

Variation in trait trade-offs allows differentiation among predefined plant functional types: implications for predictive ecology

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Summary

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Received: 22 April 2015

Accepted: 28 July 2015

New Phytologist (2016) **209**: 563–575

doi: 10.1111/nph.13623

Key words: kernel density estimation, plant functional types, plant strategies, plant traits, trade-offs, trait variation.

- Plant functional types (PFTs) aggregate the variety of plant species into a small number of functionally different classes. We examined to what extent plant traits, which reflect species' functional adaptations, can capture functional differences between predefined PFTs and which traits optimally describe these differences.
- We applied Gaussian kernel density estimation to determine probability density functions for individual PFTs in an n -dimensional trait space and compared predicted PFTs with observed PFTs. All possible combinations of 1–6 traits from a database with 18 different traits (total of 18 287 species) were tested.
- A variety of trait sets had approximately similar performance, and 4–5 traits were sufficient to classify up to 85% of the species into PFTs correctly, whereas this was 80% for a bioclimatically defined tree PFT classification. Well-performing trait sets included combinations of correlated traits that are considered functionally redundant within a single plant strategy.
- This analysis quantitatively demonstrates how structural differences between PFTs are reflected in functional differences described by particular traits. Differentiation between PFTs is possible despite large overlap in plant strategies and traits, showing that PFTs are differently positioned in multidimensional trait space. This study therefore provides the foundation for important applications for predictive ecology.

Introduction

Plant functional type (PFT) classifications are used to aggregate the enormous number of plant species into a relatively small number of functionally different classes. As the term implies, a PFT classification should be functional, based on ecological concepts, and differentiate between groups of plants with similar responses to changes in their environment and with comparable impacts on this environment (Diaz & Cabido, 1997; Lavorel & Garnier, 2002). Classifications of plants have a long history (for an overview of the development of the PFT concept, see Ustin & Gamon, 2010; Wullschlegel *et al.*, 2014) and are broadly applied in ecology as well by the modeling community. Especially when making predictions at regional to global scales, there is a need to aggregate species into a simplified, workable number of functional groups, thereby reducing the need for knowledge on the underlying species.

Although there are different conceptualizations of PFTs, for example based on structural aspects (growth forms), environmental constraints or plant traits (Box, 1996; Lavorel *et al.*, 1997, 2007; Woodward & Kelly, 1997; Harrison *et al.*, 2010), (global) applications of PFTs are often classified 'a priori' based on

growth form. The idea behind such classification is that growth forms reflect structural adaptations to different environmental conditions, that is 'form follows function' (Box, 1996). In addition to basic growth forms, depending on the application, characteristics related to, for example leaf phenology (deciduous vs evergreen), leaf structure (broadleaved vs needleleaved) or photosynthetic pathway add subdivisions within growth forms. Growth forms and their derived PFTs are a basic first division reflecting and explaining differences in plant functioning in relation to environmental conditions (Lavorel *et al.*, 1997; Reich *et al.*, 2007; Kattge *et al.*, 2011). Such a classification is commonly used in applications such as global vegetation mapping and investigations on the impacts of climate change, land use change or management strategies on vegetation cover.

A way to quantitatively test how functional differences between PFTs are related to (structural) plant properties is to investigate their positioning in multidimensional domains of plant functional traits. Plant traits are a suitable tool for describing different functional aspects of plants and their relations to environmental conditions, because the different growth and survival strategies of plants in response to (a)biotic determinants such as water, light and nutrient availability, competition and

disturbances are reflected by a plant's set of trait values (Westoby *et al.*, 2002; Reich *et al.*, 2003; Reich, 2014). As a consequence of the different strategies of plants, trait values vary between species (both within and between habitats). By relating this variation in traits to a number of largely independent strategy axes (or 'axes of trait variation'; Westoby, 1998), differences in plant strategies between species can be explained. For example, the leaf–height–seed strategy scheme (Westoby, 1998) distinguishes three functionally different strategy axes, which relate variation in leaf traits, like specific leaf area (SLA) and leaf life span (LLS) (so called 'leaf economics' traits), to differences in growth and resource acquisition (Reich *et al.*, 1999; Wright *et al.*, 2004; Reich, 2014), variation in seed mass (SM) and output to variation in reproductive strategies (Moles & Westoby, 2004; Moles *et al.*, 2004) and variation in plant height to differences in strategies concerning light competition and disturbances (Westoby, 1998; Westoby *et al.*, 2002).

Different methods that use traits to distinguish among vegetation types or to describe functional classifications have been developed (Diaz & Cabido, 1997; Pillar & Sosinski, 2003). Combinations of traits with different functional roles may be particularly useful for differentiating between different plant strategies and consequently allow classification of functionally different groups of plant species (Diaz *et al.*, 2004; Boulangéat *et al.*, 2012). However, the extent to which predefined growth form-based PFTs can be described from a bottom-up, functional traits-based approach has not been quantified yet. Global scale analyses can clarify which traits are most important in explaining functional differences between growth forms and, as such, reveal which functional aspects of plants underlie differences in growth forms. In addition, knowing both the extent to which plant traits can quantitatively discriminate between PFTs as well as knowing the most important traits is highly relevant, as it would allow global vegetation mapping based on trait maps. Such global trait maps can be constructed relatively easily based on the relationships between traits and climate (Van Bodegom *et al.*, 2014). Even though there is large overlap in traits between growth forms or PFTs (Reich *et al.*, 2003, 2007; Wright *et al.*, 2005; Kattge *et al.*, 2011; Van Bodegom *et al.*, 2012; Verheijen *et al.*, 2013), suggesting substantial overlap between functional strategies of PFTs, combinations of (functional different) traits might allow discrimination between PFTs. With this information, changes in vegetation distribution upon climate change can be predicted based on modifications in plant trait values.

We investigated to what extent plant traits can capture functional differences between growth forms and their derived PFTs by analyzing how well these PFTs can be differentiated from each other based on plant traits, and which (sets of) traits are needed to describe these functional differences between PFTs. We did not define *a priori* the most important traits, but tested a whole range of traits from different plant strategy dimensions, including various 'core' traits, related to dispersal, establishment and persistence of plants (Weiher *et al.*, 1999; Cornelissen *et al.*, 2003b). We asked whether combinations of traits that reflect different functional aspects within plants (e.g. competition for water, light, drought tolerance) will capture functional differences between

PFTs best and consequently will have the highest potential to differentiate among PFTs.

