

## GLOBAL BIOMES AND ECOZONES – CONCEPTUAL AND SPATIAL COMMUNALITIES AND DISCREPANCIES

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With 6 figures, 2 tables and 3 appendices

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**Summary:** Various facets of global changes and related problems and challenges are asking for sound impact assessments and corresponding coping strategies. The human impact on nature is a major driver of biodiversity loss and restricted ecosystem functioning and services. Assessing such global changes is often done by using biomes as benchmarks. However, even if the wording and terminology seem common sense ('tropical rain forest', 'steppe', 'boreal forest') global biome units and maps deviate in many ways. This is well justified by their individual intention, expert opinions, disciplinary background, and methodology of creation. A closer look reveals linkages between spatial accordance and common origin in climate classifications and maps. Their original influence, however, is rarely evident. In consequence, it is difficult if not impossible for users to realize and understand differences in these global maps. Furthermore, it is difficult to accept the fact that there is no common standard for global biomes. Even more surprising is the fact that some approaches are uncritically taken for common sense and are perpetuated over decades. This study aims to review established global biome concepts. Regions that are consistently assigned to comparable types of biomes shall be detected and also regions where ambiguity exists. For this purpose, we shortly review the history of existing concepts and the generic relations between them. Biomes, ecozones and climate classifications are considered. We digitized the most prominent biome classifications. Spatial match and mismatch between concepts were analyzed globally. We detect areas of spatial agreement and regions with ambiguous classifications. A clustering approach including 287 individual biomes originating from 12 established global biome concepts and their classifications/units revealed 12 terrestrial biome clusters among which 8 can be assigned to terrestrial ecological units. One cluster on ice caps adds to this. And finally, 3 clusters represent rather transition zones (ecotones), high mountain plateaus or are of minor areal extent. The spatial arrangement of these emerging clusters is displayed on a global map. Additionally, regions of uncertainty related to class assignment were identified. Those primarily occur in the vicinity of mountainous regions. The findings of this study should be seen as a work in progress and as a basis for further optimization of global biome concepts.

**Zusammenfassung:** Die vielfältigen Facetten des globalen Wandels, sowie die damit zusammenhängenden Herausforderungen erfordern in wachsendem Umfang fundierte Folgenabschätzungen und entsprechende Anpassungsstrategien. Die menschliche Beeinflussung der Natur ist eine Hauptursache von Biodiversitätsverlust und eingeschränkten Ökosystemfunktionen und -dienstleistungen. Die globalen Biome dienen häufig als Referenz-Systeme für diesen Einfluss. Selbst wenn allgemein verwendete Begrifflichkeiten wie „Tropischer Regenwald“, „Steppe“ oder „Borealer Wald“ verständlich sind, so finden sich doch vielfache Abwandlungen und räumliche Abweichungen hierzu. Solche Abweichungen sind in individuellen Intentionen, Expertenmeinungen, disziplinärem Hintergrund, und methodischem Vorgehen begründet. Bei genauerer Betrachtung, finden sich allerdings auch Übereinstimmungen, welche sich lediglich aus ursprünglich gemeinsamen Bezugssystemen, wie Klimaklassifikationen und -karten, ergeben. Deren Beitrag zur Abgrenzung aktueller, beziehungsweise fortgeschriebener Karten ist jedoch selten evident. Als Folge ist es für die Nutzer solcher globaler Karten schwer, wenn nicht unmöglich, Unterschiede in diesen globalen Kartenwerken zu erkennen und zu verstehen. Es fällt schwer zu verstehen, dass aktuell kein Standard für globale Biome existiert und darüberhinaus einzelne Konzepte oft unkritisch übernommen und über Jahrzehnte unverändert fortgeschrieben werden. Ziel dieser Studie ist ein Vergleich etablierter Konzepte und die Identifikation von Ähnlichkeiten in der klassifizierenden Zuordnung von Raumeinheiten zu Biomen, aber ebenso die Identifikation von Spezifika einzelner Konzepte. Des Weiteren wird die Kennzeichnung von Gebieten mit hohen Übereinstimmungen oder abweichenden Zuordnungen zwischen den verschiedenen Biom-Klassifikationen angestrebt. Auf der Grundlage einer eingehenden Literaturanalyse arbeiteten wir den generischen Zusammenhang zwischen Klassifikationen heraus, um eine entsprechende Auswahl von Konzepten zu gewährleisten. Biome, Ökozonen und Klimaklassifikationen werden gleichermaßen berücksichtigt. Für diese Studie wurden globale Karten der bekanntesten Biom-Klassifikationen digitalisiert. Auf dieser Grundlage wurden Korrelationen zwischen den Konzepten berechnet, um Beziehungen zwischen den einzelnen Ansätzen aufzuzeigen. Auf globaler Skala wurde ermittelt, welche Biom-Typen und welche geografischen Regionen übereinstimmend zugeordnet werden. Eine Clusteranalyse 287 individueller Biome aus insgesamt 12 etablierten Biomkonzepten ergab 12 terrestrischen Biom Cluster, von welchen 8 sehr klar terrestrischen ökologischen Einheiten zugeordnet werden können. Ein Cluster betrifft Eisflächen. Weitere 3 Cluster repräsentieren entweder Übergangszonen



(Ökotope), Hochgebirgsplateaus, oder sind von geringer räumlicher Fläche. Die räumliche Verbreitung der emergenten Cluster ist in einer globalen Karte dargestellt. Zusätzlich wurde die Ungewissheit in der Flächenzuordnung visualisiert. Jene Regionen, welche durch eine hohe Unsicherheit der Klassenzuordnung charakterisiert sind, konzentrierten sich vor allem in der Nähe von Gebirgszonen. Die Ergebnisse dieser Studie sollten als Work in Progress auf dem Weg zur weiteren Optimierung globaler Biome Konzepte angesehen werden.

**Keywords:** biodiversity, biogeography, biome shift, biome stability, biosphere, climate change, climate zones, ecosystems, ecozones, evolutionary arenas, global ecology, global reference, global vegetation models

## 1 Introduction

The global perspective on the ecosystems and the biodiversity of the world is becoming increasingly important due to the global nature of environmental changes and is facilitated by access to big data and geo-information technology. Biomes that were considered in the past as one way of describing global ecological patterns are receiving more and more attention as reference systems for studies on global environmental and ecological changes (MONCRIEFF et al. 2016; HOFFMANN et al. 2019), and also for phylogenetic and evolutionary research (PENNINGTON et al. 2004; CRISP 2006; DONOGHUE and EDWARDS 2014, NÜRK et al. 2020; RINGELBERG et al. 2020).

Exploring nature across large spatial scales, however, is not a recent ambition. As early as in Greek antiquity, THEOPHRASTUS assessed the large-scale structures of ecosystems and landscapes (mangroves, Mediterranean forest, deserts, etc.) for the military campaigns of Alexander the Great (BEIERKUHNEIN 2007). In the following centuries, Roman, Arab, and Chinese campaigns extended biogeographical knowledge, but historical evidence and sources are scarce. The period of European colonization enhanced not only the knowledge on land surface distribution but also on the ecological conditions of these lands, even if this was not explicitly formulated.

It was the work of ALEXANDER VON HUMBOLDT that initiated a new era in geoscience. A very modern aspect of his works was how he linked natural vegetation with climatic conditions, but also to typical forms of human land use to modify natural ecosystems. He developed this viewpoint for zonal vegetation and elevational zones.

Already 100 years before RAUNKIAER (1905) established a concept for plant life-forms, HUMBOLDT (1807) attributed characteristic plant forms to vegetation zones pointing out that morphological traits and types of plants are more informative than the 'natural system of botanists' for characterizing vegetation zones. He suggested classifying plants into 14 categories defined by growth form (banana, palm, tree ferns, aloe, pothos, needle-leaved trees, orchid,

mimosa, malva, vine, lily, cactus, cassuarine, and grass) plus mosses, lichens and fungi as additional types. Today we would label these categories as plant functional types. HUMBOLDT was aiming for generality. He was convinced that many things (and processes) are interlinked in natural systems. He was fascinated by emerging vegetation structures beyond individual taxa, which were also of interest for his studies. Although HUMBOLDT expressed the desire to develop a 'physique du monde' (his major publications were in French) his vision remained incomplete (HUMBOLDT 1845–1862). Nevertheless, he paved the way for global ecology.

In the second half of the 19<sup>th</sup>-century geographical knowledge on the spatial distribution and structural components of vegetation developed rapidly. GRISEBACH (1872, 1884/1885) assembled for the first time a global perspective on the vegetation of the world by compiling individual reports and maps. The blank spots on the map slowly disappeared. This work can hardly be praised enough considering historic limitations in scientific knowledge and mobility. Being strongly influenced by ALEXANDER VON HUMBOLDT, GRISEBACH travelled frequently but never left Europe on his excursions.

As a consequence of the impossibility to consider all species and their global distribution, it was vegetation structure, including phenology, taken as a criterion for global patterns. However, most approaches were quite descriptive and there was no common sense about terminology. KERNER VON MARILAUN (1888) criticized the chaotic terminology during this period: he expressed the need to develop clear and quantitative criteria to categorize large units of vegetation. Based on specific plant traits and forms he introduced the term 'formation' to characterize such structural units. His concept strongly promoted classifications of large spatial units of vegetation such as deciduous temperate forests, steppe, or savanna.

SCHIMPER (1898) promoted new insights directed towards global vegetation patterns with his physiological and functional understanding of plant geography. He travelled to the Caribbean, to Venezuela, Chile, Brazil, Sri Lanka, and Java. This personal experience

provided insights into global patterns of zonal vegetation. Among other seminal contributions, he introduced the notion of ‘tropical rain forest’.

In climate geography, KÖPPEN’S (1884, 1931, and continued by GEIGER 1961) deductive concept introduced a global classification of climatic conditions, that are controlling ecological processes and patterns. A whole series of global concepts are based on climatic classifications from different angles (also on THORNTHWAITE 1933). KÖPPEN’S climate-based approach towards a global ecological overview is still successful and widely reflected in biome maps (e.g. WOODWARD et al. 2004, PEEL et al. 2007; BECK et al. 2018). And, in the face of climate change, the interaction between global circulation models (GCMs) and global vegetation models (GVMs) based on plant functional types is experiencing massive attention (e.g. PRENTICE et al. 1992; SITCH et al. 2003; PRENTICE et al. 2007; GONZALEZ et al. 2010).

The term ‘biome’ is derived from bioformation for the entire plant community of a larger area. It was first used by the vegetation scientist FREDERIC E. CLEMENTS (1916), even if he did not clearly define the scope of the subject (MUCINA 2019). Hence, the term ‘biome’ was established earlier than the word ‘ecosystem’ which was introduced into scientific literature by ARTHUR TANSLEY only in 1935. This may sound surprising as we see biomes today as being composed of and characterized by ecosystems. The origin of this notion reflects the fact that biomes are mainly characterized by vegetation. MERRIAM (1892) was definitively ahead of his time when he characterized large-scale life zones for mammals in Northern America. However, this work was taken up with a significant delay. It was CLEMENTS’ (1916) work on successional trajectories and the concept of zonal climax vegetation, representing the climatic conditions of a region, that shaped an entire era of ecological research.

At the same time, VERNADSKY (1926, 1945) coined the term ‘biosphere’ and gave a theoretical framework for global ecology, relating biota to the abiotic environment in a three-dimensional global context but again this work was ignored for many years. During this period, access to information and international knowledge exchange was quite limited. National researchers often worked on their own, restricted by political and linguistic barriers. Regional schools and paradigms evolved and academia was not requested to address societal needs.

In Central Europe, the school of phytosociology dominated phytogeography and vegetation science for decades. This explains why many approaches were restricted to vegetation composition and struc-

ture (e.g. RÜBEL 1930). During the entire 20<sup>th</sup> century, the paradigm of potential natural vegetation (TÜXEN 1956) largely dominated the perception of biomes as hypothetically natural units.

The modern ecological perspective is based on the works of two outstanding scientists: Robert Harding WHITTAKER (1975) and Heinrich WALTER (1964, 1968, 1973; WALTER and BOX 1991; WALTER and BRECKLE 1985, 1991). WHITTAKER introduced a conceptual linkage between biomes and climatic conditions with his simple but prominent biome diagrams. The restriction to average climatic conditions, however, can be misleading. Mid- and high-latitude ecosystems exhibit significant seasonality in light availability, temperature, and precipitation regime. Deciduous forests, for instance, perform a highly synchronized phenological fluctuation, which is not associated with mean annual conditions.

