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RESEARCH PAPER

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Assessing the reliability of predicted plant trait distributions at the global scale

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Abstract

Aim: Predictions of plant traits over space and time are increasingly used to improve our understanding of plant community responses to global environmental change. A necessary step forward is to assess the reliability of global trait predictions. In this study, we predict community mean plant traits at the global scale and present a systematic evaluation of their reliability in terms of the accuracy of the models, ecological realism and various sources of uncertainty.

Location: Global.

Time period: Present.

Major taxa studied: Vascular plants.

Methods: We predicted global distributions of community mean specific leaf area, leaf nitrogen concentration, plant height and wood density with an ensemble modelling approach based on georeferenced, locally measured trait data representative of the plant community. We assessed the predictive performance of the models, the plausibility of predicted trait combinations, the influence of data quality, and the uncertainty across geographical space attributed to spatial extrapolation and diverging model predictions.

Results: Ensemble predictions of community mean plant height, specific leaf area and wood density resulted in ecologically plausible trait–environment relationships and trait–trait combinations. Leaf nitrogen concentration, however, could not be predicted reliably. The ensemble approach was better at predicting community trait means than any of the individual modelling techniques, which varied greatly in predictive performance and led to divergent predictions, mostly in African deserts and the Arctic, where predictions were also extrapolated. High data quality (i.e., including

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intraspecific variability and a representative species sample) increased model performance by 28%.

Main conclusions: Plant community traits can be predicted reliably at the global scale when using an ensemble approach and high-quality data for traits that mostly respond to large-scale environmental factors. We recommend applying ensemble forecasting to account for model uncertainty, using representative trait data, and more routinely assessing the reliability of trait predictions.

KEYWORDS

ensemble forecasting, environmental filtering, intraspecific trait variation, leaf nitrogen concentration, plant height, specific leaf area, trait–environment relationships, trait model, wood density

1 | INTRODUCTION

Global trait-based models have proliferated in recent years owing to the increasing availability of plant trait data (Kattge, 2019). Fitting and projecting trait–environment relationships over large spatial scales is becoming increasingly common to study trait trade-offs (e.g., Díaz et al., 2016; Wright et al., 2004), to relate traits to environmental gradients (e.g., Moles et al., 2009; Wright et al., 2005) and to describe geographical patterns of traits (e.g., Madani et al., 2018; Yang et al., 2016). Trait-based models can not only increase our understanding of trait–environment relationships, but can also allow us to estimate how plant traits might respond to global environmental change (Bjorkman et al., 2018). This, in turn, is considered particularly useful for predicting the impact of environmental change on vegetation (Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010), because trait-based models allow to directly link plant fitness to environmental filters, including climate, soil properties and disturbance (Keddy, 1992).

Recent attempts to model global plant trait distributions as a function of environmental conditions have yielded different trait patterns (e.g., Butler et al., 2017; Madani et al., 2018; Moreno-Martínez et al., 2018; Van Bodegom, Douma, & Verheijen, 2014). For example, Butler et al. (2017) and Moreno-Martínez et al. (2018) predicted specific leaf area to be low in western Canada and high in northern Russia and eastern Brazil, whereas Van Bodegom et al. (2014) and Madani et al. (2018) predicted the opposite. Such discrepancies among existing global trait models might arise from differences in: (a) the sources of the underlying trait data (floras and measurements in natural areas, manipulated field experiments, botanical gardens and greenhouses); (b) the representativeness of the sampled species for the entire natural plant community; (c) the selection of environmental predictors; and (d) the model fitting techniques. The first difference translates to the use of global species trait averages, which may cause a potential mismatch of trait and environmental data. The second and third differences may result in different spatial patterns of uncertainty owing to extrapolations of trait–environment relationships (Thuiller, Brotons, Araujo, & Lavorel, 2004). The fourth difference may render considerable variation among predictions (Thuiller, Guéguen, Renaud, Karger, & Zimmerman, 2019). Furthermore, the ecological realism of the combination of predicted plant traits needs to be tested against observed trait combinations, which has, to our knowledge, not yet been done at the global scale. Additionally, although all studies reported the variance explained by the trait-based models, the predictability of independent samples (i.e., data not used to train the models) has not yet been assessed thoroughly. A necessary step forward to increase macroecological insights in global trait–environment relationships with potential application in ecological impact or conservation assessments (e.g., Lavorel & Garnier, 2002; Madani et al., 2018) is to perform a thorough assessment of the reliability of global plant trait predictions.

Here, we predict community mean plant traits at the global scale and present a systematic evaluation of the reliability of the predictions in terms of the models' accuracy, ecological realism and various sources of uncertainty. We systematically selected locally measured, representative data focusing on four widely studied plant traits (specific leaf area, leaf nitrogen concentration, height and wood density). These traits reflect the global spectra in plant form and function, are responsive to the abiotic environment and show physical trade-offs with other traits (Table 1; Díaz et al., 2016; Lavorel & Garnier, 2002). For each of the traits, we calculated community mean trait values and predicted global patterns at

TABLE 1 Expectations for community mean trait–environment relationships

Predictor	Rationale	Impact and adaptations	Expectations
Minimum temperature of the coldest month (Tmin)	Temperature-induced leaf damage, at low and high Tmin, affects plant performance[1]	Lower damage risk with increased tolerance via decreasing SLA[2]	^ SLA
		Enhanced metabolic activity and frost tolerance with increased LNC[1,3]	↓ LNC[4]
	Lower frost-induced mortality risk with increasing Tmin		↑ Plant height[4]
			↑ Wood density[4]
Humidity index (HumInd)		Increased drought tolerance with low transpiration rates via decreased SLA	↑ SLA[2]
			↑ LNC[2]
	Lower drought-induced mortality risk with increasing HumInd	Cavitation risk increases with height[5]	↑ Plant height
		Increasing wood density increases plant performance at low HumInd[6]	↓ Wood density
Precipitation in the driest quarter of the year (PrecDryQ)			o SLA
			o LNC
	Lower drought-induced mortality risk with increasing PrecDryQ	Cavitation risk increases with height[5]	↑ Plant height
			o Wood density
Precipitation seasonality (PrecSeas)	Moisture availability affects plant survival	Changing leaf habit (deciduousness) not traits[7]	– SLA
			– LNC[4]
			↓ Plant height[4]
			↓ Wood density[4]
Soil cation exchange capacity (CEC)	Higher CEC indicates a greater capacity to retain easily attainable nutrients (i.e., higher soil fertility)[8]	Less durable structures can be maintained[9,10]	↑ SLA
			– LNC
			o Plant height
			↓ Wood density
Soil pH	Higher pH increases the available phosphorus and nitrogen in the soil (i.e., higher soil fertility)[11]	Less durable structures can be maintained[9,10]	↑ SLA
			– LNC
			o Plant height
			↓ Wood density

Note: Hypotheses are indicated as follows: ↑ = positive relationship; ↓ = negative relationship; – = flat relationship; **^** = unimodal response. Hypotheses are based on theory (no reference) or on significant, biologically relevant trends found at the community level in literature (reference included). o indicates relationships between trait and predictor that have not been discussed at the community level in literature.

Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area.

References in table: [1]Went (1953); [2]Wright et al. (2005); [3]Reich, Oleksyn, and Tjoelker (1996); [4]Swenson and Weiser (2010); [5]Tyree and Sperry (1989); [6]Reich (2014); [7]Borchert (1998); [8]Ross and Ketterings (1995); [9]Chave et al. (2009); [10]Wright et al. (2004); [11]Maire et al. (2015).

a 0.5° resolution (*c*. 55 km × 55 km at the equator) using an ensemble modelling approach based on two regression and two machine learning techniques. Subsequently, we evaluated the predictive performance of the models and assessed their ecological plausibility in terms of the trait–environment relationships and the correlations and combinations of individually predicted community mean trait values (Díaz et al., 2016; Lavorel & Garnier, 2002). Finally, we evaluated the effect of various sources of uncertainty: (a) the effect of data quality in terms of representativeness of the sampled species to the entire plant community and the use of global species trait averages versus local trait measurements; (b) the uncertainty across geographical space attributed to extrapolation of traits outside the applicability domain (i.e., the geographical area with environmental variation covered by the environmental variation of the trait data); and (c) the uncertainty across geographical space owing to discrepancies among the predictions of the four modelling techniques. We build upon this assessment to provide guidelines for the further development, interpretability and usability of global trait-based models.

2 | METHODS

2.1 | Plant functional traits

We selected four plant functional traits: specific leaf area (SLA; in square millimetres per milligram), leaf nitrogen concentration (LNC; in milligrams per gram), height (in metres) and wood density (in milligrams per cubic millimetre). The SLA and LNC are both linked to photosynthetic capacity and nutrient investment, where a high SLA

and high LNC represent a fast return on investment at the expense of a shorter life span (Wright et al., 2004). Plant height is considered to be indicative of the ecological strategy of carbon distribution, indirectly determining growth and reproduction and their initial response to climate change (Moles et al., 2009). Last, wood density is a measure of carbon investment, representing a trade-off between growth (e.g., to overcome light limitation) and strength (e.g., mechanical support and drought tolerance), with higher wood density reflecting slower growth but increased strength at a similar stem diameter (Chave et al., 2009; Larjavaara & Muller-Landau, 2010).

The selected traits are easily measured according to standardized measurement procedures (Perez-Harguindeguy et al., 2013), which facilitates the integration of data from multiple datasets and reduces trait variation caused by seasonal changes (Bloomfield et al., 2018). To optimize between the number of observations and the consistency of the measurement methods, we included SLA measurements on both sun-leaves and shade-leaves, wood density measurements on both heartwood and sapwood, and plant height measurements on both vegetative and generative plant organs (see also Siefert et al., 2015).

2.2 | Data collection and selection procedure

Our main source for plant trait data was the TRY database (Kattge et al., 2011), from which we received 964,464 trait records on 85,437 species from 168 datasets. We also obtained data from the Tundra Trait Team (TTT) database (Bjorkman et al., 2018) and from various other published and unpublished datasets (Supporting Information Appendix S1). A list of data sources is provided in the Appendix. All species names were standardized using The Plant List (2013).

We selected trait observations based on six criteria. First, we included only georeferenced observations in order to enable a meaningful link with environmental covariates. Second, we considered only real measurements of plant traits (i.e., no species-level averages) in order to include intraspecific trait variation, which can contribute substantially to the trait variation within and between communities (Albert et al., 2010; Bloomfield et al., 2018; Siefert et al., 2015). Third, we considered only measurements obtained from natural vegetation, to minimize the influences of local management practices and legacy effects of historical land use (Perring et al., 2017). Fourth, we included observations only from studies that measured all or the most abundant species present in the entire plant community or in the dominant vegetation structure, in order to account for the representativeness of the sampled species for the plant community. This is in line with previous studies on this topic (e.g., Poorter et al., 2017) and in accordance with the biomass ratio hypothesis (Grime, 1998). Fifth, we included observations only from studies that targeted all life stages and/or size classes and from studies that targeted only adults. Thus, we excluded observations from studies focusing only on early-successional plant communities and studies measuring only seedlings or juveniles in a more established vegetation, in order to reduce confounding effects of ontogeny (e.g., Thomas & Bazzaz, 1999) and succession (e.g., Purschke et al., 2013). Sixth, we included only measurements conducted from 1980 onwards, in order to link up with the environmental covariate data, which span from 1979 to 2013. We excluded trait observations for which the listed criteria could not be checked. The Supporting Information (Appendix S2) contains an overview of the number of datasets excluded per criterion. In total, we removed 63.1% of all the datasets we originally received from TRY and 54.5% of all datasets in the TTT database.

2.3 | Data processing

We checked and corrected for possible errors in our database, such as duplicates, coordinate and unit inaccuracies and outliers (see Supporting Information Appendix S2). We then calculated location-specific community means per trait and per study to represent the mean response of the plant community to the local environment (Ackerly & Cornwell, 2007). Using unweighted community means was the better compromise over abundance-weighted community means, mainly because previous studies were not conclusive on the superiority of abundance-weighted means and because > 50% of our data did not include species abundances (for further discussion, see Supporting Information Appendix S3). We averaged the location-specific community means to 0.5° grid cells (with a median of 22 communities per grid cell) in order to describe large-scale patterns in traits. This is a common resolution used in global plant trait studies (Butler et al., 2017; Van Bodegom et al., 2014) and a good compromise, accounting for the effect of climatic filtering on plant traits, the coordinate uncertainty of the trait data, avoidance of pseudo-replicates and the uncertainty related to interpolated climatic variables (Stoklosa, Daly, Foster, Ashcroft, & Warton, 2015). These community means represent plant community average trait values, thereby making values not directly transferable to a specific species or a class of species. The final dataset used as input for model fitting included community mean trait values based on data from 76 studies and 8,955 species averaged to 486 grid cells, including 361 grid cells for SLA, 338 for LNC, 217 for height and 125 for wood density (Supporting Information Figure S4).

