

The significance of geographic range size for spatial diversity patterns in Neotropical palms

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We examined the effect of range size in commonly applied macroecological analyses using continental distribution data for all 550 Neotropical palm species (Arecaceae) at varying grain sizes from 0.5° to 5°. First, we evaluated the relative contribution of range-restricted and widespread species on the patterns of species richness and endemism. Second, we analysed the impact of range size on the predictive value of commonly used predictor variables. Species sequences were produced arranging species according to their range size in ascending, descending, and random order. Correlations between the cumulative species richness patterns of these sequences and environmental predictors were performed in order to analyse the effect of range size. Despite the high proportion of rare species, patterns of species richness were found to be dominated by a minority of widespread species (~20%) which contained 80% of the spatial information. Climatic factors related to energy and water availability and productivity accounted for much of the spatial variation of species richness of widespread species. In contrast, species richness of range-restricted species was to a larger extent determined by topographical complexity. However, this effect was much more difficult to detect due to a dominant influence of widespread species. Although the strength of different environmental predictors changed with spatial scale, the general patterns and trends proved to be relatively stable at the examined grain sizes. Our results highlight the difficulties to approximate causal explanations for the occurrence of a majority of species and to distinguish between contemporary climatic factors and history.

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The uneven distribution of diversity is one of the most prominent patterns in ecology and has attracted massive scientific interest since the beginnings of biogeography (Humboldt 1808). The debate about possible determinants of large-scale patterns of species richness has led to a plethora of hypotheses during the last decades and even recently further hypotheses have been proposed (Fischer 1960, Pianka 1966, MacArthur 1972, Stevens 1989, Rohde 1992, Colwell and Hurtt 1994, Rosenzweig 1995, Gaston 1996, 2000, Ritchie and Olff 1999, Chown and Gaston 2000, Dynesius and Jansson 2000, Jansson and Dynesius 2002, Hawkins et al. 2003b, Willig et al. 2003). Searching for determinants of large-scale patterns

of diversity, conventional approaches analyse species richness maps dependent on environmental variables, e.g. temperature, precipitation, ambient energy, productivity, topographical complexity, or habitat heterogeneity (Currie and Paquin 1987, Currie 1991, Kerr and Packer 1997, O'Brien 1998, O'Brien et al. 1998, Qian and Ricklefs 2000, Rahbek and Graves 2001, Jetz and Rahbek 2002, Francis and Currie 2003, Hawkins et al. 2003a).

The vast majority of studies uses species occurrence data in the form of range maps or museum records to document and analyse large-scale patterns of species richness and endemism (Currie and Paquin 1987, Lovett

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et al. 2000, Rahbek and Graves 2001). Thus, geographic ranges of species are the basic unit of biogeography and one of the most prominent biogeographic features is that species differ in the size of their geographic ranges (Brown et al. 1996). Within a given assemblage of species most species tend to have relatively small ranges (Gaston 1994, 1998, Brown et al. 1996) and it has been argued that this reflects one of the most fundamental ways of how species share space (Brown 1995). Differences in range size may reflect interspecific differences in ecological tolerance, dispersal ability, and evolutionary history (Hengeveld 1990, Brown 1995, Gaston 1998, Cowling and Lombard 2002, Pither 2003, Lloyd et al. 2003) or may reflect ecological traits associated with different life-forms (Kelly 1996, Kessler 2002, Hunter 2003).

Overall species richness patterns thus emerge from a complex spatial interaction of many species with small ranges and relatively few species with very large ranges. So far, relatively little attention has been paid to this issue. Since species richness maps emerge from superimposed range maps of individual species, exploring the influence of range size may substantially improve our understanding of large-scale diversity patterns. Consequences of the highly skewed range size frequency distributions (RSFD) on spatial patterns of species richness and on our perception of environmental determinants of species richness have so far been tested exclusively with vertebrates (Jetz and Rahbek 2002, Ruggiero and Kitzberger 2004, Lennon et al. 2004). Plants in general appear to be largely under-represented in macroecological studies, because reliable distribution data especially for tropical families is insufficient.