Independently, HAGGETT (1972) and WALTER (1973) developed comparable zonal concepts. WALTER (1973) explicitly differentiated ‘zono-biomes’ from ‘oro-biomes’ and ‘zono-ecotones’. The latter account for the fact that there are no sharp boundaries of such complex, large-scale units. These transitional zones differ in their extent depending on topography and exhibit substantial intrinsic heterogeneity.

All those concepts are deeply rooted in climatology and vegetation science. Vegetation is a key structure in all terrestrial ecosystems that serve as a proxy for the entire system and its processes, drivers and continental patterns. In consequence, vegetation zones and biomes are almost redundant (SCHMITHÜSEN 1976). Until today, vegetation structure and the role of plant life forms are the main aspects of biome concepts (FORSETH 2010; PFADENHAUER and KLÖTZLI 2014) (Fig. 1).

For many years, ecosystem studies were primarily linked with the biological processes, physiology, and ecology of plants (WALTER 1964, 1968). Vegetation zones as introduced by GRISEBACH or SCHIMPER, mainly based on scholarly reports from different parts of the world, became increasingly clear during the 20<sup>th</sup> century through improved accessibility, travelling options, and empirical evidence (RICHTER 2001; PFADENHAUER and KLÖTZLI 2014). However, the question remains to which degree the human footprint modified natural patterns.

If biomes are just a theoretical construct of conditions related to a historic climate, how can they serve as a reference? Fundamental critical perception arises from the fact that several established bi-



Fig. 1: Ecosystems from major global biomes: a) polar tundra (Sweden); b) boreal forest (Norway); c) temperate forest (Korea); d) steppe (USA); e) subtropical forest (New Zealand); f) desert (Tunisia); g) savanna (South Africa); h) tropical rain forest (Brazil)

ome and ecozone concepts are focused on potential natural vegetation patterns, which are mainly derived from an assumed steady state that reflects historic climatic classifications.

As biomes and ecozones are aiming to reflect more than vegetation, which is seen just as a proxy for ecosystems, it is surprising that in most concepts, the contribution of animals and microbiota is almost neglected. Vegetation is dependent on soil fertility and nutrient availability and is controlled by herbivory and other disturbances such as wildfires.

More process-based approaches and ecosystem models were initially restricted to fluxes of energy and matter (e.g. ODUM 1953) and implemented in concepts on large-scale biogeochemical cycles (LIKENS 1981). However, this bias and the fact that zonal climatic conditions, soil conditions, and land use are not only reflected in or driven by vegetation provoked the development of alternative concepts and terminology in neighbouring disciplines such as climatology or physical geography (e.g. MÜLLER-HOHENSTEIN 1979; SCHULTZ 1988).

The ecoregions and ecozones, respectively, of SCHULTZ (e.g. 1988, 1995, 2016) are focused on ecotopes, i.e. the locations of ecosystems, but less on the processes within ecosystems. Spatial units of these ecozones follow historic climatic classifications without basic updates for decades. Nevertheless, this concept is still textbook knowledge in Central Europe (but mostly ignored in other parts of the world). Terminological issues related to local ecosystem conditions were addressed as early as 1932 by SHELFORD and by TANSLEY in 1935. Nevertheless, confusion about these definitions and notions still exists.

The explicit contribution of bedrock and soil types is rarely highlighted. Soil is rather seen as a consequence of the current climate. Besides historic climatic conditions, soils are characterized by bedrock and relief. Nevertheless, the concept of pedobiomes is rather seen as an option to categorize specific site conditions within biomes (e.g. MUCINA 2018) and is not widely applied in the scientific literature. Generally, the dynamics of ecosystem processes, and particularly short-term events, which are important drivers of ecosystem functioning and structure are ignored when the focus is restricted to long-term average conditions of climate. Many ecosystems on Earth involve fire regimes as inherent processes (BOND et al. 2004). Other disturbances such as herbivory are key for biomass turnover and nutrient cycling (WOHLGEMUTH et al. 2019). Only in regional studies (RUTHERFORD et al. 2006) disturbances are explicitly included as traits of biomes.

In this study, the concepts related to the terms biome and ecoregion/ecozone (BAILEY 1998; OLSON et al. 2001; SCHULTZ 2016; DINERSTEIN et al. 2017) are taken as congruent. We understand a biome in a wider sense including a series of ecosystems that are interacting at landscape scales and being characterized by climate, site conditions, disturbance regimes, vegetation structure, and ecophysiology. This approach has a clear functional component (VALENTINE 1968) and it includes temporal scales and turnover as well as all kinds of biota and environmental site conditions. With an increasing interest in the processes driving global patterns of ecosystems and vegetation structures, the combination of plant physiology and climate regimes needs to be complemented by the interactions with physical impacts such as fire regimes and other disturbances and by biological processes within ecosystems such as herbivory. Such a process-based ecological perspective is somehow intrinsic in several historic approaches but also partly hidden if not ignored.

However, the ecological approach to global biomes should not be equated with biogeographical regions or provinces that are based on phylogenetic relatedness of biotic taxa (e.g. floristic realms) (ANTONELLI 2017) even if the history of biomes and their shift can be reflected in phylogenetic radiations and cladistics (PENNINGTON et al. 2004; DONOGHUE and EDWARDS 2014). Nevertheless, related taxa are likely to occur under comparable conditions provided within biomes.

Biomes also have a history. Tropical rain forests have existed very probably with comparable structures for long periods of time. Species composition changed over evolutionary periods but in some cases the constancy of higher taxa and plant functional traits is stunning. The Miocene Laurel Forest, for instance, is well documented in Central European lignite deposits (KONDRASKOV et al. 2015), indicating a much warmer and moister climate when the Tethys Ocean was not closed to become the Mediterranean Sea and global temperatures were significantly warmer than under current conditions. However, it is difficult if not impossible to disentangle the interactions between environmental conditions and biota with their evolutionary consequences.

Nevertheless, the criterion for labelling biogeographical regions and provinces is phylogeny and not ecosystem structure and functioning. The phylogenetic perspective to large-scale units is not directly linked to biomes as it is evident in South Africa, of which parts are a stand-alone floristic realm (*Capensis*) but part of the global Mediterranean biome, at least in many biome classifications (but see MONCRIEFF et al. 2015). Evidence suggests that the types of dominant

ecosystems determined by climatic and soil conditions affect plant species richness (e.g. BARTHLOTT et al. 2007).

Modelling approaches for global biomes emerged in the early 1990ies (PRENTICE et al. 1992). With increasing data availability (e.g. GBIF), and strongly promoted by the development of the plant functional TRY database (KATTGE et al. 2019) and free climatic data (e.g. KARGER et al. 2017), modelling approaches are increasingly performing based on plant distribution data (KAPLAN et al. 2003; HENGL et al. 2018). This includes their physiology and structural dominance, but also soil properties and climate (HIGGINS et al. 2016). Process-based functional approaches in biome research are on the rise as well (GRIFFITH et al. 2019). Remote sensing approaches on photosynthetic activity, NDVI, productivity, etc. are feeding into modern biome models (SAYRE et al. 2014). Nevertheless, the divide between real and potential ecosystem performance remains.

To sum up: Global classifications of biomes are based on different criteria and combinations thereof such as climate, topography, natural vegetation, ecosystems, and land cover. The diversity of concepts results from the parallel development under different foci and from a variety of disciplinary backgrounds (Fig. 2).

The most recent review on biome concepts has been provided by MUCINA (2019) from a biological perspective. He points out that this framework is aiming to understand and characterize the patterns and drivers of life at a large spatial scale. Nevertheless, MUCINA does not offer a clear perspective for improved future approaches. The development of modern Dynamic Global Vegetation Models (DGVMS) that are currently used to project global changes of biogeochemical cycles may seem as a solution. Their appeal and their limitation, however, are both related to their simplicity and reductionist understanding of plant functional traits and types. Currently, there is no concept that receives general consent, but the need for data-based biome classification that is less biased by single criteria is growing with global and climate change (GEO ECO 2020).

The aim of our study, however, is not to evaluate different approaches and their pros and cons. The need for a better understanding of natural global patterns is evident. The complexity of biomes that are composed of many different types of ecosystems each, asks for the consideration of a broad spectrum of expertise, and questions individual viewpoints. This is why we do not want to grapple with single biological processes or climatic data but rather want to compare established concepts for global terrestrial

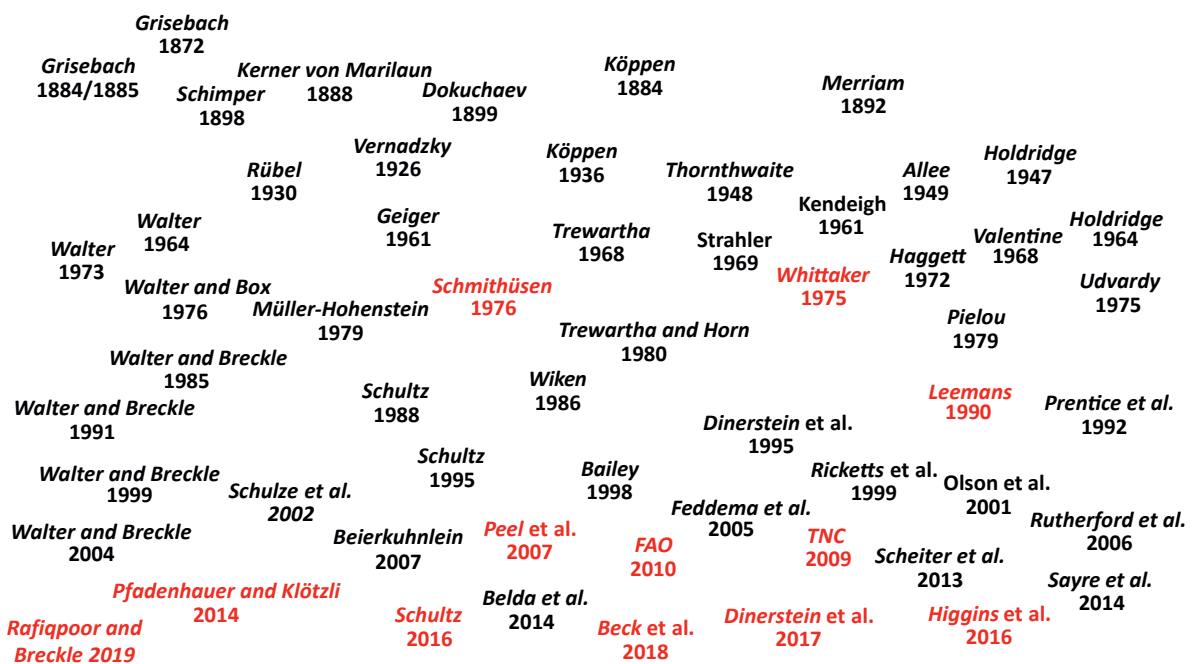


Fig. 2: Pedigree of selected published concepts on biomes (in red) including published concepts not considered in this study (in black). The position in the diagram from above to below hints at the temporal development. The sequence of approaches does not indicate a direct continuation of influence but indicates a legacy of related approaches. The neighbourhood of authors is reflecting similarities in methodological approaches. This overview indicates interdependencies between concepts. Our study aims to cover a broad spectrum of approaches.

biomes, ecozones and climate regions from a geographical perspective in order to identify communalities and discrepancies.

We hypothesize that certain land surfaces are likely to be classified similarly into large spatial and ecological units, independent of the applied criteria because climatic drivers are controlling vegetation and ecosystems. In consequence, we do not expect that classifications that are more focused on either climatic or ecological criteria would deviate considerably. On the other hand, some biomes are rather unanimous and others are not covered as separate units in all cases (e.g. temperate rain forest, laurel forest). In addition, transition zones (zono-ecotones) between biomes are more or less pronounced resulting in problems of attribution.

## 2 Methods

Screening the literature on global products for biomes, ecozones and climate zones yielded a series of published map products. Many of those are digitally available, including HOLDRIDGE's life zone classification by IIASA 1989 compiled by LEEMANS 1990; PEEL et al. 2007; TNC 2009 (based on TNC, USDA and USGS 1995); FAO 2010; HIGGINS et al. 2016; DINERSTEIN et al. 2017 (closely related to OLSON and DINERSTEIN 2002) and BECK et al. 2018. In addition, we digitized the following global maps: WHITTAKER 1975; SCHMITHÜSEN 1976; PFADENHAUER and KLÖTZLI 2014; SCHULTZ 2016; RAFIQPOOR and BRECKLE 2019. As maps were available in different projections, all digital maps were re-projected to the equal-area Mollweide projection.

