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Trait-based projections of climate change effects on global biome distributions

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Abstract

Aim: Climate change will likely modify the global distribution of biomes, but the magnitude of change is debated. Here, we followed a trait-based, statistical approach to model the influence of climate change on the global distribution of biomes.

Location: Global.

Methods: We predicted the global distribution of plant community mean specific leaf area (SLA), height and wood density as a function of climate and soil characteristics using an ensemble of statistical models. Then, we predicted the probability of occurrence of biomes as a function of the three traits with a classification model. Finally, we projected changes in plant community mean traits and corresponding changes in biome distributions to 2070 for low (RCP 2.6; +1.2°C) and extreme (RCP 8.5; +3.5°C) future climate change scenarios.

Results: We estimated that under the low climate change scenario (sub)tropical biomes will expand (forest by 18%–22%, grassland by 9%–14% and xeric shrubland by 5%–8%), whereas tundra and temperate broadleaved and mixed forests contract by 30%–34% and 16%–21%, respectively. Our results also indicate that over 70%–75% of the current distribution of temperate broadleaved and mixed forests and temperate grasslands is projected to shift northwards. These changes become amplified under the extreme climate change scenario in which tundra is projected to lose more than half of its current extent.

Main conclusions: Our results indicate considerable imminent alterations in the global distribution of biomes, with possibly major consequences for life on Earth. The level of accuracy of our model given the limited input data and the insights on how trait–environment relationships can influence biome distributions suggest that trait-based correlative approaches are a promising tool to forecast vegetation change and to provide an independent, complementary line of evidence next to process-based vegetation models.

KEYWORDS
biome distribution, climate change, Gaussian mixture model, global vegetation, plant height, specific leaf area, traits-based model, wood density

1 | INTRODUCTION

Climate change is affecting ecosystems globally. Effects on terrestrial plants include changes in physiology, species composition and biomass production (Boone et al., 2018; Esquivel-Muelbert et al., 2019; Wadgymar et al., 2018), which in turn may translate into changes in vegetation and, ultimately, the global distribution of biomes. For example, studies have been reporting a poleward shift of temperate and boreal forest at high latitudes (Bjorkman et al., 2018; Myers-Smith & Hik, 2018), and the encroachment of tropical forest into tropical grasslands (Esquivel-Muelbert et al., 2019; Stevens et al., 2017). Such changes in the distribution of biomes may alter local biotic interactions, changing the structure of ecological communities and the provision of ecosystem services (e.g. Coops et al., 2018; Lavorel and Grigulis, 2012).

Process-based dynamic global vegetation models (DGVMs) are typically used to forecast biome shifts due to climate change. Generally, DGVMs describe how climate affects plant physiology (e.g. plant photosynthesis and evapotranspiration) through a hypothesized mechanism, which in turn determines the population dynamics and vegetation structure. This way, DGVMs help to understand mechanisms that may result in biome changes (Gonzalez et al., 2010; Sakschewski et al., 2015; Scholze et al., 2006; Sitch et al., 2008). Yet, due to the complex nature of ecological processes, DGVMs simplify real-world variability in plant traits into a limited number of plant functional types (Sitch et al., 2008; Yang et al., 2016). Moreover, while these mechanistic models explicitly include processes that underpin scenario specific changes (Connolly et al., 2017), the combination of many processes modelled simultaneously may result in emergent properties that may be difficult to validate.

As an alternative, correlative plant functional trait-based models may also contribute to predict biome changes due to climate change. These statistical models rely on the direct link between community mean plant traits and the local environment (Boonman et al., 2020), where an equilibrium state is assumed and processes are implicitly described via the impact of the environment on individual plant fitness (e.g. effects on growth, reproduction and survival; Keddy, 1992; Violle et al., 2007). Similar to how DGVMs use physiological processes as an intermediate step between climate and vegetation structure, this intermediate step allows us to include trait variation of different species in similar environments and trait adaptation of similar species in different environments. In addition, this intermediate step introduces a causal link between climate and biomes (e.g. the conversion of water availability to respiration via specific leaf area, and of temperature to metabolism via wood density and height), therefore reducing the risk of establishing spurious relationships (e.g. Fourcade et al., 2018; Santini et al., 2021). Assuming that these models capture the causal relationships between climate and community mean trait values, the relationships are in principle transferable to future scenarios (Dormann et al., 2012; Yang et al., 2016, 2019). Here, the environmental constraints on traits are used as a backbone

for predicting biome changes in response to climate change (van Bodegom et al., 2014; Yang et al., 2016, 2019).

As argued in the field of distribution modelling (Dormann et al., 2012), these two families of modelling approaches should not be seen as competing, but as complementary approaches with their own strengths and weaknesses. Although the mechanistic approach is common for large-scale vegetation predictions, the fundamentally different statistical, trait-based models may provide an independent line of evidence and may bring new prospects for understanding climate change impacts on vegetation distributions (Lavorel and Grigulis, 2012; Yang et al., 2015; Yang et al., 2016). The comparison between two fundamentally distinct modelling approaches, each with its own limitations, provides insight in the models' ability to capture the right mechanisms and make meaningful predictions (e.g. Newbold et al., 2017). While biomes and future trait distributions have already been predicted using a trait-based approach, this technique has not yet been used to predict the change in global biome distributions due to climate change (Bodegom et al., 2014; Madani et al., 2018).

In this study, we aim to predict the impact of climate change on the global distribution of biomes. We project future biome distribution changes via global community mean trait–environment relationships of specific leaf area, plant height and wood density. Specifically, we investigate how predicted changes in geographic patterns of plant traits can translate into biome contractions, expansions or shifts. By comparing the results of our study to the results of process-based models predicting global vegetation changes (e.g. Alo & Wang, 2008; Gonzalez et al., 2010; Scholze et al., 2006; Sitch et al., 2008), this study may bring new insights into the underlying causes of vegetation change (Boonman et al., 2020; Madani et al., 2018; van Bodegom et al., 2014). In addition, this may help to assess ecological consequences of climate change and may ultimately aid the allocation of large-scale conservation efforts (Laughlin, 2014).

