



# Geographical variation and environmental correlates of functional trait distributions in palms (Arecaceae) across the New World

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Functional traits play a key role in driving biodiversity effects on ecosystem functioning. Here, we examine the geographical distributions of three key functional traits in New World palms (Arecaceae), an ecologically important plant group, and their relationships with current climate, soil and glacial–interglacial climate change. We combined range maps for the New World ( $N = 541$  palm species) with data on traits (leaf size, stem height and fruit size), representing the leaf–height–seed plant strategy scheme of Westoby, to estimate median trait values for palm species assemblages in  $110 \times 110$ -km grid cells. Spatial and non-spatial multi-predictor regressions were used with the Akaike Information Criterion to identify minimum adequate models. Present-day seasonality in temperature and precipitation played a major role in explaining geographical variation of all traits. Mean annual temperature and annual precipitation were additionally important for median leaf size. Glacial–interglacial temperature change was the most important predictor for median fruit size. Large-scale soil gradients played only a minor role overall. These results suggest that current climate (larger median trait values with increasing seasonality) and glacial–interglacial temperature change (larger median fruit size with increasing Quaternary temperature anomaly) are important drivers for functional trait distributions of New World palms. © 2015 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2015, **179**, 602–617.

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## INTRODUCTION

Functional traits play a key role in driving biodiversity effects on ecosystem functioning (Mason *et al.*, 2005; Swenson *et al.*, 2012). They are defined as traits which impact fitness indirectly through effects on growth, reproduction and survival (Diaz & Cabido, 2001). Furthermore, functional traits can be divided into effect and response traits (Violle *et al.*, 2007), with the former modulating impacts on ecosystem functioning and the latter shaping responses to environmental conditions (Diaz *et al.*, 2013). In recent years, a few studies have started to explore the relationships between geographical patterns of plant functional trait

distributions and their underlying environmental drivers. Geographical variation of plant functional traits can be strongly related to the current environment. For example, median seed mass of plant assemblages across Germany correlates with soil pH and soil moisture (Tautenhahn *et al.*, 2008), different morphological and physiological variables of North American trees (e.g. mean tree height, seed mass) correlate with current precipitation and temperature (Swenson & Weiser, 2010), and mean leaf area of tropical forest trees in Panama and China is mainly related to soil fertility and acidity (Liu *et al.*, 2012). Moreover, average maximum tree height across species correlates with mean annual temperature and precipitation along the Bolivian Andes (Kessler, Böhner & Kluge, 2007), mean leaf size across vascular plant species is

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related to mean annual precipitation in south-eastern Australia (McDonald *et al.*, 2003) and Amazonia (Malhado *et al.*, 2009), and abundance-weighted assemblage average seed size is related to soil characteristics in tropical forests of the Guiana Shield (ter Steege & Hammond, 2001) and Amazonia (ter Steege *et al.*, 2006). Assemblage-level means of other plant traits such as leaf size have also been found to change along elevational (Gurevitch, 1988), latitudinal (Hulshof *et al.*, 2013) and soil gradients (Liu *et al.*, 2012).

Palms (Arecaceae) are an important plant family in tropical and subtropical regions, with high species richness, a variety of growth forms and keystone ecological importance in many areas (Dransfield *et al.*, 2008; Balslev *et al.*, 2011). Arecaceae comprise *c.* 2400 species worldwide (Govaerts & Dransfield, 2005) and are a major canopy and understorey element in many tropical and subtropical forests (Gentry, 1988). Palms play an important role in biogeographical theory and represent a suitable model organism group for understanding the drivers of high tropical biodiversity and its geographical variation (Eiserhardt *et al.*, 2011). Their global distribution and diversity are strongly linked to temperature and precipitation and historical regional drivers (Kissling *et al.*, 2012a) and palms are considered to be indicators for warm and humid climates in palaeo-ecological reconstructions (Greenwood & Wing, 1995; Morley, 2000). Further, there is evidence that their species diversity is driven by both current and palaeoclimatic factors (Blach-Overgaard *et al.*, 2010, 2013; Eiserhardt *et al.*, 2011; Kissling *et al.*, 2012a,b), but no studies have so far focused on large-scale patterns of functional trait distributions and how they may be constrained by present-day environment and long-term historical constraints, e.g. glacial–interglacial climatic oscillations. Here, we focus on this issue for palms in the New World, where they are diverse and ecologically important (Dransfield *et al.*, 2008).

The leaf–height–seed (LHS) plant ecology strategy scheme (Westoby, 1998) suggests that variables related to leaf morphology [especially specific leaf area (SLA)], stem height and seed size (usually seed mass) capture the main trait axes of responses of a plant species to competition, stress and disturbance. We focus here on maximum leaf size, stem height and fruit size to represent these major trait axes for palms. We use maximum leaf size, measured as rachis length of the longest individual leaf, as a unidimensional measurement to represent leaf morphology as data on leaf area or SLA are not widely available for palms and because maximum leaf size is commonly used in analyses of leaf traits (e.g. McDonald *et al.*, 2003). Furthermore, fruit size (here fruit volume) was used as a proxy for seed mass

because data on the latter are limited for palms. In the LHS scheme, the leaf component is regarded to be a representative of the light-catching area, which is responsible for photosynthetic capacity, and hence energy production of the plant and therefore also directly involved in competition for light with other competitors (Westoby, 1998). In palms, leaf size is relevant for tall species to reach canopy gaps, e.g. in disturbed forests (de Granville, 1992). By contrast, leaf size is also relevant for understorey palms because reduced light availability causes leaves to be shaped towards sizes and structures that maximize the effectiveness of photosynthesis and the tolerance to increased shading, e.g. by decreasing leaf area to reduce biomass costs of leaf support (Chazdon, 1991). Maximum stem height represents the accessibility of a plant to light and its exposure to heat load, humidity and wind speeds (Westoby, 1998). Further, in forests with a tall, dense canopy layer, stem height of many palm species might be small as small stature affords greater shade tolerance (Chazdon, 1991). In contrast, in disturbed forests erect solitary palms may be frequent due to their ability to exploit tree-fall gaps to grow to the canopy (de Granville, 1992). Seed and fruit size further determine the establishment success of plants because larger seed masses enable seedlings to survive hazards such as drought better (Westoby *et al.*, 1996). Moreover, dispersal distances of animal-dispersed plants rely on seed size as large seeds can only be dispersed by animals large enough to swallow them (de Almeida & Galetti, 2007; Andreazzi *et al.*, 2012; Galetti *et al.*, 2013).

Several questions concerning functional trait distributions and their environmental correlates remain unanswered and only few studies have focused on functional traits across broad macroecological scales (ter Steege *et al.*, 2006; Tautenhahn *et al.*, 2008; Ordoñez *et al.*, 2009; Peppe *et al.*, 2011; Moles *et al.*, 2014). Previous studies have detected mean leaf size across plant species to decrease towards dry (Giliberto & Estay, 1978; McDonald *et al.*, 2003) and cold climates (Peppe *et al.*, 2011) and acidic soil conditions (Liu *et al.*, 2012), whereas high mean leaf sizes are associated with warm, moist areas with low annual seasonality (Murphy & Lugo, 1986; Dransfield *et al.*, 2008; Balslev *et al.*, 2011), e.g. in low latitudinal moist rainforests such as the Amazon (Hulshof *et al.*, 2013). In other studies it has been shown that tree height correlates positively with temperature and precipitation (e.g. Kessler *et al.*, 2007), peaking in warm and moist climates (Swenson & Weiser, 2010), whereas the small-stemmed understorey palm genus *Geonoma* Willd. was shown to be most species-rich in moist, warm lowland forests (Chazdon, 1991). Furthermore, soils may also play a role, e.g. with Amazonian palms having low assemblage-level mean stem height on poor

soils (Balslev *et al.*, 2011). Several studies have focused on fruit and seed sizes and their environmental drivers. In Australia, plant seed mass was found to be high in habitats with high mean annual temperature, possibly due to increased metabolic costs and expenditure (Murray *et al.*, 2004). Furthermore, precipitation in North America (Swenson & Weiser, 2010), poor soils in a Malaysian rainforest (Katabuchi *et al.*, 2012) and acidic soils in Germany (Tautenhahn *et al.*, 2008) were shown to be positively related to seed size. Soil variation is often important for plant assemblage composition (Vormisto *et al.*, 2000; Tuomisto *et al.*, 2002) and trait distributions at local spatial scales (Liu *et al.*, 2012). However, edaphic gradients also exist across broad spatial scales, notably in the Neotropics where nutrient-poor soils exist in parts of the cerrado and on the Guiana Shield (Furley & Ratter, 1988; ter Steege *et al.*, 2006) and nutrient-rich soils in the Chaco, north-eastern Brazil and the eastern Andean slopes (Ratter *et al.*, 1978; Pennington, Prado & Pendry, 2000). Poor soil conditions may lead to reduced disturbance with lower turnover of individual trees, smaller canopy gaps and more shading, thereby favouring larger seeds by reducing stress tolerance to seedlings (ter Steege & Hammond, 2001; ter Steege *et al.*, 2006). Although the focus has been on contemporary environmental drivers of functional trait composition, historical factors may also play a role. Notably, strong Quaternary climate oscillations could also influence large-scale distribution patterns of traits because environmental filtering might favour species with specific traits (Ordóñez & Svenning, 2015), e.g. large seed size due to survival benefits under relatively harsh glacial climatic conditions (Kissling *et al.*, 2012b).

