



# Patterns and drivers of plant functional group dominance across the Western Hemisphere: a macroecological re-assessment based on a massive botanical dataset

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*Received 9 March 2015; revised 9 October 2015; accepted for publication 2 November 2015*

Plant functional group dominance has been linked to climate, topography and anthropogenic factors. Here, we assess existing theory linking functional group dominance patterns to their drivers by quantifying the spatial distribution of plant functional groups at a 100-km grid scale. We use a standardized plant species occurrence dataset of unprecedented size covering the entire New World. Functional group distributions were estimated from 3 648 533 standardized occurrence records for a total of 83 854 vascular plant species, extracted from the Botanical Information and Ecology Network (BIEN) database. Seven plant functional groups were considered, describing major differences in structure and function: epiphytes; climbers; ferns; herbs; shrubs; coniferous trees; and angiosperm trees. Two measures of dominance (relative number of occurrences and relative species richness) were analysed against a range of hypothesized predictors. The functional groups showed distinct geographical patterns of dominance across the New World. Temperature seasonality and annual precipitation were most frequently selected, supporting existing hypotheses for the geographical dominance of each functional group. Human influence and topography were secondarily important. Our results support the prediction that future climate change and anthropogenic pressures could shift geographical patterns in dominance of plant functional groups, with probable consequences for ecosystem functioning. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **180**, 141–160.

**ADDITIONAL KEYWORDS:** Anthropocene – biodiversity – biogeography – boosted regression trees – climate change – disturbance – macroecology – model averaging – plant functional groups – vegetation modelling.

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## INTRODUCTION

The biosphere can be divided into a number of vegetation zones, thought to be largely determined by climate, that occur in a repeated pattern across the continents (Holdridge, 1947; Küchler, 1949; Olson *et al.*, 2001). The transitions between these zones are believed to be controlled by a variety of primarily climatic factors (Walter, 1973; Whittaker, 1975; Lavorel *et al.*, 1997) that determine the presence and frequency of different functional groups of plants (Dansereau, 1951; Penfound, 1967). However, the extent to which the distributions of these vegetation zones are determined by climate is debated. Other environmental factors related to the availability of resources, or possibly top-down control by grazing or fires, are also believed to influence the distribution of plant vegetation zones (Bond, 2005). The delimitation of such vegetation zones is largely based on dominance patterns among major plant functional groups (Vasquez & Givnish, 1998; Duckworth, Kent & Ramsay, 2000).

We define plant functional groups as species using similar resources and sharing morphological and physiological traits (Lauenroth, Dodd & Sims, 1978; Diaz & Cabido, 1997; Duckworth *et al.*, 2000). The division of plants into functional groupings on the basis of functional traits has been recognized as an important way to simplify ecological complexity and to reveal general patterns (Box, 1996; Cornelissen *et al.*, 2003). Many studies have focused on the connection between functional traits in local communities and environmental factors (Chapin *et al.*, 1996; Bernhardt-Romermann *et al.*, 2011), whereas fewer have looked into continental-scale patterns (e.g. Moles *et al.*, 2009; Swenson *et al.*, 2012; Lamanna *et al.*, 2014). Studies that quantitatively investigate continental-scale patterns of plant functional group dominance are lacking. For most species, we have limited knowledge of their individual response to environmental change and, in turn, how their response might affect the entire community (Bellard *et al.*, 2012). Species in the same functional group are assumed to respond more similarly to changes in their environment, and therefore functional groups can be used as a proxy to investigate the links between species distributions and environmental changes on regional and even global scales (Duckworth *et al.*, 2000; Voigt, Perner & Jones, 2007). Furthermore, plant functional groups based on structure can be easily assigned in the field and are globally comparable among studies and sites (Dormann & Woodin, 2002; Harrison *et al.*, 2010).

The dominance of different plant functional groups has been linked previously to climate, but the strength and direction of the relationships need

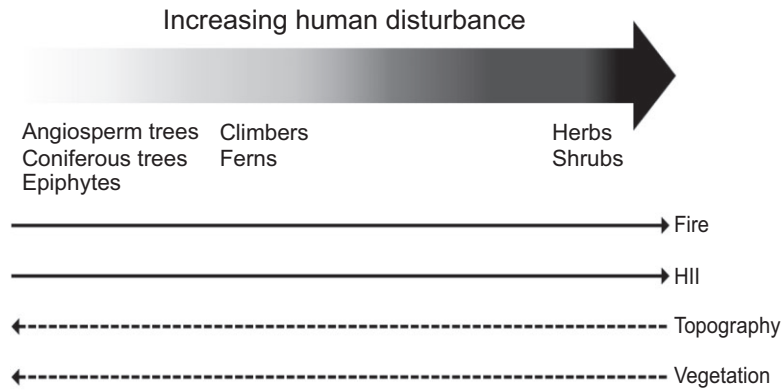
further assessment, especially to improve predictions of climate change effects (Box, 1996; Diaz & Cabido, 1997; Harrison *et al.*, 2010). However, the general importance of geographical variability in other environmental factors, such as topography, soil conditions and disturbance, is less certain. Humans increasingly change the global environment, exerting a growing pressure on natural ecosystems, and even change natural biomes to anthromes (Ellis, 2011). This is likely to change community composition through different effects on different functional groups (Chapin *et al.*, 2000). Which of these multiple factors are the most important for each plant functional group and how they influence geographical patterns of dominance are yet to be determined.

Here, we leverage a massive botanical dataset to provide the first continental-scale quantitative analysis of the factors underlying the geographical distribution of major plant functional groups. We define and compile a new dataset on seven vascular plant functional groups that describe important differences in plant structure and function and large-scale vegetation types: ferns and fern allies (hereafter referred to as ferns); coniferous trees; angiosperm trees; shrubs; herbs; climbers; and epiphytes. The aims of this article are: (1) to quantify and compare geographical patterns in the dominance of these plant functional groups across the New World; (2) to identify the underlying environmental drivers; and (3) to determine the relative influence of natural factors compared with human-related disturbance. We assess three hypotheses: (H<sub>1</sub>) the dominant factors controlling plant functional group distributions are the natural drivers climate and soil; (H<sub>2</sub>) human influence is now so pervasive that drivers related to anthropogenic disturbance are also important at the continental scale; and (H<sub>3</sub>) coniferous and angiosperm trees and epiphytes decline in dominance with increasing disturbance, whereas herbs and shrubs increase and climbers and ferns exhibit intermediate responses (Fig. 1, see also subsection on 'Specimen data and predictions' in 'Material and methods' section).

## MATERIAL AND METHODS

## PREDICTOR VARIABLES

We used 12 environmental and biotic predictor variables, all of which have been proposed to be influential for the geographical distribution of plant functional groups (Table 1, Fig. 1). All data layers were resampled to 100 × 100-km<sup>2</sup> resolution grid cells and projected to the Lambert azimuthal equal area projection. Collinearity among the predictor variables was checked with the pairwise Pearson product-moment correlation coefficient (Supporting Informa-



**Figure 1.** Hypothetical relationship between plant functional groups and human disturbance. The large arrow represents a gradient of increasing human disturbance. The positions of the functional groups on the disturbance gradient represent the tolerance of each group based on predictions from the existing literature. The thin arrows show the relationship between human disturbance and our representative environmental predictors: arrows to the right show predictors that increase disturbance, whereas arrows to the left show predictors that decrease disturbance. HII, human influence index.

