

1 **Title**

2 Can we reliably predict plant traits globally? A critical data selection and assessment of
3 modelling uncertainty.
4

5 **Running title**

6 Reliability of global plant trait predictions
7

8 **Abstract**

9 **Aim:** Plant trait data is becoming increasingly available, and global predictions over space or
10 time are in high demand. A necessary first step forward is to assess the reliability of global
11 trait predictions. In this study, we predict community mean plant traits at the global scale, and
12 present a systematic evaluation of their reliability in terms of the model's accuracy, ecological
13 realism, and modeling uncertainty.
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15 **Location:** Global.
16

17 **Time period:** Present.
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19 **Major taxa studied:** Vascular plants.
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21 **Methods:** We predicted global distributions of community mean specific leaf area, leaf
22 nitrogen concentration, plant height, and wood density with four modelling techniques using
23 georeferenced, locally measured trait data representative of the plant community. We assessed
24 models' predictive performance, plausibility of predicted trait combinations, effect of data

quality, and uncertainty across geographic space due to extrapolation and diverging models' predictions.

Results: Models for plant height, specific leaf area, and wood density, had high predictive performance and showed ecologically realistic trait-environment relationships and trait combinations. Leaf nitrogen content could not be predicted. Data quality had a large impact on trait predictability, where consideration of intra-specific trait variation and a representative species sample resulted in highest predictability. Predictions were mostly within the applicability domain, except for the Arctic and in deserts. Different modelling techniques varied in their predictive performance per trait and lead to divergent predictions in some regions.

Main conclusions: Plant traits can be reliably predicted at the global scale when data quality is high, but prediction accuracy differs per trait and model, and varies over space. More high-quality data and improved geographic coverage is needed to further increase reliability of global trait predictions. We recommend the use of ensemble forecasting to account for the diverse performance of statistical methods, and to more routinely assess the reliability of trait predictions.

Keywords

ensemble forecasting, environmental filtering, height, intra-specific trait variation, leaf nitrogen concentration, specific leaf area, trait model, trait-environment relationships, wood density

1 | Introduction

Global trait-based models have proliferated in the last years due to the increasing availability of plant trait data (Jens Kattge, 2019). Fitting and projecting trait-environment relationships over large spatial scales is becoming increasingly common to study trait trade-offs (e.g. Bruelheide et al., 2018; Díaz et al., 2016; Wright et al., 2004), trait relationships with environmental gradients (e.g. Moles et al., 2009; Wright et al., 2005), and describe geographic patterns of plant traits (e.g. Yang et al., 2016; Madani et al., 2018). Such models can not only increase our understanding of trait-environment relationships, but also allow us to estimate how plant traits might respond to global environmental change (Bjorkman et al., 2018; Wullschlegel et al., 2014). Traits are indeed considered particularly useful for predicting the impact of environmental change on vegetation (Webb, Hoeting, Ames, Pyne, & LeRoy Poff, 2010), as they allow to directly link plant fitness to environmental filters like climate, soil properties, and disturbance (Joner, Anand, & Pillar, 2012; Keddy, 1992).

Recent attempts to model global plant trait distributions as a function of environmental conditions have yielded different trait patterns so far (e.g. Butler et al., 2017; Madani et al., 2018; Moreno-Martínez et al., 2018; Van Bodegom, Douma, & Verheijen, 2014; Wright et al., 2017). For example, Butler et al. (2017) and Moreno-Martínez et al. (2018) predicted specific leaf area to be low in the west of Canada and high in the Northern Russia and East of Brazil, while Van Bodegom et al. (2014) and Madani et al. (2018) predicted the opposite. Such discrepancies among existing global trait models may arise from a variety of reasons. These reasons include differences in (i) the underlying trait data originating from various sources (floras and measurements in natural areas, manipulated field experiments, botanical gardens, and greenhouses), (ii) the representativeness of the sampled species towards the entire natural plant community, (iii) the selection of environmental predictors, and (iv) the techniques for model fitting.

The first discrepancy translates to the use of global species trait averages and a mismatch of trait and environmental data, while the second and third combined translate to different spatial patterns of uncertainty due to extrapolations of trait-environment relationships (Thuiller, Brotons, Araujo, & Lavorel, 2004), and the fourth may translate to considerable differences among predictions (Thuiller, 2007). Additionally, the ecological realism of the combination of predicted plant traits has so far not been tested against observed trait combinations. Finally, while all studies reported the variance explained by the trait models, the predictability of independent samples has not been assessed, yet. To further increase macroecological insights on global environment-trait relationships with potential application for conservation assessments, e.g. climate change impact (Lavorel & Garnier, 2002), or when trait predictions are used as input for further modelling step, e.g. Dynamic Global Vegetation Models (Sakschewski et al., 2015), a necessary step forward is to perform a thorough assessment of the reliability of global trait predictions.

Here, we predict community mean plant traits at the global scale, and present a systematic evaluation of their reliability in terms of the model's accuracy, ecological realism, and modeling uncertainty. We systematically selected data focusing on four widely studied plant traits (specific leaf area, leaf nitrogen concentration, height, and wood density). These traits reflect global spectra in plant form and function, are responsive to the abiotic environment, and show physical tradeoffs (Díaz et al., 2016; Lavorel & Garnier, 2002). For each of the traits we calculated the community mean trait value per cell and modeled the trait patterns at the global scale. Then we proceeded by evaluating the three main components. First, we evaluated the predictive performance of the models. Second, we assessed the ecological plausibility of the models in terms of the trait-environment relationships, and correlations and combinations of individually predicted trait values (Díaz et al., 2016; Lavorel & Garnier, 2002). Third, we evaluated the effect of various sources of modelling uncertainty: (i) the

effect of data quality in terms of representativeness of the sampled species towards the entire natural plant community and the use of global trait averages vs. local trait measurements; (ii) the uncertainty across geographic space due to extrapolating traits outside the environmental coverage of the data; and (iii) the uncertainty across geographic space due to discrepancies in the predictions of four different modelling techniques. We build upon this assessment to provide guidelines for the further development, interpretability and usability of global plant trait-environment models.

2 | Methods

2.1 | Plant functional traits

We selected four plant functional traits: specific leaf area (SLA; $\text{mm}^2.\text{mg}^{-1}$), leaf nitrogen concentration per leaf mass (LNC; mg.g^{-1}), height (m), and wood density (mg.mm^{-3}). The leaf traits 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 on the expense of a shorter life-span (Wright et al., 2004). Plant height is considered to be indicative of initial species responses to climate change and its competitive ability (Guittar, Goldberg, Klanderud, Telford, & Vandvik, 2016; 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 (Chave et al., 2009).

The selected traits have the advantage of being easily measured, according to a standardized measurement procedure (Perez-Harguindeguy et al. 2013). This facilitates the integration of data from multiple datasets and reduces trait variation caused by seasonal changes (Bloomfield et al., 2018). To increase our dataset, we allowed for slightly different measures per trait, including measurements for SLA on shade-leaves instead of sun-leaves (but see

Keenan & Niinemets, 2016), for wood density on sapwood instead of heartwood, and for height on generative instead of vegetative plant organs (also done by e.g. Siefert et al., 2015).

2.2 | Data collection and selection procedure

Our main source for plant trait data was the TRY database (J. 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 various other datasets, both published (Bloomfield et al., 2018; Cornelissen et al., 2003; Gleason, Butler, Ziemińska, Waryszak, & Westoby, 2012; Kraft, Valencia, & Ackerly, 2008; Meir, Levy, Grace, & Jarvis, 2007; Simpson, Richardson, & Laughlin, 2016; van der Sande et al., 2017, 2018; Van Der Sande et al., 2016) and unpublished (Schamp, B.; Santini, L.). For the additional datasets, we standardized all species names using The Plant List (2013) to make data comparable to the data from TRY. Then, we selected trait observations based on the following six criteria. First, we only included georeferenced observations in order to enable a meaningful link with environmental covariates. Second, we only considered actual measurements of plant traits (i.e. no species-level averages) in order to include intra-specific trait variation which can substantially contribute to the trait variation within and between communities (Albert et al., 2010; Bloomfield et al., 2018; Siefert et al., 2015). Third, we only considered measurements obtained from natural vegetation, to minimize influences of local management practices and legacy effects of historical land-use (Perring et al., 2017). Fourth, we only included observations from studies that measure 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 towards the local, natural vegetation. This is in line with previous studies on this topic (e.g. Poorter et al. (2017); Wüest et al. (2017)) and in accordance with the biomass ratio hypothesis (Grime, 1998). Fifth, we

only included observations from studies that targeted all life-stages and/or size-classes and from studies that targeted only adults. We, thus, excluded observations from studies focusing only on early-successional plant communities and studies measuring only seedlings or juveniles in a more established vegetation. This reduces confounding effects of ontogeny (e.g. Thomas & Bazzaz, 1999) and succession (e.g. Purschke *et al.*, 2013). Sixth, we only included measurements conducted from 1980 onwards, in order to link up with the environmental covariate data, which spans from 1979 till 2013. We excluded trait observations for which the listed criteria could not be checked. The Supplementary Information contains an overview of the number of datasets excluded per criterion (Appendix S1) as well as an overview of the datasets and studies from the TRY and the TTT database we included in our final database (Appendix S2). 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 by doing the following: 1) we removed duplicate entries, which are defined by having the same coordinates and references or the same coordinates and trait values but different dataset identification numbers; 2) for observations not located on land, we checked the original reference and corrected coordinates according to the site description; 3) we excluded obvious errors in trait observations (e.g. SLA = 0); and 4) we evaluated outliers in trait values against values of the same species reported by other studies in our database and/or external sources (local floras), and corrected them when appropriate (adjustment of decimal separator). 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). The main reason for using unweighted community means was that previous studies did not provide a conclusive answer

to which is better to use, and since >50% of our data did not include species abundances unweighted means were the better compromise (see Supplementary Information Appendix S4 for further discussion and comparison between the two approach). Then, we averaged the location-specific community means to 0.5 degree grid cells (~ 55×55km at the equator, with an median of 22 communities per grid cell) in order to describe large-scale patterns in traits. This is a common resolution used in previous studies modeling traits globally (Butler et al., 2017; Van Bodegom et al., 2014) and a good compromise accounting for the effect of climatic filtering on plant traits, resolution of global biodiversity models for conservation (Pollock, Thuiller, & Jetz, 2017), coordinate uncertainty of data collection, and uncertainty related to interpolated climatic variables (Stoklosa, Daly, Foster, Ashcroft, & Warton, 2015). These community means represent the average trait values of the entire vegetation in a grid cell, 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 (Figure 7).

