

Determinants of palm species distributions across Africa: the relative roles of climate, non-climatic environmental factors, and spatial constraints

Anne Blach-Overgaard, Jens-Christian Svenning, John Dransfield, Michelle Greve and Henrik Balslev

A. Blach-Overgaard (anne.overgaard@biology.au.dk), J.-C. Svenning, M. Greve and H. Balslev, *The Ecoinformatics and Biodiversity Group, Dept of Biological Sciences, Aarhus Univ., Ny Munkegade 114, DK-8000 Aarhus C, Denmark.* – J. Dransfield, *Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK.*

Most of the Earth's biodiversity resides in the tropics. However, a comprehensive understanding of which factors control range limits of tropical species is still lacking. Climate is often thought to be the predominant range-determining mechanism at large spatial scales. Alternatively, species' ranges may be controlled by soil or other environmental factors, or by non-environmental factors such as biotic interactions, dispersal barriers, intrinsic population dynamics, or time-limited expansion from place of origin or past refugia. How species ranges are controlled is of key importance for predicting their responses to future global change. Here, we use a novel implementation of species distribution modelling (SDM) to assess the degree to which African continental-scale species distributions in a keystone tropical group, the palms (Arecaceae), are controlled by climate, non-climatic environmental factors, or non-environmental spatial constraints. A comprehensive data set on African palm species occurrences was assembled and analysed using the SDM algorithm Maxent in combination with climatic and non-climatic environmental predictors (habitat, human impact), as well as spatial eigenvector mapping (spatial filters). The best performing models always included spatial filters, suggesting that palm species distributions are always to some extent limited by non-environmental constraints. Models which included climate provided significantly better predictions than models that included only non-climatic environmental predictors, the latter having no discernible effect beyond the climatic control. Hence, at the continental scale, climate constitutes the only strong environmental control of palm species distributions in Africa. With regard to the most important climatic predictors of African palm distributions, water-related factors were most important for 25 of the 29 species analysed. The strong response of palm distributions to climate in combination with the importance of non-environmental spatial constraints suggests that African palms will be sensitive to future climate changes, but that their ability to track suitable climatic conditions will be spatially constrained.

It is well known that the tropics harbour a major fraction of the World's biodiversity; yet, little is known regarding the drivers of tropical species distributions (Gentry 1988). In fact, while understanding the controls of geographic distributions of species is a central issue in ecology and biogeography (Gaston 2009a, b), we still do not have a thorough understanding of the limiting factors for the distribution of any species, despite decades of research (Gaston 2009b). While substantial theory on species distributions exists, it needs better validation from empirical work (Gaston 2009a). In particular, a better understanding of non-equilibrium range dynamics is needed (Holt et al. 2005), as this will have crucial importance for robust conservation planning in the face of global change (Midgley and Thuiller 2005). Notably, tropical biodiversity is foreseen to be critically threatened not only by climate change, but also by land-use changes and contingent habitat loss

and fragmentation (Bradshaw et al. 2009). At the same time, the distributions of tropical species are particularly poorly documented (Collen et al. 2008). Hence, there is a special need for understanding the determinants of the current distributions of tropical species.

Species distribution studies have primarily focused on the role of the environment, with climate often being assumed to be the main range-limiting factor (Gaston 2003), especially at large spatial scales (Pearson and Dawson 2003). Tropical regions experience little intra-annual climatic variability, particularly in terms of temperature. As a result, tropical species may have evolved narrow climatic tolerances; hence, steep climatic gradients have been hypothesised to provide stronger barriers to range expansion in the tropics than elsewhere (Janzen 1967). Consistent with this hypothesis, elevational range size has been found to increase with latitude in most vertebrate

groups investigated (McCain 2009). In contrast to climate, non-climatic environmental factors such as topography, land use and soil type are thought to increase in importance at increasingly finer scales (Pearson and Dawson 2003). Numerous studies have shown that topographic and edaphic factors often limit the distribution of tropical species at local to landscape scales (Svenning 1999, Jones et al. 2006). Although there are indications that non-climatic environmental factors may also be important range determinants at larger scales (Tuomisto 2007, Buermann et al. 2008), the relative importance of climatic and non-climatic environmental factors for determining the distributions of tropical species at continental scales is not well understood.

Whilst it is often argued or assumed that species range limits are determined by environmental constraints (McInnes et al. 2009), range limits may also be caused by non-environmental constraints, notably biotic interactions and dispersal limitations (Soberon 2007, Gaston 2009a), or a combination of both (Tuomisto et al. 2003). A species may be excluded from a region due to the presence of a competitor, by the absence of a mutualist or prey species, or by more complex biotic interactions (Case et al. 2005). Biotic interactions have been proposed to be particularly strong in the tropics, where they may limit species distributions more strongly than at higher latitudes (Brown et al. 1996). More generally, there is some evidence that species' low-latitude range limits are more often determined by biotic interactions than their high-latitude range limits (Normand et al. 2009). Alternatively, species distributions may simply be spatially constrained by limited dispersal (Gaston 2009a). It is widely accepted that species distributions can be constrained by major dispersal barriers (e.g. oceans), while the extent to which dispersal limits distributions at smaller scales is contentious (Gaston 2009b). Nevertheless, there is increasing evidence that dispersal can indeed be an important constraint on species distributions within continents and smaller regions (Svenning and Skov 2004, Normand et al. 2006, Munguia et al. 2008). Dispersal limitation may reflect physical dispersal barriers such as mountain ranges within regions (Brown et al. 1996, Gaston 2003), or time-limited expansion from place of origin or refugia (Svenning and Skov 2004, Paul et al. 2009). Ranges may also simply fail to expand due to intrinsic population dynamics: e.g. Allee effects (growth-rate depressions at low population densities) may potentially restrict species range expansions even in the absence of external drivers (Holt et al. 2005). The extent to which species distributions are limited by biotic interactions or dispersal have strong implications for nature conservation, especially in relation to climate change (Thomas et al. 2004); hereunder for predictive distribution modelling, which generally relies on species' distributions being at least close to equilibrium with the contemporary abiotic environment (Guisan and Thuiller 2005). If these assumptions are violated, model calibration may be inaccurate, potentially jeopardising the predictive ability of models, e.g. in relation to the consequences of future climate change (Guisan and Thuiller 2005).

Here, we assess the controls of the African continental-scale species distributions of a keystone tropical organism group, the palms (Arecaceae). Palms constitute important components of tropical and subtropical ecosystems across the World, with only few species occurring in warm-temperate regions (Dransfield et al. 2008). Both cultivated and wild palms are a much utilised resource in rural communities throughout the tropics (Dransfield et al. 2008). The species richness of palms is highest in tropical Asia (>1200 species) and the Americas (730 species), while only 65 species occur in Africa (Dransfield et al. 2008). Wild palms, nevertheless, constitute a keystone resource for African rural communities (Cunningham and Milton 1987, Dransfield 1988), as well as for wildlife (Yamakoshi 1998). The majority of African palms inhabit the humid rain forests, or low-lying swamplands, while only rather few species are associated with dry, open habitats (e.g. savannas or even deserts), and then often in the riparian zone or where the water table is locally high (Dransfield 1988, Tuley 1995). Recently, it has been found that climate and soil constitute important controls of continental- and regional-scale palm species distributions in the New World, although purely spatial constraints are generally of similar or greater importance (Bjorholm et al. 2008). However, the continental-scale controls of African palm distributions have not previously been quantitatively investigated. The smaller-scale distributions of New World palms have been related to topography, hydrology, human impact and dispersal, with the relative importance of these factors varying among studies (Clark et al. 1995, Svenning 1999, Normand et al. 2006, Svenning et al. 2006). Few analogous studies have been made in Africa, but there is evidence that similar factors influence the local distribution of palms here (Mwaura and Kaburu 2009).

