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## METHOD

# How to map biomes: Quantitative comparison and review of biome-mapping methods

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### Abstract

Biomes are large-scale ecosystems occupying large spaces. The biome concept should theoretically facilitate scientific synthesis of global-scale studies of the past, present, and future biosphere. However, there is neither a consensus biome map nor universally accepted definition of terrestrial biomes, making joint interpretation and comparison of biome-related studies difficult. “Desert,” “rainforest,” “tundra,” “grassland,” or “savanna,” while widely used terms in common language, have multiple definitions and no universally accepted spatial distribution. Fit-for-purpose classification schemes are necessary, so multiple biome-mapping methods should for now co-exist. In this review, we compare biome-mapping methods, first conceptually, then quantitatively. To facilitate the description of the diversity of approaches, we group the extant diversity of past, present, and future global-scale biome-mapping methods into three main families that differ by the feature captured, the mapping technique, and the nature of observation used: (1) *compilation* biome maps from expert elicitation, (2) *functional* biome maps from vegetation physiognomy, and (3) *simulated* biome maps from vegetation modeling. We design a protocol to measure and quantify spatially the pairwise agreement between biome maps. We then illustrate the use of such a protocol with a real-world application by investigating the potential ecological drivers of disagreement between four broadly used, modern global biome maps. In this example, we quantify that the strongest disagreement among biome maps generally occurs in landscapes altered by human activities and moderately covered by vegetation. Such disagreements are sources of bias when combining several biome classifications. When aiming to produce realistic biome maps, biases could be minimized by promoting schemes using observations rather than predictions, while simultaneously considering the effect of humans and other ecosystem engineers in the definition. Throughout this review, we provide comparison and decision tools to navigate the diversity of approaches to encourage a more effective use of the biome concept.

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**KEYWORDS**

biogeography, ecology, map comparison, paleoecology, plant functional traits, remote sensing, vegetation, vegetation modeling

## INTRODUCTION

“A biome is a large-scale ecosystem occupying large spaces at least at the (sub)continental scale, or found in the form of a complex of small-scale, isolated patches scattered across those large spaces” (Mucina, 2019). Biomes are ecological and biogeographical tools intended to represent the basic biological units of the terrestrial biosphere (Hanks, 2011; Mucina, 2019), such as “tropical rainforest,” “temperate deciduous forest,” “savanna,” or “grassland.” The biome concept facilitates qualitative and quantitative comparisons of such categories at the global scale. Since the first written mention of the term “biome” in the early 20th century (Clements, 1917; Mucina, 2019; Nicolson, 2013), several dozen global biome-classification schemes have emerged (e.g., Ellis et al., 2021; Melillo et al., 1993; Myneni et al., 1997; Running et al., 1995; and 35 references in table 2 in Mucina, 2019). The ensuing diversity of biome-delimitation criteria gave rise to various global biome maps (e.g., Ellis & Ramankutty, 2008; Friedl et al., 2010; Haxeltine & Prentice, 1996; Higgins et al., 2016; Leemans, 1990a, 1990b; Melillo et al., 1993; Olson et al., 2001; Prentice et al., 1992; Walter, 1973; Figure 1).

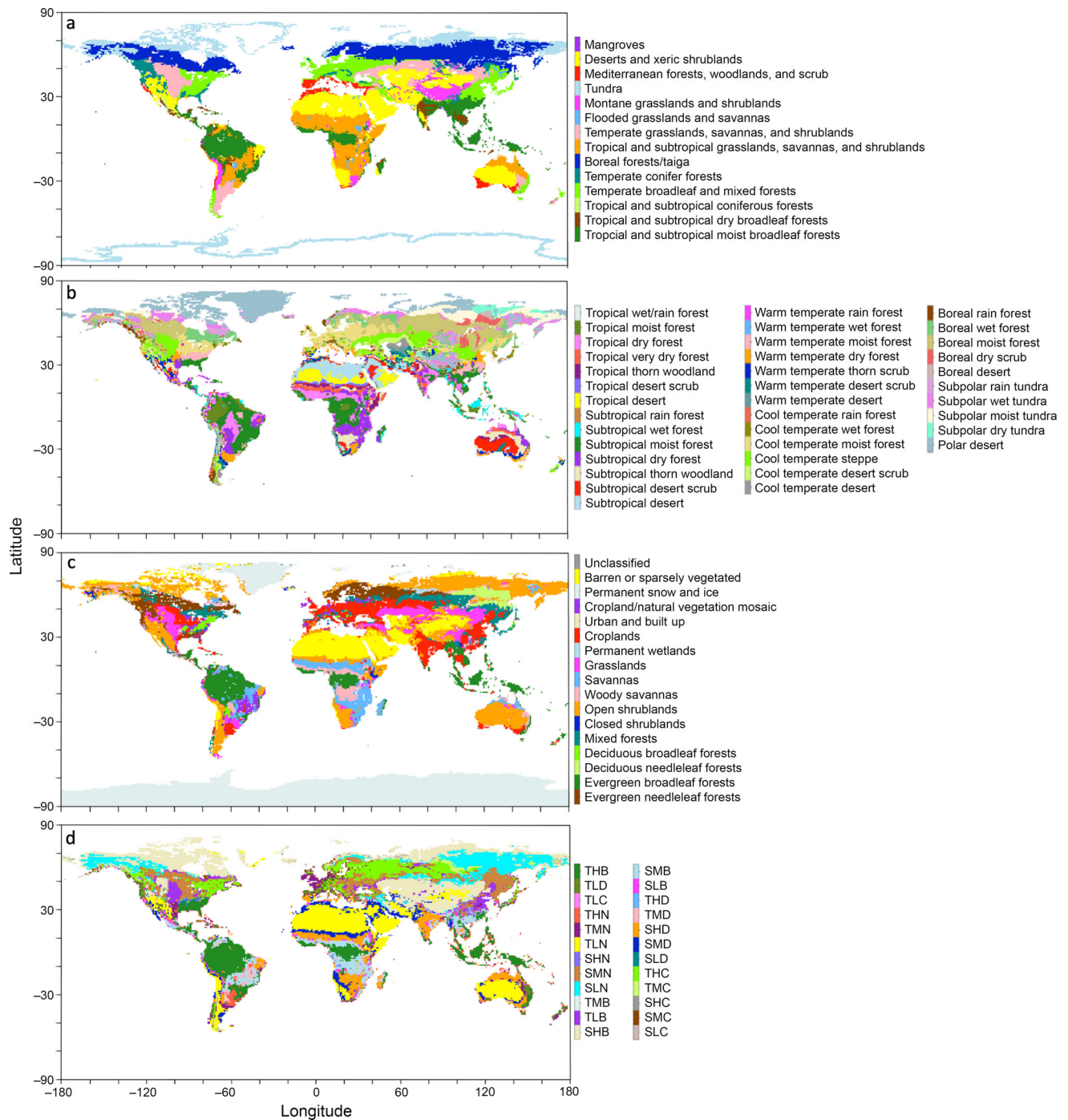
Four main drivers are responsible for this diversification: (1) the diversity of vegetation, climate, soil, and topography that can be interpreted differently depending on expertise, application, and objective (Moncrieff et al., 2016; Running et al., 1995); (2) the rise of analytical tools that facilitate the study of the biosphere at global scales (e.g., remote sensing, vegetation modeling); (3) the evolution of the concept from descriptions of the physical environment toward those quantifying ecosystem functions such as productivity or habitat (Mucina, 2019); and (4) the diversification of uses of biomes from conservation biology to the assessment of global fluxes of matter and energy (Mucina, 2019). Although there are many definitions of biome, in this review, for practical reasons we adopt the definition of Mucina (2019).

In the absence of data on the effect of the diversity of biome-delimitation criteria used on the variability of biome maps, using different criteria to distinguish and map biomes can be an obstacle for effective comparison, validation, understanding, and application of the concept. Results emerging from one type of classification cannot be used when studying another because a universal translation protocol does not yet exist. Studies referring to biomes

should therefore acknowledge the assumptions and approaches underlying different biome-classification schemes and the impact of these on ensuing spatial differences. While some studies have arbitrarily decided to use only one set of criteria while ignoring other classification schemes (e.g., da Silva Junior et al., 2020; Mittermeier et al., 2003; Stocker et al., 2018), others have attempted to work around this problem by considering expert knowledge-based equivalencies among categories (Werner et al., 2018) or by using low-level classification (i.e., by aggregating biomes into fewer, simplified categories) (Dallmeyer et al., 2017; Harrison & Bartlein, 2012; Monserud & Leemans, 1992).

However, there is no effort to converge toward a single universal scheme or to reject others, even with the advent of fully automated classification schemes (i.e., without follow-up expert assessment required for quality control) designed to produce “objective” biome maps but relying on expert selections of biome-delimitation criteria (e.g., Conradi et al., 2020; Higgins et al., 2016; Moncrieff et al., 2016; Woodward et al., 2004). New biome-classification schemes rather aim to facilitate new applications of the biome concept, but it is sometimes unclear which approach fits which purpose best. In this context, it makes more sense to learn how to navigate carefully through the diversity of approaches, rather than trying to develop a consensus map.

In this review we describe why and how different global-scale terrestrial biome-mapping methods differ. In the first section, we describe the conceptual differences among biome-mapping methods by grouping past, present, and future maps into three main families of methods: (1) compilation, (2) functional, and (3) simulated biome maps. In the following two sections, we aim to quantify the spatial differences among biome maps. In the next section, we provide an algorithmic protocol for comparing existing georeferenced global biome maps spatially. In the third section, we provide a real-world demonstration to illustrate the use of a unified protocol by quantifying and mapping the spatial agreement among classifications to identify the correlations between the spatial distribution of agreement among biome-classification schemes and several environmental descriptors. Ultimately, we discuss how to choose between biome-classification schemes depending on the research question, scope, and audience.



**FIGURE 1** Global biome maps compared in this study. (a) Compilation biome map of World Wildlife Fund Terrestrial Ecoregions of the World (Olson et al., 2001). (b) Simulated biome map from Holdridge's (1967) life zones (Leemans, 1990a, 1990b) and two functional biome maps: (c) MODIS-IGBP land-cover-type product (Friedl et al., 2010; Loveland & Belward, 1997) and (d) dominant biome distribution over 31 years from global functional biome scheme from Higgins et al. (2016, 2017). Biome names are derived from three letters (1) tall versus short, (2) low, medium, and high vegetation productivity index, and (3) cold, dry, both cold and dry, nonseasonal for growth limitation index.

