RESEARCH ARTICLE

Biome classification influences current and projected future biome distributions

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Abstract

Aim: Biome classification schemes are widely used to map biogeographic patterns of vegetation formations on large spatial scales. Future climate change will influence biome patterns, and vegetation models can be used to assess the susceptibility of biomes to experience transitions. However, biome classification is not unique, and various classification schemes and biome maps exist. Here, we aimed to assess how the choice of biome classification schemes influences current and projected future biome patterns.

Location: Africa, Australia, Tropical Asia.

Time period: 2000–2099.

Major taxa studied: Tropical vegetation.

Methods: We used the adaptive dynamic global vegetation model version 2 (aDGVM2) to simulate vegetation in the study region. We classified vegetation into biomes using (1) a classification scheme based on the cover of functional types, (2) a cluster analysis based on the cover of functional types and (3) a cluster analysis based on trait patterns simulated by the aDGVM2. We compared the resulting biome maps to multiple observation-based biome maps and quantified differences in projected biome changes under the RCP8.5 scenario for the different classification schemes.

Results: As expected, biome patterns were strongly related to the scheme used for biome classification. The highest data-model agreement was derived for a cluster analysis using 21 simulated traits. Traits related to size were most important for classification. Considering all classification schemes, the area projected to undergo biome transitions under climate change varied between 16.5% and 32.1%. Despite this variability, different schemes consistently showed that grassland and savanna areas are most susceptible to climate change, whereas tropical forests and deserts are stable. Our results demonstrate that traits simulated by aDGVM2 are appropriate to delimit biomes.

Main conclusions: Studies projecting biome patterns and transitions under current and future climate should consider applying different biome classification schemes to avoid biases in such projections caused by biome classification schemes.

1 | INTRODUCTION

Biomes are widely used to map biogeographic patterns of vegetation formations on large spatial scales and to study changes in the spatial extent and distribution of vegetation formations under past, current and future climate (e.g. Allen et al., 2020; Conradi et al., 2020; Fischer et al., 2022; Martens et al., 2020). However, while the value of the biome concept has been proven, a consensus on a single biome or land cover classification scheme that fits all purposes is lacking. Rather, the range of classification schemes varies from simplified schemes with a low number of mega-biomes to detailed schemes (Beierkuhnlein & Fischer, 2021; Fischer et al., 2022). The differences between classification schemes imply that the choice of the classification scheme influences projected changes in biome patterns under future climate change: While a region may experience a biome change under one classification scheme, it may remain stable under another classification scheme. Robust studies of climate change impacts on biome patterns therefore require assessments of the sensitivity of regions threatened by biome changes to the choice of the classification scheme.

Early biome classification schemes were based on dominant life forms with similar physiological characteristics (Schimper, 1903), climate zones (Köppen, 1936) or climatic and orographic features (Walter, 1973). More recent biome maps included information on ground cover, vegetation structure and physiognomy (Prentice et al., 1992). The increased availability of remote sensing products facilitated the development of biome classification at high spatial resolution that emphasizes the features of the land surface and represents bioclimatic conditions only implicitly (e.g. Higgins et al., 2016). A comprehensive compilation of different biome classification methods and associated biome maps has recently been provided by Beierkuhnlein and Fischer (2021) and Fischer et al. (2022).

To assess the impacts of future climate change on the distribution of biomes at large spatiotemporal scales, dynamic global vegetation models (DGVMs, Prentice et al., 2007) have been widely used. These models simulate the dynamics of different plant functional types (PFTs), species or ecological strategies based on the prevailing environmental conditions. Model variables such as the leaf area index (LAI) of different PFTs or their fractional cover in a simulated grid cell can be used to classify vegetation into different biome types. Simulated changes in those variables due to climate change translate into biome transitions and allow identifying regions and biomes most susceptible to climate change (Martens et al., 2020; Scheiter et al., 2020). Open ecosystems, that is savannas and grasslands, are expected to be particularly susceptible to climate change. Some of these areas support alternative biome states (Pausas & Bond, 2020) maintained by grass–tree interactions, fire and herbivory. Climate change may influence these factors and cause rapid transitions between alternative states (Higgins & Scheiter, 2012).

During the last decade, plant traits have gained considerable attention in observational studies and among DGVM developers. Trait data have been assembled in databases such as TRY (Kattge et al., 2020) or sPlot (Bruelheide et al., 2018). Statistical methods and machine learning approaches have been applied to create trait distributions at a global scale from site data (Boonman et al., 2020; Butler et al., 2017). Such global trait maps are suitable to develop trait-based biome classification schemes. For instance, Boonman et al. (2022) classified vegetation into the ecoregions provided by Olson et al. (2001) by using global maps of specific leaf area (SLA), wood density and vegetation height and projected climate change impacts on biome patterns.

DGVM modellers made use of the trait data to represent trait variability in DGVMs (Sakschewski et al., 2015; Scheiter et al., 2013). While such trait-based DGVMs allow simulations of trait patterns at large spatial scales, simulated traits have rarely been used to define biomes (Reu et al., 2011). It, therefore, remains to be tested if biome patterns derived from simulated traits differ from those using cover fractions or LAI of different PFTs, and if the likelihood of biome transitions under climate change differs.

Here, we used the adaptive dynamic global vegetation model version 2 (aDGVM2, Scheiter et al., 2013) to test how the selection of model variables and traits as well as the selection of biome maps used to develop biome classification schemes influence simulated biome patterns. We further assessed areas most susceptible to biome transitions under climate change for different classification schemes, focusing on Africa, tropical Asia and Australia. We hypothesized (1) that the agreement between observed and simulated biomes is strongly related to the biome map used to develop classification schemes, as well as to the model variables and traits used for biome classification; (2) that the considered traits are not equally important and appropriate for biome classification; (3) that regions and the total area projected to undergo biome transitions under climate change differ among biome schemes; and (4) that open ecosystems are most susceptible to biome transitions as indicated by previous studies.

2 | METHODS

2.1 | Model description and simulation protocol

We used the aDGVM2 to simulate current and future vegetation and classified vegetation into biomes using different approaches. A short model description is provided in Supplement S1. The original model version is described in Scheiter et al. (2013) and Langan et al. (2017);

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the updated model version used in this study is described in Kumar et al. (2021). The aDGVM2 was previously benchmarked using multiple remote sensing products for South Asia (Kumar et al., 2021), tropical Asia (Scheiter et al., 2020) and Africa (Gaillard et al., 2018, using a previous model version). These benchmarking results are not reproduced in this study, yet, here we benchmarked aDGVM2 at the biome level (Sections 2.3 and 2.4).

We conducted aDGVM2 simulations following the modelling protocol described in Kumar et al. (2021) and Scheiter et al. (2020), see Supplement S2. Simulations were conducted for potential natural vegetation in the presence of fire.