2.4 | Environmental data

We considered environmental variables that are expected to affect plant performance (e.g. Varela et al., 2015), including climate, and soil properties. This allowed us to check the ecological plausibility of the resulting trait-environment relationships. Based on ecological relevance, we selected bioclimatic variables from CHELSA version 1.2 (Karger et al., 2017) and soil characteristics from SoilGrids250m (Hengl et al., 2017). For the latter, we averaged data to a depth of 30 cm, which we considered most relevant for plant establishment. As an additional predictor, we calculated the aridity index as the mean annual precipitation divided by the mean annual potential evapotranspiration (Zomer et al. 2008). 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). The final selection included six predictors: minimum temperature of the coldest month (T_{min} ; °C), aridity index (dimensionless), precipitation in the driest quarter (mm), precipitation seasonality (coefficient of variation based on monthly precipitation; dimensionless), soil cation exchange capacity (CEC; $\text{cmol}^+ \text{kg}^{-1}$), and soil pH ($-\log(\text{H}^+)$). As lower values of the aridity index indicate higher aridity, for clarity we will refer to this predictor as ‘humidity index’ from now on. All environmental covariates were resampled to a resolution of 0.5 degrees in order to match the resolution of the plant community mean trait data.

2.5 | Model fitting and validation

To quantify the relationships between the plant traits and environmental variables, we fitted four different models per trait: two statistical models (Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs)) and two machine learning models (Random Forest (RF) and Boosted Regression Trees (BRT)). An overview of the model parameterization is provided in the Supplementary Information Appendix S5. We validated all models by running a 10-fold cross-validation using a split-sampling procedure (80-20%) and evaluated the models’ predictive performance (cross-validated pseudo- R^2) 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, and correlated those predictions with predictions of the model using the original data, and quantified relative variable importance as 1 minus the correlation coefficient (Thuiller, Lafourcade, Engler, & Araújo, 2009).

2.6 | Testing sensitivity to data quality

To test the effect of data quality, we created four different datasets with trait values for the same communities, but that differed in terms of trait values, i.e. intra-specific trait variation versus species-specific trait values, and in terms of representativeness, i.e. a representative sample of species versus an specific selection of species in the plant community (Figure 1). The community mean trait values excluding intra-specific trait variation were calculated by averaging trait values per species for all data we originally gathered (see Appendix S6), and replacing the original trait values with these species averages. Datasets where species representativeness of the entire plant community was not considered was simulated by randomly selecting one plant species from each community, and replicating this process 10 times. This one-species-sample mimicks common practice where data from the Global Biodiversity Information Facility (GBIF) or of studies targeting a single species is included in a dataset. For each dataset, community means were then calculated as described in section 2.3. To ensure pure effects of trait values and species representativeness, and not of sample size effects or differences in applicability domain, we only adjusted communities that are present in the dataset with the actual community means. These actual community means are the ones that included the intra-specific trait variation and had species representative of the entire plant community. Thus, plot 1 in Figure 3 is the actual community mean dataset, plot 2 is representative but has local trait values replaced with species means, for plot 3 species were removed, and for plot 4 species were removed and local trait values were replaced with species means. To ensure sample size would not change when removing species, we retained a minimum of one species per community.

For each dataset (N=102), we ran the parameter selection for the four different models for each of the four traits, ran all models with the selected parameters, and evaluated each model

by confronting predictions of the cross-validation with community mean trait values from the dataset with the actual community means (Appendix S6).

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). Similarly, we estimated ensemble variable importance and partial response curves. To quantify model uncertainty, i.e. the variability in predictions across algorithms, the coefficient of variation was calculated as the weighted difference of each of the four individual models' predictions compared to the ensemble prediction (see Supplementary Information Appendix S7 for further explanation). To identify geographic areas outside the environmental domain covered by our data, we calculated and mapped the multivariate environmental similarity surface (MESS) as described by Elith *et al.* (2010). This analysis quantifies the difference of the most extrapolated environmental predictor in a certain location and the environmental range of that predictor covered by the dataset, while considering the distribution of data within the environmental range.

Furthermore, we checked if among-trait correlations observed in the data were retained in the predictions by correlating the trait correlation matrix of the dataset (i.e. the 0.5 degree grid cell trait averages used for model fitting) with the trait correlation matrix of the predictions (i.e. across all 0.5 degree grid cells). Additionally, we assessed whether predicted trait combinations were realistic by comparing them with a hypervolume of all trait combinations existing in our dataset. To build the hypervolume, we used the original trait values before calculating community means or grid cell averages, as we want to check if predicted trait combinations can actually occur, and because this ensured enough observations with all four

traits measured to build the hypervolume. For this analysis, we used the ‘hypervolume_svm’ function and the ‘hypervolume_inclusion_test’ function of the ‘hypervolume’ R package (Blonder *et al.* 2014). Note that this test does not necessarily imply that predicted trait combinations do not or cannot exist, but only that they might be unrealistic and should be interpreted with caution.

3 | Results

3.1 | Predicted global plant trait variation

The variation explained by the environmental variables clearly varied among traits (Figure 2). Model predictive performance was highest for plant height, followed sequentially by wood density, SLA, and leaf nitrogen concentration (Figure 2). The projected global trait maps revealed low SLA in arid areas and high SLA in temperate climates (Figure 3a), whereas LNC was found to be low in dry tropical regions (Figure 3c). We further found lower plant height at higher latitudes, with the tallest vegetation in wet tropical areas, and shorter vegetation in temperate climates (Figure 3e). Finally, wood density, representing the potential average wood density for all woody vegetation in a location, was predicted particularly low in areas with low precipitation seasonality (Figure 3g).

3.2 | Ecological assessment

3.2.1 | Trait-environment relationships

SLA was mostly explained by humidity index and minimum temperature of the coldest month (Figure 4a). As expected, SLA showed a unimodal response to minimum temperature and a monotonic increase with humidity index, but we did not find a response of SLA to soil pH (Table 1, Figure 5). We further found a decrease of SLA with increasing precipitation in the driest quarter of the year and soil CEC, and a small increase of SLA with precipitation seasonality (Figure 5).

LNC was mostly explained by minimum temperature of the coldest month (Figure 4b). We expected LNC to decrease with minimum temperature and humidity index, but found a unimodal response of LNC with minimum temperature around 0 °C, and found LNC to increase strongly from very arid to less arid environments after which it declined again (Table 1, Figure 5). We further found LNC to decrease with precipitation seasonality (Figure 5). Plant height was mostly explained by the amount of precipitation in the driest quarter of the year (Figure 4c). As expected, height increased with increasing minimum temperature and minimum precipitation, whereas in contrast to our original expectation, we found height to decrease with humidity index, and to increase with precipitation seasonality (Table 1, Figure 5). Wood density was mostly explained by minimum temperature of the coldest month (Figure 4d). As expected, wood density decreased with humidity (Table 1, Figure 5). Contradicting our expectations, wood density increased with minimum temperature, and showed a unimodal response to soil CEC (Table 1, Figure 5). Furthermore, we found no response of wood density with changing precipitation in the driest quarter of the year, precipitation seasonality, or soil pH (Figure 5).

3.2.2 | Combinations of predicted traits

The predicted trait values largely preserved the global trait correlations present in the training data ($r=0.83$). Further, for 99.9% of all grid cells, the predicted trait combination of community means does not violate the trait combinations found in individual plants or species. Locations with unrealistic predicted trait combinations are presented in the Supporting Information Appendix S8, Figure S8.

3.3 | Modelling uncertainty assessment

3.3.1 | Data quality

Predictive accuracy of traits on average reduced by 9% when intra-specific trait variation was excluded (Figure 6; Appendix S6 Table S6). Predictably, the representativeness of the species sample towards the community also reduced the predictive accuracy on average by 19% (Figure 6). The combination of not considering intra-specific trait variation and using a non-representative species sample amplified the negative effects and reduced the predictive accuracy of traits by 31% (Figure 6). Yet, the decrease in predictability was not as pronounced as expected.

3.3.2 | Applicability domain

Despite a lack of trait data in large areas of the world (e.g. India, Asian Russia and Africa; Figure 7), the data covered a large part of the global environmental space (Figure 7; Appendix S9 Figure S9), indicating that predictions were mostly within the applicability domain of the models. However, deserts, tropical islands, and some parts of the Arctic were out of the environmental domain covered by the trait data, meaning that predictions for these areas should be interpreted carefully.