2 | METHODS

2.1 | Modelling approach

We followed a three-step trait-based approach to model the influence of climate change on the global distribution of biomes (Figure 1). This paragraph provides an overview of these steps, and each step is discussed in more detail in the following sections. As the first step, we predicted the current global distributions of plant community mean specific leaf area (SLA), height and wood density at a 0.5-degree resolution in the WGS84 coordinate system based on recently developed global trait–environment relationships (Boonman et al., 2020). Second, we applied a clustering model that predicts the probability of occurrence of each biome as a function of the combination of the three traits. We trained this model based on the predicted present-day global trait patterns and a map of the present biome distributions (Olson et al., 2001) and predicted current biome distributions based on the highest probability of occurrence of all biomes per grid cell. Third, we projected changes in plant
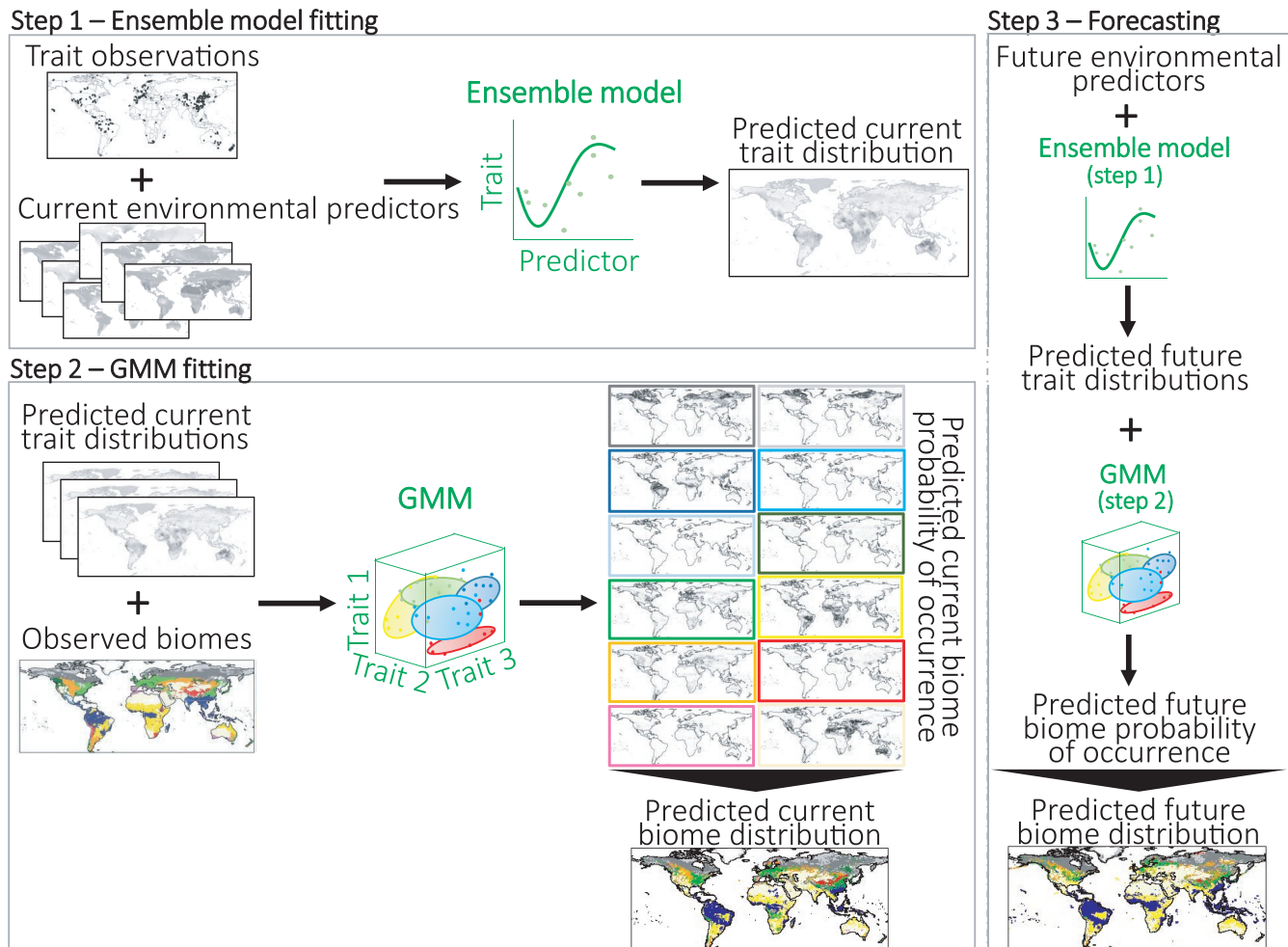
FIGURE 1 Modelling overview. Trait–environment relationships are established and, using an ensemble modelling approach, global plant trait distributions are predicted (step 1). These are linked to observed biome distributions with a classifying Gaussian Mixture Model (GMM) (step 2). For future predictions of biome distributions, future climate predictions are used as input for the fitted ensemble model resulting in future plant trait distributions, which, in turn, are used as input for the fitted GMM resulting in future biome distributions (step 3)

community mean traits and corresponding changes in global biome distributions under two alternative future greenhouse gas emission scenarios, representing a low (RCP 2.6) and extreme (RCP 8.5) emission scenario corresponding to an increase of global mean annual temperature of +1.2°C and +3.5°C in 2070, respectively.

2.2 | Trait modelling

We established global trait–environment relationships using the plant community mean trait dataset from Boonman et al. (2020), which includes georeferenced, locally measured trait data representative of natural plant communities. As plant traits, we selected specific leaf area (SLA), plant height and wood density, which are related with plant form and growth rate (Griffin-Nolan et al., 2018), are known to vary with environmental gradients and across geographic regions and biomes (Charles-Dominique et al., 2018; Chave et al., 2009; Freschet et al., 2011; Griffin-Nolan et al., 2018) and could be modelled with sufficient predictive power (Boonman et al., 2020).

For each trait, we first calculated community mean trait values for each community in each study and then combined multiple community means in one grid cell by taking their mean, in order to limit spatial pseudo-replicates. This led to 361, 217 and 125 0.5-degree grid cell average community means for SLA, plant height and wood density, respectively. We fitted the trait–environment relationships at a resolution of 0.5 degrees using six environmental variables: minimum temperature of the coldest month, humidity index, precipitation in the driest quarter of the year, precipitation seasonality and, averaged to a depth of 30 cm, soil cation exchange capacity and soil pH (Figure 1, step 1). We selected these variables for their ecological relevance while minimizing collinearity (for details see Boonman et al., 2020). We obtained the current bioclimatic variables (averages for 1979–2013) from CHELSA version 1.2 (Karger et al., 2017) and the soil characteristics from SoilGrids250 m (Hengl et al., 2017). The latter were resampled to match the 0.5-degree resolution of the trait and climate data. The humidity index was calculated as the mean annual precipitation divided by the mean annual potential evapotranspiration (Zomer et al., 2008).

