollagüe Volcano, Atacama Puna, Potosí, Bolivia, 3820 m); **D.** Tropical low montane hyperdesert (Lima, Perú, 760 m); **E.** Tropical lowland evergreen flooded forest (Amazonian Várzea, Río Beni, Pando, Bolivia, 120 m). (Photos: Gonzalo Navarro).

climate and environmental factors. The recent IUCN global proposal (Keith et al. 2020) is cartographically based on Olson et al. (2001), and its approach is explicitly functional, with a focus on the traits and ecological drivers of biomes. Many of these traits and ecological drivers can be derived directly or indirectly from the interactions between climate and vegetation. The IUCN biomes are roughly equivalent to our zonal biomes; the typology of this IUCN system is discussed in detail by the authors, but so far there is a lack of explicit standard nomenclatural protocol to systematically name the ecosystem functional group (EFG), which may be equivalent to our biomes, although the difference in delimitation and nomenclatural criteria makes this comparison uncertain.

Ecological Systems of NatureServe (Josse et al. 2003) differs from our proposal in terms of bioclimatic criteria and the dynamic-successional concept of ecosystem, and in the scale of application. In general, ecological systems are partially equivalent to our regional biomes, and related ecological systems ensembles are roughly equivalent to our biomes. Ecological land units (Sayre et al. 2014, 2015) are conceptually related to ecological systems, and their cartographic expression produces units with a finer level of detail than what is often accepted for biomes. These units are based on the geospatial superposition of several objective physical and ecological criteria (elevation, landforms, geology, bioclimate, land cover), thus conferring the advantage of repeatability. The results are a global map with a detailed map of terrestrial ecological units (ELUs) for South America and the world (Sayre et al. 2014, 2015); however, unlike ecoregional approaches, cartographic units have a much finer scale that goes beyond the required and generally accepted scale for biomes. Our work largely agrees with Sayre et al. (2014) in the general hierarchy of land units.

Functional approaches use geospatial variables, methodologies and models (whose main inputs are spatial vegetation layers or the distributions of several species attributes) to address the cartographic delimitation of biomes. The correspondence between the resulting functional units and known biogeographic or biome units, which are based on more structural characters, has in many cases failed. Paruelo et al. (2001) modelled the ecosystem functional types (EFT) for Temperate South America based on the seasonal dynamics of the normalized difference vegetation index (NDVI) from NOAA/AVHRR satellites, which reflect similar seasonal patterns of biomass or productivity, and they did not find a clear correspondence between EFT and phytogeographical provinces. Conradi et al. (2020) used range modelling of plant species to reveal spatial attractors for different growth-form assemblages that define biomes but contain no ecological hypothesis of why these growth forms co-occur and how they interact with one another. Echeverría-Londoño et al. (2019) examined distributions of functional diversity of plant species across the biomes of North and South America, finding that widespread species in any biome tend to be functionally similar whereas the most functionally distinctive species are restricted in their distribution. These authors proposed a functional diversity biome classification for the Americas and their equivalence with the biome classification of Olson et al. (2001).

Table 3. A comparison between the key criteria in our approach and some other related proposals. The weaknesses and strengths of each proposal can be derived from this comparison.