3.3.3 | Model selection

Predictive performance differed between models per trait, where the random forest technique showed the highest predictive performance for SLA, LNC, and wood density, while the generalized linear model best predicted height (Figure 2). The consistency in the predictions among the four modelling techniques varied geographically (Figure 3b,d,f,h), where uncertainty across geographic space due to model selection was highest for plant height. The coefficient of variation of SLA was mostly low apart from some areas in Africa. LNC had 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. And wood density had an overall low coefficient of variation 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-scale trait predictions. We assessed these trait predictions by models' predictive performance, ecological realism, data quality, the applicability domain for predictions, and model choice uncertainty. Our results showed that models for SLA, plant height, and wood density could predict trait variation well. The trait-environment relationships were mostly as hypothesized, and our trait predictions preserved the observed among-trait correlations and combinations. Furthermore, we showed that most of the global environmental variation was covered by the available trait data that met our criteria for quality, that including intra-specific trait variation and having a representative species sample improved the predictability of traits at the resolution and extent applied here, and that different modelling techniques demonstrated different predictive performances for different traits. Overall, this suggests that global predictions aimed at describing broad geographic plant trait patterns are reliable with the data currently available, but caution is needed for certain traits and areas.

4.1 | Global trait patterns

The performance of our models in predicting trait values along environmental gradients is comparable with other global or large-scale trait-based studies (Van Bodegom *et al.*, 2014; Yang *et al.*, 2016; Butler *et al.*, 2017; Madani *et al.*, 2018). Predicted spatial patterns were also consistent with those predicted by previous studies for some areas. For example, we

found lower SLA values in central Australia compared to the coast (Figure 3a), which shows the leaf adaptation to dryer conditions (Butler et al., 2017; Madani et al., 2018; Moreno-Martínez et al., 2018; Van Bodegom et al., 2014). Similarly, we found lower SLA values in the Amazon compared to the South American Cerrado (Figure 3a), which was also found before (Butler et al., 2017; Moreno-Martínez et al., 2018). Further, we found that vegetation in tropical climates was taller than in temperate climates (Figure 3e), similar to Madani et al. (2018).

On the contrary, in some areas SLA, LNC, and wood density predictions were inconsistent with previous studies. For example, we predicted higher SLA values for boreal forests compared to desert areas, similar to Van Bodegom et al. (2014), whereas Butler et al. (2017) predicted the opposite. Additionally, predicted patterns for LNC and wood density did not coincide with other maps (Figure 3; Butler et al., 2017; Moreno-Martínez et al., 2018; Van Bodegom et al., 2014).

When trait predictions 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 to the North West and South West (Figure 3g), 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 makes it difficult to conclude which predictions are more accurate. Nevertheless, our models for LNC had poor predictive accuracy, making LNC predictions unreliable (Figure 2).

4.2 | Ecological evaluation of global trait predictions

Most trait-environment relationships established at the community-scale were found at the global scale, too. In general, we found traits to vary more with climatic factors than with soil characteristics (Figure 4). This may reflect the greater variation in soil characteristics at smaller scales compared to climatic variables, which makes the relative predictor importance scale-dependent. Furthermore, all predicted trait combinations and correlations were found within the composed dataset.

Our results mostly showed the hypothesized relationships between SLA and the environmental variables (Table 1, Figure 5). However, we found SLA to decrease with minimum precipitation and increase with precipitation seasonality (Figure 5). This can be explained by the phylogenetic trend where areas with more and more frequent rain have relatively more gymnosperms, which have a low SLA (Díaz et al., 2016). Further, we expected SLA to increase with soil fertility, but found the opposite (Table 1, Figure 5). The expected responses of LNC with the environmental variables were not found (Table 1, Figure 5). The partial responses of LNC showed great variation over small environmental ranges, possibly due the nature of machine learning models to over-fit. Together with the low models' predictive performance, this might reflect that LNC responds more to small-scale environmental variation or that LNC is too plastic in relation to multiple environmental factors leading to non-universal adaptations (Bloomfield et al., 2018; Reich & Oleksyn, 2004) and different responses when considering intra-specific variation or not (Albert et al., 2010). This plasticity makes it difficult to reliably predict LNC distributions at this resolution.

Our results mostly showed the hypothesized relationships between average community height and the environmental variables (Table 1, Figure 5). However, we found mean plant height to decrease with humidity index (Table 1, Figure 5), which, in the absence of a biological explanation, might merely show that more humid environments are dominated by shorter vegetation (e.g. grasses, herbs, and shrubs). The unexpected increase in height with

precipitation seasonality (Table 1, Figure 5) can be explained by the fact that many species in areas with seasonal rainfall can shed leaves, which makes deciduous vegetation less vulnerable to cavitation compared to evergreen vegetation. Furthermore, taller plants are better able to reach the water from the previous rain season due to deeper root systems (Canadell et al., 1996).

Our results mostly conflicted with the hypothesized relationships between wood density and the environmental variables (Table 1, Figure 5). The unexpected higher wood densities with minimum temperature (Table 1, Figure 5) can be an effect of decreased xylem vulnerability for cavitation. However, it could also be a phylogenetic trend where colder areas are more dominated by soft-wooded gymnosperms, and warmer areas are dominated by angiosperms with generally denser wood (Swenson & Enquist, 2007). We expected a decrease in wood density with soil CEC as higher soil fertility can sustain increased growth rates. Nevertheless, the unexpected increase in wood density at the lower end of the CEC spectrum can be explained as the result of extreme limitation to soil nutrients. As no global relationships have been described for wood density with different environmental factors (Moles, 2018), these patterns should be investigated further.

Literature reports that some trends between traits and environmental factors at the local scale may vary with leaf habit, plant growth forms, and photosynthetic pathway (e.g. Šímová *et al.*, 2018), and likewise, that trends are affected by other factors, such as land-use type, and disturbance (e.g. Chen *et al.*, 2018). However, we expect that this variation will not create great deviations in results, since we model at the global scale community mean values estimated from local measurements in natural vegetation. At this scale, environmental filtering effects on species traits are expected to be much less confounded by variation in biotic interactions and not-considered disturbances than at a smaller scale.

4.3 | Modelling uncertainty evaluation

4.3.1 | Data quality

We found that considering intra-specific trait variation contributed to the predictability of traits (Figure 6; Supplementary Information Appendix S6, Table S6). This improvement of the accuracy of trait predictions at the global scale highlights the importance of considering intra-specific trait variation over and above the conclusion made by previous small-scale studies that intra-specific trait variation contributes largely to community trait variation (Albert et al., 2010; Bloomfield et al., 2018; Poorter, Castilho, Schiatti, Oliveira, & Costa, 2018; Siefert et al., 2015). Additionally, we show that the representativeness of the selected species towards the entire plant community also affected the predictability of traits, and that the combination of not considering intra-specific trait variation and using unrepresentative species samples led to even lower trait predictability. The relatively small change between predictive performance of datasets with a representative and non-representative species sample is a reflection of the fact that our dataset contained not only communities where all species were sampled, but also communities where only representative species were sampled. When randomly selecting a species from a representative species sample, the community mean trait value might not be that different from the actual community trait value. Though our analysis quantifies the difference of using different quality datasets, also conceptually it leads to different results. Including or excluding intra-specific trait variation leads to results that represent actual community dynamics or potential trait values, respectively (Poorter et al., 2018). Using the same line of reasoning, using data representative of the local vegetation captures environmental trait filtering better than using community means estimated from a random sample of plants. Thus, both statistically and theoretically, including intra-specific trait variation and, more importantly, including data that is

representative of the local vegetation should be preferred when the aim is community mean trait predictions.

4.3.2 | Applicability domain

The strict selection criteria we set greatly reduced the amount of available data (Supplementary Information Appendix S1, Table S1). Nevertheless, despite the limited coverage of geographic space, our dataset still covered the major part of the global terrestrial environmental space indicating that predictions can be made without extrapolation for most areas (Figure 7). However, predictions for wood density are extrapolated for a larger part of the terrestrial world compared to the other traits. A reason for the fewer wood density community mean data points is that species mean values are generally considered appropriate for most studies since inter-specific variation in wood density is larger than the intra-specific variation, and so new wood density data are rarely collected in the field (Siefert et al., 2015). However, wood density does show variation even within a species (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 as it does not match the current local environment. Another reason for the environmental and geographical bias in wood density community mean data points is that measurements of wood density on small shrubs and other woody vegetation with low height (i.e. in the Arctic regions) is difficult and maybe imprecise, making that this data is almost never reported (Perez-Harguindeguy et al., 2013).

4.3.3 | Model selection

The selection of a specific modelling technique greatly affected the ability to predict traits (Figure 2). As predictive performance differed among both modelling techniques and traits,

we could not identify a single ‘best’ technique. Though the predictive performance is one of the major aspects, besides the applicability domain, to assess the reliability of trait predictions, it can be biased: machine learning models tend to have higher predictive performances but are also more prone to overfitting. The ensemble forecasting approach as employed here can be used to retrieve a single prediction relying mostly on the best performing models, while considering the variability in model predictions between similarly supported models. Areas with high variation in values predicted by different models, like the Sahara and the North of India for plant height, can then be assumed to not provide reliable predictions. Thus, though ensemble forecasting might not necessarily be better in predicting traits compared to a single best model, it reduces the uncertainty due to subjective model technique selection and enables the quantification and mapping of the uncertainty due to divergent model predictions. Finally, it allows for one general modelling approach for multiple traits.