tion, Table S1). We chose annual mean temperature, temperature seasonality, annual precipitation, precipitation seasonality, actual evapotranspiration and the sand content of the soil to represent natural climate- and soil-related factors. The human influence index (HII) and fire were chosen as direct measures of human-related disturbance. HII represents anthropogenic impacts on the environment as an index value based on nine global data layers related to human population pressure, land use, and infrastructure and accessibility (Wildlife Conservation Society, 2005). Fire was calculated as the mean burnt area per year using data from Tansey *et al.* (2008), which provides the Julian date of fire detection each year at 1-km resolution. Tree height also partially captures the effects of human-related disturbance. Tree height contains a natural signal reflecting its dependence on climate and other natural environmental factors, but will also strongly reflect anthropogenic land cover change, notably deforestation. In addition, tree height may capture ecological interactions between trees and other functional groups, e.g. negative, competitive interactions with herbs and positive interactions with tree-dependent epiphytes. To avoid issues of circularity, tree height was excluded as a predictor of coniferous and angiosperm trees. We also included elevation, topographical heterogeneity and slope as topographical predictors. Topography will capture natural variation in vegetation structure and disturbance regime (e.g. landslides in steep terrain). However, it is also likely to contain a human impact signal, as natural vegetation in many regions is increasingly constrained to steep terrain (Sandel & Svenning, 2013). Slope was calculated from elevation as a percentage using the slope tool in the SDMtools

package. Topographical heterogeneity was also calculated from elevation as the standard deviation. Slope and topographical heterogeneity were highly correlated ( $r = 0.97$ ). We chose to retain slope, as this variable is more closely linked to our predictions. Mean annual temperature, temperature seasonality, annual precipitation and actual evapotranspiration were also highly correlated. We defined three sets of models which kept the highly correlated variables separate (Supporting Information, Table S2). Based on improvement in model performance, measured as  $R^2$  values, of the three model sets, we only report results from the model with temperature seasonality (model set 2). We also included sampling intensity, calculated as the number of georeferenced observations within a grid cell, as a predictor variable to control further for sampling effects.

#### SPECIMEN DATA AND PREDICTIONS

We defined seven different vascular plant functional groups, describing important differences in plant structure and function: ferns; coniferous trees; angiosperm trees; shrubs; herbs; climbers; and epiphytes. Data on plant functional groups were compiled from multiple data sources. We extracted information on plant functional groups from the Botanical Information and Ecology Network (BIEN 2.0) herbarium collection dataset based on the specimen description field (Enquist *et al.*, 2009; <http://bien.nceas.ucsb.edu/bien/>), the Plant Trait Database (TRY) (Kattge *et al.*, 2011), the SALVIAS database (The SALVIAS Project, 2002; [http://www.salvias.net/pages/database\\_info.php](http://www.salvias.net/pages/database_info.php)), the USDA PLANTS database (USDA, 2008) and Tropicos@ ([www.tropicos.org](http://www.tropicos.org)) (Tropicos, 2014). Species were

**Table 1.** Names, references and original resolution of environmental predictor variables used in the analyses

Variable	Unit	Reference	Classification	Time span	Original resolution
Annual mean temperature (Bio 1)	°C	Hijmans <i>et al.</i> , 2005	Natural	1950–2000	5'
Temperature seasonality (Bio 4)	Standard deviation × 100	Hijmans <i>et al.</i> , 2005	Natural	1950–2000	5'
Annual precipitation (Bio 12)	mm	Hijmans <i>et al.</i> , 2005	Natural	1950–2000	5'
Precipitation seasonality (Bio 15)	Coefficient of variation	Hijmans <i>et al.</i> , 2005	Natural	1950–2000	5'
Actual evapotranspiration	mm/year	Trabucco & Zomer, 2010	Natural	1950–2000	30'
Elevation	m	Hijmans <i>et al.</i> , 2005	Natural/anthropogenic	2000	1 km
Slope (derived from elevation)	%	Hijmans <i>et al.</i> , 2005	Natural/anthropogenic	2000	1 km
Topographical heterogeneity (derived from elevation)	Standard deviation	Hijmans <i>et al.</i> , 2005	Natural/anthropogenic	2000	1 km
Sand content	%	Fischer <i>et al.</i> , 2008	Natural	1971–2008	30'
Human influence index	Index value	Wildlife Conservation Society, 2005	Anthropogenic	1995–2004	1 km
Fire (burnt area)	Mean	Tansey <i>et al.</i> , 2008	Anthropogenic	2000–2007	1 km
Tree height	m	Lefsky, 2010	Anthropogenic	2003–2007	500 m

All datasets were resampled to 100-km resolution. ' indicates arc seconds.

assigned a functional group value when more than two-thirds of the sources agreed on the same functional group (84 434 species). Otherwise, the species was excluded (5629 species). We then reclassified the species to fit our seven vascular plant functional groups by first dividing the data into three major phylogenetic groups based on their fundamental functional differences: ferns; gymnosperms; and angiosperms. The gymnosperms were subdivided into conifers (mainly trees, although a few are shrubs) and several functionally divergent small groups (e.g. cycads), which were excluded from further consideration in this study because of the small sample size. The angiosperms were subdivided into five functional subgroups: angiosperm trees; shrubs; herbs; climbers; and epiphytes. The shrubs category included both true shrubs and suffruticose species. The climbers were similarly constructed by combining herbaceous vines and woody lianas. Herbs are non-woody herbaceous plants that are not epiphytes or ferns.

Each of our seven functional groups is characterized by unique and ecologically relevant traits. We used this to generate specific predictions about the most influential drivers of the distribution and dominance of each functional group based on the existing literature (see also Table 2). **Ferns** are vascular cryptogams that disperse via spores (Taylor, Kerp & Hass, 2005). They are also characterized by an independent, free-living gametophyte life stage that is dependent on water (Kato, 1993), and their lack of stomatal control makes them vulnerable to drought (Brodribb & McAdam, 2011). Ferns are limited by water availability, as only a few have adaptations to drought (Schuettpelz *et al.*, 2007). They are therefore expected to peak at *sloped regions* at *mid-high elevation* and *high precipitation* (Aldasoro, Cabezas & Aedo, 2004; Kessler *et al.*, 2011). **Epiphytes** grow on other plants, which they rely on only for support, i.e. non-parasitically (Benzing, 1990). They are mostly herbaceous, but also include some woody species (e.g. *Clusia* L.). The aerial position of epiphytes creates a need for high humidity and hence *high precipitation* (Walter, 1973; Benzing, 1990). Furthermore, epiphytes are strongly dependent on available substrate and their distribution is expected to be correlated with the distribution of humid *forests*. As these forests are often found in mountainous regions, epiphyte richness is expected to peak in *sloped regions* at *intermediate elevation*, with drought constriction at lower elevations, and frost and treeline constriction at higher elevations (Janzen, 1975; Gentry & Dodson, 1987; Kromer *et al.*, 2005). **Climbers** are defined as herbaceous or woody plants that also non-parasitically rely on other plants for support, but are rooted in the ground. Climbers are more frequent in the tropics because of the vulnerability of their wide vessels to embolisms under freezing conditions (Gentry, 1991). In

**Table 2.** Predictions for plant functional groups

	Climate			Topography			Edaphic			Disturbance			Vegetation		
	TSEAS	AP	PSEAS	Elevation	Slope	Sand	HII	Fire	TreeH.	References					
Ferns	L	H	L	M–H	M–H	M–H									Walter, 1973; Janzen, 1975; Gentry & Dodson, 1987; Benzing, 1990; Puigdefábragas & Pugnaire, 1999; Kromer <i>et al.</i> , 2005; Moorhead, Philpott & Bichier, 2010
Epiphytes	L	H	H	M–H	M	L			H						Walter, 1973; Gentry, 1991; Schnitzer, 2005; Jiménez-Castillo, Wiser & Lusk, 2007; Cai <i>et al.</i> , 2009
Climbers	L	L	H				M		H						Kato, 1993; Aldasoro <i>et al.</i> , 2004; Bhattarai, Vetaas & Grytnes, 2004; Karst, Gilbert & Lechowicz, 2005; Schuettpelz <i>et al.</i> , 2007; Walker & Sharpe, 2010; Brodribb & McAdam, 2011; Kessler <i>et al.</i> , 2011
Herbs	M–H	M	H	H		M–H			L						Crawley, 1997; Vasquez & Givnish, 1998; Gurevitch <i>et al.</i> , 2006; Keddy, 2007; Harrison <i>et al.</i> , 2010
Shrubs	M	L	H					H							Givnish, 1995; McIntyre <i>et al.</i> , 1999; Puigdefábragas & Pugnaire, 1999; Gurevitch <i>et al.</i> , 2006; Keddy, 2007; Eldridge <i>et al.</i> , 2011; Zizka <i>et al.</i> , 2014
Coniferous trees	M–H	L	L	H		H	L	L							Bond, 1989; Schulze, Beck, & Müller-Hohenstein, 2002; Gurevitch <i>et al.</i> , 2006; Keddy, 2007
Angiosperm trees	L	H	L	M–H		L	L	L							Bond, 1989; Crawley, 1997; Puigdefábragas & Pugnaire, 1999; Schulze <i>et al.</i> , 2002; Gurevitch <i>et al.</i> , 2006; Keddy, 2007; Harrison <i>et al.</i> , 2010; Staver <i>et al.</i> , 2011; Toledo <i>et al.</i> , 2011; Sandel & Svenning, 2013

