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RESEARCH REVIEW

Going beyond limitations of plant functional types when predicting global ecosystem–atmosphere fluxes: exploring the merits of traits-based approaches

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ABSTRACT

Aim Despite their importance for predicting fluxes to and from terrestrial ecosystems, dynamic global vegetation models have insufficient realism because of their use of plant functional types (PFTs) with constant attributes. Based on recent advances in community ecology, we explore the merits of a traits-based vegetation model to deal with current shortcomings.

Location Global.

Methods A research review of current concepts and information, providing a new perspective, supported by quantitative analysis of a global traits database.

Results Continuous and process-based trait–environment relations are central to a traits-based approach and allow us to directly calculate fluxes based on functional characteristics. By quantifying community assembly concepts, it is possible to predict trait values from environmental drivers, although these relations are still imperfect. Through the quantification of these relations, effects of adaptation and species replacement upon environmental changes are implicitly accounted for. Such functional links also allow direct calculation of fluxes, including those related to feedbacks through the nitrogen and water cycle. Finally, a traits-based model allows the prediction of new trait combinations and no-analogue ecosystem functions projected to arise in the near future, which is not feasible in current vegetation models. A separate calculation of ecosystem fluxes and PFT occurrences in traits-based models allows for flexible vegetation classifications.

Main conclusions Given the advantages described above, we argue that traits-based modelling deserves consideration (although it will not be easy) if one is to aim for better climate projections.

Keywords
Assembly theory, bioclimatic limits, DGVM, earth system models, functional traits, habitat filtering, land surface model, PFT, plant strategies, trait convergence.

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INTRODUCTION

Our climate is partly driven by interactions among atmospheric, oceanic and terrestrial components. Earth system models are the only tools that account for the complex set of processes that affect these interactions (Murphy *et al.*, 2004). Models that predict fluxes of energy, water and CO_2 from terrestrial components play a pivotal role in earth system models. These so-called dynamic global vegetation models (DGVMs; hereafter called 'vegetation models') are essential to understand fluxes to and from terrestrial ecosystems interacting with climate controls like temperature, precipitation and atmospheric CO_2 concentrations in the present and future climate (reviewed by, e.g., Friedlingstein *et al.*, 2006). Vegetation models also aid the understanding and prediction of feedbacks between terrestrial ecosystems and the atmosphere.

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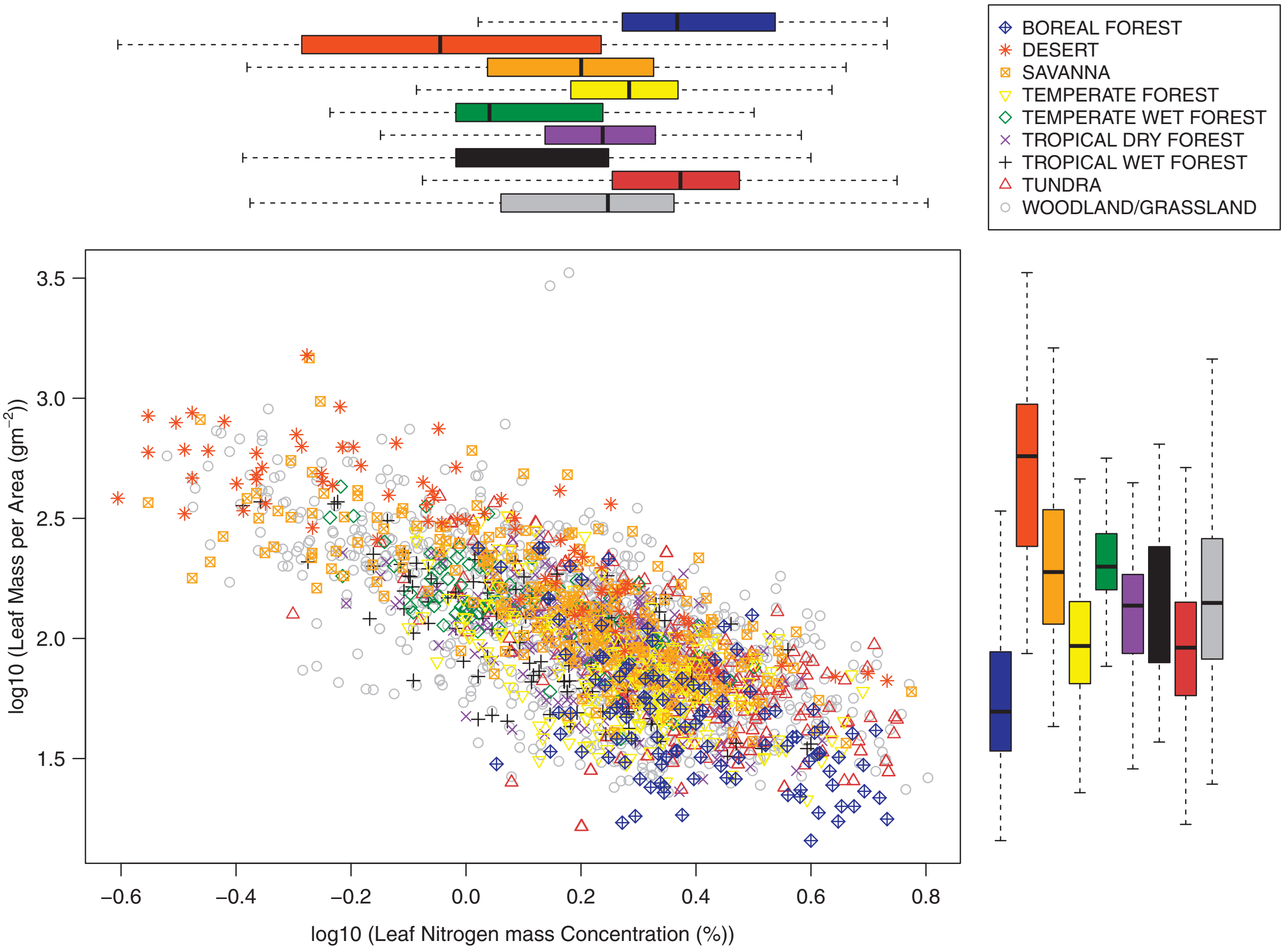