2.2 | Observation-based biome maps

For data-model comparison and to develop biome schemes, we used the data set compiled by Fischer et al. (2022), hereafter abbreviated as F31 biome maps. This data set includes 31 different biome and land cover maps at 10×10 km spatial resolution (provided in appendix S4 in Fischer et al., 2022). We aggregated the data to the $1 \times 1°$ grid of the aDGVM2 simulations using the nearest neighbour method. We used the 'raster' R package for data processing (Hijmans, 2020).

2.3 | Biome classification

We applied a biome classification scheme based on a previous aDGVM2 study (Kumar et al., 2021). Vegetation was classified into seven biomes (desert, C_4 grassland, C_3 grassland, shrubland, woodland, deciduous forest and evergreen forest) based on the cover of six PFTs (C_4 grasses, C_3 grasses, deciduous shrubs, evergreen shrubs, deciduous trees and evergreen trees). Details of the classification scheme are provided in Supplement S3 and Table S1.

The biome map derived from the classification was compared to each F31 biome map. We intended to use the κ statistics (Monserud & Leemans, 1992) for the comparisons. This measure quantifies the agreement between categorical data sets. It considers the likelihood that agreement can occur by chance and is more robust than calculating overlap. Values <0 indicate no agreement, between 0 and 0.2 slight agreement, between 0.2 and 0.4 fair agreement, between 0.4 and 0.6 moderate agreement, between 0.6 and 0.8 substantial agreement and between 0.8 and 1 almost perfect agreement.

The κ statistics requires equal numbers of classes in the data sets to be compared, whereas the number of biomes differs between the modelled and the F31 biome maps. Therefore, a matching between modelled and each F31 biome map was established using the Hungarian algorithm (Kuhn, 1955) implemented in the 'RcppHungarian' R package (Silverman et al., 2022). The Hungarian algorithm identifies one observed biome for each modelled biome such that the matching overlap is maximized. After this matching, the number of simulated biomes and the corresponding F31 map was equal, and the κ value was calculated.

2.4 | Cluster analysis for biome classification

Following the approach by Boonman et al. (2022), we used Gaussian mixture models (GMM) to classify simulated vegetation into the biome types given in each of the F31 biome maps. Biome types covering less than 40 grid cells were excluded. We used the 'MclustDA' function implemented in the 'mclust' R package (Scrucca et al., 2016) for the cluster analysis. The cluster analysis was supervised, that is, the biome information (number of biomes and their spatial distribution) of each F31 biome map was used. We used different sets of model variables for the cluster analysis: the cover of different PFTs used in the biome classification (see Section 2.3) and 30 plant traits simulated by aDGVM2 (Table S2). For the analyses using traits, we calculated mean trait values for each grid cell by averaging the trait values of all plants within a grid cell. Binary traits describing phenology were averaged, and the averages represent the proportion of plants with those strategies in a grid cell. As the range of values differs between traits, traits were standardized for the cluster analysis such that the mean value is 0 and the standard deviation is 1.

In addition to using all 30 plant traits (hereafter denoted Trait Cluster 1, TC1), the cluster analysis was repeated for 10 different subsets of the traits to assess how the inclusion or exclusion of different trait assemblages influences data-model agreement (Table S2). We considered only 25 inheritable traits according to the aDGVM2 design (TC2), only variable traits (TC3), only phenology traits (TC4), only traits describing carbon allocation (TC5), only architectural traits (TC6), all traits excluding phenology traits (TC7), excluding allocation traits (TC8), excluding architectural traits (TC9), traits commonly used in the trait literature (TC10, e.g. Díaz et al., 2016) and all traits excluding traits commonly used in trait literature (TC11). The difference between inheritable and variable traits in aDGVM2 is that inheritable traits are constant during the lifetime of a plant and only change during reproduction by mutation and crossover. Variable traits change during the lifetime of a plant and are essentially model state variables.

Overall, we conducted 12 cluster analyses (one using PFT covers, 11 using trait clusters) for each of the F31 biome maps, and obtained 372 biome maps. We compared each simulated biome map with the corresponding F31 biome map used for the clustering by calculating the κ value.

We created biome maps for current and future conditions by evaluating the GMMs with the simulated current and future covers of PFTs and traits. We identified areas projected to experience biome transitions until the end of the century and calculated the number of grid cells with biome transitions for each map. To create a consensus map indicating areas most susceptible to biome changes, we stacked the 31 maps indicating biome changes derived from cluster analysis using covers of PFTs and the 31 maps derived from the best cluster analysis using traits (TC8, see Section 3). Then, we counted the number of maps projecting a biome transition for each simulated grid cell.

To test if traits characterizing biomes differ between cluster analyses using different F31 maps, we calculated mean trait values

of clusters representing tropical evergreen forest for all F31 maps. We only analysed those forests because they are represented in all F31 maps, while biomes outside forests strongly differ between the F31 maps.

2.5 | Land use

Large proportions of the study area are affected by human land use. We used the land cover map provided by Potapov et al. ([2022](#)) and classified a grid cell as utilized by humans if the fraction covered cropland and built-up areas of a grid cell exceeded 15% ([Figure S1](#)). We masked out these grid cells and calculated the area affected by biome shifts based on the remaining grid cells.

2.6 | Importance of traits

We assessed how the number of traits and the subset of traits used in cluster analyses influence the data-model agreement. A randomized approach was necessary as testing all possible combinations of 30 traits was computationally not feasible. We conducted this analysis for the biome map with the highest data-model agreement (map 3, Beck et al. ([2018](#)), see Section [3](#)).

Sets of 2, 3, …, 29 traits were randomly selected out of the 30 traits simulated by aDGVM2. For each set, a cluster analysis was conducted. For each number of traits, this analysis was repeated 150 times to obtain cluster analyses with different subsets of traits. We also conducted 150 analyses including all 30 traits. As the clustering algorithm is not deterministic, the replicates for 30 traits differ. Overall, 4350 (=29 ×150) models were fitted. For each model, we calculated the κ value to quantify data-model agreement.

To assess the importance of different traits in the 4350 models, we identified the best models by calculating the 98% percentile of the κ values. Models with a κ value greater than the 98% percentile were selected, and as a measure of importance we counted how often each of the 30 traits was included in those models.

Some traits and state variables in the aDGVM2 are correlated. We therefore repeated the analysis for 17 weakly correlated traits, that is, traits with pairwise correlation <0.9 (WC in [Table S2](#)). Models were fitted for sets of 2, 3, …, 17 traits, with 150 replicates each. Overall, 2400 (=16×150) models were fitted for this analysis.