Predictions were compiled from the existing literature on functional group dominance along environmental gradients. Dominance along the gradients was classified as low (L), medium (M), high (H) or unknown (blank). TSEAS, temperature seasonality; AP, annual precipitation; PSEAS, precipitation seasonality; Slope, percentage change in elevation; Sand, percentage of sand in soil; HII, human influence index; Fire, burnt area; TreeH., tree height. For details on the calculation of the variables, see the 'Material and methods' section.

tropical forests, their density increases with drought occurrence as a result of their competitive advantage in the assimilation of carbon and utilization of nitrogen and water compared with trees. Hence, the fraction of climbers should increase with *increasing precipitation seasonality* and *decreasing precipitation* (Schnitzer, 2005; Cai, Schnitzer & Bongers, 2009). Connected tree crowns support and facilitate climber occurrence by enabling their climbing, and climber distribution should follow the distribution of *forests* (Toledo *et al.*, 2011), with increases in *disturbed areas* as a result of strong pioneering abilities (Schnitzer & Bongers, 2011). **Herbs** generally have low water-storing ability and are increasingly found in areas with *high precipitation* (Gurevitch, Scheiner & Fox, 2006). As they require less carbon for construction, they can occupy colder and *more seasonal* environments than can trees (Harrison *et al.*, 2010), and competition for light results in higher frequencies of herbs in areas with *open canopies* in unfertile or drought-prone areas with *high soil sand* content (Vasquez & Givnish, 1998). **Shrubs** are self-standing woody plants that have more than one main stem arising from near the ground, which can prevent fires and herbivores from damaging the innermost stems. Furthermore, the basal meristem ensures regrowth in the case of damage to above-ground parts (Zizka, Govender & Higgins, 2014). Shrubs dominate in dry to very dry areas as a result of high drought tolerance (Givnish, 1995), and the shrub fraction should thus increase along an increasing temperature and *decreasing precipitation* gradient (Gurevitch *et al.*, 2006). The distribution of shrubs can be promoted by *disturbance* in the form of fires and grazing, which limit the distribution of tree competitors and favour the regenerative ability of shrubs (McIntyre *et al.*, 1999; Eldridge *et al.*, 2011). **Trees** are self-standing woody plants with a single main stem (Penfound, 1967). We considered two groups of trees: conifers (gymnosperms in the order Pinales); and angiosperm trees. **Coniferous trees** have mostly evergreen needle-like leaves with deciduous species being rare, whereas **angiosperm trees** include both evergreen and deciduous species, with leaves that are usually broader. The needle-like leaves of conifers have lower photosynthetic ability than the broader leaves of angiosperm trees that dominate productive environments. However, the majority of conifers with evergreen needles have year-round photosynthesis and are more resistant to drought (Bond, 1989). Coniferous trees have low photosynthetic ability of leaves and slow growth, which are competitive disadvantages compared with angiosperm trees in forest openings. This should limit their geographical distribution to colder, *more seasonal*, *drier* and nutrient-poor areas with *sandy soils*, where angiosperm tree seedlings are unable to establish (Bond, 1989). Angiosperm trees

require higher amounts of carbon than herbaceous plants for construction, and their frequency should increase with higher water and nutrient availability (Harrison *et al.*, 2010), and dominance should be higher in *wetter* and *less seasonal* regions (Crawley, 1997; Toledo *et al.*, 2011). *Disturbance* in the form of grazing and fires is limiting for the occurrence of both coniferous and angiosperm trees, as it hinders the establishment of seedlings (Bond, 1989; Staver, Archibald & Levin, 2011).

The functional group classification was combined with standardized georeferenced plant species occurrence data, also from the BIEN 2.0 database. This gave us a total of 83 854 species and 3 648 533 georeferenced observations with functional group assignments across the New World. The BIEN 2.0 database contains georeferenced plant observations from herbarium specimens, vegetation plot inventories, species distribution maps and plant traits covering the whole New World and spanning a wide time period from the beginning of the 17th century to 2011. Most data, however, were from the last few decades. All original data sources can be found on the BIEN website (<http://bien.nceas.ucsb.edu/bien/biendata/bien-2/sources/>). Before inclusion in the database, all species names were taxonomically standardized and synonyms updated to the most recent accepted name with the Taxonomic Name Resolution Service (version 1; Boyle *et al.*, 2013), with Tropicos® as the taxonomic authority (<http://www.tropicos.org>) Tropicos, 2014. Also, all specimens in the database were 'geoscrubbed' to ensure reliability of georeferenced data. We also excluded all specimens that were categorized as cultivated to focus on the naturally occurring patterns of plant functional groups.

Two measures of dominance for each functional group were calculated: relative species richness (proportion of total plant species richness per 100 × 100-km<sup>2</sup> grid cell) and relative frequency (proportion of total number of plant occurrences registered per grid cell). We calculated both measures to ensure that our results were robust. The data were analysed as proportions to represent dominance and to reduce any bias affecting the sampling of different functional groups differentially in a given grid cell. We define the dominance of a given functional group as high relative frequency of occurrences or species richness, and refer to it as such in the subsequent sections. The functional group observations were rasterized to 100 × 100-km<sup>2</sup> grid cells in a Lambert's azimuthal equal-area projection to eliminate area effects on species frequency and richness estimates. Total and functional group species richness per grid cell were corrected for differences in sampling intensity between grids using Margalef's diversity index, before calculating relative richness (Margalef, 1958). This

index standardizes the number of species in a sample in relation to the number of observations following the formula  $d = S - 1/\ln N$ , where  $S$  is the number of species and  $N$  is the number of specimens in the sample (we consider occurrences as specimens and grid cells as samples) (Gamito, 2010). As both of the functional group measures were proportions, they were arcsine transformed before statistical analysis. Sampling intensity varied greatly among cells (range, 1–70 518; median, 48), with poorly sampled cells possibly giving unreliable estimates of growth form dominance. Thus, we excluded cells with < 50 observations from all statistical analyses, even though this resulted in decreased spatial coverage (Supporting Information, Fig. S1).

#### STATISTICAL ANALYSIS

We tested the strength of the relationship between the relative richness and relative frequency of each functional group and the predictor variables with boosted regression trees (BRTs). The greatest strength of the BRT models is their ability to model non-linear responses and interactions between predictors to optimize model fits, whilst overcoming the drawbacks of simple classification and regression trees (CARTs) which have poor predictive performance (De'ath, 2007; Elith, Leathwick & Hastie, 2008). Non-linear responses and interactions are both likely to influence the relationship between functional groups and environmental predictors, and the BRT models will therefore provide highly reliable estimates of variable influence. BRTs combine large numbers of CART models adaptively to optimize predictions (Elith *et al.*, 2006; De'ath, 2007). Boosting differs from model averaging by being a stagewise procedure. Each CART is fitted randomly, but sequentially, until the addition of new trees no longer increases the accuracy of the model, as measured by model residuals (Greve *et al.*, 2011). We fitted the BRT models to the data using a slow learning rate of 0.001 and allowed for interactions of predictors by setting tree complexity to 5 for increased predictive ability (Leathwick *et al.*, 2008). The influence of interactions between the predictor variables was estimated with the `gbm.interactions` function in the `gbm` package. Ten-fold cross-validation was used to determine the optimal number of trees for each functional group, which ranged from 4950 to 11 500 (Table 3, Supporting Information, Table S3), and the bag fraction was set to 0.5 with observations being chosen at random (Elith *et al.*, 2008). The performance of the models was calculated as the cross-validation correlation (Tables 3, S3). We fitted response curves of functional group relative frequency and richness and the environmental variables to illustrate the direction of the relationship.