Here we used a novel implementation of species distribution modelling (SDM) to estimate the degree to which the continental-scale distributions of African palm species are controlled by 1) climate, 2) non-climatic environmental factors such as habitat and human impact, or alternatively, 3) non-environmental spatial constraints, potentially reflecting the effects of biotic interactions and/or dispersal limitations. Distributions were analysed by the SDM algorithm Maxent in combination with climatic and non-climatic environmental predictors (habitat, human impact), as well as spatial eigenvector mapping (Borcard and Legendre 2002, Griffith 2003). The inclusion of eigenvectors (spatial filters, Griffith 2003) in SDM has recently been shown to effectively capture non-environmental constraints caused by dispersal-limited non-equilibrium range dynamics (De Marco et al. 2008). Our specific study questions concerning the range-limiting factors for the African palm species were: 1) what is the relative importance of environmental factors and non-environmental spatial constraints? 2) What is the relative importance of climatic and non-climatic environmental factors? 3) What is the relative importance of water- vs. temperature-related factors as climatic controls? By providing answers to these questions, we contribute to an improved quantitative basis for understanding what determines species distributions as well as for predicting the extent to which keystone tropical

organism groups, such as the palms, will be sensitive to future climate changes.

Materials and methods

Palm data

In general, there is a dearth of high-quality tropical biodiversity data; however, we have assembled a high-quality database on African palm species occurrences ($n = 1920$ unique species records, Fig. 1A), which is representative of the distribution of each palm species, and in general well distributed across each species' range, i.e. with no apparent geographical sampling bias. The occurrence data came primarily from herbarium collections from the Royal Botanic Gardens, Kew; the Nationaal Herbarium Nederland; the Missouri Botanical Garden and herbarium collections accessed through the Global Biodiversity Information Facility (GBIF) data-portal (Botanic Garden and Botanical Museum Berlin-Dahlem; Herbarium of the Aarhus Univ.; Museum National d'Histoire Naturelle; European Environment Agency; Fairchild Tropical Botanic Garden; National Herbarium of New South Wales; Royal Museum of Central Africa). Additional data was obtained through literature surveys, and from private databases and observations. For the present study, we selected all African palm species with ≥ 20 unique georeferenced observations ($n = 29$) (Supplementary material Table S1). The remaining 36 palm species are particularly rare (20) or in general widespread, yet, inadequately sampled (6), or with a questionable taxonomy (10). The selected palm species represent the variation in range sizes and ecological requirements amongst the African palms.

Predictor variables

Predictor variables were compiled to represent potential climatic and non-climatic range controls, dividing the latter into three subgroups (habitat, human impact, and spatial constraints). Variable selection was initially based on correlation tests using Pearson's correlations and one-way ANOVA tests to minimise potential collinearity issues (for further explanation, see Supplementary material Appendix S1 and Table S2). We used seven climatic variables commonly used in species distribution modelling to represent the climatic controls, hereof three variables representing temperature (annual mean temperature, AMT; temperature seasonality, TSEA; minimum temperature of the coldest month, TMIN) and four variables primarily representing water availability (annual precipitation, PREC; precipitation seasonality, PSEA; precipitation of driest quarter, PDRY; water balance, WATBAL, computed as the annual sum of monthly differences between potential evapotranspiration and precipitation). These variables were all from the Worldclim data set (Hijmans et al. 2005), except WATBAL, which was computed following Skov and Svenning (2004) using the CRU CL 2.0 data set (New et al. 2002) (Supplementary material Fig. S1).

The non-climatic factors were represented by five habitat, two human impact and fourteen spatial constraint variables. The habitat variables to represent the environmental variability of the area were: slope (SLOPE), derived from the U.S. Geological Survey GTOPO30 digital elevation model, and soil type (SOIL) from the Harmonised World Soil Database, which for Africa is derived from regional SOTER (soil and terrain) studies and the Digital Soil Map of The World at 30" (Fisher et al.

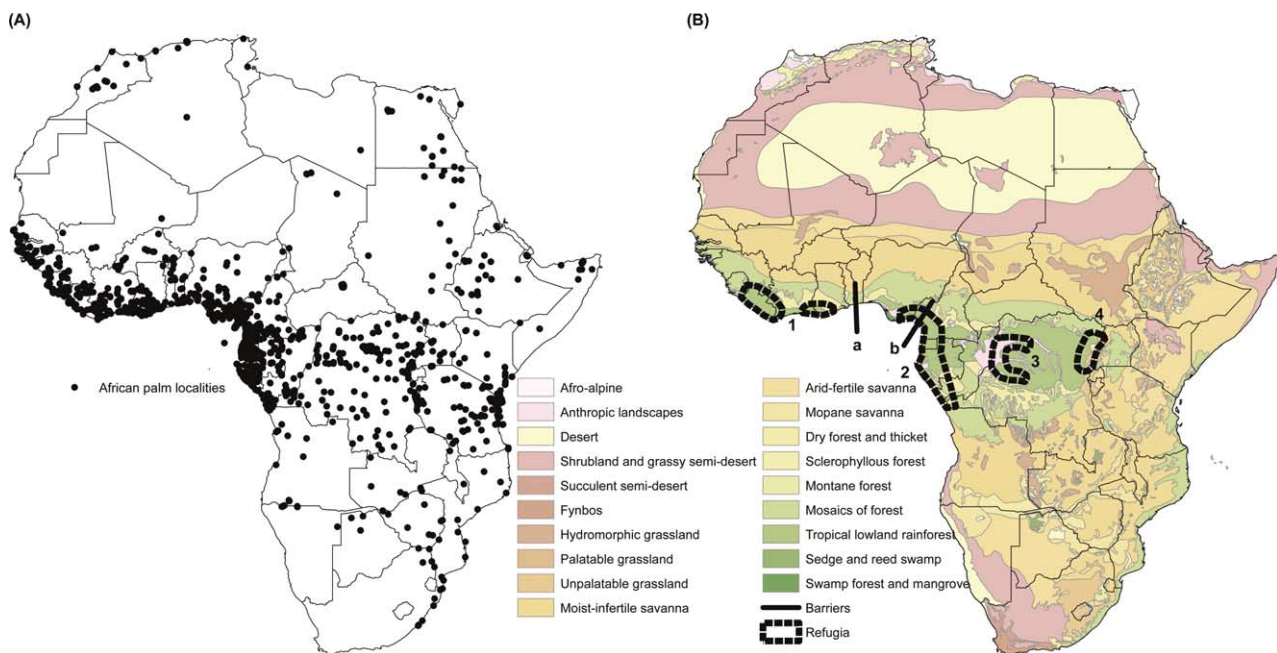


Figure 1. (A) Georeferenced point localities for all African palm species ($n = 1920$), (B) White's vegetation map of Africa (White 1983), overlaid with physical barriers for plant migration according to Richards (1973) and Tuley (1995) (a, the Dahomey Gap; b, the Cameroon Range), and the major forest refugia recognised for Africa for the Last Glacial Maximum (LGM): 1, Upper Guinea; 2, Cameroon-Gabon; 3, Congo Basin; and 4, Eastern Congo DRC (Hamilton and Taylor 1991, Maley 1991, Morley 2000).