Figure 1 Two central traits in vegetation models; leaf nitrogen concentration and leaf mass per area (LMA) of individual species. Data compiled from Pâques (1994), Eguchi *et al.* (2004), Wright *et al.* (2004), Withington *et al.* (2006), Cornwell *et al.* (2008) and Ordoñez *et al.* (2009). The relationship between LMA and leaf nitrogen follows the expected trade-off (Wright *et al.*, 2004). The biome classification of Whittaker (1975) was chosen here to classify plant functional types (PFTs) to be independent of classifications used in particular current vegetation models. Many of such PFT classifications, as for example applied in the Lund–Potsdam–Jena (LPJ) dynamic global vegetation model (Sitch *et al.*, 2003), show strong resemblances to this biome classification and yield similar patterns (results not shown), i.e. heavily spread PFTs across the figure instead of clustering of PFTs. Note that the order of the box-and-whisker plots on the x-axis (top to bottom) and the y-axis (left to right) matches the order of the key.

Despite their importance, effects of feedbacks between ecosystems and atmosphere are amongst the biggest uncertainties in climate change predictions (e.g. Friedlingstein *et al.*, 2006). The Millennium Ecosystem Assessment (Carpenter *et al.*, 2006) indicates that we lack a robust theoretical basis for linking vegetation to ecosystem dynamics and, in turn, to ecosystem services like the regulation of energy, water and CO_2 fluxes (hereafter called ‘ecosystem functions’). Recent advances in community ecology have provided important insights. The aim of our paper is to explore whether these advances may provide a robust basis for a next generation of vegetation models.

One reason for the large uncertainties is that all current vegetation models predicting ecosystem functions have been built around the concept of plant functional types (PFTs). PFTs are a priori defined discrete classes that group species with presumed similar roles in ecosystem functions (Lavorel *et al.*, 1997). The use of PFTs confines the complexity of the analysis, although the concept recognizes that all species are ecologically different (Chapin *et al.*, 1996). A condition of using PFTs is that they are functionally different. Unfortunately, plant species attributed to different PFTs as defined in vegetation models do in reality not differ much in, for example, the temperature acclimation potential of photosynthesis (Cunningham & Read, 2002) or in specific leaf area and leaf nitrogen (determining photosynthesis and affecting decomposition of plant litter, two important CO_2 exchanges between vegetation and atmosphere) (Fig. 1). In fact, the functional differences between PFTs seem to be too small to predict the distribution of these PFTs in the absence of bioclimatic controls (Brovkin *et al.*, 1997). Due to the close resemblance of PFTs to biome classifications, bioclimatic controls prescribed for the present climate, like minimum and maximum temperatures, strongly determine the global distribution of PFTs in most vegetation models. This was not a problem when vegetation models were used to predict vegetation distribution

(Prentice *et al*., 1992), but is a problem when calculating ecosystem functions. In addition, the use of any PFT classification with fixed attributes has several drawbacks.

1. There is a clear mismatch between allocating vegetation to discrete entities (PFTs) to calculate continuously varying fluxes through vegetation (Reich *et al*., 2007). The majority of fluxes are continuous by definition, while any classification limits the number of possible outcomes, particularly because each PFT is assumed to have constant attribute values across the globe. This is a particular problem because the functional differences among PFTs as defined in current vegetation models are marginal (with a lot of functional variation within a PFT).

2. Constant PFT attributes do not allow for adaptation to the environment. Within and between PFTs, vegetation attributes (and consequently ecosystem functions) differ strongly depending upon climate (Moorcroft, 2006), soil fertility (Ordoñez *et al*., 2009) and hydrology (e.g. Wright *et al*., 2005). Accounting for adaptation is also essential when quantifying the mechanisms involved in carbon–water–nutrient feedbacks between terrestrial ecosystems and the atmosphere. In vegetation models with constant PFT attributes, feedbacks can only be detected through shifts in abundance between PFTs. Recent advances to include carbon-nutrient feedbacks in vegetation models (e.g. Gerber *et al*., 2010; Zaehle & Friend, 2010) have shown that PFT approaches with fixed attributes have reached their limits and that (some) vegetation attributes need to be allowed to vary in order to model feedbacks.

3. Current models assume equilibrium between climate and vegetation distribution, and moreover assume that PFT attributes are invariable upon climate change. These steady-state assumptions are questionable given that: (1) future environmental drivers are expected to lead to different realized niches (e.g. Guisan & Thuiller, 2005); (2) future climate is expected to have no analogue in present-day climates, probably leading to no-analogue PFTs for significant parts of the globe (e.g. Williams *et al*., 2007): such no-analogue PFTs in a future climate (Thuiller *et al*., 2005) potentially have a different resource use and interactions with the atmosphere; and (3) dramatic differences in dispersal rates among species, even within PFTs (unaccounted for in current models), will further amplify the expected changes in PFT composition.