## MAPPING PAST, PRESENT, AND FUTURE BIOMES: METHODS AND PROXIES

The biome concept engendered dozens of classification schemes and various biome maps. In this section, we first

describe how the biome concept fits with other biogeographical concepts. Next, we describe the different methods for mapping the current distribution of biomes by grouping them into three main families of methods: (1) compilation biome maps from expert elicitation, (2) functional biome maps from vegetation physiognomy,

and (3) simulated biome maps from vegetation modeling. We then use these same families to describe methods for mapping the past and future distribution of biomes. We use these categories to describe the diversity of approaches, although other categorizations could be used based on other criteria.

## Biomes among other biogeographical concepts

The general biome concept is derived from five previous and disconnected, finer-scale notions that all attempted to define a group of life forms living together as a single, universal unit (Mucina, 2019). These were (1) *community* (Clements & Shelford, 1939)—a generic term for a group of organisms at any scale; (2) *association* (Nicolson, 2013; von Humboldt & Bonpland, 1805)—a local-scale community describing a common and predictable grouping of populations of species with consistent physiognomy; (3) *formation* (Grisebach, 1838 in Egerton, 2017; Schimper, 1903; Clements & Shelford, 1939; Whittaker, 1957)—a landscape-scale community grouping various associations, characterized by its dominant growth form, developing through a succession of definite stages in response to a specific climate; (4) *biocoenosis* (Möbius, 1877; Clements & Shelford, 1939)—a term coupling association with the biological interactions within it; and (5) *life zone* (Holdridge, 1967; Merriam, 1892, 1894)—representing a finite combination of physical properties of the environment that host a specific biological formation.

The biome concept provides broad-scale studies with a simple, natural “background” of major ecosystems that transcends parochial community composition, regionally specific species distributions, and other spatially unique processes. Biomes are not uniform in terms of physiognomy. Disturbances such as fires and windstorms create spatial variability by favoring the coexistence of different successional stages in close proximity. Therefore, biomes are large-scale ecosystems incorporating “a complex of fine-scale biotic communities” encompassing both plant and animal life (Mucina, 2019). Additionally, two separate biomes can share common ecological, functional, or climatic traits (Beierkuhnlein & Fischer, 2021; Moncrieff et al., 2015; Mucina, 2019).

When it comes to naming and mapping, biomes are usually attributed to the dominant plant formation they host (Box & Fujiwara, 2005). Biome names are often combinations of adjectives describing dominant plant functional (e.g., evergreen, deciduous, broadleaf, woody) or climatic traits (e.g., “warm,” “dry,” “seasonal,” “tropical,” “boreal”) of communities (Figure 1, Appendix S1: Table S1).

Sometimes, biome names refer instead to a specific place that serves as a reference for describing comparable biological communities around the world, such as “savanna,” first used to describe the mixed tree and grass vegetation of the Venezuelan *llanos* (Oviedo, 1535 in Balátová-Tuláčková & Surli, 1983; Cole, 1960), or “taiga,” initially designating northern Russian coniferous forests (Marcuzzi, 1979). Grouping distinct communities around the world under the banner of a specific place suggests that the definition of such biomes depends on the characteristics of the place of reference, thus representing a challenge to map biomes objectively.

The biome concept complements Earth-scale categorizations of the biosphere that are based more on species identity, such as the 846 “ecoregions” distributed across 14 biomes (Dinerstein et al., 2017; Olson et al., 2001), the 198 “biotic provinces” (Dasmann, 1974), the 193 “biogeographic provinces” (Udvardy, 1975), or even the continent-sized “realms” like the six “floristic realms” (Walter & Straka, 1970) or the eight “biogeographic realms” (Dinerstein et al., 2017; Udvardy, 1975). By their very nature, the four latter, region-specific units are based on taxonomic similarity, with a strong imprint of geological history such as continental arrangements, past glaciations, or the establishment of temporary land bridges in the Pleistocene (Olson et al., 2001). But unlike biomes, region-specific units do not consider structural and functional similarities of the vegetation among regions. The biome concept is thus rooted in the phenomenon of functional convergence, which states that several taxa from different phylogenetic background can evolve to share some functional traits to adapt to similar environmental conditions (Moncrieff et al., 2015; Prentice & Webb III, 1998).

By grouping spatially distinct biological communities with different species compositions, biomes therefore attempt to make these communities uniform to provide some form of standardized comparison. For example, mapping biome distributions in conservation biology provides the basis for drawing the boundaries of endangered areas and habitats at a global scale in a standardized way (e.g., Bond & Parr, 2010; Brancalion et al., 2019; Dinerstein et al., 2017; Olson et al., 2001; Olson & Dinerstein, 1998). Another example pertains to the assessment of human land-use impacts on the biosphere, which includes the concept of anthropogenically defined biomes (“anthromes”) (Dinerstein et al., 2017; Ellis & Ramankutty, 2008) that provides a means to compare human-modified systems across regions (Bodart et al., 2013; Ellis & Ramankutty, 2008; Loveland et al., 2000; Myneni et al., 1997). The analogy between the concept of anthromes and biomes can be debated depending on whether one considers people and cultures as part of nature or as an anomaly that merely disrupts nature. In this review, we

have considered global-scale maps of anthromes and land use as “biome” maps in the broadest sense, following other studies (e.g., Conradi et al., 2020; Ellis et al., 2021; Ellis & Ramankutty, 2008; Higgins et al., 2016; Moncrieff et al., 2015). Biomes also provide a framework of homogeneous units to assess and predict the consequences of climate change on the biosphere for both past and future distributions of life on Earth (Allen et al., 2010; Gonzalez et al., 2010; Huntley et al., 2021; Li & Zhang, 2017; Prentice et al., 1992), to compare long-vanished landscapes to modern analogs (e.g., Dallmeyer et al., 2017; Prentice & Webb III, 1998; Sobol et al., 2019), and to represent spatially the global-scale exchanges of matter and energy such as the carbon cycle or nitrogen fixation (e.g., da Silva Junior et al., 2020; Stocker et al., 2018; Turner et al., 2006; Yi et al., 2010; Zheng et al., 2019).

## Approaches to derive modern biome maps

Several classification approaches have facilitated global-scale biome mapping. For describing and subdividing the entirety of nature—from individuals, populations, and species to ecosystems—it might seem desirable to know the distributions of every single species, genotype, or phenotype on the planet. But such information is obviously impossible to acquire, so biome maps must rely instead on the patchy and incomplete data available (Holdridge, 1967; Moncrieff et al., 2016; Udvardy, 1975), even considering the recent advances in data collection and sharing. The resulting maps are thus limited by the quality and completeness of the underlying data, even at local scales. In addition, the diversity of classifications itself stems from the growing diversity of criteria used to define biomes. Biome-mapping criteria often depend on a selection of proxies such as local physical and biological observations of climate, geomorphology, soils, and plant and animal communities (Mucina, 2019). Given the gradual spatial arrangement of biological communities (e.g., Box, 1981; Woodward et al., 2004), mapping biomes commonly involves drawing hard spatial boundaries based on a set of criteria that include precise thresholds, the choice of which is inherently arbitrary and imperfect.

The set of *biomes* used is then designed to match the specific needs of a particular application or research question, assuming explicitly that the definition of biomes cannot be universally useful (Conradi et al., 2020; Higgins et al., 2016). For example, while biome maps aiming to represent the actual distribution of biological communities facilitate the monitoring of changes in terrestrial ecosystems (e.g., Friedl et al., 2010; Higgins et al., 2016), other biome maps reflecting biome distribution as might be expected when considering only some

environmental factors as drivers are more useful for projecting changes in ecosystem distribution through time (e.g., Gonzalez et al., 2010; Huntley et al., 2021). Many biome maps aim to represent the distribution of potential natural vegetation, which is the expected state of mature vegetation without human intervention (Chiarucci et al., 2010; Tüxen, 1956). For example, potential natural vegetation maps would represent an agricultural landscape as a forest or grassland that it once was under similar environmental conditions, or as it would become if human activities ceased. While being a traditional tool in vegetation science, the definition, realism, and usefulness of the potential natural vegetation concept remain strongly debated (e.g., Box & Fujiwara, 2005; Chiarucci et al., 2010; Kowarik, 1987; Loidi & Fernández-González, 2012; Mucina, 2010). Often it is unclear what is “natural.” For example, it is still debated to what extent the glacial steppes of the Northern Hemisphere disappeared as a result of climate change or because humans drove large megafauna grazers (which acted as ecosystem engineers), such as the woolly mammoth (*Mammuthus primigenius*), to extinction (Owen-Smith, 1987; Zimov, 2005; Zimov et al., 1995). The natural extent of grasslands in Europe is also debated, which has important implications for conservation (Feurdean et al., 2018).

In what follows, we differentiate among three families of methods to map biomes (Table 1) that differ by the feature captured, the mapping technique, and the nature of observation used (i.e., compilation maps from expert elicitation, functional maps from vegetation physiognomy, and simulated biome maps from vegetation modeling). We identify the pros and cons of each family of methods. In delineating their specific sources of uncertainty, we use Dietze’s (2017) first-principle concepts of prediction uncertainty (Appendix S1: Table S2), which are applicable across the three families of biome-mapping approaches.

## Compilation biome maps from expert elicitation

Biome maps derived from ground observations attempt to capture in a single map the real diversity of local perceptions of biological community distributions (i.e., based on local classification systems). Such maps were first generated by expert elicitation, gathering reports of field observations by local experts, and assigning them to particular biomes based on an almost unlimited quantity of ground observations (e.g., plant and animal species composition and diversity, vegetation structure and successional relationships, climate, soil, topography). First, local observations are extrapolated

**TABLE 1** Biome-classification families and how to apply them.

Biome-mapping family	Underlying data	Features captured	Global mapping method	Examples of global biome maps
Compilation	Unlimited field observations (e.g., plant and animal species composition and diversity, vegetation structure and successional relationships, climate, soil, topography)	Subjectively expected state of mature vegetation (i.e., in equilibrium with climate) without human impact, global patchwork of local perceptions	Compilation of preexisting regional maps using expert elicitation for category equivalencies	Melillo et al. (1993), Olson et al. (2001)
Functional	Vegetation physiognomy, temperature profiles, population density	Actual distribution of vegetation functional traits	Combinations of vegetation functional traits derived from satellite imagery	Ellis and Ramankutty (2008), Friedl et al. (2010), Higgins et al. (2016, 2017)
Simulated	Physical environment (e.g., soil, climate, CO <sub>2</sub> concentrations), relationships between vegetation traits and physical environment	Statistically expected vegetation distribution under theoretical assumptions	Correlative or mechanistic modeling	Walter (1973), Leemans (1990a, 1990b), Holdridge (1967), Prentice et al. (1992) Haxeltine and Prentice (1996)

*Note:* We grouped existing biome classifications by how they define and map biomes, that is, the method and underlying data used for mapping and the features captured.

spatially to draw continuous regional biome maps derived from various biome-delineation criteria. Second, regional maps are combined using category equivalencies defined by expert elicitation to produce global maps (Friedl et al., 2010).