2008). Three additional habitat variables were derived from remote sensing: 1) The Global Land Cover 2000 (GLC), assembled from various remote sensing data sources (SPOT vegetation, JERS and ERS radar, and The Defence Meteorological Satellite Program data) at 1-km spatial resolution (Mayaux et al. 2004); 2) Generalised Global Vegetation Index (GVI), obtained from Advanced Very High Resolution Radiometer (AVHRR) data as a series of monthly mean values for 1985–1988 (Kineman and Hastings 1992), which were averaged to derive an annual mean at 10' resolution; 3) The Vegetation Continuous Field product (VCF) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) data which provides a measure of percent tree cover for the year 2001 at 500-m resolution (Hansen et al. 2002) (Supplementary material Fig. S2). Current anthropogenic factors are also believed to control species ranges; hence, human impact was represented by: 1) human population density (POP), obtained from population statistics at 2.5' resolution for the year 2000 (CIESIN and CIAT 2005); 2) Human Influence Index (HMNINFL), consisting of values representing low (0) to high (64) human influence, and estimated for each grid cell based on several proxy data layers for human influence such as population density, land transformation, accessibility from road, rivers and coastlines, and electric power infrastructure (Sanderson et al. 2002) (Supplementary material Fig. S3).

To account for spatial constraints on the palm distributions, hereunder dispersal limitation-generated patterns, we used spatial filters (eigenvectors) (Griffith 2003) as spatial constraint variables. Spatial filters are orthogonal variables (Supplementary material Table S2), which represent the spatial relationship amongst spatial units (here: grid cells), and capture the geometry of the study area at a range of scales (Diniz-Filho and Bini 2005). The spatial filters were computed in SAM 3.0 (Rangel et al. 2006) by constructing a pairwise distance matrix amongst all grid cells using their geographical coordinates (latitude and longitude). The distance matrix was subsequently truncated at a given distance (default settings in SAM 3.0), and from this modified distance matrix 991 spatial filters were computed using principal coordinate analysis (Borcard and Legendre 2002). Only positive filters were retained. Due to computational limitations the filters were computed at a coarse resolution (100 × 100-km), but subsequently interpolated to 1 × 1-km resolution using the Inverse Weighted Distance method in GIS. This method was applied due to its inherent property that if point x_0 (point to be interpolated) coincide with point x_i (known value), the interpolation $z(x_0)$ always takes on the value of $z(x_i)$ (Webster and Oliver 2007). Griffith (2003) has proposed several strategies for selecting suitable spatial filters for regression analyses including: 1) maximisation of R^2 by using the stepwise regression procedure, 2) minimisation of regression residual spatial autocorrelation to obtain independent variable components, and 3) a significant correlation between the response and each spatial filter to use only meaningful eigenvectors. However, none of these strategies seem applicable in this particular case, where a key aim was to assess the relative importance of environmental factors and non-environmental spatial constraints for species distributions. In this case it was of paramount importance not to

introduce bias in the modelling towards either environment predictors or spatial filters. Hence, as a fixed number of predetermined environmental predictors were used, we also used the same number of spatial filters (first 7 or first 14 filters, depending on the environmental predictor set). These filters may represent relatively broad- to medium-scale spatial patterns (Supplementary material Fig. S4) such as those potentially resulting from major dispersal barriers (e.g. the Dahomey Gap in western Africa; Mayr and O'Hara 1986), dispersal-limited expansions from glacial refugia (Svenning and Skov 2004), other time-limited range expansions (Paul et al. 2009), or other non-environmental range constraints (Holt et al. 2005). Our approach is in line with De Marco et al. (2008) who included the first five spatial filters to explicitly include broad-scale spatial constraints into species distributions modelling.

All layers were reprojected to the Lambert Azimuthal Equal Area projection and resampled or aggregated to 1-km grid size using the nearest neighbour or bilinear resampling techniques for categorical and continuous variables respectively. All GIS operations were conducted in ArcGIS 9.2 (ESRI, Redlands, CA, USA).

Species distribution modelling

Species distribution modelling was implemented using the maximum entropy approach (Maxent) of Phillips et al. (2006) due to its high performance compared to other predictive algorithms in a recent comparative methodological study (Elith et al. 2006). To address the study questions, we ran Maxent with nine models based on different combinations of the predictors for each species. The combinations were: I) a full environmental model (clim + hab + hum) that included all the climatic, habitat and human impact predictors, II) a combined climate and habitat model (clim + hab) that included just the climatic and habitat predictors, III) an environment and filter model (clim + hab + hum + filters) that included all environmental predictors and all spatial filters. Additionally, we tested the performance of IV) a climate and filter model (clim + filters) that included the seven climatic predictors, and for balance, just the first seven filters to examine a simpler and potentially more parsimonious model compared to the clim + hab + hum + filters model. The remaining models included single groups of predictors in isolation V) climate (clim), VI) habitat (hab), VII) human impact (hum) variables, or VIII–IX) only the spatial filters (seven or fourteen filters, for use in different model comparisons) (Supplementary material Table S3).

The default settings for Maxent were used, with the allowed response types (linear, quadratic, product, threshold and hinge functions of the variables) for a species being determined by its number of point localities, as these settings have been shown to provide good predictive performance over a range of datasets (Phillips and Dudik 2008). To assess the relative influence of each predictor variable for a given species in the best performing model, we examined the contribution of each predictor to the final regularised training gain when all variables of the particular model were included in the Maxent run. The climatic variable with the highest gain (highest contribution to the

prediction for each species) was subsequently used in isolation in a model for all the point localities to also estimate its overall contribution to the prediction for a given species without the influence of the other predictors. This was done to ensure that our findings were not affected by the remaining collinearity among the predictors. If pairs of variables are highly correlated, the importance of one may be wrongly diminished by Maxent when both are included in the predictor set (Phillips et al. 2004).

Statistical analyses

Model performance was assessed by dividing the species occurrence data into random training (80%) and test (20%) datasets, and using 10 000 randomly selected pseudo-absences from the whole study area. Random selection of pseudo-absences has recently been found to outperform selection of pseudo-absences in low suitability areas (Wisz and Guisan 2009). A given model was calibrated on the training data and evaluated on the test data using two threshold-independent assessment measures: the Area Under the receiver operating characteristics Curve (AUC) and the point-biserial correlation (COR). AUC provides a measure of the accuracy of predictive distribution models (Lobo et al. 2008), a value of 0.5 indicating that the model is no better than random, while AUC values ≥ 0.750 are considered in the “best” model category (Phillips and Dudik 2008). However, comparing models across species using AUC scores is problematic as AUC is influenced by species’ prevalence, nonetheless, AUC can safely be applied to evaluate model performance within species (Lobo et al. 2008). Another issue regarding AUC, notably for presence-only methods, is that in theory the maximum achievable AUC can only be $1-a/2$, where a is the fraction of grids covered by a species’ distribution. However, a is often unknown (as in our case), and in practice the maximum AUC computed this way can be exceeded by the test AUC (AUC based on the test data set) (Phillips et al. 2006), although the reasons for this are largely unexplained in the

literature. We minimised these problems by only comparing AUC values among models within species (see below), thereby keeping prevalence constant. The point-biserial correlation (COR) was calculated as Pearson’s correlation between model predictions (suitability scores) and presence (1)/pseudoabsence (0) in the test data set (Elith et al. 2006, Phillips and Dudik 2008).

We primarily assessed the relative importance of the different predictor sets by comparing the performance of the various models using Wilcoxon sign rank tests with species as the sampling unit (i.e. a paired test). Two-tailed tests were used for model comparisons between the models based on non-overlapping sets of predictors, while one-tailed tests were used for comparisons of nested models. These tests were conducted in JMP 7.0 (SAS Inst., Cary). We additionally addressed the study questions by testing if certain groups of predictor variables contributed the strongest predictor variables for a species more often than expected by chance. This was assessed by classifying the most important variable (variable with the highest contribution to the training gain) for each species in the best performing model based on the Wilcoxon sign rank test (clim+filters) into various pairs of mutually exclusive groups (most important variable: environment vs spatial filters; most important climate variable: water vs temperature), and testing the group frequencies against the null expectation based on the number of variables in a group using Goodness of fit- (G -) tests (Sokal and Rohlf 1995).