Because of these drawbacks, a new approach is urgently needed. Here, we will discuss the potential merits of a traits-based vegetation model to predict ecosystem functions, like ecosystem–atmosphere fluxes of energy, water and CO_2, directly from plant traits instead of through PFTs. Its potential to complement or replace current vegetation models is discussed by evaluating the ability of and challenges facing traits-based vegetation models in solving some drawbacks of current vegetation models. A final section is devoted to the feasibility of translating traits to global vegetation maps, as maps provide a powerful communication tool to PFT-based vegetation models. A traits-based vegetation model fits the important paradigm shift in ecology (Webb *et al*., 2010) that occurred since the first vegetation models were developed from describing species or vegetation types to vegetation functions. Fukami *et al*. (2005) provided the first experimental proof that the environment governs trait composition, but not necessarily species composition. So far, traits-based modelling has, however, hardly been applied to vegetation models.

A TRAITS-BASED APPROACH TO DESCRIBE GLOBAL VEGETATION FUNCTIONING

Current vegetation models predict the occurrence of PFTs as a function of environmental conditions; climate, soil and hydrology, leading to a discrete palette of predicted vegetation patterns (or semi-continuous if the vegetation model allows the co-occurrence of several PFTs within a grid). Continuous changes in vegetation attributes are, however, central to ecosystems, e.g. in succession (Garnier *et al*., 2004) and in response to environmental conditions like soil fertility (e.g. Harley *et al*., 1992). Functional traits provide such a continuous, process-based link between ecosystem functions and soils and climate (e.g. Suding *et al*., 2008). In a traits-based vegetation model, flux calculations – previously based on vegetation identities – are replaced by direct calculations based on functional traits (compare Fig. 2a,b). Current vegetation models implicitly assume that the difference in trait values between PFTs is larger than the 95% confidence interval of values within PFTs. Instead, a traits-based vegetation model allows direct calculation of the continuous global differences in selected plant traits and the effects on ecosystem–atmosphere fluxes. Therefore, within a traits-based vegetation model, there is no need to predict whether differences in vegetation attributes occur due to within-species plasticity, species turnover within a PFT or by PFT replacements. Another conceptual attraction lies in the fact that selecting for plant attributes, instead of complete PFTs, is more closely related to the evolutionary selection mechanisms active in ecosystems in which traits are selected based on adaptations to environmental and biotic pressures. Thanks to these improvements in ecological realism, it is worthwhile to pursue a fully traits-based model.

In a traits-based vegetation model, appropriate traits need to be selected to predict vegetation–environment interactions. Plant strategy schemes (e.g. Grime, 2001; Westoby *et al*., 2002) summarize the important traits and position them along a number of orthogonal axes. Available information (Westoby *et al*., 2002; Díaz *et al*., 2004; Laughlin *et al*., 2010; Fig. 3) indicates partial independent functions of life-history traits, like seed mass, and leaf traits, like the so-called leaf economics traits (Wright *et al*., 2004).

Current vegetation models already use several of these traits, but as PFT-specific constants. In particular, leaf economics traits – determining photosynthetic processes – are well presented in current vegetation models as PFT-specific parameters. Unfortunately, few vegetation models use life-history traits, wood density or maximum height despite their importance in differentiating among plant strategies (Grime, 2001; Westoby *et al*., 2002; Chave *et al*., 2009; Fig. 3). This is a missed opportunity, not only to functionally distinguish among PFTs, but also because wood density and height affect transpiration, growth potentials and

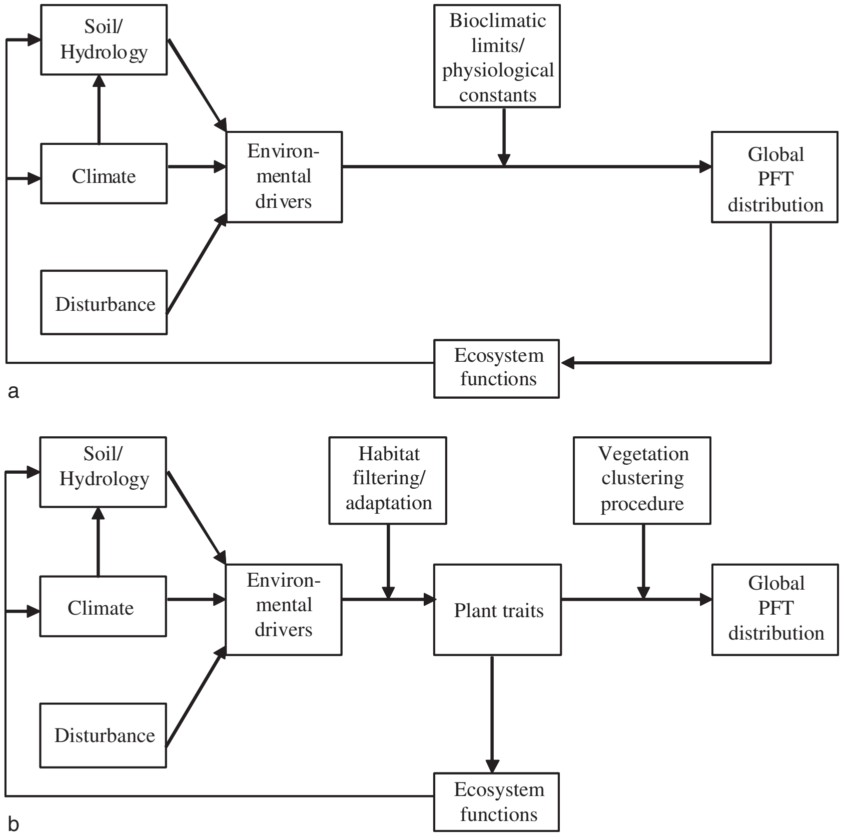

Figure 2 Conceptual representation of global vegetation models, comparing the structure of (a) a current vegetation model and (b) a traits-based vegetation model, highlighting their similarities and differences in terms of pathways involved in predicting ecosystem functions.

light partitioning (Falster & Westoby, 2003; Maherali *et al.*, 2004), while seed mass determines the light-use efficiency of juveniles, survival and plant life span (Moles & Westoby, 2004) with subsequent effects on fluxes of energy, water and CO_2.