Uncertainty in compiled biome maps then relates predominantly to accuracy and density of underlying observations (driver uncertainty), as well as equivalency definitions (Appendix S1: Table S2). Global biome maps resulting from the compilation of regional maps ensure compatibility with preexisting regional maps, thereby facilitating their broad understanding and acceptance. The large time span among the various observations makes these maps timeless representations of the biosphere, usually focusing on potential natural vegetation. Olson et al. (2001) used this approach by combining observations from over a thousand regional experts to produce one of the most widely used global biome maps in existence today (Figure 1a), endorsed by the World Wildlife Fund and the Intergovernmental Science-Policy Platform of Biodiversity and Ecosystem Services (IPBES, 2019). Similarly, Melillo et al. (1993) combined ground-deduced local vegetation maps from 12 different continental-scale sources to produce a global “potential natural vegetation” map. Pfadenhauer and Klötzli (2014) also combined 16 regional sources to produce a global map of “Earth’s vegetation,” using sources different from those used by Melillo et al. (1993). However, Melillo et al. (1993), Olson et al. (2001), and Pfadenhauer and Klötzli (2014) mapped the global distribution of biomes without providing any definition of

a biome or vegetation type, even if Melillo et al. (1993) provided some basic, ecosystem-based estimates and predictions regarding their total area, net primary production, and nitrogen uptake.

The absence of proper biome definitions contributes to the general subjectivity and lack of repeatability of compilation biome maps (Higgins et al., 2016; Moncrieff et al., 2015) because such derived, global-scale maps must be necessarily based on the compilation of incompatible, local-scale classifications. Although often considered “biome” maps by others, compilation biome maps are not based on any generalized classification system and do not “map” biomes *stricto sensu*. Considering regional map compilation as a proper mapping method can therefore be legitimately debated.

## Functional biome maps from vegetation physiognomy

Functional biome maps summarize the distribution of structural and functional attributes of existing vegetation. Such biomes can be efficiently delineated at the global scale by converting satellite imagery data into vegetation attributes such as plant ground cover (e.g., leaf area index [LAI]), leaf physiognomy (e.g., needle, broadleaf), leaf phenology (e.g., deciduous, evergreen, semi-evergreen), plant height, or leaf orientation (e.g., erectophile, planophile) (Friedl et al., 2010; Higgins et al., 2016; Myneni et al., 1997; Woodward et al., 2004).

Satellite products also include the impacts of human activities, ultimately culminating in the concept of “anthromes” (i.e., anthropogenic biomes) that explicitly treat people and cultures as part of nature rather than as an anomaly that merely disrupts it (Ellis et al., 2021; Ellis & Ramankutty, 2008). Some vegetation functional traits can be locally measured from the ground, and increasing data availability, for example, through the TRY plant functional trait database (Kattge et al., 2020), makes it possible to derive global map estimates (e.g., Butler et al., 2017). Satellite imagery provides measurements in poorly studied areas, such as inaccessible or dangerous places (Popkin, 2015).

Satellite imagery has provided a means to automate the delineation of biomes using standard observations at the global scale, thereby reducing subjectivity. The subjectivity in biome classification algorithms based on remote sensing is open to scrutiny, but the observations and analyses are in digital form, as opposed to the personal experiences of local experts. Remote sensing most notably gave rise to the well-known Moderate Resolution Imaging Spectrometer—International Geosphere Biosphere Programme (MODIS-IGBP) land-cover types, using images from MODIS satellites and following the IGBP biome classification (Friedl et al., 2010; Loveland & Belward, 1997; Figure 1c). Arguing that the IGBP classification uses preconceived ideas of what biomes should look like to decide on their definition, Higgins et al. (2016) more recently developed a global functional biome scheme based on combinations of three global vegetation attributes of height, productivity, and seasonality (Figure 1d). Ellis and Ramankutty (2008) mapped the first global anthrome distribution by combining land-use and land-cover data from satellite imagery with human-population census data.

Satellite-derived functional biome definitions still exclude many data describing botanical, ecological, and some functional characteristics of plants (e.g., Friedl et al., 2010; Higgins et al., 2016; Moncrieff et al., 2016). Limitations also include strict numerical thresholds of ground cover that can only be inferred from space, such as a threshold of 60% of trees used to define “forest” biomes in the IGBP classification (Loveland & Belward, 1997). Nor does the use of such thresholds consider the large uncertainties associated with the translation of remote-sensing signals into biological descriptors (Houborg et al., 2015). For example, the combination of many factors related to the signal received and its treatment methods can cause >50% of relative uncertainty in the measurement of the LAI from remote sensing (Fang et al., 2019). In summary, correlating remote sensing with ecological “groundtruthing” hinges on model parameterization and calibration, and could thus suffer from concomitant

parameter-related uncertainties (Appendix S1: Table S2). Consequently, this type of classification is difficult to compare to ground observations and is equivocal for vegetation communities scoring close to the threshold.

## Simulated biome maps from vegetation modeling

Biome maps from vegetation modeling are predictions of the distribution of vegetation considering a set of precise assumptions. Broad-scale vegetation modeling stems from preestablished climate classifications that have been linked to the global distribution of vegetation types (e.g., Bagnouls & Gaussen, 1957; Bailey, 1989a, 1989b; Köppen & Geiger, 1954; Walter, 1973). When mapping biomes at the global scale, vegetation modeling often maps the distribution of biomes predicted from climate, soil, and, increasingly, atmospheric chemistry (CO<sub>2</sub> concentration, nitrogen deposition) data (e.g., Smith et al., 2014). Recently, the incorporation of human land use has attracted more interest (e.g., Pugh et al., 2019; Yue et al., 2018). However, unlike maps from expert elicitation or vegetation physiognomy, maps from vegetation modeling are statistically or more process-based predictions that do not necessarily aim to represent the current state of vegetation or modern potential natural vegetation. Instead, they often test our current understanding of the role of different drivers, or they are used to project changes in biome distributions through time (e.g., Gonzalez et al., 2010; Huntley et al., 2021).

Modeled predictions often differ from observation-based biome maps because the models try to explain the distribution of biomes rather than mapping them, for example, concerning the role of fire disturbance on global tree cover (Lasslop et al., 2020). When compared to ground- or satellite-based observations, modeled biome maps represent means of testing hypothetical relationships between environmental factors and the distribution of vegetation types.

One might distinguish approaches that directly correlate biome distribution with environmental conditions from more process-based approaches that consider ecological mechanisms to simulate biome distributions, such as dynamic global vegetation models. However, the distinction blurs where otherwise highly mechanistic models restrict plant distribution by predefined bioclimatic limits (e.g., Smith et al., 2001). Both correlative and process-based approaches can aim either to elucidate ecological processes or predict biome distributions accurately. As an example of a correlative approach, Whittaker’s broadly used diagram (Whittaker, 1970) considers only mean annual precipitation and temperature to predict a worldwide distribution of biomes. Similarly,

Leemans (1990a, 1990b) mapped what Holdridge (1967) described as “life zones” (a synonym for “biome”) based on actual climate data, where precipitation, evapotranspiration, and altitude are physical limitations of the local environment to support specific life forms (Figure 1b). Prentice et al. (1992) then emphasized the need to consider plant physiological mechanisms explicitly in the choice of predictor variables, such as the minimum winter temperature, which is clearly related to the frost tolerances of different plant or vegetation types, instead of mean annual variables. Recently, it has become more popular to use fewer a priori assumptions on drivers and more potential predictors in combination with advanced “big data” statistics, including machine learning (Hengl et al., 2018).

On the other hand, process-based biome models map the distribution of biomes by simulating competition among plant types under given environmental conditions based on their physiology. Process-based vegetation models often group plants with similar functional characteristics into a few functional types or growth forms. This approach treats species’ groupings functionally as a single “average” species that ignores phylogenetic relationships (Duckworth et al., 2000). Competition among plant types (defined by a combination of functional traits) is then simulated as a result of simulated physiological processes and competition for resources (water, light, and, increasingly, soil nutrients, in particular nitrogen) in dynamic global vegetation models (e.g., Levis et al., 2004; Smith et al., 2014). This simplification predicts the coarse-scale distribution of all plant species by simulating competition among only a few (commonly 5–15) “virtual” plant functional types. Their high mechanistic detail might cause overparameterization in process-based models as a source of uncertainty (Appendix S1: Table S2).

Lasslop et al., 2020). For example, maps produced by Haxeltine and Prentice (1996) and Hickler et al. (2006) agreed approximately ( $\kappa > 0.5$ ) with an expert-based compilation biome map primarily derived from Melillo et al. (1993). Recently, within-plant type trait variability has also been included (e.g., Dantas de Paula et al., 2021; Sakschewski et al., 2016), and the Adaptive dynamic global vegetation model (version 2) also simulates trait inheritance (Scheiter et al., 2013). Together with promising ambitions of including data assimilation in global dynamic vegetation models (Luo & Schuur, 2020), these developments could help reduce uncertainty from parameter variability (sensu Dietze, 2017).

Biome maps from correlative or process-based models simplify the relationships between vegetation and environmental conditions. While model simulations might be able to reproduce the general distribution pattern of

biomes accurately, they do not account for all processes leading to the actual biome distribution.

## Past and future biomes

The biome concept is a useful tool when reconstructing past or predicting future landscapes because it provides a means to compare long-vanished or expected future landscapes with modern analogs. Past and future biome projections relate to the three families of biome maps, that is, compilation from expert elicitation, functional from vegetation physiognomy, and simulated from vegetation modeling. Depending on the method used to infer biomes, such reconstructions potentially provide insight into past environmental changes or into the potential effects of future climate changes to the distribution of biological communities and functional traits at regional to global scales. However, inferring past or future biomes requires hindcasting or predicting characteristics from limited information regarding their extent and properties.

The functional traits and taxonomic diversity of past vegetation remains (e.g., pollen, leaves, phytoliths or leaf waxes) can indicate past biome characteristics. This information provides valuable evidence of past environments that can be used to infer past biomes. Biome reconstructions based on past vegetation remains or vegetation model simulations assume that at least as far back as the Cretaceous-Paleogene extinction event (66 million years ago), landscapes hosted modern-analog floras, even if this assumption weakens with the age of the studied flora due to ensuing evolutionary and environmental changes (Carvalho et al., 2021; Peppe et al., 2011). Features of past biomes can be inferred from (1) expert knowledge combining all the information available from the fossil record (i.e., compiled biomes), (2) functional traits and taxonomic diversity of past vegetation remains (i.e., functional biomes), (3) correlative or mechanistic models based on past climate data deduced from fossil remains or climate model simulations (i.e., simulated biomes). Vegetation modeling also enables future simulated biome projections from simulated climate data.