2.4 | Environmental data

We considered environmental variables that are expected to affect plant performance (e.g., Kimball, Gremer, Angert, Huxman, & Venable, 2012). This allowed us to check the ecological plausibility of the resulting trait–environment relationships. Based on ecological relevance, we selected bioclimatic variables from CHELSA v.1.2 (Karger et al., 2017). Given that water availability to plants is not determined by precipitation alone, we calculated the aridity index as the mean annual precipitation divided by the mean annual potential evapotranspiration, which in turn was calculated using the Penman–Monteith model (Zomer, Trabucco, Bossio, & Verchot, 2008). However, given that lower values of the aridity index indicate higher aridity, to avoid confusion this predictor will be referred to as the "humidity index" from now on. Furthermore, we

selected soil characteristics from SoilGrids250m (Hengl et al., 2017) and resampled them to a resolution of 0.5° to match the resolution of the plant community mean trait data. We averaged the soil data to a depth of 30 cm, which we considered most relevant for community composition via plant establishment and by influencing plants in later life stages, for example, through the potentially high nutrient availability (e.g., Vitousek & Sanford, 1986).

To avoid collinearity, we reduced the number of predictors based on variance inflation factors (VIF < 4), while ensuring a combination of different environmental factors (i.e., both climatic and soil characteristics; Franklin, Serra-Diaz, Syphard, & Regan, 2016). A complete list of the predictors considered and more details on our selection procedure can be found in the Supporting Information (Appendix S5). The final selection included six predictors: minimum temperature of the coldest month (Tmin; in degrees Celsius), humidity index (HumInd; dimensionless), precipitation in the driest quarter of the year (PrecDryQ; in millimetres), precipitation seasonality (PrecSeas, coefficient of variation based on monthly precipitation; as a percentage), soil cation exchange capacity (CEC; centimoles of positive charge per kilogram of soil) and soil pH.

2.5 | Model fitting and validation

For each relationship between the plant traits and environmental variables, we formulated expectations on the shape of the response based on existing literature (Table 1). To quantify the trait–environment relationships, we fitted four different models per trait: two statistical models [generalized linear model (GLM) and generalized additive model (GAM)] and two machine learning models [random forest (RF) and boosted regression trees (BRT); for full details on model parameterization, see Supporting Information Appendix S6]. We validated all models by running a 10-fold cross-validation using a split-sample procedure (80%–20%) and evaluated the predictive performance (cross-validated pseudo-R^2) of the models by regressing the predicted and observed trait values from all repetitions of the cross-validation.

To quantify the relative importance of each predictor in a consistent way across the models, we predicted traits using permuted values for the predictor of concern, correlated those predictions with predictions of the model using the original data and quantified relative variable importance as one minus the Spearman rank correlation coefficient (Thuiller, Lafourcade, Engler, & Araújo, 2009).

2.6 | Testing sensitivity to data quality

To test the influence of data quality on the performance of the trait models, we created three alternative datasets differing in terms of trait values (i.e., including intraspecific trait variation versus using species-specific trait values) and in terms of species representativeness (i.e., a representative sample of species versus the random selection of one species in the plant community; Supporting Information, Figure S7). For each alternative dataset, we fitted the four different models for each of the four traits, following the procedure described above for our default dataset. We then evaluated each model separately, where the predictions are confronted with the observed community means of the full dataset (Supporting Information Appendix S7).

2.7 | Spatial predictions and their assessment

To derive spatial predictions per trait, we used an ensemble forecasting procedure, which averages the predictions of the four algorithms weighted by their cross-validated pseudo-R^2 values (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). Likewise, we estimated ensemble variable importance and partial response curves. Furthermore, we calculated the accuracy of the ensemble predictions by regressing the 20% test data of the cross-validations against the observed trait values. We checked whether among-trait correlations observed in the data were retained in the predictions by correlating the trait correlation matrix of the original dataset with the trait correlation matrix of the predictions. Additionally, we assessed whether predicted trait combinations were realistic by comparing them with a hypervolume of all trait combinations existing in our dataset. We built the hypervolume with the "hypervolume_svm" function of the "hypervolume" R package using the original trait values before calculating community means or grid cell averages, because we wanted to check whether predicted trait combinations occurred naturally and because this ensured enough observations with all four traits measured to build the hypervolume (Blonder, Lamanna, Violle, & Enquist, 2014). Note that this test does not necessarily imply that predicted trait combinations do not or cannot exist, but merely that they did not occur in the input data and should therefore be interpreted with caution.

To identify the applicability domain, we calculated and mapped the multivariate environmental similarity surface (Elith, Kearney, & Phillips, 2010). This analysis quantifies, per grid cell, the difference of the most extrapolated environmental predictor 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. Finally, to quantify model uncertainty (i.e., the variability in predictions across models), the coefficient of variation was calculated as the difference in the predictions of each of the four individual models compared with the ensemble prediction weighted by the predictive performance of each of the models (further explanation in Supporting Information Appendix S8).

3 | RESULTS

3.1 | Predicted global plant trait variation

The variation explained by the environmental variables varied among traits (Figure 1). Model predictive performance was highest for plant height, followed by wood density, SLA and LNC (Figure 1). The

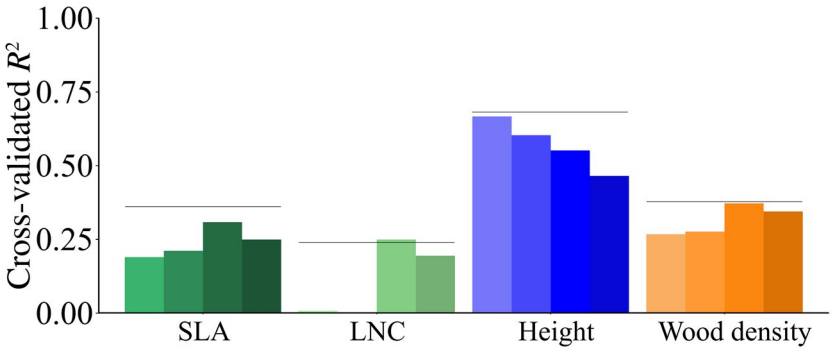


FIGURE 1 Model performance for different traits and different models presented as the cross-validated R^2 values. Per trait, the bars represent the predictive performance of GLM, GAM, RF, and BRT from left to right. The horizontal black lines represent the accuracy of the ensemble predictions. Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area [Colour figure can be viewed at wileyonlinelibrary.com]

projected global trait maps revealed low SLA in arid areas and high SLA in temperate climates (Figure 2a), whereas LNC was found to be low in dry tropical regions (Figure 2c). We also found lower community plant height at higher latitudes, with the tallest vegetation in wet tropical areas and shorter vegetation in temperate climates (Figure 2e). Height values, like the other predicted traits, represent community means and thus cannot be transferred directly to a specific species or a class of species. Finally, wood density, representing the potential average wood density for all woody vegetation in a location, was predicted to be particularly low in areas with low PrecSeas (Figure 2g).

