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The resolution-dependent role of landscape attributes in shaping macro-scale biodiversity patterns

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Abstract

Aim To assess if and to what extent the role of local landscape attributes in shaping macroscopic biodiversity patterns is sensitive to spatial and thematic resolutions of land cover data.

Location Sub-Saharan Africa and continental China.

Time Period Early 21st century.

Taxa studied Terrestrial mammals.

Methods We conducted spatial and thematic scaling analyses to generate land cover datasets of different spatial (0.3 km, 0.5 km, 1.0 km and 9.0 km) and thematic (2, 3 and 5 classes) resolutions. We calculated landscape metrics based on the resulting land cover maps, and examined the power of landscape metrics for explaining species richness patterns, using non-spatial (OLS) and spatial (SAR) linear models, as well as random forest (RF) models. We systematically assessed resolution-dependence of explanatory power for different geographic regions, different scaling approaches, and different model types. We also compared the explanatory power of landscape attributes with that of macro-climate.

Results Local landscape attributes collectively generally had strong explanatory power for species richness. For the African system, the largest explanatory power was *c.* 60% based on the OLS models and random forest models, and *c.* 35% based on the non-spatial components of the SAR models. For the Chinese system, the largest explanatory power was *c.* 35% based on the OLS models and *c.* 40% based on the SAR and random forest models. We observed a linear scaling relation, which is robust to studied systems, scaling approaches, and model types. In contrast, scaling relations varies substantially among single landscape metrics. At coarse resolutions, the addition of landscape attributes collectively would not improve climate-envelope models significantly, whereas at finer resolutions, landscape attributes collectively have explanatory power that is close to or even exceed climate.

Main conclusions Local landscape attributes play an important role in shaping macroscopic biodiversity patterns. However, their strength is highly sensitive to both spatial and thematic resolutions of land cover data, with stronger explanatory power detected at finer resolutions. Strong sensitivity to spatial and thematic resolutions makes landscape attributes highly plastic determinants, leading to contrasting conclusions if based on largely differed resolutions of land cover data. Scaling analyses are

needed to systematically examine such cross-scale effects of macroecological determinants.

Key words: cross-scale effect, landscape pattern, macroecology, mammal, scale, scaling, species richness.

Introduction

Geographic patterns of biodiversity at broad spatial scales have long fascinated ecologists. For instance, the latitudinal gradients of increasing species richness from polar to tropical regions are considered ‘*among the most universal features of nature*’ (Rohde, 1992). Extensive research efforts devoted to understanding broad-scale biodiversity patterns have given rise to many hypotheses (see Willig et al., 2003; Hawkins et al. 2003; Field et al., 2009 for reviews/synthesis) postulating a large set of potential determinants of these patterns, such as energy (Hutchinson, 1959; Connell and Orias 1964), water (Wright, 1983), dispersal (Tscharntke et al., 2012) and habitat conditions (Ricketts et al., 2008; Stein, Gerstner, & Kreft, 2014).

While there is consensus that many of these factors can jointly shape species distributions and diversity patterns, their relative importance at macro (e.g., continental or global) scales remains controversial. Previous studies have been focusing on the abiotic environmental factors operating at large spatial extents, such as climate (Peterson et al., 2011; Soberón & Nakamura, 2009), whereas ignoring factors that occur within small spatial domains, such as biotic interactions between individual organisms (Soberón, 2007). Such exclusion of small-scale interactions has been based on the presumption that different driving factors operate at distinct characteristic domains (Pearson & Dawson, 2003), and that at macro scales, small-scale interactions would mostly act as noise that can be averaged out (Soberón & Nakamura, 2009). Although this presumption makes intuitive sense, recent findings surprisingly suggest the opposite: biotic interactions as a typical class of small-scale factors have an important shaping role that can in fact scale up to macro scales, determining species distribution and richness to a substantial degree (Gotelli, Graves, & Rahbek, 2010; Hortal, Roura-Pascual, Sanders, & Rahbek, 2010; Reino, Beja, Araújo, Dray, & Segurado, 2013; Araújo & Rozenfeld, 2014; Pedersen, Sandel, & Svenning, 2014; Ilsøe, Kissling, Fjeldså, Sandel, & Svenning, 2017). The validation of this cross-scale effect has produced profound implications to the paradigm of macroecology, as seen for instance from the increasing incorporation of biotic interactions in macroecological modelling frameworks (Elith & Leathwick, 2009; Guisan & Rahbek, 2011; Wisz et al., 2013; Maynard, Crowther, & Bradford, 2017). It also calls important attention to systematically assessing if and to what extent

cross-scale effects can drive macroecological processes. A first step towards this aim is to investigate if there exist other factors (like biotic interactions) that have been assumed to typically operate at narrow scales, but can substantially shape broad-scale ecological patterns.