**Table 3.** Percentage contribution of each of the predictor variables for plant functional group species richness dominance

	TSEAS	AP	PSEAS	Elevation	Slope	Sand	HII	Fire	TreeH.	Sampling	No. of trees	CV correlation
Ferns	<b>12.0</b>	8.5	4.1	5.3	9.9	11.8	<b>19.1</b>	7.2	6.1	<b>16.0</b>	10 300	0.68
Epiphytes	<b>26.5</b>	<b>11.4</b>	4.6	3.6	5.8	5.3	4.4	6.6	4.4	<b>27.4</b>	7 150	0.80
Climbers	<b>54.0</b>	3.4	2.7	<b>9.8</b>	3.4	2.6	2.2	2.1	2.8	<b>17.1</b>	6 000	0.86
Herbs	<b>75.4</b>	<b>3.5</b>	2.7	2.8	1.4	1.5	2.2	3.4	2.5	<b>4.6</b>	6 100	0.91
Shrubs	<b>16.4</b>	<b>18.1</b>	<b>14.2</b>	8.6	3.4	6.6	6.8	5.8	6.7	13.4	10 200	0.74
Coniferous trees	9.1	5.8	3.7	1.5	8.9	2.3	<b>13.7</b>	<b>13.6</b>	–	<b>41.5</b>	5 350	0.83
Angiosperm trees	<b>58.6</b>	<b>9.7</b>	1.1	5.7	5.6	1.5	<b>7.1</b>	5.0	–	5.5	5 300	0.90

Bold indicates the three most important variables for each functional group in the boosted regression tree (BRT) model. Abbreviations: TSEAS, temperature seasonality; AP, annual precipitation; PSEAS, precipitation seasonality; HII, human influence index; TreeH., tree height; Sampling, total number of observations; No. of trees, number of trees fitted; CV correlation, cross-validation correlation.

To supplement the BRT results, we fitted single and multiple ordinary least-squares (OLS) regression models generated with an all subsets selection approach. We used all subsets selection to generate all possible combinations of models from the nine variables in the model set containing temperature seasonality. No pairwise interactions between model parameters were fitted to limit model complexity and to ease the interpretation of parameter coefficients. The model parameters were then calculated as averaged means weighted with the Akaike information criterion (AIC) of each model, following Burnham & Anderson (2002). Model averaging based on all of these models allowed us to use the models predictively and to compare both the strength and direction of parameter estimates (Symonds & Moussalli, 2010). Model performance was estimated as  $R^2$  values and model support as the summed AIC weights across all predictors. Predictor importance was calculated as the summed AIC weight for each individual predictor across all models following the zero method, which substitutes coefficients of predictors not included in the model with zero (Nakagawa & Freckleton, 2010).

Spatial autocorrelation is often present in species occurrence data and can bias parameter estimates (Dormann *et al.*, 2007). We tested for spatial autocorrelation by examining Moran's I value correlograms (Supporting Information, Fig. S2) for the residuals of the OLS model with all the variables for a given predictor variable set. The correlograms showed considerable spatial autocorrelation in all of the global OLS model residuals. Spatial autocorrelation is only handled to a limited degree by BRT models (Crane, Liedloff & Wintle, 2012), and we therefore repeated all subset selection and model averaging with simultaneous autoregressive (SAR) models, and only show regression results from these. We fitted the SAR models as spatial error models, as these have been shown to account effectively for spatial autocorrelation in response and explanatory variables and to provide reliable parameter estimates (Kissling & Carl, 2008). Similar to the OLS models, no interactions were fitted for the SAR models. Model performance was estimated as pseudo- $R^2$  values without the spatial terms, and model support as the summed AIC weights across all predictors. As a result of computational limits, we only averaged models with  $\Delta\text{AIC} < 10$ , as models with higher values have little influence on the final parameter estimates.

All GIS (packages 'raster', 'rgdal', 'SDMTools' and 'sp') and statistical (packages 'ape', 'dismo', 'fossil', 'gbm', 'gtools', 'Hmisc', 'leaps', 'MuMIn', 'ncf', 'plyr', 'qpcR', 'spdep' and 'vegan') operations were performed in R 3.0.0 (R Development Core Team, 2013).

## RESULTS

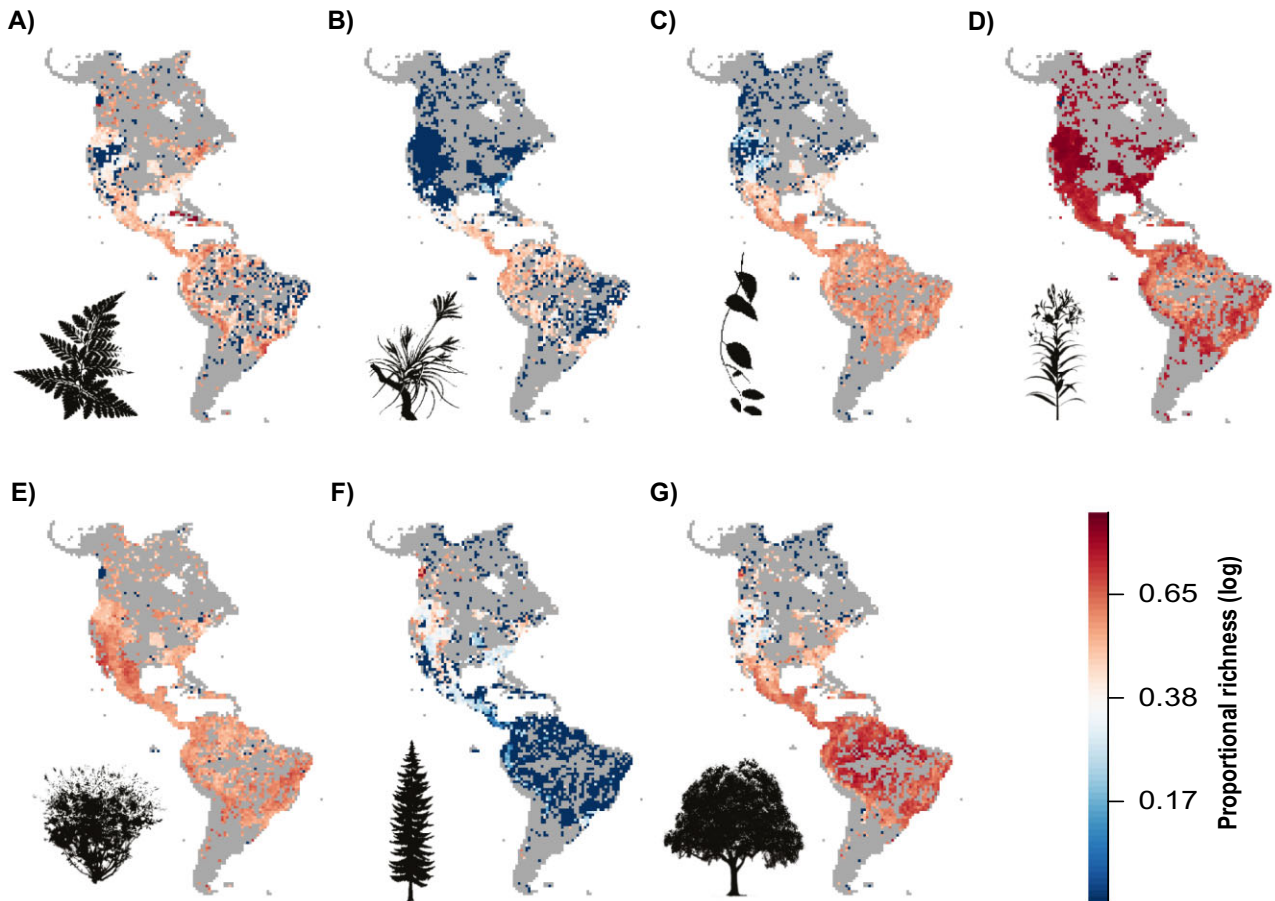
### SPATIAL PATTERNS OF FUNCTIONAL GROUP DOMINANCE