We used four modelling techniques (generalized linear model, generalized additive model, random forest and boosted regression trees) and combined their predictions using an ensemble forecasting approach, calculating the current global trait distributions as the average predictions of the four models weighted by the models' predictive performance (cross-validated R^2; Appendix S1). Specifics on model settings can be found in Boonman et al. (2020). Further, we assessed the applicability domain of the models using a multivariate environmental similarity surface (MESS) analysis (Appendix S1). This analysis quantifies per grid cell the difference of the most extrapolated environmental predictor (i.e. the predictor with a grid cell value that is furthest outside that predictor's range of values within the dataset compared to all other included predictors) and the environmental range of that predictor covered by locations in the plant trait dataset, while considering the distribution of these data within the global environmental range (Elith et al., 2010).

2.3 | Biome modelling

To predict biomes from trait combinations, we fitted a Gaussian Mixture Model (GMM) (Witte et al., 2007). This clustering model links trait combinations to biomes by estimating the probability of occurrence of each biome based on densities of trait combinations found in a specific biome. We calibrated the GMM by overlaying the predicted current global trait distributions with an observed biome map from Olson et al. (2001) (Figure 1, step 2). For this calibration step, we excluded grid cells where at least one of the traits was predicted to have an extreme value (i.e. > the 99th quantile of the predicted values), which resulted in the removal of 3% of all grid cells. From the observed biome map, we omitted the biome "rock and ice" because soil data on ice are not available, and the biomes "lakes," "flooded grassland and savanna" and "mangroves" because water-dependent plant communities were not covered by the trait dataset (Boonman et al., 2020). We included the following biomes: 1) tundra; 2) boreal forest and taiga (hereafter boreal forest); 3) (sub)tropical moist broadleaf forest (hereafter tropical moist forest); 4) (sub)tropical dry broadleaf forest (hereafter tropical dry forest); 5) (sub)tropical coniferous forest (hereafter tropical coniferous forest); 6) temperate coniferous forest; 7) temperate broadleaf and mixed forest (hereafter temperate mixed forest); 8) (sub)tropical grassland, savanna and shrubland (hereafter tropical grassland); 9) temperate grassland, savanna and shrubland (hereafter temperate grassland); 10) montane grassland and shrubland (hereafter montane grassland); 11) Mediterranean forest, woodland and scrub (hereafter Mediterranean woodland); and 12) desert and xeric shrubland (hereafter xeric shrubland). We used untransformed trait predictions rather than the underlying community mean trait observations to calibrate the GMM to ensure a sufficiently large number of replicates per biome to properly train the model, enabling us to predict more biomes (Yang et al., 2016).

We then applied the GMM to predict the present-day distribution of biomes by assigning each 0.5-degree grid cell the biome with the maximum probability of occurrence (Figure 1, step 2). A clustering model assumes perfect matches between the vegetation types as

recorded in the original trait dataset and the observed biome map used to train the GMM. However, biomes naturally include small-scale variations, which may be defined as vegetation mosaics intrinsic to biomes, for example grassland or heathland patches in the temperate forest biome. Nevertheless, we checked for (dis)similarities between the recorded vegetation type and the observed biome on the Olson global map and found a good match between the recorded vegetation type and the biome or vegetation type common to the matching biome (Appendix S2). We assessed the performance of the GMM by using a 10-fold split-sample cross-validation (80% training; 20% testing) and calculating biome-specific True Skills Statistics (TSS) values (Allouche et al., 2006). The overall TSS value was calculated as the average value weighted by the relative extent of each biome.

2.4 | Forecasting

We extracted climate projections for 2070 (averages from 2061 to 2080) from three divergent general circulation models (GCMs), CCSM4, CNRM-CM5 and MRI-CGCM3 (Varela et al., 2015), forced with the emission scenarios RCP 2.6 and RCP 8.5 (from now on referred to as low and extreme climate change scenarios). We downloaded the climate data associated with the emission scenarios from CHELSA version 1.2 (Karger et al., 2017). We selected these scenarios to cover a wide range of vegetation changes for the considered range of possible projected changes in climate (Thuiller et al., 2019). For each combination of GCM and climate change scenario, we projected future trait distributions using the fitted ensemble model (Figure 1, step 3), assuming soil characteristics to remain unchanged given the relatively short time period considered in this study. We then averaged the projections across the GCMs for each of the two climate change scenarios. In turn, we used the future trait distributions as input to the trained GMM to estimate the future probability of occurrence of the different biomes (Figure 1, step 3). Finally, we projected future biome distribution maps under both climate change scenarios by superimposing the future probabilities of occurrences of all biomes and presenting the one with the highest probability for each grid cell (Figure 1, step 3).

To draw sufficiently grounded conclusions on biome expansions, contractions and shifts in response to climate change, the extent of biomes should be large enough to have a good predictive accuracy (Table 1), which is why we focused on the seven most widespread biomes (jointly covering 88% of the global terrestrial vegetated surface and each covering more than 5% of the land surface): tundra, boreal forest, tropical moist forest, temperate mixed forest, tropical grassland, temperate grassland and xeric shrubland. Biome surface areas were calculated by grid cell size in km^2 using the "area" function of the raster package.

To account for the uncertainty in biome predictions for both the present and future, and thus relax the assumption that cells correspond to the biome with the highest probability of occurrence, we generated 100 alternative biome maps for the present as well as each of the two future scenarios. Each map was generated by resampling each grid cell using the predicted probability of occurrence of each

TABLE 1 Confusion matrix with 12 biomes. The numbers represent the total number of grid cells averaged over the model runs predicted (row) and observed (column) to be a specific biome. Per observed biome, the shade of the cell indicates the relative difference in number of grid cells predicted to be a specific biome, where darker shades represent larger differences. The colour of each biome matches the colours in the biome maps (Figure 4). The first column of the table shows the relative surface area (km^2) of each biome according to the observed biome map. The second column shows the predictive accuracy of the GMM as TSS values per biome. Bold values indicate the biomes with a large enough extent and good predictive accuracy, which are considered in analyses on future biome distributions.