To our knowledge, no study has so far focused on palm functional traits at a macroecological scale or linked palm functional trait patterns to long-term historical drivers such as palaeoclimate. Here, we test the relationships of assemblage-level medians of three key functional palm traits (leaf size, stem height and fruit size) to three classes of potential drivers, namely current climate, soil and palaeoclimate. We assess whether environmental predictor variables related to climate (Kissling *et al.*, 2012a), soil (Balslev *et al.*, 2011; Eiserhardt *et al.*, 2011) and palaeoclimate (Kissling *et al.*, 2012a,b; Blach-Overgaard *et al.*, 2013) are important for explaining functional trait distributions (Swenson & Weiser, 2010; Liu *et al.*, 2012). More specifically, we test the following hypotheses:

1. Median leaf size in palm species assemblages is highest in currently warm, moist areas with low annual seasonality and low soil acidity and sand content, but also in areas with reduced glacial–interglacial oscillations in climate.
2. Median stem height of palm species assemblages is low on poor soils, but high in disturbed landscapes with open canopies driven by hot or dry current and glacial climates.
3. Median fruit sizes of palm species assemblages are large on poor soils and in habitats with high mean annual temperature and precipitation. Furthermore, Quaternary climate change could have shaped assemblage median fruit size patterns through environmental filtering, favouring clades with large fruit sizes in areas that have been exposed to strong palaeoclimatic oscillations.

## MATERIAL AND METHODS

### PALM DISTRIBUTION AND TRAIT DATA

Distributional data for nearly all palm species (Arecaceae,  $N = 541$ ) across the Americas were digitized in ArcView 9.2 (ESRI Inc.) based on the range maps from Henderson (1995). These palm distribution maps are mostly based on expert information and represent conservative extent-of-occurrence extrapolations of the geographical ranges of palm species. We excluded the coconut (*Cocos nucifera* L.) from our analysis due to its unexceptionally large fruit size and its dispersal mode via floating seeds (Dransfield *et al.*, 2008). Range maps were overlaid onto a grid in cylindrical equal area projection with  $110 \times 110$ -km resolution (equivalent to c.  $1^\circ \times 1^\circ$  near the equator) and the presence of each palm species was then recorded for each grid cell. We excluded grid cells with species richness less than three to calculate meaningful median values per grid cell ( $N = 1474$ ). This represented a total of 36 422 grid cell occurrences across all palm species.

For the palm traits, we focused on leaf size [maximum rachis length (m)], stem height [maximum height (m)] and fruit size [volume ( $\text{cm}^3$ ), based on information of maximum fruit length, width, diameter and shape]. These traits are not identical to, but nevertheless in line with, the traits of the LHS plant ecology strategy scheme and represent one trait for each category (Westoby, 1998). We chose leaf size and fruit size rather than SLA and seed size, because little information is available for the latter pair for palms. Palm leaves are often large compared with other families. Furthermore, palms can have palmate or pinnate leaves, which also complicates the measurement of leaf area. For instance, for pinnate leaves it requires additional information on leaflets (number, length, width, etc.), which is often not available. We therefore worked with leaf/rachis length which is the best proxy for leaf size that can be consistently obtained across all species. Fruit size can be seen as a proxy for seed size because many palm genera are mainly one-seeded so that fruit and seed size are often highly correlated (Tomlinson, 1990; Henderson, 1995).

Trait data for palm species were extracted from Henderson (2002) for the majority of species. Additional data were collated from other sources, including monographs and species descriptions, the Aarhus University Herbarium and the palmweb database from the Royal Botanic Gardens, Kew (<http://palmweb.org/>). A detailed overview of the trait data sources for each species is provided in Supporting Information (Table S1). To calculate fruit size, we derived a measure of fruit volume based on information of fruit length, width and diameter (cm). Additional information for three-dimensional fruit shapes (e.g. globose, ellipsoid, pyramidal, cylindrical) was then used together with geometrical formulas to calculate fruit size volume (cm<sup>3</sup>) for each palm species. Globose fruit shapes were calculated by the formula for spheres ( $V = 4/3\pi \times \text{radius}^3$ ), ellipsoid shapes by the formula for ellipsoids ( $V = 4/3\pi \times \text{height} \times \text{length} \times \text{width}$ ), pyramidal shapes by the formula for pyramids ( $V = 1/3 \times \text{length}^2 \times \text{height}$ ) and cylindrical shapes with the formula for cylinders ( $V = \pi \times \text{radius}^2 \times \text{height}$ ). Where trait values were missing for individual species, we used the mean of species in the same genus to estimate the value of the missing species. This was done with

leaf size for 87 species, stem height for four species and fruit size for 18 species. A detailed overview of the mean and median trait values per genus and the number of estimated species per genus is provided in Supporting Information (Table S2). In a final step, we computed median values for each of the three trait variables across all species that were present in a given 110 × 110-km grid cell; these assemblage-level medians were then used as response variables in the statistical analyses (see below). To assess whether acaulescent species (i.e. palms with no or only a short stem concealed in the ground) have a major influence on geographical trait variability in palms, we examined species richness and trait distributions of acaulescent and non-aculescent palms separately (see Supporting Information, Figs S1, S2).

#### ENVIRONMENTAL DETERMINANTS

To explain geographical variation in functional traits of New World palms, we focused on three categories of predictor variables: present-day climate (three variables), soil (three variables) and palaeoclimate (two variables) (Table 1). These drivers have previously

**Table 1.** Predictor variables to explain the geographical variation and environmental correlates of functional trait distributions in palms across the New World

Abbreviation	Predictor variable (units)	Data source
Current climate		
PC-ANNU	High PC-ANNU values mainly represent high annual precipitation (mm year <sup>-1</sup> ), precipitation of the driest month (mm) and mean annual temperature (°C)	Worldclim dataset (Hijmans <i>et al.</i> , 2005)
PC-SEAS	High PC-SEAS values mainly represent high seasonality of temperature (SD of monthly means, °C) and seasonality of precipitation (coefficient of variation of monthly total, mm)	Worldclim dataset (Hijmans <i>et al.</i> , 2005)
PC-DRYM	High PC-DRYM values mainly represent high precipitation of the driest month (mm)	Worldclim dataset (Hijmans <i>et al.</i> , 2005)
Soil		
pH	pH in topsoil (−log(H <sup>+</sup> ))	Harmonized World Soil Database (FAO <i>et al.</i> , 2012)
sand%	Sand fraction in topsoil (%)	Harmonized World Soil Database (FAO <i>et al.</i> , 2012)
CEC	Cation exchange capacity in topsoil (cmol kg <sup>-1</sup> )	Harmonized World Soil Database (FAO <i>et al.</i> , 2012)
Quaternary climate change		
LGM ANOM TEMP	Anomaly in mean annual temperature between Last Glacial Maximum (LGM) and present (°C)	Calculated in ArcGIS using the Worldclim and the PMIP2 dataset (Hijmans <i>et al.</i> , 2005; Braconnot <i>et al.</i> , 2007)
LGM ANOM PREC	Anomaly in annual precipitation between Last Glacial Maximum (LGM) and present (mm year <sup>-1</sup> )	Calculated in ArcGIS using the Worldclim and the PMIP2 dataset (Hijmans <i>et al.</i> , 2005; Braconnot <i>et al.</i> , 2007)



been shown to be important for explaining species richness and assemblage composition in palms or geographical trait variation in other plant families (ter Steege *et al.*, 2006; Tautenhahn *et al.*, 2008; Balslev *et al.*, 2011; Kissling *et al.*, 2012a,b). We used the same grid (110 × 110-km grid resolution) as for the palm distribution data to extract the environmental data. All environmental variables were calculated in ArcGIS (version 10.1, ESRI) and mean values were extracted for each grid cell.

#### CURRENT CLIMATE

Current climatic factors have been shown to be important drivers of palm species distributions and diversity patterns (Eiserhardt *et al.*, 2011; Kissling *et al.*, 2012a) and trait distributions of other plants (Giliberto & Estay, 1978; Swenson & Weiser, 2010). To represent current climate, we used all 19 climate variables from the WORLDCLIM database (version 1.4; <http://www.worldclim.org>), a set of global climate layers with a spatial resolution of c. 1 km<sup>2</sup> (Hijmans *et al.*, 2005). We performed a principal component analysis (PCA) based on the correlation matrix to reduce collinearity among the 19 climate variables. We retained the first three PCA axes, which together explained 81% of the variability in the data (see Supporting Information, Table S3). The first axis was strongly positively related to mean annual precipitation, precipitation of the wettest quarter and mean annual temperature (hereafter PC-ANNU, Supporting Information, Table S3). The second axis showed a positive relationship to temperature seasonality and precipitation seasonality (hereafter PC-SEAS, Supporting Information, Table S3). The third axis showed a negative relationship with precipitation of the driest month (hereafter PC-DRYM, Supporting Information, Table S3).

#### SOIL

Soil variables can play an important role for fine-scale (Balslev *et al.*, 2011) and broad-scale species distributions of palms (Eiserhardt *et al.*, 2011) and for functional trait distributions in other plant families (Tautenhahn *et al.*, 2008). We focused on three topsoil variables, namely acidity of topsoil (pH), percentage sand fraction in topsoil (sand%) and cation exchange capacity in topsoil (CEC) (see Table 1). This corresponds to palms mainly forming short roots at ground level or slightly below (Dransfield *et al.*, 2008). Soil data were derived from the Harmonized World Soil Database (FAO *et al.*, 2012) and mean values within grid cells were calculated for all three soil variables in ArcGIS. Soil information in the Harmonized World Soil Database is relatively coarse, but the data capture the large-scale edaphic gradients in the New World such as the differences between the nutrient-poor soils of the Guiana Shield and the Cerrado

versus the nutrient-rich soils in the Chaco, north-eastern Brazil and the eastern Andean slopes. Correlations between the three soil variables were low to moderate (Spearman rank:  $r < 0.53$ ) and we therefore included all three soil variables in the analyses. We initially also explored mean base saturation in the topsoil per grid cell as potential predictor variable, but this was highly correlated with soil pH ( $r = 0.86$ ) and therefore not included in the analyses.