The tropics of the New World exhibit the richest flora of all floristic kingdoms (Gentry 1982b, Kier et al. 2005). The vast majority of studies on continental-scale patterns of species richness in the Neotropics rely on atlas data for vertebrate groups like birds and mammals (Kaufman and Willig 1998, Rahbek and Graves 2001, Willig et al. 2003, Ruggiero and Kitzberger 2004, Tognelli and Kelt 2004), or use other data from plots (ter Steege et al. 2003) or other floristic inventories (Barthlott et al. 1996, Kier et al. 2005). However, knowledge about the distribution of Neotropical palms is reasonably good and appropriate distribution data with a continent-wide coverage is available (Henderson et al. 1995). Following the work of Jetz and Rahbek (2002) and expanding the approach of Lennon et al. 2004, this study aims to investigate the contribution of species with different range sizes to two frequently used measures of spatial variation of diversity: species richness and range size rarity. Furthermore, we analyse the influence of range size on the perception of environmental determinants of these patterns.

Methods

Distribution data

We examined a continent-wide data set of all 550 native palm species (Arecaceae) of the Americas. The palm family has an essential tropical distribution and includes ca 2700 species in 200 genera worldwide. In the Neotropics, palms occur between ca 36°N and 34°S and dominate vast landscapes by their high abundance and conspicuous appearance.

Range maps of all New World species of palms were compiled from Henderson et al. (1995) and digitized in ArcView 3.2. Presence and absence of every single species was extracted across a 0.5° latitude × 0.5° longitude grid resulting in a map of 6638 grid cells with a total of 140 860 positive grid records. Range size was measured as the number of grid cells where a species is present.

Statistical analysis

To analyse the relative contribution of range size to patterns of species richness, we ranked all species according to their range size in ascending order (i.e. starting with the species with the smallest range, small-to-large sequence) and in descending order (i.e. starting with the species with the largest range, large-to-small sequence) (cf. the procedure of Lennon et al. 2004). We also generated a random sequence of species based on 2000 runs.

Species richness maps of subassemblages were generated by starting with either the most widespread or most range-restricted species and adding the next species in the sequence to the sequential species richness pattern at that stage. For each of the range size sequences (ascending, descending and random) we correlated at each step the generated species richness patterns with the overall pattern of species richness (number of species per grid cell) and range size rarity (sum of the inverse range sizes of all species occurring in one grid cell, a measure that combines species richness and endemism (Usher 1986, Williams 1993)).

Different species contribute varying amounts of spatial information to species richness patterns depending on their range size. To investigate the volume of spatial information that different species contribute to the species richness patterns along the different sequences we applied the information index suggested by Lennon et al. (2004). Accordingly, each species was weighted according to its range size, calculated as $p^*(1-p)$, where p is the occupancy of a given species. This measure takes into account that the potential spatial information is at maximum for species with 50% occupancy, while species with, e.g. 30 and 70% occupancy contain an equivalent amount of spatial

information, i.e. the distribution of information is symmetrical around 50% occupancy. We used two different plots that allow observing the increase of correlations between species richness patterns of all species and of subassemblages with increasing numbers of species and with increasing volume of spatial information along the sequences, respectively.

The effect of range size in ecological analyses was analysed by correlating species richness patterns of the three different kinds of sequences with predictor variables which are frequently attributed to account considerably for the spatial variation of species richness (actual evapotranspiration, potential evapotranspiration, precipitation, productivity, and topographical heterogeneity). Data for potential and actual evapotranspiration were obtained from Ahn and Tateishi (1994) and Tateishi and Ahn (1996), data for mean annual precipitation from New et al. (2002) and data for net primary productivity from Cramer et al. (1999). Elevation data in a 30 arc second resolution ($\sim 1 \text{ km}^2$) were taken from the GTOPO30 data set developed by the U.S. Geological Survey EROS Data Center (<http://edcdaac.usgs.gov/gtopo30/gtopo30.asp>). We used altitudinal range per grid cell as a surrogate for habitat heterogeneity (compare Kerr and Packer 1997, Rahbek and Graves 2000, 2001, O'Brien et al. 2000, Hawkins et al. 2003a, Tognelli and Kelt 2004).

It has been frequently shown that determinants of species richness and endemism are scale dependent (Böhning-Gaese 1997, Rahbek and Graves 2000, 2001, Willis and Whittaker 2002) and it has been hypothesized that this is because different driving processes act at different spatial scales (Whittaker et al. 2001). To examine the effect of spatial scale, we repeated all analyses at grain sizes between 1° and 5° (see Appendix for a complete documentation of the results).

