

A fully traits-based approach to modeling global vegetation distribution

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Edited by Peter B. Reich, University of Minnesota, St. Paul, MN, and accepted by the Editorial Board October 22, 2013 (received for review May 16, 2013)

Dynamic Global Vegetation Models (DGVMs) are indispensable for our understanding of climate change impacts. The application of traits in DGVMs is increasingly refined. However, a comprehensive analysis of the direct impacts of trait variation on global vegetation distribution does not yet exist. Here, we present such analysis as proof of principle. We run regressions of trait observations for leaf mass per area, stem-specific density, and seed mass from a global database against multiple environmental drivers, making use of findings of global trait convergence. This analysis explained up to 52% of the global variation of traits. Global trait maps, generated by coupling the regression equations to gridded soil and climate maps, showed up to orders of magnitude variation in trait values. Subsequently, nine vegetation types were characterized by the trait combinations that they possess using Gaussian mixture density functions. The trait maps were input to these functions to determine global occurrence probabilities for each vegetation type. We prepared vegetation maps, assuming that the most probable (and thus, most suited) vegetation type at each location will be realized. This fully traits-based vegetation map predicted 42% of the observed vegetation distribution correctly. Our results indicate that a major proportion of the predictive ability of DGVMs with respect to vegetation distribution can be attained by three traits alone if traits like stem-specific density and seed mass are included. We envision that our traits-based approach, our observation-driven trait maps, and our vegetation maps may inspire a new generation of powerful traits-based DGVMs.

functional variation | global vegetation map | probabilistic model | trait-environment relationships | vegetation attributes

To understand and predict the impacts of climate change on system Earth, it is essential to predict global vegetation distribution and its attributes. Vegetation determines the fluxes of energy, water, and CO₂ to and from terrestrial ecosystems. So-called Dynamic Global Vegetation Models (DGVMs) (reviewed in ref. 1) are indispensable tools to make predictions on such biosphere–climate interactions. Despite their importance, DGVMs are among the most uncertain components of earth system models when predicting climate change (2).

DGVMs have been built around the concept of Plant Functional Types (PFTs) (3). Traditionally, various functional attributes (or traits) were assumed to be constant for a given PFT. This assumption has various drawbacks (reviewed in ref. 4). For instance, it implies assuming that trait values used to parameterize PFTs are valid under past environmental conditions and will be valid under future conditions. As such, this assumption neglects acclimation and adaptation (5), nonrandom species extinction (6), and major differences in dispersal rates among species and within PFTs (7). Moreover, this assumption strongly hampers quantifying feedback mechanisms between vegetation and its environment.

For these reasons, the application of traits in DGVMs is increasingly refined. Trait responses to, for example, different soil fertility conditions are described as an emergent property in relation to nutrient feedbacks (8). Also, acclimation processes are increasingly included by replacing constant photosynthesis and respiration parameters by functions of temperature or CO₂ (9, 10), with profound impacts on predicted carbon fluxes (11). Within current DGVMs, traits are varied within a PFT (12), not

allowing for assessing the direct impacts of traits relative to its indirect effects (for example, through productivity, biomass, or feedbacks changing environmental conditions). A comprehensive analysis of the direct impacts of trait variation as such (within and between PFTs) on global vegetation functioning and distribution does not yet exist. However, the paradigm shifts from species-centered approaches to traits-based approaches (13), the rapid increase in the compilation and application of traits-based analyses (14, 15), and the associated conceptual advances (e.g., in assembly theory) (16) allow for such analyses independent of a DGVM.

Our aim was to describe global trait variation and evaluate whether trait variation alone already allows for predicting the global distribution of vegetation types, which is one of the principle aims of DGVMs. We first empirically describe global trait distribution and global trait maps—*independent of vegetation type*—as a function of multiple environmental drivers. Subsequently, in a posterior calculation, we predict the occurrence probability of vegetation types. This way, we derive a DGVM-independent trait-driven estimate of global vegetation distribution. We envision that our approach may inspire a new generation of powerful traits-based DGVMs applying (fully) traits-based concepts to predict carbon, water, and energy fluxes.