Obvious differences between these products exist in terms of the non-uniform consideration of the Antarctic. Several classifications include this continent (SCHMITHÜSEN 1976; PEEL et al. 2007; TNC 2009; FAO 2010; PFADENHAUER and KLÖTZLI 2014; SCHULTZ 2016; DINERSTEIN et al. 2017; BECK et al. 2018), others don't (WHITTAKER 1975; LEEMANS 1990; HIGGINS et al. 2016; RAFIQPOOR and BRECKLE 2019). For this reason, Antarctica was excluded which causes a bias towards an underrepresentation of the polar region.

A big challenge was the inconsistent representation of mountains. Mountains may host a series of biomes within a small area. This can hardly be reflected in global maps. However, it is not an easy task to classify mountain regions on a global scale. Several authors did this quite roughly, others in a differentiated way. WALTER (1973) classifies orobiomes

as separate spatial units due to their three-dimensional organization of ecosystems, which results in the occurrence of several biomes along the altitudinal zonation of large mountain slopes. In consequence, there would be a spatial overlap within one mountain range. The coarse grain of information in global maps, however, impedes a realistic graphic representation of this fact in two-dimensional maps. Several authors (PFADENHAUER and KLÖTZLI 2014; SCHULTZ 2016; RAFIQPOOR and BRECKLE 2019) explicitly mark large mountain areas (e.g. the Andes, the Rocky Mountains, or the Himalayas) as such. However, this was not done in a standard or reproducible procedure. Others did not particularly consider the specifics of mountain ranges (WHITTAKER 1975; SCHMITHÜSEN 1976; LEEMANS 1990; PEEL et al. 2007; TNC 2009; FAO 2010; HIGGINS et al. 2016; DINERSTEIN et al. 2017; BECK et al. 2018). Such an inconsistency also is attributed to the consideration of large inland waters. To achieve comparability between the individual approaches, we developed and applied a mask to crop out high mountains (data source: KARAGULLE et al. 2016) as well as large inland water bodies (data source: WESSEL and SMITH 2017). In doing so, the geospatial data were limited to the zonal biomes by a reduction of 10% of the full areal coverage. Zono-ecotones were considered as individual units if they were mapped as such.

The considered spatial products differ in classification criteria (Tab. 1). Classifications by SCHMITHÜSEN (1976), PFADENHAUER and KLÖTZLI (2014) and HIGGINS et al. (2016) are based on vegetation structure. In PEEL et al. (2007) and BECK et al. (2018), the categories are determined by climatic conditions. The maps from the various sources differed not only in the terminology of mapping units (biomes, ecozones, etc.) but also in the number of recognized units. The number of mapping units excluding inland and maritime waters, oceanic islands and mountains ranged from 12 (WHITTAKER 1975) to 38 (LEEMANS 1990) with an average of 24 units per classification (Fig. 3).

As we were not aiming to characterize the current surface and land cover but rather wanted to compare established concepts for the potential natural conditions, we did not exclude areas strongly modified by settlements, infrastructure, and agriculture or forestry.

The spatial comparison was carried out in R Studio with the 'raster' package (HIJMAN and VAN ETEN 2012). Correlation matrices for all pairwise comparisons were calculated with the 'sabre' package (NOWOSAD and STEPINSKI 2018) to identify the

**Tab. 1: Major classification categories and criteria for biome concepts considered in this study**

Classification	Category of concept	Criteria for class distinction
WHITTAKER 1975	climate and vegetation	temperature, precipitation, plant community distribution
SCHMITHÜSEN 1976	biogeography	geographic location, elevation, temperature, potential evapotranspiration, ecology
LEEMANS 1990	vegetation	vegetation distribution based on temperature, precipitation, potential evapotranspiration
PEEL et al. 2007	climate	monthly temperature and precipitation threshold values and variances
TNC 2009	ecology	biodiversity, climate, vegetation
FAO 2010	biogeography	temperature, precipitation, evapotranspiration, soil, landform, distribution of vegetation types
PFADENHAUER and KLÖTZLI 2014	vegetation	life forms of plants, soil, relief, agricultural and forestry productivity, climate
SCHULTZ 2016	geo-ecology	climate, hydrology, soil, relief, vegetation, fauna, human influence
HIGGINS et al. 2016	climate and vegetation	vegetation (NDVI), soil moisture, radiation, temperature
DINERSTEIN et al. 2017	biogeography	flora and fauna distribution
BECK et al. 2018	climate	monthly temperature and precipitation threshold values and variances
RAFIQPOOR and BRECKLE 2019	climate and vegetation	temperature, precipitation, radiation, soil, vegetation, fauna, continentality and maritime influence, snow cover

degree of spatial association between classifications. As a result of the analysis, the degrees of association between two maps are calculated and expressed in three values (value range: 0-1); Homogeneity, Completeness and V-measure. Homogeneity shows the average homogeneity of the regions in the second map in relation to the regions in the first map, while Completeness is the homogeneity of the regions in the first map in relation to the regions in the second map. V-measure (cf. ROSENBERG and HIRSCHBERG 2007) expresses the degree of general agreement (NOWOSAD and STEPINSKI 2018). Classified biomes were analyzed to identify fitting units among multiple biome classification schemes.

In order to identify the drivers of global patterns, the classification of biome clusters was linked to 21 modelled climate parameters from the CHELSA data set (KARGER et al. 2017) for current climatic conditions on a global scale. In contrast to the still very popular global climate data set from WORLDCLIM

(HIJMANS et al. 2005; FICK and HIJMANS 2017), this data base has been developed from a biogeographical perspective. The considered parameters in our study include a variety of temperature and precipitation variables as well as potential evapotranspiration and solar radiation. A complete list can be found in Appendix I. To group the individual biomes ( $n=287$ ) of all biome concepts according to their environmental/climate characteristics, a dissimilarity matrix was generated based on the Euclidean distance of their mean climatic conditions. Ward's minimum variance criterion was implemented in divisive hierarchical clustering (MURTAGH and LEGENDRE 2014). 12 biome clusters were derived to form the base of the novel global biome distribution (Fig. 4, revised global biome map). Those computations were completed with the R 'stats' package (R Core Team 2021).

The frequency of overlap among the 12 dominant zones was derived from the number of different biomes per location.



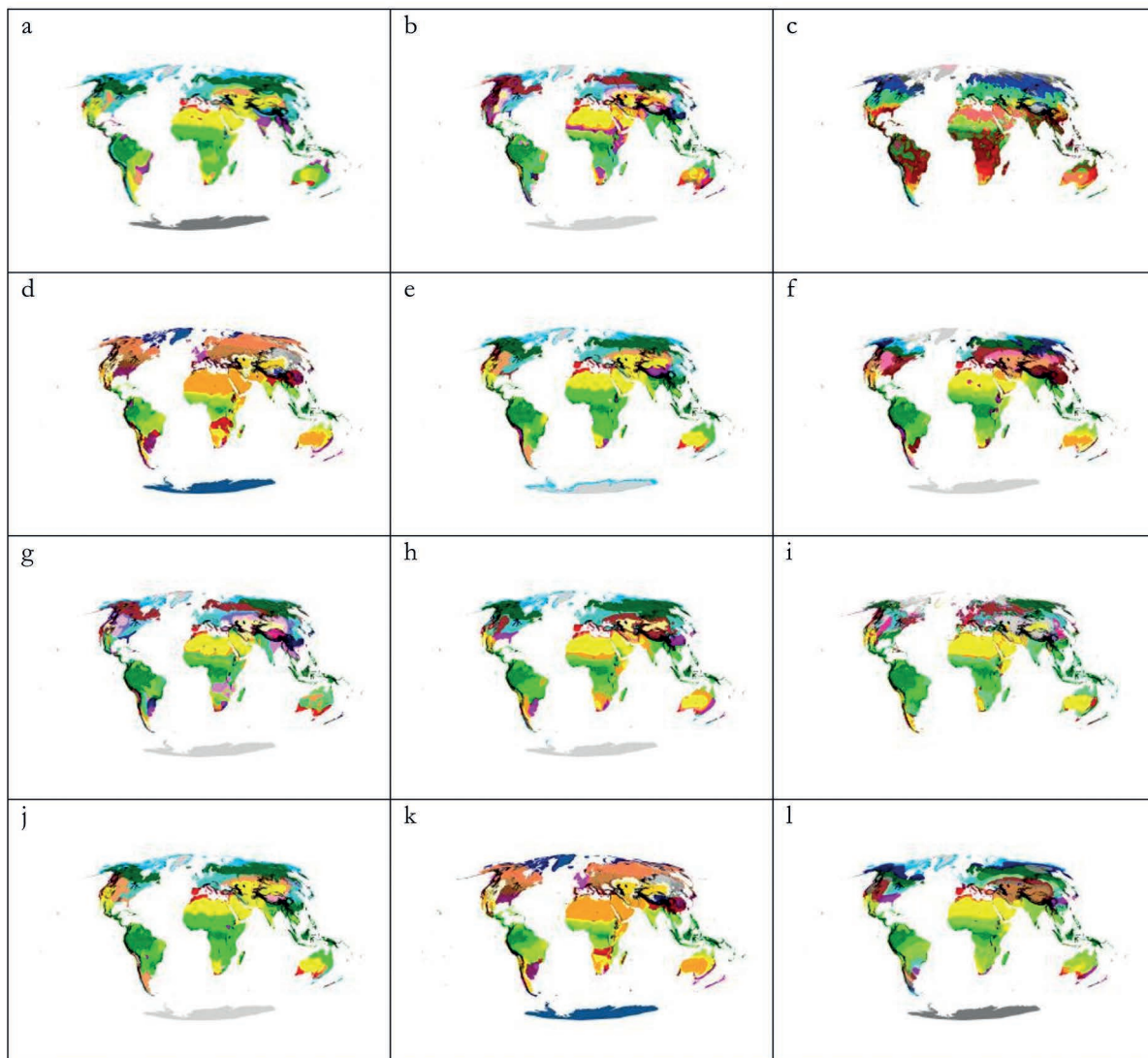


Fig. 3: Map display of established global concepts for biomes, ecozones, and climate zones: a) WHITTAKER 1975; b) SCHMITHÜSEN 1976; c) LEEMANS 1990; d) PEEL et al. 2007; e) TNC 2009; f) FAO 2010; g) PFADENHAUER and KLÖTZLI 2014; h) SCHULTZ 2016; i) HIGGINS et al. 2016; j) DINERSTEIN et al. 2017; k) BECK et al. 2018; l) RAFIQPOOR and BRECKLE 2019. Legends and digital information at high spatial resolution are available in the [electronic Appendix II](#).

### 3 Results

A comparison of 12 major biome concepts illustrates that some concepts (SCHMITHÜSEN 1976 and PFADENHAUER and KLÖTZLI 2014; PEEL et al. 2007 and BECK et al. 2018 TNC 2009 and DINERSTEIN et al. 2017, FAO 2010 and SCHULTZ 2016 as well as SCHULTZ 2016 and BECK et al. 2018) are closely related. Their products show above-average scores of the measures of spatial agreement. Others (WHITTAKER 1975; HIGGINS et al. 2016) provided complementary information and yielded less overlap with other approaches (Tab. 2). Due

to the coarse form of the data from HOLDRIDGE's life zone assignment by IIASA 1989 compiled by LEEMANS 1990 in a raster-like style, this concept could not be compared to the others and was therefore excluded from the similarity analysis.

As a result of the applied hierarchical biome clustering, the spatial representation of the derived biomes resulted in 12 remaining dominant classes (biome clusters) with associated congruencies (Fig. 5).