Because many traits covary predictably, only a limited number of traits may be needed to fully predict the range of ecosystem functions. Thanks to extensive recent global database compilations (e.g. Díaz *et al.*, 2004; Wright *et al.*, 2004), quantitative descriptions of plant trait covariation are increasingly available. Examples are short leaf life span covarying with high specific leaf area and high maximum leaf respiration rates with high maximum photosynthesis rates (Wright *et al.*, 2004). Trait covariation is recurrent and globally applicable (Díaz *et al.*, 2004) and due to fundamental physiological (Shipley *et al.*, 2006), allometric (Enquist *et al.*, 2007) and evolutionary (Falster & Westoby, 2003; Cavender-Bares *et al.*, 2009) trade-offs. They are therefore expected to be relatively stable in a changing climate. These trade-offs play a pivotal role in determining ecosystem–atmosphere fluxes.

The behaviour of current vegetation models heavily depends on bioclimatic controls. These bioclimatic controls are partly correlative in nature and may be caused by ecophysiological traits related to climate responses, such as frost tolerance (Körner, 1999) or optimal temperatures for photosynthesis (Medlyn *et al.*, 2002). However, limitations imposed by soil, hydrology, dispersal and historic effects and correlated to current climate distribution may also have caused these apparent bioclimatic controls. In that case, bioclimatic controls may change unpredictably in a changing climate. Unfortunately, there has been surprisingly little experimental work done to guide the choice of bioclimatic variables that really limit vegetation (Thuiller *et al.*, 2005). In contrast to the traits discussed previously, the role of the above-mentioned ecophysiological traits in plant strategies is poorly understood. Neither the importance of these traits nor their role in modulating ecosystem fluxes is currently known. A recent publication (Hallik *et al.*, 2009), however, suggests that drought tolerance, for example, covaries with leaf economics traits. This may imply that predicting leaf economics traits values in a traits-based vegetation model may be sufficient to predict fluxes.

TRAITS-BASED APPROACH TO DEAL WITH CURRENT DRAWBACKS

Continuous responses of vegetation to the environment

Decoupling vegetation functions from vegetation identity shifts the challenge of vegetation models to how to predict plant trait values. This requires a coherent and integrative framework (Webb *et al.*, 2010). While implicit in current modelling approaches, a traits-based vegetation modelling approach explicitly assumes that the environment filters the occurrence of traits (Keddy, 1992). The most important filters are known and include light availability, water availability, nutrient availability