The seven functional groups showed distinct distribution patterns in dominance (Fig. 2,  $r = 0.01$ – $0.83$ , Supporting Information, Table S4). Epiphytes, climbers, ferns and angiosperm trees were most dominant in the tropics, especially in the Amazonian lowland. Herb dominance was highest in the temperate regions and decreased towards tropical regions. Shrub dominance was more patchily distributed, but with reoccurring high dominance in drier regions of both North and South America. Conifers were mainly dominant in North America, with only a few records in South America. The patterns of relative frequency were similar to those of relative richness for all functional groups, and these results are shown in Supporting Information (Figs S3, S4, S5a, S6a; Tables S3–S6).

### ENVIRONMENTAL PREDICTORS OF FUNCTIONAL GROUP DOMINANCE

The BRT models showed that temperature seasonality and annual precipitation were most common among the three variables explaining most of the variation in relative dominance for all functional groups, followed by HII and sampling intensity (Table 3). The cross-validation correlation values for the BRT models ranged from 0.68 to 0.91. The fitted response plots from the BRT models showed that epiphytes, climbers, shrubs and angiosperm trees dominated at low temperature seasonality, whereas herbs and conifers peaked at high temperature seasonality (Figs 3, S5b). Ferns had maximum dominance at high temperature seasonality, but lowest dominance at intermediate temperature seasonality. Epiphytes, ferns and angiosperm trees all had the highest dominance at high annual precipitation, whereas climbers, herbs, shrubs and coniferous trees dominated at low annual precipitation (Figs 3, S5b). Precipitation seasonality was also an important predictor of shrub dominance, with dominance peaking at high seasonality (Fig. S5b). Sand content was only among the more important predictors for ferns and epiphytes, which both peaked at low sand content. Elevation ranked high for climbers, but was generally less important than climatic factors (Table 3). HII was among the most important predictors for ferns and coniferous and angiosperm trees, but was much less important for the other functional groups. Ferns and herbs had highest dominance at medium to high HII, whereas epiphytes, climbers, shrubs and angiosperm trees peaked at low to intermediate levels of HII. Conifers were only dominant at the lowest levels





**Figure 2.** Geographical distribution of relative functional group species richness. All maps show the proportion of individual functional group species richness relative to the total species richness. A, Ferns. B, Epiphytes. C, Climbers. D, Herbs. E, Shrubs. F, Coniferous trees. G, Angiosperm trees. The maps illustrate the unique spatial patterns of relative species richness for the individual functional groups. Richness was calculated as the number of species of a given functional group within a  $100 \times 100\text{-km}^2$  grid cell. Cells with  $< 50$  observations (Fig. S1C) were excluded. Grey shows cells without any observations. Projection: Lambert azimuthal equal area.

of HII (Figs 3, S5b). Sampling ranked high for all functional groups, except shrubs and angiosperm trees (Table 3). Interaction effects were generally weak, but often included a combination of temperature and precipitation variables (Table S6). The only strong interaction was found between sand and HII for ferns, which peaked at low sand content and high HII (Supporting Information, Fig. S7).

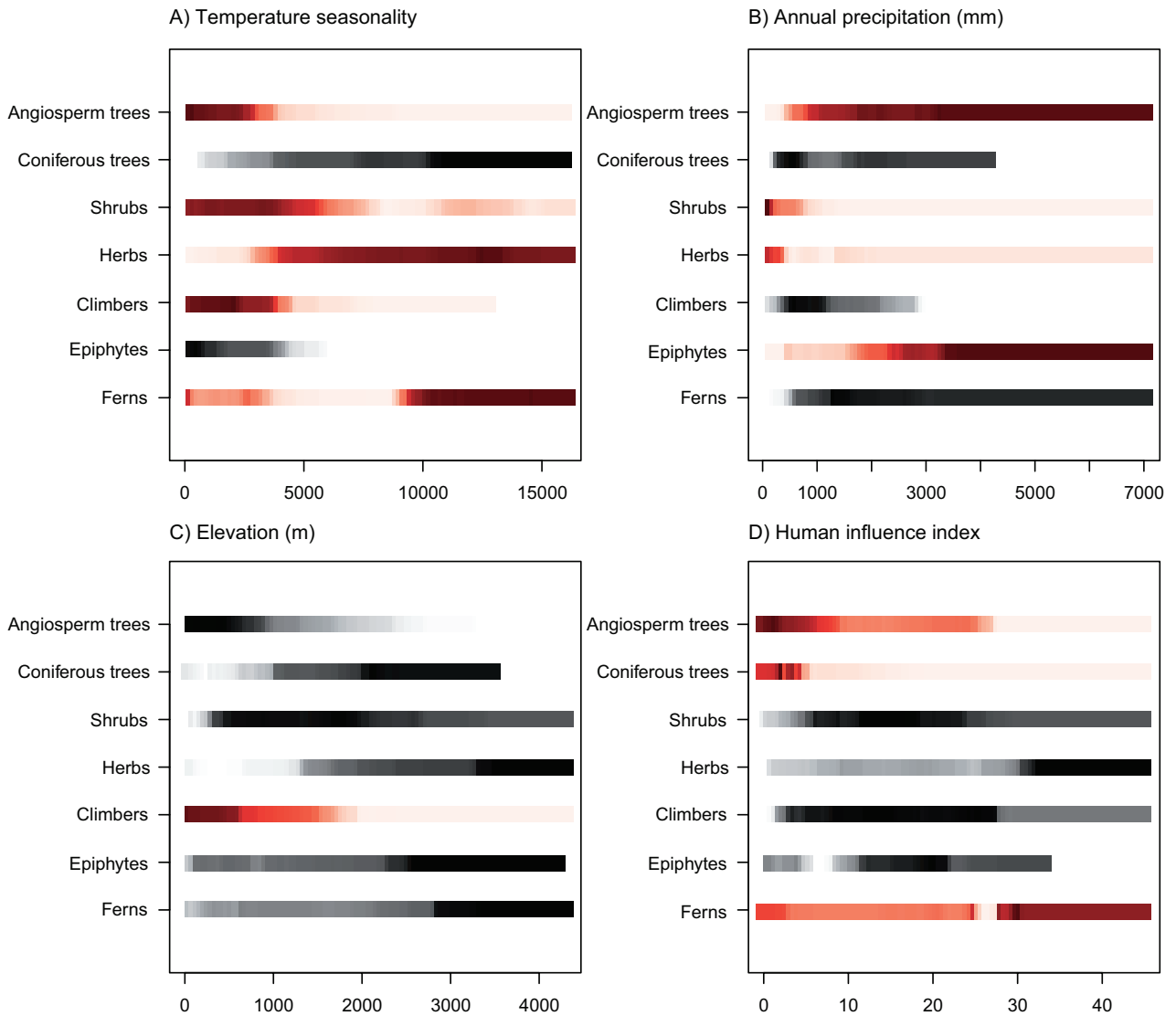
Model performance from the SAR multiple regression with all subsets selection was in the range  $R^2 = 0.25\text{--}0.70$ . The best predictor model for each functional group consisted of nearly all predictor variables, and so we used model averaging to quantify variable influence. Model averaging showed that temperature seasonality was always among the three most important predictors for all functional groups (Table 4). The importance of other predictors varied across the functional groups, but annual precipitation

and sampling were often among the most important predictors. The estimated variable effects were, with few exceptions, consistent with the results from the BRT models (Tables 3, 4).