Materials and Methods

Data collection and selection

We collected plant trait data related to different functional roles in plants. The main source was the TRY database (Kattge *et al.*, 2011) (accession date 16 November 2010), which included data from both unpublished studies (H. Kurokawa, unpublished; W. J. Bond, unpublished; F. S. Chapin III, unpublished; A. Siefert, unpublished; E. E. Sosinski, unpublished; E. Weiher, unpublished) and published studies (Leishman & Westoby, 1992; Shipley, 1995; Cornelissen, 1996; Cornelissen *et al.*, 1996, 1997; Bahn *et al.*, 1999; Medlyn & Jarvis, 1999; Medlyn *et al.*, 1999; Meziane & Shipley, 1999; Niinemets, 1999; Pyankov *et al.*, 1999; Wohlfahrt *et al.*, 1999; Fonseca *et al.*, 2000; White *et al.*, 2000; Craine *et al.*, 2001; Medlyn *et al.*, 2001; Niinemets, 2001; Klotz *et al.*, 2002; Shipley & Vu, 2002; Cornelissen *et al.*, 2003a; Loveys *et al.*, 2003; Ogaya & Penuelas, 2003; Pillar & Sosinski, 2003; Poschlod *et al.*, 2003; Queded *et al.*, 2003; Cornelissen *et al.*, 2004; Diaz *et al.*, 2004; Moles & Westoby, 2004; Moles *et al.*, 2004; Wright *et al.*, 2004; Craine *et al.*, 2005; Han *et al.*, 2005; Kirkup *et al.*, 2005; Louault *et al.*, 2005; Moles *et al.*, 2005; Soudzilovskaia *et al.*, 2005; Bakker *et al.*, 2006; Cavender-Bares *et al.*, 2006; Cornwell *et al.*, 2006; He *et al.*, 2006; Kazakou *et al.*, 2006; Ogaya & Penuelas, 2006; Preston *et al.*, 2006; Wright *et al.*, 2006; Ackerly & Cornwell, 2007; Blanco *et al.*, 2007; Campbell *et al.*, 2007; Duarte *et al.*, 2007; Muller *et al.*, 2007; Ogaya & Penuelas, 2007; Swaine, 2007; Wright *et al.*, 2007; He *et al.*, 2008; Kleyer *et al.*, 2008; Kurokawa & Nakashizuka, 2008; Ogaya & Penuelas, 2008; Pakeman *et al.*, 2008; Paula & Pausas, 2008; Reich *et al.*, 2008; Sardans *et al.*, 2008a,b; Van Bodegom *et al.*, 2008; Baker *et al.*, 2009; Chave *et al.*, 2009; Craine *et al.*, 2009; Fortunel *et al.*, 2009; Fyllas *et al.*, 2009; Kattge *et al.*, 2009; Laughlin & Moore, 2009; Pakeman *et al.*, 2009; Paula *et al.*, 2009; Poorter *et al.*, 2009; Reich *et al.*, 2009; Wirth & Lichstein, 2009; Zanne *et al.*, 2009; Freschet *et al.*, 2010a,b; Laughlin *et al.*, 2010; Messier *et al.*, 2010; Ordoñez *et al.*, 2010; Wright *et al.*, 2011; Onipchenko *et al.*, 2012; Soudzilovskaia *et al.*, 2013). Additional data was collected from other publicly available and private databases (Hendricks *et al.*, 2000; Pregitzer *et al.*, 2002; Craine & Lee, 2003; Comas & Eissenstat, 2004, 2009; Tjoelker *et al.*, 2005; Kerkhoff *et al.*, 2006; Pittermann *et al.*, 2006; Roumet *et al.*, 2006; Green, 2009; Liu *et al.*, 2010; Zanne *et al.*, 2010; Holdaway *et al.*, 2011; Choat *et al.*, 2012; Douma *et al.*, 2012b; McCormack *et al.*, 2012; Fort *et al.*, 2013; Tobner *et al.*, 2013) or unpublished data (P. M. van Bodegom, unpublished). The traits are listed in Table 1. In light of the debate on area- vs mass-based photosynthesis-related traits (Lloyd *et al.*, 2013; Westoby *et al.*, 2013), both mass- and area-based estimates of leaf traits were investigated for leaf nitrogen content (LNC_{mass} and LNC_{area}), maximum photosynthetic rate ($A_{\text{max, mass}}$ and $A_{\text{max, area}}$) and leaf dark respiration (Rd_{mass} and Rd_{area}). To eliminate a small

Table 1 List of traits used in the different plant functional type (PFT) classification analyses

Trait	Abbreviation	Unit	Classification		
			7-PFT	6-PFT	Tree PFT
Leaf life span	LLS	months		x	x
Specific leaf area	SLA	mm ² mg ⁻¹	x	x	x
Mass based maximum photosynthetic rate	A _{max, mass}	μmol g ⁻¹ s ⁻¹	x	x	x
Area based maximum photosynthetic rate	A _{max, area}	μmol m ⁻² s ⁻¹	x	x	x
Mass based leaf dark respiration	Rd _{mass}	μmol g ⁻¹ s ⁻¹		x	x
Area based leaf dark respiration	Rd _{area}	μmol m ⁻² s ⁻¹		x	x
Mass based leaf nitrogen content	LNC _{mass}	mg g ⁻¹	x	x	x
Area based leaf nitrogen content	LNC _{area}	g m ⁻²	x	x	x
Leaf phosphorus content	LPC _{mass}	mg g ⁻¹	x	x	x
Leaf carbon content	LCC _{mass}	mg g ⁻¹	x	x	x
Leaf area	LA	mm ²	x	x	x
Stomatal conductance	G _s	mol m ⁻² s ⁻¹	x	x	x
Leaf dry matter content	LDMC	g g ⁻¹	x	x	x
Maximum plant height	MPH	m	x	x	x
Seed mass	SM	mg	x	x	x
Stem specific density	SSD	mg m ⁻³		x	x
Vessel area	VA	mm ²			x
Water potential at which 50% loss of conductivity occurs	Ψ50	MPa			x
Minimum rooting depth	MinRD	m	x	x	x
Root nitrogen content	RNC _{mass}	mg g ⁻¹	x	x	
Specific root length	SRL	cm g ⁻¹	x	x	

number of biologically impossible trait values while preventing selective removal of entries in PFTs occurring at the upper and lower boundaries of trait values, only data within the 99% quantiles of every PFT separately were selected. For most individuals of a species, only a subset of the traits was measured, which resulted in a database with many trait gaps. By calculating species means, the database became smaller, but the number of traits per species increased, allowing us to investigate more trait combinations. This database based on species means consisted of 18 287 species for which information for one or more traits was available.