#### PALAEOCLIMATE

Palaeoclimate has been shown to be an important predictor of regional, continental and global palm diversity patterns (Kissling *et al.*, 2012a; Blach-Overgaard *et al.*, 2013; Rakotoarinivo *et al.*, 2013), but it has rarely been explored as a driver of trait distributions in plants (Ordonez & Svenning, 2015). To represent Quaternary climate change, we calculated the anomalies (differences) between the climate during the Last Glacial Maximum (LGM; c. 21 000 years ago) and the present-day climate. Using annual precipitation and annual mean temperature, we computed the anomaly of temperature (LGM ANOM TEMP, in °C) and the anomaly of precipitation (LGM ANOM PREC, in mm year<sup>-1</sup>) as palaeoclimatic predictor variables (see Table 1). The former can be seen as roughly representative of the major climatic oscillations of the Quaternary (the last several 10<sup>5</sup> years) because these temperature anomalies cover the full glacial–interglacial climate cycle with a geographical pattern that is consistent with these orbitally driven climatic oscillations over at least a large portion of the period (see Jansson, 2003). We used two different climate simulations (the Community Climate System Model version 3, CCSM3, and the Model for Interdisciplinary Research on Climate version 3.2, MIROC3.2) of the Paleoclimate Modeling Intercomparison Project (PMIP2; <http://pmip2.lscce.ipsl.fr/>) to quantify these palaeoclimatic changes (Braconnot *et al.*, 2007). These data were downloaded from worldclim ([www.worldclim.org](http://www.worldclim.org)). Both climate simulations provide temperature and precipitation data for the LGM and data were resampled in ArcGIS with a bilinear interpolation from the original 2.5° resolution to the resolution of the contemporary climate data. We then calculated mean anomaly values across these two climate simulations per 110 × 110-km grid cell. Large positive anomaly values indicate a higher precipitation and temperature in the present than in the past, whereas small or negative anomaly values indicate the opposite, i.e. higher precipitation and temperature in the past than in the present.

#### STATISTICAL ANALYSES

We analysed geographical variation in three assemblage-level median palm traits (leaf size, stem

height, fruit size) and their relationships with environmental predictor variables related to climate (PC-ANNU, PC-SEAS, PC-DRYM), soil (pH, sand%, CEC) and Quaternary climate change (LGM ANOM TEMP, LGM ANOM PREC). We used non-spatial ordinary-least-squares (OLS) linear regression models as well as spatial autoregressive (SAR) models (Kissling & Carl, 2008). We excluded cells with  $\leq 10\%$  land area or less than three palm species and those for which no environmental or trait variables (see below) were available. In a first step, we included all eight predictor variables in full OLS models (separate models with all predictors for each trait) and then performed a model selection with the Akaike Information Criterion (AIC) to identify the minimum adequate model (i.e. the one with the lowest AIC value). Response variables (Supporting Information, Fig. S3) and model residuals were checked to approximate a normal distribution and bivariate relationships were examined for non-linearity. As a consequence, the response variables leaf size and fruit size and the explanatory variables CEC and LGM ANOM TEMP were  $\log_{10}$ -transformed. We further tested for non-linear relationships by comparing OLS models with and without second-order polynomials using an ANOVA (Crawley, 2007). As spatial autocorrelation can affect significance tests and coefficient estimates of statistical models (Legendre & Legendre, 1998; Kissling & Carl, 2008), we used Moran's  $I$  and residual maps based on the residuals of the selected minimum adequate OLS models to quantify the presence of spatial autocorrelation (see Supporting Information, Fig. S4). Because Moran's  $I$  values were significant for OLS model residuals, we implemented SAR models of the error type (Kissling & Carl, 2008). We used the same variables as in the minimum adequate OLS regression models and included a spatial weight matrix in the SARs to account for residual autocorrelation (Kissling & Carl, 2008). To define the neighbourhood of the spatial weight matrix, we used the minimum distance needed to connect a grid cell to at least one nearest neighbour (158 km) and row-standardization for the weighting (Kissling & Carl, 2008). We further used correlograms to quantify spatial autocorrelation in the response variables (raw data), the residuals of the non-spatial OLS models and the residuals of the SAR models (see Supporting Information, Fig. S5). This allowed us to assess the amount of spatial autocorrelation with increasing geographical distance by plotting distance classes (bins) of grid cells on the  $x$ -axis and Moran's  $I$  values on the  $y$ -axis (Kissling & Carl, 2008).

For the SAR models, we quantified how much of the explained variance could be attributed to the predictor variables only, or to additional spatially structured factors (e.g. unmeasured environmental

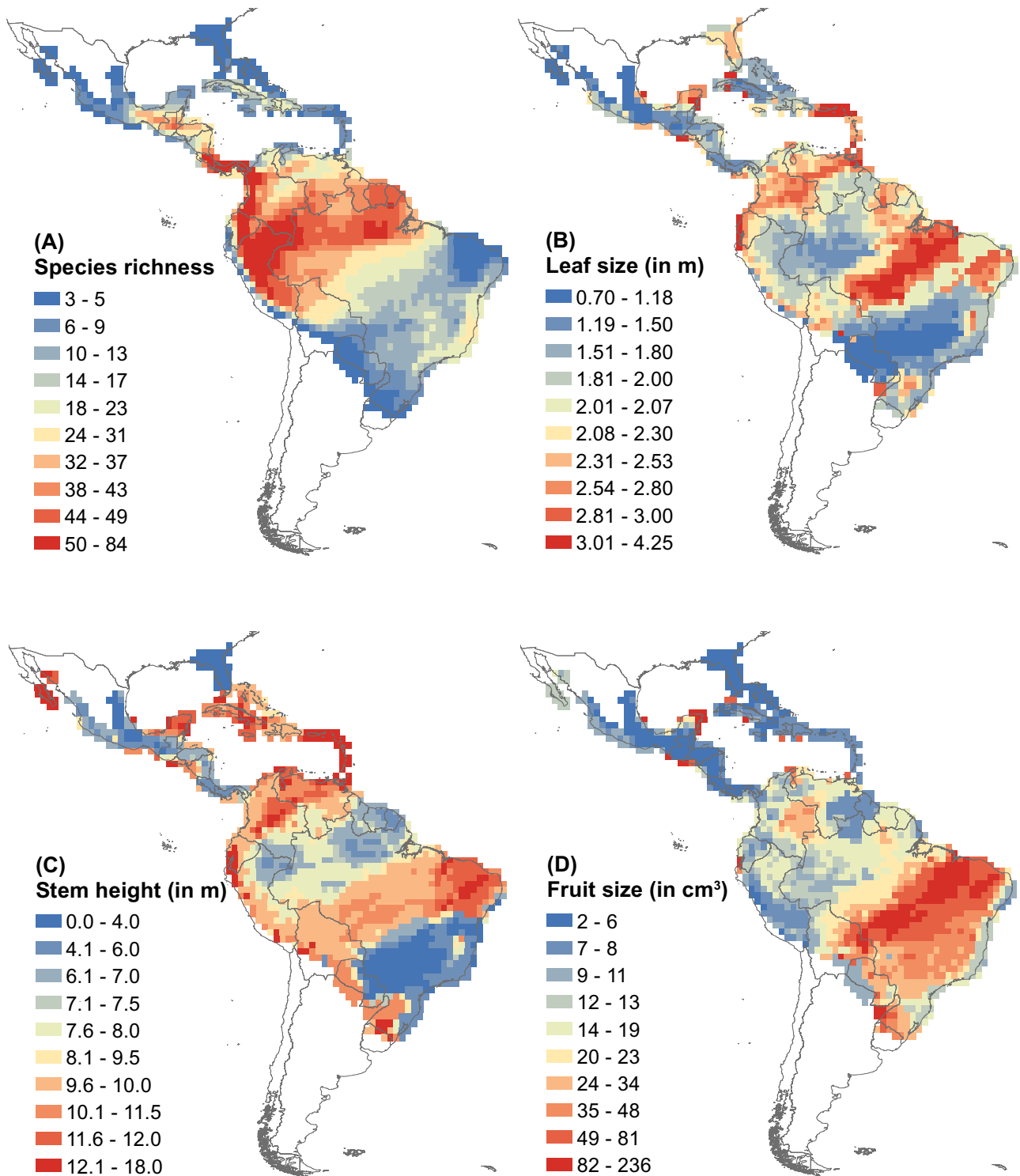
variables or dispersal limitation). We quantified the explained variance of the environmental predictors for each selected SAR model ( $R^2_{\text{PRED}}$ ) and the total explained variance ( $R^2_{\text{FULL}}$ ) of the full SAR models (including environmental predictors and the spatial weights matrix) (Kissling & Carl, 2008). This was done using pseudo- $R^2$  values, which were calculated as the squared Pearson correlation between predicted and true values (Kissling & Carl, 2008).

All statistical analyses were performed with R version 3.0.1 (R Core Team, 2013). Spatial analyses were performed using the R package 'spdep' version 0.5-71 (2014, R. Bivand). Correlograms were calculated with the function `correlog()` from the R package 'ncf' version 1.1-5 (Bjørnstad, 2005). Means  $\pm$  SD are given unless indicated otherwise.