Rel. extent	TSS						Observed								
				Tun	BoF	TrMF	TrDF	TrCF	TeCF	TeBF	TrG	TeG	Mon	Med	Des
0.06	0.61		Tun	4161	2518	0	0	0	193	229	5	122	85	14	44
0.12	0.59		BoF	2500	5317	2	0	0	344	634	25	470	257	14	240
0.15	0.66		TrMF	0	3	3469	260	85	72	301	1318	68	69	53	457
0.02	0.01		TrDF	0	1	278	97	13	16	53	338	41	19	18	170
0.00	0.00	Predicted	TrCF	0	0	86	12	9	6	21	74	12	6	4	40
0.03	0.05		TeCF	184	383	73	13	4	217	418	115	207	83	46	166
0.10	0.48		TeBF	214	625	297	45	20	365	2166	434	554	301	164	378
0.16	0.45		TrG	12	36	1353	326	75	112	425	2539	396	127	129	1239
0.08	0.33		TeG	96	560	99	38	13	204	616	364	1388	214	191	868
0.04	0.23		Mon	67	224	77	18	5	77	311	124	225	357	20	290
0.02	0.18		Med	9	11	42	16	4	50	157	132	176	23	206	345
0.21	0.66		Des	44	143	521	179	43	161	355	1282	831	225	305	5649

Abbreviations: BoF, boreal forest; Des, xeric shrubland; Med, Mediterranean woodland; Mon, montane grassland; TeBF, temperate mixed forest; TeCF, temperate coniferous forest; TeG, temperate grassland; TrCF, tropical coniferous forest; TrDF, tropical dry forest; TrG, tropical grassland; TrMF, tropical moist forest; Tun, tundra.

biome per grid cell as weights. The results on biome changes are based on the comparison of each of the 100 current maps to each of the 100 alternative future biome maps per future scenario (Appendix S3). We further assessed the reliability of independently predicted future traits and their combinations by assessing the applicability domain of the future predictions (Appendix S1), comparing observed and projected among-trait correlations (Appendix S1) and checking the degree of overlap between hyper-volumes built with projected community mean trait combinations and observed plant trait values (Appendix S1).

We performed all analyses in R version 3.4.1 (R Core Team, 2016), using the following packages for the main modelling steps: penalized (Goeman, 2010), mgcv (Wood, 2017), randomForest (Breiman, 2001), gbm (Ridgeway, 2017), mclust (Fraley and Raftery, 2003), raster (Hijmans & van Etten, 2012) and hypervolume (Blonder et al., 2014).

3 | RESULTS

3.1 | Trait predictions

The ensemble model for each of the predicted traits performed similar to other models predicting global or large-scale trait distributions (Appendix S1; Boonman et al., 2020). Community mean specific leaf area was the lowest in more arid areas and regions with the highest temperatures (Figure 2a). Community mean plant height was the highest in wet, tropical regions and the lowest in temperate and arctic

regions (Figure 2b). Community mean wood density was the lowest in areas with a low precipitation seasonality and the highest in warm, humid regions (Figure 2c). These global trait predictions include uncertainty due to model fitting and extrapolation. The former is indicated in the trait–environment relationships (Appendix S4, plotted spatially by Boonman et al., 2020) and suggests uncertain specific leaf area, height and wood density predictions in Africa, arid regions and arctic regions, respectively. As most observations are done in the Americas, Europe and Southeast Asia, current and future trait predictions are extrapolated in Africa, and for wood density also in Russia and Canada (Appendix S1).

Projected changes in trait distributions were less pronounced under the low than the extreme climate change scenario (Figure 2). Overall, community mean SLA was predicted to decrease by up to 21% and 31% under the low and extreme climate change scenarios, respectively. Yet, it increased by up to 12% and 18% (low and extreme climate change scenario) in extreme dry and tropical wet areas (Figure 2d,g). Community mean plant height generally increased by up to 207% under the low climate change scenario and up to 388% under the extreme climate change scenario, but decreased up to 59% and 60% (low and extreme climate change scenario) in parts of Western Europe, the West Siberian Plain, the boreal shield of Canada and around the Mato Grosso Plateau (Figure 2e,h). Finally, community mean wood density overall increased up to 7% and 11% under the low and extreme climate change scenarios, respectively, but decreased up to 3% and 4% (low and extreme climate change scenario) in the most xeric areas of the world (Figure 2f,i).
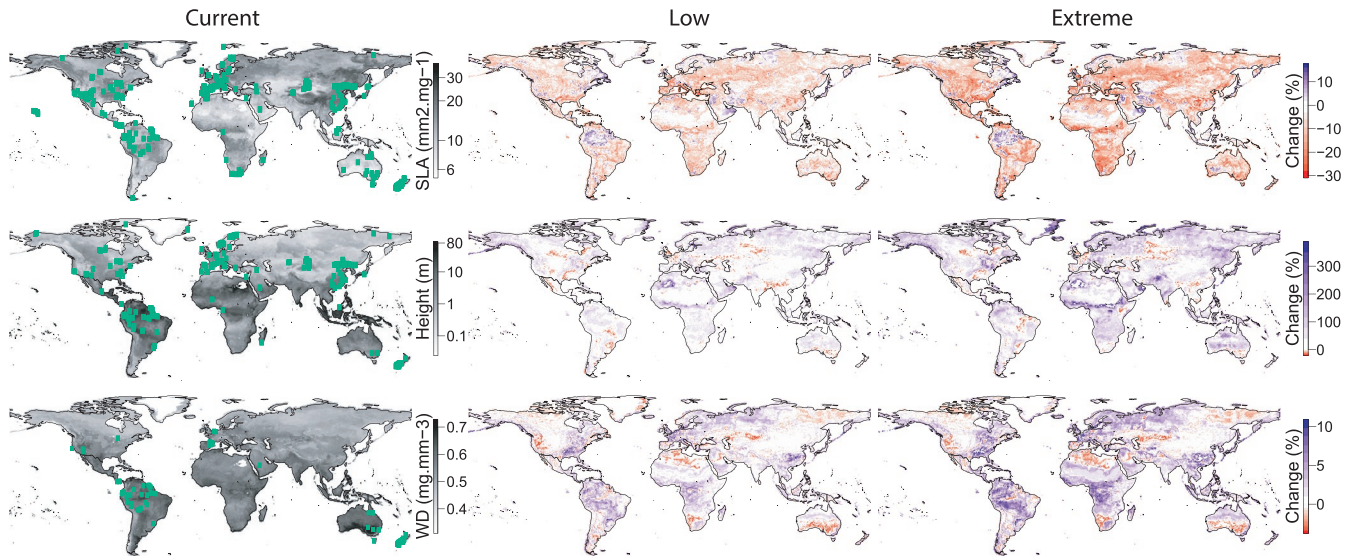
FIGURE 2 Trait predictions under the current climate, and the relative change per trait for the low (RCP 2.6) and extreme (RCP 8.5) climate change scenarios, using fitted trait-environment models and future climate (Appendix S4). The first row indicates predictions for Specific Leaf Area (SLA), the second row for height, and the third row for wood density (WD). The green squares represent the grid cells with community mean trait observations. The most extreme future changes (values smaller than the 0.01 percentile and larger than the 0.99 percentile) were removed from these plots to enhance interpretation. No predictions were made for Greenland or the south of Egypt, as there are no soil predictions and precipitation seasonality is zero, respectively
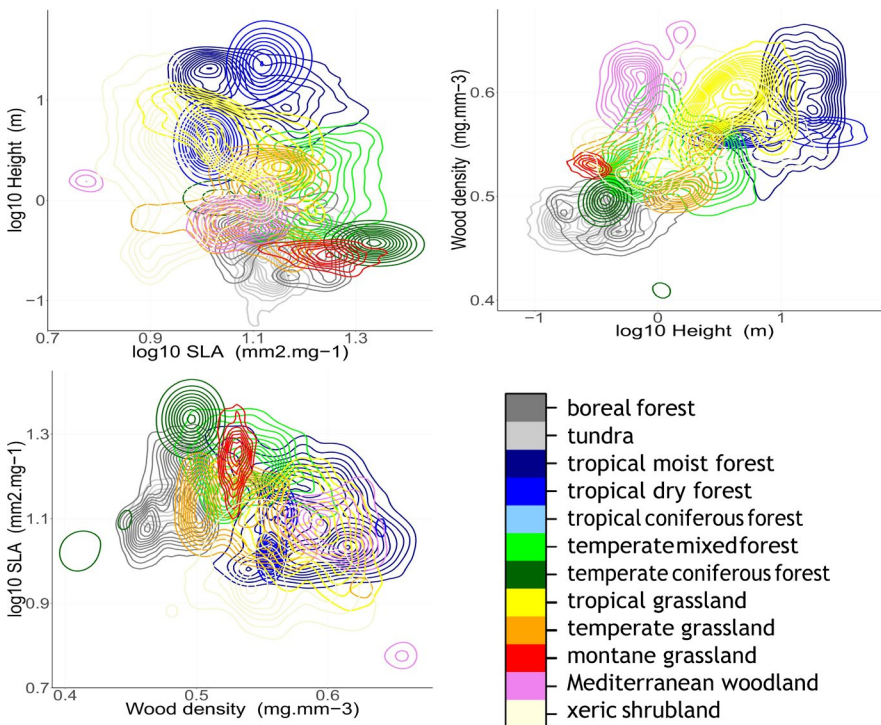