PFT classification

Species were assigned to a PFT based on the categorical data available from multiple trait data sources, the most important being the TRY database. These included plant growth form, leaf phenology, leaf type and photosynthetic pathway. When no information about C₃- or C₄-photosynthesis was available, the species was assumed to be a C₃-species. Species that could not be classified because of missing or ambiguous categorical data were omitted. Species known not to belong to the seed plants, species with crassulacean acid metabolism (CAM)-photosynthesis, succulent species (e.g. cacti), climbers or vines, (hemi-)parasitic species, aquatic species, (hemi-)epiphytes, crops and palmoids were left out as well, because little data trait was available for these plant types.

Different PFT classifications were evaluated. The first PFT classification consisted of seven broadly applied PFTs (including only angiosperms and gymnosperms): C₃- and C₄-graminoids (including grasses, sedges and rushes), (C₃-)forbs, (C₃-)shrubs, broadleaved deciduous trees, broadleaved evergreen trees and

needleleaved evergreen trees. Needleleaved deciduous trees could not be included, because of trait data limitations (a minimum of seven species per trait (set) per PFT was needed, explained in the next section). For this classification, there were 15 traits with sufficient species per PFT to be included in the analyses (see Table 1). The number of species within the C₄-graminoid PFT was too low to include a number of traits considered to be important in plant survival strategies (stem specific density, SSD, and LLS). Therefore, a six-PFT classification was constructed, with C₄- and C₃-graminoids merged into a single graminoids PFT. This allowed additional inclusion of LLS, SSD and Rd_{mass} and Rd_{area}. The distribution and number of observations (species' means) per PFT and per trait are listed in Supporting Information Fig. S1.

We also tested a PFT classification of trees only, which included bioclimatic descriptions. This classification de-emphasizes the role of plant height as a descriptor of growth form and allowed the inclusion of a number of additional traits; vessel area (VA) and the water potential at which 50% loss of conductivity occurs (Ψ50). To associate each species to a climate zone, species distributions were determined based on their spatial occurrences in the Global Biodiversity Information Facility (<http://www.gbif.org>, data accessed 18 October 2014), extracted with the R-package RGBIF (Chamberlain *et al.*, 2014). The climate zone within the Köppen–Geiger climate classification (Kottek *et al.*, 2006) with most occurrences was taken to represent the correct climate zone that a species originated from. For species occurring mostly in deserts, the climate zone with the second most occurrences for this species was taken. The different climatic zones were aggregated into tropical (equatorial climates), extratropical (warm temperate climates, snow and polar climates,

and steppes from the arid climates) and deserts (arid climates). An extra subdivision of extratropical climates into temperate and boreal climates was not possible due to limited data on boreal species. This resulted in five PFTs with sufficient trait data: tropical broadleaved deciduous and evergreen trees and extratropical broadleaved deciduous and evergreen trees and needleleaved evergreen trees. The traits used for analysis with this tree PFT classification were broadly similar to the six-PFT classification described earlier, except that there were not sufficient data to include root nitrogen content (RNC_{mass}) and specific root length (SRL), whereas VA and Ψ_{50} were additionally included. In Fig. S2, the data distribution per trait is given.

Kernel density estimation

We analyzed which trait or set of traits had the highest power to discriminate between PFTs by using (Gaussian) kernel density estimation (*kde*) from the kernel smoothing ('ks') package in R (Duong, 2014). This technique allowed estimation of probability density functions for the different PFTs within an n -dimensional space of traits (with n varying between 1 and 6, the latter being the maximum possible using the 'ks'-package). Estimated density functions in a two-dimensional trait space are visualized in Fig. 1. For a given set of traits, we only selected species for which all selected traits were available. This resulted in sets containing a variable number of species, depending on both the selected traits as well as the number of traits. Only trait sets where at least seven species per PFT were available were tested, as seven species is the minimum number of entries needed to create a complete density kernel for a PFT within a six-dimensional trait space (and one additional species for validation). This low threshold did not

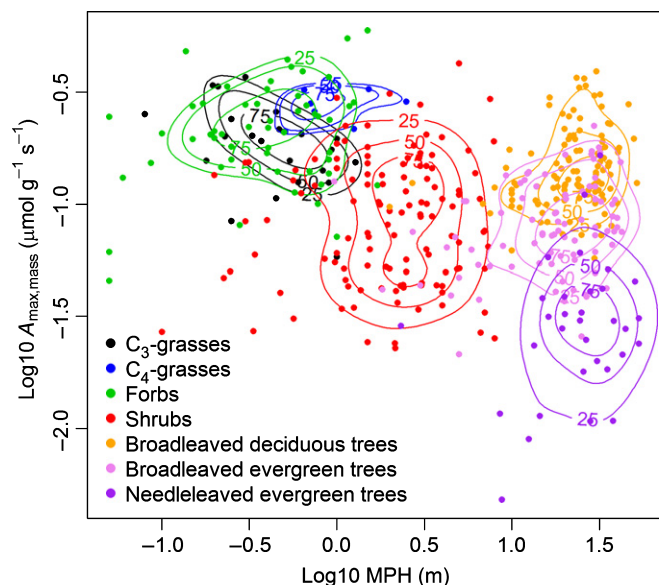


Fig. 1 Probability densities of seven plant functional types (PFTs) in a two-dimensional trait-space (\log_{10} -transformed maximum plant height, MPH, and mass-based maximum photosynthetic capacity, $A_{max, mass}$). The contour lines of the different PFTs reflect upper percentages of different density regions (from inside to outside: 75, 50 and 25%).

strongly affect the estimate of the probability density function (Fig. S3).