Landscape attributes (defined as amounts and configurations of spatially mosaicked ecosystems, usually characterized by a set of landscape metrics) may be a class of such overlooked determinants. In the field of landscape ecology, it is central to understand how landscape attributes influence biodiversity patterns at spatial extents of tens to hundreds of kilometers (landscape scales), involving a variety of spatial processes such as optimal foraging (Shochat, Lerman, Katti, & Lewis, 2004), meta-population dynamics (Hanski, 1999) and disturbance spread (Forrestel, 2013; Turner, Gardner, Dale, & O'Neill, 1989). For example, extensive studies have suggested that human induced habitat modification (including loss and fragmentation) can substantially influence biodiversity at landscape scales, through many mechanisms including population isolation, territory compression, and edge effects (Fahrig, 2003). At a minimum, even if species richness is predominately driven by the sample area effect, the amount of habitat in the local landscape can act as a key factor influencing species richness (the habitat amount hypothesis; *sensu* Fahrig, 2013). By contrast, in the field of macroecology there has been a revived interest on landscape attributes for explaining broad-scale patterns of species distribution and richness. Typical of traditional view, earlier work has reported that they have rather weak effects (except for the long recognized effects of landscape heterogeneity in terms of topography, e.g., White & Miller, 1988; Kerr & Packer, 1997; Nichols, Killingbeck & August, 1998; Thuiller, Araujo, & Lavorel, 2004; Reino, Triviño, Beja, Araújo, Figueira, & Segurado, 2018). However, recent studies suggested that they have strong, unneglectable power shaping macro-scale biodiversity patterns in areas with strong anthropogenic landscape modifications (Martins, Proença, & Pereira, 2014; Ramesh, Kalle, & Downs, 2016; Xu et al., 2014). To ascertain whether landscape attributes are indeed the ‘unusual suspect’ (a metaphor by Martins et al., 2014), we need to understand what underlies these two contradictory lines of evidence.

While system-specific relationships might (partly) explain this contradiction, one possibility is that it is simply a result of different resolutions of land cover data used for the characterization of landscape

attributes (the resolution dependence may also apply to biodiversity data, but it's beyond the scope of this paper). This possibility can be derived from the distinction that weak effects of landscape attributes were often found in the studies based on coarse-resolution data (e.g., 10 km in Thuiller et al., 2004; Triviño, Thuiller, Cabeza, Hickler, & Araújo, 2011), whereas strong effects were mostly reported in more recent work employing newer landscape datasets with finer resolutions (e.g., *c.* 0.5 km in Reino, Beja, Araújo, Dray, & Segurado, 2013; 1 km in Xu et al., 2014). In this sense, testing whether resolution of land cover data is indeed responsible for these contrasting findings can help to clarify the role of landscape attributes in shaping macroecological patterns.

Characterization of landscape attributes have largely relied on remotely sensed products of land cover. Data selection in terms of 'optimal resolution' is beyond a technical issue. Instead, it represents an essential element of observational scale. Although it has been a textbook knowledge that ecological patterns must be studied at relevant scales (Levin, 1992), it is always notoriously intractable to determine the optimal scale *a priori* (Jackson & Fahrig, 2012). Also, there may not even be a single adequate scale, if ecological phenomena are products of processes acting across a range of scales. So far, selection of land cover data resolutions (reflecting observational scales) is usually not well justified, leaving its role unknown in relevant macroecological studies.