## Past compilation biomes from expert elicitation

Features of past compilation biomes can be inferred by combining all the information available from a paleoenvironment record (e.g., past vegetation, mammals, climate). Like modern compilation biomes from expert elicitation, the quantity of information is not limited to any standard biome definition, and biomes are defined

based on expert elicitation. The general functional characteristics and taxonomic diversity of a paleoenvironment record often recall one or several modern associations of local vegetation, formations, or biomes (e.g., Adams & Faure, 1997; Dyke, 2007; Ray & Adams, 2001; Willis & McElwain, 2002; Ziegler, 1990). Experts combine information about the biogeographical origin and/or the modern habitat of the nearest living related taxa and/or the environment to which the functional traits are adapted. This approach aims to approximate, albeit subjectively, a natural framework facilitating the interpretation of the data, rather than to describe the environment precisely. Because this approach relies on compiling information from multiple sources using category equivalencies based on expert knowledge, it can be compared to modern compilation biomes (e.g., Olson et al., 2001).

### Past functional biomes from proxies of vegetation physiognomy

The general characteristics of past functional biomes can be inferred from leaf compressions, pollen records, and leaf waxes. Like modern ones from remote sensing, past functional biomes focus exclusively on vegetation traits and are independent of estimations of past environmental conditions. For example, information about leaf physiognomy (deciduous, evergreen) can arise from petiole width of leaf compressions, assuming that heavy and thick evergreen leaves have a wider petiole than light and thin deciduous leaves (e.g., Peppe et al., 2018). Leaf physiognomy and the relative proportions of woody and herbaceous vegetation can be deduced from the taxonomic composition of pollen or phytolith records (e.g., Bremond et al., 2008; Forbes et al., 2020). Stable isotope analysis of organic matter ( $\delta^{13}\text{C}$ ) like leaf waxes can also provide insights into photosynthetic pathways (i.e.,  $\text{C}_3$  or  $\text{C}_4$ ) (O'Leary, 1988), potentially indicating the proportion of woody vegetation at the lowest latitudes because  $\text{C}_4$  grasses have dominated herbaceous vegetation on all continents since the late Pliocene (e.g., Andrae et al., 2018; Forbes et al., 2020).

While deduced independently of different paleoproxies, these vegetation functional traits, once combined, represent functional biome definition criteria. By calibrating biome definitions to local records of modern vegetation, several methods automate the process of drawing inferences about past functional biomes (Prentice & Webb III, 1998; Sobol & Finkelstein, 2018). Such methods define biomes regionally as combinations of taxa or plant functional types. For example, the BIOME6000 project mapped paleobiomes from pollen records for the Last Glacial Maximum and mid-Holocene using a

“biomization” technique (Harrison & Bartlein, 2012; Prentice & Webb III, 1998). Biomization is a process where identified pollen taxa are translated into one or more plant functional types for each site. Then the biome with the highest affinity to the composition of specific plant functional types represents that site over the relevant period. Biomization usually relies on representative plant taxa and expert-based links among pollen taxa, plant functional types, and biomes. Sobol and Finkelstein (2018) alternatively developed a machine-learning method to assign pollen taxa programmatically to biomes. These functional characteristics are comparable to modern functional biomes mapped from remote sensing using the same functional traits (e.g., Friedl et al., 2010; Higgins et al., 2016).

### Past and future simulated biomes from vegetation modeling

Past reconstructions of biome changes are an important source to evaluate biome models: an obvious prerequisite to applying such models to project future changes and to inform climate-adaptation and climate-mitigation measures. However, data from paleoenvironmental records are often very sparse. In the case of deep-time studies going back millions of years, biome models rest on only very few data points (e.g., Salzmann et al., 2008). For time periods with better data coverage, vegetation simulations might actually be able to test hypotheses about what drove past biome shifts. For example, Harrison and Prentice (2003) showed that the BIOME3 model only reproduced landscape openness in the tropics during the Last Glacial Maximum if the model limited  $\text{C}_3$  photosynthesis through low atmospheric  $\text{CO}_2$ . Huntley et al. (2013) showed that glacial variability associated with Heinrich events is crucial to simulate landscape openness comparable to pollen-based reconstructions, in western Europe in particular. Forrest et al. (2015) combined fossil plant data, climate, and vegetation modeling to infer that atmospheric  $\text{CO}_2$  concentrations during the last Miocene were probably at the low end of current estimates. Future scenarios of biome shifts have been mostly interpreted in terms of climate-adaptation needs (e.g., in forestry) and their impact on biodiversity (Gonzalez et al., 2010; Huntley et al., 2021).

To simulate past and future biome distributions, model forcing data can be obtained from various and complementary sources, including model hindcasts and predictions, or paleoproxies. First, vegetation models predicting modern biomes from modern climate data can also simulate biomes from hindcasted climate data (e.g., Allen et al., 2010, 2020; Forrest et al., 2015; François et al., 2011;

Prentice et al., 2011; Salzmann et al., 2008; Tardif et al., 2021) or future climate scenarios (Gonzalez et al., 2010; Huntley et al., 2021; Leemans, 1990a, 1990b; Monserud & Leemans, 1992). Second, many past climate characteristics can be inferred from paleoproxies, thereby providing independent training data at regional scales against which climate models can be calibrated. For example, past climate characteristics can be deduced from fossil leaf compressions assuming that modern climate dependencies of plant functional traits also apply to the past and that most plant communities are in equilibrium with their local climates (Peppe et al., 2018 and references therein), regardless of the few exceptions arising from rapidly changing climates (e.g., Blonder et al., 2015; Davis, 1986; Svenning & Sandel, 2013).

## Uncertainties of past vegetation paleoproxies and biome modeling

The interpretation of paleoproxies to infer biomes must also consider the preservation biases resulting from different structural and chemical properties among species or plant parts (Schopf, 1975). Preservation processes prevent several proxies from being recorded simultaneously in the same place, because good preservation conditions for one organism or part of an organism can promote decomposition conditions for others (Schopf, 1975), causing poor taxonomic resolution due to missing identification criteria. Whichever proxy is used, only some organisms are recorded, so that one record represents only a small sample of its original environment, biased toward the most resistant species (Sangster & Dale, 1964) and deposit environments with high preservation potential (e.g., riparian forests, riverbeds). Finally, whereas microfossil records such as pollen are often assumed to represent the regional environment, macrofossils such as leaves and wood more likely represent the local environment given the latter are not dispersed as much as the former (e.g., DiMichele et al., 2019). Hence, pollen cores can accumulate species-composition information across a much broader spatial range than the immediate vicinity in which the sample was collected. If inferring past biomes from actual vegetation remains is an evidence-based method, the sparse spatial distribution of paleovegetation records provides only temporal snapshots and local reconstructions.

More comprehensive biome maps can only be generated via paleovegetation modeling. Model forcing data, such as paleoclimate, might diverge from observations (Lorenz et al., 2016). In fore- or hindcasting models, driver uncertainty thus becomes an additional source of uncertainty (Appendix S1: Table S2). Therefore, and in

spite of the incomplete process representation in biome models, paleovegetation data and proxies and biome models are sometimes combined to reconstruct past biomes (e.g., Salzmann et al., 2008).

Overall, fossil records represent direct evidence of past environments at a given time, while model simulations generate past and future biome maps at a regional to global scale. Using a consistent biome-classification scheme for past, modern, and future reconstitutions is essential to assess changes in biome distributions through time and to evaluate climate and biome models that are used for future predictions. Plant remains or simulations can inform different elements of the environment, from modern, expert-based analogs and taxonomic diversity to functional traits and paleoclimate features. Such information must then be combined to describe biomes based on vegetation physiognomy, the physical environment (vegetation modeling), or the compilation of nonstandard observations (expert elicitation).

## COMPARING GLOBAL BIOME MAPS QUANTITATIVELY

The diversity of biome classifications has resulted in various geographic divisions, biome names, and number of biomes (from <10 to several dozen globally; Beierkuhnlein & Fischer, 2021). Two different biome-classification schemes can even use the same biome name to describe different entities. For example, the “tundra” of Olson et al. (2001) does not correspond to the spatial combination of the four “tundra” biomes of Leemans (1990a, 1990b) (Figure 1). However, the scale and nature of these discrepancies remain cryptic and underestimated (Beierkuhnlein & Fischer, 2021). In this context, it is essential to explore, quantify, and map the global agreement among biome maps. In what follows, we briefly review published comparison methods and then introduce a new algorithm to quantify pairwise agreement between biome maps.

### Shortcomings of methods to compare biome maps

Several methods can be used to compare biome maps, even if each has shortcomings. A contingency table is a straightforward tool to illustrate how two classifications overlap spatially (Higgins et al., 2016). Such a table describes how the distribution of categories in Map A relates to that of Map B as a fraction of the entire map, with the sum of all fractions equaling 1 (see also Hagen, 2002). However, summarizing the agreement as a single or a few numbers makes the result easier to interpret,

especially when there are many categories. Map-comparison measures based on such contingency tables, such as the broadly used Cohen's kappa ( $\kappa$ ) (Cohen, 1960; Monserud & Leemans, 1992) or the more recent quantity-and-allocation agreement (Pontius Jr & Millones, 2011), both consider the percentage of pixels of the map attributed to the same category in two maps and take into account the likelihood of agreement occurring by chance.

Quantifying the overall spatial agreement between two biome maps with the methods mentioned earlier would require classifications to share equivalent sets of categories, which is not the case. Setting up an expert-based equivalency table (or a similarity matrix) between two sets of biomes based on their names or definition similarities, that is, deciding on theoretical equivalencies among biomes to facilitate map comparison (Fritz & See, 2005; Hagen-Zanker et al., 2005), could be circular, subjective, and nonrepeatable. Alternatively, Beierkuhnlein and Fischer (2021) grouped categories from 12 global biome maps based on common climate and environmental characteristics and mapped the frequency of overlap among categories at global scale. This type of approach is effective at identifying the existence of differences between biome maps, but their distribution still depends on the criteria chosen to group the categories (here, mainly climate).

To avoid using subjective equivalencies among categories, it is possible to quantify the agreement between each biome pair by measuring their spatial overlap compared to a distribution of overlap occurring by chance. The quantity-and-allocation-agreement statistics suggested by Pontius Jr and Millones (2011) to replace Cohen's  $\kappa$  make sense for global comparisons; unfortunately, Pontius and Millones's (2011) single-category statistics are weighted by the total number of locations on the map and are therefore not designed for single-category comparisons. In contrast, Cohen's  $\kappa$  on a single category (Monserud & Leemans, 1992) is weighted by the area covered by the category under examination, that is, weighted by the size of the biome. Because of these challenges, we present here an alternative approach to measuring and representing spatially the pairwise agreement between biome maps by merging categories based on spatial overlap and by calculating Cohen's  $\kappa$  on a single category (Monserud & Leemans, 1992), thereby considering differences in biome size.