Results

The AUC and COR measures provided highly consistent estimates of model performance (Table 1). Overall both environmental factors and spatial constraints were important controls of palm species distributions across Africa. The clim+hab+hum+filters model had superior predictive ability to the clim+hab+hum model, and was also significantly better than the filters model according to

Table 1. Wilcoxon sign rank test comparisons of the predictive ability among species distribution models based on different sets of predictors for 29 African palm species with ≥ 20 unique occurrence records. The tests compare two measures of model predictive ability: the Area Under the receiver operating Curve (AUC) and the point-biserial correlation (COR). Three model comparisons (MC1-3) are shown.

	Model	AUC		COR	
		Median	[min-max]	Median	[min-max]
MC1	Clim+hab+hum+filters	0.984 ^{a(a)}	0.749–1.000	0.181 ^{a(a)}	0.022–0.433
	Clim+hab+hum	0.975 ^b	0.608–0.999	0.156 ^b	0.022–0.346
	Filters	0.979 ^{ab}	0.897–1.000	0.151 ^b	0.044–0.408
MC2	Clim+filters	0.983 ^{a(a)}	0.855–1.000	0.153 ^{a(a)}	0.050–0.416
	Clim	0.976 ^b	0.759–1.000	0.135 ^b	0.037–0.330
	Filters	0.976 ^b	0.858–1.000	0.139 ^b	0.039–0.390
MC3	Clim+hab+hum	0.975 ^a	0.608–0.999	0.156 ^a	0.022–0.346
	Clim	0.976 ^a	0.759–1.000	0.135 ^{ab}	0.037–0.330
	Clim+hab	0.974 ^a	0.608–1.000	0.146 ^b	0.018–0.354
	Hab	0.931 ^b	0.630–0.998	0.101 ^c	0.009–0.250
	Hum	0.805 ^c	0.518–0.959	0.035 ^d	–0.001–0.084

Clim+hab+hum, (all environmental layers: climate, habitat, human impact); Filters, first 14 (MC1) or 7 (MC2) spatial filters; Clim, climate; Clim+hab, climate+habitat; Hum, human impact. Different superscript letters (a–d) indicate models which were significantly different (only tested within groups, MC1-3). All significantly different models differed at $p < 0.0001$ except for clim+filters vs filters at $p = 0.0057$ and clim+hab+hum vs hab at $p = 0.0023$ (in the AUC test), and clim+hab+hum+filters vs filters at $p = 0.0021$ and clim+hab+hum vs clim+hab at $p = 0.0182$ (in the COR test). The superscript (a) indicates no significant difference between the clim+hab+hum+filters and clim+filters models in AUC and COR.

COR (but not AUC; Table 1). Furthermore, the clim+filters model provided superior predictive ability to the clim and filters models, while the latter two models performed equally well (Table 1). These results indicate that palm distributions are not only limited by environmental factors, but also by spatial constraints, as was also apparent from the mapped predicted distributions for most species (Fig. 2, Supplementary material Fig. S5, S6). However, despite the fact that filters were an important component in structuring African palm distributions, the most important range predictor for a given species was significantly far more often a climatic variable (25 spp.) than a spatial filter (4 spp.; Table 2).

Among the environmental factors, only climate was important in determining distributions. There were no significant differences between the clim model, with only climatic predictors, and the more complex environmental models (clim+hab+hum, clim+hab) (Table 1). The clim model and the two more complex models including climatic variables were all superior to the non-climatic hum and hab models (Table 1). Hence, the simplest of these three climate models, the clim model with just seven climate predictors, was sufficient to account for the environmental control of the palm species ranges, with no significant additional effect of the non-climatic environmental factors. Supporting this conclusion, the clim+hab+hum+filters model also did not exhibit significantly better performance than the clim+filters model (Table 1).

As climate and spatial filters were sufficient to optimally predict palm species distributions across Africa; we assessed the relative importance of water- vs temperature-related factors using the clim+filters model. Water-related variables strongly predominated over temperature-related variables as the most influential individual predictor (Table 2, Fig. 3A–F). In terms of the specific species responses to climate, most of the species showed a positive response to increasing precipitation or water balance (Fig. 3A, D), with many species' responses peaking at approximately 2000–3000 mm (Fig. 3B, C), i.e. tropical rain forest climate. Just a few palm species were associated with low precipitation regimes and negative water balance (Fig. 3C).

Discussion

Our analyses showed that the continental-scale distributions of the African palms are not only limited by environmental controls, but also by spatial constraints (Table 1). Of the environmental controls, climate exhibited the greatest influence, while habitat or human impact had negligible impact on the distributions (Table 1). In terms of climate, the African palms were more dependent on water-related variables than temperature (Table 2).

We found that environmental factors (just climatic factors, in fact) had a strong effect on the African palm distributions. Hereby our results agree with most current thinking which emphasises climate as the main range determinant at large spatial scales (Pearson and Dawson 2003). Other studies have also shown that palm species distributions are sensitive to climate at multiple spatial scales (Salm 2007, Walther et al. 2007, Bjorholm et al. 2008). In addition, the paleo-record documents that past

climate change has had profound effects on the diversity and distribution of African palms (Morley 2000, Pan et al. 2006). Nevertheless, by including spatial filters in the modelling (De Marco et al. 2008) we found evidence that African palm species distributions are also often strongly spatially constrained beyond the effects of environmental control, i.e. in contrast to the equilibrium postulate (the assumption that species are in equilibrium with the contemporary abiotic environment; Guisan and Thuiller 2005). Notably, considering the predicted distributions, the clim model clearly overpredicted the distributions for most species relative to the clim+filters model (Fig. 2, Supplementary material Fig. S5).

We cannot firmly establish the mechanisms behind the purely spatial range constraints, but in many cases they are consistent with dispersal limitation in relation to dispersal barriers or glacial refugia. For example, the Mediterranean *Chamaerops humilis* (Tuley 1995) was predicted to also occur widely across southern Africa by the clim model, while the inclusion of spatial filters (clim+filters) removed this overprediction (Fig. 2). The effect of spatial filters, in this case, probably reflects dispersal limitation caused by the broad band of unsuitable non-Mediterranean climate between northern and southern Africa, hindering the southwards dispersal of this species. We note that numerous plant species that are native to either northern or southern Africa have become naturalised or even invasive after introduction to the other region (Fox 1990).

The overpredictions of the clim model in comparison to the predictions of the clim+filters model for several other species could be explained by geographic features that have been proposed as dispersal barriers in the phytogeographical literature (Richards 1973, Tuley 1995). *Podococcus barteri*, *Eremospatha wendlandiana*, *Laccosperma robustum* and *Raphia palma-pinus* all fail to fill both parts of their disjunct suitable areas in the Guineo-Congolian phytoregion (White 1983), in contrast to many other forest palm species of this region (Fig. 2, Supplementary material Fig. S5). The suitability disjunction corresponds to an intrusion of savanna in the distribution of tropical lowland rain forest in Ghana, Togo and Benin (Fig. 1B), known as the Dahomey Gap (Mayr and O'Hara 1986). The Dahomey Gap likely arose in the Holocene (cf. Maley 1991), but was also present during dry Pleistocene glacials (Dupont and Weinelt 1996), and has been suggested as a barrier for the dispersal for many other organisms in the region (Richards 1973). Another proposed dispersal barrier is the Cameroon Range (Fig. 1B), which forms a divide between the coastal West African and Congolian floras (Tuley 1995), and appears to constitute a dispersal barrier to some palm species (notably, *Eremospatha cabrae* and *Eremospatha cuspidata*) according to our results (Supplementary material Fig. S5).