Results

Global Maps of Traits. We selected traits that reflect plant fitness and play critical roles in common plant strategy schemes (17, 18): seed mass (in milligrams), leaf mass per area (LMA; in grams per meter²), and stem-specific density (SSD; in grams per centimeter³). Seed mass expresses a tradeoff between seed

Significance

Models on vegetation dynamics are indispensable for our understanding of climate change impacts. These models contain variables describing vegetation attributes, so-called traits. However, the direct impacts of trait variation on global vegetation distribution are unknown. We derived global trait maps based on information on environmental drivers. Subsequently, we characterized nine globally representative vegetation types based on their trait combinations and could make valid predictions of their global occurrence probabilities based on trait maps. This study provides a proof of concept for the link between plant traits and vegetation types, stimulating enhanced application of trait-based approaches in vegetation modeling. We envision that our approach, our observation-driven trait maps, and vegetation maps may inspire a new generation of powerful traits-based vegetation models.

Author contributions: P.M.v.B. designed research; P.M.v.B., J.C.D., and L.M.V. performed research; P.M.v.B. analyzed data; and P.M.v.B., J.C.D., and L.M.V. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. P.B.R. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1304551110/-DCSupplemental.

dispersal and seedling survival (19). Leaf traits, like LMA, indicate a tradeoff between fast growth and short lifespan of tissues to cope with available water and nutrient resources (15). SSD indicates a tradeoff between fast growth and mechanical support (20). Moreover, SSD does not only relate to competition for light (like height), but also relates to drought tolerance (20). Available information (18, 21) shows that the selected traits are partially independent, thus maximizing traits space available to differentiate among vegetation types.

We related community mean trait values to environmental information from climate and soil maps in a multiple regression analysis to describe the effects of environmental drivers on the functional composition of species assemblages. This analysis builds on previous analyses that showed significant trait convergence (22) for several biomes, which was attributed to environmental differences (16, 23, 24). These studies also suggest that the functional differences among communities can be conveniently represented by community mean trait values (25).

Indeed, a reasonably high proportion of the global variance in traits was explained by a combination of environmental drivers (*SI Appendix, section 2* and *SI Appendix, Fig. S2.2*). A combination of soil and climate variables explained SSD best ($R_{\text{adj}}^2 = 0.52$) followed by seed mass ($R_{\text{adj}}^2 = 0.41$) and LMA ($R_{\text{adj}}^2 = 0.35$). The R^2 values of LMA are lower than in a previous study using locally observed soil C and soil N (26), but the use of local observations (and the lack of such observations in concert with trait observations) comes at the cost of fewer data points and a potential selection bias.

Based on the regressions, we prepared global spatially explicit trait maps (Fig. 1). Thus far, trait maps exist for the Americas (24, 27) but not the globe. Our global trait maps (Fig. 1) illustrate the huge variability in trait values within and across regions: 11 times for LMA, 15 times for SSD, and 10^5 times for seed mass. Only part of this variation is accounted for in current DGVMs. In addition, we prepared maps containing SEs of our predictions to facilitate assessing the accuracy of our trait maps for applications in the context of DGVM evaluation (*SI Appendix, Fig. S2.3*).

LMA did not show a profound latitudinal pattern (Fig. 1A), which reflects the multiple drivers acting on LMA, like drought, fertility, and shade (26). Across the globe, LMA was predicted to be lowest in fertile (temperate) regions and highest in dry tropical environments, which coincides with earlier findings (28). The higher selective pressure of the environment on SSD is reflected in its clustered distribution with high values in very dry environments and low values in temperate climates and regions dominated by herbaceous species. Seed mass is highest at low latitudes (19), but the trait maps also show high additional variation in seed mass within latitudes (e.g., within India and Southeast Asia). Particularly, fertile conditions seem to cause a decrease in seed mass. Note that the trait analysis was done without considering whether a particular trait combination actually leads to viable vegetation. Thus, traits may be predicted at locations where no (or sparse) vegetation occurs (e.g., ice or deserts). SEs of predictions also tended to be high in regions with sparse vegetation (*SI Appendix, Fig. S2.3*).