## Algorithmic protocol to represent spatial distribution of map agreement

### Merging biomes based on spatial overlap

To compare two sets of biomes with different category names and numbers (Figure 2a), we must first have the

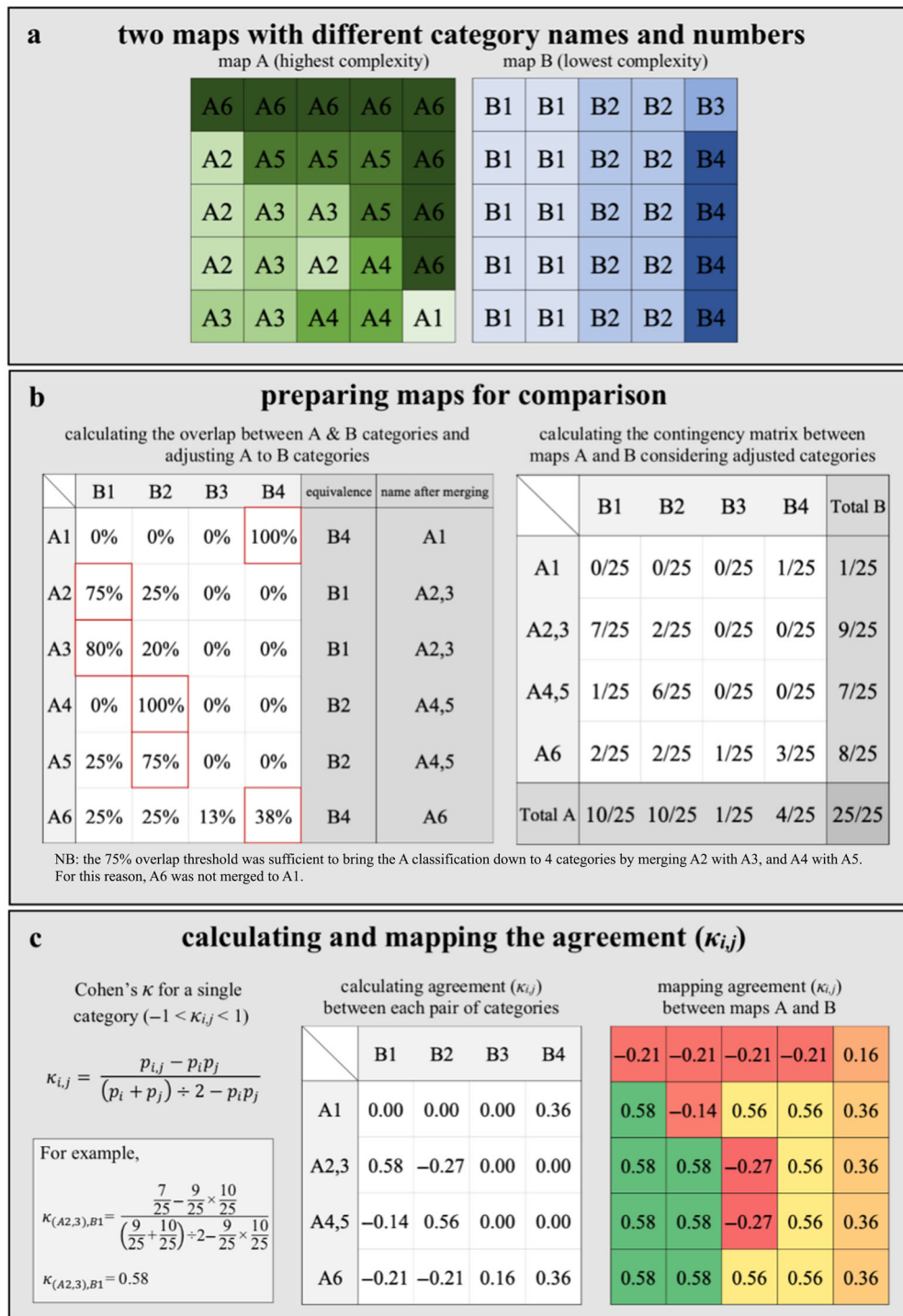
same number of biomes for each set. For each pair of biome classifications, we adjusted the number of biomes of the classification with the highest number of biomes (Map A in Figure 2a) to the classification with the lowest number of biomes (Map B, in Figure 2a,b). To avoid deciding arbitrarily on equivalencies among categories, we merged biomes programmatically based on spatial overlap. Two categories from A were merged if the regions they covered were generally classified in the same category from B, irrespective of biome names or definition similarities. We generated a contingency table between the two rasters, from which we derived the percentage of spatial overlap (ranging from 0 to 100%) for each category from A in categories from B (Figure 2b, left panel). Starting from the highest overlap, we then associated each category from A to its highest overlapped category from B. When two categories from A were associated in this way with the same category from B, we merged them, and we repeated this process until the two classifications had an equal number of categories (Figure 2b, left panel). The merged biomes from the first map are not biologically equivalent, but the regions they cover are mostly classified in a single category on the second map to which they are compared.

### Generating agreement maps

We then generated spatial agreement maps based on Cohen's  $\kappa$  on a single category. We calculated a new contingency table between Maps A and B considering merged categories (Figure 2b, right panel). Next, we calculated the  $\kappa$  agreement of a single pair of categories  $i,j$  ( $\kappa_{i,j}$ ) by successively considering each possible pair of biomes as a single category and compared their distribution against the union of all other categories in both classifications (Figure 2c, left and middle panels). We excluded from the analysis locations not assigned to any terrestrial biomes in at least one of the two maps. We then calculated  $\kappa_{i,j}$  of each biome pair (Figure 2c, center panel) to plot the global distribution of agreement in each a pair of classifications, based on where each pair was located (Figure 2c, right panel).  $\kappa_{i,j}$  ranges from no agreement ( $\kappa_{i,j} < 0.05$ ) to perfect agreement ( $0.99 < \kappa_{i,j} < 1.00$ ; sensu Monserud & Leemans, 1992).

## EXAMPLE OF A REAL-WORLD APPLICATION OF OUR ALGORITHMIC PROTOCOL

To demonstrate the utility of quantifying classification agreements, we first compare four global



**FIGURE 2** Protocol to spatially compare two raster maps with different classifications. (a) Example of maps to be compared. (b) Map preparation procedure including category merging. (c) Agreement calculation and mapping.

biome maps using the algorithmic protocol presented earlier. We then discuss the ecological characteristics of areas of low agreement between biome maps, in particular by testing correlations between the agreement and six potential ecological predictors.

## Comparing four global biome maps

We calculated the similarity between biome pairs for a panel of four broadly used (i.e., biome map or classification cited in thousands of scientific papers and textbooks) or recent georeferenced global biome maps at a

0.5° × 0.5° spatial resolution. We compared the compilation biome map from the World Wildlife Fund Terrestrial Ecoregions of the World (Olson et al., 2001, Figure 1a), the simulated biome map from Holdridge's (1967) life zones (Leemans, 1990a, 1990b, Figure 1b), and two functional biome maps: MODIS-IGBP land-cover-type product (Friedl et al., 2010; Loveland & Belward, 1997, Figure 1c), and the dominant biome distribution over 31 years from the global functional biome scheme from Higgins et al. (2016, 2017) (Figure 1d) (all biome names for each classification are listed in Appendix S1: Table S1). We did the analysis in R using the terra and diffeR packages (Hijmans et al., 2023; Pontius Jr & Santacruz, 2019; R Core Team, 2022). All input, output data, and code used to run the analyses, including original and merged biome maps, contingency matrices, agreement maps, and the algorithm shown in Figure 2, are provided in a Zenodo archive (Champreux et al., 2023).

For each of the six interclassification comparisons, biomes were merged based on an overlap threshold ranging between 37% (Higgins et al., 2016, 2017 adjusted to Friedl et al., 2010) and 74% (Friedl et al., 2010 adjusted to Olson et al., 2001). The resulting merged categories are based on spatial overlap with a category from the other classification and, thus, are not designed to be ecologically or functionally meaningful. For example, the evergreen needleleaf forests, deciduous needleleaf forests, and permanent wetlands from Friedl et al. (2010) were merged based on their overlap with the boreal forests/taiga from Olson et al. (2001). We merged up to 11 biomes based on a single merging reference, that is, 11 biomes from Leemans (1990a, 1990b) corresponded to the open shrublands from Friedl et al. (2010) (Figure 3a). In this example, the result shows that the 11 biomes from Leemans (1990a, 1990b), which represent 11 different typical combinations of annual precipitation and potential evapotranspiration, today mainly host vegetation characterized by a 10%–60% cover of 1- to 2-m-high woody plants corresponding to the “open shrublands” of Friedl et al. (2010). We provide all biome-merging settings in Appendix S1: Table S3, as well as all global biome maps with merged categories in Appendix S1: Figures S1 and S2.

## Worldwide pattern of agreement

The global distribution of  $\kappa_{i,j}$  demonstrates that the strength of the agreement among global biome maps varies widely across regions. The six interclassification comparison maps generally share the same spatial distribution pattern of agreement (Figure 4, Appendix S1: Figure S3). This common pattern is independent of the biome-map family compared. In Figure 4a, we calculated

the average  $\kappa_{i,j}$  for each grid cell of the world map across the six interclassification comparisons (Figure 3, Appendix S1: Figure S3). High mean agreements (>0.55, sensu Monserud & Leemans, 1992) occur in the equatorial rainforests of the Amazon basin, Congo basin, and Southeast Asia and the tropical deserts of the Sahara and the Arabian Peninsula. Conversely, low or no agreement (<0.05; sensu Monserud & Leemans, 1992) were spread sparsely among many zones of the world, such as in eastern Patagonia, the Caatinga, eastern South Africa and Lesotho, southeastern and southwestern Australia, New Zealand, western Europe, Turkey, and large areas of North America and Asia (Figure 4a).