Displaying the biome clusters in the form of a combined global map (Fig. 4) results in a meaningful ecological pattern. Certain areas are

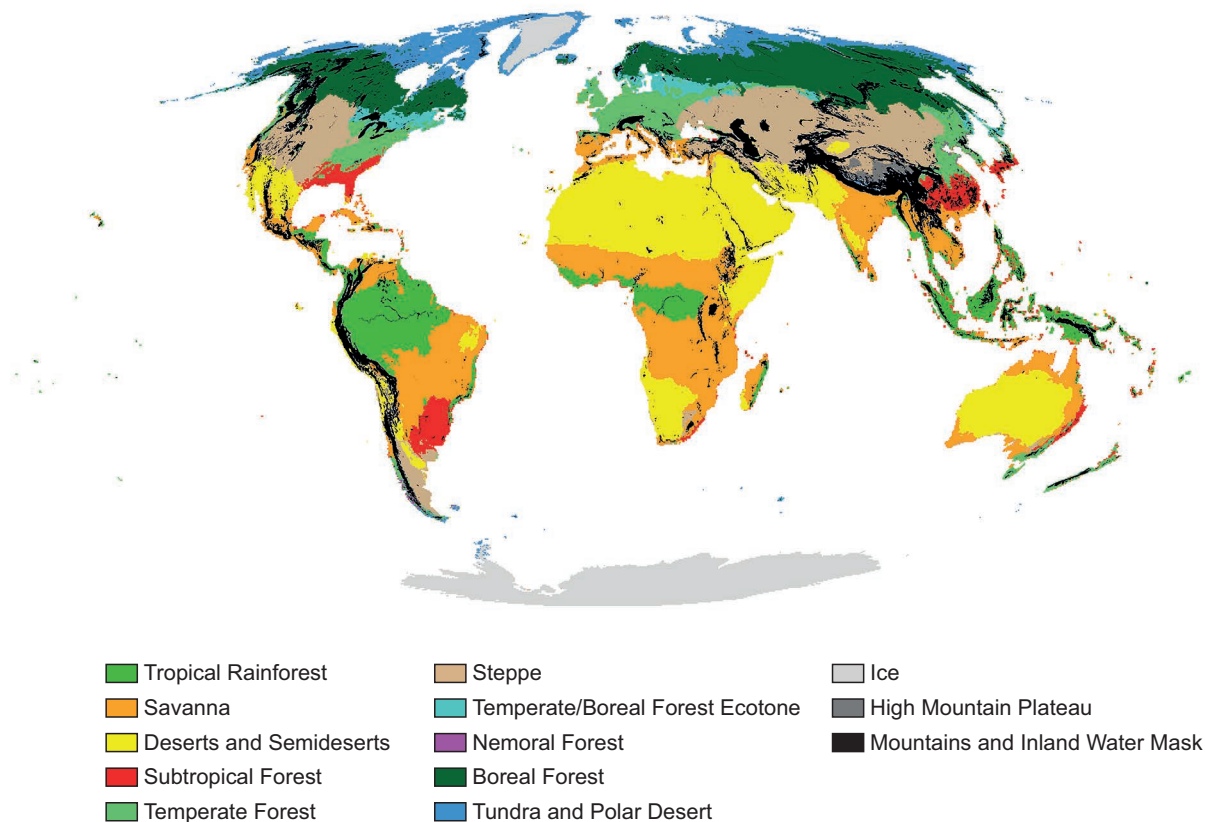


Fig. 4: Revised global biome map based on cluster analysis of spatial characteristics in 12 published biome concepts. The terms used in the legend are attributed to the resulting classes and were not defined a priori. Orobiomes and inland waters are masked out and displayed in black.

attributed to a common ground in the understanding of biomes because they perform similarly in different classification approaches. Deserts and Semideserts, Tropical Rainforest and Boreal Forest zones exhibited the highest degree of consistency within the analyzed concepts.

Besides nine biome clusters that can be well understood as zonal ecological conditions (Tropical Rainforest, Savanna, Deserts and Semideserts, Subtropical Forest, Temperate Forest, Temperate Steppe, Boreal Forest, Tundra and Polar Desert, Ice), three exceptional biomes are emerging (Nemoral Forest, High Mountain Plateau, Temperate/Boreal Forest Ecotone). One biome cluster (Nemoral Forest) that is identified by our geostatistical approach is restricted to a very small area in South America. Another one is representing mainly the specific situation of the Tibetan plateau (High Mountain Plateau). These high elevation ecosystems were not marked out completely because they did not fulfil the criteria for the mountains mask (topography, slope).

And finally, it was surprising, that the Temperate/Boreal Forest Ecotone emerged as an individual biome cluster unit. However, this category is not well characterized and may vanish during further studies. Nevertheless, it indicates a large area of gradual transition.

Surprisingly, other biomes that are commonly accepted such as the Mediterranean biome, the Subtropical Rain Forest, the Succulent Scrub etc. do not emerge individually in this cumulative approach. In these cases, there is a considerable amount of disagreement in individual biome classifications.

Zones of high spatial uncertainty resulted from individual biomes which partially cover identical zones but statistically got assigned to different clusters. Those are primarily detected in the vicinity of mountainous regions (especially in the Andes and Himalayas), as well as in the southeastern United States, eastern South America, South Africa and along Australia's eastern coastal region (Fig. 5).

Tab. 2: Correlation matrix between biome concepts illustrating redundancy and complementarity of spatial information. Strong similarity scores among individual pairs are marked in blue (V-measure), red (homogeneity) and green (completeness). The threshold for their identification was set to a 75% quartile of all values for each measure.

Compared classifications		SCHMITHÜSEN 1976	PEEL et al. 2007	TNC 2009	FAO 2010	PFADENHAUER and KLÖTZLI 2014	SCHULTZ 2016	HIGGINS et al. 2016	DINERSTEIN et al. 2017	BECK et al. 2018	RAFIQPOOR and BRECKLE 2019
WHITTAKER 1975	V-measure	0.49	0.48	0.50	0.47	0.51	0.52	0.33	0.52	0.49	0.53
	Homogeneity	0.55	0.52	0.49	0.51	0.58	0.53	0.35	0.51	0.52	0.59
	Completeness	0.44	0.44	0.51	0.44	0.45	0.51	0.31	0.53	0.46	0.48
SCHMITHÜSEN 1976	V-measure		0.53	0.55	0.56	0.62	0.58	0.42	0.55	0.55	0.58
	Homogeneity		0.51	0.48	0.54	0.63	0.53	0.39	0.49	0.53	0.57
	Completeness		0.56	0.63	0.59	0.62	0.64	0.46	0.64	0.58	0.60
PEEL et al. 2007	V-measure			0.52	0.57	0.56	0.61	0.46	0.54	0.73	0.60
	Homogeneity			0.48	0.58	0.59	0.58	0.44	0.50	0.72	0.61
	Completeness			0.58	0.57	0.53	0.64	0.47	0.60	0.73	0.58
TNC 2009	V-measure				0.59	0.55	0.58	0.39	0.88	0.54	0.56
	Homogeneity				0.66	0.64	0.60	0.43	0.88	0.60	0.63
	Completeness				0.54	0.48	0.55	0.37	0.88	0.50	0.50
FAO 2010	V-measure					0.60	0.64	0.45	0.60	0.60	0.60
	Homogeneity					0.63	0.60	0.43	0.55	0.59	0.61
	Completeness					0.57	0.67	0.48	0.66	0.60	0.59
PFADENHAUER and KLÖTZLI 2014	V-measure						0.61	0.43	0.56	0.58	0.61
	Homogeneity						0.55	0.39	0.48	0.55	0.59
	Completeness						0.68	0.47	0.65	0.61	0.62
SCHULTZ 2016	V-measure							0.47	0.59	0.63	0.64
	Homogeneity							0.48	0.57	0.66	0.69
	Completeness							0.46	0.62	0.61	0.60
HIGGINS et al. 2016	V-measure								0.39	0.49	0.46
	Homogeneity								0.37	0.50	0.48
	Completeness								0.43	0.48	0.43
DINERSTEIN et al. 2017	V-measure									0.56	0.57
	Homogeneity									0.62	0.64
	Completeness									0.52	0.51
BECK et al. 2018	V-measure										0.60
	Homogeneity										0.62
	Completeness										0.59

Projecting the identified biomes into a two-dimensional representation of mean annual temperature and precipitation illustrates the specific characteristics of the identified biome clusters in terms of these climatic factors (Fig. 6). However, seasonality, continentality and other climatic drivers are adding to these long-term average values when the spatial distribution of biomes is addressed.

#### 4 Discussion

A series of global terrestrial biome concepts including ecozones and climatic zones were comprehensively analyzed, spatially matched and compared according to their climatologic characteristics. Global patterns of biomes are generally consistent across different approaches. Spatial gradients such

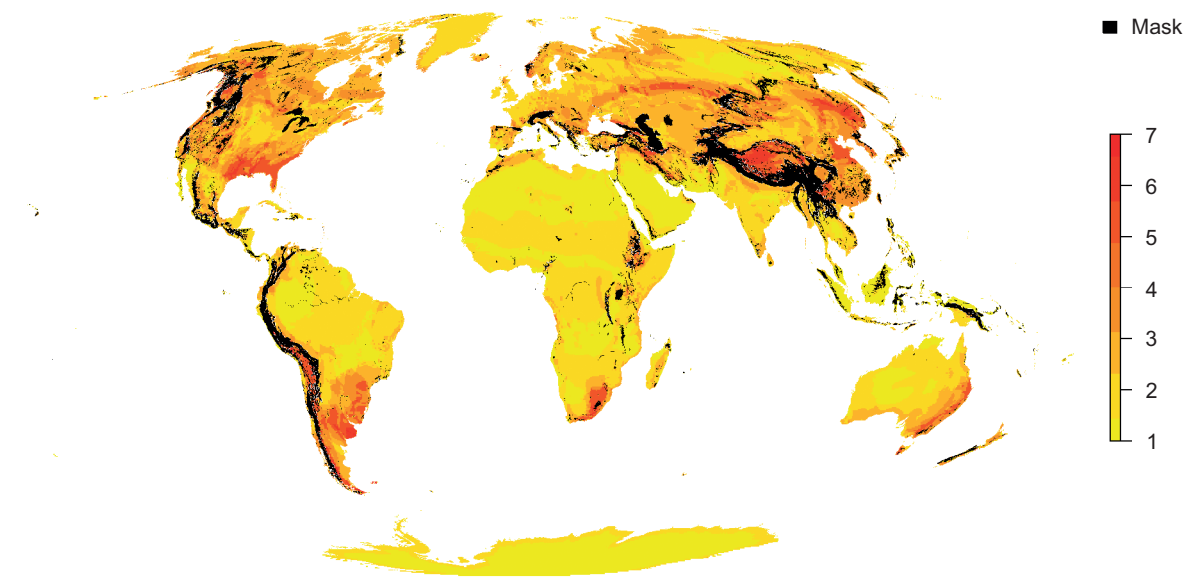


Fig. 5: Regions with high spatial overlap between global biome mapping units considered in this study. The frequency of overlap is translated into the yellow-to-red colour gradient in regions of considerable deviations in classification. Reddish colours indicate low agreement between published concepts. Certain subtropical regions, as well as transition zones (e.g. in Central Asia), are inconsistently attributed to biomes (high degree of overlap). The same applies to regions with pronounced topography in the vicinity of mountain regions. Orbiomes and inland waters are masked out and displayed in black.

as latitude, continentality and orography play a major role in driving these important ecological units that are mostly expressed through vegetation cover as they translate into climatic conditions such as temperature, precipitation and seasonality. The advantage of this ambition to search for biome clusters by integrating a broad spectrum of different approaches is to reduce bias from individual concepts. All of them may have their pros and cons, even if there is not always a clear protocol for the applied procedure. Expert-knowledge based maps can be based on implicit knowledge and holistic understanding of nature, ignoring individual elements and their functioning. Biome maps that are derived from remotely sensed data cannot identify ecosystem assemblages and are strongly influenced by the current human footprint of land use and settlements. Process-based models are restricted to the knowledge about individual components (e.g. plant functional types) and would require explicit information about their mechanistic contribution to functional interactions within ecosystems, which is almost completely lacking. In consequence, there is no best practice or most convincing single approach. Users have the choice between holistic and reductionistic approaches, and between concepts where the main criteria are related to meanwhile historic climatic conditions and others that are based on the limited significance and informative value of current data on plant species distribution.

Here, we don't suggest deciding on one specific option. We rather aim to highlight global patterns that emerge, when products that are based on different disciplinary viewpoints are combined. Such a critical perception can hardly be achieved when only one published concept is selected.

Recognizing the importance and need for global biome maps should not ignore their limitations. These constraints refer to the criteria for classification and spatial delineation of mapping units. When comparing different expert- and data-based approaches considerable differences not only in the number of classes or mapping units (biome types) become apparent, but also their spatial arrangement differs significantly. The here documented compilation of a series of 12 established classification schemes and their respective map products can help to identify individual biases that are inherent in global reference systems. However, it cannot replace the detection of attributions of areas and classifications of units that are not well justified.