The discontinuous distribution patterns of many forest plants and animals in Africa are thought to reflect retractions to forest refugia during cold and dry glacial periods of the Pleistocene in combination with limited postglacial range expansion (Mayr and O'Hara 1986, also cf. Hamilton and Taylor 1991). The predicted distributions by the clim+filters and clim+hab+hum+filters models (Fig. 2, Supplementary material Fig. S5, S6) for some species (*E. wendlandiana*, *Laccosperma acutiflorum*,

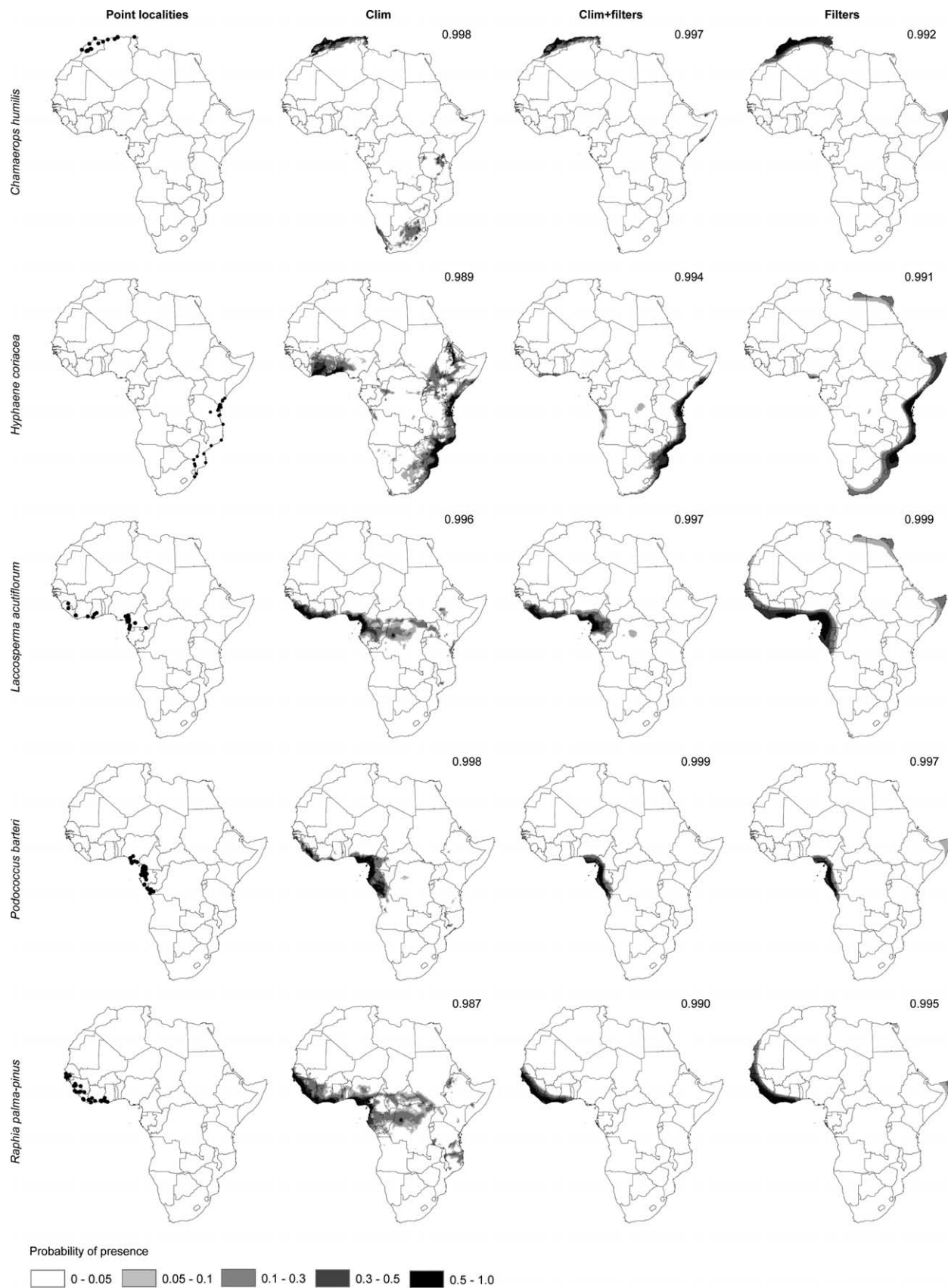


Figure 2. Presence localities and predicted distributions of five selected African palm species based on Maxent models fitted to all the presence localities per species using only climate predictors (clim), climate predictors and spatial filters (clim + filters), or just seven spatial filters (filters). AUC scores are displayed in the upper right-hand corner of each predicted distribution map. Corresponding maps for the remaining 24 palm species are provided in Fig. S5 in the Supplementary material.

Table 2. Goodness of fit- (G -) tests for whether the observed frequency of the most important predictor variable for each species (based on the best performing model (clim+filters)) across two pairs of two mutually exclusive predictor classes deviates from random expectation (expected frequency = $n \times$ [number of predictor variable in the class/number of predictor variables in the two classes combined], $n = 29$ species). The number of predictor variables in a class is given in parentheses. The G -tests were implemented using Williams' correction for the two-cell case (G_{adj}).

Classes	Observed	Expected	G_{adj}
Environment (7)†	25	14.5	16.65***
Filters (7)	4	14.5	
Water balance (4)	25	16.6	11.30***
Temperature (3)	4	12.4	

†, just the seven climatic variables, given that the analyses were based on the clim+filters model; ***, $p < 0.001$.

Laccosperma laeve, *Oncocalamus mannii*, *Oncocalamus tuleyi*, *Podococcus acaulis* and *P. barteri*) coincided broadly with recognised glacial refugia for rain forest in Africa. Despite some disagreement in the literature, there is a general consensus that the following four regions acted as refugia: Upper Guinea, Cameroon-Gabon, the Congo Basin, and Eastern Congo DRC (Fig. 1B) (Hamilton and Taylor 1991, Maley 1991, Morley 2000). The distributions of *E. wendlandiana*, *P. acaulis*, *P. barteri*, *O. mannii* and *O. tuleyi* are restricted to the vicinity of the Cameroon-Gabon refuge and *L. acutiflorum* and *L. laeve* to both the Upper Guinea and Cameroon-Gabon refuges despite suitable areas occurring much more widely. Similar refuge-restricted patterns are also known from other regions and taxa, e.g. European trees (Svenning and Skov 2007, Svenning et al. 2008).

The extent to which a species fills its full potential distribution (range-filling, Svenning and Skov 2004) has for other plant groups been shown to be related to species' dispersal ability or time for dispersal (Schurr et al. 2007, Paul et al. 2009). For African palms, such assessments have not yet been conducted, but palms are generally thought to be poor dispersers (Dransfield 1981). A number of studies have found evidence that New World palms are dispersal limited at both continental (Bjorholm et al. 2008) and smaller scales (Charles-Dominique et al. 2003, Normand et al. 2006, Svenning et al. 2006). Palms are mainly dispersed by mammals or birds, but there is substantial variability among palm species in the types of dispersers within these groups (Zona and Henderson 1989), and thereby potentially also in dispersal ability. As spatial filters simply capture spatial range constraints of any nature, the evidence for constraints beyond those caused by environmental limitation could also reflect mechanisms other than dispersal, e.g. biotic interactions. However, we found little evidence that biotic interactions limit the African palm species distributions at large scale. Notably, even within the larger genera (*Hyphaene*, *Eremospatha* and *Laccosperma*), many, and often the majority, of the species tend to co-occur at least sometimes in the same regions. The most obvious potential exception would be *Hyphaene petersiana* and *Hyphaene thebaica* (Fig. 2, Supplementary material Fig. S5, S6).