## RESULTS

### GEOGRAPHICAL VARIATION OF FUNCTIONAL TRAIT DISTRIBUTIONS

In contrast to the high palm species richness in Panama, along the eastern slopes of the Andes and in the Amazon basin (Fig. 1A), the trait values mostly peaked north of the Amazon and in the central and southern parts of Brazil (Fig. 1B–D). Assemblage-level median leaf sizes peaked in areas north of the central Amazon basin (including eastern Colombia and western Venezuela), the Lesser Antilles in the Caribbean and a broad belt from north-eastern Bolivia to eastern Brazil. Low values for median leaf size were located in central Amazonia, southern Brazil and most parts of Central America (Fig. 1B). The palm species with the highest overall maximum leaf size in our dataset was *Attalea funifera* Mart. (12 m), which is only found in eastern Brazil. More generally, the genus *Attalea* Kunth contains many species with large leaf sizes (median  $\pm$  SD:  $6.72 \pm 2.78$  m; Supporting Information, Table S2) and this increases assemblage-level median leaf sizes in many areas of the New World, e.g. through *A. maripa* Mart. along the belt south of the Amazon and *A. butyracea* (Mutis ex L.f.) Wess.Boer in central Venezuela. The comparably dry regions of south-eastern Brazil (e.g. Cerrado) showed median leaf sizes that were generally small. This coincides with a low overall palm species richness in this region and with the presence of small-leaved species in genera such as *Butia* Becc. and *Syagrus* Mart. In general, the most species-rich understory genera all have small leaves: *Bactris* Jacq. ( $1.41 \pm 0.48$  m), *Geonoma* ( $0.80 \pm 0.53$  m) and *Chamaedorea* Willd. ( $0.64 \pm 0.56$  m) (Supporting Information, Table S2). These genera decrease assemblage-level median leaf sizes in regions where they are species rich, e.g. in the Amazon.



**Figure 1.** Species richness (A) and assemblage-level median values of (B) leaf size (m), (C) maximum stem height (m) and (D) fruit size (cm<sup>3</sup>) for palm assemblages across the New World. Quantile classification is shown across a grid with 110 × 110-km cell size (equivalent to c. 1° × 1° near the equator) and a WGS 1984 projection. Grid cells with fewer than three species were excluded.

For maximum stem height, assemblage-level medians peaked along the Pacific coast, in the Andes, the Caribbean, northern Colombia, Venezuela and the Cerrado (Fig. 1B). In contrast, species-rich areas such as the Amazon basin, south-eastern Brazil and Central America were dominated by relatively small-statured understorey palm species (Fig. 1C). The palm species with the largest maximum stem height was *Ceroxylon quindiuense* H.Wendl (60 m), which mainly occurs along the central and eastern Cordillera of the Colombian Andes. This and other species of *Ceroxylon* Bonpl. ex DC. contribute to the high assemblage-level median stem heights along the Andes. In the Brazilian Cerrado, the genus *Attalea* is species-rich and most of the species are tall ( $9.78 \pm 10.50$  m; Supporting Information, Table S2), resulting in high assemblage-level median stem heights. Similarly, the genera *Roystonea* O.F.Cook ( $21.50 \pm 7.84$  m; Supporting Information, Table S2) and *Coccothrinax* Sarg. ( $10.71 \pm 3.27$  m) in the Caribbean and the genus *Wettinia* Poepp. ex Endl. ( $12.38 \pm 4.55$  m) in Colombia are all species-rich and most species have large stem heights, leading to high assemblage-level median stem heights in these areas. Low assemblage-level median stem heights were congruent with high species richness of understorey genera such as *Geonoma* ( $3.00 \pm 2.54$  m; Supporting Information, Table S2) and *Bactris* ( $4.00 \pm 3.18$  m; Supporting Information, Table S2) in Central Amazonia, *Chamaedorea* ( $2.84 \pm 2.87$  m; Supporting Information, Table S2) in Central America and *Syagrus* ( $7.95 \pm 7.81$  m; Supporting Information, Table S2) in south-eastern Brazil, with several low-statured species (e.g. *S. vagan* Bondar and *S. werdermannii* Burret) in this region.

In contrast to leaf size and stem height, median fruit sizes of palm species assemblages peaked in a broad band from the savannah regions of the Brazilian Cerrado towards the Atlantic coast of eastern Brazil (Fig. 1D). A few species-rich genera with relatively large fruits and the low species richness of small-fruited understorey genera in this region drove high median fruit sizes. Large-fruited species in the Cerrado and the eastern Brazilian Atlantic coast are mainly members of *Attalea* ( $957 \pm 1020$  cm<sup>3</sup>; Supporting Information, Table S2), but this region shows a general scarcity of small-fruited (understorey) species. Furthermore, small values in assemblage-level median fruit sizes were found in central and southern Amazonia and along the eastern Andes slopes from Colombia to Peru where small-fruited genera such as *Geonoma* ( $1.77 \pm 2.19$  cm<sup>3</sup>), *Bactris* ( $18.72 \pm 34.05$  cm<sup>3</sup>) and *Desmoncus* Mart. ( $22.48 \pm 32.48$  cm<sup>3</sup>; Supporting Information, Table S2) occur with many species.

Fifty-eight species (11%) in our dataset had an acaulescent growth form (i.e. a woody stem below or

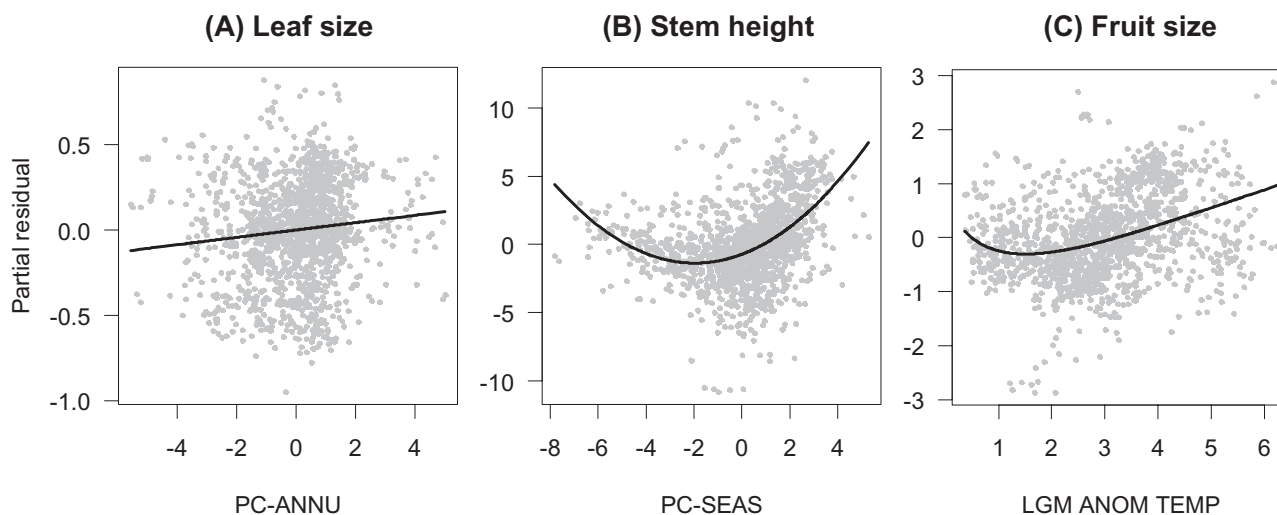
just at the ground). The distribution of species richness in these acaulescent palm genera (e.g. *Attalea* and *Phytelephas* Ruiz & Pav) differed from non-aculescent palms (Supporting Information, Fig. S1), with peaks of acaulescent species richness being located in the Brazilian Cerrado and the lowlands of Ecuador, Colombia and northern Brazil. This contrasting distribution could potentially influence geographical variability of assemblage-level traits such as leaf size, stem height and fruit size. For acaulescent palms, median leaf and fruit size distribution mainly peaked in the northern parts of Amazonia and median fruit size additionally peaked in the Brazilian Cerrado. This contrasted with the median trait distributions of non-aculescent palms (Supporting Information, Fig. S2). However, species richness of acaulescent palms was comparably low and median trait distributions of non-aculescent palm species (Supporting Information, Fig. S2A–C) were consistent and highly correlated (Spearman rank:  $r_{\text{leaf}} = 0.84$ ;  $r_{\text{stem}} = 0.80$ ;  $r_{\text{fruit}} = 0.97$ ) with those of all palm species (Fig. 1). In contrast, correlations of median trait distributions between all palm species and acaulescent palms were low or intermediate (Spearman rank:  $r_{\text{leaf}} = 0.43$ ;  $r_{\text{stem}} = 0.33$ ;  $r_{\text{fruit}} = 0.44$ ). In the following, we present analyses for all palm species which therefore predominantly reflects the drivers of non-aculescent palms. We further highlight here and below that functional traits vary across genera (Supporting Information, Table S2) and geographical space (geographical variations in standard deviations plotted in Supporting Information, Fig. S6).

#### TRAIT AND ENVIRONMENTAL CORRELATES

Assemblage-level median leaf size was positively related to annual temperature and precipitation (PC-ANNU) (Fig. 2A) and to seasonality (PC-SEAS) (Table 2). Moreover, median leaf size was negatively correlated to topsoil sand fraction (Table 2). CEC only showed a significant relationship with median leaf size in the non-spatial OLS models (Table 2). Other included environmental variables such as soil pH and Quaternary climate change (LGM ANOM TEMP, LGM ANOM PREC) did not show statistically significant relationships with median leaf size (Table 2).