One fundamental limitation of our approach is related to spatial autocorrelation between concepts. If, for instance, the ecozones of SCHULTZ (1988) follow the climate map of TROLL and PAFFEN (1964), which in turn has been constructed based on vegetation patterns, climate and vegetation cannot be disentangled at all. Spatial limitations of units were evidently also copied in other products, which can artificially increase those borders in spatial statistics. However,

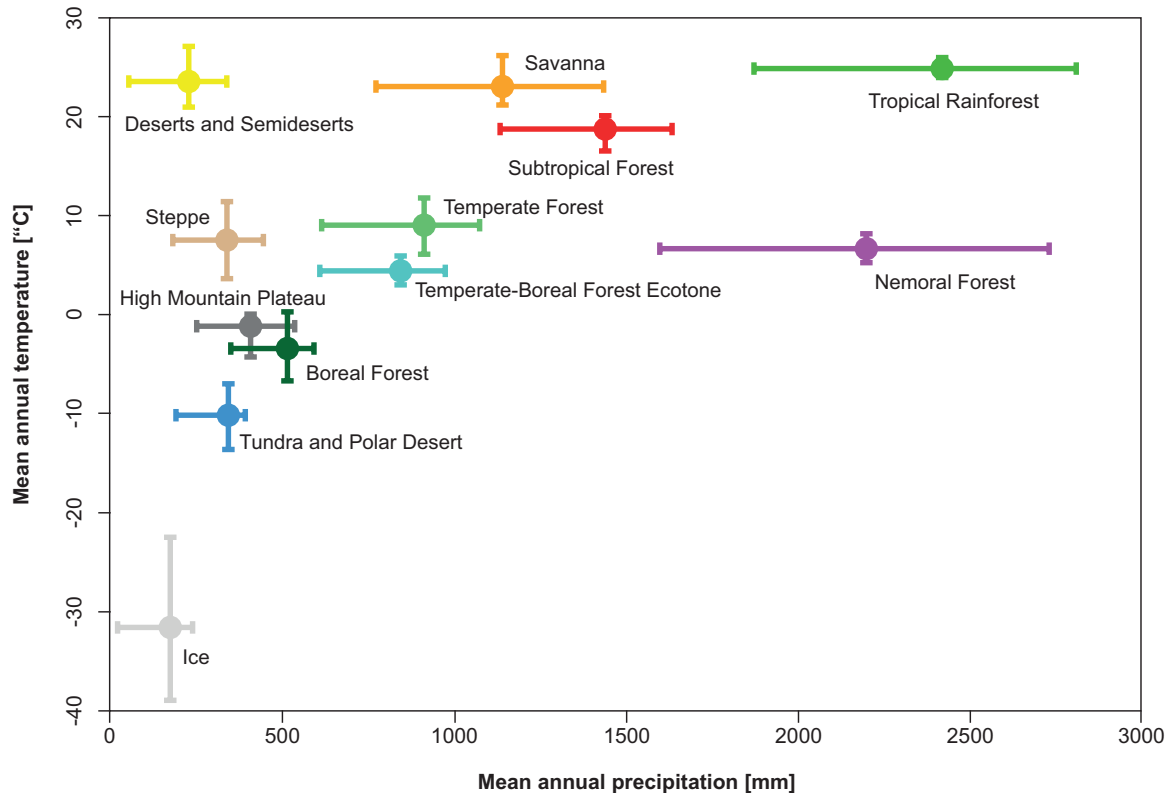


Fig. 6: Mean annual temperature and precipitation values for 12 condensed biome clusters to visualize their relative position in the climate space. 25 and 75 quantiles in x- and y-dimensions are shown by the horizontal and vertical bars extending off the mean values. The underlying climate data were derived from KARGER et al. 2017. 2D kernel density plots for all condensed biomes are documented in an [electronic Appendix III](#).

this cannot be explicitly identified in individual and widespread expert-opinion-based approaches. This study, however, contributes to the discussion about these problems and aims at a more critical perception of established global biome products.

Early approaches (e.g., WHITTAKER 1975) and modern ones (e.g., HIGGINS et al. 2016) are rather stand alone for different reasons. Since first publications, viewpoints were replenished by improved access to geo-information. HIGGINS et al. (2016) on the other hand provide an approach that considers data on structural and functional plant attributes.

The very high degree of similarity between TNC (2009) and DINERSTEIN et al. (2017) is not surprising because both concepts have been developed based on OLSON et al. (2001). PEEL et al. (2007) and BECK et al. (2018) share a comparable classification method, which explains their similarity. Comparably, it had to be expected that approaches that focus on vegetation units such as SCHMITHÜSEN (1976) and PFADENHAUER and KLÖTZLI (2016) exhibit a high similarity (redundancy of information), too.

Although the FAO (2010) approach seems to be strongly driven by climatic conditions, obviously there are also close links to a series of other concepts. Also, the approaches by SCHULTZ (2016) and RAFIQPOOR and BRECKLE (2019) are overlapping with other concepts that are quite different in nature. This provokes the request for more explicit documentation of procedures, data, and criteria for classification and delimitation of units. On the other hand, it seems obvious that potential auto-correlation and hidden interdependencies should be identified. There is generality within the larger picture, but discrepancies on a significant surface of the planet as well.

As a result of our spatial analysis, nine major biome clusters are emerging in this comprehensive approach. These spatial units are designated as follows to consistent global biomes: Tropical Rainforest, Savanna, Deserts and Semideserts, Subtropical Forest, Temperate Forest, Temperate Steppe, Boreal Forest, Tundra and Polar Desert. In addition, ice-covered surfaces build one terrestrial unit as

expected. Three units, however, are less representative for zonal biomes for different reasons. These units are the small cluster of the Nemoral Forest at the southern coast of South America, the High Mountain Plateau in Central Asia, and finally, the Temperate/Boreal Forest Ecotone in north-eastern Europe and North America. We do not make a plea to rank these units finally at the equal level as other global biomes. Nevertheless, these areas exhibit unique conditions that may be considered in global strategies for nature conservation and protected area designation.

The Nemoral Forest cluster is driven by approaches that are focused on vegetation types. Additionally, high amounts of precipitation combined with rather low temperatures are indicating the specific character of a temperate rain forest, which is displayed in some concepts but with high inconsistency. As biome concepts should aspire to characterize global ecological patterns, this cluster needs to be treated with caution. One problematic aspect here are inconsistencies in the predominantly climatic characterization of vegetation-based biome classifications (MONCRIEFF et al. 2016).

Comparably, the High Mountain Plateau cluster is restricted to one region, which is the Tibetan Plateau. As there, topographical diversity is less pronounced compared to the blanked-out surface of high mountains, it is not identified as a high mountain region in this study. This cluster should be linked with high mountains in terms of ecosystems and climate, even if it does not exhibit relief diversity and steep slopes.

Finally, one cluster, the Temperate/Boreal Forest Ecotone, emerges from the geostatistical analyses, which is a transition zone between the deciduous Temperate Forest biome and the Boreal Forest biome. This category, too, cannot serve as a global biome, even if it is appearing on various continents. The close vicinity to the climatic conditions of the temperate biome is indicating that this cluster should be rather added to the temperate and not to the boreal cluster.

From a global perspective, we identify regions that are considered as clear spatial units across classifications and criteria, and on the other hand, we discover areas where global concepts of biome classification disagree considerably. Regions with a high degree of overlapping neighbouring biomes can refer to zono-ecotones (in the understanding of Heinrich WALTER (1964, 1968)), but also uncertainty in classification schemes. It cannot be decided at this stage, which aspect is of greater influence for such areas that are not attributed to biomes.

There is uncertainty in these transition zones in terms of the local conditions and their attribution to a neighbouring unit, but there is also variation among these zones where classifications from various authors and methodological approaches diverge. Additionally, uncertainty is related to the superimposed human impact that can hide original natural patterns. Low human impact areas are rare on the planet and restricted to the arctic and boreal zone, deserts and humid tropical lowlands (JACOBSON et al. 2019). On the other side of the coin, fragmentation mostly affects high natural value and protected areas in the temperate zone (IBISCH et al. 2016). In consequence, certain biomes are more and others less overshadowed by the human footprint. And finally, uncertainty arises from climatic changes and their repercussions on disturbance regimes and short-term climatic events (HEGERL et al. 2011). Topographic diversity within protected areas, and biomes, respectively, can contribute to buffer possible negative impacts and to maintain ecosystem functioning in face of ongoing climate change (LAWRENCE et al. 2021). Topographic diversity within spatial units of biomes is not apparent in global maps but can be identified indirectly through point information from weather stations located within the frame of a mapping unit (KARGER et al. 2017). As all of these conditions and processes can modify the spatial patterns with increasing speed and intensity, any product about global biomes must be considered as a moving target. Biomes that were previously considered to be stable and constant, which is the basis of maintaining biodiversity, are identified to change (HUNTLEY et al. 2021).

There is a fundamental shortcoming in all comprehensive approaches, which is the lack of temporal dynamics beyond ecological processes such as succession or climatic aspects such as seasonality. Biome concepts, like the idea of potential natural vegetation, are implicitly characterizing a hypothetical stable state which is no longer granted and may never have existed (CHIARUCCI et al. 2010). The dynamics of processes and disturbances within units is not neglected but considered to be inherent in addressed systems of a given latitude and climate. The problem with many biome concepts is that this is not illustrated or analyzed in detail.

In the same way as the variety of really existing ecosystems at a fine spatial resolution is included in a more general understanding of potentially developed climax vegetation, short-term dynamics and successional trajectories are expected to shape global biomes. This can translate into circular reasoning as

these processes are not explicitly analyzed. Soil formation, nutrient and carbon turnover, life cycles, biotic interactions, wildfires, seasonality, and impacts of extreme weather conditions are major natural processes and drivers in all biomes. It would be naïve to think that all these can be explained by long-term average annual temperature or precipitation values. The fact that zonal vegetation and biomes are reflecting large-scale climatic conditions is hardly evidence for clear causality. For biome concepts that are based on expert knowledge, there is even the risk of circular arguments when biomes are delineated based on climatic data and then climate is identified as the best explanation of biome patterns. This is not necessarily a fallacy, as both, climate and biomes are integrals of heterogeneous units and complex mechanisms. Effective mechanisms, resulting in emerging patterns of ecosystems with a certain degree of resemblance in structures, phenology, trophic cascades, or biodiversity can be hidden behind the holistic syndrome.

In that respect, it is not surprising that there is a high degree of accordance between concepts, and depending on the viewpoints and classification criteria and the chosen number of mapping units also deviations between concepts emerge. The fact that in many cases biomes are constructed based on climatic information and reflected (or reduced) to vegetation cover and dominant plant life forms in combination with the fact that several global climatic maps have been constructed based on vegetation patterns, however, is calling for greater sensitivity in the use and application of these products. Furthermore, the legacy of global biome products can be seen also as the uptake of previous approaches (e.g. PFADENHAUER and KLÖTZLI 2014). Global biome maps are rarely independent and data-based (e.g. HIGGINS et al. 2016). There seems to be a tradeoff between reproducibility and comprehensiveness. Additionally, it should be noted that non-data-based holistic models can serve only as a theoretical historic comparison, but they cannot be adapted to the changing conditions during the 21<sup>st</sup> century.

We are all aware that the human impact is superimposed on the natural background of climate (seasonality, temperature regime, precipitation variability, insolation), vegetation, trophic cascades, natural disturbance regimes, and soil (RAMANKUTTY and FOLEY 1999). Wilderness areas, where natural processes would still be governing ecosystem functioning, have become rare and remote. They are limited to inaccessible regions (HENNING 2016) and to places where human activities are restricted for various rea-

sons. Additionally, they are reflecting past climatic conditions, if their turnover is low and life cycles are long. Technological development and economic interests, for instance, to access mineral resources, are rapidly reducing these places on Earth. Profound and far-reaching consequences for natural biota are documented (SANDERSON et al. 2002).

Soil conditions, climate, topography and other site conditions enable or suppress certain kinds of land use. In landscape ecology, this was realised at an early date and gave rise to the term ‘cultural landscapes’, but culture and history are not the only drivers of cultural landscapes. Realizing the human footprint in the Anthropocene, new viewpoints are emerging such as anthropogenic biomes (ELLIS and RAMANKUTTY 2008). Pure physical detection of surface conditions by remote sensing would reflect these patterns but hide the ecological background that is addressed by the biome concept in cases where land use has modified the land cover substantially (see SAYRE et al. 2014). This is why land use is ignored in this study as we are aiming to identify the natural background even if it might be hypothetical. In consequence, providing the natural basis will enable us to assess the role of land use and human impact in general within global biomes (e.g. ARINO et al. 2012; CONGALTON et al. 2014).