Here, we aim to determine if and to what extent the strength of local landscape attributes (as a collective) in shaping broad-scale biodiversity patterns is sensitive to resolutions of land cover data. To this end, we conducted systematic scaling analyses on the power of landscape attributes in explaining species richness of terrestrial mammals in sub-Saharan Africa (a continental scale) and continental China (a nationwide scale). To date, dozens of standard land cover datasets with broad (from national to global) coverage are freely available, presenting a wide range of spatial resolutions from *c.* 10 m (e.g., EEA, 2010, 2011) to 10 km (Channan, Collins, & Emanuel, 2014; Friedl et al., 2010) as well as thematic resolutions (defined as number of land cover classes as a measure of ability for distinguishing between different ecosystem types) from only one (Schneider, Friedl, & Potere, 2009) to tens of land cover classes (Arino et al., 2008; ESA 2008). We conducted scaling analyses in terms of both spatial and thematic resolutions. For the spatial scaling analyses, we 1) systematically manipulated spatial

resolution of the land cover dataset through data resampling, and 2) compared between a handful of standard, commonly used land cover datasets with inherently different spatial resolutions. We examined how explanatory power of landscape attributes for species richness varied across the studied spatial/thematic resolutions (i.e., scaling relations), and checked if the scaling relations are robust to different statistical models that have been widely used for detecting macroecological patterns. We used both linear regression models (including non-spatial, ordinary least square models and simultaneous autoregressive models that account for spatial autocorrelation) and non-linear, decision tree based (random forest) models. Our specific objectives are to assess if and to what extent resolution-dependence exists for different geographic regions (Africa vs. China), different scaling approaches (standard vs. resampled data), and different statistical models (linear vs. non-linear, spatial vs. non-spatial). In addition, macro-climate is often the strongest driver of macroscopic biodiversity patterns (Hawkins et al., 2003), setting a reference for understanding the strengths of other determinants. Therefore, we also compared the strength of landscape attributes with that of macro-climate to provide a quantitative assessment of whether landscape attributes can be neglected or add valuable information for unravelling the drivers of broad-scale biodiversity patterns. We expect to fill the gap of understanding on resolution-dependent role of landscape determinants in shaping macroecological patterns, and highlight the importance and complexity of scale issue in macroecological studies.

Methods

Study regions and species richness data

Both sub-Saharan Africa and continental China are rich in mammal species (Fig. 1). The species richness data for the African mammals were compiled based on their distribution range maps from the African Mammal Databank (AMD) including 281 mammal species, an atlas of medium to large mammals (see Boitani, 1998; Boitani et al., 2008 for detailed descriptions). The species richness data for Chinese mammals were compiled based on their distribution range maps derived from China Species Information Service (CSIS) including 575 mammal species (Xie, Zhang, & Wang, 2009). We

excluded islands in both study areas. Since the distribution range data for small mammals are usually less reliable (Prins, Olff, Newbery, Prins, & Brown, 1998), mammal species with average body mass $\leq$ 2 kg were excluded from the analyses. As a result, our study included 281 and 131 mammal species in sub-Saharan Africa and China, respectively. For both study areas, species richness was calculated per 50 km $\times$ 50 km grid cells. This cell size is equivalent to the average grain size of the distribution range data in the CSIS. The grid cells intersect with coastal lines or the country border (of continental China) were excluded.

Land cover data and scaling analyses

We used two scaling approaches to produce land cover maps with different spatial resolutions. In the first approach, we collected four standard global remotely sensed products of land cover that have been published and are freely available to download (hereafter referred to as standard data). These standard data were produced with inherently different spatial resolutions, i.e., the GlobCover 2005 data of 0.3 km resolution (Arino et al., 2008; ESA 2008), the GLCNMO Version 3 data of 0.5 km resolution, the GLCNMO Version 1 data of 1 km resolution (Tateishi et al., 2011; Tateishi et al., 2014), and the GLCF data of 9 km resolution (Friedl et al., 2010; Channan, Collins, & Emanuel, 2014).

In the second approach, we used the standard data of 0.3 km resolution (i.e., the GlobCover data) as a basis, and aggregated it to coarser spatial resolutions of 0.5 km, 1 km and 9 km, respectively. The majority resampling method was used for this aggregation, i.e., the land cover type of a given coarse-grained output (resulting) grid cell is determined by the most dominant land cover type of the 0.3 km-resolution input grid cells that are located within this coarse-grained target cell. Doing so we produced the resampled data that have consistent spatial resolutions with corresponding standard data as in the first approach. Note that the two spatial scaling approaches have the same data basis for the 0.3 km-spatial-resolution data.