3 | RESULTS

3.1 | Biome patterns under current conditions

The comparison between the biomes of the biome classification scheme (BC) and the F31 biome maps revealed an average value of $\kappa=0.263$. The highest agreement was observed for the Pfadenhauer and Klötzli ([2014](#)) map with $\kappa=0.367$ ([Figure 1, 2a](#)), indicating fair agreement. In cluster analyses using the cover of PFTs, κ was highest

for the Dinerstein et al. ([2017](#)) map ($\kappa=0.406$, [Figures 1](#) and [2d](#), [Table 1](#)), indicating moderate agreement. The average κ for all biome maps using the cover of PFTs was $\kappa=0.278$.

When using traits for the classification, the highest average κ value for all F31 biome maps was obtained for trait cluster 8 (TC8, $\kappa=0.427$), which uses all traits except the carbon allocation traits ([Figures 1](#) and [2g](#), [Table 1](#)). The highest κ of all models was obtained with TC8 and the Beck et al. ([2018](#)) biome map ($\kappa=0.518$). When using traits commonly used in the literature (TC10), κ was highest for the Olson et al. ([2001](#)) map with $\kappa=0.191$.

Different classification methods reproduce clusters in northern Africa, western Asia and for the cluster analyses in central Australia ('Des' in [Figure 2a](#), cluster 8 in [Figure 2d,g](#)) and clusters in central Africa and southeast Asia ('EvF' in [Figure 2a](#), cluster 1 in [Figure 2d,g](#)). These clusters overlap with deserts and tropical forests in the F31 maps respectively. The agreement was lower in areas outside tropical forests and deserts, particularly in areas covered by savannas and grasslands. We conclude that tropical forests and deserts were best represented by the different classification approaches.

Mean trait values differed between biomes, here exemplified for the cluster analysis using traits and the Beck et al. ([2018](#)) biome map ([Table 2](#), [Figure S2](#)). Tropical rainforest and tropical monsoon forest showed the highest mean vegetation height and lowest mean stem count, indicating tree dominance. In contrast, hot arid deserts showed the lowest vegetation height and highest stem count, indicating shrub dominance. Mean tree age was low in tropical rainforest and monsoon forests and temperate regions without a dry season ([Table 2](#)). Those regions were almost exclusively dominated by evergreen vegetation, whereas phenology in other biomes was a mixture of evergreen and deciduous vegetation. Communities dominated by evergreen vegetation showed the lowest SLA values and temperate dry winter hot summer regions with the highest proportion of deciduous plants showed the highest SLA. Carbon allocation traits showed relations across different biomes ([Figure S3](#)). For instance, leaf allocation was negatively related to storage and reproduction allocation, and it was positively related to wood and root allocation. Despite these relations, variation of the values of allocation traits was low ([Table 2](#)). Mean trait values of the tropical rainforest biome differed between cluster analyses for all F31 biome maps, particularly age, height, SLA and phenology ([Figure 3](#)).

3.2 | Importance of traits for classification

Data-model agreement increased with the number of traits used for the cluster analysis while variation between replicates decreased ([Figure S4a](#)). For trait cluster TC1 using all traits, the highest data-model agreement was observed for a classification using 21 traits ($\kappa=0.553$, [Table S3](#)). The 98% percentile of κ for all models was $\kappa=0.514$. Crown area was included in most of the models exceeding this value (81 models, [Figure 4a](#)), followed by stem diameter, height and age (76, 73 and 68 models). Allocation to wood biomass, wood density and SLA were the least important (40, 38 and 36 models).
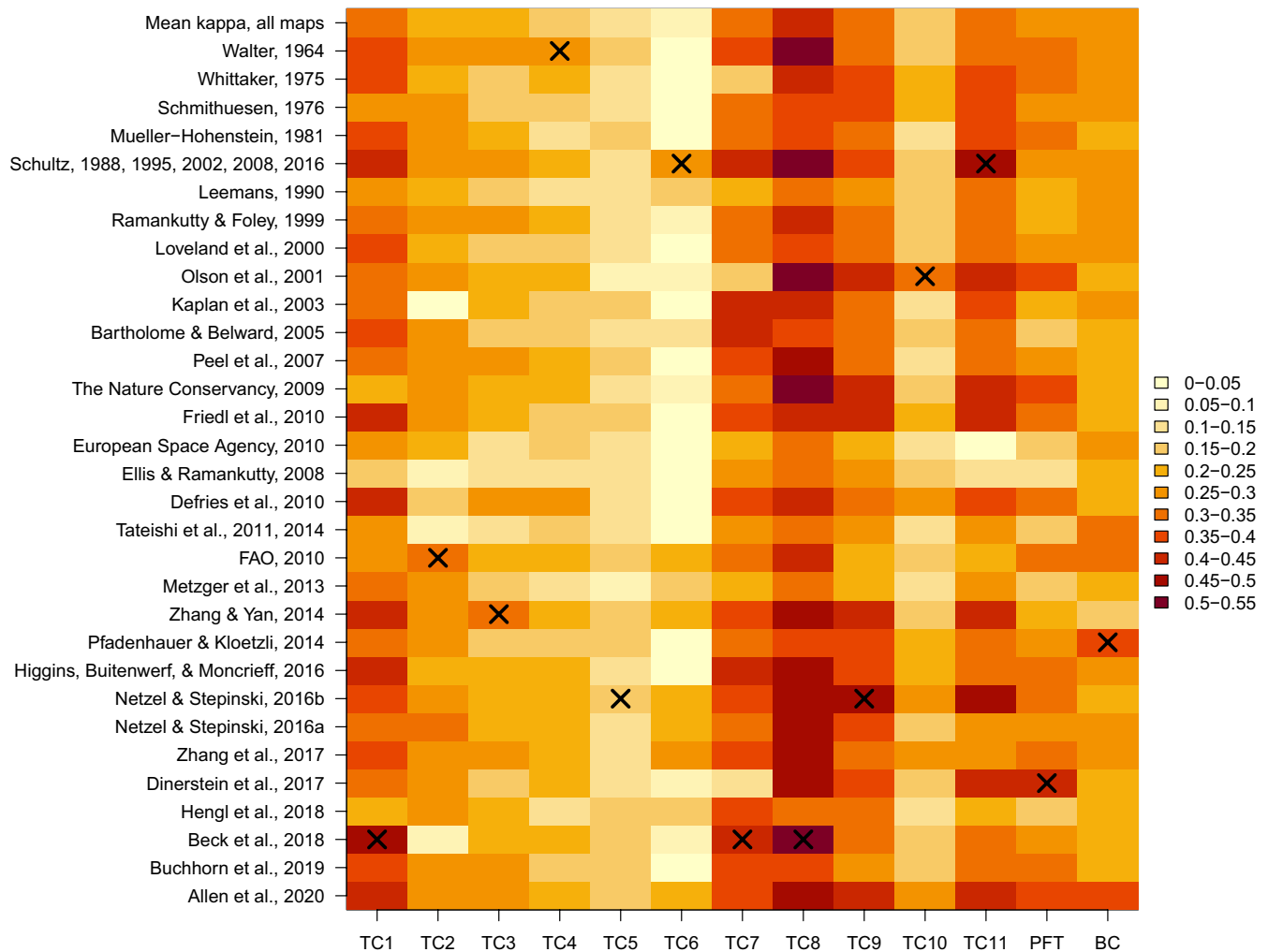
FIGURE 1 Data-model agreement for different biome maps and biome classification methods. The figure shows κ values for all of the 31 biome maps provided by Fischer et al. (2022) for different trait clusters (TC) as defined in Table S2, for the cluster analysis using cover of different PFTs (PFT) and for the biome classification using cover of different PFTs (BC). The 'X's denote the biome map that maximized κ within each trait cluster. The first row is the mean κ value for each trait cluster.