Inevitably, remote sensing-based assessments of ecological units at the global scale will reflect this human footprint and result in complex categories due to a broad spectrum of options for deviation from expectation (SAYRE et al. 2014). Nevertheless, it makes sense to compare expected natural conditions with the current situation. With technological progress, the spectral, spatial and temporal resolution of sensors is improving. Combining active and passive sensors in remote sensing is providing fascinating options for earth observation. However, when the question is to assess the deviation from natural conditions, a solid reference system is required.

At the scale of plant communities, the concept of potential natural vegetation (*sensu* TÜXEN 1956) is no longer accepted as a practical tool, both because of methodological issues and, even more important, due to rapid environmental and biotic changes (KOWARIK 1987; CHIARUCCI et al. 2010). A rapidly changing world will force questioning the concept of biomes that have been developed as hypothetical constructs for large-scale natural conditions years ago. This is a paradox in face of global changes. Global overviews and natural references are increasingly needed, and those that are available are increasingly outdated. There is no way back in the short run to a hypo-

thetical nature that may have served for orientation in the last century. Novel ecosystems are emerging, with previously unobserved species assemblages and traits (HOBBS et al. 2009). Their novelty only partly derives from direct human construction and management. Indirect effects such as enhanced biotic exchange (invasive species), biodiversity loss (local and regional population decline and species extinction), modified fluxes of energy (climate change), nutrients (nitrogen deposition) and toxic compounds (nuclear fallout, pollution, release of xenobiotic substances) are forcing long-lasting changes in ecosystems with uncertain consequences for the future of biomes.

Global climate change will trigger substantial ecosystem responses. In consequence, biome shifts are very likely to occur (GONZALEZ et al. 2010; DALE et al. 2021), but it is unlikely, that they will shift as complete units in a synchronized way with climate changes (MARTENS et al. 2020). Species exhibit very different life cycles and dispersal capacities; ecosystems are characterized by very different degrees of inertia, and by a wide range in turnover. Nevertheless, the composition and structure, as well as the processes and ecosystem functioning of biomes, will experience modifications in the future. This will translate into challenges for nature conservation and beyond for instance related to modern forestry practices and the urge for maintained levels of carbon sequestration. However, also novel opportunities are discussed and the transition to future ecosystems could be facilitated in a pro-active way (TOOT et al. 2020). Changes in regional spatial patterns are most expected in sensitive and vulnerable regions (GUIOT and CRAMER 2016), whereas other regions will respond less to climatic changes. This explains the need to question historic approaches beyond a mere categorization of their criteria. It also explains the need for evidence-based updated approaches and a revision of the current global biome concept (MONCRIEFF et al. 2016). The increasing knowledge and data availability at the planetary scale combined with methodological progress creates new options for consistent global surveys (e.g. DELGADO-BAQUERIZO and ELDRIDGE 2019; HOFFMANN et al. 2019).

The added value of our approach is beyond a mere comparison. For certain intentions, individual global reference systems with a clear focus, for instance on vegetation, will make sense in the future. In a changing world a wider perspective, as well as more data-based approaches, are needed. If the climatic forcing of ecosystems and biomes is changing, also their potential spatial distribution will change. It is unlikely that the ecological responses to the

changing environmental background will be synchronized with a changing climate. Deviation from expectation then will not only be related to the direct human impact but in addition also to climatic changes, which are modifying the natural reference. In consequence, more solid and differentiated biome maps capable to consider biomes as a moving target will be needed. Even ecosystems that are considered recently as natural representations of biomes, may become elusive but would be recorded in situ (and maybe considered to be still natural) until they will be removed by disturbances and replaced in the long run by ecosystems that would be better adapted to future climatic conditions. Evaluation of such possible developments is not the aim of this work. Rather, we want to create sensitivity about reliability, bias, aims, approaches, and history of established biome concepts, and where they agree or disagree. As the societal challenges and environmental problems to a global extent are rapidly increasing, the need for the critical perception of the biogeographical basis for decision making and naturalness or wilderness is required.

This synthesis of existing biome concepts is not aiming to provide a ready-made final product. Combining spatial information from different sources does not necessarily improve a resulting map. Theoretically, there can be one correct and a series of erroneous approaches and then the averaged product would not be better than the best single contribution. Hence, it is not our ambition to provide a 'best practice' global map, but to hint at communalities and discrepancies in the application of established biome concepts. What we intend is to stimulate the discussion on global geographical and ecological reference systems. This includes the awareness of circular reasoning in cases where natural vegetation is derived from climate and vice versa. It is worth recommending a more critical perception of existing concepts and global maps that are teaching material in schools and an orientation for nature conservation and global change impact studies.

### Acknowledgement

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## References

- ALLEE, W.C. (1949): Principles of animal ecology. Philadelphia
- ANTONELLI, A. (2017): Biogeography: drivers of bioregionalization. In: *Nature Ecology & Evolution* 1, 0114. <https://doi.org/10.1038/s41559-017-0114>
- ARINO, O.; RAMOS PEREZ, J. J.; KALOGIROU, V.; BONTEMPS, S.; DEFOURNY, P. and VAN BOGAERT, E. (2012): Global land cover map for 2009 (GlobCover 2009). <https://doi.org/10.1594/PANGAEA.787668>
- BAILEY, R. G. (1998): Ecoregions: the ecosystem geography of oceans and continents. New York.
- BARTHLOTT, W.; HOSTERT, A.; KIER, G.; KÜPER, W.; KREFT, H.; MUTKE, J.; RAFIQPOOR, M. D. and SOMMER, H. (2007): Geographic patterns of vascular plant diversity at continental to global scales. In: *Erdkunde* 61, 305–315. <https://doi.org/10.3112/erdkunde.2007.04.01>
- BECK, H. E.; ZIMMERMANN, N. E.; MCVICAR, T. R.; VERGOPOULAN, N.; BERG, A. and WOOD, E. F. (2018): Present and future Köppen-Geiger climate classification maps at 1-km resolution. In: *Scientific Data* 5, 180214. <https://doi.org/10.1038/sdata.2018.214>
- BEIERKUHNLEIN, C. (2007): Biogeographie – Die räumliche Organisation des Lebens in einer sich verändernden Welt. Stuttgart. <https://doi.org/10.36198/9783838583419>
- BELDA, M.; HOLTANOVÁ, E.; HALENKA, T. and KALVOVÁ, J. (2014): Climate classification revisited: from Köppen to Trewartha. In: *Climate Research* 59, 1–13. <https://doi.org/10.3354/cr01204>
- BOND, W. J.; WOODWARD, F. I. and MIDGLEY, G. F. (2004): The global distribution of ecosystems in a world without fire. In: *New Phytologist* 165 (2), 525–538. <https://doi.org/10.1111/j.1469-8137.2004.01252.x>
- CHIARUCCI, A.; ARAUJO, M. B.; DECOCQ, G.; BEIERKUHNLEIN, C. and FERNANDEZ-PALACIOS, J. M. (2010): The concept of Potential Natural Vegetation: an epitaph? In: *Journal of Vegetation Science* 21 (6), 1172–1178. <https://doi.org/10.1111/j.1654-1103.2010.01218.x>
- CLEMENTS, F. E. (1916): Plant succession: analysis of the development of vegetation. Carnegie Institution of Washington Publication Sciences 242. <https://doi.org/10.5962/bhl.title.56234>
- CONGALTON, R.; GU, J.; YADAV, K.; THENKABAIL, P. and OZDOGAN, M. (2014): Global land cover mapping: a review and uncertainty analysis. In: *Remote Sensing* 6, 12070–12093. <https://doi.org/10.3390/rs61212070>
- CRISP, M. D. (2006). Biome assembly: what we know and what we need to know. In: *Journal of Biogeography* 33, 1332–1333. <https://doi.org/10.1111/j.1365-2699.2006.01551.x>
- DALE, E. E.; LARCOMBE, M. J. and LEE, W. G. (2021): The effect of single biome occupancy on the estimation of biome shifts and the detection of biome conservatism. In: *PLoS ONE* 16 (3), e0248839. <https://doi.org/10.1371/journal.pone.0248839>
- DELGADO-BAQZERIZO, M. and ELDRIGE, D. J. (2019): Cross-biome drivers of soil bacterial alpha diversity on a worldwide scale. In: *Ecosystems* 22, 1220–1231. <https://doi.org/10.1007/s10021-018-0333-2>
- DINERSTEIN, E.; OLSON, D. M.; GRAHAM, D. J.; WEBSTER, A. L.; PRIMM, S. A.; BOOKBINDER, M. P. and LEDEC, G. (1995): A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. Washington (DC).
- DINERSTEIN, E.; OLSON, D.; JOSHI, A.; VYNNE, C.; BURGESS, N. D.; WIKRAMANAYAKE, E.; HAHN, N.; PALMINTERI, S.; HEDAO, P.; NOSS, R.; HANSEN, M.; LOCKE, H.; ELLIS, E. C.; JONES, B.; BARBER, C. V.; HAYES, R.; KORMOS, C.; MARTIN, V.; CRIST, E.; SECHREST, W.; PRICE, L.; BAILLIE, J. E. M.; WEEDEN, D.; SUCKLING, K.; DAVIS, C.; SIZER, N.; MOORE, R.; THAU, D.; BIRCH, T.; POTAPOV, P.; TURUBANOVA, S.; TYUKAVINA, A.; DE SOUZA, N.; PINTEA, L.; BRITO, J. C.; LLEWELLYN, O. A.; MILLER, A. G.; PATZELT, A.; GHAZANFAR, S. A.; TIMBERLAKE, J.; KLÖSER, H.; SHENAN-FARPÓN, Y.; KINDT, R.; BARNEKOW LILLESØ, J. P.; VAN BREUGEL, P.; GRAUDAL, L.; VOGEL, M.; AL-SHAMMARI, K. F. and SALEEM, M. (2017): An ecoregion-based approach to protecting half the terrestrial realm. In: *Bioscience* 67(6), 534–545. <https://doi.org/10.1093/biosci/bix014>
- DOKUCHAEV, V. V. (1899): Report to the Transcaucasian Statistical Committee on Land Evaluation in general and especially for the Transcaucasia. Horizontal and vertical soil zones (Tipogr. kantselyarii Glavnonachal'stvuyushchego grazhdanskoi chast'yu na Kavkaze. Tiflis [in Russian]).
- DONOGHUE, M. and EDWARDS, E. (2014). Biome shifts and niche evolution in plants. In: *Annual Review of Ecology, Evolution, and Systematics*, 45, 547– 572. <https://doi.org/10.1146/annurev-ecolsys-120213-091905>
- ELLIS, E. C. and RAMANKUTTY, N. (2008): Putting people in the map: anthropogenic biomes of the world. In: *Frontiers in Ecology and the Environment* 6 (8), 439–447. <https://doi.org/10.1890/070062>
- FAO (Food and Agriculture Organization of the United Nations) (2015): Global ecological zones for FAO forest reporting: 2010 Update. <http://www.fao.org/3/ap861e/ap861e00.pdf>
- FEDDEMA, J. J.; OLESON, K. W.; BONAN, G. B.; MEARNES, L. O.; BUJA, L. E.; MEEHL, G. A. and WASHINGTON, W. M.