We found that climatic factors were important determinants of African palm species distributions, as already

discussed, while the non-climatic environmental factors had no discernable influence. These results agree with the a priori notion that climate is the main environmental control of species ranges at large scales, while non-climatic environmental factors such as human impact and soil type mainly are important at smaller scales (Pearson and Dawson 2003). At local to landscape scales, habitat and human impact are important determinants of palm species distributions in the New World (Clark et al. 1995, Svenning 1999, Normand et al. 2006, Svenning et al. 2006). There is no reason to think that African palm species distributions would not be similarly influenced by these factors, and some evidence for this does indeed exist (Cunningham and Milton 1987, Tuley 1995). However, at the continental scale the importance of these variables is not strong enough to be apparent with the data presently available. Yet, we note that soil, notably the response to soils associated with good water retention and high water tables, appeared as an important predictor for dry-climate palms in the hab, clim+hab and clim+hab+hum models (results not shown) indicating that hydrology is an important aspect for these palms. Especially for *Hyphaene petersiana* does soil constitute a stronger predictor than any climatic variables, according to a recent study of this species (Blach-Overgaard et al. 2009). However, these relationships are not frequent enough to affect the overall model comparisons, where the simple climatic model performed as well as models including both climatic and non-climatic environmental predictors. The limited overall importance of habitat factors such as soil is likely caused by the 1-km spatial resolution of the present study, which may cause much of the variation in habitat and human influence to be within grid cells.

In terms of the climatic predictors, water-related variables were found to strongly predominate over temperature variables as range-controlling factors for the African palms (Table 2). The superior importance of water-related factors is consistent with the idea that water availability has greater importance than temperature in subtropical and tropical zones for controlling patterns of species diversity (Hawkins et al. 2003). Moreover, water is in general of greatest importance for palm occurrences worldwide (Dransfield et al. 2008); even dry-climate palms are dependent on locally high water tables to persist in dry environments (Tuley 1995). Similarly to our findings, Salm et al. (2007) found that a water-related climatic variable was the main predictor of palm species distributions and species richness in Brazil, whereas temperature was only of secondary importance. We note that our findings on the relative importance of the various factors will most likely be specific to our study group, the African palms, and further studies will be needed to assess to what extent they can be generalised to other species groups with other geographies, ecologies, and evolutionary histories.

Our variable selection approach limited collinearity problems. Nevertheless, there were fairly high correlations among some of the predictor variables (Supplementary material Table S2). These correlations had no overall influence on our major conclusions. Maxent may only use one of the variables in a pair of highly correlated variables, and thus has an ability to deal with such cases; however overall model performance will not be affected (Phillips et al. 2004). More importantly, in our case, the only highly

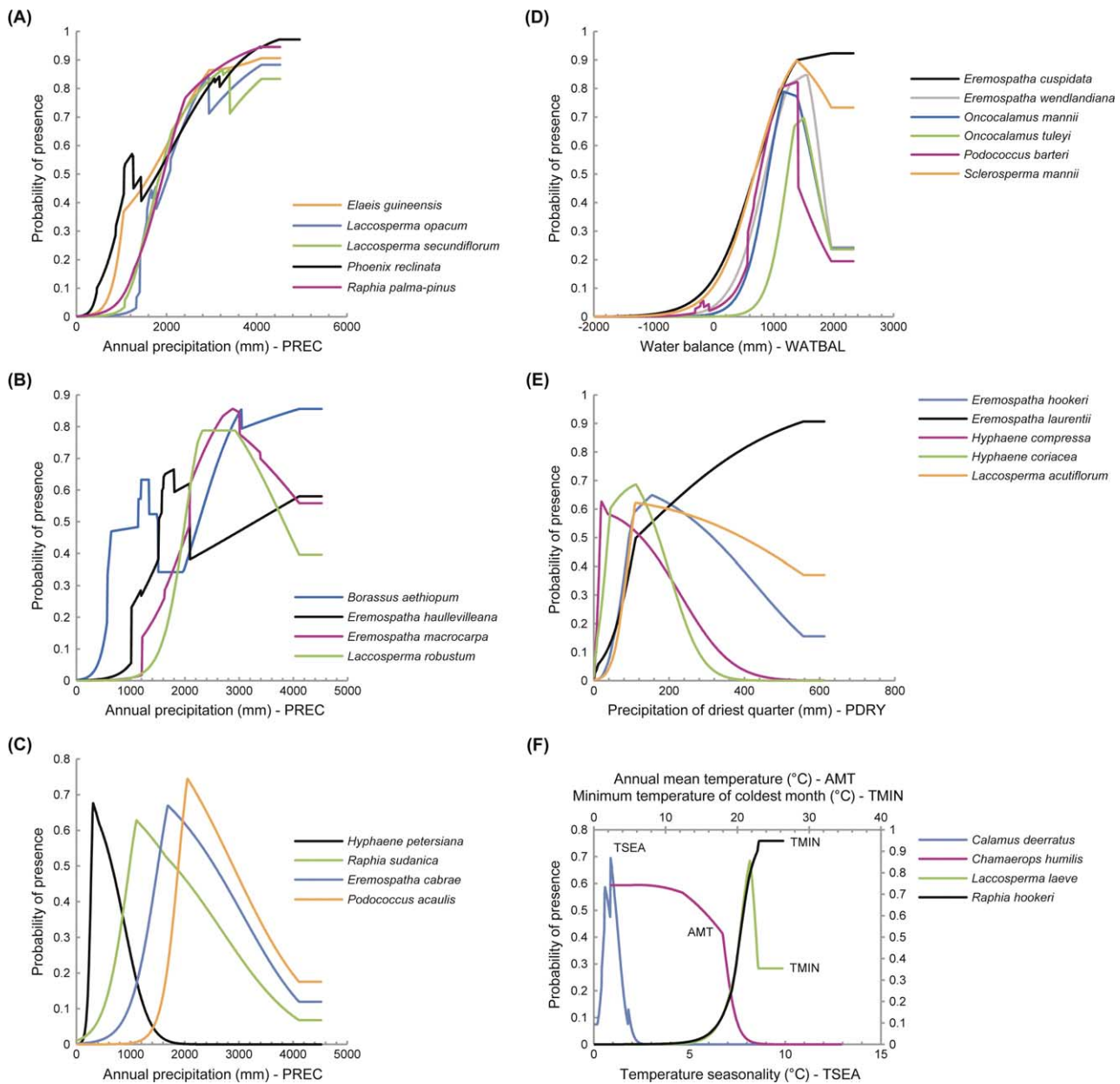


Figure 3. Response curves to the most important climatic predictors for 28 African palm species. For each species, the response curve for the climatic predictor with the highest relative contribution in the clim+filters Maxent model is shown. For 25 species this climatic variable had the highest relative contribution among all 14 predictors, while for three species (*Eremospatha haullevilleana*, *Hyphaene petersiana* and *Raphia sudanica*) it ranked second in importance after a spatial filter. The response curves were estimated by Maxent modelling based on all presence localities per species using just the selected climatic predictor. For the 29th species, *Hyphaene thebaica*, precipitation seasonality was the second-most important predictor after a filter (response curve not shown).

correlated predictors were WATBAL and PREC (Supplementary material Table S2), which both belong to the same predictor category (water-related climate variables); ensuring that any collinearity effects on the relative importance of variables would not be relevant for any of our study questions.