	The present integrated approach	**Ecoregional approaches** Bailey (1996a, 1996b), Olson et al. (2011), [Keith et al. (2020) – maps based on ecoregions]	**Eco-vegetational approaches** IVC-EcoVeg (Faber-Langendoen et al. 2014, 2017, 2020)	**Ecosystem based approaches**: ELUs (Sayre et al. 2015), Ecological Systems (Josse et al. 2003)
Tentative equivalences between several types of units	Zonobiome (macrobiome) Biome Regional biome	Biome Ecoregion Ecosystem functional type (EFT)	Formation Division Macrogroup or group	Uncertain equivalences with the former, as ecological land units (ELUs) have a finer scale and are not comparable with biomes. However, several ecological systems defined for Latin America may correspond to regional or subregional biomes, and groups of related ecological systems may correspond to our biome concept.
Standardized nomenclatural protocol for naming units	Systematic use of the same sequence of naming criteria and in this order: macrobioclimate, plant formation, bioclimatic level, biogeography, which apply according to the macrobiome-biome-regional biome levels. E.g.: Step 1. Macrobiome (zonal biome): *Tropical evergreen forest* Step 2. Biome: *Tropical montane evergreen forest* Step 3. Regional biome: *Tropical montane Andean Yungas evergreen forest*.	Heterogeneous nomenclature with no consistency or homogeneity in the GFS names assigned. Detailed principles designed for a global ecosystem typology, but lacking an objective, consistent and explicit protocol or keys to properly name the units. As the authors say: "Names of functional groups are vernacular — we adopt names and descriptors frequently applied in the literature that reflect key functional features. A vernacular (rather than systematic) approach" (Keith et al 2020). e.g. T4.3 Hummock savannas T2.1 Boreal and temperate montane forests and woodlands T5.3 Sclerophyllous deserts and semi-deserts T6.5 Tropical alpine meadows and shrublands	Use of a similar and consistent sequence of criteria to name the units: Formation criteria: macrobioclimate-plant formation-bioclimatic level (not always applied) Division criteria: biogeography (ca. region level) Macrogroup-group criteria: Biogeography (ca. province level), Floristic composition However, biogeographical names are not standardized or somewhat ambiguous: biogeographical names mixed with purely geographic or plant names at the same hierarchical level. e.g. D227 1. A.2.Ek Brazilian-Parana lowland humid forest: M597 Cerrado humid forest M595 Brazilian Atlantic forest D006 1. B.1.Na Southeastern North American forest & woodland: M007 Longleaf pine woodland US M885 South-eastern coastal plain Evergreen oak – mixed hardwood	Ecological Systems use somewhat inconsistent nomenclature without a standardized protocol. ELUs cartographic unit labels follow the same more or less consistent descriptors: bioclimate, land form, lithology, Coberture. E.g.: "Cool moist mountains on metamorphic rock with mostly deciduous forest" "Cold wet mountains on acidic volcanic rocks with mostly needleleaf/evergreen forest"