3.2 | Ecological assessment

3.2.1 | Trait–environment relationships

In our models, community mean SLA was mostly explained by HumInd and Tmin (Figure 3a). As expected, SLA showed a unimodal albeit mostly decreasing response to Tmin, an increase with HumInd and a flat response to PrecSeas. However, we did not find the expected response of SLA to soil CEC and soil pH (Table 1; Figure 4). We also found a flat response of SLA to PrecDryQ (Figure 4). Community mean LNC was mostly explained by Tmin (Figure 3b). We expected LNC to decrease with Tmin, to increase with HumInd and to show a flat response to PrecSeas, but we found a unimodal response of LNC with Tmin around 0 °C, and a decrease of LNC with HumInd and PrecSeas (Table 1; Figure 4). We also found LNC to increase with PrecDryQ and, as expected, to show a flat response to soil CEC and soil pH (Table 1; Figure 4). Community mean plant height was mostly explained by PrecDryQ (Figure 3c). As expected, height increased with increasing Tmin and PrecDryQ, whereas in contrast to our original expectation, we found height to decrease with HumInd and to increase with PrecSeas (Table 1; Figure 4). Height showed a flat response to soil CEC and a unimodal response to soil pH. Community mean wood density was mostly explained by Tmin (Figure 3d). As expected, wood density increased with Tmin, decreased with HumInd and decreased overall with soil CEC (Table 1; Figure 4). Against our expectations, wood density showed a flat response to PrecSeas and soil pH (Table 1; Figure 4). Furthermore, we found a flat response of wood density to PrecDryQ (Figure 4).

3.2.2 | Combinations of predicted traits

The predicted trait values largely preserved the global trait correlations present in the training data (r = .83). Furthermore, for 99.9% of all grid cells, the predicted trait combination of community mean traits was found within the existing trait combinations found in individual plants or species. Locations with unrealistic predicted trait combinations are presented in the Supporting Information (Figure S9).

3.3 | Uncertainty assessment

3.3.1 | Data quality

The predictive accuracy decreased by 11% on average across all traits and models when intraspecific trait variation was excluded (Figure 5; Supporting Information Table S7). When species were sampled randomly (i.e., an unrepresentative sample), the predictive accuracy of the models decreased on average by 19% (Figure 5). The combination of ignoring intraspecific trait variation and using a non-representative species sample amplified the reduction in accuracy to 28% compared with the default models (Figure 5).

3.3.2 | Applicability domain

Despite data paucity in large areas of the world (e.g., India, Asian Russia and Africa; Figure 6), the trait data covered a large part of the global environmental space (Figure 6; Supporting Information Figure S10). However, deserts, tropical islands and some parts of the Arctic were outside the environmental domain covered by the trait data.