Ecological and environmental data sets generally show spatial autocorrelation which violates the assumption of independence and can affect parameter estimates of most traditional statistic procedures (Legendre 1993, Lennon 2000, Diniz-Filho et al. 2003). In order to examine patterns of spatial autocorrelation in our analyses, we calculated spatial correlograms using Moran's I coefficient for raw species richness and for residuals after fitting the examined environmental predictors. Spatial statistics were performed in SAM 1.0 (Rangel et al. 2005).

Results

Range size frequency distribution (RSFD)

Range size varies strongly among Neotropical palm species. Extremely rare species occurring in one or two grid cells (e.g. *Sabal bermudana*, *Roystonea violacea*) are contrasted by very few widespread species occurring in

more than half of all grid cells (e.g. *Bactris gasipaes*, *Desmoncus orthacanthos*). However, most species have small to medium ranges (median range size = 56 grid cells) with ca 79% of the species having smaller ranges than the mean (mean range size = 256 grid cells). The range size frequency distribution (RSFD) is highly right skewed (skewness = 4.38) and approximates a normal distribution if log-transformed (Fig. 1).

Regional RSFDs of various biogeographic regions differ markedly from each other (Fig. 1). We recognize two coarse types of richness centres: centres that have a high portion of restricted species (e.g. Chocó biogeographic region or Mesoamerica; Fig. 1a, b) and those that are mainly produced by the overlap of many widespread species (e.g. western and eastern Amazonia; Fig. 1c, d).

Partitioning of species into range size quartiles (each quartile contains 25% of the species; ca 137 spp.) exhibits distinct spatial centres (compare Fig. 2). The Mesoamerican cordilleras and the Chocó biogeographic region are especially rich in range-restricted species. The coastal rain forests of eastern Brazil show up as an important centre for species with medium range size, but are less

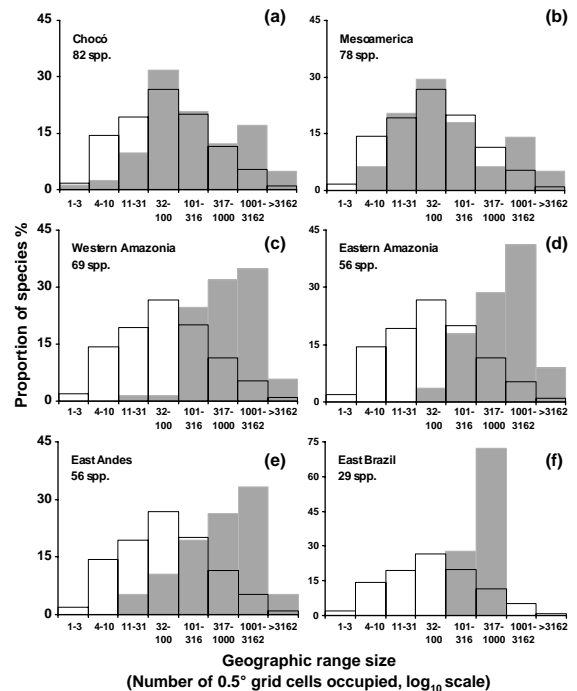


Fig. 1. Range size frequency distributions (RSFD) of the species occurring in the most species rich grid cell located in each of six different biogeographic regions (grey bars) in comparison to the RSFD of the total continental assemblage (transparent bars) on a logarithmic scale. Geographic position (latitude and longitude in decimal degree) of the analysed grid cells: (a) Chocó (6.75°N , 76.25°W); (b) Mesoamerica (9.25°N , 82.75°W); (c) western Amazonia (3.75°S , 73.25°W); (d) eastern Amazonia (2.25°S , 54.25°W); (e) east Andes (0.25°S , 77.25°W); (f) east Brazil (18.25°S , 39.75°W).