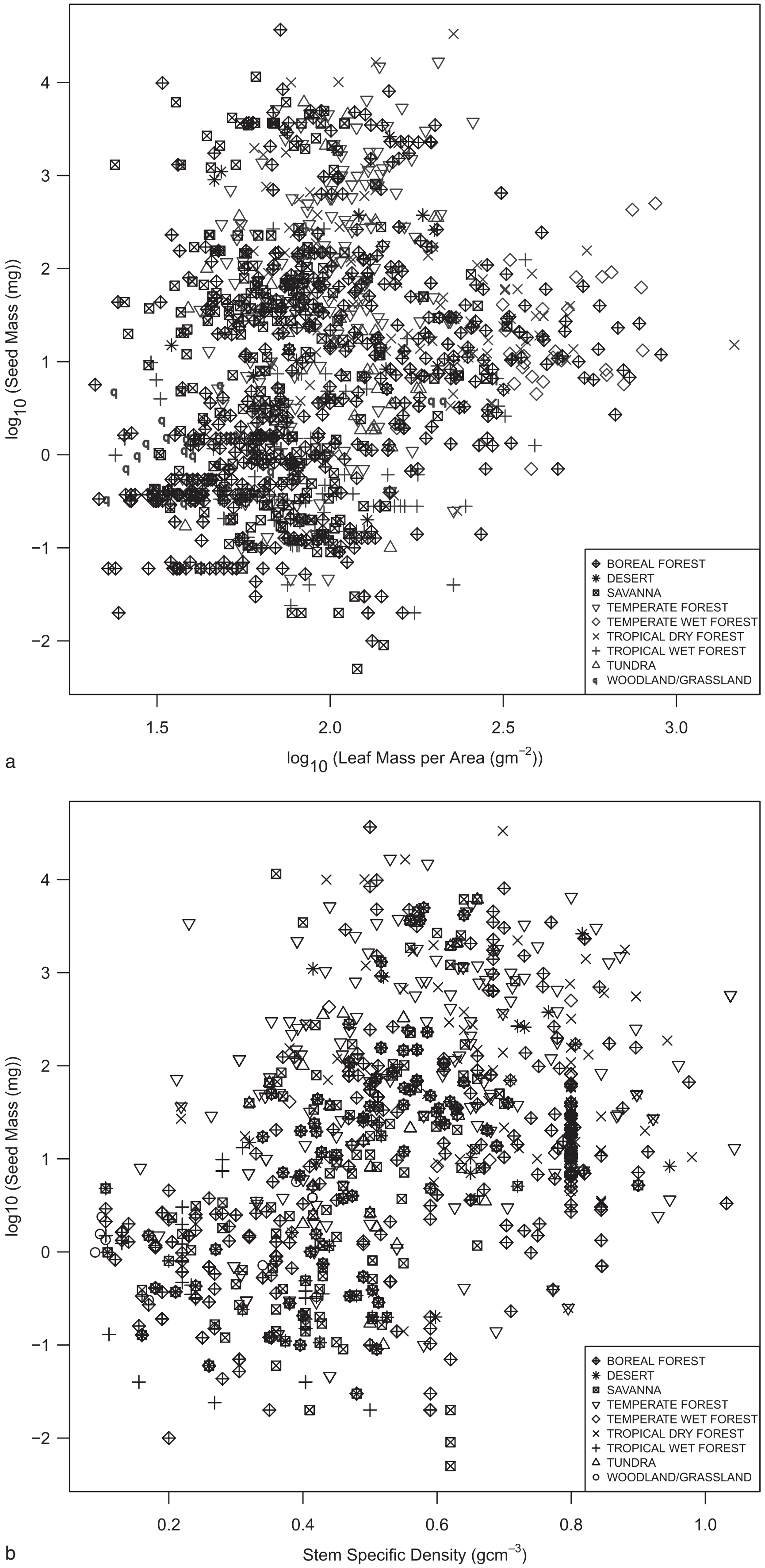

Figure 3 Configuration of the three-dimensional trait space comprising traits from individual species common to most plant strategy schemes: seed mass (primarily related to disturbance), stem specific density (SSD; primarily related to water and light availability) and leaf mass per area (LMA; primarily related to water and nutrient availability). To facilitate visual interpretation, trait space has been split into two panels: (a) LMA versus seed mass and (b) SSD versus seed mass. Correlations among these traits are low, i.e. they show orthogonality, both within and between plant functional types (classified according to Whittaker, 1975) and much lower than for the leaf economics traits of Fig. 1. Together, the three traits fill major portions of the three-dimensional trait space.

and disturbance regime (Grime, 2001; Westoby *et al.*, 2002). The impact of environmental conditions on traits can be predicted through these drivers. Thanks to the increasing availability of large global trait databases, these predictions have become increasingly quantitative and accurate (which is urgently needed; McGill *et al.*, 2006). Traits have been related to climate variables, e.g. leaf economics traits in relation to temperature and precipitation (Wright *et al.*, 2005; Swenson & Weiser, 2010), leaf shape to temperature (Royer *et al.*, 2005), plant height to precipitation (Moles *et al.*, 2009; Swenson & Weiser, 2010) and hydraulic conductivity in relation to soil moisture (Cavender-Bares & Holbrook, 2001), precipitation and temperature (Maherali *et al.*, 2004). Also the effects of temperature (Medlyn *et al.*, 2002) and (elevated) atmospheric CO_2 concentrations (Medlyn *et al.*, 1999) on photosynthesis parameters, like the Farquhar parameters (Farquhar *et al.*, 1980), have been quantified. Likewise, disturbance, as another important driver of vegetation dynamics, has been linked to life-history traits and plant height (Falster & Westoby, 2005). Recently, Ordoñez *et al.* (2009) showed that combinations of climate and soil fertility predicted global patterns in leaf economics traits better than climate variables alone. The number of ecological drivers and their relation to one another should thus be carefully considered in analysing and predicting trait values.

For a traits-based model, environmental filtering has to be strong, i.e. the predictive power of the relationships should be high. Unfortunately, many of the relationships between traits and environmental drivers show high unexplained trait variability (Fig. 4). This trait variability is not only noise or uncertainty in the estimates of trait–environment relationships: many ecosystem functions critically depend on trait variation (Westoby *et al.*, 2002; Ackerly & Cornwell, 2007) and trait variability is a key component of ecosystem resilience (Díaz *et al.*, 2006). Part of this variability may be caused by direct phylogenetic effects upon trait values, independent of habitat filtering. Another, probably larger, part of trait variability is due to competitive exclusion that tends to dominate local trait patterns (the scale at which most trait–environment databases have been compiled). Competition and other biotic interactions tend to lead to trait divergence (Cavender-Bares *et al.*, 2009). On a larger scale, however, environmental filtering and thus trait selection and trait convergence is expected to be more important (Swenson *et al.*, 2007; Kraft *et al.*, 2008). Therefore, the use of site or regional trait averages allows the quantification of environmental filtering and indeed leads to lower residual variance (Fig. 4).

Trait variability, unexplained by environmental conditions, may also be reduced by analysing multiple traits simultaneously (Webb *et al.*, 2010). Additional traits, known to have a physiological trade-off with the trait of interest (as discussed above), may be included as covariates in trait–environment relationships to reduce the residual variability in predicted trait values. For instance, variation in canopy height explained a large fraction of variation in specific leaf area of chaparral vegetation (Ackerly & Cornwell, 2007). Alternatively, integrative traits that already include trade-offs may be used, as these are expected to show less variability. For example, nutrient use efficiency integrates several correlated traits, like leaf life span and leaf nitrogen (Wright *et al.*, 2004), and plays an important role in ecosystem functions related to soil fertility (Aerts & Chapin, 2000). Likewise, water use efficiency integrates photosynthetic adaptations (like C_3 versus C_4 photosynthetic pathways; Ehleringer & Monson, 1993) related to drought and transpiration demands. Finally, traits related to ecosystem functions may be simultaneously predicted by determining trait combinations that maximize plant survival or plant productivity through cost–benefit analyses, e.g. based on plant energy/carbon economics (*sensu* Bloom *et al.*, 1985).