FIGURE 3 Density plots showing the locations of the biomes in two-dimensional trait space for each of three pairwise combinations of traits. Colours represent biomes and the centre(s) of each contour plot corresponds to the most common combination(s) of traits for that specific biome

- boreal forest
- tundra
- tropical moist forest
- tropical dry forest
- tropical coniferous forest
- temperate mixed forest
- temperate coniferous forest
- tropical grassland
- temperate grassland
- montane grassland
- Mediterranean woodland
- xeric shrubland

3.2 | From traits to biomes

Biomes were characterized by different ranges of values for the three traits. The lowest specific leaf area values were mostly associated to xeric shrublands, while we found the highest specific leaf area values for temperate mixed forests (Figure 3, Appendix S6). Community mean plant height decreased with latitude, with the highest values for tropical

biomes (Figure 3, Appendix S6). Similarly, community mean wood density was the highest for tropical biomes and decreased in more temperate environments (Figure 3, Appendix S6). Combining the three traits better characterized biomes and increased their identifiability (Figure 3). Some biomes included limited variation of trait values (e.g. the temperate grassland biome), while others encompassed a wide variety of trait value combinations (e.g. the tropical grassland biome).

The predictive accuracy (TSS) varied greatly between the 12 terrestrial biomes (Table 1). The TSS values partly related to the biomes' extent (Spearman correlation *r* = .92), where biomes with low predictability generally had a low extent. For the seven most widespread biomes, the largest mismatches were tundra for boreal forest and vice versa, tropical grassland for tropical moist forest and xeric shrubland, and temperate grassland for xeric shrubland. Biomes with relatively low TSS values were confused with 1 biomes of larger extent but similar traits, for example tropical dry forest being confused with tropical moist forest (Table 1, Figure 3 or 2) biomes identified during the original trait measurements, for example Mediterranean woodland being confused with temperate grassland (Appendix S2).

Despite fine-scale differences, the weighted average TSS across all biomes was 0.51, resulting in a global pattern of predicted biomes broadly consistent with the actual distribution of biomes (Figure 4a,b and Appendix S5).

3.3 | Biome predictions

Tropical biomes were projected to flourish under climate change (Figures 4 and 5). Overall, tropical moist forest was projected to expand by 19.9% (17.7%–22.3%; mean [min-max]) under the low climate change scenario and by 32.0% (29.8%–33.7%) under the extreme scenario (Figure 5), mostly reflecting projected increases in community mean plant height (Appendixes S4,S6,S7). These expansions are expected to occur mostly in central Africa and the north of South America (Figure 4) replacing tropical grassland (Figure 6). Tropical grassland, in turn, was projected to expand by
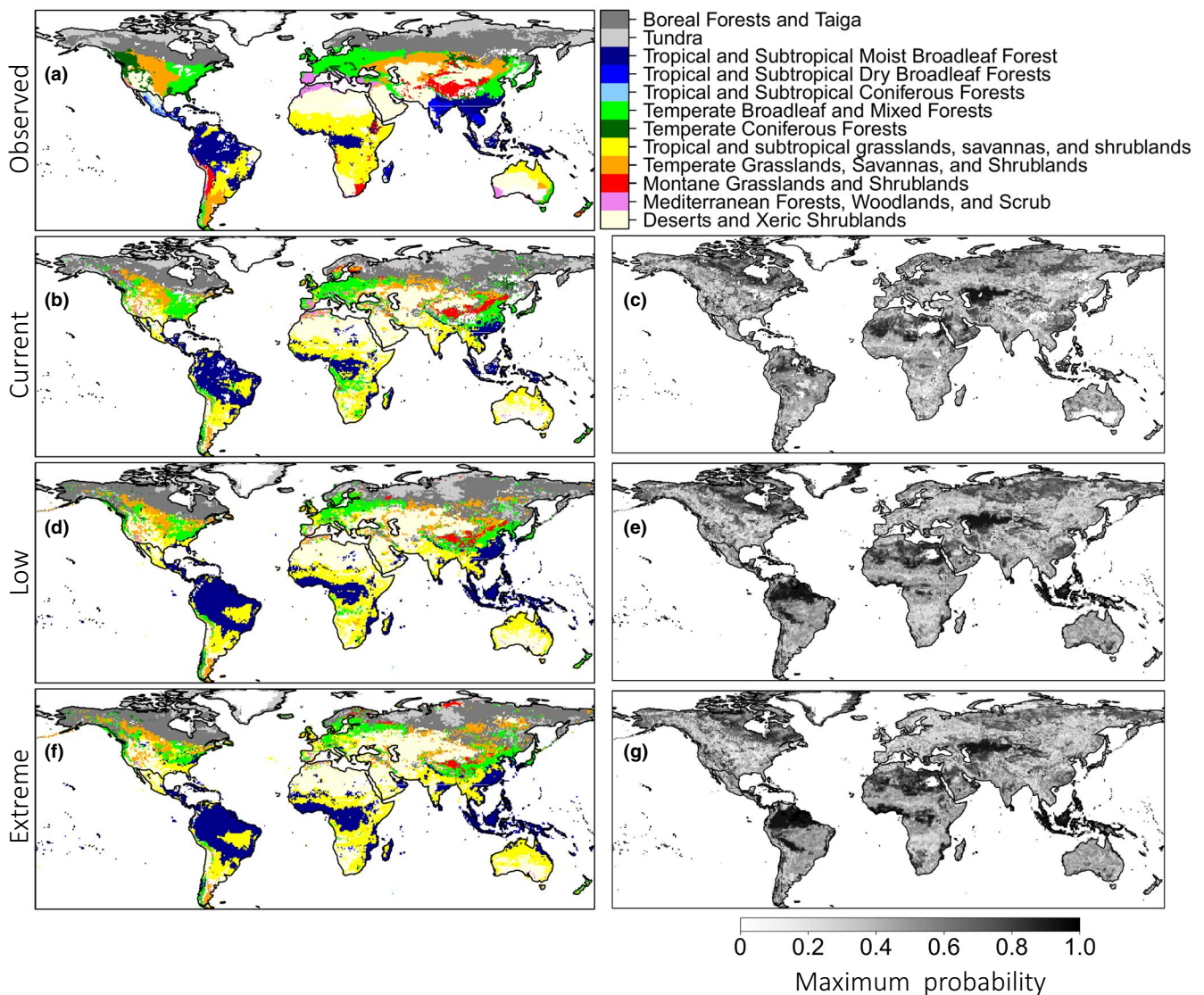