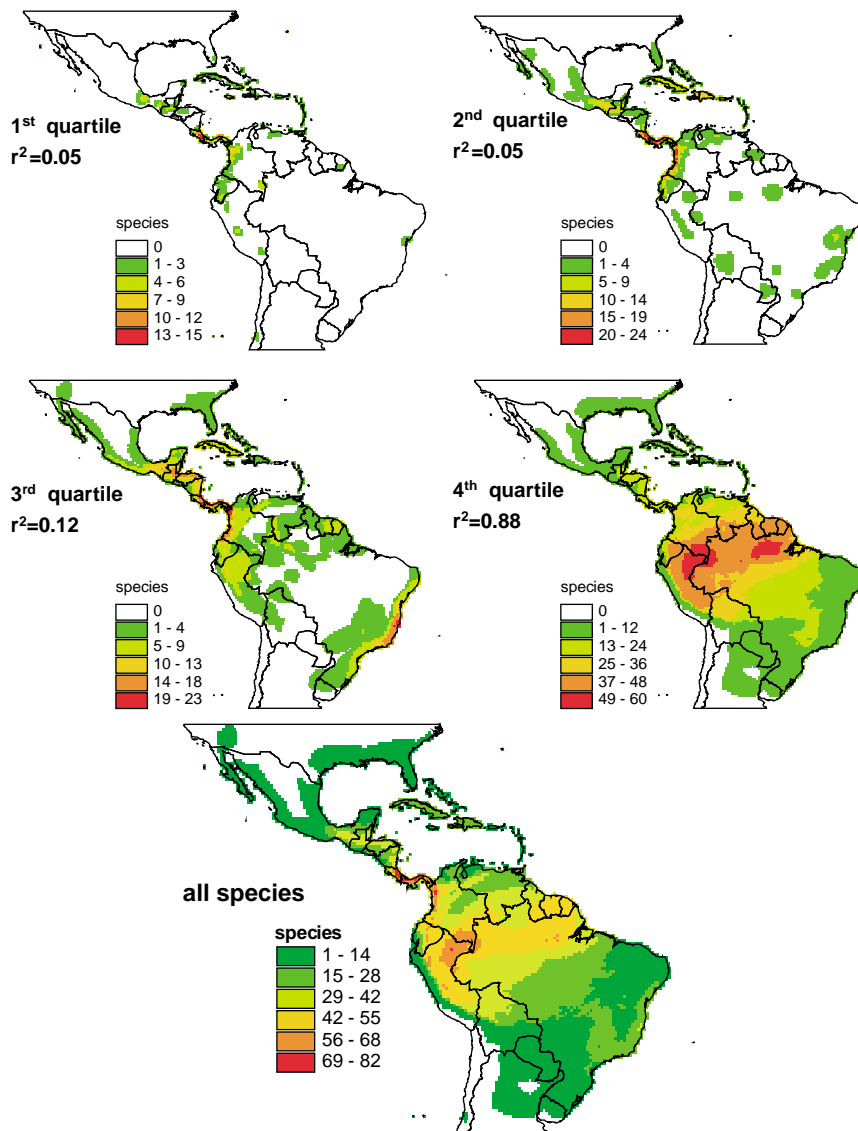


Fig. 2. Spatial variation of species richness per 0.5° grid square of ranges size quartiles and all Neotropical palms species. Correlation coefficients (r^2) between species richness of quartiles and overall species richness are given.

important for overall species richness of palms. The first three quartiles show only very poor correlations to overall richness (r^2 between 0.05 and 0.12, respectively), whereas the fourth quartile is strongly correlated with overall richness ($r^2=0.88$).

Contribution of range size to species richness and endemism

The contribution of range size to patterns of species richness is shown in Fig. 3a. Correlation coefficients along the large-to-small, small-to-large, and random sequences increase in fundamentally different ways. The correlation coefficients of the large-to-small sequence rise quickly and subassemblage patterns become

rapidly congruent with the overall richness pattern. The small-to-large sequence, on the other hand, shows three distinct phases. The first 20% of range-restricted species raise the correlation coefficients to a moderate level. By adding more species, correlation coefficients remain on the same level. Adding the ~20% most widespread species to the sequence leads to remarkably higher correlation coefficients. Correlations of the random sequence increase quickly and in logarithmic shape. Correlations of the large-to-small sequence are at any stage higher than the small-to-large and the random sequence, respectively.