4.4 | Reliability of global plant trait predictions

We conclude that plant traits can reliably be predicted at the global scale with high quality data, but predictions are more accurate for some traits than others, and certainty varies over space. Higher certainty in predictions is found for traits that have low plasticity to small-scale differences in predictors and primarily respond to large-scale environmental factors. The results of our trait models can improve the mechanistic understanding of global plant trait-environment relationships and adds to the central question in functional ecology of the predictability of traits by the environment. Further, our assessment opens a new avenue to test impacts of global change on trait distributions, and, eventually, on community assemblages. Based on our results, we recommend to systematically select data and modelling techniques, and more routinely assess the reliability of trait models 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 traits will enhance our ability to build upon previous modelling attempts and eventually improve our understanding on trait-environment relationships. Moreover, the results of global trait models are contingent on the quality and distributions of the trait data. Modelling efforts will greatly be enriched by improving data collection or data availability in areas where no or little data is available and for locations characterized by unique environmental conditions.

References

- Ackerly, D. D., & Cornwell, W. K. (2007). A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters*, 10, 135–145. <http://doi.org/10.1111/j.1461-0248.2006.01006.x>
- Albert, C. H., Thuiller, W., Yoccoz, N. G., Soudant, A., Boucher, F., Saccone, P., & Lavorel, S. (2010). Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, 98, 604–613. <http://doi.org/10.1111/j.1365-2745.2010.01651.x>
- Ambrose, A. R., Sillett, S. C., Koch, G. W., Van Pelt, R., Antoine, M. E., & Dawson, T. E. (2010). Effects of height on treetop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*). *Tree Physiology*, 30(10), 1260–1272. <http://doi.org/10.1093/treephys/tpq064>
- Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., ... Martínez, R. V. (2004). Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, 10, 545–562. <http://doi.org/10.1111/j.1529-8817.2003.00751.x>
- Bjorkman, A. D., Myers-Smith, I. H., Elmendorf, S. C., Normand, S., Rüger, N., Beck, P. S.

547 A., ... Weiher, E. (2018). Plant functional trait change across a warming tundra biome.
 548 *Nature*, 562, 57–62. <http://doi.org/10.1038/s41586-018-0563-7>
 549 Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional
 550 hypervolume. *Global Ecology and Biogeography*, 23, 595–609.
 551 <http://doi.org/10.1111/geb.12146>
 552 Bloomfield, K. J., Cernusak, L. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Wright, I. J.,
 553 ... Atkin, O. K. (2018). A continental-scale assessment of variability in leaf traits: within
 554 species, across sites and between seasons. *Functional Ecology*, 1–15.
 555 <http://doi.org/10.1111/1365-2435.13097>
 556 Borchert, R. (1998). Responses of tropical trees to rainfall seasonality and its long-term
 557 changes. In A. Markham (Ed.), *Potential Impacts of Climate Change on Tropical Forest*
 558 *Ecosystems* (pp. 241–253). Dordrecht: Springer.
 559 Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M.,
 560 ... Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature*
 561 *Ecology and Evolution*, 2(12), 1906–1917. <http://doi.org/10.1038/s41559-018-0699-8>
 562 Butler, E. E., Datta, A., Flores-moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., ... Reich,
 563 P. B. (2017). Mapping local and global variability in plant trait distributions.
 564 *Proceedings of the National Academy of Sciences*, 114, E10937–E10946.
 565 <http://doi.org/10.1073/pnas.1708984114>
 566 Canadell, J., Jackson, R., Ehleringer, J., Mooney, H. A., Sala, O. E., & Schulze, E.-D. (1996).
 567 Maximum rooting depth of vegetation types at the global scale. *Oecologia*, 108(4), 583–
 568 595. <http://doi.org/10.1007/BF00329030>
 569 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009).
 570 Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351–366.
 571 <http://doi.org/10.1111/j.1461-0248.2009.01285.x>

572 Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., Chen, D., ... Bai, Y. (2018). Plant diversity
573 enhances productivity and soil carbon storage. *Proceedings of the National Academy of*
574 *Sciences*, 115, 4027–4032. <http://doi.org/10.1073/pnas.1700298114>

575 Cornelissen, J. H. C., Cerabolini, B., Castro-Díez, P., Villar-Salvador, P., Montserrat-Martí,
576 G., Puyravaud, J. P., ... Aerts, R. (2003). Functional traits of woody plants:
577 Correspondence of species rankings between field adults and laboratory-grown
578 seedlings? *Journal of Vegetation Science*, 14(3), 311–322. [http://doi.org/10.1111/j.1654-](http://doi.org/10.1111/j.1654-1103.2003.tb02157.x)
579 [1103.2003.tb02157.x](http://doi.org/10.1111/j.1654-1103.2003.tb02157.x)

580 Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., ... Gorné, L. D.
581 (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171.
582 <http://doi.org/10.1038/nature16489>

583 Efreteui, A. (2016). The soils cation exchange capacity and its effect on soil fertility.
584 Retrieved from [https://permaculturenews.org/2016/10/19/soils-cation-exchange-](https://permaculturenews.org/2016/10/19/soils-cation-exchange-capacity-effect-soil-fertility/)
585 [capacity-effect-soil-fertility/](https://permaculturenews.org/2016/10/19/soils-cation-exchange-capacity-effect-soil-fertility/)

586 Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species.
587 *Methods in Ecology and Evolution*, 1, 330–342. [http://doi.org/10.1111/j.2041-](http://doi.org/10.1111/j.2041-210X.2010.00036.x)
588 [210X.2010.00036.x](http://doi.org/10.1111/j.2041-210X.2010.00036.x)

589 Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and
590 terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*,
591 113, 3725–3734. <http://doi.org/10.1073/pnas.1519911113>

592 Gleason, S. M., Butler, D. W., Ziemińska, K., Waryszak, P., & Westoby, M. (2012). Stem
593 xylem conductivity is key to plant water balance across Australian angiosperm species.
594 *Functional Ecology*, 26, 343–352. <http://doi.org/10.1111/j.1365-2435.2012.01962.x>

595 Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder
596 effects. *Journal of Ecology*, 86, 902–910.

597 Guittar, J., Goldberg, D., Klanderud, K., Telford, R. J., & Vandvik, V. (2016). Can trait
598 patterns along gradients predict plant community responses to climate change? *Ecology*,
599 97(10), 2791–2801. <http://doi.org/10.1002/ecy.1500>

600 Hengl, T., Jesus, J. M. De, Heuvelink, G. B. M., Ruiperez Gonzalez, M., Kilibarda, M.,
601 Blagoti, A., ... Kempen, B. (2017). SoilGrids250m: Global gridded soil information
602 based on machine learning. *PLoS ONE*, 12(2).
603 <http://doi.org/10.1371/journal.pone.0169748>

604 Joner, F., Anand, M., & Pillar, V. (2012). Trait-convergence and divergence assembly
605 patterns in a temperate forest herbaceous layer along the gradient of canopy closure.
606 *Community Ecology*, 13(2), 178–184. <http://doi.org/10.1556/ComEc.13.2012.2.7>

607 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., ... Kessler,
608 M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific*
609 *Data*, 4, 170122. <http://doi.org/10.1038/sdata.2017.122>

610 Kattge, J. (2019). TRY Plant Trait Database. Retrieved from www.try-db.org/

611 Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bonisch, G., ... Wirth, C. (2011).
612 TRY - a global database of plant traits. *Global Change Biology*, 17(9), 2905–2935.
613 <http://doi.org/10.1111/j.1365-2486.2011.02451.x>

614 Keddy, P. A. (1992). A pragmatic approach to functional ecology. *Functional Ecology*, 6,
615 621–626.

616 Keenan, T. F., & Niinemets, Ü. (2016). Global leaf trait estimates biased due to plasticity in
617 the shade. *Nature Plants*, 3. <http://doi.org/10.1038/nplants.2016.201>

618 Kraft, N. J. B., Valencia, R., & Ackerly, D. D. (2008). Functional traits and niche-based tree
619 community assembly in an Amazonian forest. *Science*, 322, 580–582.

620 Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and
621 ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*,

622 16, 545–556. <http://doi.org/10.1046/j.1365-2435.2002.00664.x>

623 Madani, N., Kimball, J. S., Ballantyne, A. P., Affleck, D. L. R., Van Bodegom, P. M., Reich,
624 P. B., ... Running, S. W. (2018). Future global productivity will be affected by plant trait
625 response to climate. *Scientific Reports*, 8(1), 1–10. [http://doi.org/10.1038/s41598-018-](http://doi.org/10.1038/s41598-018-21172-9)
626 21172-9

627 Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., van Bodegom, P. M., ...
628 Santiago, L. S. (2015). Global effects of soil and climate on leaf photosynthetic traits and
629 rates. *Global Ecology and Biogeography*, 24(6), 706–717.
630 <http://doi.org/10.1111/geb.12296>

631 Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation
632 of consensus methods in predictive species distribution modelling. *Diversity and*
633 *Distributions*, 15, 59–69. <http://doi.org/10.1111/j.1472-4642.2008.00491.x>

634 Meir, P., Levy, P. E., Grace, J., & Jarvis, P. G. (2007). Photosynthetic parameters from two
635 contrasting woody vegetation types in West Africa. *Plant Ecology*, 192(2), 277–287.
636 <http://doi.org/10.1007/s11258-007-9320-y>

637 Moles, A. T. (2018). Being John Harper: Using evolutionary ideas to improve understanding
638 of global patterns in plant traits. *Journal of Ecology*, 106, 1–18.
639 <http://doi.org/10.1111/1365-2745.12887>

640 Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., ...
641 Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97(5), 923–
642 932. <http://doi.org/10.1111/j.1365-2745.2009.01526.x>

643 Moreno-Martínez, Á., Camps-Valls, G., Kattge, J., Robinson, N., Reichstein, M., van
644 Bodegom, P., ... Running, S. W. (2018). A methodology to derive global maps of leaf
645 traits using remote sensing and climate data. *Remote Sensing of Environment*, 218, 69–
646 88. <http://doi.org/10.1016/J.RSE.2018.09.006>

647 Ordoñez, J. C., Bodegom, P. M. Van, Witte, J. M., Wright, I. J., Reich, P. B., & Aerts, R.
 648 (2009). A global study of relationships between leaf traits, climate and soil measures of
 649 nutrient fertility. *Global Ecology and Biogeography*, 18, 137–149.
 650 <http://doi.org/10.1111/j.1466-8238.2008.00441.x>

651 Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., ...
 652 Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant
 653 functional traits worldwide. *Australian Journal of Botany*, 61, 167–234.