FIGURE 4 Original biome map (a) and modelled current and future biome distributions (b,d,f) with associated maximum probabilities (c,e,g). The higher the maximum probability, the higher the likelihood of the depicted biome being the true biome occurring in that area. Current corresponds to predictions under the current climate (b,c); Low corresponds to projections under RCP 2.6 climate change scenario (d,e); Extreme corresponds to projections under the RCP 8.5 climate change scenario (f,g)
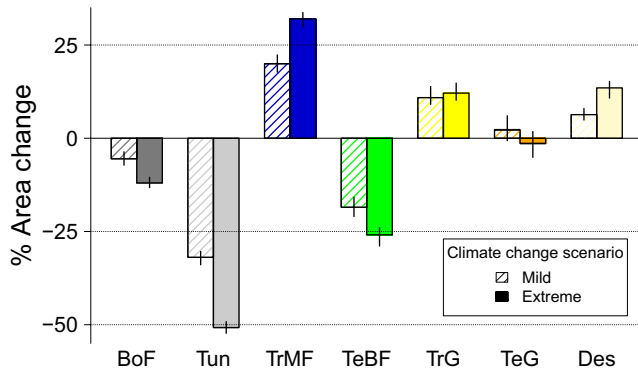
FIGURE 5 Projected changes in surface area (%) of the seven biomes with the highest predictive performance (TSS>0.3) for the low (dashed bar) and extreme (full bar) climate change scenario. Bars represent the average change over the 10,000 current and future comparisons (resulting from the 100-fold sampling), and the error bars represent the minimum and maximum change. Actual values, including medians, can be found in Appendix S3. BoF, boreal forest; Tun, tundra; TrMF, tropical moist forest; TeBF, temperate mixed forest; TrG, tropical grassland; TeG, temperate grassland; Des, xeric shrubland

10.9% (9.09%–13.9%) to 12.2% (10.2%–14.8%; low to extreme climate change scenario) in Europe, the east of North America, and Australia (Figures 4 and 5). This reflects projected changes in community mean plant height and wood density (Figure 3, Appendixes S4,S6,S7). The expansion of tropical grassland in these areas would likely happen at the expense of temperate mixed forest, temperate grassland and xeric shrubland (Figures 4 and 6). Yet, we also predicted tropical grassland expansion at the expense of tropical moist forest, which reflects the battle of occurrence between tropical moist forests and grasslands, both having a high probability of occurrence in tropical climates (Figures 4 and 6 and Appendix S8). Xeric shrublands were projected to expand by 6.4% (4.9%–8.0%) to 13.4% (10.8%–15.3%; low and extreme climate change scenario) in the Kalahari and Gobi regions, Australia and North America, replacing tropical and temperate grassland (Figures 4–6). This is mostly reflecting projected decreases of community mean SLA (Appendixes S4,S6,S7).

In contrast to the expansion of tropical biomes, major biome contractions and shifts were expected in the temperate and arctic regions of the Northern Hemisphere (Figure 4). Our projections indicated a loss in tundra area of 32.0% (30.4%–33.9%) under the low climate change scenario and 50.8% (49.2%–52.3%) under the extreme scenario, making tundra the biome mostly affected by climate change (Figure 5). These changes reflect projected increases in community mean plant height under climate change in northern regions (Appendixes S4,S6,S7), indicative of woody encroachment and replacement of tundra by boreal forest in North America and Russia (Figures 4 and 6). Specifically, we projected that 51.2% (49.3%–53.1%) to 55.5% (53.6%–57.3%) of the current extent of boreal forest will shift northwards under low and extreme climate change, respectively (Figures 4 and 6). As a result, the southern border of the

Eurasian boreal forest would be displaced northwards (Figure 4). In turn, temperate mixed forest was projected to shift 72.6% (70.2%–74.8%) to 79.8% (78.0%–81.7%) of its current extent under the two climate change scenarios, moving northwards into the boreal forests of Europe, North America and Asia (Figures 4 and 6). Alongside these shifts we found decreases in extent of 5.5% (3.6%–7.2%) to 11.9% (10.5%–13.2%) for boreal forest and 18.5% (15.8%–21.0%) to 26.0% (24.0%–28.9%) for temperate mixed forests (low and extreme change scenarios; Figure 5). Declines in temperate mixed forest were expected to occur mostly in Europe, the east of North America and China, along the southern edge of the biome (Figure 4), and reflect projected, climate change-induced decreases in community mean SLA and height (Appendixes S4,S6,S7). While the extent of the temperate grassland biome was projected to remain relatively constant (+2.4% [−0.6 to +6.0%] and −1.5% [−5.1 to +1.8%] under the low and extreme change scenarios, respectively), temperate grassland was projected to shift 73.8% (71.6%–76.3%) to 78.8% (76.8%–81.1%) of its current distribution to new locations (Figures 4 and 5). More specifically, it was expected to expand towards eastern Russia and disappear from central Eurasia, where it would be replaced by xeric shrubland (Figures 4 and 6). This reflects projected decreases in community mean SLA and increases in community mean height and wood density in these areas (Appendixes S4,S6,S7).