For every species within a set, the Gaussian probability density for each PFT was calculated. This calculation was based on the density kernels fitted for each PFT as constructed from the remaining data in the set (leave-one-out method). Because kernels were fitted independently across PFTs, probability densities of a given species were normalized to probabilities per PFT to enable comparisons between PFTs. To allow this normalization, probability densities were also calculated for each PFT for a dummy trait set. Normalization was obtained by dividing the species' probability density estimates for each PFT by the sum of the density estimates calculated in the dummy trait set. This unique dummy trait set was created for every trait set by evenly distributing trait values between the minimum to the maximum trait value in the dataset with a fixed number of intervals. The size of the dummy matrix (i.e. the number of dummy trait combinations) depended on the number of traits involved. Because the size of the matrix may affect model performance we did not set a fixed number of intervals. Instead, an optimal matrix size was chosen for each number of traits (see Methods S1 and Fig. S4).

Due to overlapping probability density functions of PFTs (Fig. 1), species may have probabilities larger than zero for multiple PFTs. For each species, the PFT with the highest probability was taken as the predicted PFT and compared with the observed PFT to which the species actually belonged. In this way, for each set, a so-called confusion matrix was constructed, which shows for each PFT the number of correctly classified and misclassified PFTs (e.g. Table 2). With this matrix, the fraction of correctly predicted entries per PFT was calculated (\overline{fcp}), as well as the mean performance (\overline{fcp}), the fraction of correctly categorized entries per PFT averaged over all PFTs. We used \overline{fcp} instead of other performance measures, such as Cohen's kappa (κ) (Cohen, 1960) which includes a correction for the agreement caused by chance. However, κ weighs all species equally independent of PFT identity, whereas \overline{fcp} gives equal weight to each PFT. This \overline{fcp} therefore allows the determination of the traits that lead to the highest differentiating power among PFTs, even in the presence of unbalanced data distribution across PFTs.

Most traits (except for LCC_{mass} , SSD and Ψ_{50}) were log-transformed, even though the applied *kde* method does not demand a normal distribution of the data, but normalization of the traits by log-transformation did improve model performance.

The database was not completely filled, leading to trait sets of varying sizes. Fortunately, for the same number of traits, different dataset sizes did not significantly affect model performance except for sets with three and four traits ($P=0.040$ and 0.045 , respectively), but R_{adj}^2 were very low ($R_{adj}^2=0.021$ and 0.020 , respectively) and slopes very flat (0.000027 and 0.000042 , respectively) (Fig. S5). This suggests that differences in model performance are trait-related and not much confounded by dataset size.

We also investigated whether the performance of trait sets could increase when adding traits without functional information. We tested this by adding a random, nonfunctional trait (with a similar mean and SD for all PFTs) to an existing trait set. This almost always decreased the performance of the trait set

Table 2 Confusion matrix of mean of best performing trait sets for the seven-plant functional type (PFT) classification, with in bold the fraction correctly classified PFTs

Obs	Pred						
	C ₃ -graminoids	C ₄ -graminoids	Forbs	Shrubs	Bl dec trees	Bl ev trees	Nl ev trees
C ₃ -graminoids	0.57	0.15	0.20	0.07	0.01	0.00	0.00
C ₄ -graminoids	0.26	0.53	0.11	0.10	0.00	0.00	0.00
Forbs	0.27	0.10	0.58	0.04	0.00	0.00	0.00
Shrubs	0.13	0.07	0.06	0.65	0.04	0.04	0.01
Bl dec trees	0.00	0.00	0.00	0.04	0.76	0.18	0.01
Bl ev trees	0.01	0.00	0.00	0.06	0.30	0.59	0.04
Nl ev trees	0.00	0.00	0.00	0.07	0.01	0.06	0.87

Obs, observed PFT; Pred, predicted PFT; Bl dec trees, broadleaved deciduous trees; Bl ev trees, broadleaved evergreen trees; Nl ev trees, needleleaved evergreen trees.

(Fig. S6), suggesting that the Gaussian kernels perform appropriately in relation to nonfunctional trait additions.

Results

Differentiating power of trait sets

For the seven-PFT classification, the mean fraction of correctly predicted PFTs (\overline{fcp}) for each trait set was plotted against the number of traits included per trait set (Fig. 2). \overline{fcp} increased with an increasing number of traits included and increased to 0.73 (with a set of five traits). From four traits onwards, trait sets did not significantly differ from each other ($P > 0.85$), whereas sets with three and six traits were not significantly different from each other ($P = 0.18$). For sets of six traits, the predictive power decreased in comparison to sets of five traits. Although there was no clear relationship between \overline{fcp} and the number of species per

trait set, the number of traits that were available for six-trait sets was much lower than for the other trait sets and might have affected the performance of the six-trait sets.

Predictability of PFTs in the best performing trait sets

The 10% trait sets (for 2–6 traits) with the highest \overline{fcp} ('best performing trait sets') were selected for further analyses. For seven PFTs, it comprised trait sets with a \overline{fcp} of 0.62–0.73 (κ range 0.45–0.70): this included one two-trait set, nine three-trait sets, 22 four-trait sets, 15 five-trait sets and two six-trait sets (total of 49). The proportion of correctly predicted species, averaged per PFT (Table 2), reflecting the extent to which a PFT could be distinguished functionally from other PFTs, ranged from 0.53 for C₄-graminoids to 0.87 for needleleaved evergreen trees. Although the average number of species per PFT differed among PFTs, this did not significantly affect performance of PFTs ($P = 0.60$).

C₄-graminoids were correctly classified least often (0.53), followed by C₃-graminoids (0.57) and forbs (0.58). For both graminoids and forbs, species were only occasionally misclassified as shrubs or trees. Similarly, trees were almost never confused with herbaceous PFTs or shrubs. For the trees, needleleaved evergreen trees could be distinguished from other PFTs most reliably (0.87), followed by broadleaved deciduous trees (0.76), whereas predictability of broadleaved evergreen trees was clearly lower (0.59). Shrubs had intermediate predictability (0.65) and most misclassifications were as C₃-graminoids, but shrubs were confused with any other PFT as well. Better predictability of some PFTs was not necessarily caused by a more detailed PFT definition, as reflected in less variation in trait values (Fig. S1); shrubs were the third best performing PFT (Table 2), but encompassed a wide range of species and associated trait values.