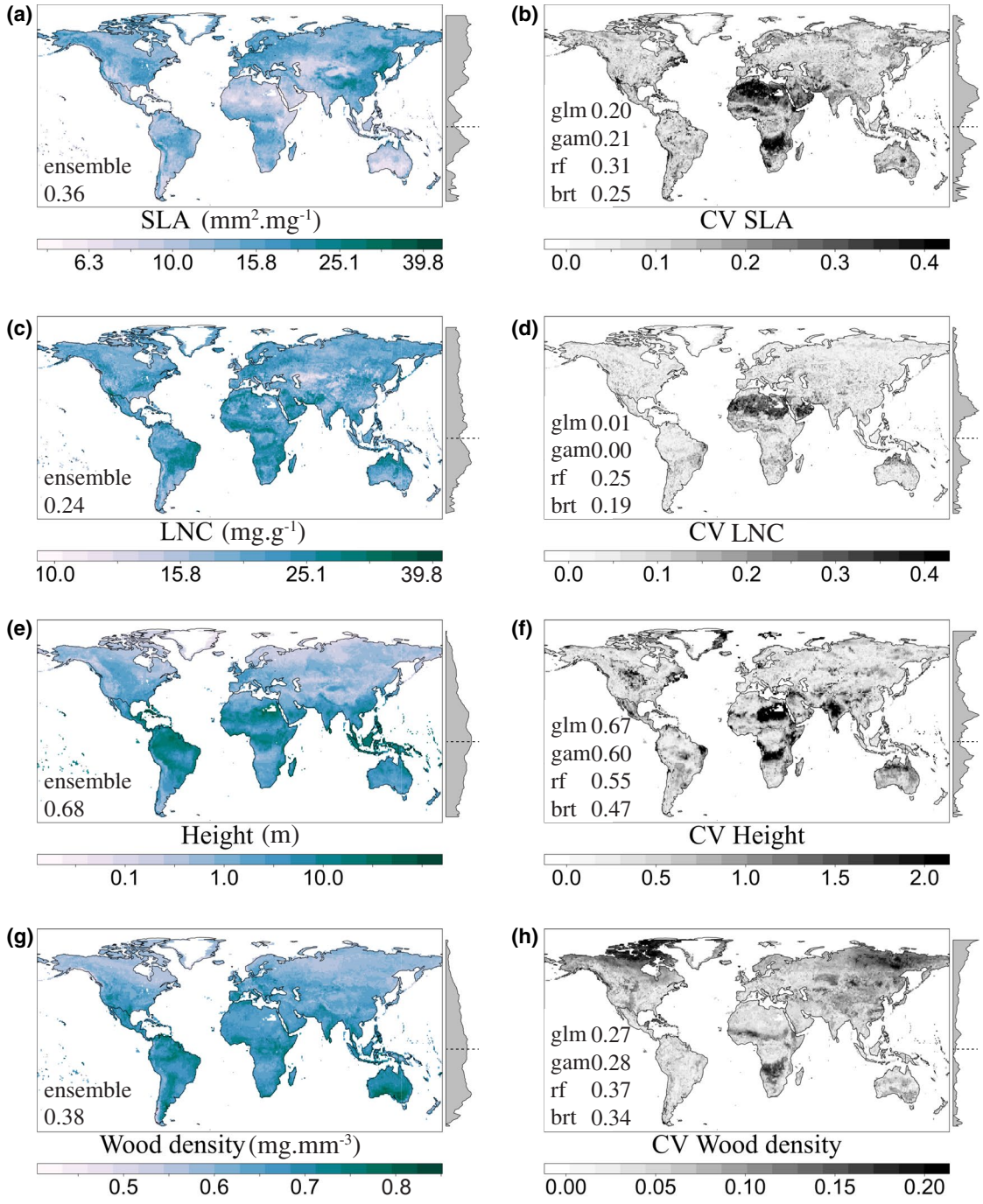


FIGURE 2 Global plant trait predictions. The left column presents the ensemble trait predictions, and the right column presents the ensemble coefficient of variation (CV) of different model predictions. The grey margin in each plot depicts the mean latitudinal value, and the horizontal dashed line indicates the Equator. Values in plots (a), (c), (e), (g) indicate the accuracy of the ensemble predictions (cross-validated R^2). Values in plots (b), (d), (f), (h) indicate the predictive performance (cross-validated R^2) of the different models, where glm indicates values of the GLMs, gam of GAMs, rf of RFs, and brt of BRT. These values indicate how well traits are predicted, while the CV maps only identify locations where predictions are divergent between models with high and/or similar predictive power. For extrapolation areas, see Figure 6. No predictions were made for Greenland (no soil data) , nor for the south of Egypt (no precipitation seasonality). All predictions represent potential trait values, as not all terrestrial world is vegetated or includes woody vegetation. Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area [Correction added on 16 April 2020, after first online publication: Figure 2 was previously incorrect and has been updated in this version.] [Colour figure can be viewed at wileyonlinelibrary.com]

3.3.3 | Model selection

Predictive performance differed between models per trait, where RF showed the highest predictive performance for SLA, LNC and wood density, and GLM for height (Figure 1). The ensemble predictions were always equal to or better than the individual models (Figure 1). The consistency in the predictions among the four modelling techniques varied geographically (Figure 2b,d,f,h). The

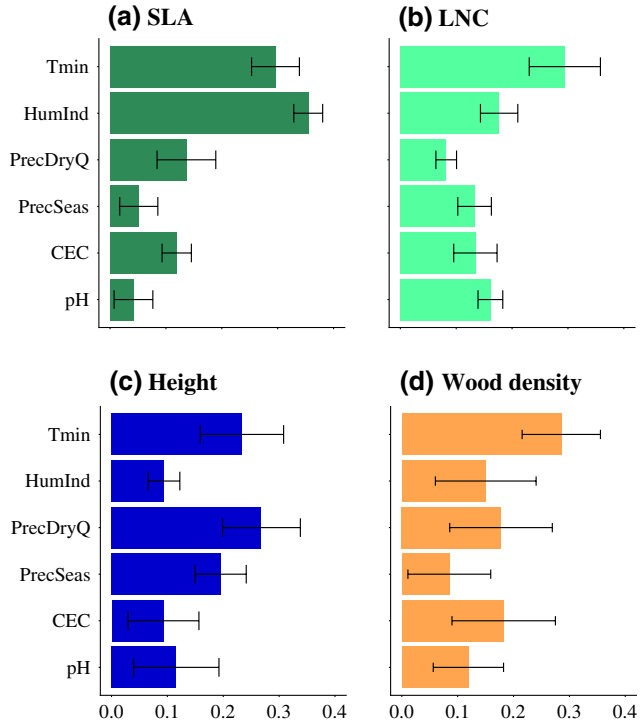


FIGURE 3 Relative predictor importance, calculated as 1—Spearman rank correlation coefficient (see Section 2.5), where high values indicate high importance. The bars represent the ensemble relative predictor importance and the error bars show the ensemble coefficient of variation. Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area; Tmin = minimum temperature; HumInd = humidity index; PrecDryQ = precipitation in the driest quarter of the year; PrecSeas = precipitation seasonality and CEC for soil cation exchange capacity [Colour figure can be viewed at wileyonlinelibrary.com]

coefficient of variation of SLA was mostly low, apart from some areas in Africa. LNC had an overall low coefficient of variation, except for the Sahara. Plant height showed a shifting pattern of high and low coefficients of variation over the globe. Wood density had an low coefficient of variation overall but was predicted with more uncertainty in parts of Africa and most of the Arctic.

4 | DISCUSSION

In this study, we established global plant trait models based on locally measured trait data representative of natural vegetation and used these models to make global trait predictions. We evaluated these trait predictions based on the predictive performance of the models, their ecological realism, the influence of the quality of input data, the applicability domain of the predictions and model choice uncertainty. Our results showed that the models predicting community mean SLA, plant height and wood density were well able to explain trait variation. Although the trait–environment relationships were as expected only in part, our trait predictions preserved the observed among-trait correlations and combinations. Furthermore, we showed that most of the global environmental variation was within the applicability domain for trait predictions, that including intraspecific trait variation and having a representative species sample improved the predictability of traits at the resolution and extent applied here, that different modelling techniques demonstrated different predictive performances for different traits and that the ensemble approach was better at predicting traits. Overall, these findings suggest that global predictions aimed at describing broad geographical plant community mean trait patterns are reliable with the data currently available, but caution is needed for certain traits and areas.

4.1 | Global trait patterns

The variance explained by our models predicting global community mean trait values along environmental gradients is comparable with other global or large-scale trait-based studies (Butler et al., 2017; Madani et al., 2018; Van Bodegom et al., 2014; Yang et al., 2016). For some areas, predicted spatial patterns were consistent with those predicted by previous studies. For example, we found lower SLA values in central Australia compared with the coast (Figure 2a), demonstrating the adaptation of leaves to drier conditions (Butler et al., 2017; Madani et al., 2018; Moreno-Martínez et al., 2018; Van Bodegom et al., 2014). Likewise, we found lower SLA values in the Amazon compared with the South American Cerrado (Figure 2a; Butler et al., 2017; Moreno-Martínez et al., 2018). Furthermore, we predicted vegetation in tropical climates to be taller than in temperate climates (Figure 2; Madani et al., 2018).