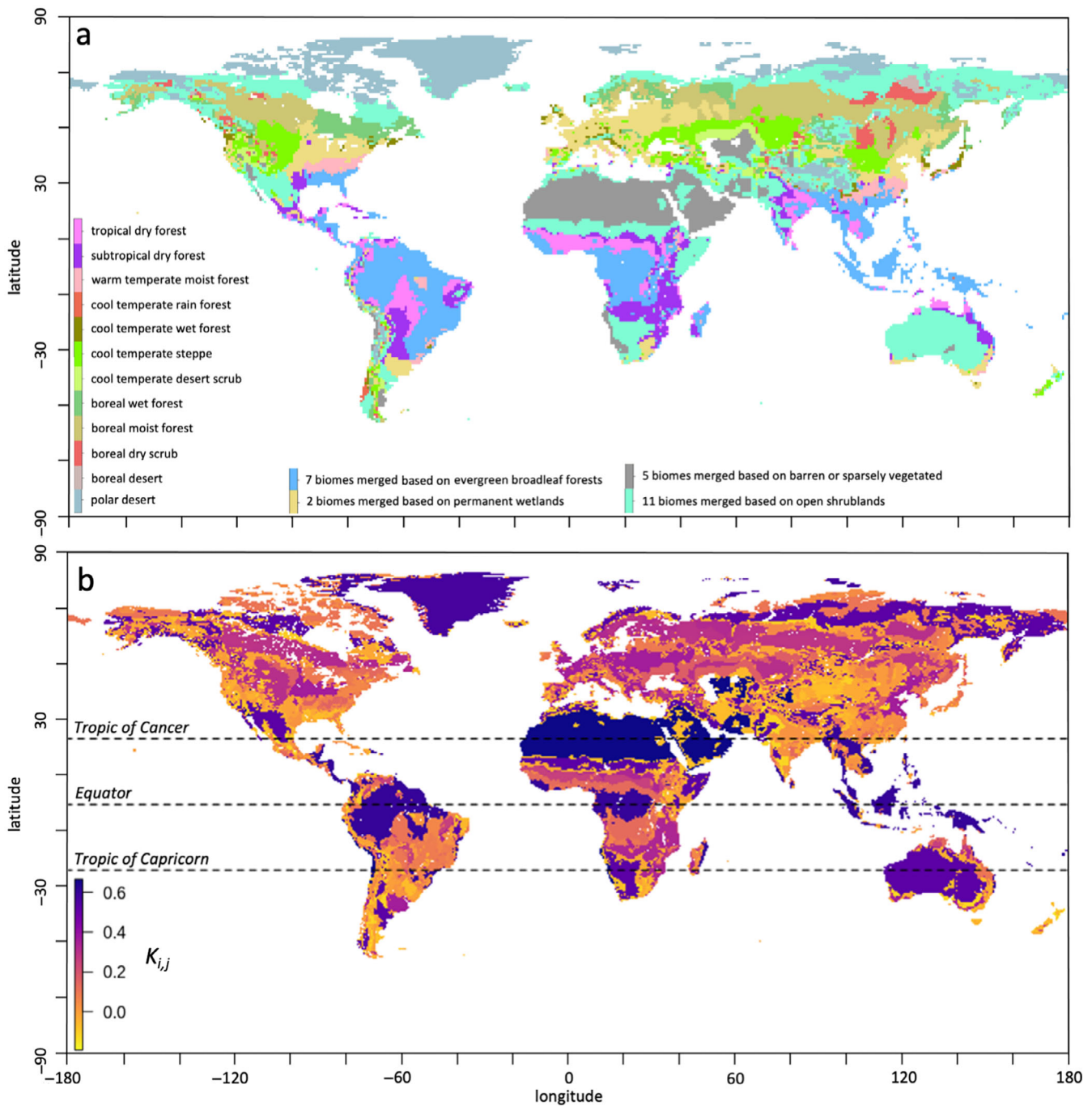
The worldwide distribution of  $\kappa_{i,j}$  also highlights a common latitudinal pattern of agreement among classifications (Figure 4b). At the same latitude,  $\kappa_{i,j}$  is generally lower in the Southern Hemisphere than in the Northern Hemisphere. The highest  $\kappa_{i,j}$  are located around the Equator, the tropics, and boreal latitudes, despite lower values at temperate latitudes (~35° to 60° from the Equator), and in the transition regions between the Tropics of Cancer and Capricorn and the Equator (~5° to 15° from the Equator). Such a pattern suggests that classification agreement depends on one or several latitude-related processes like changes in vegetation cover, species diversity, or natural disturbances.

## Explaining the distribution of spatial agreement

Discrepancies among biome maps stem from the differences among mapping strategies and illustrate the lack of consensus on how to classify certain areas. Identifying the ecological characteristics of such low-agreement areas optimizes the use and further development of the biome concept. In this section, we first discuss theoretically the potential causes of disagreement among biome maps. Then we quantify the relative effect of six potential predictors in explaining the overall distribution of agreement.

### Potential drivers of biome-map disagreement

The position of biomes and their boundaries depends on the characteristics of the ecosystems and on the biome-mapping method used (i.e., biome definition and data collection). One of the main conceptual differences between biome maps is whether they consider human activities. As a result, in areas of high human activity it is likely that biome maps intending to represent potential natural vegetation (Olson et al., 2001, Figure 1a;

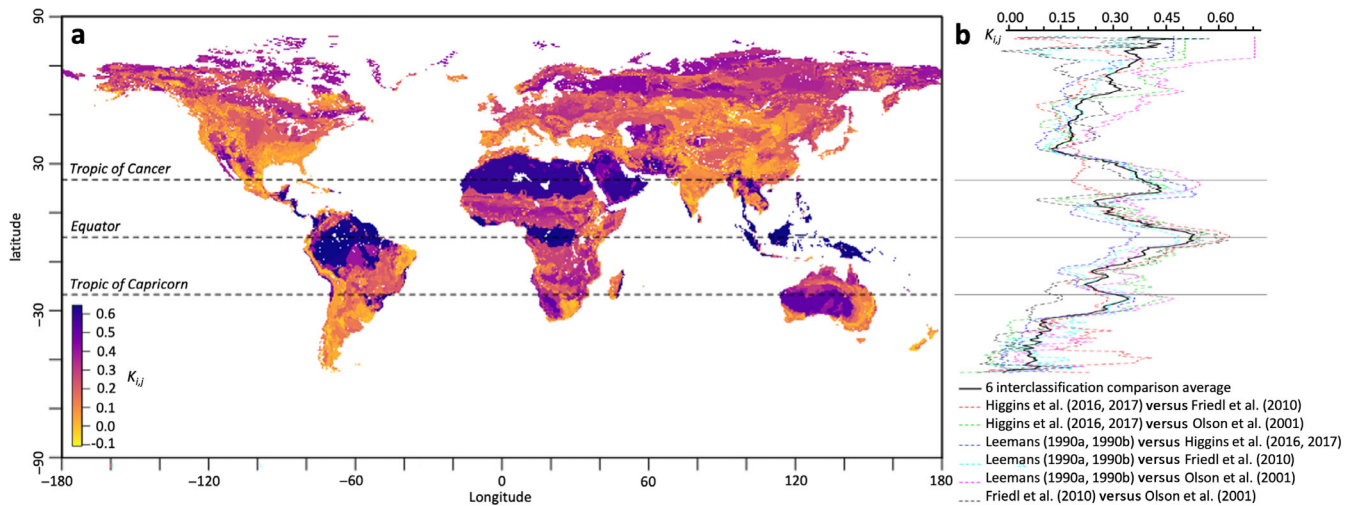


**FIGURE 3** Example of biome map comparison. (a) Example of biome map with merged categories. Categories from Leemans (1990a, 1990b, highest complexity) were merged based on their spatial overlap with categories from Friedl et al. (2010, lowest complexity). (b) Distribution of agreement (Cohen's  $\kappa_{i,j}$ ) on a single category between global biome maps from Leemans (1990a, 1990b, with merged categories) and Friedl et al. (2010).

Leemans, 1990a, 1990b, Figure 1b) should intentionally differ markedly from maps considering the effect of human activities (Loveland & Belward, 1997; Friedl et al., 2010, Figure 1c). Beyond the effect of such conceptual differences, some ecological characteristics could generate disagreement by making the classification of a given area ambiguous. For example, human activities

could cause disagreement in any pair of maps if one map unintentionally underestimated them, which could occur between two potential natural vegetation maps.

Weak agreement can also arise in ecosystems that are poorly studied. For example, using the biome map of Ramankutty and Foley (1999), Martin et al. (2012) demonstrated that ecologists focused more on protected



**FIGURE 4** Distribution of mean agreement (Cohen’s  $\kappa_{i,j}$ ) on a single category. Mean  $\kappa_{i,j}$  is calculated as average across the six interclassification comparison rasters, at a  $0.5^\circ \times 0.5^\circ$  resolution and ranges from “no” agreement ( $-1 < \kappa_{i,j} < 0.05$ ) to “perfect” agreement ( $0.99 < \kappa_{i,j} < 1$ ). (a) Average for each grid cell of map. (b) Average across all grid cells of same latitude for six interclassification comparisons and their total average.

natural environments, which could produce disagreements in the most anthropogenically altered areas. Similarly, Martin et al. (2012) demonstrated that relatively open biomes such as “savanna,” “open shrublands,” and “desert and barren” tended to be undersampled compared to more forested biomes such as “tropical deciduous woodland,” “temperate evergreen woodland,” and “temperate deciduous woodland.”

We identified two possible main causes of low agreement among global biome maps: (1) high landscape heterogeneity and (2) impact of landscape-modification processes. First, grid cells hosting landscapes of high heterogeneity such as mixed tree and grass vegetation (e.g., with intermediate LAI) or potentially hosting many different biological associations (e.g., with high mammal or plant species richness) might be classifiable into several biomes depending on the scale (e.g., one observation on a finer-scale vegetation formation, or average vegetation for the whole grid cell) and the location (e.g., in a mosaic, observation in the more or less forested area) of observations. In such cases, functional and simulated biomes from satellite imagery and modeling might tend to consider average observations, while compilation biomes from field observations could focus on and select localized features. Second, landscapes impacted by modification processes like the effect of ecosystem engineers (e.g., humans via agricultural practices or other effects depending on population density, and/or mammals by their diverse diets and habits) or disturbances (e.g., fire) may yield gaps between expected and existing biome distributions. When the actual vegetation is different than expected, compilation and

simulated biomes theoretically differ from functional biomes, because field observations and model predictions generally downplay the impact of modification processes by focusing on well-preserved, “natural” landscapes. Additionally, these differences might not be permanent due to the possible temporal variation of disturbance intensity, characterizing areas with multiple stable biome states such as in subtropical savannas and forests (Dantas et al., 2016; Moncrieff et al., 2014; Sankaran et al., 2008; Staver et al., 2011).