Traits-Based Probabilistic Vegetation Descriptions. The occurrence probability of different vegetation types was described as a function of three traits applying a Gaussian mixing density (GMD) model (Fig. 2). Based on the GMD model, 56% (Cohen $\kappa = 0.47$) of the vegetation type observations in the calibration database were predicted correctly. The biggest mismatches were that desert vegetation was mistaken for woodland, savanna was mistaken for tropical dry forest and woodland, and tropical wet forest was mistaken for tropical dry forest (*SI Appendix, Fig. S3.1*), which may be understood from the functional similarity among these vegetation types. Many vegetation types were confused for temperate forests, indicating that temperate forests cannot be fully characterized by the three traits chosen.

Based on the predicted combination of traits in a grid cell and one moderate bioclimatic constraint, the probability of a grid cell

to contain a given vegetation type was determined by applying the GMD models (which may be interpreted as the fundamental functional niche of each vegetation type) (*SI Appendix, Fig. S3.3*). In some regions, multiple vegetation types were predicted to have a similar probability, indicating that alternative vegetation types may occur. In those cases, initial conditions and/or stochastic events may determine the vegetation type that is observed (29). Multiple probable vegetation types, coinciding with low maximum probabilities types (Fig. 3A), seem to prevail particularly in the wet tropics and wet temperate regions of Europe and North America. In contrast, high maximum probability (and thus, unique position in terms of traits) occurred in grasslands in the chernozem region of Eurasia and Canada and the tundra in parts of Siberia.

For each grid cell, we selected the most probable vegetation type. The resulting vegetation map (Fig. 3B) describes the observed global vegetation distribution reasonably well. Our vegetation map is patchier, which might actually be real, given that local heterogeneities and gradual transitions among vegetation types are not accounted for in current vegetation maps. The validation with observed vegetation yielded $\kappa = 0.34$. The κ is somewhat lower than the κ obtained for existing global vegetation models [e.g., BIOME1 ($\kappa = 0.49$) (30), Lund–Potsdam–Jena

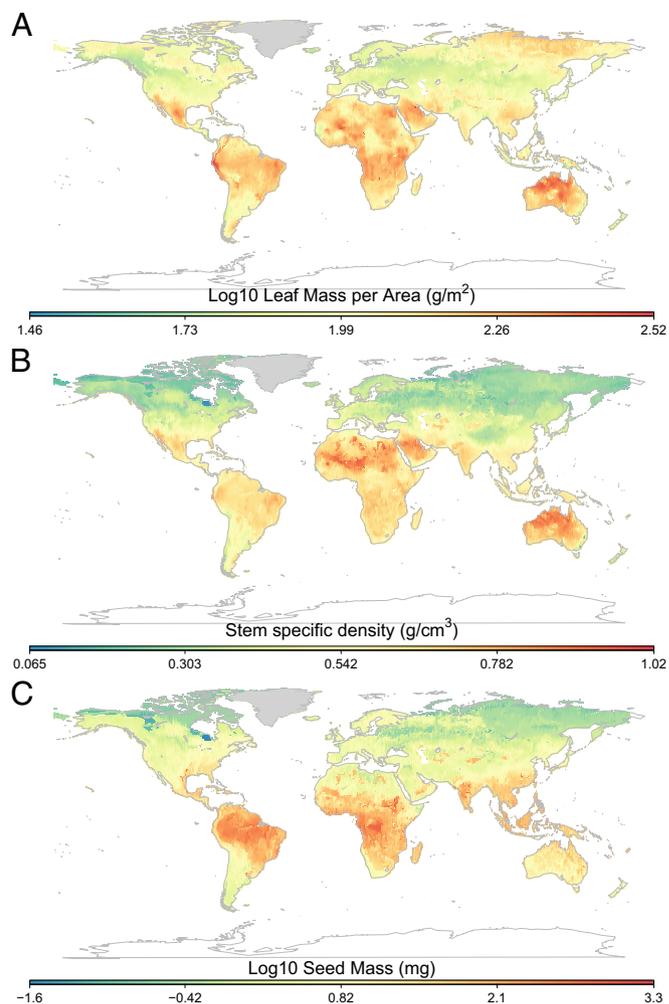


Fig. 1. Global community mean trait maps for (A) \log_{10} LMA (grams per meter⁻²), (B) SSD (grams per centimeter⁻³), and (C) \log_{10} seed mass (milligrams) derived by linking global trait databases to environmental drivers obtained from global climate and soil maps. Greenland has been masked, because climate predictions for this region are bound to be biased (43).