654 Perring, M. P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L.,
 655 ... Verheyen, K. (2017). Global environmental change effects on plant community
 656 composition trajectories depend upon management legacies. *Global Change Biology*,
 657 24(4), 1722–1740. <http://doi.org/10.1111/ijlh.12426>

658 Pollock, L. J., Thuiller, W., & Jetz, W. (2017). Large conservation gains possible for global
 659 biodiversity facets. *Nature*, 546(7656), 141–144. <http://doi.org/10.1038/nature22368>

660 Poorter, L., Castilho, C. V., Schiatti, J., Oliveira, R. S., & Costa, F. R. C. (2018). Can traits
 661 predict individual growth performance? A test in a hyperdiverse tropical forest. *New*
 662 *Phytologist*, 219(1), 109–121. <http://doi.org/10.1111/nph.15206>

663 Poorter, L., Sande, M. T. Van Der, Aerts, E. J. M. M., Ascarrunz, N., Enquist, B., Finegan,
 664 B., ... Peña-Claros, M. (2017). Biodiversity and climate determine the functioning of
 665 Neotropical forests. *Global Ecology and Biogeography*, 26, 1423–1434.
 666 <http://doi.org/10.1111/geb.12668>

667 Purschke, O., Schmid, B. C., Sykes, M. T., Poschlod, P., Michalski, S. G., Durka, W., ...
 668 Prentice, H. C. (2013). Contrasting changes in taxonomic, phylogenetic and functional
 669 diversity during a long-term succession: Insights into assembly processes. *Journal of*
 670 *Ecology*, 101, 857–866. <http://doi.org/10.1111/1365-2745.12098>

671 Reich, P. B. (2014). The world-wide “fast–slow” plant economics spectrum: a traits

672 manifesto. *Journal of Ecology*, 102, 275–301. <http://doi.org/10.1111/1365-2745.12211>

673 Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to
674 temperature and latitude. *Proceedings of the National Academy of Sciences of the United*
675 *States of America*, 101, 11001–6. <http://doi.org/10.1073/pnas.0403588101>

676 Reich, P. B., Oleksyn, J., & Tjoelker, M. G. (1996). Needle respiration and Nitrogen
677 concentration in Scots Pine populations from a broad latitudinal range: A common
678 garden test with field-grown trees. *Functional Ecology*, 10(6), 768–776.

679 Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., ... Thonicke, K.
680 (2015). Leaf and stem economics spectra drive diversity of functional plant traits in a
681 dynamic global vegetation model. *Global Change Biology*, 21, 2711–2725.
682 <http://doi.org/10.1111/gcb.12870>

683 Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle,
684 D. A. (2015). A global meta-analysis of the relative extent of intraspecific trait variation
685 in plant communities. *Ecology Letters*, 18, 1406–1419. <http://doi.org/10.1111/ele.12508>

686 Šimová, I., Violle, C., Svenning, J. C., Kattge, J., Engemann, K., Sandel, B., ... Enquist, B. J.
687 (2018). Spatial patterns and climate relationships of major plant traits in the New World
688 differ between woody and herbaceous species. *Journal of Biogeography*, 45(4), 895–
689 916. <http://doi.org/10.1111/jbi.13171>

690 Simpson, A. H., Richardson, S. J., & Laughlin, D. C. (2016). Soil–climate interactions
691 explain variation in foliar, stem, root and reproductive traits across temperate forests.
692 *Global Ecology and Biogeography*, 25, 964–978. <http://doi.org/10.1111/geb.12457>

693 Stoklosa, J., Daly, C., Foster, S. D., Ashcroft, M. B., & Warton, D. I. (2015). A climate of
694 uncertainty: Accounting for error in climate variables for species distribution models.
695 *Methods in Ecology and Evolution*, 6, 412–423. <http://doi.org/10.1111/2041-210X.12217>

696 Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key

697 plant functional trait: wood density and its community-wide variation across latitude and
698 elevation. *American Journal of Botany*, 94(3), 451–459.
699 <http://doi.org/10.3732/ajb.94.3.451>

700 Swenson, N. G., & Weiser, M. D. (2010). Plant geography upon the basis of functional traits:
701 an example from eastern North American trees. *Ecology*, 91, 2234–2241.
702 <http://doi.org/10.1890/09-1743.1>

703 Ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., ...
704 Vásquez, R. (2006). Continental-scale patterns of canopy tree composition and function
705 across Amazonia. *Nature*, 443(7110), 444–447. <http://doi.org/10.1038/nature05134>

706 The Plant List. (2013). Version 1.1. Retrieved from [Www.theplantlist.org](http://www.theplantlist.org)

707 Thomas, S. C., & Bazzaz, F. A. (1999). Asymptotic height as a predictor of photosynthetic
708 characteristics in Malaysian rain forest trees. *Ecology*, 80(5), 1607–1622.

709 Thuiller, W. (2007). Biodiversity: Climate change and the ecologist. *Nature*, 448, 550–552.
710 <http://doi.org/10.1038/448550a>

711 Thuiller, W., Brotons, L., Araujo, M. B., & Lavorel, S. (2004). Effects of restricting
712 environmental range of data to project current and future species distributions.
713 *Ecography*, 27, 165–172.

714 Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD - A platform for
715 ensemble forecasting of species distributions. *Ecography*, 32, 369–373.
716 <http://doi.org/10.1111/j.1600-0587.2008.05742.x>

717 Tyree, M. T., & Sperry, J. S. (1989). Cavitation and Embolism. *Water*, 19–38.
718 <http://doi.org/10.1146/annurev.pp.40.060189.000315>

719 Van Bodegom, P. M., Douma, J. C., & Verheijen, L. M. (2014). A fully traits-based approach
720 to modeling global vegetation distribution. *Proceedings of the National Academy of*
721 *Sciences of the United States of America*, 111, 13733–8.

722 <http://doi.org/10.1073/pnas.1304551110>

723 Van Der Sande, M. T., Arets, E. J. M. M., Peña-Claros, M., De Avila, A. L., Roopsind, A.,
724 Mazzei, L., ... Poorter, L. (2016). Old-growth Neotropical forests are shifting in species
725 and trait composition. *Ecological Monographs*, 86(2), 228–243.
726 <http://doi.org/10.1890/15-1815.1>

727 van der Sande, M. T., Arets, E. J. M. M., Peña-Claros, M., Hoosbeek, M. R., Cáceres-Siani,
728 Y., van der Hout, P., & Poorter, L. (2018). Soil fertility and species traits, but not
729 diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest.
730 *Functional Ecology*, 32, 461–474. <http://doi.org/10.1111/1365-2435.12968>

731 van der Sande, M. T., Peña-Claros, M., Ascarrunz, N., Arets, E. J. M. M., Licona, J. C.,
732 Toledo, M., & Poorter, L. (2017). Abiotic and biotic drivers of biomass change in a
733 Neotropical forest. *Journal of Ecology*, 105, 1223–1234. [http://doi.org/10.1111/1365-](http://doi.org/10.1111/1365-2745.12756)
734 [2745.12756](http://doi.org/10.1111/1365-2745.12756)

735 Varela, S., Lima-Ribeiro, M. S., & Terribile, L. C. (2015). A short guide to the climatic
736 variables of the last glacial maximum for biogeographers. *PLoS ONE*, 10(6), 1–15.
737 <http://doi.org/10.1371/journal.pone.0129037>

738 Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., & LeRoy Poff, N. (2010). A structured
739 and dynamic framework to advance traits-based theory and prediction in ecology.
740 *Ecology Letters*, 13(3), 267–283. <http://doi.org/10.1111/j.1461-0248.2010.01444.x>

741 Went, F. W. (1953). The effect of temperature on plant growth. *Annual Review of Plant*
742 *Physiology*, 4(1), 347–362. <http://doi.org/10.1146/annurev.pp.04.060153.002023>

743 Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., ... Wilf, P. (2017).
744 Global climatic drivers of leaf size. *Science*, 357(6354), 917–921.

745 Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., ...
746 Westoby, M. (2005). Modulation of leaf economic traits and trait relationships by

climate. *Global Ecology and Biogeography*, 14(5), 411–421.
<http://doi.org/10.1111/j.1466-822x.2005.00172.x>

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., ... Gulias, J. (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.