Most selected traits in best performing trait sets

Because the number of sets in which a trait occurred varied, we did not compare the absolute number of occurrences in the best performing trait sets. Instead, we compared occurrences of a trait in these best performing trait sets relative to the occurrence of a trait in the full multitrait dataset (2–6 trait sets). The trait with the highest relative occurrence was specific root length (SRL)

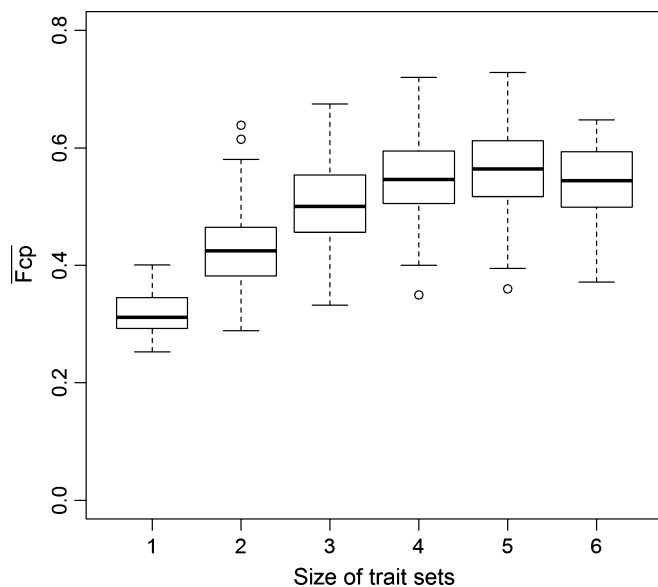


Fig. 2 Mean fraction correctly predicted (\overline{fcp}) of all tested trait sets against size of tested trait sets for the seven-plant functional type (PFT) classification. Box plots show the median (middle line), the 25 and 75% quartiles (hinges), the outer value within the 1.5 × interquartile range (whiskers) and outliers (open circles).

(Fig. 3), but this trait occurred only seven times in the full multitrait dataset, so its actual performance in a database without gaps remains unknown. Maximum plant height (MPH) had the second highest relative occurrence (22.0%), followed by leaf area (LA) (18.6%). After these traits, a range of traits performed similarly well (relative occurrences between 10–15%): minimum rooting depth (MinRD), LNC_{mass} , mass-based leaf phosphorus content (LPC_{mass}), SLA and $A_{max,area}$. Other traits had a lower occurrence than would be expected by chance (< 10%), or were never selected (stomatal conductance, G_s , and mass-based root nitrogen content, RNC_{mass}), although they had a low occurrence in the full multitrait dataset as well (see Table S1 for occurrences of traits within 2–6-trait sets). However, other traits with low occurrences (SRL, $A_{max,mass}$; see Table S1) did occur in the best performing trait sets, suggesting that these nonselected traits have a low differentiating ability.

Co-selection of traits with maximum plant height and leaf area or leaf life span

The high occurrence of MPH and LA in the best performing trait sets is not unexpected, because these traits are included in the

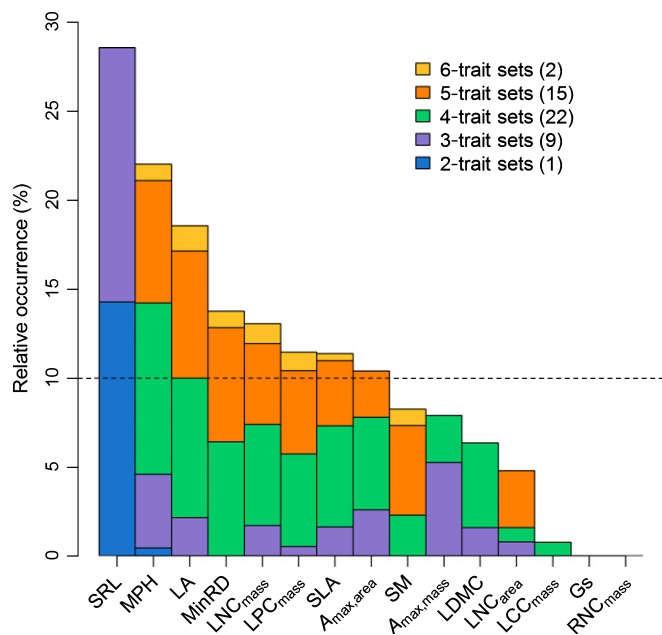


Fig. 3 Relative occurrence (%) of traits in best performing trait sets (i.e. occurrences relative to occurrences in the full multitrait dataset) for the seven-plant functional type (PFT) classification. Colors reflect relative occurrence of traits for trait sets with different sizes. Absolute number of combinations that occurred in the best performing trait sets in brackets behind size of trait set. Dashed line indicates threshold for chance occurrences: above the line occurrences of traits are higher than by chance, below the line lower than by chance. SRL, specific root length; MPH, maximum plant height; LA, leaf area; MinRD, minimum rooting depth; LNC_{mass} , mass-based leaf nitrogen content; LPC_{mass} , mass-based leaf phosphorus content; SLA, specific leaf area; $A_{max,area}$, area-based maximum photosynthetic rate; SM, seed mass; $A_{max,mass}$, mass-based maximum photosynthetic rate; LDMC, leaf dry matter content; LNC_{area} , area-based leaf nitrogen content; LCC_{mass} , mass-based leaf carbon content; G_s , stomatal conductance; RNC_{mass} , mass-based root nitrogen content.

definition of PFTs (e.g. MPH distinguishes trees from the other PFTs, and LA separates broadleaved from needleleaved trees). Therefore, including these two traits is likely to increase the chance of achieving a high \overline{fcp} . Looking at the traits that were selected together with these two traits can reveal which traits add additional functional information. From the 49 best performing trait sets in the seven-PFT classification, 26 trait combinations (53.1%), contained both MPH and LA. Traits that occurred with these two traits more often than what would be expected by chance alone (i.e. occurrence of > 53.1%) were SM (13 times, which is 72.2% of its occurrences in the best performing trait sets), followed by LNC_{area} (four times, 66.7%), MinRD (nine times, 60%) and LPC_{mass} (13 times, 59.1%) (Fig. 4), whereas other traits had lower occurrences than 53.1%, or did not occur at all in combination with MPH and LA.