(LPJ) ($\kappa = 0.42$) (31), or a consensus map among DGVMs ($\kappa = 0.42$) (32)]; however, direct comparison is difficult, because each study used a different vegetation map. This result indicates that vegetation types are functionally sufficiently dissimilar, such that the majority of the predictive ability of DGVMs with respect to vegetation distribution can be attained by three traits alone (and no vegetation dynamics).

However, the ability to differentiate among some vegetation types—particularly among woodlands, tropical dry forests, and deserts—was poor. The majority of the mismatches had already occurred in the calibration, showing that there is overlap in the trait combinations characterizing these vegetation types. Functional similarity among vegetation types thus strongly hampers predicting global vegetation distribution when using as few traits as we have used here. In correspondence with this interpretation, on merging savanna, woodlands, and dry forests into one vegetation type, a much higher κ (0.52) was obtained.

To evaluate the robustness of our vegetation distribution predictions, we ran two control analyses. The vegetation map of the first control analysis (a rerun without our bioclimatic constraint) (*SI Appendix, Fig. S3.5A*) shows deviations from observations, particularly in Scandinavia and around the great lakes of Northern America, where now, tropical dry and wet forests are predicted to occur. Interestingly, these regions are dominated by wetlands (33) with high organic matter according to the soil map. Apparently, for those corresponding positions in traits space, these tropical vegetation types are functionally similar to (and even more probable than) temperate terrestrial vegetation types. A separate class for wetland vegetation (and information on their traits, for which no global database currently exists) might aid in dealing with these misclassifications.

As a second control analysis, we analyzed vegetation predictions for regions where the conditions (according to their position in traits space) were considered unsuitable for vegetation. These locations are the Sahara, the Arabic peninsula, and parts of South America (*SI Appendix, Fig. S3.4*), which are known to be barren. If we determine vegetation probabilities for these locations, primarily woodlands, desert vegetation, and savannas are predicted, which seems ecologically reasonable (*SI Appendix, Fig. S3.5B*). Arctic barren regions are predominantly converted to tundra (*SI Appendix, Fig. S3.5B*). The control analyses, thus, indicate that the results are ecologically consistent.

Discussion

Fully Traits-Based Approach to Predict Vegetation Distribution. We provided a proof of principle for modeling global vegetation distribution by making use of two ecological paradigms: (i) community mean traits vary predictably along environmental gradients, and (ii) the spatial distribution of vegetation is determined by its traits and probabilistic processes. By integrating these two paradigms, we show the feasibility to reasonably accurately calculate the global vegetation distribution based on the global variation in three traits alone (see below).

We chose traits central to plant strategy schemes to functionally differentiate among vegetation types. Such differentiation was not possible based on leaf economics traits alone, because the functional overlap among vegetation types along individual trait axes was considerable. Whereas leaf economics traits tend to receive the most emphasis in current DGVMs (*Discussion, Future Prospects to Improve DGVMs*), we integrated information on the (local) value of three functionally independent traits simultaneously to better determine the probability of occurrence of a particular vegetation type (as well as predict non-suitable conditions for vegetation).

As an intermediate step in this analysis, we derived global traits maps that are independent of the vegetation type information and independent of a DGVM model, and they may be valuable for DGVM modeling (*Discussion, Future Prospects to Improve DGVMs*). The global trait variation shown in the trait maps likely reflects the global importance of varying environmental conditions in driving trait variation (16, 24).