- (2005): The importance of land cover change in simulating future climates. In: *Science* 310, 1674–1678. <https://doi.org/10.1126/science.1118160>
- FICK, S. E. and HIJMANS, R. J. (2017): WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. In: *International Journal of Climatology* 37 (12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- FORSETH, I. (2010): Terrestrial biomes. In: *Nature Education Knowledge* 3 (10), 11. <https://www.nature.com/scitable/knowledge/library/terrestrial-biomes-13236757/>
- GEIGER, R. (1961): Überarbeitete Neuauflage von GEIGER, R.: Koeppen-Geiger / Klima der Erde. Wandkarte 1:16 Mill. Gotha.
- GEO ECO (2020): Implementation Plan 2020-2022.. [https://earthobservations.org/documents/gwp20\\_22/GEO-ECO.pdf](https://earthobservations.org/documents/gwp20_22/GEO-ECO.pdf)
- GONZALEZ, P.; NEILSON, R. P.; LENIHAN, J. M. and DRAPEK, R. J. (2010): Global patterns in the vulnerability of ecosystems to vegetation shifts due to climate change. In: *Global Ecology and Biogeography* 19, 755–768. <https://doi.org/10.1111/j.1466-8238.2010.00558.x>
- GRIFFITH, D. M.; STILL, C. J. and OSBORNE, C. P. (2019): Editorial: revisiting the biome concept with a functional lens. In: *Frontiers in Ecology and Evolution*. <https://doi.org/10.3389/fevo.2019.00144>
- GRISEBACH, A. (1872): *Vegetation der Erde nach ihrer klimatischen Anordnung*. 2 Volumes. Leipzig.
- (1884/1885): *Vegetation der Erde nach ihrer klimatischen Anordnung*. 2. ed., 2 Volumes Leipzig.
- GUIOT, J. and CRAMER, W. (2016): Climate change: the 2015 Paris Agreement thresholds and Mediterranean basin ecosystems. In: *Science* 354 (6311), 465–468. <https://doi.org/10.1126/science.aah5015>
- HAGGETT, P. (1972): *Geography. A modern synthesis*. New York.
- HEGERL, G.; HANLON, H. and BEIERKUHNEIN, C. (2011): Elusive extremes. In: *Nature Geoscience*, 4 (39), 142–143. <https://doi.org/10.1038/ngco1090>
- HENGL, T.; WALSH, M. G.; SANDERMAN, J.; WHEELER, I.; HARRISON, S. P. and PRENTICE, I. C. (2018): Global mapping of potential natural vegetation: an assessment of machine learning algorithms for estimating land potential. In: *PeerJ*, 6:e5457. <https://doi.org/10.7717/peerj.5457>
- HENNIG, B. D. (2016): Visualising spaces of global inaccessibility. In: CARVER S. and FRITZ, S. (eds.): *Mapping wilderness: concepts, techniques and applications of GIS*. Heidelberg, 103–116. [https://doi.org/10.1007/978-94-017-7399-7\\_7](https://doi.org/10.1007/978-94-017-7399-7_7)
- HIGGINS, S. I., BUTTENWERF, R. and MONCRIEFF, G. R. (2016): Defining functional biomes and monitoring their change globally. In: *Global Change Biology* 22, 3583–3593. <https://doi.org/10.1111/gcb.13367>
- HIJMANS, R. J. and VAN ETTEN, J. (2012): raster: geographic analysis and modeling with raster data. R package version 2.0-12. <http://CRAN.R-project.org/package=raster>
- HIJMANS, R. J., CAMERON, S. E., PARRA, J. L., JONES, P. G. and JARVIS, A. (2005): Very high resolution interpolated climate surfaces for global land areas. In: *International Journal of Climatology* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>
- HOBBS, R. J.; HIGGS, E. and HARRIS, J. A. (2009): Novel ecosystems: implications for conservation and restoration. In: *Trends in Ecology & Evolution*. 24 (11), 599–605. <https://doi.org/10.1016/j.tree.2009.05.012>
- HOFFMANN, S.; IRL, S. and BEIERKUHNEIN, C. (2019): Predicted climate shifts within terrestrial protected areas worldwide. In: *Nature Communications* 10, 4787. <https://doi.org/10.1038/s41467-019-12603-w>
- HOLDRIDGE, L. R. (1947): Determination of world plant formations from simple climatic data. In: *Science* 105(2727), 367–368. <https://doi.org/10.1126/science.105.2727.367>
- (1964): *Life zone ecology*. San Jose, Costa Rica.
- HUMBOLDT, A. v. (1807): *Ideen zu einer Geographie der Pflanzen nebst einem Naturgemälde der Tropenländer: auf Beobachtungen und Messungen gegründet, welche vom 10ten Grade nördlicher bis zum 10ten Grade südlicher Breite, in den Jahren 1799, 1800, 1801, 1802 und 1803 angestellt worden sind*. Tübingen. <https://doi.org/10.5962/bhl.title.9310>
- HUMBOLDT, A. v. (1845–1862): *Kosmos – Entwurf einer physischen Weltbeschreibung*. Stuttgart und Tübingen. <https://doi.org/10.5962/bhl.title.4717>
- HUNTLEY, B.; ALLEN J. R. M.; FORREST, M.; HICKLER, T.; OHLEMUELLER, R.; SINGARAYER, J. S. and VALDES, P. J. (2021): Projected climatic changes lead to biome changes in areas of previously constant biome. In: *Journal of Biogeography* 48 (10), 2418–2428. <https://doi.org/10.1111/jbi.14213>
- IBISCH, P. L.; HOFFMANN, M. T.; KREFT, S.; PE’ER, G.; KATI, V.; BIBER-FREUDENBERGER, L.; DELLASALA, D.A.; VALE, M.M.; HOBSON, P. and SELVA, N. (2016): A global map of roadless areas and their conservation status. In: *Science* 354, 1423–1437. <https://doi.org/10.1126/science.aaf7166>
- JACOBSON, A. P.; RIGGIO, J.; TAFT, A. M. and BAILLIE, J. E. M. (2019): Global areas of low human impact (‘Low Impact Areas’) and fragmentation of the natural world. In: *Scientific Reports* 9, 14179. <https://doi.org/10.1038/s41598-019-50558-6>
- KAPLAN, J. O.; BIGELOW, N. H.; PRENTICE, I. C.; HARRISON, S. P.; BARTLEIN, P. J.; CHRISTENSEN, T. R.; CRAMER, W.; MATVEYEVA, N. V.; MCGUIRE, A. D.; MURRAY, D. F.; RAZZHIVIN, V. Y.; SMITH, B.; WALKER, D. A.; ANDERSON, P. M.; ANDREEV, A. A.; BRUBAKER, L. B.; EDWARDS, M. E. and LOZHKIN, A. V. (2003): Climate change and Arc-

- tic ecosystems: 2. Modeling, paleodata-model comparisons, and future projections. In: *Journal of Geophysical Research- Atmospheres* 108(D19), 8171, <https://doi.org/10.1029/2002JD002559>
- KARAGULLE, D.; FRYE, C.; SAYRE, R.; BREYER, S.; ANIELLO, P.; VAUGHAN, R. and WRIGHT, D. (2017): Modeling global hammond landform regions from 250-m elevation data. In: *Transactions in GIS* 22 (1), <https://doi.org/10.1111/tgis.12265>
- KARGER, D. N.; CONRAD, O.; BÖHNER, J.; KAWOHL, T.; KREFT, H.; SORIA-AUZA, R.W.; ZIMMERMANN, N. E.; LINDER, H. P.; KESSLER, M. (2017): Climatologies at high resolution for the earth's land surface areas. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.kd1d4>
- KATTGE, J. et al. (2019): TRY plant trait database - enhanced coverage and open access. In: *Global Change Biology*. <https://doi.org/10.1111/gcb.14904>
- KENDEIGH, S. C. (1961): *Animal ecology*. Prentice-Hall, Englewood Cliffs. <https://doi.org/10.5962/bhl.title.7351>
- KERNER VON MARILAUN, A. (1888): *Pflanzenleben*. 1. Band: *Gestalt und Leben der Pflanze*. Leipzig.
- KONDRASKOV, P.; SCHÜTZ, N.; SCHÜSSLER, C.; DE SEQUEIRA, M. M.; GUERRA, A. S.; CAUJAPÉ-CASTELLS, J.; JAÉN-MOLINA, R.; MARRERO-RODRÍGUEZ, Á.; KOCH, M. A.; LINDER, P.; KOVAR-EDER, J. and THIV, M. (2015): Biogeography of Mediterranean hotspot biodiversity: re-evaluating the 'Tertiary Relict' hypothesis of Macaronesian laurel forests. In: *PLoS ONE* 10 (7), e0132091. <https://doi.org/10.1371/journal.pone.0132091>
- KÖPPEN, W. (1884): Die Wärmezonen der Erde, nach der Dauer der heißen, gemässigten und kalten Zeit und nach der Wirkung der Wärme auf die organische Welt betrachtet. In: *Meteorologische Zeitschrift* 1, 215–226.
- (1931): *Grundriss der Klimakunde*. Berlin.
- (1936): *Das geographische System der Klimate*. Handbuch der Klimatologie. Band 1, Teil C. Berlin.
- KOWARIK, I. (1987): Kritische Anmerkungen zum theoretischen Konzept der potenziellen natürlichen Vegetation mit Anregungen zu einer zeitgemäßen Modifikation. In: *Tuexenia* 7, 53–68.
- LAWRENCE, A.; HOFFMANN, S. and BEIERKUHNLEIN, C. (2021): Topographic diversity as an indicator for resilience of terrestrial protected areas against climate change. In: *Global Ecology and Conservation* 25, e01445. <https://doi.org/10.1016/j.gecco.2020.e01445>
- LEEMANS, R. (1990): Possible changes in natural vegetation patterns due to global warming. IIASA Working Paper. IIASA, Laxenburg, Austria, WP-90-008. <http://pure.iiasa.ac.at/3443/>
- LIKENS, G. E. (ed.) (1981): *Some perspectives of the major biogeochemical cycles*: Scope 17. Chichester.
- MARTENS, C.; HICKLER, T.; DAVIS-REDDY, C.; ENGELBRECHT, F.; HIGGINS, S. I.; VON MALITZ, G. P.; MIDGLEY, G. F.; PFEIFFER, M. and SCHEITTE, S. (2020): Large uncertainties in future biome changes in Africa call for flexible climate adaptation strategies. In: *Global Change Biology* 27, 340–358. <https://doi.org/10.1111/gcb.15390>
- MERRIAM, C. H. (1892): The geographical distribution of life in North America with special reference to the Mammalia. In: *Proceedings of the Biological Society of Washington* 7, 1–64.
- MONCRIEFF, G. R.; BOND, W. J. and HIGGINS, S. I. (2016): Revising the biome concept for understanding and predicting global change impacts. In: *Journal of Biogeography* 43, 863–873. <https://doi.org/10.1111/jbi.12701>
- MONCRIEFF, G. R.; HICKLER, T. and HIGGINS, S. I. (2015): Intercontinental divergence in the climate envelope of major plant biomes. In: *Global Ecology and Biogeography* 24, 324–334. <https://doi.org/10.1111/geb.12257>
- MUCINA, L. (2018): Vegetation of Brazilian campos rupestres on siliceous substrates and their global analogues. In: *Flora* 238, 11–23. <https://doi.org/10.1016/j.flora.2017.06.007>
- (2019): Biome: evolution of a crucial ecological and biogeographical concept. In: *New Phytologist* 222, 97–114. <https://doi.org/10.1111/nph.15609>
- MÜLLER-HOHENSTEIN, K. (1979): *Die Landschaftsgürtel der Erde*. Stuttgart. <https://doi.org/10.1007/978-3-663-14175-4>
- MURTAGH, F. and LEGENDRE, P. (2014): Ward's hierarchical agglomerative clustering method: which algorithms implement Ward's criterion? In: *Journal of Classification* 31, 274–295. <https://doi.org/10.1007/s00357-014-9161-z>
- NOWOSAD, J. and STEPINSKI, T. F. (2018): Spatial association between regionalizations using the information-theoretical V-measure. In: *International Journal of Geographical Information Science* 32, 2386–2401. <https://doi.org/10.1080/13658816.2018.1511794>
- NÜRK, N. M.; LINDER, H. P.; ONSTEIN, R. E.; LARCOMBE, M. J.; HUGHES, C. E.; FERNÁNDEZ, L. P.; SCHLÜTER, P. M.; VALENTE, L.; BEIERKUHNLEIN, C.; CUTTS, V.; DONOGHUE, M. J.; EDWARDS, E. J.; FIELD, R.; FLANTUA, S. G. A.; HIGGINS, S.; JENTSCH, A.; LIEDE-SCHUMANN, S. and PIRIE, M. D. (2020): Diversification in evolutionary arenas – Assessment and synthesis. In: *Ecology and Evolution* 10, 6163–6182. <https://doi.org/10.1002/ece3.6313>
- ODUM, E. P. (1953): *Fundamentals of ecology*. Philadelphia.
- OLSON, D. M. and DINERSTEIN, E. (2002): The Global 200: priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* 89, 125–126. <https://www.jstor.org/stable/3298564>
- OLSON, D. M.; DINERSTEIN, E.; WIKRAMANAYAKE, E. D.; BURGESS, N. D.; POWELL, G. V. N.; UNDERWOOD, E. C.; D'AMICO, J. A.; ITOUA, I.; STRAND, H. E.; MORRISON, J. C.; LOUCKS, C. J.; ALLNUTT, T. F.; RICKETTS, T. H.; KURA, Y.