Six-PFT classification performance

When merging C_3 - and C_4 -graminoids, resulting in a six-PFT classification, \overline{fcp} increased to 0.85 (Fig. S7) and κ increased to 0.79, meaning that performance increased even when corrected for chance effects. The \overline{fcp} of the best performing trait sets (240 sets) ranged from 0.69 to 0.85 (κ range 0.51–0.79). The confusion matrix for this classification (Table S2) was broadly similar to that for the seven-PFT analysis.

The traits with the highest relative occurrence in the best performing trait sets was (again) MPH (22.0%), followed by traits

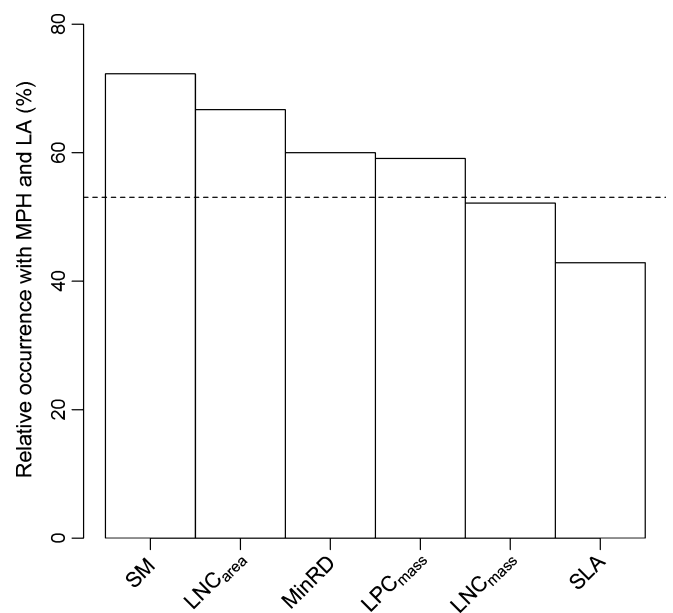


Fig. 4 Relative occurrence of traits (%) together with maximum plant height (MPH) and leaf area (LA) in the best performing trait sets (i.e. occurrences of traits with MPH and LA in best performing trait sets relative to occurrences of traits in all best performing trait sets) for the seven-plant functional type (PFT) classification. Dashed line indicates threshold for chance occurrences: above the line occurrences of traits are higher than by chance, below the line lower than by chance. SM, seed mass; LNC_{area} , area-based leaf nitrogen content; MinRD, minimum rooting depth; LPC_{mass} , mass-based leaf phosphorus content; LNC_{mass} , mass-based leaf nitrogen content; SLA, specific leaf area.

that were not present in the seven-PFT classification: LLS (relative occurrence of 19.5%), and SSD (17%) (Fig. S8). Traits with a relative occurrence between 15 and 10% included again a number of leaf traits (LA, LNC_{mass} and SLA) and MinRD.

Only 20% of the 240 best performing trait sets contained both MPH and LA (48 sets). The traits that were co-selected more often than expected by chance with these traits were MinRD and LPC_{mass} (27.0 and 22.6%, respectively) as in the seven-PFT classification, but also SSD (24.5%) (Fig. S9). By contrast, SM and LNC_{area} were no longer selected more often than expected by chance. Like MPH and LA, LLS is also part of the PFT-definition (for trees), suggesting that LLS will also have a high differentiating power. Indeed, 107 combinations out of the 240 best performing trait combinations (44.6%) contained LLS and MPH. Traits which had a higher occurrence than expected by chance (44.6%) were $A_{max, mass}$ and LNC_{area} (60.5 and 50.8%, respectively), whereas in contrast to traits associated with MPH and LA, MinRD and SSD were selected less often.

Bioclimatic tree classification

For classifications with trees only, as separated into extratropical and tropical trees, \overline{fcp} ranged from 0.68 to 0.80 (κ range 0.44–0.77) in the best 10% performing trait sets (302 trait sets). Because the tree PFT classification comprised five PFTs, the fraction correctly predicted averaged per PFT was expected to increase by 3.3% to 5.7% by chance alone. However, the percentage correctly predicted increased only for the tropical and extratropical broadleaved evergreen trees (by 7–10% and 13–16%, respectively) (Table S3), suggesting that traits are less effective at distinguishing among bioclimatic classifications than growth forms.

In the best performing trait sets, LLS appeared to be the dominant trait (Fig. 5). By comparing different tree PFTs with each other, height as a major determinant of growth form was removed, but MPH was still selected, although less often than in the seven and six PFT classification analyses. In contrast to these PFT classifications, traits directly related to carbon assimilation and release, $A_{max, mass}$, $A_{max, area}$, G_s and Rd_{mass} were much more frequently selected in the tree PFT classification. By contrast, traits that did well in the general PFT classifications, like MinRD and SSD, were not often selected to distinguish among tree PFTs. The additional traits, $\Psi 50$ and VA, did not occur very often either, but this can be due to the fact that they occurred in a lower number of trait sets. Looking at trait associations with LLS, the traits that were co-selected more often than expected by chance (81.5%) with LLS were $\Psi 50$ (100%, but occurring only once in the best 10% dataset), LNC_{area} (98.5%) $A_{max, mass}$ (93.3%) and Rd_{mass} (87.1%), followed by G_s (85.9%) and SSD (85.3%) (Fig. S10).

Discussion

Functional dissimilarity of PFTs

Many studies describe which traits are considered important in distinguishing between different plant ecological strategies