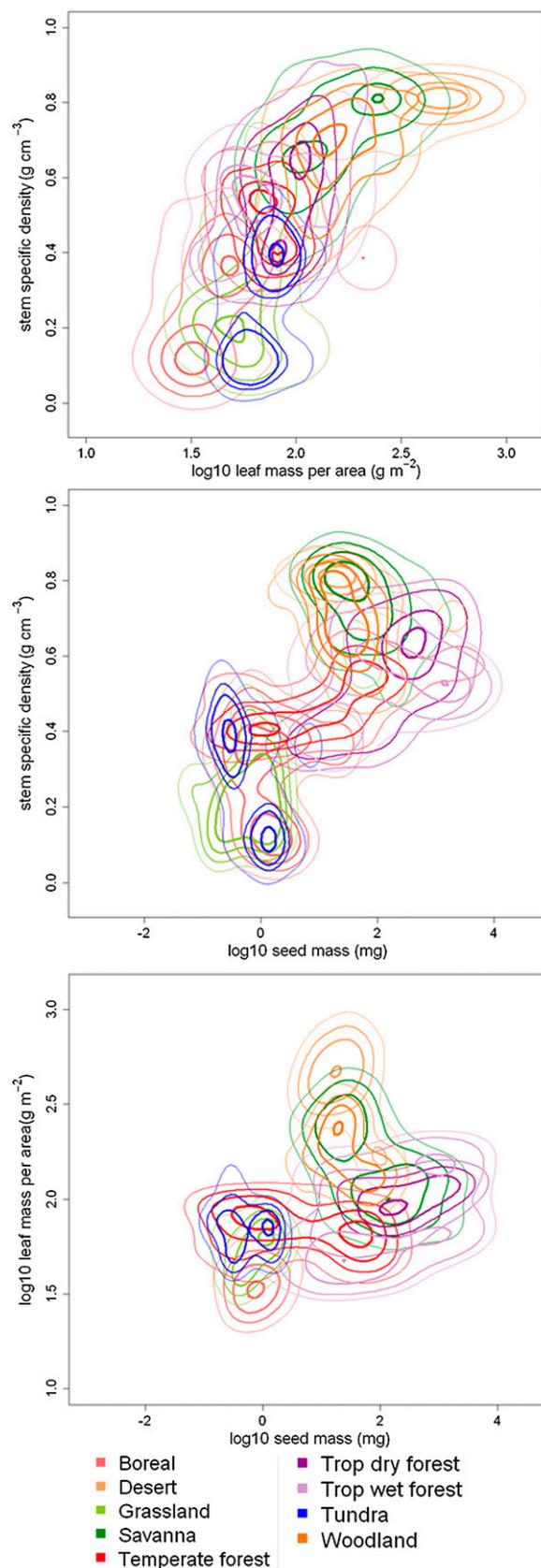


Fig. 2. Probability densities (increasing line thickness coincides with higher densities; it also illustrates the flexibility of the method to fit any structure) of vegetation types in 3D traits space, which were defined by \log_{10} LMA (grams per meter²), SSD (grams per centimeter³), and \log_{10} seed mass (milligrams) and projected onto the respective axes.

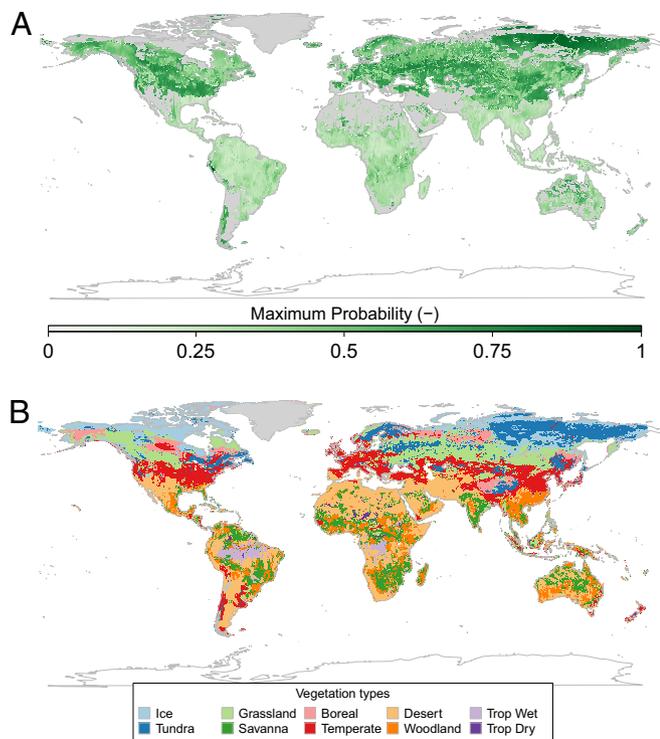


Fig. 3. Global vegetation distribution predictions. (A) Probability of the vegetation type with the highest probability for each $0.5^\circ \times 0.5^\circ$ terrestrial location. (B) Global vegetation map derived by selecting the vegetation type with the highest occurrence probability at a given functional characterization of the local vegetation (provided by the trait predictions shown in Fig. 1).