Wüest, R. O., Münkemüller, T., Lavergne, S., Pollock, L. J., & Thuiller, W. (2017). Integrating correlation between traits improves spatial predictions of plant functional composition. *Oikos*, 1–9. <http://doi.org/10.1111/oik.04420>

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., ... Xu, X. (2014). Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany*, 114(1), 1–16. <http://doi.org/10.1093/aob/mcu077>

Yang, Y., Zhu, Q., Peng, C., Wang, H., Xue, W., Lin, G., ... Li, S. (2016). A novel approach for modelling vegetation distributions and analysing vegetation sensitivity through trait-climate relationships in China. *Scientific Reports*, 6, 24110.
<http://doi.org/10.1038/srep24110>

Zomer, R. J., Trabucco, A., Bossio, D. A., & Verchot, L. V. (2008). Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture, Ecosystems and Environment*, 126, 67–80.
<http://doi.org/10.1016/j.agee.2008.01.014>

Data accessibility statement

Community trait mean data used in this paper are provided in the supplementary information. Due to regulations of the major trait database used, the raw data cannot be openly shared. The predicted trait distributions maps generated in this study are provided as raster objects in the

771 supplementary information. Furthermore, the Rscripts for model parameter selection and of
772 the final models are provided in the supplementary information.

Table and figure legends

Table 1. Hypotheses on environmental variables impact on plant performance, and how this affects traits.

Figure 1. Overview of data quality types.

Figure 2. Model performance for different models and different traits.

Figure 3. Global plant trait predictions.

Figure 4. Relative predictor importance.

Figure 5. Partial response curves.

Figure 6. Models performances of different quality datasets.

Figure 7. Trait observations and their environmental coverage.

Table 1. How plant performance is affected by environmental variables. Reported trait-environment relationships are significant and/or biologically relevant. ↑ indicates an increase of trait value with an increase in value of the predictor, ↓ indicates a decrease, – indicates that no relationship was found, ^ indicates a unimodal response, and ○ indicates that this relationship has not been discussed in literature.

Predictor	Rationale	Impact	Hypothesis
Minimum temperature of the coldest month (Tmin)	Temperature-induced leaf damage affects plant performance. Frost-induced cavitation risk increases with decreasing temperatures.	Leaf habit change and their changes to be extreme temperature tolerant. Cavitation risk increases with decreasing wood density.	^ SLA ^{1,2} ↓ Nmass ^{3,4,5} ↑ Plant height ⁶ ↓ Wood density ^{7,8,9}
Humidity index	Drought-induced cavitation risk increases with decreasing humidity index.	Drought tolerant leaves Cavitation risk increases with height ¹⁰ .	↑ SLA ¹ ↓ Nmass ³ ↑ Plant height ^{3,11} ↓ Wood density ⁸
Precipitation in the driest quarter of the year (PrecDryQ)	Drought-induced cavitation risk increases with decreasing precipitation.	Cavitation risk increases with height ¹⁰ .	○ SLA ○ Nmass ↑ Plant height ⁶ ○ Wood density
Precipitation seasonality (PrecSeas)	Moisture availability affects plant survival.	Leaf-shedding. Stature change.	– SLA ¹² – Nmass ¹² ↓ Plant height ⁶ ○ Wood density
Soil cation exchange capacity (CEC)	Higher CEC increases soil fertility ¹³ .	Less durable structures can be maintained ^{7,14} .	– SLA ^{3,15} – Nmass ^{3,15} ○ Plant height ↓ Wood density ¹⁶
Soil pH (pH)	Lower pH increases soil fertility.	Less durable structures can be maintained ^{7,14} .	↓ SLA ¹⁵ ○ Nmass ○ Plant height ○ Wood density

¹Wright et al., 2005

²Went, 1953

³Ordoñez et al., 2009

⁴Reich & Oleksyn, 2004

⁵Reich, Oleksyn, & Tjoelker, 1996

⁶Moles et al., 2009

⁷Chave et al., 2009

⁸Reich, 2014

⁹Swenson & Weiser, 2010

¹⁰Tyree & Sperry, 1989

¹¹Ambrose et al., 2010

¹²Borchert, 1998

¹³Efretuei, 2016

¹⁴Wright et al., 2004

¹⁵Maire et al., 2015

¹⁶Ter Steege et al., 2006

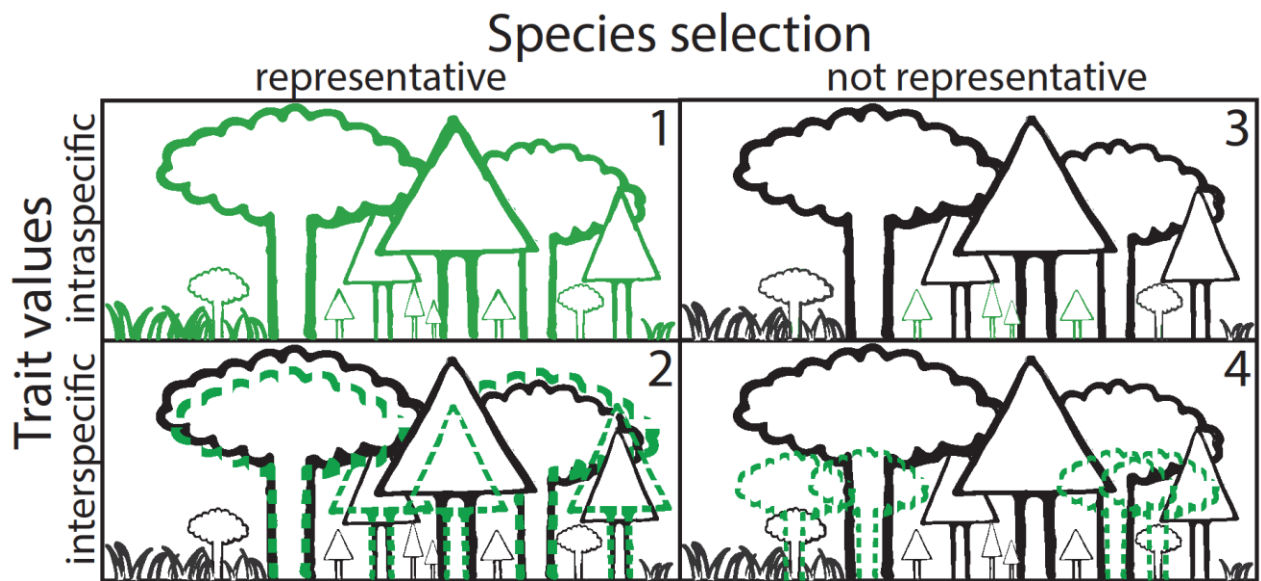


Figure 1. Overview of data quality types. Each plot presents the same plant community, where the individuals selected to sample are displayed in green. These samples are merely an example of how samples can be representative or not representative (as defined in Methods section 2.2, criterion 4). Dashed lines represent species mean values. In plot 1, all individuals in the entire community are selected for sampling, thus a representative sample of the community, and intra-specific trait variation is included. In plot 2, all species from the dominant vegetation type are selected for sampling, thus a representative sample of the community, but intra-specific trait variation is excluded. In plot 3, only saplings are sampled, thus a not representative sample of the community, and intra-specific trait variation is included. In plot 4, only one specific species from the dominant vegetation type is selected, thus a not representative sample of the community, and intra-specific trait variation is excluded.

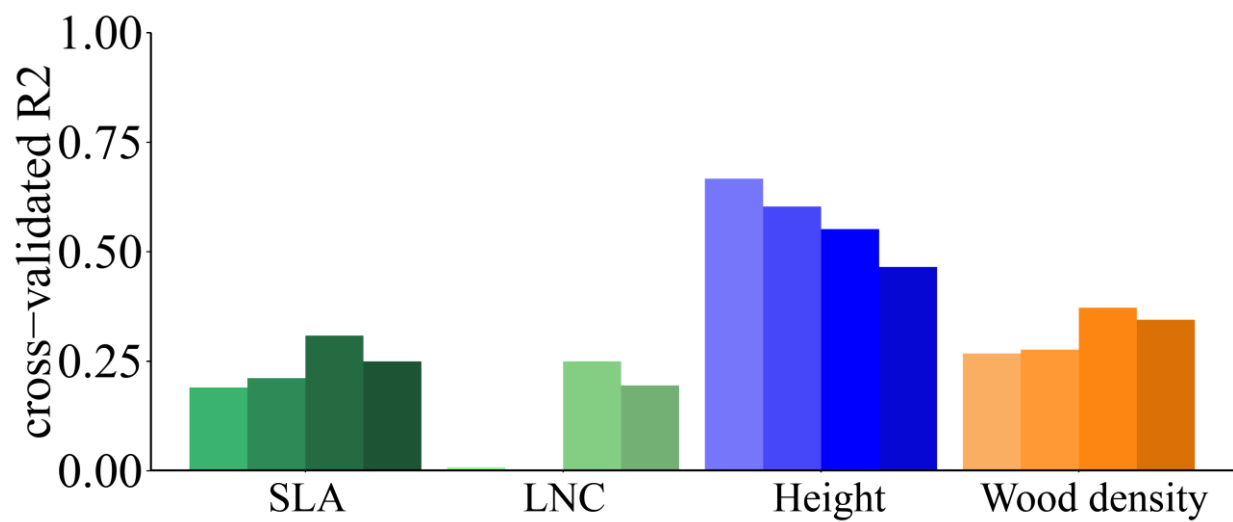


Figure 2. Model performance for different traits and different models presented as the cross-validated R^2 values. Per trait, the bars represent the predictive performance of the Generalized Linear Model, the Generalized Additive Model, the Random Forest, and the Boosted Regression Trees.