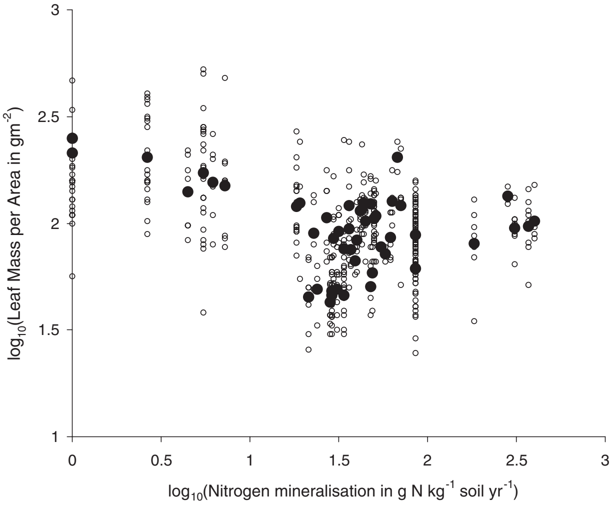

Figure 4 Relationship between nitrogen availability and leaf mass per area (LMA) per individual species (small open circles) and per site (larger black circles) based on a global database (Ordoñez *et al.*, 2009). The variability orthogonal to the nitrogen mineralization–LMA relation is significantly reduced when focusing on site averages: A mixed model with site as a random factor has an *F*-value of 5.85 ($P = 0.020$) for the slope of nitrogen mineralization, while a regression model on site averages has an *F*-value of 8.31 ($P = 0.006$) for the slope of nitrogen mineralization.

To improve existing trait predictions as a function of the environment, it will be essential to better quantify the local impacts of environmental drivers of vegetation – like nutrient availability and water availability – and of global disturbance patterns. Temporal and spatial (depth) scales essential to describe these drivers need to be defined appropriately. Also impacts of past variations in environmental conditions need to be better accounted for. Bartholomeus *et al.* (2008) showed that time series of groundwater levels as long as 30 years may be needed to properly predict the responses of vegetation to hydrology. Incorporation of these issues will improve trait predictions, although in the near future no set of relations between functional traits and its environmental drivers is likely to capture all sources of trait variation. Still, such imperfect relationships, coupled functionally within a vegetation model (Fig. 2), will allow a first test of the real effects of trait variation (implicitly assumed to be negligible in current vegetation models) on ecosystem functions at a global scale.

Quantifying adaptation and feedbacks as they affect ecosystem functions

Coupling traits directly to environmental conditions also takes care of another fundamental challenge in current vegetation models: accounting for adaptation and feedback mechanisms. Plant adaptations to the environment directly affect ecosystem functions, but also indirectly as trait adaptations modify the feedbacks between vegetation, soil and atmosphere. For instance, at low nutrient availability, species have low leaf nitrogen concentrations and low specific leaf area (Ordoñez *et al.*, 2009), higher concentrations of secondary compounds that decrease leaf palatability (Coley *et al.*, 1985) and a higher nutrient resorption (Kobe *et al.*, 2005), reducing leaf litter decomposability and nitrogen mineralization in nutrient-poor environments (Parton *et al.*, 2007; Cornwell *et al.*, 2008). This reinforces the prevailing low plant biomass (e.g. Aerts & Chapin, 2000) and causes lower fluxes of water and CO_2. Likewise, a traits-based approach may shed light on the role of water–nitrogen–carbon feedbacks and plant adaptations in the much debated CO_2-fertilization effect (Hungate *et al.*, 2003). Plant adaptations to elevated CO_2 are not only reflected in a (temporarily) enhanced photosynthetic capacity and reduced water consumption. Elevated CO_2 also causes a changed biomass allometry, decreased leaf nitrogen and decreased specific leaf area (Hyvönen *et al.*, 2007). In turn, these trait adaptations feed back to the cycling of soil nutrients and moisture. Trait changes in combination with (modified) nutrient and drought limitations may have precluded enhanced tree growth upon increasing atmospheric CO_2 (Peñuelas *et al.*, 2011). This contrasts to a continued rise in biomass carbon sequestration predicted by all current vegetation models. A traits-based approach will allow simultaneous quantification of the relative importance of these constraints on productivity and ecosystem functions across a range of ecosystems.

As long as PFT parameters are assumed to be constant, feedbacks cannot be modelled and have to be approached indirectly, e.g. through the displacement of complete PFTs, instead. Indeed, all recent vegetation models that included the N cycle (e.g. Gerber *et al.*, 2010; Zaehle & Friend, 2010) allowed for variation in one or more PFT parameters that had hitherto been fixed. This has led to hybrid models that share some characteristics of traits-based models and some of PFT-based vegetation models.

Even the most elaborate model of vegetation N cycling to date (Zaehle & Friend, 2010) still has several traits linked to and affected by N cycling – like specific leaf area, nutrient resorption and leaf life span – fixed. Moreover, carbon–water–vegetation interactions and feedbacks to the water cycle are insufficiently characterized, because either they are not accounted for in current vegetation models or because the (root) traits involved are fixed. For instance, rooting depth and cavitation resistance respond to drought, but also determine the extent to which transpiration may continue during drought (Schenk & Jackson, 2002). Root architecture, mostly unaccounted for, determines the soil infiltration capacity (Rietkerk & van de Koppel, 1997). In addition, high vegetation productivity also leads – via higher soil organic matter content – to an increased soil water holding capacity.