Challenges of Traits-Based Approaches for Predicting Vegetation Distribution. Our analysis showed that, based on the global variation in three traits alone, we can predict 42% of the observed vegetation distribution correctly. There are some large and systematic errors, including the underestimation of wet tropical and boreal forests and the inability to discriminate among savannas, woodlands, and tropical dry forests. Within the current framework, several improvements may be achieved by reducing uncertainties of the individual steps.

First, when predicting global trait distributions, we could describe about one-half or less of the trait variance by the regression equations. Despite these large uncertainties, the remaining global variance was generally homogeneously distributed, with somewhat larger prediction errors in desert regions and the boreal zone (*SI Appendix*, Fig. S2.3). This regionally increased uncertainty might have contributed to the underestimation of boreal forests. Moreover, there was a tendency to level off the minimum and maximum trait values, which is common to linear fitting procedures. Although this leveling did not strongly affect the trait patterns themselves, it will have led to underestimation of vegetation type occurrences with more extreme trait values, like boreal forests (low in SSD) and wet tropical forests (high in seed mass).

A full explanation of trait values by current environmental drivers will principally be impossible given the additional influences of historical events, stochastic processes, biotic interactions, and phylogenetic constraints (although the latter only seems to have a limited influence on the traits considered here) (34). Improvements may be obtained, however, when better global and spatially explicit estimates of local soil, hydrology, and climate conditions relevant to vegetation become available. Special attention should be paid to global quantitative estimates of disturbance, because disturbance is an important driver of many traits, including seed mass. The availability of global maps of disturbance by fire or grazing (the latter not included in

current DGVMs) would likely have aided higher predictive power for seed mass. Moreover, for predictions of future trait patterns, atmospheric CO_2 concentration should be considered as additional driver of trait variation (35). Finally, the incorporation of more physiological information may improve the predictions. For instance, the incorporation of trait–trait constraints and the application of physiological thresholds combined with asymptotic regressions may force trait combinations at a given location to realistic ranges. Theoretical advances on the physiological background of such constraints are essential to allow full development of these extensions.

Second, for predicting the occurrence probabilities of vegetation types, the most obvious improvement is the inclusion of more traits (preferably those traits that represent different plant functions) (36). The TRY database (with many more observations) (14) may provide such an opportunity. In our analysis based on three traits, wet tropical forests were confused with dry tropical forests, and boreal forests were confused with tundra, which contributed to their underestimation. An increased ecological understanding of the traits distinguishing these types would provide a major advance to functionally classifying global vegetation types. Ideally, classifications would also allow for the occurrence of no-analog vegetation types that may arise in a future climate (6). An advantage of the approach presented here is that vegetation occurrences are calculated after the trait calculations, allowing for easy incorporation of adapted classifications or testing of multiple classification schemes.

Future Prospects to Improve DGVMs. Our traits-based approach may inspire the next generation of DGVMs, in which the observed variability in vegetation characteristics (as a driver of fluxes and vegetation distribution) will play an even more prominent role. Our vegetation distribution map indicates that (i) the combination of selected traits is sufficiently different to distinguish among vegetation types and (ii) the trait maps alone (independent of biomass dynamics) are sufficiently exact to describe a considerable fraction of the global vegetation distribution. Such predictions are one of the principle aims of DGVMs. Our analysis aids additional appreciation of the critical importance of trait variation within and between vegetation types, and including this variation does not impair the ability to predict vegetation distribution. Enhanced appreciation of trait variation should lead to incorporation of additional traits as well as continued incorporation of internal and external drivers of trait variation in DGVMs. Additional traits to be considered include drought-tolerance traits (linked to vegetation resistance in the Amazon basin) (37)—like SSD—and dispersal or establishment traits—like seed mass. Previously, seed mass and canopy height were shown to be more important than leaf traits for discriminating among vegetation types (36). Given that these traits codetermine vegetation productivity, their inclusion may also improve predictions of carbon and water fluxes.