For median stem height, the hypothesized increase in assemblage-level medians with hot and dry conditions was supported in the statistical models (Table 2). The strongest and most important environmental predictor variable was PC-SEAS, which showed a non-linear relationship with median stem height (Fig. 2B; Table 2). This indicated that median stem height increased with increasing seasonality (Fig. 2). Other included environmental variables had





**Figure 2.** Partial residual plots illustrating the relationship of three assemblage-level median traits (A, leaf size; B, stem height; C, fruit size) with their most important environmental predictor variable (based on standardized coefficients from Table 2). Partial residuals represent the relationship between a response and a predictor variable when all other predictor variables in the model are statistically controlled for. Specifically, these partial residual plots are plots of  $r + b \times Environment$  vs.  $Environment$  (x-axis), where  $r$  is the ordinary residuals from the multiple-predictor model and  $b$  is the regression coefficient estimate for  $Environment$  from the same multiple-predictor model. Abbreviations of predictor variables are given in Table 1.

small standardized coefficients and did not show a statistically significant relationship with stem height once spatial autocorrelation was accounted for (Table 2).

In contrast to leaf size and stem height, assemblage-level median fruit size showed a strong and mostly positive, non-linear relationship with LGM ANOM TEMP (Fig. 2C). This indicated that median fruit size was large in areas that had been exposed to strong Quaternary temperature oscillations. In addition, there was a positive relationship with seasonality (Table 2) and a weaker, but statistically significant, relationship with precipitation of the driest month (PC-DRYM, Table 2). Other predictor variables did not show strong or statistically significant effects in the SAR models (Table 2).

The explanatory power ( $R^2$ ) of the environmental variables in OLS models (0.287–0.507) and SAR models (0.233–0.465) varied among traits (Table 2). A good proportion of geographical variation in traits was explained by the included environmental factors for median leaf size (OLS:  $R^2_{OLS} = 0.40$ ; SAR:  $R^2_{PRED} = 0.43$ ), whereas the smallest amount was explained for stem height (OLS:  $R^2_{OLS} = 0.29$ ; SAR:  $R^2_{PRED} = 0.23$ ). In contrast, geographical trait variation was most strongly explained by the included environmental factors for median fruit size (OLS:  $R^2_{OLS} = 0.51$ ; SAR:  $R^2_{PRED} = 0.47$ ). All non-spatial OLS models showed statistically significant spatial autocorrelation in model residuals, whereas SAR models

successfully accounted for the spatial structure in model residuals (Table 2; Supporting Information, Figs S4, S5).

## DISCUSSION

We tested the relationships between geographical distributions of key functional traits (assemblage-level medians of leaf size, stem height and fruit size) and current climate, soil and palaeoclimatic temperature and precipitation change across the New World for *Areaceae*, a major plant lineage of tropical and subtropical ecosystems. We found that the geographical distributions of all trait variables were related to current environment, with seasonality in temperature and precipitation (all traits), mean annual temperature and precipitation (leaf size), and precipitation of the driest month (fruit size) playing a major role. We further found that palaeoclimate, notably Quaternary temperature change, was the most important predictor of assemblage-level median fruit size. The latter suggests that average fruit sizes tend to be larger in areas with more pronounced glacial–interglacial climatic oscillations. Our results thus reveal important imprints of both current and past climate on functional trait composition of palm assemblages in the New World, with large-scale gradients in soil properties playing a comparably minor role.

We expected median leaf size to be high in currently moist and warm climates with low soil acidity

**Table 2.** Results from non-spatial (ordinary least squares: OLS) and spatial autoregressive (SAR) multi-predictor models to explain geographical variation of assemblage-level functional traits (median leaf size, median stem height and median fruit size) in palm assemblages across the New World

Explanatory variable	Coefficient					
	Leaf size		Stem height		Fruit size	
	OLS	SAR	OLS	SAR	OLS	SAR
Intercept	1.340***	1.215***	10.388***	11.110***	6.667***	7.557***
PC-ANNU	<b>0.289***</b> (0.252)	<b>0.226***</b> (0.230)	–	–	0.098* (0.090)	0.040 (0.031)
PC-SEAS	<b>0.220***</b> (0.201)	<b>0.177***</b> (0.187)	<b>0.304***</b> (0.286)	<b>0.185***</b> (0.113)	<b>0.501***</b> (0.328)	<b>0.441***</b> (0.305)
PC-SEAS <sup>2</sup>	–	–	<b>0.372***</b> (0.299)	<b>0.368***</b> (0.280)	–	–
PC-DRYM	0.002 (0.001)	–0.005 (–0.053)	–	–	<b>0.194**</b> (0.177)	<b>0.089*</b> (0.123)
pH	–0.000 (–0.000)	0.000 (0.002)	0.104* (0.097)	0.063 (0.034)	–0.013 (–0.009)	–0.023 (–0.027)
sand%	<b>–0.162**</b> (–0.104)	<b>–0.104*</b> (–0.097)	–	–	–	–
CEC	0.082* (0.087)	0.041 (0.050)	0.090* (0.081)	0.046 (0.031)	–0.026 (–0.022)	–0.005 (–0.004)
LGM ANOM TEMP	0.029 (0.016)	0.001 (0.021)	0.106* (0.089)	0.061 (0.069)	<b>0.506***</b> (0.561)	<b>0.588***</b> (0.471)
LGM ANOM TEMP <sup>2</sup>	–	–	–	–	<b>0.536***</b> (0.501)	<b>0.509***</b> (0.412)
LGM ANOM PREC	–0.000 (–0.000)	–0.000 (–0.030)	–0.000 (–0.002)	–	0.003 (0.002)	–
$R^2_{OLS}$	0.404	–	0.287	–	0.507	–
$R^2_{PRED}$	–	0.429	–	0.233	–	0.465
$R^2_{FULL}$	–	0.844	–	0.832	–	0.969
AIC	5672	–2653	2578	4788	972	1821
Moran's $I$	0.587	0.013	0.640	0.011	0.518	0.008
$P$ (Moran's $I$ )	***	n.s.	***	n.s.	***	n.s.

Predictors that are statistically significant in both OLS and SAR models are indicated by bold type. Standardized coefficients are given in parentheses. Explanatory variables include current climate (PC-ANNU, PC-SEAS, PC-DRYM), soil (pH, sand%, CEC) and Quaternary climate change (LGM ANOM TEMP, LGM ANOM PREC). For each functional trait variable, a minimum adequate model was selected with the Akaike information criterion (AIC) based on a non-spatial OLS model with all explanatory variables (variables not selected are indicated by '–'). This model was then fitted with a SAR model. The response variables leaf size and fruit size and the predictor variables CEC and LGM ANOM TEMP were log<sub>10</sub>-transformed and PC-SEAS<sup>2</sup> and LGM ANOM TEMP<sup>2</sup> are quadratic polynomial terms of the predictor variables (see Methods). Sample sizes are 1474 grid cells of 110 × 110-km resolution in all analyses. Abbreviations of predictor variables are given in Table 1. For each model, the regression coefficients, the explained variance of the OLS ( $R^2_{OLS}$ ) and SAR models ( $R^2_{FULL}$ ,  $R^2_{PRED}$ ), the AIC, Moran's  $I$  and the  $P$ -value of Moran's  $I$  are given.

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; n.s., not significant; '–' not selected in the minimum adequate model.

and low sand content. This was generally supported by our results, albeit with weak negative relationships to soil conditions (Table 2). The smaller median leaf size in the central Amazon basin (Fig. 1B) can be explained by shade tolerance causing a small leaf size, but also by allometric constraints of having a small stature (Chazdon, 1991). Small-leaved under-

storey palm species (e.g. *Geonoma*, *Chamaedorea*, *Bactris*, *Hyospathe* Mart.) are particularly diverse in warm, moist and aseasonal climates of the central Amazon basin (Dransfield *et al.*, 2008; Balslev *et al.*, 2011). Towards the more seasonal parts in the north-western and south-eastern Amazon basin, median leaf size increased (Fig. 1B), mainly due to the pres-

ence of several species in genera such as *Attalea* (and to a lesser extent *Mauritia* L.f.). Increased drought stress and less shading in these seasonal areas might reduce the diversity of small-leaved understorey palms (Chazdon, 1991; Wright, 1992) and thereby increase the assemblage median leaf size. The comparably dry regions of south-eastern Brazil (e.g. Cerrado) showed median leaf sizes to be rather small, probably reflecting an adaptation to drought stress and water loss (e.g. Givnish, 1984). The overall negative (but weak) relationships with soil conditions probably reflect the fact that smaller leaves are advantageous on soils with low moisture and nutrient contents (e.g. sandy soils) (Gilberto & Estay, 1978; Givnish, 1984; Liu *et al.*, 2012). In contrast, clayey soils usually have higher water storage capacity and could therefore provide water even during longer drought periods (Ritchie, 1981), benefitting palms with large leaves such as species in the genera *Manicaria* Gaertn. and *Astrocaryum* G.Mey. on waterlogged soils (Balslev *et al.*, 2011). Besides producing larger leaves, an alternative strategy on better soils might be to modify leaf morphology, e.g. increasing leaf narrowness and leaf number to enhance photosynthetic capacity (Malhado *et al.*, 2009). Palms with palmate leaves are often found in dry and seasonal areas with nutrient-poor soils, which could indicate a morphological adaptation to those environmental factors (Balslev *et al.*, 2011). We suggest that soil data at finer spatial resolutions and other environmental predictors related to fine-scale topography (Tomer & Anderson, 1995) could additionally reveal interesting insights into how leaf sizes of palms vary with soil properties (cf. Ackerly & Cornwell, 2007; Balslev *et al.*, 2011; Eiserhardt *et al.*, 2011).