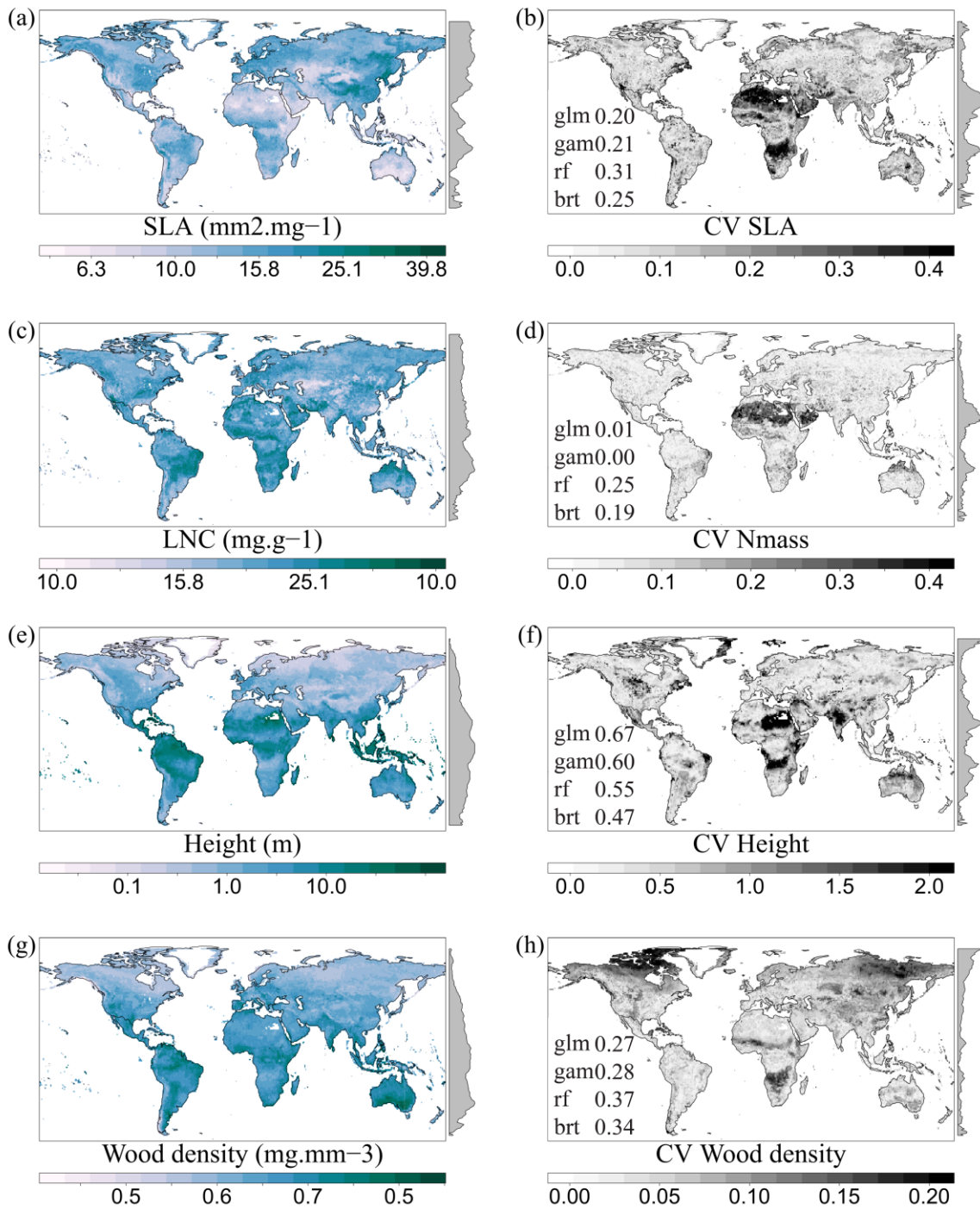


Figure 3. Global plant trait predictions. The left column presents the ensemble trait predictions, and the right column presents the ensemble coefficient of variation (CV) of different model predictions. The grey margin in each plot depicts the mean latitudinal value. Values in plots (b), (d), (f), (h) indicate the predictive performance of the different models, where glm indicates values of the Generalized Linear Models, gam of Generalized Additive

830 Models, rf of Random Forests, and brt of Boosted Regression Trees. These values indicate
831 how well trait are predicted, while the CV maps only identify locations where predictions are
832 divergent between models with high and/or similar predictive power. For extrapolation areas,
833 see Figure 7. No predictions were made for Greenland, as no soil predictions are available,
834 nor for the south of Egypt, as there is no precipitation seasonality. All predictions report
835 potential trait values, as not all terrestrial world is vegetated or includes woody vegetation.

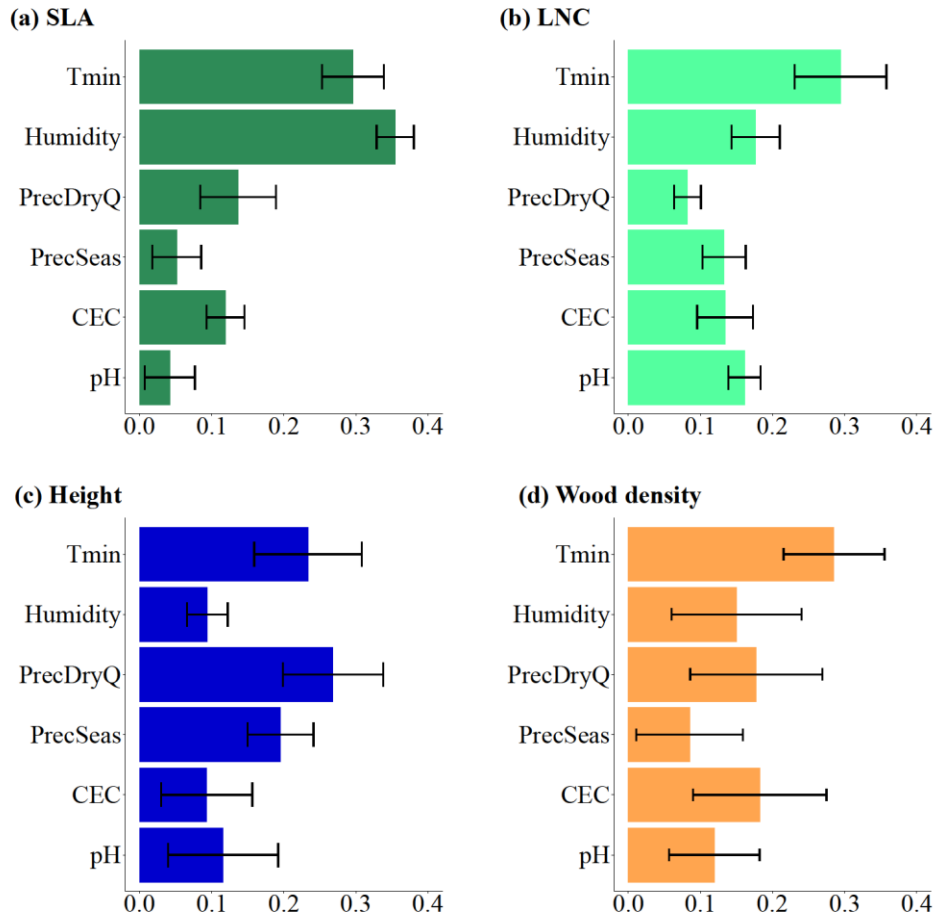
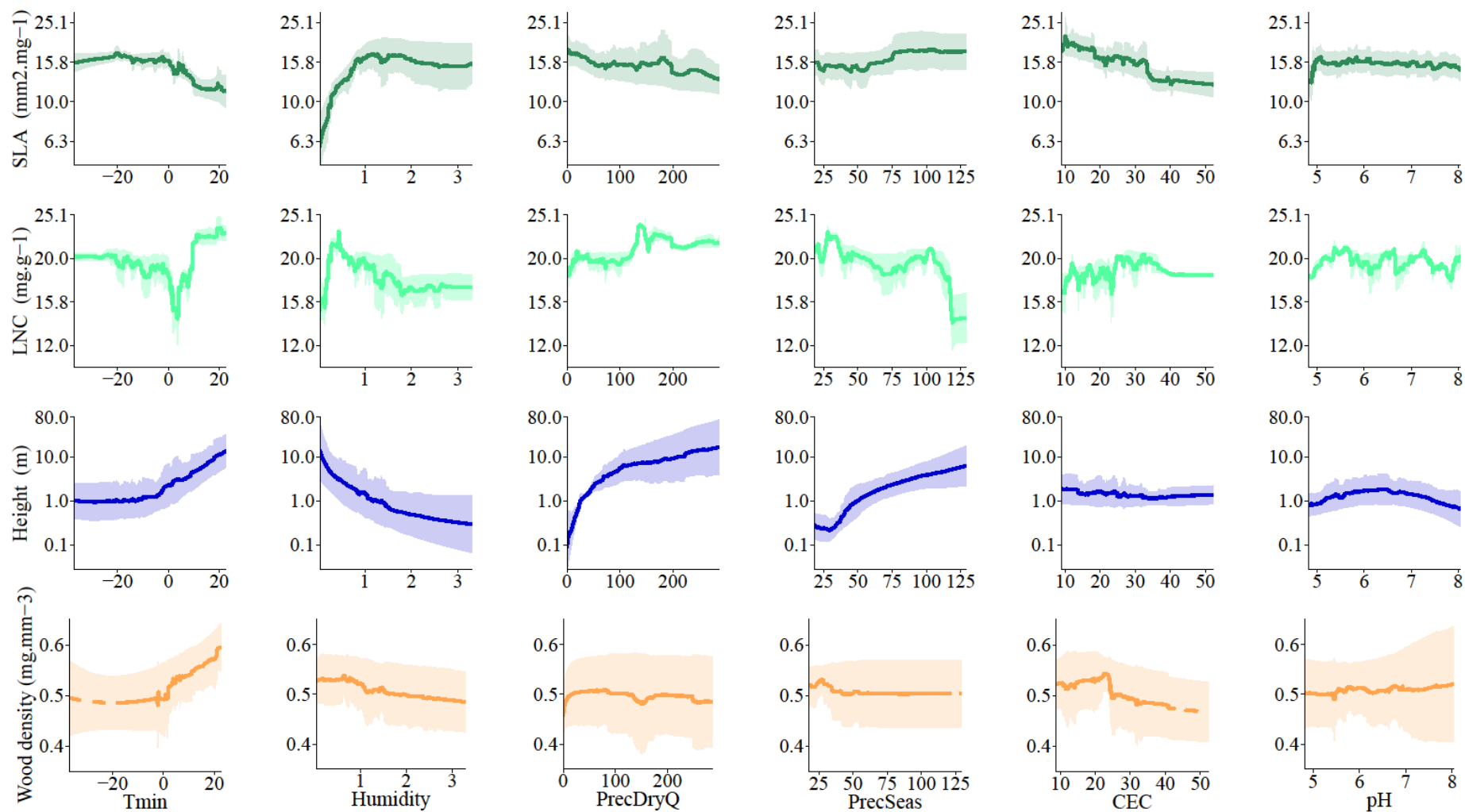