### Methods: Testing correlations with potential ecological drivers of disagreement

Beyond the expected effect of conceptual differences, such as the choice either to map or erase the impact of human activities, we assessed the relative effect of (1) high landscape heterogeneity and (2) landscape modification on agreement among biome maps. We decomposed the two potential drivers of disagreement into six quantifiable potential predictors, that is, three landscape-heterogeneity characteristics (LAI, mammal species richness, and native plant diversity) and three possible markers of landscape modification including the presence of ecosystem engineers represented by humans (anthropogenic habitat loss [HL], human population density), and a disturbance (monthly burned area). We included anthropogenic HL in the analysis to account for both its expected effect on biome map agreement when human activities are explicitly considered in only one of the two maps compared and its potential additional effect

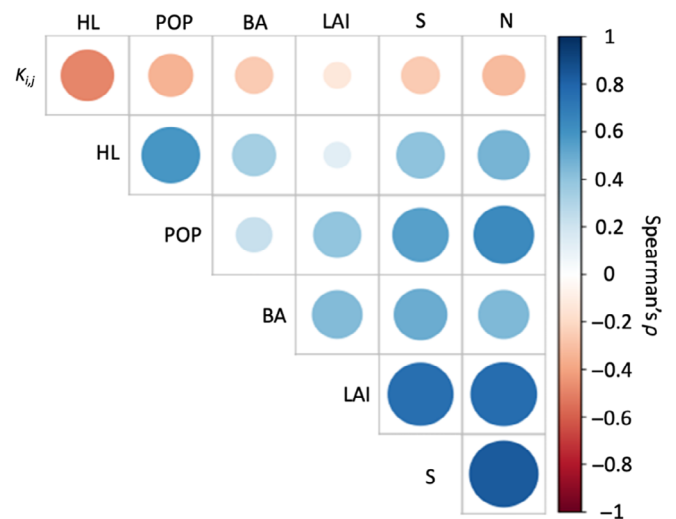
when it is unintentionally underestimated in any map, including in potential natural vegetation maps.

We derived data representing the six potential predictors from published sources as follows. (1) We calculated the average LAI from global remote-sensing data at monthly intervals between 1981 and 2015 (Mao & Yan, 2019). (2) We derived global mammal species richness from the International Union for Conservation of Nature and the Center for International Earth Science Information Network (2015), (3) the global distribution of native plant species richness, and (4) anthropogenic HL from Ellis et al. (2012). Ellis et al. (2012) estimated the distribution of native plant species richness from the species-richness model of Kreft and Jetz (2007) and anthropogenic HL as the sum of the percentage of land use for cultures, urban areas, and two thirds of pasture area from the HYDE 3.1 data model (Klein Goldewijk et al., 2010, 2011). (5) We derived human population density in 2015 from the Gridded Population of the World database (Center for International Earth Science Information Network, 2018). (6) We calculated the average monthly burned area from 1997 to 2015 from the remote sensing-derived Global Fire Emission Database version 4 (Randerson et al., 2017). We formatted all data to a  $0.5^\circ \times 0.5^\circ$  resolution, 1-year average, and excluded grid cells containing missing data. Missing LAI data correspond to low cover, so we replaced missing data on continental areas with an arbitrary low value (=0.0001) to prevent any statistical misrepresentation.

Relying on these six products can be debated because they are inevitably associated with particular biases and uncertainties. For example, there are uncertainties and differences among available anthropogenic land-cover products depending on the mapping method, including the classification scheme and input data used (Klein Goldewijk et al., 2007, 2011; Buchhorn et al., 2020). The quality of the anthropogenic habitat-loss data set from Ellis et al. (2012) can be questioned because the input data are not standardized among countries (Klein Goldewijk et al. 2007, 2011). In contrast to Ellis et al. (2012), Buchhorn et al. (2020) provided some estimates of uncertainty and accuracy, and they standardized data collection at the global scale and at high spatial resolution using machine learning. However, the two products have some similarities. For example, despite methodological differences, the estimated total percentage of cropland cover is of the same order of magnitude in the product used by Ellis et al. (2012) (i.e., ~10% in 2000; Klein Goldewijk et al., 2011) as that used by Buchhorn et al. (2020) (i.e., ~12% in 2015; Buchhorn et al., 2019). In this exploratory analysis, we assumed that the product of Ellis et al. (2012) adequately represented the main spatial trends of anthropogenic land cover, but at a low spatial resolution. We also chose to use Ellis

et al. (2012) because they explicitly estimated the rate of anthropogenic HL by grid cell and because they also included an estimate of the percentage of pasture areas. While rarely considered in land-cover products, the percentage of pasture is important for biome distribution because livestock grazing can potentially impact vegetation at broad spatial scales. In addition, we included a measure of the monthly burned area in the analysis to consider, at least partially, the effect of fire on biome map disagreement. However, such a product does not adequately describe the fire regimes given that some aspects of fire regimes are not specified (e.g., frequency, severity, seasonality) (Hély et al., 2019); as yet there is no global, georeferenced, and gridded data set representing those aspects. Moreover, the remote-sensing record covers 19 years, so environments with long fire-return intervals are not considered in the burned area product from Randerson et al. (2017).

The assumption that mammal species richness is related to landscape heterogeneity can be debated. Mammal species richness strongly correlates positively with native plant diversity and LAI (Figure 5). We suggest that extremely high or low mammal species richness best characterizes “extreme” biomes (in terms of diversity and vegetation cover), which tend to represent



**FIGURE 5** Spearman's  $\rho$  between variables included in generalized least-squares models. Correlations between mean Cohen's  $\kappa$  (agreement) for a single category ( $\kappa_{ij}$ ), variables describing landscape modification (HL, habitat loss; POP, human population density; BA, yearly burnt area), and landscape heterogeneity (LAI, leaf area index; N, native plant species richness; S, mammal species richness) per grid cell. We used the `corrplot` R package (Wei & Simko, 2017). The size of the dots represents the strength of the correlation. Based on uniformly resampled data from total list of grid cells where we calculated mean  $\kappa_{ij}$  across the six interclassification comparison rasters ( $\times 10,533$  grid cells).

more homogeneous landscapes. Extreme biomes correspond to high mammal richness in equatorial rainforests (>150 species) or low mammal richness in deserts (<10 species). In contrast, biome distinction might be more ambiguous in regions with midrange mammal richness ( $50 < S < 100$ ). Mammal richness generally increases with ecosystem primary productivity (Toszogyova & Storch, 2019). Midrange mammal richness thus represents midrange productivity environments. Such environments often correspond to multiple stable biome states, thus heterogeneous landscapes that might prevent agreement on biome identity in large areas, such as in subtropical savannas and forests (Dantas et al., 2016; Moncrieff et al., 2014; Sankaran et al., 2008; Staver et al., 2011). Multiple stable states have mostly been linked to the effects of both fire and herbivores (Dantas et al., 2016). We did not test the effects of herbivores on agreement among biome maps due to the lack of suitable, global-scale data.

We measured the correlations among  $\kappa_{i,j}$  and the six potential predictors (Spearman's  $\rho$ ). Negative values of Spearman's  $\rho$  indicated that the selected predictors are likely to affect the agreement among biome classifications negatively. For each of the six pairwise agreement maps and their average, we built and compared 64 generalized least-squares models (accounting for spatial autocorrelation) to identify which predictor among landscape (1) heterogeneity and (2) modification variables best described the variation in agreement for a single category  $\kappa_{i,j}$  (Appendix S1: Table S4). The 64 models expressed  $\kappa_{i,j}$  as a function of all possible combinations of the six potential predictors excluding their interactions, that is, LAI, plant species richness, anthropogenic HL, human population density, mammal species richness, and monthly burned area. To account for computational limitations, we built the generalized least-squares models based on a sample of 471 to 486 grid cells selected at regular intervals of five latitude and five longitude degrees among valid grid cells. We designed a metric for the goodness of fit of each model as the difference between the sum of squares of the residuals of the generalized least-squares model and the sum of squares of the dispersion of the data around the observed mean, divided by the sum of squares of the dispersion of the data around the observed mean (Saltr e et al., 2019). High values (>80%) of the model's goodness of fit indicated that the model performed well in predicting agreement.

We ranked the 64 models based on their Akaike's information criteria corrected for small samples ( $AIC_c$ ) (Akaike, 1973; Hurvich & Tsai, 1989). The ranking penalizes models with more covariant parameters, thereby accounting for collinearity. The top-ranked model indicated the most probable combination of predictors and rejected other hypotheses. From this top-ranked model, we quantified the relative importance of each predictor variable (including their interactions) by measuring the

change in the model's goodness of fit and the Nagelkerke pseudo-R-squared ( $R^2$ ; Nagelkerke, 1991) when removing this variable from the model. All input and output data, including potential ecological driver data, resampled data, and generalized least-squares model outputs, are provided in a Zenodo archive (Champreux et al., 2023).

## Results: Correlations of spatial agreement with landscape heterogeneity and modification factors

All six of our selected predictors were negatively correlated with the average agreement among biome classifications  $\kappa_{i,j}$  ( $\rho < 0$ ), with HL emerging as the predictor with the greatest explanatory power as expected from discrepancies among biome classification in accounting for human activities (Figure 5). Unsurprisingly, the negative correlations with the six selected predictors confirm our expectations that both landscape heterogeneity and the presence of landscape-modification processes relate to a reduction of the agreement among biome classifications.

In terms of average map agreement (Figure 4), generalized least-squares models including anthropogenic HL generally explained the distribution of the biome-map agreement better than other models (Appendix S1: Table S4A). The top-ranked generalized least-squares model included HL, mammal species richness, and LAI (>93% goodness of fit and lowest  $AIC_c$ ; Table 2, S4A). When considering interactions among these three variables, interactions between LAI and either HL or mammal species richness (S) had the strongest effect (HL  $\times$  LAI: highest percent of change of the model's goodness of fit,  $\Delta\%$  goodness of fit = 2.61; LAI  $\times$  S: highest pseudo- $R^2$  relative to the full model,  $R^2 = 0.05$ ; Tables 3 and 4 and Appendix S1: Table S4).

However, when investigating the six pairwise agreement maps (Table 4, Appendix S1: Tables S5–S10), all top-ranked models included anthropogenic HL and the LAI. When considering the interaction terms, the most important predictors generally considered anthropogenic HL interacting with another predictor (LAI or mammal diversity). High anthropogenic HL was also among the leading ecological characteristics explaining disagreement when comparing the two potential natural vegetation maps (Table 4, Appendix S1: Table S9; Olson et al., 2001, Figure 1a; Leemans, 1990a, 1990b, Figure 1b). This highlights the difficulties in predicting what nature would look like without the impact of human activities and suggests their underestimation when mapping potential biome distribution. We provide the details of the generalized least-squares analyses for the pairwise agreement maps in Appendix S1: Tables S5–S10.

The top-ranked models indicate that biome-classification agreement is highest where anthropogenic impacts are lowest. Conversely, areas with more anthropogenic impacts (cultures, pasture, and urban areas) are more likely to correspond to disagreement among different biome classifications. In addition, biome maps often tend to disagree more in areas characterized by midrange LAI. Assuming that areas with high LAI are

characteristic of forested landscapes and that low values instead reflect more grassland-like ecosystems, we then argue that intermediate LAI indicates mixed tree and grass ecosystems, which tend to represent more heterogeneous landscapes. Overall, the results suggest that biome distribution is generally more sensitive to the choice of mapping method in areas with moderate vegetation cover and higher human activity. Further local/regional data and analyses are required to investigate the underlying ecological processes leading to these agreements/disagreements. Our protocol helped to identify the areas of focus on a global/continental perspective.