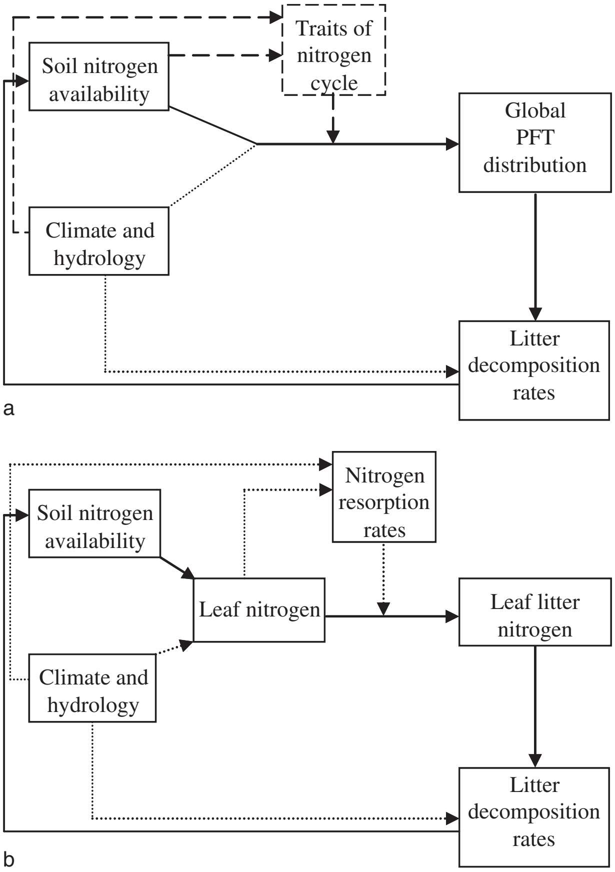

Figure 5 Conceptual representation for modelling feedbacks – in this example a feedback between plants and soil fertility – in global vegetation models based on the structure of Fig. 2, comparing the structure and concepts of (a) a current vegetation model and (b) a traits-based vegetation model, highlighting their similarities and differences. Lines show the flow of nitrogen, whereas dashed lines indicate modifiers of flows. Large dashes show the recent additions in current vegetation models (e.g. Zaehle & Friend, 2010) to calculate feedbacks in the nitrogen cycle.

In comparison to the hybrid models developed recently, a traits-based vegetation model would allow all traits to fully vary in response to the environment. Through the effects of traits (at a given plant biomass) on the environment, such an approach allows us to fully capture the feedback mechanisms (compare Fig. 5a,b). Plant biomass can be calculated by linking traits to photosynthesis (e.g. Kattge *et al.*, 2009) and respiration equations as incorporated in current vegetation models. Together, this would allow for an integrative treatment of vegetation–environment interactions and potentially an integrative treatment of carbon-nutrient cycling in ecosystems.

Non-constant vegetation attributes in a changing climate

A third drawback of current vegetation models, identified in the Introduction, is that PFT attributes, and thus indirectly species composition within PFTs, are assumed to be invariable upon climate change. This problem does not exist in a traits-based vegetation model, as trait composition and not species composition is predicted. In a traits-based vegetation model, it is irrelevant to know which species contributed to a calculated trait value. Moreover, in a traits-based vegetation model, trait values change as a function of environmental dynamics as implied by trait–environment relationships, implicitly accounting for physiological adaptation (Moorcroft, 2006) and species shifts (Thuiller *et al*., 2005).

In analogy to the assumption in many current vegetation models that species dispersal is not limiting, a traits-based vegetation model may assume that climate or geography does not limit the available trait space, in order to apply trait–environment relationships directly in a changing climate. The assumption of no limitation to the dispersal of trait values is much less stringent, however, as dispersal of traits is not only facilitated by species dispersal but also by genotypic adaptations and phenotypic plasticity within species. Moreover, species from different PFTs have similar trait values (Fig. 1), reducing adverse effects of phylogenetic constraints on the dispersal of traits even if phylogenetic constraints occur independently of habitat filtering (Losos, 2008). Even so, not all traits may respond promptly. Traits related to biomass allometry or particular stem features, like stem specific density, may respond more slowly. Unfortunately the response times of such traits are currently unknown. As a first approximation, it may be assumed that the relative change of such traits is maximally equal to the relative turnover rate of plant biomass, as assumed in several current vegetation models.

If the mechanisms for trait value selection are well understood and quantitatively correctly incorporated, a traits-based approach may in principle also predict trait combinations that do not exist in present-day climates (which is analogous to new PFTs). For a proper prediction, it may be particularly important to better understand and quantify the impacts of extreme climatic events on trait value selection. In principle, a traits-based vegetation model may thus predict the no-analogue ecosystem functions that may arise in the near future (Thuiller *et al*., 2005). Predictions of no-analogue ecosystems are less likely, if not impossible, in a PFT-based approach with fixed classes and in which vegetation composition has fixed attributes (and implicitly fixed composition).

FROM TRAITS TO GLOBAL VEGETATION MAPS

In a traits-based vegetation model, there is no need to calculate global vegetation distributions. Instead, maps of trait values (see Swenson & Weiser, 2010, for one of the first published examples) or of ecosystem functions important to earth system models (including their changes) are produced directly and can be validated for current climatic conditions by comparison with observations. Such trait maps are, however, less attractive from a communication and policy point of view than vegetation maps produced by current vegetation models, as they are harder to interpret.

For such communication aims, sets of trait values may be translated into PFTs to produce global vegetation maps (Fig. 2). Given that trait combinations are functionally coupled to vegetation strategies (as discussed above), an appropriate choice of traits (in contrast to those of current vegetation models) should allow discrimination among PFTs. Differences among PFTs may even be more pronounced in extreme trait values (another set of attributes that is not accounted for in current vegetation models) given that, for example, PFTs made up of fast-growing plant species show more extreme trait values than those for slow-growing species (Grime & Mackey, 2002). An *n*-dimensional space of trait values can be statistically distributed among different PFTs, e.g. by multivariate analysis or by Gaussian mixture density fitting (Witte *et al*., 2007). In the latter case – applied to PFTs and validated successfully in the Netherlands using three traits (Witte *et al*., 2007) – probability density functions of individual PFTs are described in an *n*-dimensional trait space (Fig. 6). Given these densities, a Bayesian occurrence probability of PFTs is calculated for each position in trait space. Each grid cell of the traits-based vegetation model concurs with a particular predicted position in trait space, which is subsequently translated into probabilities of the respective PFTs.