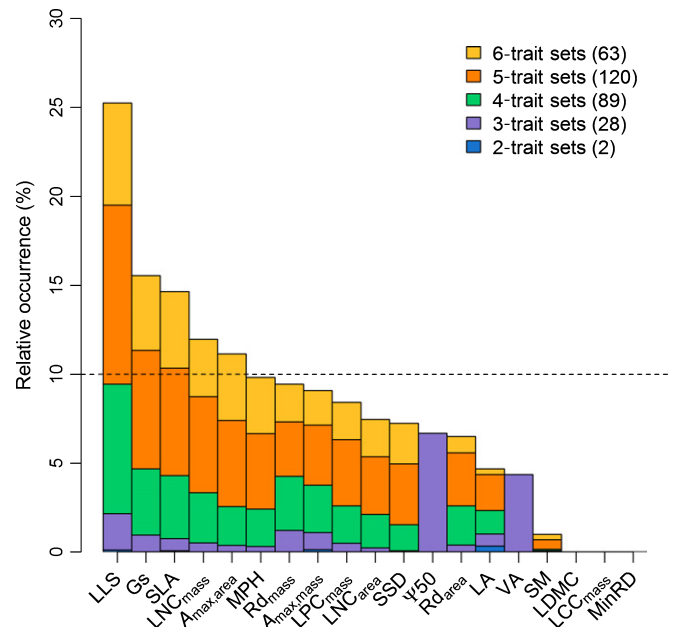


Fig. 5 Relative occurrence (%) of traits in best performing trait sets (i.e. occurrences relative to occurrences in the full multi-trait dataset) for the tree plant functional type (PFT) classification. Colors reflect relative occurrence of traits for trait sets with different sizes. In brackets behind size of trait set, absolute number of combinations that occurred in the best performing trait sets. Dashed line indicates threshold for chance occurrences: above the line occurrences of traits are higher than by chance, below the line lower than by chance. LLS, leaf life span; G_s , stomatal conductance; SLA, specific leaf area; LNC_{mass} , mass-based leaf nitrogen content; $A_{max, area}$, area-based maximum photosynthetic rate; MPH, maximum plant height; Rd_{mass} , mass-based leaf dark respiration; $A_{max, mass}$, mass-based maximum photosynthetic rate; LPC_{mass} , mass-based leaf phosphorus content; LNC_{area} , area-based leaf nitrogen content; SSD, specific stem density; $\Psi 50$, water potential at which 50% loss of conductivity occurs; Rd_{area} , area-based leaf dark respiration; LA, leaf area; VA, vessel area; SM, seed mass; LDMC, leaf dry matter content; LCC_{mass} , mass-based leaf carbon content; MinRD, minimum rooting depth.

(Westoby, 1998; Weiher *et al.*, 1999), but different plant strategies are not restricted to specific PFTs. PFTs can include multiple plant strategies and plant strategies can overlap between PFTs as well, as is reflected by the large variation in trait values observed within PFTs and the overlap in trait values between PFTs (Kattge *et al.*, 2011; Van Bodegom *et al.*, 2012; Verheijen *et al.*, 2013). Here, we quantitatively determined to what extent plant traits can distinguish between predefined, growth form-based PFTs and which trait sets are most likely to produce a model with a high differentiating ability. We show that despite overlap in plant strategies within and between PFTs, traits are a powerful tool to distinguish between PFTs. In our study, four to five traits were found to be sufficient to classify PFTs correctly up to 85% (κ of 0.79, for six PFTs), without the need for any additional constraint. This high percentage indicates that although PFTs might overlap in single trait values and plant strategies, the kernel density estimation method shows their different positioning in multidimensional trait-space. This different positioning of PFTs reflects, at least in part, functional differentiation across several strategy axes. Our study therefore quantitatively demonstrates

that structural properties of plants (growth form, leaf shape, leaf phenology) also reflect functional differences.

Correlated traits still have differentiating ability

Some traits were selected more often than others in the best performing trait sets of the different PFT classifications. As expected, traits that are reflected in the definitions of the PFTs, such as MPH, LA and LLS, appeared most often in the best performing traits sets of the seven- and six-PFT classifications. Because PFTs differ more in terms of LLS than of LA (Fig. S1), LLS replaced LA as an important distinguishing trait, as soon as it was included in the six PFT classification (Fig. S8). MPH also occurred in the tree PFT classification, suggesting that height still plays a role in distinguishing among different types of trees, even though Moles *et al.* (2009) did not find latitudinal gradients in plant height within trees.

A range of other traits can be combined with MPH and either LA or LLS and provide additional information on the functions that relate to different growth forms and associated PFTs. This trait selection is dependent on the PFT classification, but overall, combining MinRD and either SM or SSD with these traits, as well as an additional leaf trait, either LNC_{area} , LPC_{mass} or $A_{max, mass}$, increases the chances of obtaining a trait set with a high differentiating ability between PFTs.

Although we expected that sets of traits combining different functional aspects within plants would capture functional differences between PFTs best and consequently would have the highest differentiating power, this is only partly true and trait combinations that are considered functionally redundant because they relate to similar strategy axes, for example the 'leaf economics traits' like LA, LLS, SLA, LPC or LNC, or that are involved in a trade-off with each other, like MPH and SM, MinRD or SSD, are included in the best performing trait sets as well.

This inclusion of correlated traits may be due to a number of reasons. First, because PFTs include a variety of plant strategies, these traits might be selected in combination to reflect the multiple plant strategies within a PFT. In that case, PFTs can be differentiated from each other because each PFT represents a different combination of plant strategies.

Alternatively, although not excluding the first explanation, the co-selection of correlated traits might also indicate that within a given trade-off or strategy axis, trait variation is still possible. It is known that trade-offs limit the occurrence of certain combinations of trait values due to mechanistic or physiological limitations. However, it seems that within certain trade-offs, multiple trait value combinations can still occur, reflecting alternative solutions within a strategy with about equal fitness (Marks & Lechowicz, 2006). According to this explanation, different PFTs express different (sets of) alternative solutions within a plant strategy.

For example, variation in SM, MinRD and SSD is restricted because of trade-offs between these traits and MPH: large plants need a minimum stem specific density and rooting depth to mechanistically sustain a certain height (Schenk & Jackson,

2002b; Chave *et al.*, 2009). In addition, small plants are unlikely to bear very large and heavy seeds (Moles *et al.*, 2004). However, despite these trade-offs, SM, MinRD and SSD were selected with MPH more often than expected by chance. This could mean that for a given MPH, different PFTs have different solutions to deal with (and partly avoid) these trade-offs and thus make different choices with respect to for example dispersal strategies (SM) (Westoby *et al.*, 2002; Moles & Westoby, 2004; Moles *et al.*, 2004), water transport, cavitation resistance or resistance against disturbances (SSD) (Westoby & Wright, 2006; Chave *et al.*, 2009) or water availability (MinRD) (Schenk & Jackson, 2002a, b).