Thematic resolutions were obtained by combining the abovementioned scaling approaches (standard and resampled data) at different spatial resolutions (0.3 km, 0.5 km, 1.0 km and 9.0 km) into 2, 3 and 5 land cover classes (Tables S1a-c). As a result, we obtained 21 land cover datasets (4 spatial

resolutions $\times$ 2 spatial scaling approaches $\times$ 3 thematic resolutions – 1 replicate for the 0.3 km resolution) $\times$ 3 thematic resolutions, see Fig. S1 for an illustration).

The resulting land cover datasets at different spatial and thematic resolutions were used to calculate landscape metrics. These scaling approaches have been adopted by previous studies that systematically investigated scaling behavior based on scalograms (e.g., Wu et al. 2002, Luan et al. 2018). For each of the 21 resulting land cover datasets we calculated a comprehensive set of 28 class- and landscape-level metrics describing landscape composition and structure (Table S2; see McGarigal & Marks (1995) for details on class- and landscape-level metrics). The landscape metrics were calculated within each 50 km $\times$ 50 km grid cell. At each spatial/thematic resolution, we quantified the collective power of the landscape variables in explaining species richness (see below).

Statistical analyses

As a first step to assess the effect of local landscape attributes, we fitted ordinary least square (OLS) models with landscape metrics as explanatory variables and mammal species richness as the response variable. We included all candidate explanatory variables (full models) to quantify the collective explanatory power of landscape attributes. Multicollinearity would not influence our conclusions because we focused on the maximum explanatory power (i.e. explained sum of squares) rather than inference or coefficient estimation (Stephens & Rio, 2010). For the same reason, we did not conduct any model selection or model averaging.

We found strong spatial autocorrelation (SAC) in the OLS model residuals using correlograms based on Moran's *I* coefficient (Fig. S2, S3). Therefore, we tested for the robustness of the scaling relations to SAC, using simultaneous autoregressive models (SAR) that have been proven useful to account for the SAC problem (e.g., Kissling & Carl, 2008). We constructed SAR mixed models (assuming that spatial autocorrelation can affect both response and explanatory variables, see Kissling & Carl, 2008 for the detail of the model form), as the sources of autocorrelation are unclear in our study (Teng, Xu, Sandel, & Svenning, 2018). We decomposed the explanatory power of SAR models into two components (spatial signal vs. non-spatial trends), and calculated their pseudo- R^2 (defined as the

squared Pearson correlation coefficient between the non-spatial component of the SAR prediction and observed values). Although the definition of pseudo- R^2 is rather loose, previous studies have shown that it can serve as a useful indicator of goodness of fit for assessing the performance of SAR models (Kreft et al., 2010; Xu et al., 2014). We also calculated root mean square error (RMSE) for the OLS and SAR models as a second measure of explanatory power.

Decision tree-based models (e.g., classification and regression tree and random forests) have been increasingly used for mining complex relationships that may not be sufficiently captured by simple linear models. Here, we fitted random forest (RF) models (Breiman, 2001). We did not intend to compare between the simple linear and RF models. Instead, our purpose is to check if the observed scaling relations are robust against nonlinearities. We used the default settings for the number of variables selected into each tree-building process ($mtry = 1/3$ of total number of variables) and the number of trees needed to be built of the forest ($n tree = 500$) (Cutler et al., 2007). We used permutation importance to avoid biased variable importance (Strobl, Boulesteix, Zeileis, & Hothorn, 2007; Parr, Turgutlu, Csiszar & Howard, 2018). We used a general pseudo R^2 , defined as $1 - (\text{mean square error}/\text{var}(y))$, and RMSE to represent the explanatory power of the RF models. Note that R^2 should not be directly compared between the OLS, SAR and RF models because they are calculated with different methods, and have different model conditions (Grömping 2009; Nakagawa & Schielzeth 2012).