When considering only weakly correlated traits (WC), data-model agreement increased with the number of traits used for the cluster analysis (Figure S4b). The highest data-model agreement was observed for a model using 13 traits ($\kappa = 0.506$, Table S4). The 98% percentile of κ for all replicates was $\kappa = 0.495$. Of the models exceeding this κ value, 18 models included all 17 traits. Stem diameter, bark thickness, allocation to bark and age were included in all best models (Figure 4b).

3.3 | Biome transitions under future conditions

The number of grid cells projected to experience biome transitions between current and future conditions differed between the methods used for classification. Using the biome classification scheme, 20.1% of the grid cells were projected to change, mainly in regions covered by grassland, shrubland and woodland (Figure 2a–c). Similar spatial patterns were derived from clustering using the cover of different PFTs (Figure 2d–f) and traits (Figure 2g–i).

The consensus map of biome changes derived from cluster analyses using all F31 biome maps, all traits (TC1) and cover of different PFTs also showed that regions surrounding the equatorial tropical rainforests were most susceptible to biome transitions (Figure 5). Areas currently covered by desert and tropical rainforests were projected to be less susceptible to biome changes. The pattern differed for classification approaches using traits and cover of PFTs (Figure 5c). In 28.2% of the study region, at least one of the models projected a biome shift (Figure 5d). In 5.5% of the total area, more than 50% of the models projected biome shifts, and in 0.2% of the area, more than 90% of the models projected biome shifts.

The number of grid cells projected to undergo biome transitions varied between 16.5% and 32.1% across all different models (Table 1). On average, 24.9% and 24.7% of the grid cells were projected to change their biome state in models using cover of PFTs and traits respectively. The number of grid cells projected to change and the κ value were negatively correlated for cluster
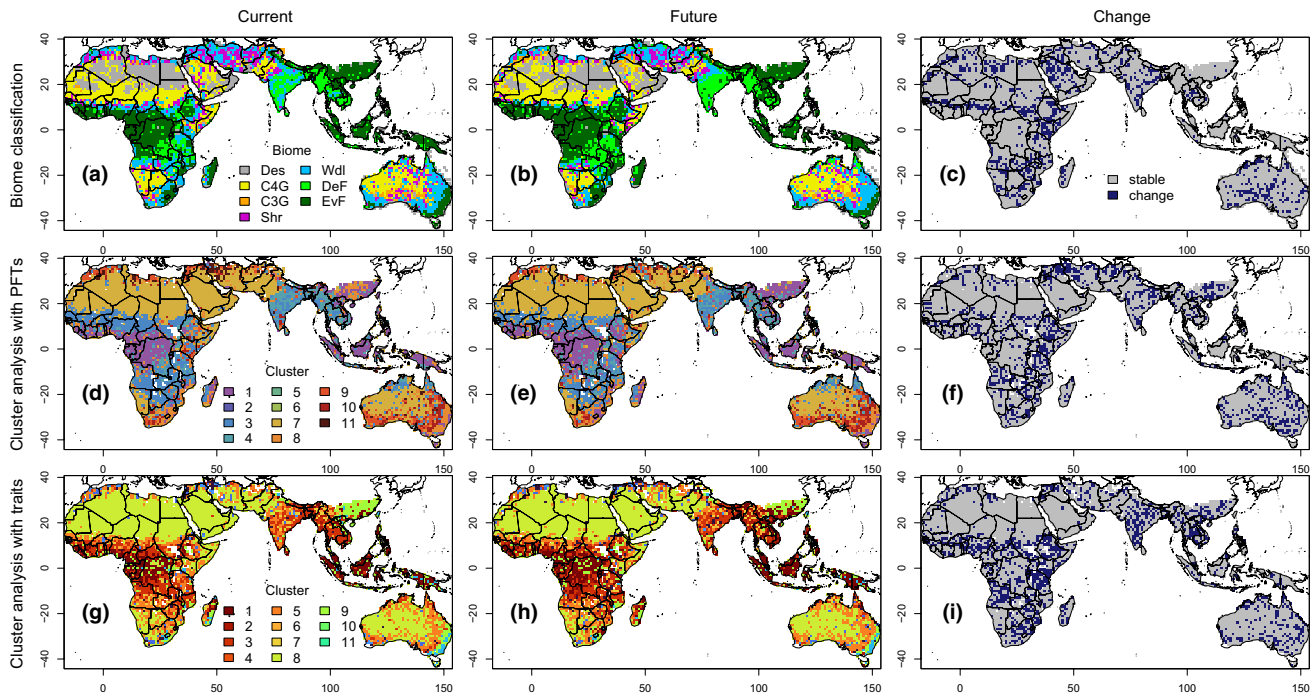
FIGURE 2 Simulated biome patterns for current and future conditions for three different classification approaches, and simulated biome changes. Out of all classification methods, we selected the biome classification scheme using PFTs (a–c), one example from the cluster analysis using PFTs (d–f), and one example from the cluster analysis using traits (g-i). For the models based on cluster analysis (d,g), models with the highest κ value were selected (see Figure 1): Dinerstein et al. (2017) for PFTs and Beck et al. (2018) with trait cluster TC8 for traits. Panels (a,d,g) represent current biome patterns, panels (b,e,h) represent future biome patterns, panels (c,f,i) represent areas where biome changes between current and future conditions are projected. Note that a separate colour scheme was used for each method (i.e. each row). Biomes in a and b: C3G, C3 grassland; C4G, C4 grassland; DeF, deciduous forest; Des, desert; EvF—evergreen forest; Shr, shrubland; Wdl, woodland.

analyses using the cover of PFTs and traits (Figure S5), indicating that biome transitions may be overestimated when data-model agreement is low whereas schemes with high agreement provide a lower bound for biome transitions. The κ value was negatively correlated with the number of biomes in the F31 maps (Figure S6), that is, biome maps with a lower number of biomes showed higher data-model agreement. The area affected by biome changes increased with the number of biomes in the F31 biome maps (Figure S7), yet, when dividing the area affected by biome changes by the number of biomes, the area per biome decreased with the number of biomes (Figure S8).