Our trait maps (and their SEs) may stimulate this development; they provide an observation-based estimate of global variation in traits derived independently from DGVM modeling, and they apply to the same scale as DGVMs. Model estimates can be confronted to these maps to gain insights that aid additional improvement of the models (in analogy to frameworks for comparing, for example, leaf area index or flux estimates) (38) by identifying missing functional modulations (missing drivers or misparameterizations in the models).

A number of fundamental unknowns constrain our ability to predict the dynamics in trait variation and vegetation distribution. (i) The first unknown is climate-induced trait acclimation and adaptation, which are presumed to be critical to accurately predict projections of carbon and vegetation (e.g., in the Amazon) (11, 39, 40). Differences in acclimation potential among vegetation types and among traits and the mutual dependencies in trait acclimation potential are not well-understood. (ii) The second unknown is the extent to which environment–trait relationships and trait–trait tradeoffs will remain the same in a future

climate (i.e., whether they reflect fundamental tradeoffs and filtering processes). Fitness maximization approaches (41, 42) may provide useful insights on this aspect. (iii) The third unknown is the extent to which current vegetation types reflect combinations of functional properties in a future climate.

Despite these uncertainties, by separating trait calculations from vegetation type calculations, we aimed to pave the way for fully traits-based models of carbon, water, and energy fluxes given the intimate link between traits and ecosystem fluxes (42).

Conclusions

Our traits-based approach to model global vegetation distribution shows that a large proportion of the predictive ability of DGVMs with respect to vegetation distribution, which is one of the principle aims of DGVMs, can be attained by accounting for variation in three traits alone. We hope this proof of principle on the critical importance of trait variation stimulates the continued incorporation of internal and external drivers of traits into the global models. Our trait maps may serve as observation-driven estimates with which to compare such improved trait representation. Ultimately, these advances are meant to inspire the next generation of DGVMs to model vegetation functioning now and in a future climate.

Methods

Global vegetation distribution was modeled in a three-step approach (dubbed TRICYCLE). First, we ran a regression of plant traits against multiple environmental drivers, which was inspired by previous findings of global trait convergence. Second, trait combinations were used to predict the occurrence probability of a vegetation type, explicitly accounting for the role of stochasticity on vegetation distribution (29) and community assembly (43). Third, our global vegetation maps were validated against observed vegetation type distributions (the conceptual diagram is shown in *SI Appendix, Fig. S1.1*).

Step 1: Predicting Traits from Climate and Soil Variables. First, we performed multiple regression with community mean traits as dependent variables and climate and soil variables as independent variables, with the aim to construct a global trait map. For this purpose, we compiled a database of field observations of LMA, SSD, and seed mass from the literature (*SI Appendix, section 2*). For those sites for which all traits were available, we calculated community mean traits values, yielding a database of community mean traits for 299 sites in all global biomes (location map is shown in *SI Appendix, Fig. S2.1*).

Based on their georeferences, trait means were related to estimates of environmental conditions. We selected environmental variables to represent environmental drivers known to affect community mean traits on a global scale (25, 28). We selected mean annual temperature (MAT), number of frost days, mean annual precipitation (MAP), net radiation, evaporative demand, and MAP/evaporative demand as climate variables. In addition, soil pH, cation exchange capacity, soil texture, total N, soil C:N ratio, and modeled net N mineralization rates were included to represent soil structural, chemical, and fertility impacts on plant traits (*SI Appendix*). Based on Akaike information criterion, the best regression model was determined for each trait (regression setup is shown in *SI Appendix, section 2* and *SI Appendix, Fig. S2.2*).

Second, we generated global trait maps by estimating the community mean traits for each 30-min pixel through coupling the regression equations to gridded soil and climate maps.