On the contrary, our SLA, LNC and wood density predictions differed from the predictions of previous studies for some areas. For example, we predicted higher SLA values for boreal forests compared with desert areas, similar to Van Bodegom et al. (2014) but opposite to Butler et al. (2017). Additionally, predicted patterns for LNC and wood density did not match other maps (Figure 2; Butler et al., 2017; Moreno-Martínez et al., 2018; Van Bodegom et al., 2014), but, given the poor predictive accuracy of the LNC models, we consider our LNC predictions unreliable (Figure 1).

Whenever trait predictions among different studies disagree, it is difficult to conclude which predictions are more reliable. One option is to validate global trait predictions against regional trait maps. For example, we found wood density to be higher in the east of the Amazon region compared with the north-west and south-west (Figure 2g), as was found by Baker et al. (2004). However, the paucity of regional trait maps makes this validation method impractical. Another option is to consider model predictive performances and the applicability domain to infer reliability of predictions. Unfortunately, the lack of quantification and indication of these in previous studies prevents us from drawing any conclusions about which predictions are more accurate.

4.2 | Ecological evaluation of global trait predictions

In general, we found community mean SLA, plant height and wood density to vary more with climatic factors than with soil

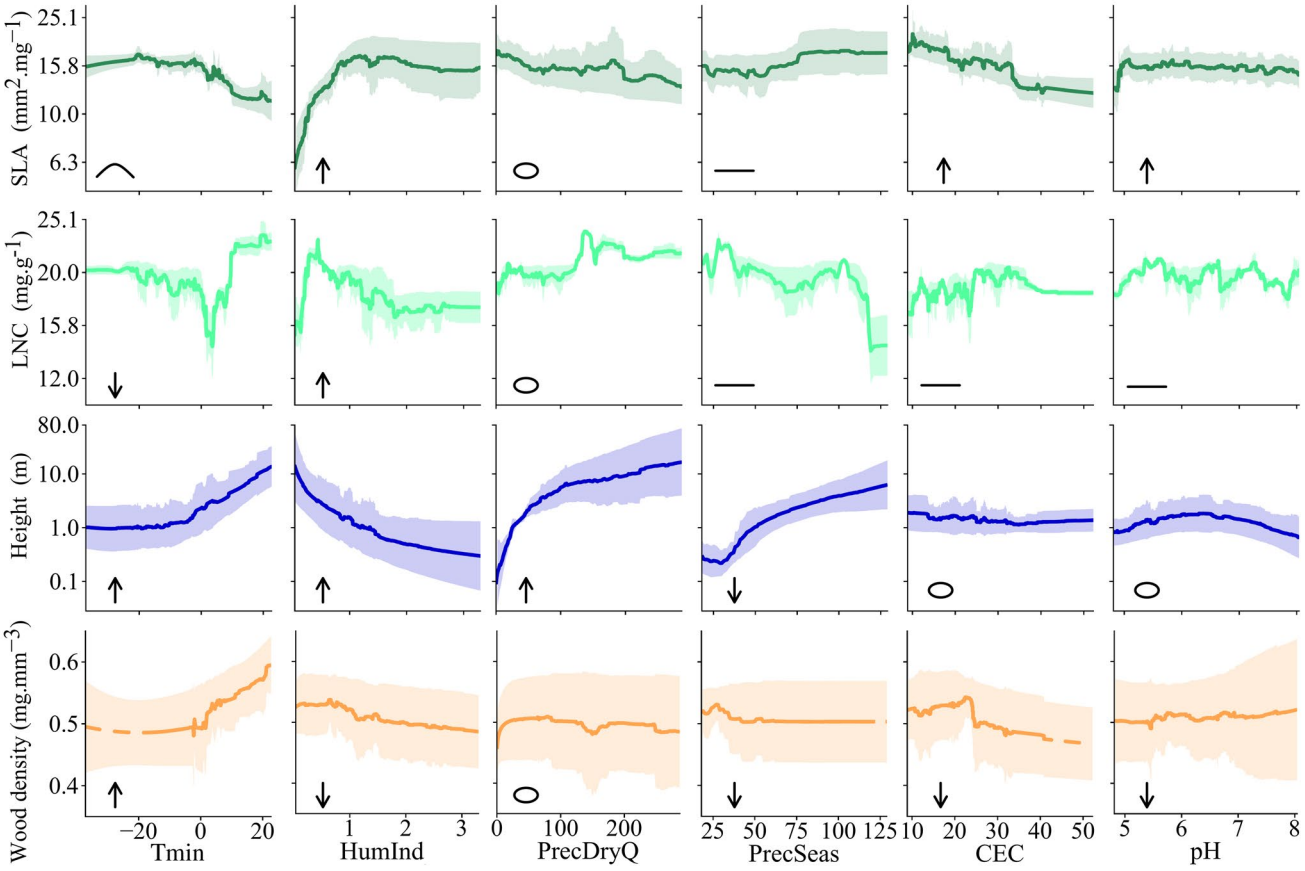


FIGURE 4 Ensemble partial trait responses. Shaded areas are the ensemble coefficients of variation. Predictors are minimum temperature (Tmin; °C), humidity index (HumInd; unitless), precipitation in the driest quarter of the year (PrecDryQ; mm), precipitation seasonality (PrecSeas; %), soil cation exchange capacity (CEC; cmol+ kg^{-1}), and soil pH. Extrapolated trait responses are shown with a dashed line. The symbols at the bottom left of each panel represent the expectation reported in Table 1: ↑ = positive relationship; ↓ = negative relationship; – = flat relationship; ^ = unimodal response; o = the relationship has not been discussed at the community level in literature. Other Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area [Colour figure can be viewed at wileyonlinelibrary.com]