Keeping the arrangement of the species in the different sequences but plotting correlations against the cumulative information achieved at a certain step along the sequence, shows that rare species contribute significantly

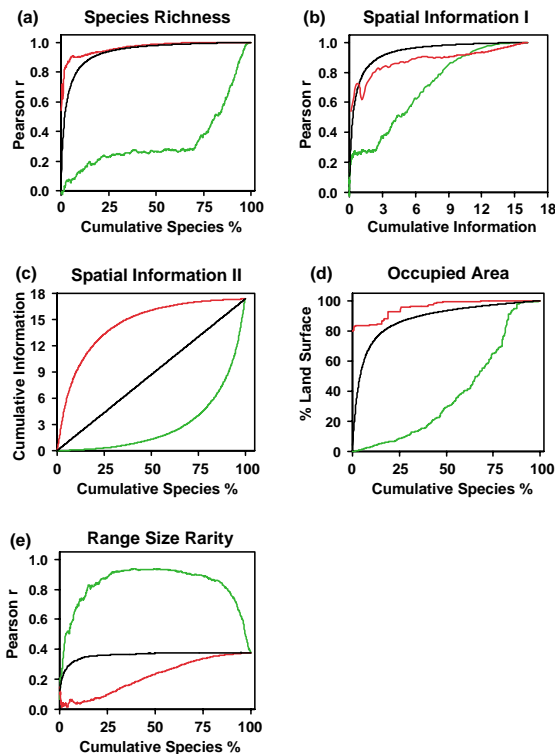


Fig. 3. Correlations of cumulative species richness patterns of three different types of species sequences at a grain size of 0.5° . Species sequences were produced by ranking species according to their range size in ascending (small-to-large, green colour), descending (large-to-small, red) and random (2000 runs, black) order. (a) Correlations between cumulative and overall species richness patterns plotted against the proportion of species in the assemblage. (b) Correlations between cumulative and overall species richness patterns plotted against the cumulative amount of spatial information. (c) The cumulative volume of spatial information at each step plotted against the portion of species in the sequence. (d) Portion of land surface covered by species sequences at each step. (e) Correlations between cumulative species richness patterns and range size rarity.

less to the species richness pattern than widespread species (Fig. 3b).

The dominance of widespread species correlates with the spatial information they contribute to the overall species richness pattern (Fig. 3c). The 20% most widespread species contain ca 80% of the spatial information that finally constitutes overall variation in species richness. Furthermore, range-restricted species show an extraordinarily uneven distribution. The 50% of the species with smaller range size occupy only <30% of all grid cells of the study area (Fig. 3d).

Surprisingly, range size rarity is only moderately correlated with overall species richness ($r=0.38$, Fig. 3e). Whereas correlation coefficients of the large-to-small sequence increase steadily to the overall correlation value, the small-to-large sequence holds a bell-shaped form. Species richness patterns of the 80% of the rarest species almost perfectly depict patterns of

range size rarity (maximum r -values = 0.94). Again, correlation coefficients of the random sequences rise quickly and logarithmically.

Environmental predictors and range size

Measures of water-energy dynamics and productivity are good predictors of overall species richness of Neotropical palms (annual precipitation: $r=0.75$; AET: $r=0.74$; PET: $r=0.65$; water balance: $r=0.65$; NPP: $r=0.61$). Latitude shows a strong negative correlation with overall species richness ($r=-0.76$). Looking at the results of the correlations between species richness patterns of subassemblages and climatic parameters, it is striking that high correlations are mainly accomplished by the influence of the most widespread $\sim 20\%$ of the species (Fig. 4a–b). Adding the $\sim 20\%$ most widespread species to the small-to-large sequence causes an exponential rise to a high level of all variables. Although only the curves for precipitation and actual evapotranspiration are shown, curves for all other mentioned variables were also examined and show a similar systematic pattern. Correlations of the random sequences rise logarithmically, reflecting the shape of the RSFD. Sequential correlation patterns of species sequences and latitude also show this notable pattern, however mirrored because of the negative relationship (Fig. 4c).