For stem height, we expected median values of palm species assemblages to peak in dry and warm environments because these tend to have an open canopy structure and less understorey diversity, as understorey palms are often vulnerable to harsh and dry climates (Chazdon, 1991; Kissling *et al.*, 2012b). Our results supported this prediction, with seasonality (an indicator of dry periods) being a better predictor than annual values of precipitation and temperature (Table 2; Fig. 2C). The positive relationship with seasonality likely reflects the fact that robust, large-stemmed palm genera are relatively more species-rich in seasonal climates than small-statured, drought-sensitive genera (Balslev *et al.*, 2011). For instance, *Roystonea* (with ten species within the Caribbean) generally shows a solitary, robust stem (15–40 m) and occurs especially in disturbed landscapes with seasonal climates (Henderson, Galeano-Garces & Bernal, 1997), resulting in high assemblage-level median stem heights across the Caribbean (Fig. 2C). Mainly in the Andes (with more seasonal climates than the low-

lands), the genus *Ceroxylon* (11 species) is widespread, with large maximum stem heights (10–50 m) increasing assemblage-level medians (Fig. 2C). As discussed above, the high diversity of understorey palms (*Geonoma*, *Bactris*, etc.) in the Amazon is particularly important because it not only decreases average leaf size, but also stem heights. Small stature in this region probably represents adaptation to shade through lower costs for biomass production (Chazdon, 1991). However, the lower diversity of these small-stemmed understorey palm species in seasonal climates might also be caused by a relatively reduced competitive ability compared with canopy species in areas with drought stress (Wright, 1992). The broadly similar geographical patterns of median leaf and stem heights (Fig. 2) reflect strong allometric leaf-height relationships in palms, but in some regions (e.g. Caribbean, Andes), for particular growth forms (e.g. acaulescent species), and in certain clades (e.g. *Mauritiella* Burret, *Coccothrinax*, *Ceroxylon*) there is considerable departure from this relationship, highlighting the need to address environmental correlates separately for these two traits.

For fruit size, we expected median values of palm species assemblages to be large on poor soils, in habitats with high mean annual temperature and precipitation and in areas that had been exposed to strong Quaternary climate change. This was partly supported (e.g. the strong positive relationship with LGM temperature anomaly), but other predictors (especially seasonality and precipitation of the driest month) were also important. Geographically, the distribution of median fruit size differed from those of leaf size and stem height (Fig. 1), with peaks being mainly found in south-eastern Brazil (e.g. Cerrado). Large seed sizes might be particularly advantageous in situations in which establishment conditions are stressful, e.g. on nutrient-poor soils (Liu *et al.*, 2012) or in areas with droughts (Wright, 1992; Westoby *et al.*, 1996). The observed relationships between median fruit sizes and large-scale soil gradients were generally weak (Table 2), but the strong relationship with present-day seasonality and palaeoclimatic temperature change supports the idea that palm clades with large fruit sizes (compared with relatively small-fruited palms) tend to survive better in areas with seasonal hazards such as droughts (Westoby, 1998). Median fruit size was the only one of the three traits that was linked to Quaternary glacial–interglacial climate change. We suggest that the relatively unstable areas exposed to strong temperature oscillations during the Quaternary tend to have more large-fruited palm species than climatically stable areas because large seed mass and fruit size allow high reproductive success (Lloret, Casanovas & Penuelas, 1999) and better establishment success of seedlings

under stressful conditions (Wright, 1992; Westoby *et al.*, 1996). This is consistent with an intercontinental comparison of palm fruit sizes, in which African palm species (which have been exposed to the strongest Cenozoic drying) have larger fruit sizes than their Neotropical counterparts (Kissling *et al.*, 2012b). It also coincides with the observation that phylogenetic clustering in South American palm assemblages increases with the magnitude of Quaternary temperature oscillations, suggesting that specific palm clades (notably, in the large-seeded tribe Cocoseae) have performed better in climatically unstable regions (Kissling *et al.*, 2012b). The underlying mechanism could be that large-fruited palms either have survival benefits (see above) or are dispersed by mobile megafauna. That was shown for lowland tapirs dispersing seeds of *Mauritia flexuosa* L.f. (Fragoso & Huffman, 2000), *Euterpe edulis* Mart. and *Syagrus romanzoffiana* (Cham.) Glassman (Galetti *et al.*, 2006; Sica, Bravo & Giombini, 2014). Such post-glacial migrational lags have been invoked as driver for the current distribution of many European trees and other plants (Normand *et al.*, 2011; Nogués-Bravo *et al.*, 2014), with stronger dispersal limitation in large-seeded species (Nogués-Bravo *et al.*, 2014). For Europe, this could perhaps reflect a lack of frugivorous megafauna dispersers during the Lateglacial and Holocene (Campbell, 1982). Our findings suggest that such post-glacial range dynamics could also be important in the tropics and at least partly dependent on traits such as fruit or seed size, reflecting their importance for plant dispersal and/or stress tolerance.

In addition to the drivers discussed above, other (unmeasured) environmental, biotic and spatial factors (e.g. unexplained spatial variation in Table 2) could play an important role in shaping trait distributions of New World palms. For instance, human behaviour could have an impact on palm trait distributions, e.g. through introductions and naturalizations of species beyond their native range (Svenning & Skov, 2005). Similarly, the spatial distribution of vertebrate seed dispersers and their traits (body size, degree of diet specialization, movement behaviour, gut retention times, etc.) might play an important role in shaping geographical variability of traits in animal-dispersed plants (e.g. Zona & Henderson, 1989; Kissling, Rahbek & Böhning-Gaese, 2007; Beaune *et al.*, 2013; Galetti *et al.*, 2013). Another important aspect that might affect functional trait distributions of palms is fire. Fire frequency is high in seasonal areas with long dry and hot periods (Furley, 1999; Grau & Veblen, 2000), but can also be modified by humans (e.g. Hoffmann, 1999; Michalski & Peres, 2005). Fire can have a strong influence on species richness and community composition (Hoffmann, 1999), e.g. in areas such as southern Amazonia and

the Cerrado (Ratter *et al.*, 1978; Pennington *et al.*, 2000; Michalski & Peres, 2005) which we have identified as areas with large average trait values for palms. Fires can therefore also influence plant functional trait distributions (Furley, 1999; Pennington *et al.*, 2000) and might lead to shifts in assemblage-level traits, e.g. towards larger and taller woody plants (Hoffmann, 1999; Williams *et al.*, 1999; Smith, 2015). Finally, our soil data are rather crude and probably underestimate the role and importance of fine-scale soil variation in Neotropical forests (e.g. Tuomisto & Ruokolainen, 1994; Vormisto *et al.*, 2000; Katabuchi *et al.*, 2012; Misiewicz & Fine, 2014), although the large-scale relationships in focus here are probably adequately represented. Future studies might shed light on the importance of such additional drivers for functional trait distributions in palms, including the role of humans, animal dispersers, fire, soil characteristics and other spatially structured factors.

Following Westoby's (1998) LHS plant strategy scheme, we have chosen three key functional traits (leaf size, stem height and fruit size) of palms and related their median assemblage values to current environment (climate, soils) and past climate change. These trait variables (especially leaf size) do not fully match those suggested in the LHS scheme, but they represent the best proxies of currently available data on broad-scale variation in functional traits across New World palms. Leaf size (here rachis length) provides less information about photosynthetic capacity and relative growth than SLA, but SLA is particularly difficult to quantify for palms with, for example, pinnate leaves (this would require information on leaflet lengths, number and width). Additionally, geographical variation in functional traits of non-aculescent species (mainly considered here) differs from aculescent palms. We assume that SLA and leaf size of palms show a positive correlation, but data are limited to test this assumption. These aspects require more in-depth analyses in the future. Overall, our results provide new insights into the role of contemporary climate (namely seasonality) in shaping continental-scale patterns of plant trait distributions and further highlight an important role of glacial–interglacial climate change for fruit size distributions in the New World. The latter is consistent with the increasing evidence that Quaternary and deeper-time palaeoclimate has left an imprint on the present-day diversity and distribution of palms (Kissling *et al.*, 2012a,b; Blach-Overgaard *et al.*, 2013; Rakotoarivivo *et al.*, 2013). The predicted future changes in climate in the Neotropical region, including an increase in mean annual temperature, a decrease in mean annual precipitation and a more seasonal climate (especially with regard to precipita-



tion) (Magrin *et al.*, 2014), will probably affect palm functional composition and hence ecosystem functioning. Likewise, the ongoing defaunation, especially of large-bodied species, is also likely to affect palm functional composition, notably with a negative effect on large-seeded palms (e.g. Fragoso & Huffman, 2000; Sica *et al.*, 2014). We suggest that trait–environment relationships such as those studied here can provide an important first step into understanding how ecological traits and ecosystem functioning vary across large spatial extents, and how this relates to biotic and abiotic drivers.