**TABLE 2** Comparison of generalized least-squares models with no interaction terms for average agreement map.

Model	<i>k</i>	LL	$\Delta\text{AIC}_c$	$w\text{AIC}_c$
~HL + S + LAI	6	295.07	0	0.15
~HL + LAI	5	293.91	0.28	0.13
~HL + S + LAI + POP	7	295.82	0.56	0.11
~HL + LAI + POP	6	294.58	0.99	0.09
~HL + LAI + N	6	294.42	1.32	0.08
~HL + S + LAI + N	7	295.25	1.71	0.06
~HL + S + LAI + BA	7	295.14	1.93	0.06
~HL + LAI + POP + N	7	295	2.2	0.05
~HL + LAI + BA	6	293.91	2.33	0.05
~HL + S + LAI + POP + N	8	295.94	2.4	0.05

*Note:* The generalized least-squares models include measures of landscape modification (HL, habitat loss; POP, human population density; BA, yearly burnt area) and landscape heterogeneity (LAI, leaf area index; N, native plant species richness; S, mammal richness) per grid cell to describe the mean agreement between the four biome classifications studied. Shown for each model are the number of parameters (*k*), maximum log-goodness of fit (LL), difference in Akaike's information criterion corrected for small sample sizes relative to the top-ranked model ( $\Delta\text{AIC}_c$ ),  $\text{AIC}_c$  weight (~model probability;  $w\text{AIC}_c$ ). Based on resampled data ( $\times 10,533$  grid cells). See details of full list of generalized least-squares models describing all combinations among predictor variables in Appendix S1: Table S4.

**TABLE 3** Relative importance of variables including interactions in top-ranked generalized least-squares model for average agreement map.

Variable removed	Model	<i>k</i>	LL	$\Delta\text{AIC}_c$	$\Delta\%$ GoF	$R^2$
S $\times$ LAI	~HL + S + LAI + (HL $\times$ LAI) + (HL $\times$ S)	8	308.75	63.24	-2.32	0.05
HL $\times$ LAI	~HL + S + LAI + (S $\times$ LAI) + (HL $\times$ S)	8	333.19	14.37	2.61	0.01
HL $\times$ S	~HL + S + LAI + (HL $\times$ LAI) + (S $\times$ LAI)	8	335.49	9.77	-1.12	0.01
HL	~S + LAI + (HL $\times$ LAI) + (S $\times$ LAI) + (HL $\times$ S)	9	341.41	<0.001	<0.001	<0.001
S	~HL + LAI + (HL $\times$ LAI) + (S $\times$ LAI) + (HL $\times$ S)	9	341.41	<0.001	<0.001	<0.001
None	~HL + S + LAI + (HL $\times$ LAI) + (S $\times$ LAI) + (HL $\times$ S)	9	341.41	<0.001	<0.001	<0.001
LAI	~HL + S + (HL $\times$ LAI) + (S $\times$ LAI) + (HL $\times$ S)	9	341.41	<0.001	<0.001	<0.001

*Note:* These models include measures of landscape modification (HL, habitat loss) and landscape heterogeneity (S, mammal richness; LAI, leaf area index) and their interactions per grid cell to describe the mean agreement between the four biome classifications we examined. Shown for each model are the number of parameters (*k*), maximum log-goodness of fit (LL), difference in Akaike's information criterion corrected for small sample sizes relative to the top-ranked model ( $\Delta\text{AIC}_c$ ), and percent of change in goodness of fit ( $\Delta\%$  GoF) for each model. The goodness of fit is calculated as the difference between the sum of squares of the residuals of the generalized least-squares model and the sum of squares of the dispersion of the data around the observed mean divided by the sum of squares of the dispersion of the data around the observed mean. The relative importance of each variable is represented by the Nagelkerke pseudo- $R^2$  (Nagelkerke, 1991) and the  $\Delta\%$  GoF of each truncated model (i.e., full model minus one of the predictive variables) relative to the full model, with higher values corresponding to higher importance. Based on resampled data ( $\times 10,533$  grid cells).

## CHOOSING A BIOME-CLASSIFICATION SCHEME

Ecology and biogeography studies refer to biomes to summarize fine-scale results at broader scales using established biogeographical units beyond the scope of their study areas, focal species, or ecosystems. Our spatial comparison of biome classifications showed widespread discrepancies among biome-classification schemes, suggesting that selecting a specific scheme or map needs careful justification for purpose, although this important aspect is often overlooked (but see Moncrieff et al., 2015; Zizka et al., 2020).

This selection process requires considering several aspects depending on the research question, scope, and audience. By better reflecting the delineation of biomes from regional maps, compilation maps should facilitate understanding and acceptance by broad, nonacademic audiences, so we recommend that they should be used

**TABLE 4** General summary of generalized least-squares models for the six pairwise agreement maps and their average.

Map A (merged)	Map B	Top ranked without interactions	Top ranked with interactions	Top predictor ( $\Delta\%$ GoF)	Top predictor ( $R^2$ )
Average of all agreement maps		~HL + S + LAI	~HL + S + LAI + (HL $\times$ LAI) + (S $\times$ LAI) + (HL $\times$ S)	HL $\times$ LAI	S $\times$ LAI
Higgins et al. (2016, 2017)	Friedl et al. (2010)	~HL + LAI + POP	~HL + POP + LAI + (HL $\times$ LAI)	HL $\times$ LAI	HL $\times$ LAI
Higgins et al. (2016, 2017)	Olson et al. (2001)	~HL + LAI + BA	~HL + BA + LAI + (HL $\times$ LAI) + (HL $\times$ BA)	HL $\times$ LAI	HL $\times$ LAI
Leemans (1990a, 1990b)	Higgins et al. (2016, 2017)	~HL + LAI + POP	~HL + LAI + POP	HL	HL
Leemans (1990a, 1990b)	Friedl et al. (2010)	~HL + LAI + S	~HL + S + LAI + (HL $\times$ LAI) + (S $\times$ LAI)	HL $\times$ LAI	S $\times$ LAI
Leemans (1990a, 1990b)	Olson et al. (2001)	~HL + LAI + S	~HL + S + LAI + (S $\times$ LAI) + (HL $\times$ S)	HL $\times$ S	S $\times$ LAI
Friedl et al. (2010)	Olson et al. (2001)	~HL + LAI	~HL + LAI + (HL $\times$ LAI)	HL $\times$ LAI	HL $\times$ LAI

Note: Models include measures of landscape modification (HL, habitat loss; POP, human population density; BA, yearly burnt area) and landscape heterogeneity (LAI, leaf area index; S, mammal richness) and their interactions per grid cell to describe the mean agreement between the four biome maps we examined. For each agreement map, models are ranked based on the Akaike's information criterion corrected for small sample sizes. For each agreement map, the most important predictor variable (top predictor) is identified by measuring the change in the model's goodness of fit and the Nagelkerke pseudo-R-squared ( $R^2$ ; Nagelkerke, 1991) when removing this variable from the top-ranked model considering pairwise predictor interactions. Abbreviation: GoF, goodness of fit.

primarily for science communication. Functional maps reflect the actual distribution of biomes at a given time, based on automated and standard observations. Such maps are thus best suited for monitoring biome dynamics (and their potential drivers) and for investigating relationships among vegetation traits and climate, biodiversity, or matter fluxes (e.g., carbon, nitrogen). Finally, simulated biome maps are derived from a set of selected hypotheses on the functioning of the biomes, making it possible to test the sensitivity of biome distribution to environmental changes, for example. Such model-generated maps are therefore useful tools to investigate ecological processes underlying present, past, and future biome dynamics. If the latter successfully reproduce the present biome distribution and further benchmarks concerning past vegetation changes (Kelley et al., 2013), they also might be useful to guide climate-adaptation measures, in particular those concerning agriculture, forestry, and conservation (Gonzalez et al., 2010; Martens et al., 2021).

## CONCLUSIONS

Ideally, the biome concept should be a tool for quantitative comparisons, but it suffers from a diversity of terrestrial biome classifications, which results in various geographic divisions, biome names, and numbers of categories. Comparing available biome-mapping methods by their

definitions and their underlying data, we identified three main families: (1) compilation biome maps from expert elicitation, (2) functional biome maps from vegetation physiognomy (remote sensing), and (3) simulated biome maps from vegetation modeling. Inferring past or future biome distributions requires hindcasting or predicting biome characteristics from limited information based on plant remains or model simulations, such as unlimited observations (compilation), plant functional traits and taxonomic diversity (functional), or physical environment data (simulated).

We developed an algorithmic protocol to spatially compare biome-classification schemes with different biome names and numbers. We compared four of the most used modern global biome maps and found strong disagreements among these maps in areas with moderate vegetation cover and in areas where human activities modify ecosystems. While biome-classification schemes agree well in some regions such as equatorial forests and several tropical deserts, they strongly differ in others. We highlighted how quantifying agreement and discrepancies between maps could help evaluate, for example, the impact of humans on global biome distributions. This may inspire further research to refine biome classifications in areas where they diverge.

To prevent and acknowledge biases, studies involving several biome classifications should identify areas of disagreement by comparing biome maps spatially. For such spatial comparison, we have provided a protocol, which

may also serve to evaluate model outputs against independently produced biome maps. Biome classifications typically disagree in areas of high human impact. These “engineered biomes” or “anthromes” deserve special attention in studies aiming to map modern-day biome distributions. To improve both the accuracy and reproducibility of biome maps and to promote maps that approach consensus, we advocate data-driven approaches. This could include not only functional biome classifications but also dynamic global vegetation models that incorporate data on plant functional traits and land use, for example.

There is neither a consensus biome map nor universally accepted definitions of biomes. “Desert,” “rainforest,” “tundra,” “grassland,” or “savanna”—while being widely used terms in common language—each have multiple definitions and no universally accepted spatial distribution. Because fit-for-purpose classification schemes are necessary, multiple biome maps should continue to co-exist, even within the three main families we identified. As a result, Earth-scale knowledge is still blurred by the extant diversity of approaches. For the time being, consensus seems to be unrealistic aim, and we must instead seek to account for the biases and uncertainties of each map more completely. We have provided comparison and decision tools to navigate this diversity and facilitate a more effective use of the biome concept, emphasizing the need for considering the way biomes are defined and mapped when using a specific biome map.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.


## DATA AVAILABILITY STATEMENT

Data and code (Champreux et al., 2023) are provided in Zenodo at <https://doi.org/10.5281/zenodo.7745096>.


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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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