Altitudinal range has no predictive value for overall species richness at a grain size of 0.5° (Pearson $r=0.01$) (Fig. 4d). Nonetheless, moderate r -values are reached in the small-to-large sequence (maximum Pearson $r=0.35$). This correlation is deflated by the $\sim 20\%$

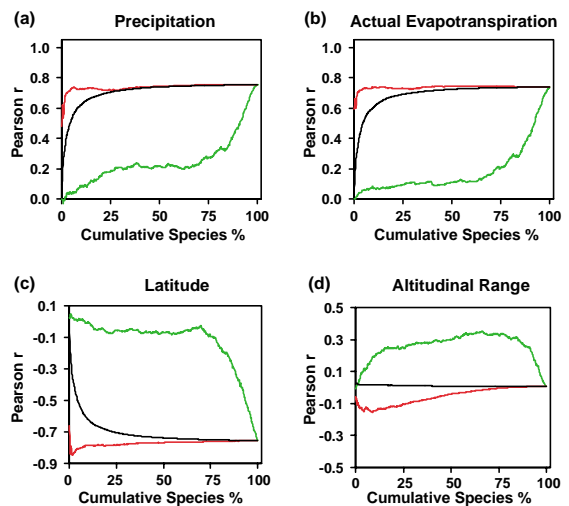


Fig. 4. Correlations between cumulative species richness patterns of the three sequences (green: small-to-large, red: large-to-small and black: random) and (a) precipitation, (b) actual evapotranspiration, (c) latitude and (d) altitudinal range at a grain size of 0.5° (only correlations of selected environmental predictors are shown).

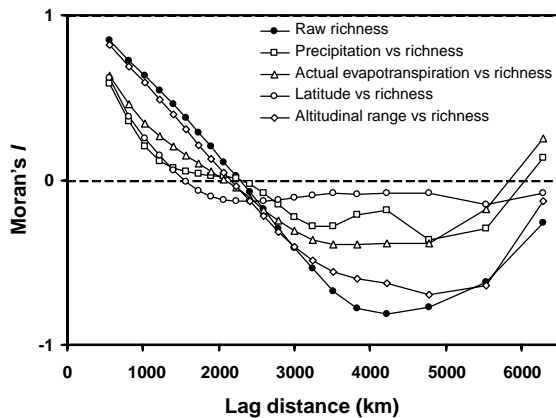


Fig. 5. Spatial correlograms using Moran's *I* of raw species richness and residual variation after fitting the examined environmental variables at a grain size of 0.5°. All correlograms are significant ($p < 0.001$ after Bonferroni correction).

most widespread species. The beginning of the large-to-small sequence even points up an opposite effect: widespread species tend to avoid highly structured landscapes.

Species richness shows positive spatial autocorrelation up to distances of ca 2000 km (Fig. 5). Linear regressions with the environmental predictors only moderately reduce spatial autocorrelation in the residuals of climatic parameters (a reduction of the original 0.85 (raw richness) to 0.58 (residuals precipitation) in the first distance class is observed) and leave positive spatial autocorrelation up to a distance of ca 1500–2000 km. This indicates that the assumption of independent errors is violated and that important additional environmental factors explaining species richness were excluded when applying a single predictor approach (compare Diniz-Filho et al. 2003).

Influence of grain size

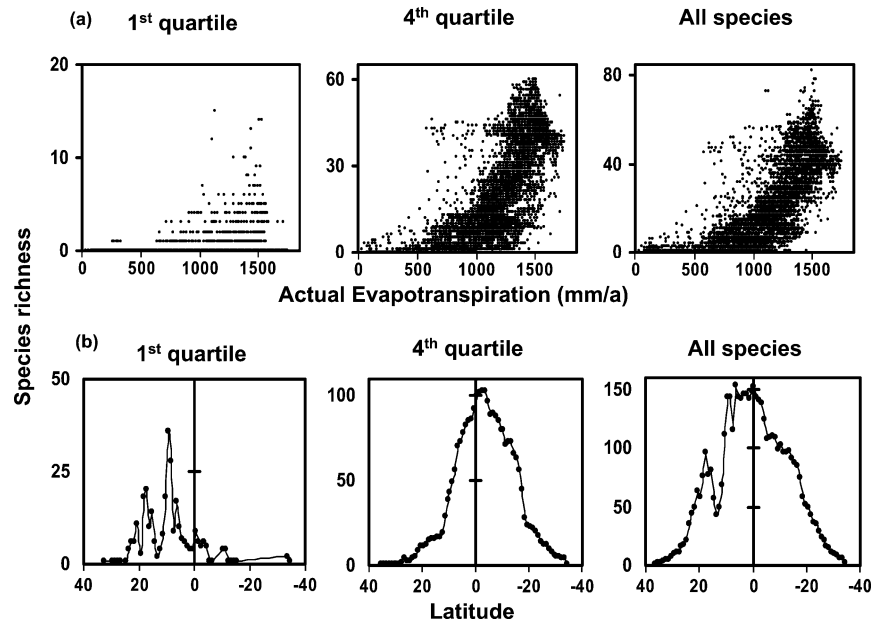
The examination at the five additional grain sizes of 1°, 2°, 3°, 4°, and 5° reveals that the general patterns shown in Figs 3 and 4 remain relatively invariant (compare the Appendix). Most conspicuously, the predictive power of altitudinal range increases with coarser resolution from $r = 0.01$ at 0.5° to $r = 0.28$ at 5°, whereas the correlations with climatic variables and latitude decrease only slightly (e.g. AET from $r = 0.74$ at 0.5° to $r = 0.63$ at 5°). Correlations between range size rarity and species richness increase at coarser grain sizes. This appears because the absolute differences in range size diminish when ranges are measured at coarser grain size, and thus the measures of range size rarity and species richness converge. Furthermore, the relative proportions between the small-to-large and large-to-small sequences change.