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## REFERENCES

- Ackerly DD, Cornwell WK. 2007. A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecology Letters* **10**: 135–145.
- de Almeida LB, Galetti M. 2007. Seed dispersal and spatial distribution of *Attalea geraensis* (Arecaceae) in two remnants of Cerrado in Southeastern Brazil. *Acta Oecologica* **32**: 180–187.
- Andreazzi CS, Pimenta CS, Pires AS, Fernandez FAS, Oliveira-Santos LG, Menezes JFS. 2012. Increased productivity and reduced seed predation favor a large-seeded palm in small Atlantic forest fragments. *Biotropica* **44**: 237–245.
- Balslev H, Kahn F, Millan B, Svenning J-C, Kristiansen T, Borchsenius F, Pedersen D, Eiserhardt WL. 2011. Species diversity and growth forms in tropical American palm communities. *The Botanical Review* **77**: 381–425.
- Beaune D, Fruth B, Bollache L, Hohmann G, Bretagnolle F. 2013. Doom of the elephant-dependent trees in a Congo tropical forest. *Forest Ecology and Management* **295**: 109–117.
- Bjornstad O. 2005. ncf: spatial nonparametric covariance functions. R package version 1.1-5. Available at <http://cran.r-project.org/web/packages/ncf/index.html>
- Blach-Overgaard A, Kissling WD, Dransfield J, Balslev H, Svenning J-C. 2013. Multimillion-year climatic effects on palm species diversity in Africa. *Ecology* **94**: 2426–2435.
- Blach-Overgaard A, Svenning J-C, Dransfield J, Greve M, Balslev H. 2010. Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints. *Ecography* **33**: 380–391.
- Braconnot P, Otto-Bliesner B, Harrison S, Joussaume S, Peterchmitt JY, Abe-Ouchi A, Crucifix M, Driesschaert E, Fichefet T, Hewitt CD, Kageyama M, Kitoh A, Laine A, Loutre MF, Marti O, Merkel U, Ramstein G, Valdes P, Weber SL, Yu Y, Zhao Y. 2007. Results of PMIP2 coupled simulations of the mid-Holocene and Last Glacial Maximum – part 1: experiments and large-scale features. *Climate of the Past* **3**: 261–277.
- Campbell JJN. 1982. Pears and persimmons: a comparison of temperate forests in Europe and eastern North America. *Vegetatio* **49**: 85–101.
- Chazdon RL. 1991. Plant size and form in the understory palm genus *Geonoma*: are species variations on a theme? *American Journal of Botany* **78**: 680–694.
- Crawley MJ. 2007. *The R book*. Chichester: John Wiley & Sons.
- Diaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution* **16**: 646–655.
- Diaz S, Purvis A, Cornelissen JH, Mace GM, Donoghue MJ, Ewers RM, Jordano P, Pearse WD. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution* **3**: 2958–2975.
- Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. 2008. *Genera palmarum: the evolution and classification of palms*. Kew: Royal Botanic Gardens.
- Eiserhardt WL, Svenning J-C, Kissling WD, Balslev H. 2011. Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. *Annals of Botany* **108**: 1391–1416.
- FAO, IIASA, ISRIC, ISSCAS, JRC. 2012. *Harmonized world soil database (version 1.2)*. Rome and Laxenburg: FAO and IIASA.
- Fragoso J, Huffman JM. 2000. Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir. *Journal of Tropical Ecology* **16**: 369–385.
- Furley PA. 1999. The nature and diversity of Neotropical savanna vegetation with particular reference to the Brazilian cerrados. *Global Ecology and Biogeography* **8**: 223–241.
- Furley PA, Ratter JA. 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. *Journal of Biogeography* **15**: 97–108.
- Galetti M, Donatti CI, Pires AS, Guimarães PR, Jordano P. 2006. Seed survival and dispersal of an endemic Atlantic

- forest palm: the combined effects of defaunation and forest fragmentation. *Botanical Journal of the Linnean Society* **151**: 141–149.
- Galetti M, Guevara R, Cortes MC, Fadini R, Von Matter S, Leite AB, Labacca F, Ribeiro T, Carvalho CS, Collevatti RG, Pires MM, Guimaraes PR Jr, Brancalion PH, Ribeiro MC, Jordano P. 2013.** Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* **340**: 1086–1090.
- Gentry AH. 1988.** Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* **85**: 156–159.
- Giliberto J, Estay H. 1978.** Seasonal water stress in some Chilean matorral shrubs. *Botanical Gazette* **139**: 236–240.
- Givnish TJ. 1984.** *Leaf and canopy adaptations in tropical forests. Physiological ecology of plants of the wet tropics.* The Hague: Springer.
- Govaerts R, Dransfield J. 2005.** *World checklist of palms.* Kew: Royal Botanic Gardens.
- de Granville JJ. 1992.** Life forms and growth strategies of Guianan palms as related to their ecology. *Bulletin de l'Institut français d'études andines* **21**: 533–548.
- Grau HR, Veblen TT. 2000.** Rainfall variability, fire and vegetation dynamics in Neotropical montane ecosystems in north-western Argentina. *Journal of Biogeography* **27**: 1107–1121.
- Greenwood DR, Wing SL. 1995.** Eocene continental climates and latitudinal temperature gradients. *Geology* **23**: 1044–1048.
- Gurevitch J. 1988.** Variation in leaf dissection and leaf energy budgets among populations of *Achillea* from an altitudinal gradient. *American Journal of Botany* **75**: 1298–1306.
- Henderson A. 1995.** *The palms of the Amazon.* New York: Oxford University Press.
- Henderson A. 2002.** *Evolution and ecology of palms.* The Bronx: New York Botanical Garden Press.
- Henderson A, Galeano-Garcés G, Bernal R. 1997.** *Field guide to the palms of the Americas.* Chichester: Princeton University Press.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005.** Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965–1978.
- Hoffmann WA. 1999.** Fire and population dynamics of woody plants in a Neotropical savanna: matrix model projections. *Ecology* **80**: 1354–1369.
- Hulshof CM, Violle C, Spaojevic MJ, McGill B, Damschen E, Harrison S, Enquist BJ. 2013.** Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Science* **24**: 921–931.
- Jansson R. 2003.** Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society B: Biological Sciences* **270**: 583–590.
- Katabuchi M, Kurokawa H, Davies SJ, Tan S, Nakashizuka T. 2012.** Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *Journal of Ecology* **100**: 643–651.
- Kessler M, Böhner J, Kluge J. 2007.** Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. *Ecological Modelling* **207**: 223–233.
- Kissling WD, Baker WJ, Balslev H, Barfod AS, Borchsenius F, Dransfield J, Govaerts R, Svenning J-C. 2012a.** Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography* **21**: 909–921.
- Kissling WD, Carl G. 2008.** Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography* **17**: 59–71.
- Kissling WD, Eiserhardt WL, Baker WJ, Borchsenius F, Couvreur TL, Balslev H, Svenning J-C. 2012b.** Cenozoic imprints on the phylogenetic structure of palm species assemblages worldwide. *Proceedings of the National Academy of Sciences of the United States of America* **109**: 7379–7384.
- Kissling WD, Rahbek C, Böhning-Gaese K. 2007.** Food plant diversity as broad-scale determinant of avian frugivore richness. *Proceedings of the Royal Society B: Biological Sciences* **274**: 799–808.
- Legendre P, Legendre LFF. 1998.** *Numerical ecology.* Amsterdam: Elsevier Science.
- Liu X, Swenson NG, Wright SJ, Zhang L, Song K, Du Y, Zhang J, Mi X, Ren H, Ma K. 2012.** Covariation in plant functional traits and soil fertility within two species-rich forests. *PLoS ONE* **7**: e34767.
- Lloret F, Casanovas C, Penuelas J. 1999.** Seedling survival of Mediterranean shrubland species in relation to root: shoot ratio, seed size and water and nitrogen use. *Functional Ecology* **13**: 210–216.
- Magrin G, Marengo J, Boulanger J-P, Buckeridge M, Castellanos E, Poveda G, Scarano F, Vicuna S. 2014.** Central and South America. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL, eds. *Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of working group II to the fifth Assessment Report of the Intergovernmental Panel on climate change.* 2014. Cambridge: Cambridge University Press, 1499–1566.
- Malhado ACM, Whittaker RJ, Malhi Y, Ladle RJ, ter Steege H, Aragao LEOC, Quesada CA, Araújo AM, Ramirez AH. 2009.** Spatial distribution and functional significance of leaf lamina shape in Amazonian forest trees. *Biogeosciences* **6**: 1837–1874.
- Mason NWH, Mouillot D, Lee WG, Wilson JB. 2005.** Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **111**: 112–118.
- McDonald PG, Fonseca CR, Overton JM, Westoby M. 2003.** Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Functional Ecology* **17**: 50–57.