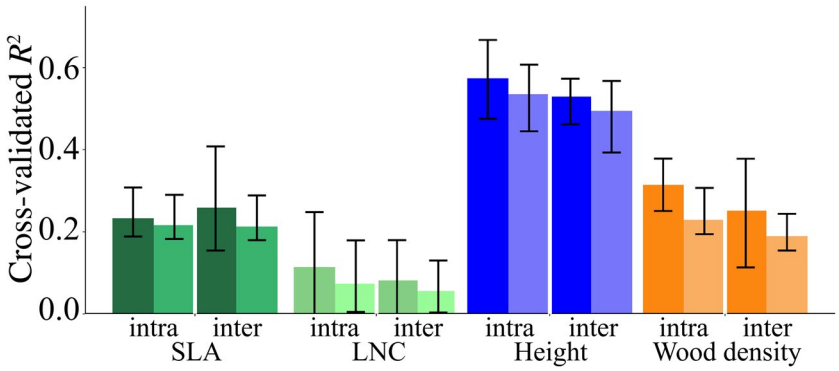


FIGURE 5 Performances of models based on datasets of different quality. The bars represent the average cross-validated R^2 values over the four different models, where the errorbars indicate the minimum and maximum cross-validated R^2 value. Datasets including and excluding intraspecific trait variation are indicated with intra and inter, respectively. Species representativeness is indicated with the shade of the bar, where darker shades represent datasets with a species sample representative of the community and lighter bars represent datasets with a non-representative species sample (Appendix S7). Thus, per trait, the bars from left to right represent plot 1, 2, 3, and 4 of Appendix Figure S7. Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area [Colour figure can be viewed at wileyonlinelibrary.com]

characteristics (Figure 3). This might reflect the greater variation in soil characteristics at smaller scales compared with climatic variables (Supporting Information Figure S11). Furthermore, all predicted trait combinations and correlations were realistic.

Our results confirmed most of the expected relationships between SLA and the environmental variables (Table 1; Figure 4). However, we found SLA to decrease with soil CEC and to show a flat response to soil pH, whereas we expected SLA to increase with soil fertility because

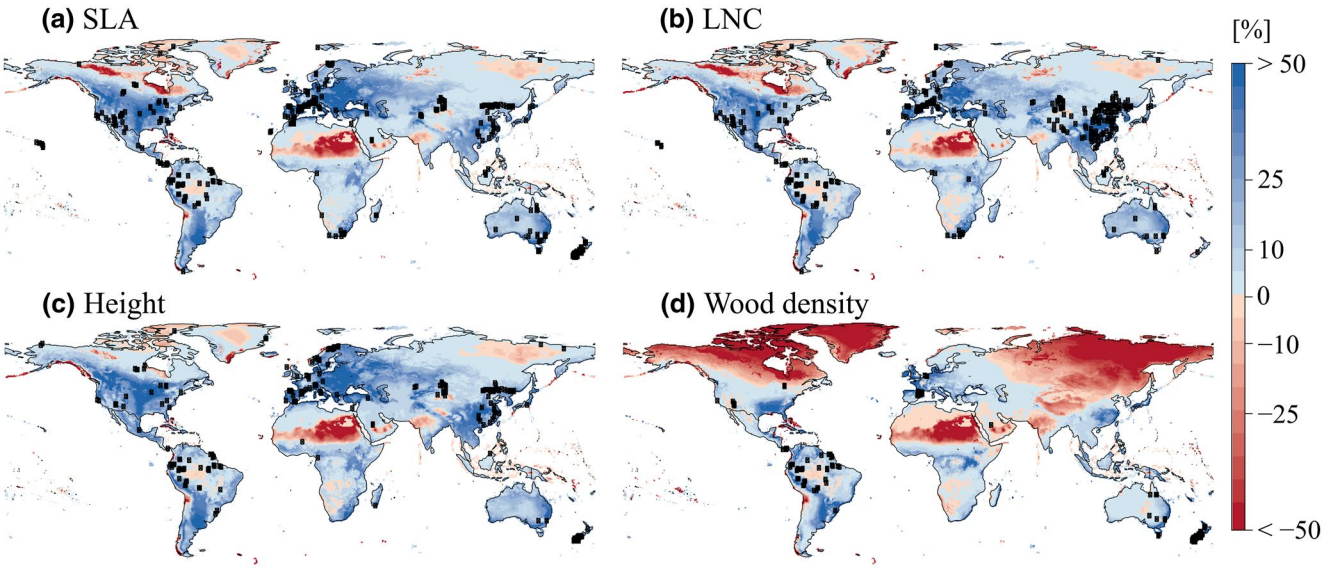


FIGURE 6 Locations of trait observations (black dots) and the environmental coverage of trait observations, that is, the multivariate environmental similarity surface (Elith et al., 2010), where blue represents interpolation and red represents extrapolation. More intense shades indicate greater similarities (blue) or differences (red) in environmental conditions of the location compared to the environmental conditions covered by the training dataset. Though values indicate percentages, each griddcell might be restrained by a different environmental variable, which is why the actual values are difficult to interpret. Abbreviations: LNC = leaf nitrogen concentration; SLA = specific leaf area [Colour figure can be viewed at wileyonlinelibrary.com]

less durable structures are thought to be maintained with higher soil fertility (Table 1; Figure 4). The flat response of SLA with soil pH might be explained by a high nutrient turnover rate in areas of low soil fertility (Vitousek & Sanford, 1986), although it might also be simply that SLA does not respond to changes in soil pH (Firn et al., 2019).

The expected responses of LNC to the environmental variables were not found (Table 1; Figure 4). The partial responses of LNC showed great variation over small environmental ranges, possibly owing to the tendency of machine learning models to over-fit. Together with the low predictive performance of the models, this might reflect that LNC responds primarily to small-scale environmental variation, whereas our models make predictions at a coarser resolution (55 km × 55 km). Our results thus support the deviating responses of LNC to environmental variables at the species level (Maire et al., 2015; Ordoñez et al., 2009; Reich & Oleksyn, 2004; Reich et al., 1996). Additionally, LNC might be highly variable in relationship to multiple environmental factors, leading to non-universal adaptations to the predictors in our model (Bloomfield et al., 2018; Reich & Oleksyn, 2004). This variability makes it difficult to interpret LNC responses to large-scale environmental gradients biologically, especially given that they will vary depending on whether intraspecific variation is considered or not (Albert et al., 2010). We conclude that it is not possible to predict LNC distributions reliably at this extent and resolution.

Our results confirmed the expected relationships between average community height and Tmin and PrecDryQ (Table 1; Figure 4). However, we found mean plant height to decrease with HumInd (Table 1; Figure 4). This might indicate that shorter vegetation (e.g., grasses, herbs and shrubs) is more abundant in more humid environments (i.e., higher annual rainfall and/or lower potential evapotranspiration). The unexpected increase in height with PrecSeas (Table 1; Figure 4) can be explained by the fact that many species in areas with seasonal rainfall can shed leaves, which makes the deciduous vegetation less vulnerable to cavitation compared with evergreen vegetation, allowing it to grow taller than expected. Furthermore, taller plants are better able to reach soil water reserves owing to deeper root systems (Borchert, 1998; Canadell et al., 1996).