## DISCUSSION

### GEOGRAPHICAL PATTERNS IN PLANT FUNCTIONAL GROUP DOMINANCE

The work of the earliest biogeographers, including Willdenow and von Humboldt, documented changing vegetation patterns along environmental gradients (Lomolino *et al.*, 2010). The differences in geographical patterns of our functional groups (Fig. 2) imply that they are driven by different underlying ecological or evolutionary mechanisms (Wiens, 2011). For instance, having a herbaceous habit has been linked



**Figure 3.** Modelled response of plant functional group dominance and environmental predictors obtained from boosted regression tree (BRT) models for the whole New World. The lines represent the relative species richness of a functional group as a function of a given environmental predictor when other predictors in the model are kept constant. Red lines show the three most important predictors for each functional group based on the BRT results (Table 3), whereas black is used for the six least important. The most intense shading shows the environmental conditions at which the functional group reaches highest dominance.

to cold adaptation (Billings, 1987). Plant functional groups are hypothesized to reflect adaptations to environmental conditions (Box, 1996), which probably explain the differences in their spatial distribution and relation to environmental drivers. Functional groups could also limit the distribution of one another through negative ecological interactions. For example, angiosperm trees are expected to outcompete the more slow-growing coniferous trees under favourable environmental conditions (Bond, 1989). This most probably explains the near-absence of coniferous trees in the Amazonian region of South America where

angiosperm tree dominance peaks (Fig. 2). However, the two functional groups overlap substantially elsewhere in the Americas, suggesting that the competitive dominance of angiosperm trees is also dependent on local conditions. The presence of certain functional groups could also promote the distribution of other functional groups through positive ecological interactions. Epiphytes and climbers both rely on woody plants for structural support and substrate, consistent with a close distributional overlap with angiosperm trees. A similar overlap is not found with coniferous trees, as climatic constraints separate

**Table 4.** Relationship between the distribution of plant functional group species richness and environmental predictors

	Ferns	Epiphytes	Climbers	Herbs	Shrubs	Coniferous trees	Angiosperm trees
Climate							
TSEAS	<b>-0.52 (1)</b>	<b>-0.19 (1)</b>	<b>-0.12 (1)</b>	<b>0.93 (1)</b>	<b>-0.13 (1)</b>	<b>-0.25 (1)</b>	<b>-0.78 (1)</b>
TSEAS <sup>2</sup>	<b>0.48 (1)</b>	-	-	<b>-0.51 (1)</b>	<b>-0.05 (0.3)</b>	-	<b>0.48 (1)</b>
AP	0.01 (0.34)	<b>0.12 (1)</b>	-0.08 (1)	-0.05 (0.8)	<b>-0.49 (1)</b>	0.09 (0.76)	<b>0.26 (1)</b>
AP <sup>2</sup>	-	-	-0.00 (0.3)	0.00 (0.3)	<b>0.09 (1)</b>	-	<b>-0.04 (1)</b>
PSEAS	-0.03 (0.7)	-0.10 (1)	0.04 (1)	0.05 (1)	0.02 (1)	0.03 (0.5)	-0.01 (0.6)
PSEAS <sup>2</sup>	-	0.00 (0.3)	0.05 (1)	0.01 (0.5)	-	-	0.01 (0.5)
Topographic							
Elevation	<b>0.20 (1)</b>	0.04 (0.6)	<b>-0.27 (1)</b>	0.06 (1)	-0.00 (0.3)	0.03 (0.48)	-0.08 (1)
Elevation <sup>2</sup>	-	-	<b>0.00 (0.3)</b>	0.02 (1)	-	-	-0.02 (0.5)
Slope	<b>0.18 (1)</b>	0.06 (0.7)	-0.12 (1)	-0.01 (0.5)	0.07 (1)	0.01 (0.38)	-0.13 (1)
Slope <sup>2</sup>	-	-	0.02 (1)	0.00 (0.2)	-	-	0.02 (1)
Edaphic							
Sand	-0.09 (1)	<b>-0.11 (1)</b>	-0.00 (0.5)	-0.00 (0.3)	<b>0.09 (1)</b>	0.02 (0.89)	-0.00 (0.4)
Sand <sup>2</sup>	0.03 (1)	-	-0.00 (0.2)	-	-	-	-0.00 (1)
Disturbance							
HII	0.02 (1)	-0.03 (0.5)	0.06 (1)	0.00 (0.3)	-0.04 (1)	<b>-0.15 (1)</b>	-0.01 (1)
HII <sup>2</sup>	0.01 (0.6)	-	-	-	-0.06 (1)	<b>0.00 (0.3)</b>	-
Fire	-0.02 (0.6)	-0.08 (0.8)	-0.00 (0.4)	0.02 (0.6)	-0.06 (1)	0.00 (0.3)	0.00 (0.4)
Fire <sup>2</sup>	-	0.01 (0.4)	0.00 (0.1)	-0.00 (0.2)	-	-	0.00 (0.14)
Vegetation related							
TreeH.	0.13 (1)	0.08 (0.9)	0.08 (1)	<b>-0.11 (1)</b>	-0.07 (1)	-	-
TreeH. <sup>2</sup>	-	-	-0.04 (1)	<b>0.04 (1)</b>	0.05 (1)	-	-
Sampling							
Samples	-0.10 (1)	0.04 (0.7)	<b>-0.23 (1)</b>	<b>0.06 (1)</b>	-0.3 (1)	<b>-0.45 (1)</b>	<b>-0.14 (1)</b>
Samples <sup>2</sup>	0.01 (1)	-	<b>0.02 (1)</b>	-	0.02 (1)	<b>0.04 (1)</b>	<b>0.01 (1)</b>
Model performance							
R <sup>2</sup>	0.26	0.30	0.58	0.70	0.25	0.31	0.60

Functional group richness is relative and proportional to the total number of species. Parameter coefficients were all standardized and calculated with the simultaneous autoregressive (SAR) model averaging procedure. Numbers in parentheses show the Akaike information criterion (AIC) weight for a given parameter. Numbers in bold indicate the three most important predictor variables for each growth form (those with the highest coefficient values). Model performance was found for the global model. Abbreviations as for Table 3.

these functional groups. Decreasing epiphyte richness at high elevation is linked to treelines, but also to low temperatures, although the physiological mechanism is unknown (Kromer *et al.*, 2005). The geographical pattern found in this study of a near-absence of epiphytes outside the tropical regions indicates a similar elevational delimitation. Climbers achieve structural support from trees and can invest heavily in their exceptionally efficient vascular system (Schnitzer, 2005). However, this also makes them vulnerable to freezing-induced embolisms (Gallagher & Leishman, 2012) and explains the low climber dominance in the colder areas inhabited by conifers.

#### CLIMATIC AND NON-CLIMATIC NATURAL DRIVERS OF GEOGRAPHICAL PATTERNS

The importance of climatic factors for all functional groups (Table 3) supports hypothesis H<sub>1</sub> and shows the strong influence of climate on plant communities through water availability (Walter, 1973), consistent with interactions between climatic predictors (Table S6). Our results were generally consistent with predictions from the literature (Table 2) and quantitatively confirm the strong link between plant functional groups and climate. The climatic predictors explained 24.6–81.6% of all explained variance (sum of percentage contribution, Table 3), emphasizing the high importance of climate for large-scale geographical patterns of plant functional groups.