When excluding areas affected by land use, the projected area affected by biome transitions averaged for all models decreased to 19.5% and 19.2% for clustering using PFT cover and traits, respectively, when the entire study region was used as reference. When considering only areas with natural vegetation, biome transitions were simulated in 22.8% and 22.4% of the area for clustering using cover and traits respectively (Table S5, Figure S9).

4 | DISCUSSION

We used different approaches to classify vegetation into biomes and assessed the agreement between simulated and observation-based

biome maps, as well as differences between projected biome changes until the end of the 21st century. While most classification schemes in the context of DGVMs use variables such as cover or LAI of different PFTs, we showed that trait patterns simulated by the aDGVM2 can be used to delimit biomes. As expected, data-model agreement differed between classification approaches and was higher for clustering methods using traits than for methods using PFTs. Areas projected to undergo transitions under climate change differed between methods using traits and PFT cover. Yet, areas covered by grasslands and savannas were most vulnerable to climate change.

4.1 | Biome patterns under current conditions

The classification methods reproduced clusters corresponding to evergreen forests and to deserts. Areas outside the forests and deserts showed disagreement among different classification approaches. This disagreement can be attributed processes that were not considered in aDGVM2 such as land use or herbivory, to uncertainties in simulated fire regimes, to uncertainties in ecological and environmental data used to parameterize aDGVM2 and to the large differences between the F31 biome maps (Fischer et al., 2022). These maps were used to inform the clustering and

TABLE 1 Data-model agreement and percent of the grid cells projected to undergo biome changes until 2099.

Biome map	κ cover	κ traits	κ class	Δ cover	Δ traits
Allen et al. (2020)	0.355	0.478	0.366	26.5	22.9
Buchhorn et al. (2019)	0.323	0.397	0.239	26.7	28.3
Beck et al. (2018)	0.264	0.518	0.228	21.3	25.5
Hengl et al. (2018)	0.192	0.348	0.200	25.6	25.8
Dinerstein et al. (2017)	0.406	0.469	0.239	22.4	18.1
Zhang et al. (2017)	0.324	0.496	0.263	18.3	24.7
Netzel and Stepinski (2016) - Map 1	0.298	0.464	0.253	23.2	23.8
Netzel and Stepinski (2016) - Map 2	0.330	0.465	0.239	24.2	21.6
Higgins et al. (2016)	0.322	0.483	0.275	23.8	19.3
Pfadenhauer and Klötzli (2014)	0.266	0.399	0.367	29.5	27.7
Zhang and Yan (2014)	0.234	0.488	0.187	18.6	24.7
Metzger et al. (2013)	0.172	0.307	0.213	28.3	27.9
FAO (2012)	0.342	0.408	0.339	27.9	25.1
Tateishi et al. (2011, 2014)	0.163	0.346	0.327	29.5	28.1
Defries et al. (2010)	0.325	0.443	0.241	21.7	24.6
Ellis and Ramankutty (2008)	0.111	0.320	0.223	27.8	29.8
European Space Agency (2010)	0.188	0.329	0.260	23.4	26.3
Friedl et al. (2010)	0.327	0.432	0.249	21.8	22.9
The Nature Conservancy (2009)	0.350	0.513	0.237	22.4	17.6
Peel et al. (2007)	0.270	0.471	0.229	21.8	24.8
Bartholomé and Belward (2005)	0.196	0.378	0.246	25.2	29.1
Kaplan et al. (2003)	0.246	0.432	0.299	27.4	27.5
Olson et al. (2001)	0.364	0.502	0.237	26.6	19.8
Loveland et al. (2000)	0.299	0.394	0.265	25.0	25.8
Ramankutty and Foley (1999)	0.217	0.435	0.292	16.5	23.2
Leemans (1990)	0.247	0.311	0.283	32.1	29.5
Schultz (1988, 1995, 2002, 2008, 2016)	0.260	0.509	0.293	22.7	22.8
Müller-Hohenstein (1981)	0.301	0.389	0.234	29.6	24.2
Schmithüsen (1976)	0.259	0.366	0.298	29.5	27.0
Whittaker (1975)	0.320	0.415	0.259	26.5	26.4
Breckle and Rafiqpoor (2019); Walter (1964, 1968); Walter & Breckle (2002)	0.343	0.517	0.283	24.8	20.2
Mean	0.278	0.427	0.263	24.9	24.7

Note: 'κ' quantifies the data-model agreement, 'Δ' represents the percent of grid cells projected to undergo biome changes, 'cover' represents models where cover of different PFTs was used for the cluster analysis, 'traits' represents models where trait cluster 8 (TC8) and the Beck et al. (2018) biome map were used for the cluster analysis, 'class' represents results from applying the biome classification scheme. For the biome classification, the percentage of grid cells projected to undergo biome changes is Δ class = 20.1%. This percentage is not related to the F31 biome maps as the maps were not used for developing the classification scheme. Simulations were conducted at 1° spatial resolution, the biome maps were aggregated to the same grid for the comparisons.

therefore cause differences between biome maps derived from aDGVM2.

The highest agreement between observed and modelled biomes was obtained for the cluster analysis using traits and the Beck et al. (2018) biome map. The Beck et al. (2018) map is a Köppen–Geiger classification based on temperature and precipitation and represents climate zones. This finding indicates that simulated biome patterns are primarily determined by the environmental conditions that drive the ecophysiological processes in the model (Kumar

et al., 2021; Langan et al., 2017). However, within communities simulated at the 1-ha scale, community assembly processes, competition and fire influence community composition and traits. For example, simulated vegetation height (Figure S10), productivity and biomass (Kumar et al., 2021) increased from desert to forest, following a rainfall gradient. In contrast, SLA was hump-shaped and community assembly selected for highest values in seasonal environments (Figure S10). Shrub abundance increased with aridity whereas trees outcompeted shrubs in humid areas. These small-scale processes

TABLE 2 Mean trait values of selected traits for the cluster analysis using the Beck et al. (2018) map.