To illustrate the strength of landscape attributes relative to macro-climate, using the same modelling approaches as abovementioned, we also quantified the explanatory power of 20 frequently used bioclimatic variables (e.g. Xu et al., 2014) as a collective (including variables characterizing mean and seasonality of temperature and precipitation, as well as those characterizing evapotranspiration regimes; see Table S3 for the specific variables and data sources).

While our focus is on the role of landscape attributes collectively, we also took a probe to resolution dependence (scaling behaviors) of single landscape metrics. In a hierarchical view, species richness is shaped by a ‘high-level’ process that aggregates the effects of all possible landscape attributes, each of which represents a ‘low-level’ process. One may expect to observe distinct scaling relations across

landscape metrics, considering that these low-level process of species richness may operate at different scales. To test this speculation (instead of a systematic assessment of scaling behaviors of all single landscape metrics), we assessed the Pearson's correlation coefficients of single landscape metrics with species richness with changing resolutions. To avoid redundancy, we selected four simple landscape-level metrics out of all 54 (class- and landscape level) metrics, i.e., number of patches, NumP; total edge, TE; mean shape index, MSI and landscape shape index, LSI (see Table S2), which are among the strongest predictors of species richness in our studied systems. We also assessed the scaling relations of the relative importance of the selected landscape metrics. The Firth's relative importance metric (Firth 2016) was calculated based on the full OLS or SAR models; the MSE-based relative importance metric (Liaw & Wiener 2002) was calculated based on the full RF models. These metrics were then standardized to sum unity for the four selected landscape metrics (Grömping 2009).

All spatial data were georeferenced using the Lambert Azimuthal Equal Area projection. The spatial data was processed using ArcGIS 10.2 and landscape metrics were calculated using Patch Analyst 5.0 (Rempel, Kaukinen, & Carr, 2012). Statistical analyses were implemented in R 3.4.1 (R Development Core Team, 2017), SAR models were fitted using the *spdep* package (Bivand, Hauke, & Kossowski, 2013; Bivand & Piras, 2015) and RF models using the *randomForest* package version 4.6-14 (Liaw & Wiener, 2002).

Results

Our statistical models consistently showed that local landscape attributes as a collective generally had strong correlations with species richness of terrestrial mammals in both sub-Saharan Africa and continental China. Specifically, for the sub-Saharan African system, the OLS models showed that the largest explanatory power (among all spatial/thematic resolutions) of landscape metrics amounted to c. 60% for both standard and resampled land cover data; while for the Chinese system the explanatory power was generally lower, but still reached considerable amounts (close to 40% at the maximum) (Fig 2). When taking into account spatial autocorrelation (i.e., looking at the non-spatial components of the

SAR models), the largest explanatory power remained at a relatively high level (*c.* 35% and 40% in the African and Chinese systems, respectively), though compared with the OLS models, the power declined substantially in the African system (Fig. 3). In contrast with the linear models, the effects of landscape attributes can be better captured by the nonlinear RF models, which showed generally stronger explanatory power (close to 65% and 45% at the maximum in the African and Chinese systems, respectively). The relative strength of local landscape attributes is clearly seen through the comparison with climate. In most cases, landscape attributes had a weaker effect. However, this relative importance was occasionally reversed, with landscape attributes outweighing climate (see Fig. 2B, Fig. 3C-D).

Our scaling analyses showed that the observed explanatory power (in terms of both R^2 and RMSE) of local landscape attributes was highly sensitive to both spatial and thematic resolutions of land cover data. Variation range of explanatory power across studied spatial/thematic resolutions can serve as a useful indicator measuring resolution sensitivity. For the African system, across the studied spatial resolutions, the explanatory power of the OLS models had a variation range (measuring sensitivity to spatial resolution) of about 20% for the resampled data (Fig. 2A) and about 35% for the standard data (Fig. 2B) at certain thematic resolutions. Such sensitivity to spatial resolution was about 10-20% for the SAR models, and about 20-30% for the RF models. Across the studied thematic resolutions, the variation ranges (measuring sensitivity to thematic resolution) amounted to 15% (for the resampled data, Fig. 2A) and 35% (for the standard data, Fig. 2B) at certain spatial resolutions. The sensitivity to thematic resolution was about 15-20% and 20-35% for the SAR and RF models, respectively. For the Chinese system, the resolution sensitivity is also strong, showing similar variation ranges with the African system (Fig. 2C-D, 3C-D, 4C-D). RMSE showed (almost) identical scaling behaviors with R^2 (Fig. S4-S6).