Trees require larger amounts of carbon for construction than do smaller plants and are expected to dominate in warmer and wetter environments, with the opposite being true for smaller plants, such as shrubs and herbs (Harrison *et al.*, 2010). Angiosperm trees are dominant in the most favourable environments, whereas herbs are dominant in areas with higher temperature seasonality and lower precipitation, and shrubs are clearly dominant in the driest areas where high precipitation seasonality increases the risk of drought events. Conifers are dominant in cold and dry areas environmentally opposite to angiosperm trees, consistent with our predictions (Table 2), but are not strongly linked to any climatic predictor. We also found the predicted division in climatic preference for epiphytes and climbers (Table 2). Both have their highest relative dominance under tropical conditions. However, the epiphytes, which require high humidity (Benzing, 1990), are dominant in wetter areas, whereas climbers are dominant in drier areas, consistent with their strong ability to extract and contain water (Schnitzer, 2005). Ferns are dominant in areas of high annual precipitation (Fig. 3), reflecting high water dependence and a preference for mesic habitats (Kato, 1993). A study from Africa, however, has shown that fern species richness is underestimated for arid

regions (Anthelme, Abdoukader & Viane, 2011). This pattern might be similar for the New World if sampling of ferns was focused on humid areas. Insufficient sampling could explain why the fern models showed low performance.

Previous climate change events have resulted in shifting communities and changing functional composition (Davis & Shaw, 2001; Cárdenas *et al.*, 2014). The strong connection to climate suggests that current and future climate change can severely influence spatial patterns of plant functional group dominance. Encroachment of woody shrubs and trees into grasslands has been documented for North American grasslands (Knapp *et al.*, 2008) and increases in climbers have been found for tropical forests (Schnitzer & Bongers, 2011), whereas epiphytes and trees have been identified as especially prone to extinction risk (Leão *et al.*, 2014). This illustrates that plant functional group responses to climate change are complex and worthy of further investigation.

The topographic predictors elevation and slope are also strong predictors of some functional groups (Table 3), consistent with local-scale studies (e.g. Waide *et al.*, 1999; Moeslund *et al.*, 2013). Both are positively related to both epiphyte and fern relative richness, confirming the prediction of high dominance of both functional groups in humid montane rainforests (Figs 3, S5b; Table 2) (Benzing, 1990). Global forest cover is strongly correlated with increasing slope as a result of anthropogenic land clearing on more accessible low slope areas (Sandel & Svenning, 2013). We also found a positive relationship between slope and both shrubs and coniferous trees, whereas the relationship was negative for angiosperm trees (Figs 3, S5b; Table 2). The generally slower growing conifers only have a competitive advantage over angiosperm trees in cold or nutrient-poor areas (Bond, 1989), consistent with a strong connection to temperature seasonality (Table 3) and clear conifer dominance in the coldest and highest areas (Figs 3, S5b).

Tree height was included as a proxy for ecological interactions between trees and other functional groups. Epiphytes and climbers dominate at increasing tree height (Fig. S5b), consistent with the need of both groups for trees for support (Benzing, 1990). Tree height generally ranks low for the functional groups. Our spatial resolution may be too coarse to determine the importance of species interactions, which more probably influence local-scale patterns (McGill, 2010). Alternatively, tree height may not be representative of interactions affecting functional group distribution, despite canopy density having strong local effects (Oberle, Grace & Chase, 2009). We also expected a strong link to soil conditions, but only found a strong effect for ferns, showing that other environmental factors are more important at this bicontinental scale.

## HUMAN INFLUENCE

Humans have transformed natural ecosystems worldwide, and future land use changes are likely to escalate anthropogenic impacts (Ellis, 2011). HII is strongly related to ferns with dominance at medium to high HII (Fig. 3). A positive connection to HII could be a result of higher sampling in areas closer to cities and infrastructure (Reddy & Da, 2003). Whether this effect influences ferns more than other functional groups is uncertain, but should be explored further. Increased sampling focused on ferns might also improve model explanatory power, which is particularly low for this functional group (Table 3). On the contrary, there is no indication that ferns are particularly poorly sampled. The connection to HII could simply be caused by ferns and humans occupying similar conditions, consistent with a strong interaction between sand and HII (Fig. S7). Many ferns are rapid colonizers and thus tolerant of disturbance, with many being clearly well adapted and even benefiting from disturbance (Arens & Baracaldo, 1998; Jenkins & Parker, 2000; Slocum *et al.*, 2004). Global forest cover has been negatively affected by land clearing (Hansen *et al.*, 2013) and is a probable cause of the strong and negative relationship between HII and coniferous and angiosperm trees. This result highlights the fact that natural forest ecosystems have been and still are pressurized by human land use changes (Butchart *et al.*, 2010). Other functional groups might benefit from human-mediated dispersal, disturbance or land use changes (Ellis, Antill & Kreft, 2012). For instance, shrubs are, in some cases, promoted by grazing (Roques, O'Connor & Watkinson, 2001), although the functional group is not strongly correlated with HII (Table 3). Grazing is difficult to measure at large scales and is unlikely to be captured well by HII, explaining the weak connection to shrub dominance.

Whether plant distributions are controlled by resources (e.g. light or water) or consumers (grazers or fire) has been much debated (Hairston, Smith & Slobodkin, 1960; Bond, 2005). We expected fire to affect shrub dominance strongly, as this functional group has been known to be promoted by fires (Knapp *et al.*, 2008; Papanikolaou *et al.*, 2011). However, the effect is rather weak (Table 3). Conifers are strongly and negatively affected by fire, consistent with deforestation after fires (Bond, 1989). Fires strongly affect local plant communities, but the effect is weak compared with the other environmental predictors at our continental scale. This pattern is consistent with results from a previous study covering the African continent (Greve *et al.*, 2011). High-impact fires are, however, expected to increase in frequency and severity with future climate change to the extent of gradu-

ally shifting vegetation zones at larger scales (Bowman *et al.*, 2011; Staver *et al.*, 2011).

Overall, these results show that natural environmental predictors are not the only influential drivers of functional group dominance at the continental scale. Human activities also shape large-scale biogeographical patterns, supporting hypothesis H<sub>2</sub>. The responses to disturbance are mostly consistent with hypothesis H<sub>3</sub>, showing that disturbance and human activities can affect broad-scale vegetation patterns via interactions with plant functional traits.

## METHODOLOGICAL CONSIDERATIONS

Increased sampling near roads, cities and rivers can create strong spatial sampling bias (Schulman, Toivonen & Ruokolainen, 2007) and can severely affect species richness estimates (Gotelli & Colwell, 2001; Engemann *et al.*, 2015). Despite the use of the Margalef correction and inclusion of sampling intensity in our models, the positive correlation to HII by epiphytes and ferns might be caused by sampling bias, although neither was the least sampled functional group (Supporting Information, Fig. S8). Coniferous trees were the least sampled functional group in our dataset and also had the strongest correlation to sampling (Table 4). Most functional groups only varied slightly with sampling intensity, whereas herbs and angiosperm trees showed more variation (Supporting Information, Fig. S9), and it is possible that the functional groups are differently sampled. The effect of spatial sampling bias could be further explored by investigating distances to roads, cities and herbaria for each functional group. The strong effect of sampling emphasizes the underlying issue of sampling bias in unstandardized datasets compiled from multiple sources (Martin, Blossey & Ellis, 2012; Amano & Sutherland, 2013). A promising new approach is stacking of species distribution models (Dubuis *et al.*, 2011) which are less affected by sampling (Loiselle *et al.*, 2008). Such maps are increasingly being made available from diversity databases (e.g. BIEN 2013, <http://bien.nceas.ucsb.edu/bien/>; Map of Life, [www.mappinglife.org](http://www.mappinglife.org)).

Spatial autocorrelation can influence the importance of parameter estimates (Kissling & Carl, 2008). We used SAR as a supplement to BRT models, as these do not entirely account for spatial dependence in model residuals. The predictive ability of BRT models and validity of cross-validation values could be improved by specifically handling spatial autocorrelation. Although sampling bias and spatial autocorrelation could influence our results (Kissling & Carl, 2008; Michalcová *et al.*, 2011), both modelling approaches concurred on the most important drivers of functional group dominance (Tables 3, 4).