- Michalski F, Peres CA. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation* **124**: 383–396.
- Misiewicz TM, Fine PV. 2014. Evidence for ecological divergence across a mosaic of soil types in an Amazonian tropical tree: *Protium subseratum* (Burseraceae). *Molecular Ecology* **23**: 2543–2558.
- Moles AT, Perkins SE, Laffan SW, Flores-Moreno H, Awasthy M, Tindall ML, Sack L, Pitman A, Kattge J, Aarssen LW, Anand M, Bahn M, Blonder B, Cavender-Bares J, Cornelissen JHC, Cornwell WK, Diaz S, Dickie JB, Freschet GT, Griffiths JG, Gutierrez AG, Hemmings FA, Hickler T, Hitchcock TD, Keighery M, Kleyer M, Kurokawa H, Leishman MR, Liu K, Niinemets U, Onipchenko V, Onoda Y, Penuelas J, Pillar VD, Reich PB, Shiodera S, Siefert A, Sosinski EE Jr, Soudzilovskaia NA, Swaine EK, Swenson NG, van Bodegom PM, Warman L, Weiher E, Wright IJ, Zhang H, Zobel M, Bonser SP. 2014. Which is a better predictor of plant traits: temperature or precipitation? *Journal of Vegetation Science* **25**: 1167–1180.
- Morley RJ. 2000. *Origin and evolution of tropical rain forests*. Chichester: Wiley.
- Murphy PG, Lugo AE. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* **17**: 67–88.
- Murray BR, Brown AHD, Dickman CR, Crowther MS. 2004. Geographical gradients in seed mass in relation to climate. *Journal of Biogeography* **31**: 379–388.
- Nogués-Bravo D, Pulido F, Araújo MB, Diniz-Filho JAF, García-Valdés R, Kollmann J, Svenning J-C, Valladares F, Zavala MA. 2014. Phenotypic correlates of potential range size and range filling in European trees. *Perspectives in Plant Ecology, Evolution and Systematics* **16**: 219–227.
- Normand S, Ricklefs RE, Skov F, Bladt J, Tackenberg O, Svenning J-C. 2011. Postglacial migration supplements climate in determining plant species ranges in Europe. *Proceedings of the Royal Society B: Biological Sciences* **278**: 3644–3653.
- Ordonez A, Svenning J-C. 2015. Geographic patterns in functional diversity deficits are linked to glacial–interglacial climate stability and accessibility. *Global Ecology and Biogeography* **24**: 826–837.
- Ordoñez JC, Van Bodegom PM, Witte JPM, Wright IJ, Reich PB, Aerts R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* **18**: 137–149.
- Pennington R, Prado DE, Pendry CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* **27**: 261–273.
- Peppe DJ, Royer DL, Cariglino B, Oliver SY, Newman S, Leight E, Enikolopov G, Fernandez-Burgos M, Herrera F, Adams JM, Correa E, Currano ED, Erickson JM, Hinojosa LF, Hoganson JW, Iglesias A, Jaramillo CA, Johnson KR, Jordan GJ, Kraft NJ, Lovelock EC, Lusk CH, Niinemets U, Penuelas J, Rapson G, Wing SL, Wright IJ. 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytologist* **190**: 724–739.
- R Core Team. 2013. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Rakotoarinivo M, Blach-Overgaard A, Baker WJ, Dransfield J, Moat J, Svenning J-C. 2013. Palaeo-precipitation is a major determinant of palm species richness patterns across Madagascar: a tropical biodiversity hotspot. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20123048.
- Ratter JA, Askew GP, Montgomery RF, Gifford DR. 1978. Observations on the vegetation of northeastern Mato Grosso. II. Forests and soils of the Rio Suia-Missu area. *Proceedings of the Royal Society B: Biological Sciences* **203**: 191–208.
- Ritchie JT. 1981. Soil water availability. *Plant and Soil* **58**: 327–338.
- Sica YV, Bravo SP, Giombini MI. 2014. Spatial pattern of pindó palm (*Syagrus romanzoffiana*) recruitment in Argentinian Atlantic forest: the importance of tapir and effects of defaunation. *Biotropica* **46**: 696–703.
- Smith N. 2015. *Attalea spectabilis*. In: Smith N, ed. *Palms and people in the Amazon*. Cham, Switzerland: Springer International Publishing, 147–152.
- ter Steege H, Hammond DS. 2001. Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* **82**: 3197–3212.
- ter Steege H, Pitman NC, Phillips OL, Chave J, Sabatier D, Duque A, Molino JF, Prevost MF, Spichiger R, Castellanos H, von Hildebrand P, Vasquez R. 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* **443**: 444–447.
- Svenning J-C, Skov F. 2005. The relative roles of environment and history as controls of tree species composition and richness in Europe. *Journal of Biogeography* **32**: 1019–1033.
- Swenson NG, Enquist BJ, Pither J, Kerkhoff AJ, Boyle B, Weiser MD, Elser JJ, Fagan WF, Forero-Montaña J, Fyllas N, Kraft NJB, Lake JK, Moles AT, Patiño S, Phillips OL, Price CA, Reich PB, Quesada CA, Stegen JC, Valencia R, Wright IJ, Wright SJ, Andelman S, Jørgensen PM, Lacher TE Jr, Monteagudo A, Núñez-Vargas MP, Vasquez-Martínez R, Nolting KM. 2012. The biogeography and filtering of woody plant functional diversity in North and South America. *Global Ecology and Biogeography* **21**: 798–808.
- Swenson NG, Weiser MD. 2010. Plant geography upon the basis of functional traits: an example from eastern North America. *Ecology* **91**: 2234–2241.
- Tautenhahn S, Heilmeyer H, Götzenberger L, Klotz S, Wirth C, Kühn I. 2008. On the biogeography of seed mass in Germany – distribution patterns and environmental correlates. *Ecography* **31**: 457–468.
- Tomer MD, Anderson JL. 1995. Variation of soil water storage across a sand plain hillslope. *Soil Science Society of America Journal* **59**: 1091–1100.
- Tomlinson PB. 1990. *The structural biology of palms*. New York: Oxford University Press.



- Tuomisto H, Ruokolainen K. 1994.** Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of Vegetation Science* **5**: 25–34.
- Tuomisto H, Ruokolainen K, Poulsen AD, Moran RC, Quintana C, Cañas G, Celi J. 2002.** Distribution and diversity of pteridophytes and Melastomataceae along edaphic gradients in Yasuni National Park, Ecuadorian Amazonia. *Biotropica* **34**: 516–533.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007.** Let the concept of trait be functional! *Oikos* **116**: 882–892.
- Vormisto J, Phillips OL, Ruokolainen K, Tuomisto H, Vásquez R. 2000.** A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. *Ecography* **23**: 349–359.
- Westoby M. 1998.** A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**: 213–227.
- Westoby M, Leishman M, Lord J, Poorter H, Schoen DJ. 1996.** Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **351**: 1309–1318.
- Williams RJ, Cook GD, Gill AM, Moore PHR. 1999.** Fire regime, fire intensity and tree survival in a tropical savanna in northern Australia. *Australian Journal of Ecology* **24**: 50–59.
- Wright SJ. 1992.** Seasonal drought, soil fertility and species density of tropical forest plant communities. *TREE* **7**: 260–262.
- Zona S, Henderson A. 1989.** A review of animal-mediated seed dispersal of palms. *Selbyana* **11**: 6–21.

## SUPPORTING INFORMATION

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

**Figure S1.** Species richness of (A) non-acaulescent palms ( $N = 483$ ) and (B) acaulescent palms ( $N = 58$ ) across the New World. Quantile classification is shown across a grid with  $110 \times 110$ -km cell size (equivalent to c.  $1^\circ \times 1^\circ$  near the equator) and a WGS 1984 projection.

**Figure S2.** Assemblage-level median values of functional traits for non-acaulescent (A–C) vs. acaulescent (D–E) palms across the New World. Median palm traits for non-acaulescent species ( $N = 483$ ) are shown for (A) leaf size (m), (B) stem height (m) and (C) fruit size ( $\text{cm}^3$ ), and for acaulescent palm species ( $N = 58$ ) for (D) leaf size (m) and (E) fruit size ( $\text{cm}^3$ ). Note that assemblage median stem height is not available for acaulescent palms as they have short erect or prostrate stem, often concealed in the ground. Quantile classification is shown across a grid with  $110 \times 110$ -km cell size (equivalent to c.  $1^\circ \times 1^\circ$  near the equator) and a WGS 1984 projection. Trait medians are shown here for all grid cells with species richness  $\geq 1$ .

**Figure S3.** Histograms for the three functional trait variables of palms illustrating the frequency distribution of the median values for leaf size (A), stem height (B) and fruit size (C). Data of leaf size and fruit size were  $\log_{10}$ -transformed.

**Figure S4.** Maps showing residuals of the non-spatial OLS models for assemblage-level median trait distributions of leaf size (A), stem height (B) and fruit size (C), and corresponding ones for the SAR models (D–F). The diameter of each dot indicates the relative amount of spatial autocorrelation (SAC) at a particular grid cell, with positive (black) and negative (grey) autocorrelation, respectively.

**Figure S5.** Moran's  $I$  correlograms of the raw trait data (white circles), of the residuals of the non-spatial OLS models (grey dots), and the residuals of the SAR model (black dots) for the three functional trait variables: median leaf size (A), median stem height (B) and median fruit size (C).

**Figure S6.** Assemblage-level standard deviation (SD) of key functional traits across all palms ( $N = 541$ ) for (A) leaf size (m), (B) stem height (m) and (C) fruit size ( $\text{cm}^3$ ) across the New World. Quantile classification is shown across a grid with  $110 \times 110$ -km cell size (equivalent to c.  $1^\circ \times 1^\circ$  near the equator) and a WGS 1984 projection. SD is only calculated for grid cells with species richness  $> 2$ .

**Table S1.** Principal component (PC) analysis for 19 present-day climate variables from the worldclim dataset extracted for a grid across the New World with  $110 \times 110$ -km grid cell resolution ( $N = 1498$  grid cells). Presented are eigenvalues, percentage of variance for each PC axis, and cumulative percentage of variance across all axes, and the correlation between the PC axes and the most important climate variables.

**Table S2.** New World palm genera and their species-level variation in key functional traits (leaf size, stem height, fruit size). For each genus, the number of all species, the number of species for which trait values have been estimated, and the trait variation (mean, median, SD) for all species with available data is given. Note that SD is not available for genera with only one species.

**Table S3.** All New World palm species within the dataset ( $N = 541$ ), the references and data sources that have been used to extract species-level trait information. The list of references and sources is provided at the end of the table.