4 | DISCUSSION

In this study, we have built upon global models linking climate to plant traits and plant traits to biomes (e.g. Boonman et al., 2020; Madani et al., 2018; van Bodegom et al., 2014) to project biome distribution changes under a low and extreme climate change scenario. Our results suggest that tropical biomes will flourish, while temperate biomes will shift northwards and reduce in extent, particularly tundra. Despite the limited number of traits used to characterize biomes, overall our projections of biome contractions, expansions and shifts are robust to uncertainty in biome classification. This indicates that trait-based models are a promising complementary approach to mechanistic models to assess the effect of climate change on biome distributions, especially as more data and traits become available in the future.

4.1 | Projected biome changes

In the northern regions, we projected a climate change-induced northward shift of temperate mixed and boreal forest into the tundra biome (Figure 4), in line with what has been found by previous studies. (Bjorkman et al., 2018; Myers-Smith & Hik, 2018). Our models indicate a better suitability for taller plant communities in tundra-dominated locations due to future increases of minimum temperature and decreases in humidity and precipitation seasonality (Appendixes S4 and S7). The predicted gradual encroachment of tundra by boreal forests has also been found by DGVM studies,
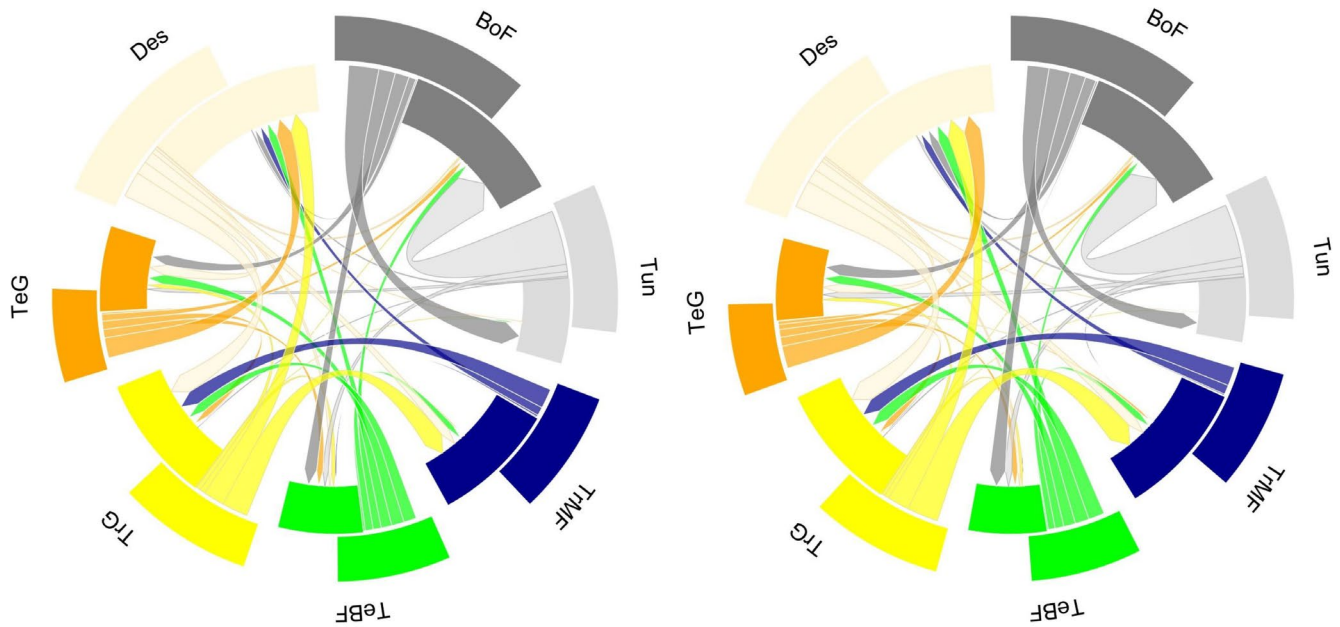
FIGURE 6 Projected shifts of the seven biomes with the highest predictive performance (TSS>0.3) for the low (left) and the extreme (right) climate change scenario, averaged over the 10,000 current and future comparisons (resulting from the 100-fold sampling). The outer circle represents the proportion of the world's land areas (km^2) assigned to each biome under the current climate. The inner circle shows the proportion of land area (km^2) per biome under a climate change scenario. The overhang of the outer circle shows the proportion of area that changes into another biome in the future. The arrows show the transitions from one biome into another one, where the size of the arrow depicts the proportion of area that changes. Thus, a fat arrow means a larger area changing to a specific biome compared to a narrow arrow. The overlap between the outer and inner circle depicts the amount of surface area of the current biome that remains the same in the future. The overhang of the inner circle shows the proportion of area that was another biome in the current situation (which can be found by tracing back the arrows) but changed into this biome in the future. Biome colours correspond to the colours in Figure 4. BoF, boreal forest; Tun, tundra; TrMF, tropical moist forest; TeBF, temperate mixed forest; TrG, tropical grassland; TeG, temperate grassland; Des, xeric shrubland

where changes have been linked to increasing temperatures and an increased atmospheric CO_2 level (Alo & Wang, 2008). Further, although woody cover increases in the tundra regions, we expect overall reductions in the area of boreal and temperate mixed forests, which will likely be replaced by temperate grassland (Figures 5 and 6). These results are also largely concordant with those produced by DGVM studies (Alo & Wang, 2008; Gonzalez et al., 2010; Scholze et al., 2006; Sitch et al., 2008). More specifically, when comparing our results to those of Park et al. (2015), who used biomes and climate change scenarios comparable to this study, our results are highly similar: we predict a 5.5% decrease in boreal forest surface area under low climate change, which matches their predicted decrease of boreal woody plant habitats of 5.3%.

We projected an increase in forest extent in tropical regions, caused by the woody encroachment into tropical grasslands (Figure 4, Appendix S7; Esquivel-Muelbert et al., 2019 and Stevens et al., 2017). The predicted increase of 20% is similar to the predicted increase of 22% by Park et al. (2015). We also predicted tropical moist forest to expand in Central Africa and the Amazon. While the African expansion is in line with the projections from Scholze et al. (2006), they predict forest dieback in Amazonia due to drought and increased frequency of wildfires. This contrast in predictions pinpoints the effect of fire on vegetation, as some biome shifts follow changes in the fire regimes as the major cause of vegetation

structure change (Scholze et al., 2006). The fact that fire is not included as a predictor in our model may partly explain our difficulty to distinguish between the tropical grassland and tropical moist forest biomes in the clustering process (Appendix S8).