Ind	Biome name	AL	AR	Ph	H	SC	SLA	Age
1	Tropical rainforest	34.36	7.52	94.2	7.83	1.60	7.53	29
2	Tropical monsoon	33.87	8.19	48.4	8.91	1.80	8.26	76
3	Tropical savanna	33.51	8.13	48.5	4.26	2.24	8.45	131
6	Temp. dry winter warm summer	33.70	7.75	61.7	4.99	1.76	7.56	98
7	Temp. dry winter hot summer	33.16	8.49	31.9	3.60	3.08	9.67	199
14	Temp. dry summer hot summer	33.21	8.26	50.9	1.40	3.26	8.58	199
9	Temp. no dry season hot summer	34.38	7.61	96.9	6.18	1.57	7.29	30
13	Temp. no dry season warm summer	34.37	7.78	97.9	5.62	1.65	7.16	29
8	Arid desert hot	32.84	7.85	40.1	0.21	5.41	7.69	44
5	Arid steppe hot	33.44	7.94	45.5	0.83	4.16	7.89	169
15	Arid desert cold	33.58	7.88	36.1	0.76	3.19	7.57	137
17	Arid steppe cold	33.28	8.23	58.0	1.75	2.85	8.15	188

Note: Ind, index of biome in Beck et al. (2018) map; Biome name, biome name in Beck et al. (2018) map; AL, allocation to leaves (%); AR, allocation to roots (%); Ph, percent of evergreen (vs. deciduous) plants (%); H, height (m); SC, stem count (number); SLA, specific leaf area (m^2/kg); Age, mean age of all trees (years). Mean trait values for all modelled traits per biome are provided in Figure S1.

can modify biome distributions, particularly where alternative biome states are possible (Pausas & Bond, 2020). To which degree biotic or abiotic factors are the main determinants of simulated biomes remains to be tested in subsequent studies.

4.2 | Importance of traits for biome classification

Our results indicate that traits describing plant size and growth form are most appropriate to distinguish biomes. These traits include height, crown area, stem diameter and a trait defining if a woody plant is a tree or shrub. Traits describing size generally increased with precipitation and from deserts and grasslands to savannas to different forest types (Figure S2). This result agrees with the observed spectrum of plant form and function, where size is one major axis (Díaz et al., 2016).

The second major axis, characterized by leaf economic traits, was less important in our sensitivity analysis. Given that SLA showed clear patterns in the study region (Figure S10), we expected high importance of this trait. This result can be explained by the high observed variability of SLA within individual plants, species and communities (Xu et al., 2020). A better representation of this variation in the model may enhance the importance of SLA for biome classification. Furthermore, it can be explained by the importance of traits related to size, that override the effects of other traits. Indeed, when we excluded traits related to size from the analysis, SLA showed higher importance for biome classification (not shown). In the aDGVM2, low and high SLA typically co-occur with evergreen and deciduous phenology respectively. Evergreen phenology emerged in tropical rainforests and non-seasonal forests while deciduous phenology emerged in seasonal environments. Phenological traits are relevant for biome classification and have previously been used to map phenological zones (Buitenwerf et al., 2015).

Different ecological strategies are characterized by carbon allocation patterns. For instance, carbon allocation in annual and

perennial vegetation prioritizes reproduction and persistence respectively (Pfeiffer et al., 2019). We therefore expected strong variation of allocation traits across biomes in the model result. Although the values of allocation traits varied only over small ranges, high carbon allocation to leaves was associated with high carbon allocation to wood but low carbon allocation to belowground storage and vice versa. This trade-off represents acquisitive strategies with rapid growth in environments with high resource availability and conservative strategies in arid and seasonal environments.

Mean traits of specific biomes differed between cluster analyses informed by different biome maps. Nonetheless, broad trait patterns were consistent. For example, tropical evergreen forests were represented by the dominance of tall evergreen trees, irrespective of the underlying biome map.

4.3 | Biome transitions under future conditions

Under future climate change, all classification methods showed that tropical rainforests and deserts were stable, whereas other biomes showed biome transitions. Yet, the area affected by biome transitions varied between 16.5% and 32.1% for different methods. Previous studies showed that vegetation changes simulated by aDGVM2 are primarily driven by increasing atmospheric CO_2 and associated CO_2 fertilization effects on woody plants, and to a lower extent by changes in precipitation and temperature (Kumar et al., 2021; Scheiter et al., 2020).

How changes in simulated traits and variables translate into biome transitions differs between classification approaches. In approaches based on the cover of PFTs, CO_2-induced increases in size and density of woody plants imply changes in the cover of different PFTs. Simulated increases in the cover of tree PFTs imply transitions to tree-dominated biome types. In the clustering methods based on traits, biome transitions can be attributed to changes in the
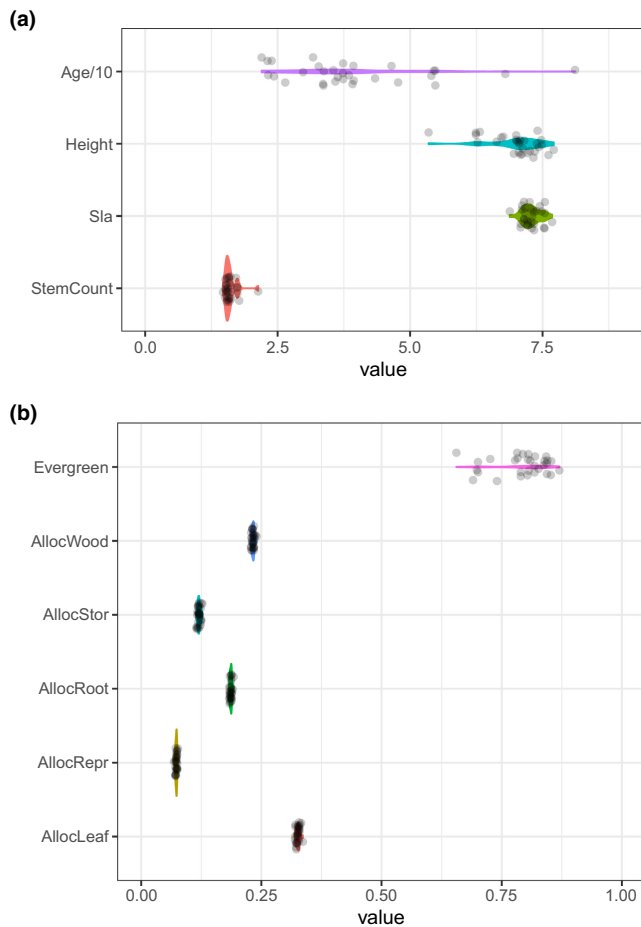
FIGURE 3 Mean traits of evergreen forest in different biome classifications. For each of the F31 biome maps, mean traits of the corresponding cluster analyses were calculated. Each point represents the mean trait value of one biome map. Units are: age—years/10; height—m; SLA—m^2/kg; stem count—number of stems per plant; evergreen—fraction of evergreen trees; allocation—fraction. Note, that age was divided by 10 and that the range of the y-axis differs between the panels. 'AllocWood', 'AllocStor', 'AllocRoot', 'AllocRepr' and 'AllocLeaf' are traits describing carbon allocation to wood biomass, storage, roots, reproduction and leaves.

community trait composition. Simulated increases in stem diameter, height, crown diameter and wood density, and decreases in SLA and the stem number of woody plants (Figure S10) indicate a higher proportion of tall and evergreen trees with low SLA and a lower proportion of shrubs in plant communities under future conditions. Such changes represent biome transitions to tree-dominated biomes. The aDGVM2 also simulated changes in carbon allocation patterns with decreases in allocation to bark, reproduction and storage and increases in allocation to leaves, roots and wood. These changes indicate transitions to acquisitive ecological strategies (Díaz et al., 2016) that invest more in growth and less in protection and reproduction.