- LAMOREUX, J. F.; WETTENGEL, W. W.; HEDAO, P. and KASSEM, K. R. (2001): Terrestrial ecoregions of the world: a new map of life on Earth. In: *Bioscience* 51 (11), 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- PEEL, M. C.; FINLAYSON, B. L. and MCMAHON, T. A. (2007): Updated world map of the Köppen-Geiger climate classification. In: *Hydrology and Earth System Sciences Discussions, European Geosciences Union*, 11 (5), 1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>
- PENNINGTON, R. T.; CRONK, Q. C. B. and RICHARDSON, J. A. (2004): Introduction and synthesis: plant phylogeny and the origin of major biomes. In: *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 359, 1455–1464. <https://doi.org/10.1098/rstb.2004.1539>
- PFADENHAUER, J. and KLÖTZLI, F. (2014) *Vegetation der Erde*. Berlin. <https://doi.org/10.1007/978-3-642-41950-8>
- PIELOU, E. C. (1979): *Biogeography*. New York.
- PRENTICE, I. C.; BONDEAU, A.; CRAMER, W.; HARRISON, S. P.; HICKLER, T.; LUCHT, W.; STICH, S.; SMITH, B. and SYKES, M. T. (2007): Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: CANADELL, J. G.; PATAKI, D. E. and PITTELKA, L. F. (eds.): *Terrestrial Ecosystems in a Changing World*. Berlin Heidelberg, 175–192. [https://doi.org/10.1007/978-3-540-32730-1\\_15](https://doi.org/10.1007/978-3-540-32730-1_15)
- PRENTICE, I. C.; CRAMER, W.; HARRISON, S. P.; LEEMANS, R.; MONSERUD, R. A. and SOLOMON, A. M. (1992): A global biome model based on plant physiology and dominance, soil properties and climate. In: *Journal of Biogeography* 19 (2), 117–134. <https://doi.org/10.2307/2845499>
- R Core Team (2021): R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- RAFIQPOOR, M. D. and BRECKLE, S.-W. (2019): *Ecology of climate and vegetation zones of the earth*. Meckenheim.
- RAMANKUTTY, N. and FOLEY, J. A. (1999): Estimating historical changes in global land cover: croplands from 1700 to 1992. In: *Global Biogeochemical Cycles* 13 (4), 997–1027. <https://doi.org/10.1029/1999GB900046>
- RAUNKJÆR, C. C. (1905): Types biologiques pour la géographie botanique. In: *Oversigt Over Det Kongelige Danske Videnskabernes Selskabs Forhandling* 5, 347–437.
- RINGELBERG, J. J.; ZIMMERMANN, N. E.; WEEKS, A.; LAVIN, M. and HUGHES, C. E. (2020): Biomes as evolutionary arenas: convergence and conservatism in the trans-continental succulent biome. In: *Global Ecology and Biogeography* 29 (7), 1100–1133. <https://doi.org/10.1111/geb.13089>
- RICHTER, M. (2001): *Vegetationszonen der Erde*. Gotha.
- RICKETTS, T. H.; DINERSTEIN, E.; OLSON, D. M.; LOUCKS, C.; EICHBAUM, W.; KAVANAGH, K.; HEDAO, P.; HURLEY, P.; CARNEY, K. M.; ABEL, R. AND WALTERS, S. (1999): Terrestrial ecoregions of North America: a conservation assessment. Washington, D.C.
- ROSENBERG, A.; and HIRSCHBERG, J. (2007): V-measure: a conditional entropy-based external cluster evaluation measure. In: *Proceedings of the 2007 joint conference on empirical methods in natural language processing and computational natural language learning (EMNLP-CoNLL)*.
- RÜBEL, E. (1930): *Pflanzengesellschaften der Erde*. Berlin.
- RUTHERFORD, M. C.; MUCINA, L. and POWRIE, L. W. (2006): Biomes and bioregions of Southern Africa. In: MUCINA, L. and RUTHERFORD, M. C. (eds.): *The vegetation of South Africa, Lesotho and Swaziland*. Pretoria, 30–51.
- SANDERSON, E. W.; JAITEH, M.; LEVY, M. A.; REDFORD, K. H.; WANNEBO, A. V. and WOOLMER, G. (2002): The human footprint and the last of the wild. In: *BioScience* 52 (10), 891–904. [https://doi.org/10.1641/0006-3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)
- SAYRE, R.; DANGERMOND, J.; FRYE, C.; VAUGHAN, R.; ANIELLO, P.; BREYER, S.; CRIBBS, D.; HOPKINS, D.; NAUMANN, R.; DERRENBACHER, B.; WRIGHT, D.; BROWN, C.; BUTLER, K.; BENNETT, L.; SMITH, J.; BENSON, L.; VAN SISTINE, D.; WARNER, H.; CRESS, J.; DANIELSON, J.; HAMANN, S.; CECERE, T.; REDDY, A.; BURTON, D.; TRUE, D.; METZGER, M.; HARTMANN, J.; MOOSDORF, N.; DURR, H.; PAGANINI, M.; DEFURNEY, P.; ARINO, O.; ANDERSON, M.; COMER, P.; MAYNARD, S. and GROSSE, A. (2014): A new map of high resolution global ecological land units from ecophysiological stratification. U.S. Geological Survey Open File Report. Washington, DC.
- SCHWEITER, S.; LANGAN, L. AND HIGGINS, S. (2013): Next-generation dynamic global vegetation models: learning from community ecology. In: *The New Phytologist* 198, 957–969. <https://doi.org/10.1111/nph.12210>
- SCHIMPER, A. F. W. (1898): *Pflanzengeographie auf physiologischer Grundlage*. Jena.
- SCHMITHÜSEN, J. (1976): *Atlas zur Biogeographie*. Mannheim.
- SCHULZE, E. D.; BECK, E. and MÜLLER-HOHENSTEIN, K. (2002): *Pflanzenökologie*. Heidelberg.
- SCHULTZ, J. (1988): *Die Ökozonen der Erde - Die ökologische Gliederung der Geosphäre*. Stuttgart.
- SCHULTZ, J. (1995): *The ecozones of the world: the ecological divisions of the geosphere*. Berlin. <https://doi.org/10.1007/978-3-662-03161-2>
- SCHULTZ, J. (2016): *Die Ökozonen der Erde*. Stuttgart. <https://doi.org/10.36198/9783838546285>
- SHELFORD, V. E. (1932): Basic principles on the classification of communities and habitats and the use of terms. In: *Ecology* 13, 105–120. <https://doi.org/10.2307/1931062>
- STICH, S.; SMITH, B.; PRENTICE, I. C.; ARNETH, A.; BONDEAU, A.; CRAMER, W.; KAPLAN, J. O.; LEVIS, S.; LUCHT, W.; SYKES, M. T.; THONICKE, K. and VENESKY, S. (2003): Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vege-

- tation model. In: *Global Change Biology* 9 (2), 161–185. <https://doi.org/10.1046/j.1365-2486.2003.00569.x>
- STRAHLER, A. N. (1969): *Physical geography*. New York
- TANSLEY, A. G. (1935): The use and abuse of vegetational concepts and terms. In: *Ecology* 16 (3), 284–307. <https://doi.org/10.2307/1930070>
- THORNTHWAITE, C. W. (1933): The climates of the Earth. In: *Geographical Review* 23, 433–440. <https://doi.org/10.2307/209629>
- (1948): An approach toward a rational classification of climate. In: *Geographical Review* 38 (1), 55–94. <https://doi.org/10.2307/210739>
- TNC (The Nature Conservancy) (2009): Global ecoregions, major habitat types, biogeographical realms and The Nature Conservancy Terrestrial Assessment Units. <https://geospatial.tnc.org/datasets/b1636d640ede4d-6ca8f5e369f2dc368b/about>
- TNC, USDA and USGS (The Nature Conservancy, SDA Forest Service and U.S. Geological Survey), based on BAILEY, R. G. (1995): Description of the ecoregions of the United States. USDA Forest Service Misc. Pub. No. 1391. <https://databasin.org/datasets/9c7bc177c6154d71b0458391f3177053/>
- TOOT, R.; FRELICH, L. E.; BUTLER, E. E. and REICH, P. B. (2020): Climate-biome envelope shifts create enormous challenges and novel opportunities for conservation. In: *Forests* 11 (9), 1015. <https://doi.org/10.3390/f11091015>
- TREWARTH, G. L. (1968): *An introduction to climate*. New York.
- TREWARTH, G. L. and HORN, L. H. (1980): *An introduction to climate*. New York.
- TROLL, C. and PAFFEN, K. H. (1964): Karte der Jahreszeiten-Klimate der Erde. In: *Erdkunde*, 18 (1), 5–28. <https://doi.org/10.3112/erdkunde.1964.01.02>
- TÜXEN, R. (1956): Die heutige potentielle natürliche Vegetation als Gegenstand der Vegetationskartierung. In: *Angewandte Pflanzensoziologie* 13, 5–42.
- UDVARDY, M. D. F. (1975): A classification of the biogeographical provinces of the world. IUCN Occasional paper 18. Morges, Switzerland.
- VALENTINE, J. W. (1968): The evolution of ecological unites above the population level. In: *Journal of Paleontology* 42, 253–267.
- VERNADSKY, W. (1926): *Biosfera*. engl. translation, *The Biosphere*. New York 1998. <https://doi.org/10.1007/978-1-4612-1750-3>
- VERNADSKY, W. (1945): The biosphere and the noosphere. In: *American Scientist* 33, 1–12.
- WALTER, H. (1964): *Die Vegetation der Erde*. Band 1. Stuttgart.
- WALTER, H. (1968): *Die Vegetation der Erde*. Band 2. Stuttgart.
- WALTER, H. (1973): *Vegetation of the earth in relation to climate and eco-physical conditions*. New York.
- WALTER, H. and BOX, E. (1976): Global classification of natural terrestrial ecosystems. In: *Vegetatio* 32, 75–81. <https://doi.org/10.1007/BF02111901>
- WALTER, H. and BRECKLE, S. (1985): *Ecological systems of the geobiosphere*. Volume 1: ecological principles in global perspective. New York. [https://doi.org/10.1007/978-3-662-02437-9\\_1](https://doi.org/10.1007/978-3-662-02437-9_1)
- (1991): *Ökologie der Erde*, Band 1 Grundlagen. Stuttgart.
- (2002): *Walter's Vegetation of the Earth*. Heidelberg, Berlin.
- WESSEL, P. and SMITH, W. H. F. (2017): A global self-consistent, hierarchical, high-resolution Geography Database. <http://www.soest.hawaii.edu/wessel/gshhg/>
- WHITTAKER, R. H. (1975): *Communities and ecosystems*. New York.
- WIKEN, E. B. (1986): *Terrestrial ecozones of Canada*. Ecological land classification Series No. 19. Hull, Quebec.
- WOHLGEMUTH, T.; JENTSCH, A. and SEIDL, R. (eds.) (2019): *Störungsökologie*. Bern. <https://doi.org/10.36198/9783838550183>
- WOODWARD, I.; LOMAS, M. R. and KELLY, C. K. (2004): Global climate and the distribution of plant biomes. In: *Philosophical Transactions of the Royal Society B: Biological Science*, 359, 1465–1476. <https://doi.org/10.1098/rstb.2004.1525>

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## Appendix

**Appendix 1: List of climatic parameters used in this study (following KARGER et al. 2017)**

Climatic parameter	Unit
Annual Mean Temperature	°C
Mean Diurnal Range	°C
Isothermality	°C
Temperature Seasonality	°C
Max Temperature of Warmest Month	°C
Min Temperature of Coldest Month	°C
Temperature Annual Range	°C
Mean Temperature of Wettest Quarter	°C
Mean Temperature of Driest Quarter	°C
Mean Temperature of Warmest Quarter	°C
Mean Temperature of Coldest Quarter	°C
Annual Precipitation	mm
Precipitation of Wettest Month	mm
Precipitation of Driest Month	mm
Precipitation Seasonality	mm
Precipitation of Wettest Quarter	mm
Precipitation of Driest Quarter	mm
Precipitation of Warmest Quarter	mm
Precipitation of Coldest Quarter	mm
Potential Evapotranspiration	mm
Surface solar radiation downwards	kJ/m <sup>2</sup>

**Appendix II: ‘High-resolution maps and legends of established global concepts for biomes, ecozones and climate zones that were processed within this study’ is available online: <https://doi.org/10.3112/erdkunde.2021.04.01a>**

**Appendix III: ‘2D Kernel graphs for all condensed biomes’ is available online: <https://doi.org/10.3112/erdkunde.2021.04.01b>**