Figure 4. Relative predictor importance, calculated as $1 - \text{spearman correlation}$ (see Methods 2.5), where high values indicate high importance. The bars represent the ensemble relative predictor importance and the error bars show the ensemble coefficient of variation. Tmin stands for minimum temperature, Humidity for humidity index, PrecDryQ for precipitation in the driest quarter of the year, PrecSeas for precipitation seasonality, and CEC for soil cation exchange capacity.



843

844 **Figure 5.** Ensemble partial trait responses. Shaded areas are the ensemble coefficients of variation. Predictors are minimum temperature (Tmin;
845 °C), humidity index (Humidity; unitless), precipitation in the driest quarter of the year (PrecDryQ; mm), precipitation seasonality (PrecSeas; -),

846 soil cation exchange capacity (CEC; $\text{cmol}^+ \text{kg}^{-1}$), and soil pH ($-\log(\text{H}^+)$). The plotted range of each predictor is the 95th quantile of the global
847 range. Extrapolated trait responses are shown with a dashed line.

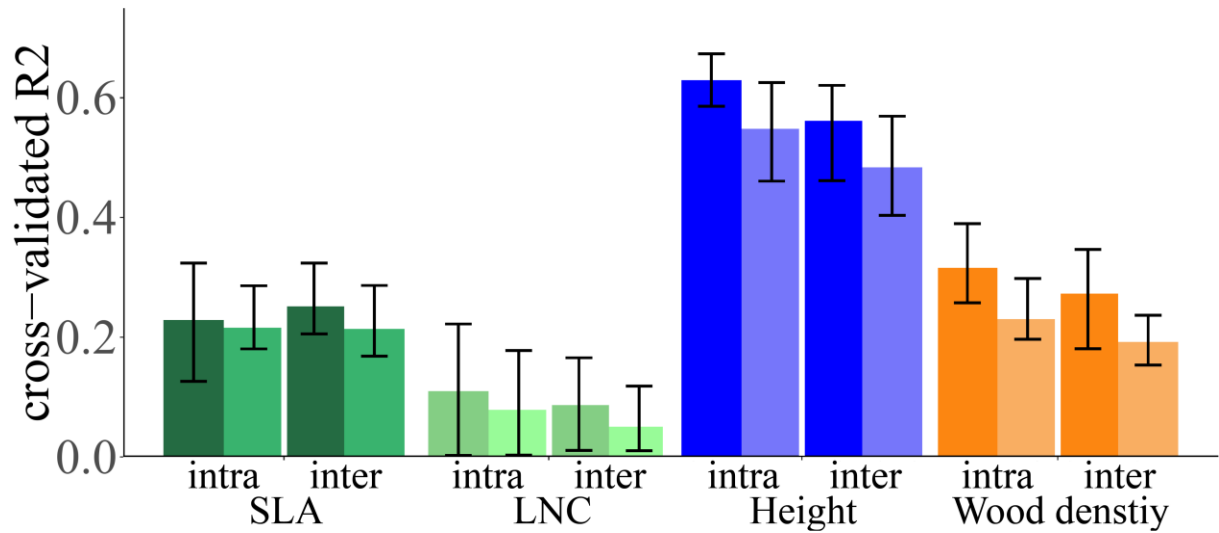
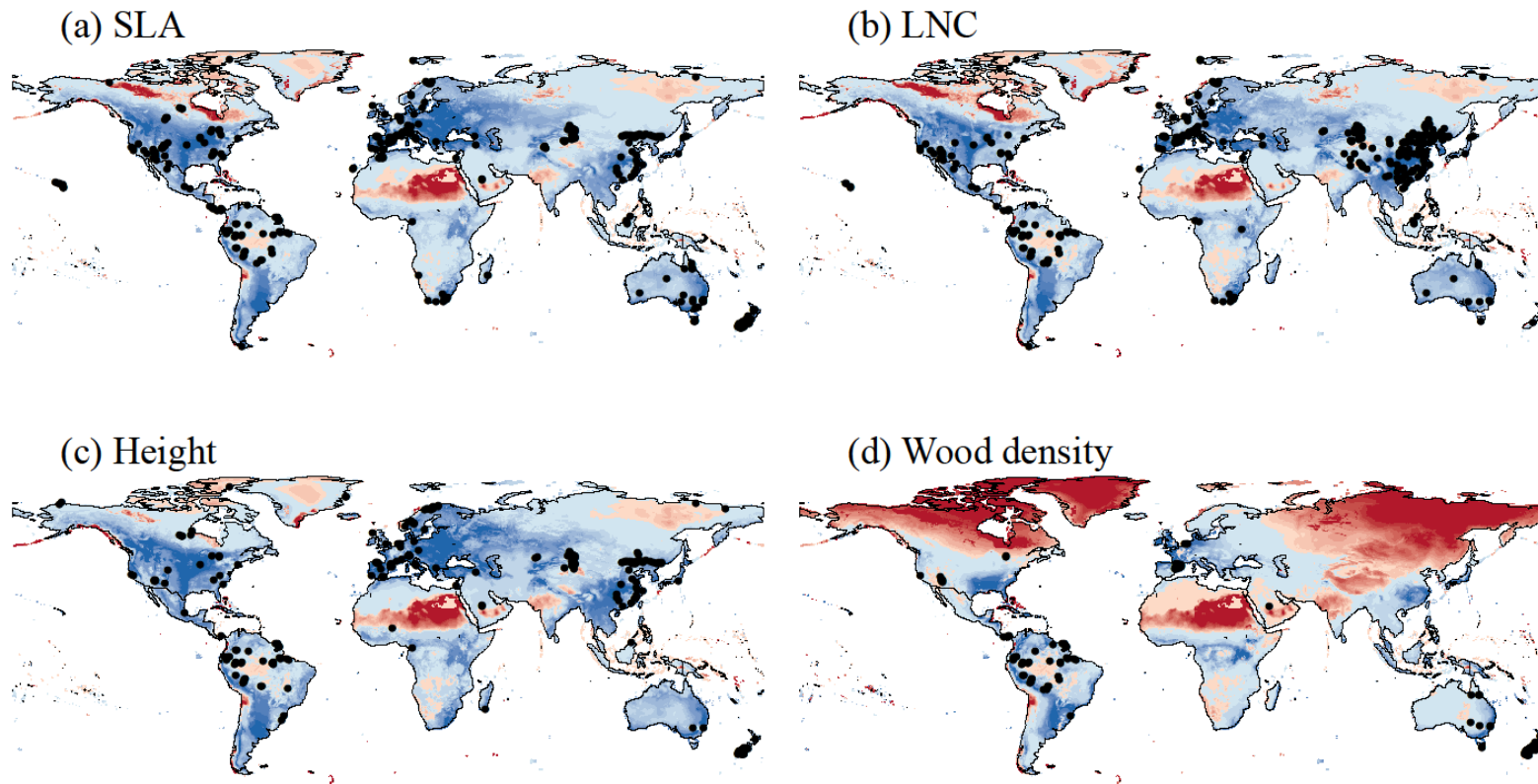


Figure 6. Model performances of different quality datasets. The bars represent the average cross-validated R^2 values over the four different models, where the errorbars indicate the minimum and maximum cross-validated R^2 value. Datasets including and excluding intra-specific trait variation are indicated with intra and inter, respectively. Species representativeness is indicated with the shade of the bar, where darker shades represent datasets with a representative species sample for the community and lighter bars represent datasets with a non-representative species sample. Thus, per trait, the bars represent plot 1, 3, 2, and 4 of Figure 1.



857

858 **Figure 7.** Locations of trait observations (black dots). Colors indicate the environmental coverage of trait observations as estimated by the MESS
 859 analysis (Elith et al., 2010). Legend: blue, interpolation; red, extrapolation. More intense shades indicate greater similarities (blue) or differences
 860 (red) in environmental conditions of the location compared to the environmental conditions covered by the training dataset.