More broadly considering our methodology, in the present study we have achieved new insights in the determinants of species distributions in a keystone tropical organism group by applying the novel implementation of SDM developed by De Marco et al. (2008). While our

study therefore illustrates the potential of this method, we note that other methodologies also may provide important insights on broad-scale species distribution patterns. Notably, species distributions can also be modelled as whole assemblages, e.g. using constrained ordinations (Svenning and Skov 2005) or using Community Dissimilarity Modelling (Ferrier and Guisan 2006). The use of spatial filters to represent non-environmental spatial constraints on the species distributions is easily implemented in many of these approaches. Several alternative methods for representing spatial structure in species distributions are also

available (Dormann et al. 2007); although unlike spatial filters most cannot be implemented in presence-only based modelling.

Since the distributions of African palms are strongly influenced by climate and are often also limited by non-environmental spatial constraints, which in many cases are consistent with dispersal limitation effects, African palms are likely to be at risk from future climate change. Continental-based climate assessments show that Africa is likely to experience marked climatic changes over the 21st century with drying and warming in most subtropical regions and slight increases in precipitation in the tropics (Boko et al. 2007). The African palms exhibit varying responses to the climate variables studied (Fig. 3). Hence, we should also expect the response of the African palm species to future climate change to vary among species. Nevertheless, the majority of species have their distributions strongly controlled by the climatic water regime, with most preferring a wet rain forest climate, and must therefore be expected to be sensitive to increasing drying. Climate change will also affect the hydrology, notably in the drier regions, and will therefore constitute a risk for the hydrology-dependent dry-climate palms (Blach-Overgaard et al. 2009). These conclusions are supported by the paleo-record, which links past palm species extinctions in Africa to increasing drought (Morley 2000). When species are exposed to major climate changes, they are forced to either adapt to the changed conditions, or to track a suitable climate by migration. However, the often strong non-environmental spatial constraints on the African palm species distributions suggest that the scope for large-scale range shifts to track the changing climate will be limited. Hereby, dispersal limitation will probably aggravate the risk posed by climate change to African palm species. The risks to the African palm flora are likely to be exacerbated by the same factors which cause Africa to be listed as the continent that is most vulnerable to future climate change, namely the additional stresses that plague the region (e.g. poverty, political instability, disasters) (Boko et al. 2007). For example, the capacity for evolutionary adaptation will be limited in populations already reduced by habitat degradation and direct over-utilisation (Cunningham and Milton 1987, Dransfield et al. 2008), while migration rates will be reduced in strongly fragmented landscapes. As the African palms also provide important resources to rural communities and wildlife in Africa (Dransfield 1988, Yamakoshi 1998), declining palm populations would exacerbate the climate-change induced problems for society and ecosystems in the region.

Conclusions

The current study implements a novel SDM approach (De Marco et al. 2008) to determine the factors which best determine species distributions by assessing the relative importance of climate, non-climatic environmental factors and non-environmental spatial constraints for the continental-scale distributions of African palms. In contrast to general theory and the typical assumption of many species distribution modelling studies (Pearson and Dawson 2003, Guisan and Thuiller 2005); our results clearly show that

although climate constitutes an important control of African palm distributions, they are also strongly controlled by spatial constraints. We note that the spatial constraints were, to a large extent, consistent with dispersal limitation in relation to physical barriers (often broad zones of unsuitable climate) as well as time-limited expansions from past refugia. Our results highlight the need for SDM approaches that are robust to violations of the equilibrium postulate, at least when the goal is accurate prediction into new temporal or spatial domains. Consistent with theory (Pearson and Dawson 2003), non-climatic environmental constraints such as human impact or soil type had no discernible influence at the large scale of the present study. The climatic control mainly represented sensitivity to the climatic water regime. From a conservation approach, the findings that many African palm species are not only sensitive to the climatic water regime, but also have distributions that are strongly constrained by purely spatial factors are worrying since Africa is predicted to experience changed precipitation patterns with strong drying in many regions during the 21st century (Boko et al. 2007), and thus the ability of the palms to track suitable climatic conditions may be spatially constrained.

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References

- Bjorholm, S. et al. 2008. To what extent does Tobler's 1st law of geography apply to macroecology? A case study using American palms (Arecaceae). – *BMC Ecol.* 8: 11.
- Blach-Overgaard, A. et al. 2009. Climate change sensitivity of the African ivory nut palm, *Hyphaene petersiana* Klotzsch ex Mart. (Arecaceae) – a keystone species in SE Africa. – *IOP Conf. Ser.: Earth Environ. Sci.* 8: 012014.
- Boko, M. et al. 2007. Africa. Climate change 2007: impacts, adaptation and vulnerability. – In: Canziani, P. M. L. et al. (eds), *Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge Univ. Press, pp. 433–467.
- Borcard, D. and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. – *Ecol. Model.* 153: 51–68.
- Bradshaw, C. J. A. et al. 2009. Tropical turmoil: a biodiversity tragedy in progress. – *Front. Ecol. Environ.* 7: 79–87.
- Brown, J. H. et al. 1996. The geographic range: size, shape, boundaries, and internal structure. – *Annu. Rev. Ecol. Syst.* 27: 597–623.