Our results confirmed the expected relationships between wood density and Tmin, HumInd and soil CEC (Table 1; Figure 4). Both the increase in wood density with increasing Tmin and the unexpected flat response with PrecSeas might reflect that colder areas with less seasonal precipitation are dominated by soft-wooded gymnosperms, whereas warmer areas with higher seasonal precipitation are dominated by angiosperms with generally denser wood (Swenson & Enquist, 2007), although xylem vulnerability for frost-induced cavitation decreases with wood density (Reich, 2014). We expected a decrease in wood density with soil CEC and soil pH because higher soil fertility is expected to sustain higher growth rates. Although the overall trend confirmed our expectation, the response to pH was very limited, and at the lower end of the CEC gradient, wood density showed a small increase. This might indicate that extreme limitation to accessible soil nutrients cannot sustain high wood density, whereas low fertility but not nutrient-limited environments promote slow growth, resulting in high wood density (Table 1). Given that no global trait–environment relationship has been described for wood density (Moles, 2018), these patterns should be investigated further.

Literature reports that some relationships between traits and environmental variables may vary with leaf habit, plant growth forms and photosynthetic pathway at the local scale (e.g., Šímová et al., 2018). Additionally, trait–environment relationships are affected by factors other than climate and soil properties, such as land-use type

and disturbance (e.g., Chen et al., 2018). However, we expect that these factors are of limited relevance at the biological scale (communities instead of species), spatial resolution and extent considered, where environmental filtering effects are expected to be much less confounded by biotic interactions and fine-grain disturbances (Pearson & Dawson, 2003).

4.3 | Evaluation of uncertainty

4.3.1 | Data quality

We found that including intraspecific trait variation contributed to improve the predictability of traits (Figure 5; Supporting Information Table S7). This improvement in trait predictions at the global scale highlights the importance of considering intraspecific trait variation over and above the conclusion from small-scale studies that intraspecific trait variation contributes greatly to community trait variation (Albert et al., 2010; Bloomfield et al., 2018; Poorter, Castilho, Schietti, Oliveira, & Costa, 2018; Siefert et al., 2015). This indicates that widespread species are likely to show adaptability in their traits, changing them in order to optimize performance for different environments. Additionally, our results emphasize the need to build community trait models on a representative sample of species (Figure 5; Supporting Information Table S7). Moreover, high-quality data not only improve models statistically, but also theoretically lead to different results (Poorter et al., 2018). Thus, the inclusion of intraspecific trait variation of species representative of the local vegetation should be preferred when the aim is to predict plant community mean trait values.

4.3.2 | Applicability domain

The strict selection criteria we set greatly reduced the amount of available community trait data (Supporting Information Table S2). Nevertheless, our dataset covered the major part of the global terrestrial environmental space, indicating a wide applicability domain of our models (Figure 6). However, trait predictions should be interpreted carefully for deserts, the Arctic and tropical islands because of the high variation in predictions between models, and for mountainous areas because of the high environmental variation within a grid cell. Furthermore, predictions for wood density are extrapolated to a larger extent in comparison to other traits. A reason for the fewer community mean data points for wood density is that species mean values are generally considered appropriate because interspecific variation in wood density is larger than the intraspecific variation; therefore, new wood density data are rarely collected (Siefert et al., 2015). Additionally, most wood density measures available were collected before 1980, meaning that taking global species averages of wood density does not consider any evolutionary responses to changes in the local environment. Finally, wood density is rarely reported because of the challenges of measuring it in small shrubs and low vegetation (Perez-Harguindeguy et al., 2013).

4.3.3 | Model selection

The selection of a specific modelling technique greatly affected the ability to predict traits, and no single "best" model could be identified (Figure 1). Nevertheless, the ensemble forecasting approach as used here is equal to or better at predicting each trait than any individual model. Additionally, this ensemble approach can be used to retrieve a single prediction relying mostly on the best-performing models, while considering the variation in predictions between models with similar support. Furthermore, large variation in values predicted by different models, such as for plant height in the Sahara and the North of India, can be used as an indication of uncertainty. Thus, ensemble forecasting is not only better in predicting traits compared with single models, it also reduces the uncertainty attributable to subjective model technique selection and it enables the quantification and mapping of the uncertainty attributable to divergent model predictions. Finally, it allows for one general modelling approach for multiple traits.

4.4 | Reliability of global plant trait predictions

Our results suggest that plant community traits can be predicted reliably at the global scale when using an ensemble approach with high-quality data (i.e., including intraspecific trait variation and a representative species sample). We show that intraspecific trait variation and the representativeness of species considered in a community are important factors to consider, even at the global scale, and that an ensemble forecasting approach helps to deal with and quantify multiple types of uncertainty. Based on these results, we recommend the systematic and careful selection of data and modelling techniques for trait–environment models, and more routine assessment of their reliability based on model predictive performance, applicability domain, model uncertainty and realism of predicted trait combinations. Such systematic presentation of validation results and applicability domain in studies presenting predictions of spatial patterns of community mean traits will enhance our ability to build upon previous modelling attempts and improve our understanding of trait–environment relationships.

Our approach also led to new insights, such as the unexpected increase of community height with the seasonality of precipitation, but the lack of proper model assessment by previous studies limits our ability to draw any objective conclusions on the observed differences in trait responses. We suggest that higher predictive accuracy can be achieved for traits that respond primarily to large-scale environmental factors, such as specific leaf area, whereas predictive accuracy at this extent and resolution would be lower for traits such as LNC that might respond primarily to small-scale environmental variation. Nevertheless, the results of our trait models can improve the mechanistic understanding of global plant trait–environment relationships and contribute to answering the central question in functional ecology of the predictability of traits by the environment. Our assessment opens a new avenue to test impacts of global change on trait distributions and, eventually, on plant communities.

Ultimately, the results of our global trait models are contingent on the quality and distributions of the trait data. Modelling efforts will be enriched greatly by improving data collection or data availability in areas where no or few data are available and for locations characterized by unique environmental conditions.

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DATA AVAILABILITY STATEMENT

Community mean trait data used in this paper and the predicted trait distributions maps generated in this study are provided via FigShare, as are all R scripts regarding data analyses (http://doi.org/10.6084/m9.figshare.11559852). Owing to regulations of the major trait database used, the raw data cannot be shared openly.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX

DATA SOURCES

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