Interestingly, Fig. 6 seems to indicate that functional distinction among PFTs is possible for a subset of PFTs (from Fig. 3) when using traits like seed mass and stem specific density in addition to those applied in current vegetation models. However, the PFT classification and trait selection applied in current vegetation models may not allow us to make such functional discriminations (based on the large within-PFT functional variation shown in Fig. 1). Instead, in this situation, the inclusion of bioclimatic controls seems to be essential to distinguish among PFTs, which is indeed done in current vegetation models. Given that the link between bioclimatic controls and ecosystems functions is not clear-cut (as discussed above), this provides another incentive for developing a traits-based model to predict ecosystems functions.

Even if a traits-based model is used to predict PFT distributions, this approach has the advantage of a strict separation between calculations of trait values (and ecosystem functions) and PFT occurrences: vegetation classifications may be adapted easily, depending on needs and preferences, without having to change a complete model structure. This flexibility could be ideal for certain policy analyses. Moreover, vegetation attributes may be calculated without having to bother with peculiarities of particular vegetation classifications. For instance, current PFT classifications may not be valid in a changing climate (as discussed above), which may lead to misinterpretations when applying those classifications. These misinterpretations may be solved in a traits-based approach by

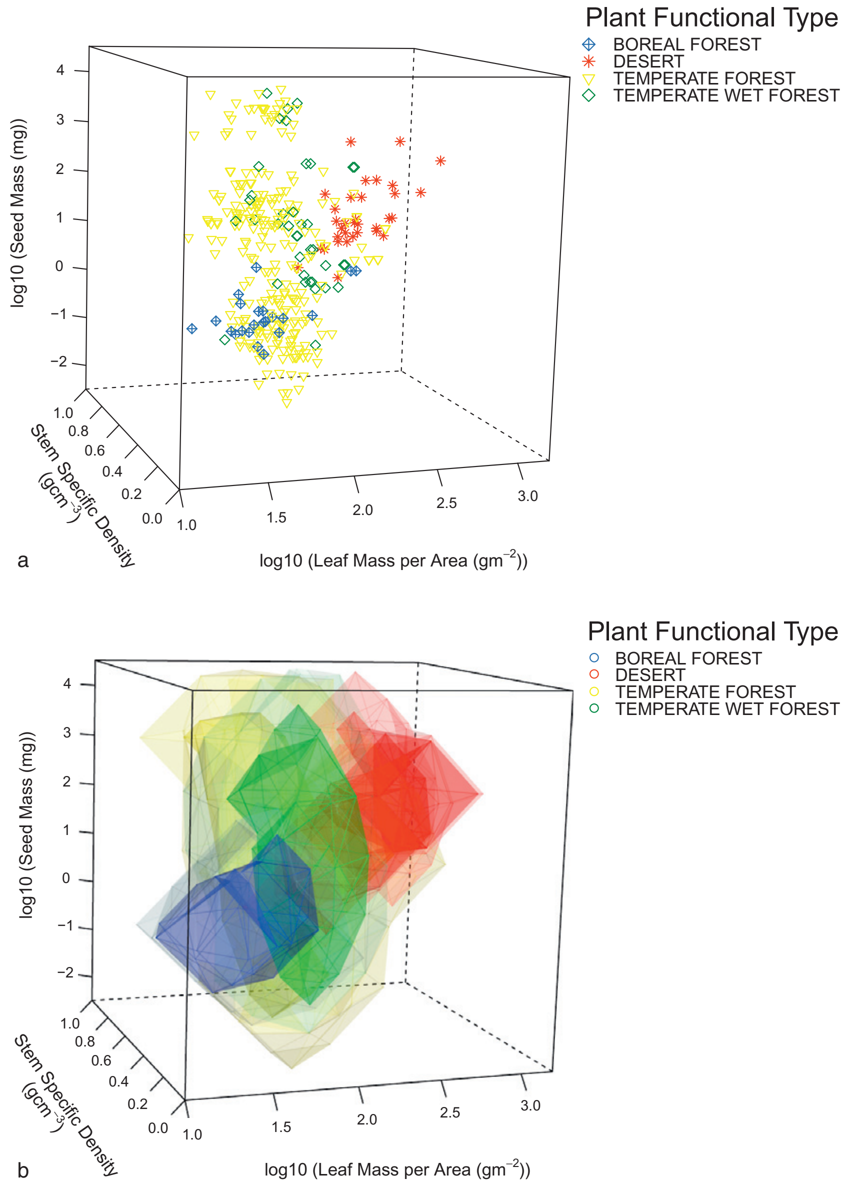

Figure 6 Measured trait values (a) for four biomes, selected from Fig. 3 based on their separation in trait space in contrast to the other biomes, and their calculated smoothed densities (b) to illustrate the Gaussian mixture density procedure for predicting plant functional types from trait combinations.

additionally predicting the occurrence of palaeo-PFTs (Jackson & Williams, 2004) and of expected future PFTs, as based on expert judgement.

CONCLUSIONS

We have shown that a traits-based vegetation model seems feasible. A traits-based vegetation model should eliminate some of the disadvantages of current models as it provides the desired robust theoretical basis to predict ecosystem functions (Moorcroft, 2006), like CO_2 and H_2O fluxes, and links vegetation models to recent conceptual developments in ecology. The development of a traits-based vegetation model will not be easy. Two particular challenges are: (1) developing trait–environment relationships with low residual trait variability, and (2) integrating trait modelling, including trait trade-offs, in a predictive framework that does justice to plant strategies and vegetation processes. Collaboration between earth science modellers and ecologists may fruitfully deal with these challenges to provide better predictions of ecosystem functions in a changing climate.

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BIOSKETCH

Peter van Bodegom is an ecologist, working at the interface between community ecology, macroecology and earth system modelling. With his group, he aims to quantify globally applicable functional relationships between vegetation, soil micro-organisms and their environment by targeted experiments, meta-analyses and process-based modelling. He applies the ecological relations thus derived to climate-proof modelling of soil–vegetation dynamics in collaboration with earth system modellers.

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