As another example, needleleaved evergreen trees (consisting exclusively of gymnosperms in our dataset), largely overlap in MPH and completely overlap in SM and SSD with the other tree PFTs (Fig. S1). However, the different vessel anatomy of gymnosperms and angiosperms (Chave *et al.*, 2009) allows for a lower SSD for a given MPH for needleleaved evergreen trees. In addition, there seems to be a different trade-off between SM and height, resulting in a different relationship between these traits for gymnosperms (Moles *et al.*, 2004), that might allow differentiation of this PFT from others based on MPH and SM. Thus, consideration of the different choices of PFTs among the various functions and related traits is therefore essential to better understand the functioning of growth form-related PFTs.

Towards further improvements of traits-based classifications

Misclassifications of PFTs occurred mostly between closely related growth forms, such as within trees or within herbs (graminoids and forbs), whereas shrubs showed functional overlap with both trees and herbs. Overlap in sets of traits between PFTs could mean that there is functional similarity between PFTs, although the high percentage correctly predicted PFTs show that structural aspects of plants indeed also reflect functional differences to a large extent. Alternatively, overlap could mean that functional differences are not completely distinguished by the traits chosen. For example, through the six-PFT classification we could add a number of traits (LLS, SSD and Rd_{mass} and Rd_{area}) to the trait sets that were not possible for the seven PFT classification due to data limitations. The inclusion of these traits resulted in a better separation of broadleaved evergreen trees from broadleaved deciduous trees (7–9% fewer misclassifications between these two PFTs; see Tables 2, S2) and a better separation of shrubs from graminoids. Additionally, other traits that were not yet available for a large number of species, but are known to have strong functional implications, might further improve PFT classifications. For example, traits related to tolerances to bioclimatic conditions such as cold tolerance thresholds of different organs or survival thresholds (Woodward & Kelly, 1997; Harrison *et al.*, 2010), or disturbances like fire (reflected by e.g. bark thickness; Hoffmann *et al.*, 2003) might increase the predictive ability of traits. C_4 -graminoids and C_3 -graminoids might be better distinguished from each other when, for example, such cold-tolerance related traits are included, because C_3 -grasses

occur in colder climates than C_4 -grasses, even though this is not true for all C_3 -lineages (Edwards & Smith, 2010).

Gaps in our dataset also hampered the testing of combinations that may be fruitful. For instance, single trait performances (Tables S4, S5 for the seven- and six-PFT classifications, respectively) suggested that for a seven-PFT classification, a combination of leaf dry matter content (LDMC), SM, RNC_{mass} , MinRD, and either $A_{max, mass}$ or LNC_{mass} might result in a high performing model. For the six-PFT classification this would be LLS, MinRD, LDMC and Rd_{mass} . Interestingly, this would mean that MPH would not necessarily be included, but currently, data gaps prevented testing these potentially important sets. In addition, some traits with low data coverage are potentially interesting for further extensions of our approach, either because they had a high relative occurrence (SRL) or due to a strong association with LLS ($\Psi 50$). Again, data limitations currently hampered making generalizations about their actual performance. Therefore, increasing the number of trait data per species is an important next step to take.

Implications

Only a limited number of strategy axes with related traits (MPH, SM, SLA) are typically used to distinguish between different plant strategies (Westoby, 1998; Diaz *et al.*, 2004). Our analysis shows that traits related to the same strategy axis or traits involved in trade-offs with each other, still add functional information about and allow discrimination between sets of plant strategies as reflected by PFTs. Therefore, although current plant ecology strategy schemes help to theoretically understand differences in the ecological behavior of plants and have identified some main traits important in plant functioning, our analysis provides new insights into how functional differences of different growth-form based PFTs are shaped by traits. Defining *a priori* the most important traits while excluding correlated traits in advance will result in a loss of differentiating capacity and consequently hamper further functional understanding. This is illustrated by a regional study that investigated which traits are needed to distinguish existing vegetation types. The analysis showed that the two or three categories used in most plant strategy schemes were insufficient to capture functional differences because they put nonredundant traits into a single category (Douma *et al.*, 2012a).

When this potential of plant traits to functionally differentiate among PFTs is acknowledged, traits can be a powerful tool for predictive ecology. The impacts of climate change on vegetation distribution can be investigated, by predicting changes in vegetation distribution based on plant traits. The PFT analysis for trees shows that trait combinations can also be used to distinguish between bioclimatically defined PFTs, enabling the differentiation among responses of tropical and extratropical (and likely also between boreal and temperate) vegetation. Van Bodegom *et al.* (2014) previously showed how vegetation maps may be constructed based on global trait maps. This vegetation map predicted a similar vegetation distribution to vegetation maps that were modeled by global dynamic vegetation models (DGVMs). In our analysis, multiple combinations of traits had a similar

ability to distinguish between vegetation types. Hence, the results of this study can be used to choose those traits that have the strongest relationship to environmental conditions in order to optimize our abilities to predict vegetation distribution, with major implications for predictive vegetation modeling.

Acknowledgements

This study has been financed by the Netherlands Organization for Scientific Research (NWO), Theme Sustainable Earth Research (project number TKS09-03) and has been supported by the TRY initiative on plant traits (<http://www.try-db.org>). TRY is currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig. The authors would also like to thank Paul Torfs from Wageningen University for his help with kernel density estimation in R.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Data distribution per trait and PFT (seven- and six-PFT classification).

Fig. S2 Data distribution per trait and PFT (tree PFT classification).

Fig. S3 Effect of number of species per PFT on the predictability of a PFT.

Fig. S4 Effect of axis evaluations points on model performance.

Fig. S5 Model performance in relation to number of species within each dataset.

Fig. S6 Change in model performance when an additional random trait is added.

Fig. S7 Model performance of tested trait sets for the six-PFT classification.

Fig. S8 Relative occurrence of traits in best performing trait sets for the six-PFT classification.

Fig. S9 Relative co-selection of traits with MPH and LA or LLS in the six-PFT classification.

Fig. S10 Relative co-selection of traits with LLS in the tree PFT classification.

Table S1 Occurrences of traits in different trait sets for the seven-PFT classification

Table S2 Confusion matrix for the six-PFT classification

Table S3 Confusion matrix for the tree PFT classification

Table S4 Fractions of correctly predicted PFTs for single traits in the seven-PFT classification

Table S5 Fractions of correctly predicted PFTs for single traits in the six-PFT classification

Methods S1 Determination of axis grid-size.

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