Step 2: Predicting the Occurrence Probability of Vegetation Types. Based on the combination of three traits, we estimated the occurrence probability of vegetation types on a global scale. We identified nine vegetation types (tropical dry forest, tropical wet forest, temperate forest, boreal forest, tundra, grassland, woodland, savanna, and desert vegetation) according to information in ref. 44. This generic classification resembles plant functional types as generally applied in DGVMs, and importantly, it can be executed based on MAT and MAP only.

We assessed the 3D traits space—defined by LMA, SSD, and seed mass—as occupied by each vegetation type. We used a calibration set of 2,208 trait observations from our database. Vegetation type was estimated from MAT and MAP based on the observation georeferences. If an observation occurred close to a climatic border according to our classification, we additionally used information on categorical traits (growth form and leaf habit) of the species involved to evaluate the classified vegetation type.

The cluster of positions of a given vegetation type in 3D traits space was quantitatively described by a probability density function using a GMD model (45) (*SI Appendix, section 3*). An important attribute of GMDs is that they do not assume any a priori distribution in traits space. This attribute requires a large number of data points (i.e., a minimum of 20 observations per trait axis per vegetation type; not allowing our analysis to extend to more than three traits given the current size of our database). At any traits combination, the probability density of a vegetation type relative to the sum of probability densities for all vegetation types equals the probability of a vegetation type to occur. The performance of this calibration was evaluated by pairwise comparison of the observed vegetation type in the database with the one predicted to have the highest probability using Cohen κ (43).

Next, to derive global maps of vegetation distribution, we superimposed the trait maps (from step 1) on top of each other to derive the position of each grid cell in 3D traits space. The multivariate combination of traits in a grid cell was input to the probability density functions of the vegetation types to determine the occurrence probability for each vegetation type. This procedure was repeated for all 67,420 land grid cells to provide occurrence probabilities of all nine vegetation types.

So far, we assumed that each grid cell contains a fully developed vegetation in equilibrium with its local environment (neglecting the influence of biotic interactions). However, some regions do not foster any vegetation at all, because the environment is too extreme. Those locations will be in the tail of probability densities of any vegetation type. Thus, the density kernels provide a measure of the habitat suitability of that grid cell. We assumed a minimum threshold density (*SI Appendix, section 3*) to avoid vegetation to be predicted in grid cells where vegetation is improbable. In our comparison with observed vegetation maps (step 3), we assume that nonsuitable habitats represent deserts or if frost days are >200 , polar deserts/ice.

Finally, we prepared vegetation maps by assuming that the most probable vegetation type will be observed. The most probable vegetation type is the most suited in terms of its traits relative to the other vegetation types that follow assembly rules (22). Multiple vegetation types may have equal probability in a grid cell (i.e., have similar functional attributes and similar fit to the local environmental conditions), although the vegetation definition may not allow the occurrence of one or more vegetation types. Thus, to avoid inappropriate predictions of tropical vegetation types, we used a weak generic bioclimatic constraint, which did not allow woodlands, savannas, and tropical dry and wet forests to occur at locations where the number of frost days exceeds 75 d. Ideally, we would have used physiological frost tolerance of species as a fourth trait axis. Unfortunately, current compilations on experimental frost tolerance (46) do not yet have a sufficient species cover to allow inclusion of frost tolerance.

Step 3: Validation of Vegetation Distribution. Our vegetation map was validated against observed vegetation using Cohen κ (47). To minimize biases and uncertainties occurring in any existing vegetation map, we chose to compare our vegetation map with a map consisting of those grid cells for which maps based on information in refs. 44 and 48 agree. This overlap had a κ of 0.48, with higher correspondence for deserts and lower correspondence for woodlands and tropical dry forest. The map in ref. 44 was derived from MAT and MAP data. The map in ref. 48, based on remote sensing information, was reclassified (*SI Appendix, Fig. S1.1*) to represent the nine vegetation types identified above.

ACKNOWLEDGMENTS. We thank Peter Reich and three anonymous reviewers for constructive comments. This study was supported by Netherlands Organization for Scientific Research (NWO) Theme Sustainable Earth Research Project Number TK509-03 and Dutch National Research Program Climate Change and Spatial Planning Project A1.

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