Discussion

A minority of widespread species dominates the spatial variation in species richness of Neotropical palms. This is mainly because widespread species contribute disproportionately more spatial information (Fig. 3b, c). On the other hand, range-restricted species are non-randomly distributed in space, but rather accumulate in distinct, confined centres (compare Figs 2 and 3d). Fifty percent of the species with the smallest ranges occupy <30% of all grid cells within the native range of the palm family in the Neotropics (compare Fig. 3d). The greater contribution of widespread species to overall richness patterns has previously been documented for regional to continental avian assemblages by Jetz and Rahbek (2002) and Lennon et al. (2004). Nevertheless, we observed even higher dominance of widespread species on the overall pattern in our data set (compare Figs 2 and 3) presumably due to a comparatively higher portion of smaller range sizes and a higher skewness of the RSFD of palms. The comparative analysis of RSFD of single regions provides interesting insights into the internal structure of regional assemblages. RSFD for different biogeographic regions can diverge strongly from the shape of the continental assemblage (Fig. 1; see also Graves and Rahbek 2005), in some cases even contradicting the otherwise general observation that most species have small ranges (Brown et al. 1996, Gaston 1998). It is likely that the biogeographic context (e.g. homogeneity of the landscape and the climate, existence of dispersal barriers) as well as historical aspects account for many of the regional differences.

Our results confirm that centres of species richness and endemism are not necessarily congruent (Prendergast et al. 1993). Because of the predominance of widespread species, overall patterns of species richness do not necessarily have much explanatory power for range-restricted species (compare Lennon et al. 2004). This idea is supported by the differences in RSFD of various centres of species richness (Fig. 1). Centres characterized by many range-restricted species can be distinguished from others where many ranges of widespread species overlap, although the top centres are characterized by both many widespread and many range-restricted species. Furthermore, the correlation between species richness and range size rarity ($r^2 = 0.14$) of Neotropical palms is surprisingly low compared to values reported from other studies of parts of the African flora (Lovett et al. 2000, Linder 2001, Taplin and Lovett 2003) and the Australian flora (Crisp et al. 2001). These authors report r^2 -values between species richness and range size rarity of 0.55–0.72. Besides continent specific geometry, topography, geological and evolutionary history, the remarkable differences between our results and the mentioned studies may in part be due to the different data sources used.

Fig. 6. Relationship between species richness of the first (25% of the most restricted-range species) and the fourth (25% of the most widespread species) range size quartile and of all species and (a) actual evapotranspiration (mm yr⁻¹) and (b) latitude (calculated as band sums per one-degree latitudinal band).