	The present integrated approach	**Ecoregional approaches** Bailey (1996a, 1996b), Olson et al. (2011), [Keith et al. (2020) – maps based on ecoregions]	**Eco-vegetational approaches** IVC-EcoVeg (Faber-Langendoen et al. 2014, 2017, 2020)	**Ecosystem based approaches**: ELUs (Sayre et al. 2015), Ecological Systems (Josse et al. 2003)
Predictive capacity and repeatability	Viable: based on numerical bioclimatic indexes and bioclimatic world maps	Difficult to standardize and repeat, as the units and their mapping are based on expert opinion. However, the IUCN approach includes detailed descriptive definition criteria.	Viable: based on explicit criteria to define the proposed units. However, there is some overlap and repetition of the defining criteria. Some difficulties for extrapolating outside the Americas	Viable: based on explicit definition criteria applied with an accurate geospatial methodology for mapping detailed units.
Consistency and propriety in the use of clear descriptors and classifiers	Consistent use of the same sequence of criteria and in the same order: *macrobioclimate*, *plant formation*, *bioclimatic belt*, *biogeography*, which apply according to the macrobiome-biome-regional biome levels. Structural consideration of biomes	Ecofunctional explicit approach Key assembly gradients: *water deficit*, *seasonality*, *temperature*, *nutrient deficiency*, *fire activity and herbivory*. (Keith et al. 2020) Mixing and overlapping of the descriptors and classifiers used: some overlaps between the vegetation structure and the bioclimate: e.g., is "humid" a vegetation term or a climate term? Do the terms "desert" and "semi-desert" refer to the physiognomy of the vegetation? or the climate? or both?	Use of a similar and consistent sequence of criteria: Formation: *macrobioclimate-plant formation-bioclimatic level (not always applied)* Division: *biogeography* (*ca. region level*) Macrogroup-group: *Biogeography (ca. province level), Floristic composition* Somewhat inconsistently applied names for descriptors and nomenclature. e.g. Mixed forest Hardwood forest & woodland	ELUs use the same criteria applied to design mapping units. Input layers: *elevation*, *landforms*, *geology*, *bioclimate*, *land cover*. Structural consideration of ecosystems: "Ecosystems can therefore be spatially delineated by mapping and integrating these structural components in geographic space" (Sayre et al. 2015).
Proper definition of the concepts used related to plant formation names	Clear and consistently applied plant formation concepts, based on the same sequence of *growth forms* and *phenological leaf persistency*. Repeatable terminology for growth forms and foliage persistency, largely based on Ellenberg & Mueller-Dombois (1967), Rivas-Martínez (2005) and EcoVeg (2014). The criterion of leaf phenology is easier to apply consistently than the commonly applied terms of humidity, which alternate or superimpose "climate humidity" with "vegetation humidity": the denomination "evergreen" is preferable to "humid" and "rainforest", as evergreen implies a pluvial bioclimate.	Glossary definition of several terms used in the EFG descriptions. The terminology of plant formations is not standardized or well-defined and delimited. Some examples: - What is the difference and clear delimitation between *steppes, grasslands and savannas?* - Some relevant Neotropical formations are not represented, e.g., the extensive woodlands and wooded or arboreal savannas of the Cerrado biome in South America (Brazil, Bolivia, Paraguay). - There is no climatic qualifier for savannas, but the proper concept of savanna is only tropical. - Inappropriate use of the term "alpine" for tropical high-montane grasslands.	Based on dominant plant growth forms. Detailed descriptions of plant growth forms, however, plant formation names remain non-standardized. e.g. Overlap between the vegetation structure and the bioclimate: Is "humid" a vegetation or a climatic term?	Global ELUs use the following land cover classes and class mosaics: *bare areas, artificial surfaces and urban areas, shrubland, closed to open, broadleaved or needle-leaved, evergreen or deciduous, herbaceous vegetation, closed to open, grassland, savannas or lichens/mosses* *mosaic forest or shrubland with grassland mosaic grassland with forest or shrubland mosaic vegetation (grassland/shrubland/forest) with cropland* South American ELUs are based on LAC NatureServe denominations of ecological systems with somewhat poorly defined and delimited or inconsistently applied plant formation names.
Proper definition of the concepts used related to bioclimates	Based on the World Bioclimatic System (Rivas-Martínez et al. 2011) that defines with numerical indexes: *thermotype, ombrotype, bioclimate, bioclimatic levels*.	*Tropical, Subtropical, Temperate, Cool temperate, Boreal, Polar, Lowland, Montane, High-montane*: there is no clear delimitation and conceptual definition for these terms, and they do not explicitly follow any bioclimatic system. Terms are not consistently applied in all EFGs: e.g. only "cool" deserts? The Mediterranean bioclimate is subsumed or immersed in the Temperate bioclimate which introduces uncertainty in several EFGs	Somewhat poorly defined and delimited or confusingly applied climatic categories e.g. Dry/Seasonal dry Temperate/Mediterranean Semi-desert/Hyperdesert Cool/warm desert	Ecological System partially uses the World Bioclimatic System of Rivas-Martínez (only ombrotypes). Global ELUs use simplified climate categories: *Arctic* *Very Cold Very Wet* *Very Cold Wet* *Very Cold Moist* *Very Cold Semi-Dry* *Very Cold Dry* *Very Cold Very Dry* South American ELUs use global meteorological raster data and formulas developed by the Rivas-Martinez bioclimatic system to delineate isobioclimate regions
Dynamic-successional character of the vegetation	Successional approach: we postulate that biome is defined by the natural potential vegetation, and that the successional states are considered (at these scales) to be included in the potential natural vegetation.	Actualistic approaches: successional states are not considered to be immersed in the potential vegetation, but rather constitute different units: e.g. (EcoVeg and Ecological Systems: "M515 Caribbean-Mesoamerican Lowland Ruderal Grassland & Shrubland"; "M123 Eastern North American Ruderal Grassland & Shrubland"; "M310 Southeastern North American Ruderal Flooded & Swamp Forest". IUCN (Keith et al. 2020) "T7: Intensive Land Use Biome" are roughly equivalent to anthromes.		