4.2 | Implications

Projected changes in biome distribution may have implications for ecosystem services. For example, changes in tundra and tropical moist forest extent may alter the global carbon budget, desertification of grasslands may have important ramifications for disease control, climate regulation, food provisioning and soil erosion control (Millennium Ecosystem Assessment, 2005), and overall biome changes may disrupt key biotic interactions (e.g. Coops et al., 2018; Zhou et al., 2017). Note, however, that by relying on traits instead of species, we recede from making assumptions on species adaptability and dispersal limitations, and refrain from making predictions on the species composition of future locations or species composition of biomes in general. Nevertheless, while changing climatic conditions may negatively influence the plant survival via traits, it may take a long time for vegetation compositions and biome distributions to change, especially for systems with long-lived plants like forests (Liu et al., 2018; Svenning & Sandel, 2013). Due to such lags in species

range expansions and delayed local extinctions in relation to climate change, but also because information on the age of vegetation structures (e.g. young versus old forests) was not included, our results must be interpreted as predictions of the distribution of biomes at equilibrium with the future climate.

We also acknowledge that additional factors may play a role in shaping vegetation patterns. First, we did not include vegetation succession nor the effect of increased carbon dioxide concentrations on plant growth, while DGVMs do include these. Second, we did not consider biotic feedback like herbivores, which influence vegetation by grazing, browsing and trampling and may thus reduce woody encroachment in low-rainfall, open areas (Stevens et al., 2017). Third, human impact, such as the increasing human land demand for food production, will likely counteract the projected future climate change-induced increases in forest cover. A recent analysis of changes in global vegetation cover indeed found a decrease of tree cover in the areas where we predicted woody encroachment of tropical grassland (e.g. West and Central Africa, the Atlantic forest and Eastern Amazon; Figure 4), mainly attributed to human impact (Song et al., 2018). In areas where human impact is lower, however, our projections are in line with recent vegetation changes (Song et al., 2018), for example expanding xeric shrublands in North America and central Asia, increasing tree cover in central Africa, and shorter vegetation in the South of Africa (Figure 4). Our projections can thus be used to assess the potential for forest regeneration (Bastin et al., 2019).

4.3 | Outlook

Even though the models in this study use only three traits and do not include complex mechanistic feedback, they were able to predict biome distributions with reasonable accuracy and project future biome shifts largely consistent to those predicted by DGVMs. Linking climate to biomes directly can increase the predictability of present biome distributions, but at the same time it is more vulnerable to spurious relationships that would become evident when projecting biomes under different climatic scenarios (see Appendix S9). The use of traits as an intermediate step linking climate to biomes allows a more mechanistic interpretation of the model, allowing a plausibility check and reducing the risk of spurious relationships. All traits used contributed to these predictions, although the relative importance of each trait in determining biome occurrences varied between biomes (Appendix S7). However, functional similarity between some of the biomes created confusion when training the GMM (van Bodegom et al., 2014). Although this contributes to the uncertainty in the modelling results, a potential mismatch between original vegetation observations and the observed biome map (i.e. the Olson map) may create an even larger discrepancy in actual versus predicted biome. On the one hand, a mismatch between survey data and the biome map may reflect the natural variation of vegetation structure within in biome (Appendix S2). On the other hand, global expert-based biome maps like the one by Olson et al. (2001) have been questioned by recent studies, which highlight

potential errors in the classification of biomes (Conradi et al., 2020). For example, the biome "dry deciduous forest" in the Indian subcontinent would more accurately fit the "mesic deciduous savanna" classification based on vegetation structure and trait composition (Ratnam et al., 2019). This confusion may have affected our results, explaining why, for example, our models predict tropical grassland in the Indian subcontinent instead of tropical dry forest (Figure 4).

Besides improvements on the biome classification side, improving trait data may also increase the accuracy of our models' predictions. For example, the extrapolation of wood density as shown in Appendix S1 may be an additional cause for the confusion between tundra and boreal forest when training the GMM, as trait predictions for these areas with similar, extrapolated climatic conditions may have resulted in largely similar traits. Additional data for the three traits included in the present study would help to reduce uncertainty of the used trait–environment relationships and to project trait changes more accurately (Figure 4c,e,g and Appendixes S2 and S9). Additionally, we are aware of the strong correlation between the extent and the predictability of biomes, where biomes with a low extent and similar traits are confused with biomes that have similar traits but a larger extent. Considering more traits may certainly improve the discriminative ability of the biome classifying model, even for those biomes with a lower extent. Good candidates for inclusion would be traits that are known to differ between biomes (e.g. root traits; Guerrero-Ramírez et al., 2020), respond to environmental factors that are expected to change into the future (e.g. hydraulic traits; Griffin-Nolan et al., 2018) and traits that are important for ecosystem functioning (e.g. diaspore size; Díaz et al., 2016). The inclusion of traits with distinct values for specific vegetation types may even allow for more refined, regional vegetation projections.

Our modelling framework can be revisited and updated as more trait data and more accurate maps of observed biomes become available. While the prediction of biome shifts remains challenging and uncertain, our findings provide an independent, complementary line of evidence for large-scale biome changes due to climate change compared to DGVMs. Our statistical modelling approach can also highlight mismatches with process-based models warranting further investigation on hypothesized mechanisms. As an example, our correlative model cannot predict vegetation that is highly dependent on factors other than climate (e.g. fire) due to the lack of suitable predictors for future scenarios (e.g. fire intensity). The differences found between our predictions of tropical moist forests and grasslands and the ones from DGVMs that do include fire can contribute to the debate between the existence of alternative stable states for tropical forest and savanna where some parties argue that the different biomes only exist due to the presence of fire (Lasslop et al., 2020) and others argue that other factors like soil determine the distribution of the two biomes (Lloyd & Veenendaal, 2016).

Ultimately, our correlative models may have the greatest potential for predicting vegetation communities and the functioning of ecosystems when integrated or in parallel with process-based models (Mokany et al., 2012; Peng et al., 2002), for example

where results of one may complement those of the other which contributes to understanding mechanisms and output. Our study might help to develop more accurate models, which can provide an independent approach for large-scale biodiversity assessments, opening up possibilities to map and project the provisioning of eco-system services.

CONFLICT OF INTEREST

All authors had no conflict of interest to declare.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13431.

DATA AVAILABILITY STATEMENT

The community mean trait data that support the findings of this study are available through the publicly accessible DANS EASY repository (https://doi.org/10.17026/dans-xf5-qdxd). In addition, we provide the R scripts for the GMM, the simulation of biome predictions, the global biome maps and the biome probability maps (https://doi.org/10.17026/dans-xf5-qdxd) in the same DANS EASY repository.

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BIOSKETCH

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