In our results, traits that are affected by climate change are not necessarily traits that are most important for biome classification. For example, SLA showed a strong response to climate change but only low importance for classification. In contrast, traits related to size showed strong responses to climate change and high importance

for classification. How traits will respond to climate change remains unresolved. Kühn et al. (2021) investigated responses of traits to changes in precipitation and temperature to assess whether specific traits maintain plant performance under climate change. These results indicate that species with lower SLA are more likely to maintain productivity and to survive when precipitation decreases. However, under increasing temperatures, the role of SLA was less clear.

The comparison of changes in trait patterns and biome patterns simulated by aDGVM2 shows broad agreement with the patterns of Boonman et al. (2022), despite the different modelling approaches. Similar to the aDGVM2 results, Boonman et al. (2022) found decreases in SLA, increases in height and increases in wood density across most of the study region under climate change (Figure S10). Boonman et al. (2022) also projected increases in wood-dominated ecosystems and forests such as an expansion of central African forests. Elevated CO_2 was not considered by Boonman et al. (2022); therefore, these biome changes were attributed to climate change effects only.

Biome shifts projected by our modelling approach are affected by several sources of uncertainty. First, aDGVM2 shows strong responses to elevated CO_2 that imply increases of productivity, carbon stocks and woody vegetation cover, thereby promoting biome transitions to more wood-dominated states (Kumar et al., 2021; Scheiter et al., 2020). The strength of CO_2 fertilization effects is, however, still debated. A second source of uncertainty is that land use activities such as pasturing or fuel wood harvesting were not explicitly simulated (Pfeiffer et al., 2019; Scheiter et al., 2019). Here, we masked out areas affected by land use (Potapov et al., 2022, Figure S1) and ignored land use changes until the end of the century. In reality, forest loss and expansion of urban areas and cropland are ongoing (Potapov et al., 2022).

4.4 | Comparison of biome classification methods

The most common approach for classifying simulation results of DGVMs into biomes is based on vegetation features such as LAI or fractional cover of PFTs that are characteristic for a biome (Hickler et al., 2012; Kumar et al., 2021). The advantages of such 'expert-based' approaches are that they use knowledge on biomes, they are reproducible and easy to interpret, and they can be tailored to specific regions and applications. Caveats of biome classification are that simulated biome patterns and transitions may be highly sensitive to the selection of threshold values that delimit biomes (Scheiter et al., 2018, 2020), and that the matching between observed biomes and model variables can be challenging.

In contrast, many clustering methods are probabilistic and provide uncertainty measures and probabilities that a grid cell belongs to a specific biome (Boonman et al., 2022). The assignment to a biome is based on the similarity of vegetation features within each biome and, in the case of unsupervised classification, not informed by a priori information on observed biome distributions (Higgins et al., 2016). Unsupervised classification was not used in this study, and its suitability remains to be tested.
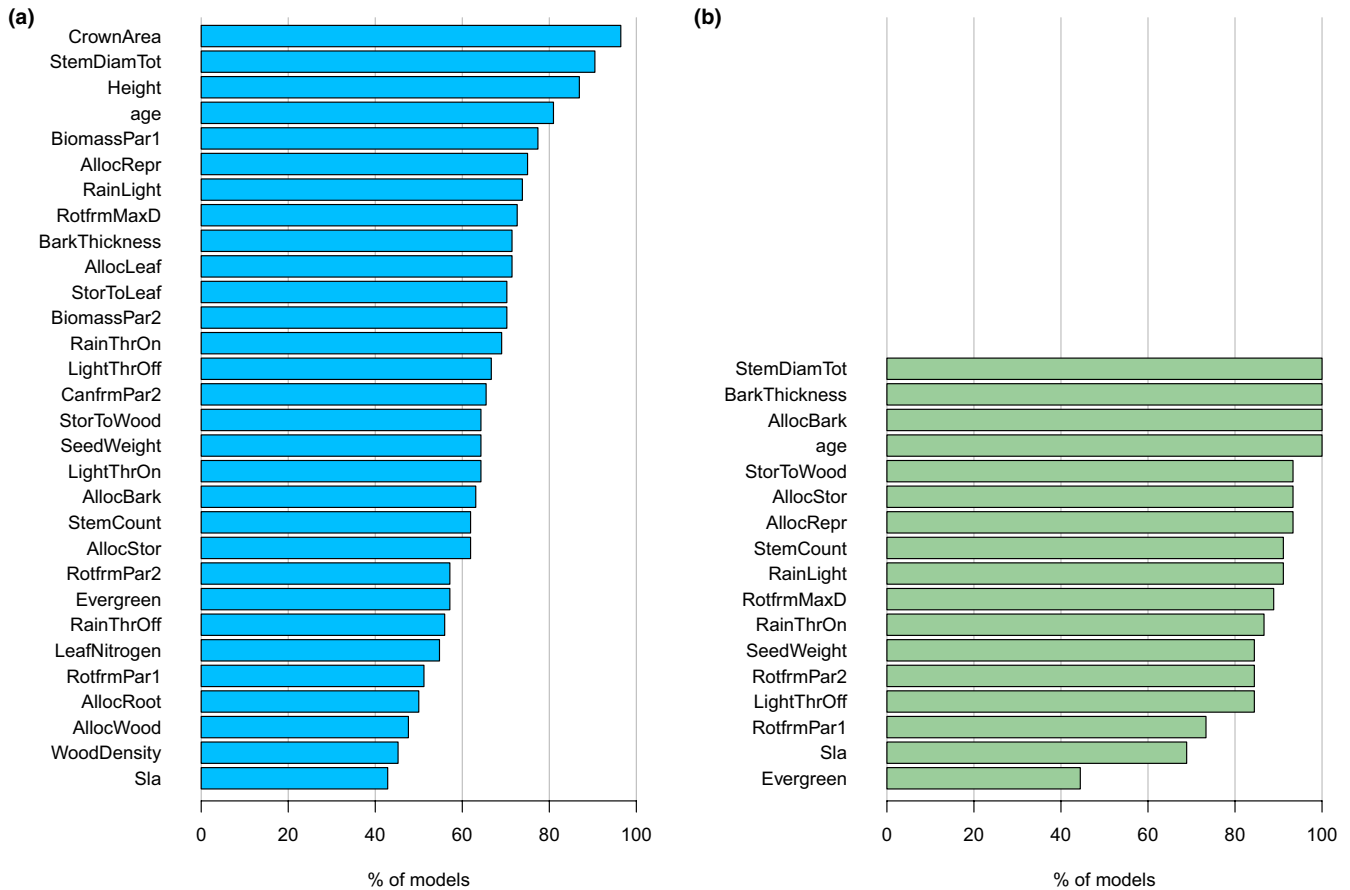
(a)