	The present integrated approach	**Ecoregional approaches** Bailey (1996a, 1996b), Olson et al. (2011), [Keith et al. (2020) – maps based on ecoregions]	**Eco-vegetational approaches** IVC-EcoVeg (Faber-Langendoen et al. 2014, 2017, 2020)	**Ecosystem based approaches**: ELUs (Sayre et al. 2015), Ecological Systems (Josse et al. 2003)
Dynamic-successional character of the vegetation	However, in highly transformed landscapes, when the dominant landscape matrix is extensively disturbed ecosystems, we still consider them as anthromes (anthro-biomes) (Ellis 2020).		Not explicit	
Ecological landscape framework to address biomes or units	We introduce a geographic-ecological framework to qualify biomes, through the concept of geoseries (geocatena, geosigmetum) that is applicable to regional biomes and biomes.	Not explicit	Not explicit	Not explicit Ecological Systems: "spatially co-occurring assemblages of vegetation types sharing a common underlying substrate, ecological process or gradient" (Josse et al. 2003)
Ecological or bioclimatic levels	We consider the altitudinal zonation as a characteristic of each biome, and one that serves to delimit it. Altitudinal levels are in accordance with the thermicity index values of Rivas-Martínez et al. (2011). We performed an operational simplification of the detailed Rivas-Martínez bioclimatic levels, based on Josse et al. (2009), in order to make them easier to apply at the biome scale.	Altitudinal belts are underrepresented (only lowland/ montane), and their delimitation criteria are not explicit.	There is no standardized use of the nomenclature of the elevation; the delimitation criteria are not explicit. Altitudinal levels are more detailed in South American units (lowland, low-montane, montane, upper montane, high-montane) than in North American units (lowland, lower montane, montane, high montane, subalpine). The criteria delimiting altitudinal levels are not explicit.	They accept elevation classes based on published literature for South American ecosystems: 0–500 m, 500–1000 m, 1000–2000 m, 2000–3300 m, and > 3300 m
Eco-functional approach	We stated that a bioclimate-based structural approach is ecofunctional in nature since the limiting climate variables condition and determine the appearance and structural adaptations of the vegetation, and the soil complexes on which it develops, thus behaving as ecosystem drivers.	Ecofunctional explicit approach. However, several IUCN ecofunctional drivers, key assembly gradients or properties described in the EFGs can be derived consistently from the respective bioclimates, in a more parsimonious way: at least water deficit, temperature and thermal seasonality in a direct way, and indirectly, nutrient deficiency, fire activity and herbivory.	Not explicit	

Conclusions

We propose a hierarchical biome classification and nomenclature in three steps. In the first step, macrobiomes or zonobiomes are defined by macrobioclimate and plant formation. In the second step, biomes are defined by bioclimatic belt and bioclimate. Finally, in a third step, regional biomes incorporate the biogeographic typology at the region level, following Rivas-Martínez et al. (2011b). Additionally, we include landscape qualifiers to define biomes and regional biomes. The overall combination of these traits enables a comprehensive and hierarchical nomenclature that offers a predictive system of global value that can be widely understood and applied. These three biome classification levels are also roughly and preliminarily equivalents to the formation, division and macrogroup levels of the International Vegetation Classification (IVC, Faber-Langendoen et al. 2014).

The main novelties or contributions of our proposal can be summarized as follows:

1. Importance of using the same nomenclatural sequence criteria to define and name biomes, namely macrobioclimate-altitudinal belt-plant formation -[biogeography]-[biogeophysical: FAO GSR (soils), hydrological variables].
2. Clear and consistently applied concepts of plant formation, based on the same sequence order of growth forms and phenological leaf or foliage persistency, largely based on Ellenberg and Mueller-Dombois (1967), Rivas-Martínez (2005) and EcoVeg (2014).
3. Standardized use of bioclimate variables and concepts based on the World Bioclimatic System (Rivas-Martínez et al. 2011a): thermotype, ombrotype, bioclimate, as well as an operational use of bioclimatic belts based on Josse et al. (2009).
4. Possibility of mapping and extrapolation of biomes based on both climate data and bioclimatic indexes.
5. Consideration of a dynamic-successional character of the vegetation in the definition of the biome.
6. An ecological landscape framework, that treats the biome as a macrogeosigmetum (macrogeoseries) which occupies a territory with a homogeneous bioclimate and biogeography.
7. A bioclimate-based proposal that serves as an eco-functional approach since the limiting climate variables condition and determines the appearance and structural adaptations of the vegetation, its biomass, and the soil complexes on which it develops, thus behaving as ecosystem drivers.

Author contributions

G.N. designed the survey and provided the core data information. J.A.M. contributed substantially to the writing and took part in shaping the proposal.

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