- Buermann, W. et al. 2008. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. – *J. Biogeogr.* 35: 1160–1176.
- Case, T. J. et al. 2005. The community context of species' borders: ecological and evolutionary perspectives. – *Oikos* 108: 28–46.
- Charles-Dominique, P. et al. 2003. Colonization front of the understory palm *Astrocaryum sciophilum* in a pristine rain forest of French Guiana. – *Global Ecol. Biogeogr.* 12: 237–248.
- CIESIN and CIAT 2005. Gridded population of the World version 3 (GPWv3): population density grids. – Socioeconomic data and applications center (SEDAC), Palisades, NY, Columbia Univ. Press.
- Clark, D. A. et al. 1995. Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. – *Ecology* 76: 2581–2594.
- Collen, B. et al. 2008. The tropical biodiversity data gap: addressing disparity in global monitoring. – *Trop. Conserv. Sci.* 1: 75–88.
- Cunningham, A. B. and Milton, S. J. 1987. Effects of basket-weaving industry on Mokola Palm and dye plants in north-western Botswana. – *Econ. Bot.* 41: 386–402.
- De Marco, P. et al. 2008. Spatial analysis improves species distribution modelling during range expansion. – *Biol. Lett.* 4: 577–580.
- Diniz-Filho, J. A. F. and Bini, L. M. 2005. Modelling geographical patterns in species richness using eigenvector-based spatial filters. – *Global Ecol. Biogeogr.* 14: 177–185.
- Dormann, C. F. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. – *Ecography* 30: 609–628.
- Dransfield, J. 1981. Palms and Wallace's line. – In: Whitmore, T. C. (ed.), *Wallace's line and plate tectonics*. Clarendon Press, pp. 43–56.
- Dransfield, J. 1988. The palms of Africa and their relationships. – In: Goldblatt, P. and Lowry, P. P. (eds), *Modern systematic studies in African botany*. Missouri Botanical Garden Press, pp. 95–103.
- Dransfield, J. et al. 2008. *Genera Palmarum*. The evolution and classification of palms. – Royal Botanic Gardens, Kew.
- Dupont, L. M. and Weinelt, M. 1996. Vegetation history of the savanna corridor between the Guinean and the Congolian rain forest during the last 150 000 years. – *Veg. Hist. Archaeobot.* 5: 273–292.
- Elith, J. et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. – *Ecography* 29: 129–151.
- Ferrier, S. and Guisan, A. 2006. Spatial modelling of biodiversity at the community level. – *J. Appl. Ecol.* 43: 393–404.
- Fisher, G. et al. 2008. Global agro-ecological zones assessment for agriculture (GAEZ 2008). – IIASA, Laxenburg, Austria and FAO, Rome, Italy.
- Fox, M. D. 1990. Mediterranean weeds: exchanges of invasive plants between the five Mediterranean regions of the world. – In: Di Castri, F. et al. (eds), *Biological invasions in Europe and the Mediterranean Basin*. Kluwer, pp. 179–200.
- Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. – Oxford Univ. Press.
- Gaston, K. J. 2009a. Geographic range limits of species. – *Proc. R. Soc. B* 276: 1391–1393.
- Gaston, K. J. 2009b. Geographic range limits: achieving synthesis. – *Proc. R. Soc. B* 276: 1395–1406.
- Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. – *Ann. Missouri Bot. Gard.* 75: 1–34.
- Griffith, D. A. 2003. Spatial autocorrelation and spatial filtering: gaining understanding through theory and scientific visualization. – Springer.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. – *Ecol. Lett.* 8: 993–1009.
- Hamilton, A. C. and Taylor, D. 1991. History of climate and forests in tropical Africa during the last 8 million years. – *Clim. Change* 19: 65–78.
- Hansen, M. C. et al. 2002. Towards an operational MODIS continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. – *Remote Sens. Environ.* 83: 303–319.
- Hawkins, B. A. et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. – *Ecology* 84: 3105–3117.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Holt, R. D. et al. 2005. Theoretical models of species' borders: single species approaches. – *Oikos* 108: 18–27.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – *Am. Nat.* 101: 233–249.
- Jones, M. M. et al. 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. – *J. Ecol.* 94: 181–195.
- Kineman, J. and Hastings, D. 1992. Monthly generalized global vegetation index from NESDIS NOAA-9 weekly GVI data (APR 1985–DEC 1988). Digital raster data on a 10-minute Cartesian Orthonormal Geodetic (lat/long) 1080 × 2160 grid (Platte Carree projection). Global Ecosystems Database Ver. 2.0. – NOAA National Geophysical Data Center, Boulder, CO.
- Lobo, J. M. et al. 2008. AUC: a misleading measure of the performance of predictive distribution models. – *Global Ecol. Biogeogr.* 17: 145–151.
- Maley, J. 1991. The African rain forest vegetation and paleoenvironments during Late Quaternary. – *Clim. Change* 19: 79–98.
- Mayaux, P. et al. 2004. A new land-cover map of Africa for the year 2000. – *J. Biogeogr.* 31: 861–877.
- Mayr, E. and O'Hara, R. J. 1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. – *Evolution* 40: 55–67.
- McCain, C. M. 2009. Vertebrate range sizes indicate that mountains may be 'higher' in the tropics. – *Ecol. Lett.* 12: 550–560.
- McInnes, L. et al. 2009. Where do species' geographic ranges stop and why? Landscape impermeability and the Afrotropical avifauna. – *Proc. R. Soc. B* 276: 3063–3070.
- Midgley, G. F. and Thuiller, W. 2005. Global environmental change and the uncertain fate of biodiversity. – *New Phytol.* 167: 638–641.
- Morley, R. J. 2000. *Origin and evolution of tropical rain forests*. – Wiley.
- Munguia, M. et al. 2008. Dispersal limitation and geographical distributions of mammal species. – *J. Biogeogr.* 35: 1879–1887.
- Mwaura, F. and Kaburu, H. M. 2009. Spatial variability in woody species richness along altitudinal gradient in a lowland-dryland site, Lokapel Turkana, Kenya. – *Biodivers. Conserv.* 18: 19–32.
- New, M. et al. 2002. A high-resolution data set of surface climate over global land areas. – *Clim. Res.* 21: 1–25.
- Normand, S. et al. 2006. Geographical and environmental controls of palm beta diversity in paleo-riverine terrace forests in Amazonian Peru. – *Plant Ecol.* 186: 161–176.
- Normand, S. et al. 2009. Importance of abiotic stress as a range-limit determinant for European plants: insights from species responses to climatic gradients. – *Global Ecol. Biogeogr.* 18: 437–449.

- Pan, A. D. et al. 2006. The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28–27 Mya) of north-western Ethiopia. – *Bot. J. Linn. Soc.* 151: 69–81.
- Paul, J. R. et al. 2009. Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant genus *Psychotria* (Rubiaceae). – *Am. Nat.* 173: 188–199.
- Pearson, R. G. and Dawson, T. P. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? – *Global Ecol. Biogeogr.* 12: 361–371.
- Phillips, S. J. and Dudik, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. – *Ecography* 31: 161–175.
- Phillips, S. J. et al. 2004. A maximum entropy approach to species distribution modeling. – In: *Proceedings of the 21st International Conference on Machine Learning*. ACM Press, pp. 655–662.
- Phillips, S. J. et al. 2006. Maximum entropy modeling of species geographic distributions. – *Ecol. Model.* 190: 231–259.
- Rangel, T. F. L. V. B. et al. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. – *Global Ecol. Biogeogr.* 15: 321–327.
- Richards, P. W. 1973. Africa, the “odd man out”. – In: Meggers, B. J. et al. (eds), *Tropical forest ecosystems in Africa and South America: a comparative review*. Smithsonian Inst. Press, pp. 21–26.
- Salm, R. et al. 2007. Cross-scale determinants of palm species distribution. – *Acta Amazon.* 37: 17–26.
- Sanderson, E. W. et al. 2002. The human footprint and the last of the wild. – *Bioscience* 52: 891–904.
- Schurr, F. M. et al. 2007. Colonization and persistence ability explain the extent to which plant species fill their potential range. – *Global Ecol. Biogeogr.* 16: 449–459.
- Skov, F. and Svenning, J.-C. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. – *Ecography* 27: 366–380.
- Soberon, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1115–1123.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry*. – W. H. Freeman.
- Svenning, J.-C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. – *J. Ecol.* 87: 55–65.
- Svenning, J.-C. and Skov, F. 2004. Limited filling of the potential range in European tree species. – *Ecol. Lett.* 7: 565–573.
- Svenning, J.-C. and Skov, F. 2005. The relative roles of environment and history as controls of tree species composition and richness in Europe. – *J. Biogeogr.* 32: 1019–1033.
- Svenning, J.-C. and Skov, F. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. – *Global Ecol. Biogeogr.* 16: 234–245.
- Svenning, J.-C. et al. 2006. The relative roles of environment, history and local dispersal in controlling the distributions of common tree and shrub species in a tropical forest landscape, Panama. – *J. Trop. Ecol.* 22: 575–586.
- Svenning, J.-C. et al. 2008. Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. – *Ecography* 31: 316–326.
- Thomas, C. D. et al. 2004. Extinction risk from climate change. – *Nature* 427: 145–148.
- Tuley, P. 1995. *The palms of Africa*. – The Trendline Press.
- Tuomisto, H. 2007. Interpreting the biogeography of South America. – *J. Biogeogr.* 34: 1294–1295.
- Tuomisto, H. et al. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. – *Science* 299: 241–244.
- Walther, G. R. et al. 2007. Palms tracking climate change. – *Global Ecol. Biogeogr.* 16: 801–809.
- Webster, R. and Oliver, M. A. 2007. *Geostatistics for environmental scientists*. – Wiley.
- White, F. 1983. *Vegetation of Africa – a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. – U.N. Educational, Scientific and Cultural Organization.
- Wisz, M. and Guisan, A. 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. – *BMC Ecol.* 9: 8.
- Yamakoshi, G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. – *Am. J. Phys. Anthropol.* 106: 283–295.
- Zona, S. and Henderson, A. 1989. A review of animal-mediated seed dispersal of palms. – *Selbyana* 11: 6–21.

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