## FUTURE PERSPECTIVES

The definition of plant functional types is an important aspect of dynamic modelling of vegetation responses (DGVMs) to climate change (Harrison *et al.*, 2010). We have quantitatively shown that plant functional group dominance shifts along natural climatic gradients across two continents. The use of functional groups ensures that our results are globally comparable (Duckworth *et al.*, 2000). The congruence between our results and predicted relationships shows that our dataset and analytical approach are robust. The results can be used complementarily to the functional types employed in DGVMs (see, for example, Scheiter & Higgins, 2009). In addition, we also showed that these large-scale patterns are influenced by anthropogenic disturbance. Synergistic effects of multiple pressures could cause greater effects than observed for each predictor alone (Brook, Sodhi & Bradshaw, 2008), and should be included in dynamic models aimed at predicting vegetation response. Different drivers work at different scales (McGill, 2010) and future work should focus on testing predictor scale dependence for functional groups. However, we found that strong sampling effects and increasing resolution to a finer grain would increase the effect of sampling bias as spatial coverage decreases.

All functional groups showed clear and strong connections to climate previously not confirmed statistically for a dataset covering the whole New World. Natural environmental predictors were not the only influential drivers of functional group dominance. Disturbance and human activities also affected dominance of the functional groups through functional responses. Future climate change in combination with increased anthropogenic pressures has the potential to shift the geographical distribution of functional vegetation groups and to affect ecosystem function through changes in plant community functional composition.

## ACKNOWLEDGEMENTS

This work was conducted as part of the Botanical Information and Ecology Network (BIEN) Working Group (PIs B.J.E., Richard Condit, R.K.P., Brad Boyle, Steven Dolins and Barbara M. Thiers) supported by the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (Grant #EF-0553768), the University of California, Santa Barbara, and the State of California. The BIEN Working Group was also supported by the iPlant collaborative (National Science Foundation #DBI-0735191; URL: [www.iplantcollaborative.org](http://www.iplantcollaborative.org)). We thank all the contributors (see <http://>

[bien.nceas.ucsb.edu/bien/people/data-providers/](http://bien.nceas.ucsb.edu/bien/people/data-providers/) for a full list) for the invaluable data provided to BIEN. We also thank Z. Wang, A. Barfod, R. Field, J. Bailey and an anonymous referee for comments on earlier versions of this paper. Funding for K.E. was provided through Aarhus University. J.-C.S. was supported by the European Research Council (ERC-2012-StG-310886-HISTFUNC). NM-H acknowledges support by an Elite-Forsk Award and the Aarhus University Research Foundation.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

**Figure S1.** Geographical distribution of species richness and occurrences for 100 × 100-km<sup>2</sup> grid cells. Maps show, for each grid cell, raw species richness (A), total occurrences (B) and occurrences for cells with at least 50 occurrences (C). Species richness was calculated as the total number of species within a grid cell and recalculated with the Margalef correction. Projection: Lambert azimuthal equal area.

**Figure S2.** Correlograms for residuals from ordinary least-squares (OLS) and simultaneous autoregressive (SAR) models. The models were fitted for the relative species richness and frequency for each plant functional group and the full set of ten environmental predictors. The spatial weights matrix of all SAR models was calculated with the smallest neighbourhood distance that ensured each observation had at least one neighbour.

The  $y$ -axis shows Moran's  $I$  value, as a measure of autocorrelation, against the distance classes on the  $x$ -axis for comparison of the spatial autocorrelation pattern with increasing distance.

**Figure S3.** Geographical distribution of functional group frequency. All maps show the proportion of individual functional group frequency to the total frequency. A, Ferns. B, Epiphytes. C, Climbers. D, Herbs. E, Shrubs. F, Coniferous trees. G, Angiosperm trees. The maps illustrate the unique spatial patterns of frequency for the individual functional groups. Frequency was calculated as the number of observations of a given functional group within a  $100 \times 100\text{-km}^2$  grid cell. Cells with  $< 50$  observations (Fig. S1C) were excluded. Grey shows cells without any observations. Projection: Lambert azimuthal equal area.

**Figure S4.** Modelled response of plant functional group dominance and environmental predictors obtained from boosted regression tree (BRT) models for the whole New World. The lines represent the relative frequency of a functional group as a function of a given environmental predictor when other predictors in the model are kept constant. Red lines show the four most important predictors for each functional group based on the BRT results (Table 3), whereas black is used for the six least important. The most intense shading shows the environmental conditions at which the functional group reaches highest dominance.

**Figure S5a.** Response curves of plant functional group dominance and environmental predictors obtained from boosted regression tree (BRT) models for the whole New World. The curves represent the relative frequency of a functional group as a function of a given environmental predictor when other predictors in the model are kept constant. For comparability, the  $y$ -axis of all curves has been scaled to the interval 0–1. Therefore, the curves show trends, not actual values.

**Figure S5b.** Response curves of plant functional group dominance and environmental predictors obtained from boosted regression tree (BRT) models for the whole New World. The curves represent the relative species richness of a functional group as a function of a given environmental predictor when other predictors in the model are kept constant. For comparability, the  $y$ -axis of all curves has been scaled to the interval 0–1. Therefore, the curves show trends, not actual values.

**Figure S6a.** Response curves of plant functional groups and environmental predictors obtained from model-averaged simultaneous autoregressive (SAR) models for the whole New World. The curves were fitted from parameter estimates from the SAR models and represent the relative frequency of a functional group as a function of a given environmental predictor when other predictors in the model are also considered.

**Figure S6b.** Response curves of plant functional groups and environmental predictors obtained from model-averaged simultaneous autoregressive (SAR) models for the whole New World. The curves were fitted from parameter estimates from the SAR models and represent the relative species richness of a functional group as a function of a given environmental predictor when other predictors in the model are also considered.

**Figure S7.** Effect of interaction between sand content of soil and human influence index (HII) for relative fern species richness.

**Figure S8.** Histograms showing the number of species (A) and the number of occurrences (B) for each functional group.

**Figure S9.** Loess regression lines between sampling and the proportion of individual functional group frequency to the total frequency (A) and the proportion of individual functional group species richness to the total species richness (B).

**Table S1.** Correlations among the environmental predictor variables. The correlations were calculated as pairwise Pearson product-moment coefficients. Abbreviations: AMT, annual mean temperature; TSEAS, temperature seasonality; AP, annual precipitation; PSEAS, precipitation seasonality; AET, actual evapotranspiration; Topo, topographical heterogeneity; HII, human influence index; TreeH., tree height; Sampling, total number of observations.

**Table S2.** Model sets. 'X' marks which variables were included in a given model set. Model set 2 showed the best performance measured as both  $R^2$  and Akaike information criterion (AIC) values across the functional groups, and was chosen for all subsequent analyses. Consensus shows the number of times a model was selected as the best fitting for a functional group for both frequency and species richness. Abbreviations: AMT, annual mean temperature; TSEAS, temperature seasonality; AP, annual precipitation; PSEAS, precipitation seasonality; AET, actual evapotranspiration; HII, human influence index; TreeH., tree height.

**Table S3.** Percentage contribution of each of the predictor variables for plant functional group frequency. Bold indicates the three most important variables for each functional group in the boosted regression tree (BRT) model. Abbreviations as for Table 3.

**Table S4.** Correlation of functional group distribution. Correlation was calculated as pairwise Pearson product-moment coefficients.

**Table S5.** Relationship between the distribution of plant functional group frequency and environmental predictors. Functional group frequency is relative and proportional to the total number of observations. Parameter coefficients were all standardized and calculated with the simultaneous autoregressive (SAR) model averaging procedure. Numbers in parentheses show the Akaike information criterion (AIC) weight for a given parameter. Numbers in bold indicate the three most important predictor variables for each growth form (those with the highest coefficient values). Model performance was found for the global model. Abbreviations as for Table 3.

**Table S6.** Interactions between environmental predictors from the boosted regression tree (BRT) models. Interactions between predictor variables with the highest median contribution to BRT models. Numbers indicate the relative degree of departure from a purely additive effect. A value of zero indicates that no interaction was present, and values above zero indicate an increasing effect of the interaction compared with a purely additive effect. Abbreviations: TSEAS, temperature seasonality; AP, annual precipitation; PSEAS, precipitation seasonality; Elev, elevation; HII, human influence index; TreeH., tree height; Samp, sampling.