Generally, maps of species richness can be based on two different types of data: points of verified occurrences (e.g. specimens or observations) or two-dimensional information (e.g. range maps based on expert estimates, bioclimatic modelling or spatial interpolation techniques). Whereas the majority of studies on geographic patterns of vertebrate diversity rely upon expert drawn maps from atlases, most continental analyses of plant diversity use point occurrences from herbarium databases or taxonomic revisions. If ranges of the examined species are poorly documented there is a great risk that macroecological or conservation-related conclusions might be flawed due to an interaction between sampling bias and range size. Even in the largest data base on African plant diversity (BISAP; compare Küper et al. 2004b), 67% of the species are documented with 10 or less geo-referenced specimen records (Küper and Sommer unpubl.). The calculation of range size in point data sets requires the projection to a reference grid and will therefore inevitably underestimate range size by producing false absences especially for widespread species. On the other hand, range maps from atlases may overestimate range size. Especially if data sets for macroecological studies are incomplete due to a lack of suitable data for the whole flora (Kress et al. 1998, Lovett et al. 2000, Linder 2001, Crisp et al. 2001, Krupnick and Kress 2003, Taplin and Lovett 2003) our findings arise the questions: is there bias towards more rare or more widespread species in incomplete data sets? How reliable are diversity patterns and analyses of their possible determinants? Our results demonstrate that overall species richness patterns can be relatively easily determined with limited taxon sampling if taxon sampling is

random. Nonetheless, systematically biased data sets towards either more widespread or range-restricted species are likely to over- or underestimate the predictive value of different abiotic factors and the relationship between species richness and range size rarity.

The strong relationship between overall species richness and water or energy related variables agrees with numerous previous studies (compare Hawkins et al. 2003a). Precipitation and actual evapotranspiration are the strongest single-predictors of species richness (Fig. 6), whereas potential evapotranspiration and temperature play a minor role. This is concordant with the water-energy theory that predicts a higher importance of water-related variables in high-energy regions such as the tropics (O'Brien 1993, O'Brien et al. 2000, Hawkins et al. 2003a).

Our results are also in accordance with previous findings on vertebrates that widespread species have a dominant influence on the predictive value of commonly used predictors of species richness (Jetz and Rahbek 2002, Ruggiero and Kitzberger 2004). Thus, there is evidence that these results might be generally valid. Conventional statistical approaches trying to explain spatial variation in species richness by focusing on overall patterns of species richness may be disproportionately inflated or deflated by a small number of widespread species (Jetz and Rahbek 2002). Hence, our results on palms support generality of the notion that conventional approaches disregarding effects of range size are limited to approximate the causative explanations for a majority of species (Jetz and Rahbek 2002, Lennon et al. 2004).

Although the overall correlation with altitudinal range is insignificant at a grain size of 0.5°, we interpret the medium correlation peak as a distinct historical and evolutionary signal (Fig. 3e) (see also Rahbek and Graves 2001). Rahbek and Graves (2000, 2001) showed that the strength of the predictive value of topography for species richness of South American birds depends on the spatial scale of the analysis and becomes stronger at a coarser spatial resolution. The same holds true in the single-predictor models at different grain sizes in the palm data set. This implies that the regional setting is more important than topographical variation within single grid cells especially at small grain sizes. For instance, west Amazonian cells are probably richer than east Amazonian ones because they are in greater proximity to the topographically and edaphically complex Andean foothills (compare Kreft et al. 2004). Furthermore, it indicates that processes responsible for species richness of range-restricted species act on a larger spatial scale (Qian and Ricklefs 2000, Jetz et al. 2004). It also highlights the difficulties to detect historical and evolutionary signals for range-restricted species on the examined spatial extent and resolution and with the presently available geographic proxy indicators.

Topographical complexity as well as the fast and recent uplift of mountain ranges in South and Central America possibly provided excellent conditions for allopatric speciation and climatic or edaphic specialization (see Küper et al. 2004a for a recent example). Highest species numbers of palms are achieved in grid cells with >3000 mm of annual rainfall and considerable portion of lowland and montane forests, respectively. This highlights the importance of the foothills of the northern Andes and the Mesoamerican cordilleras as cradles for the high diversity of the Neotropics (Gentry 1982a, 1986, Kreft et al. 2004). Recent molecular studies on the species-rich genus *Inga* have provided further evidence for rapid diversification simultaneously to the uplift of the Andes and the bridging of the Isthmus of Panama (Richardson et al. 2001).

Species with narrow ranges are particularly in the focus of conservation because they are subject to a higher risk of extinction (Gaston 1994, Purvis et al. 2000). Large-scale conservation strategies depend substantially on macroecological approaches to identify priority areas (Prendergast et al. 1999, Rahbek and Graves 2000, Margules and Pressey 2000, Whittaker et al. 2005). However, species with narrow ranges are discriminated by many conventional correlative analyses due to the small amount of spatial information they contribute to the overall species richness patterns and because their environmental predictors are difficult to determine.

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