(b)

FIGURE 4 Importance of different traits in cluster analyses. Importance is represented by the percent of models that include the trait in a randomized design with variable number of randomly selected traits. Analyses were conducted including all traits (TC1, panel a) and only weakly correlated traits (WC, panel b). Traits in the analysis represent mean trait values of all plants in simulated grid cells.
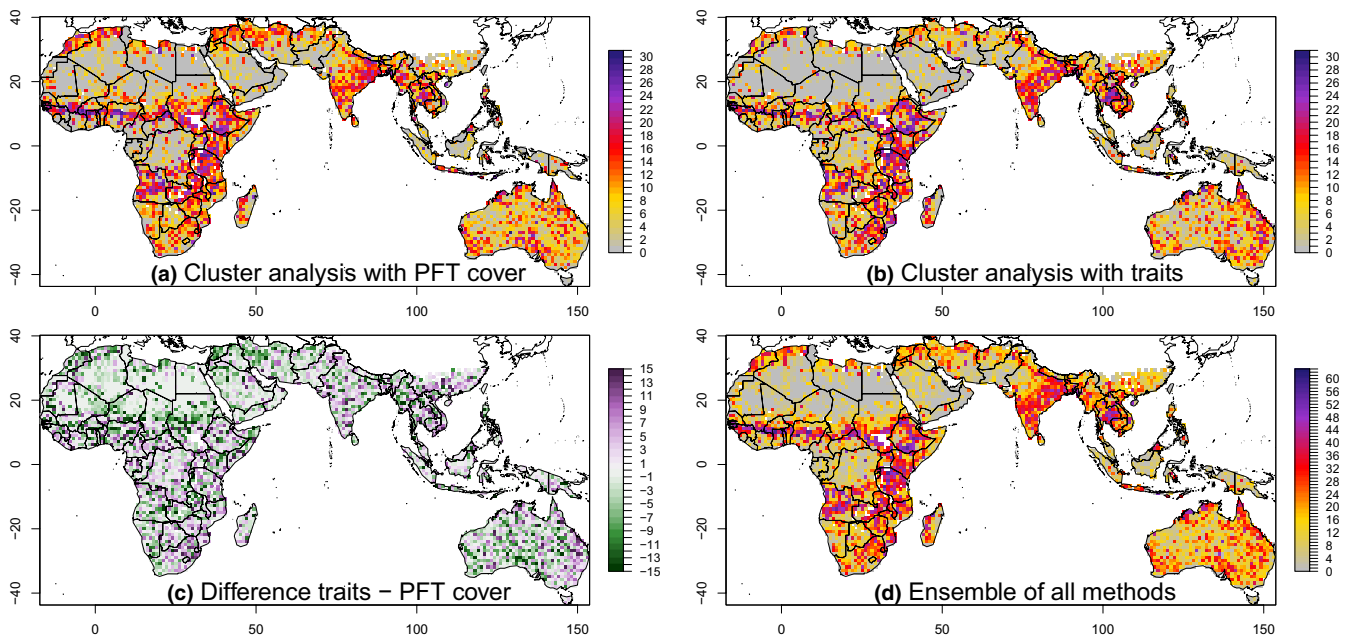

(a) Cluster analysis with PFT cover

(b) Cluster analysis with traits

(c) Difference traits − PFT cover

(d) Ensemble of all methods

FIGURE 5 Consensus maps of biome transitions until 2099. The consensus maps were derived by counting the number of models that simulate a biome change in each simulated grid cell, (a) 31 models using cover of different PFTs, (b) 31 models using traits from TC8 and (d) all 63 models (1 classification using PFTs, 31 cluster analyses using PFTs, 31 cluster analyses using traits). Panel (c) shows the difference between models using traits and models using PFT covers (difference between panels a and b), and illustrates where biome projections from clustering methods with PFTs and traits deviate. We constrained the values to a range between −15 and 15 to improve the visibility of the differences.

We demonstrated that three aspects are relevant for biome classification: (1) the model variables used for classification, (2) the classification method and (3) the biome map for developing classification methods and for data-model comparisons. Modellers need to select appropriate data and models for each aspect. The uncertainty associated with such decisions was clearly demonstrated by our analysis. For (1), we recommend to use traits for biome classification instead of PFT cover, if such information is available in the model. To maximize data-model agreement, all available traits should be included, particularly traits related to size. For (2), we recommend to apply supervised clustering methods for classification, informed by observation-based biome maps, because it showed the best performance and a priori definition of thresholds to match observation-based biomes is not necessary. For (3), we recommend to compare simulated biome patterns to multiple observation-based biome maps to account for uncertainties in biome classification. Thereby, a subset of the Fischer et al. (2022) product can be selected that is most appropriate for the study region or that best matches the PFTs and biomes simulated by the model. Classification methods with high accuracy provide a lower bound for biome transitions according to our results.

Merging different biome maps into a consensus map is challenging if they use a variable number of different biome types (Fischer et al., 2022). Yet, biome maps could be merged by first reclassifying different biome maps into a set of common biomes and then merging biome maps, for example, by identifying the most frequent biome types. Alternatively, maps representing areas with biome transitions can be merged by counting the number of maps that project biome transitions per grid cell. Such an approach provides a measure of uncertainty for biome transitions and was applied in this study.

5 | CONCLUSIONS

Our results showed that the selection of methods for classifying simulated vegetation into biomes influences both the simulated current and the future biome distributions, as well as the area at risk of experiencing a biome change. This result has important implications for management, climate mitigation and adaptation as it is crucial whether model results indicate that 32.1% of the study area may be affected by biome changes or merely 16.5%. Studies of biome changes should therefore account for uncertainties in biome classification by using different approaches. Aggregation of model results based on different climate forcing data sets or different DGVMs in model ensembles is already state of the art, and applying different methods for biome classification schemes adds a further dimension to such studies.

AUTHOR CONTRIBUTIONS

Simon Scheiter conceived the study. Dushyant Kumar conducted model simulations. Simon Scheiter conducted analyses. All authors contributed to model development. Simon Scheiter led the writing with contributions of all authors.

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SUPPORTING INFORMATION

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