Our scaling analyses demonstrated a clear scaling trend across the investigated resolutions: explanatory power of landscape attributes was enhanced at finer spatial and thematic resolutions. Although there are occasional deviations from this scaling trend (e.g., for African mammals, the strongest explanatory power was observed at the spatial resolution of 0.5 km rather than 0.3 km when comparing between the standard land cover data, Fig 2B, Fig 3B, Fig 4B), the scaling trend is quite

robust, regardless of study system (sub-Saharan Africa vs. continental China), scaling approach (standard vs. resampled data), and type of statistical model chosen (linear vs. non-linear models as well as spatial vs. non-spatial models).

For single landscape metrics, we often found similar scaling relations with that of the landscape attributes collectively, i.e., the correlations (in terms of absolute value of the correlation coefficient between a given landscape metric and species richness) increased with increasing resolutions (Fig. S7). However, there were exceptions, too. Importantly, the strongest correlations were sometimes detected at coarse or intermediate spatial resolutions; and the coarse thematic resolution (2 classes) sometimes gave rise to the strongest correlations (and an opposite sign of correlation). Moreover, the relative importance of landscape metrics varied with changing resolutions and models (Fig. S8).

Discussion

Our results demonstrate conspicuous relationships between landscape attributes and macroscopic patterns of mammal species richness in sub-Saharan Africa and continental China, supporting the previous hypothesis that the strength of local landscape attributes can scale up to biogeographic levels, substantially shaping macroscopic biodiversity patterns (Martins et al., 2014; Ramesh et al., 2016; Xu et al., 2014). Importantly, we show that their strength depends to a considerable extent on both spatial and thematic resolutions of land cover data. A linear scaling trend arises across the investigated resolution ranges (i.e., spatial resolutions of 0.3-9 km, thematic resolutions of 2-5 classes), suggesting that stronger effects of landscape attributes can be generally observed at finer spatial and thematic resolutions.

Our scaling analyses help to reconcile the contradictory evidence on the role of landscape attributes on species richness spatial patterns. At relatively coarse spatial and thematic resolutions, landscape attributes may present weak relationships with mammal species richness, in terms of both absolute value of explanatory power and their relative strength compared with climatic factors. As a primary drivers of macroscopic species richness patterns (Hawkins et al., 2003), climate can often explain a

majority of variations in the studied systems, e.g., up to 60-80% variations of African mammal species richness (Andrews & O'Brien, 2000; Said, 2003), which are close to our results. Our results showing the contrasting explanatory power of climate against coarse-resolution landscape attributes (e.g., for the OLS models, *c.* 60% vs. 10% for African mammals, and *c.* 40% vs. 5% for Chinese mammals, Fig. 1) may lead to the conclusion that landscape attributes add little to climate-envelope models for characterizing macroecological patterns (Opdam & Wascher, 2004; Reino, Triviño, Beja, Araújo, Figueira, & Segurado, 2018). However, we found that landscape attributes at fine spatial and thematic resolutions have a much-enhanced strength, which can be close to or even exceed climate (e.g., for the OLS models based on standard data, *c.* 65% vs. 60% of climate for African mammals, and *c.* 35% vs. 40% of climate for Chinese mammals, Fig. 2). Such strong resolution sensitivity can indeed make landscape factors a highly plastic determinant, leading to contrasting conclusions on their strength if based on largely differed resolutions of land cover data.

Assessing the resolution dependence of land cover data has been largely neglected in macroecological studies, though it has been reported in some landscape-scale studies (Wu, Shen, Sun & Tueller, 2002; Wu, 2004; Wu, Jones, Li & Loucks, 2006; Buyantuyev & Wu, 2007; Tsianou, Koutsias, Mazaris, & Kallimanis, 2016). The revealed linear scaling trend is in line with the general expectation that finer-resolution land cover data can be used to better quantify detailed landscape composition and structure and thereby landscape-richness relationships. However, the 'finer-is-better' assertion may not hold when extrapolated to other scales and/or other systems. An important caveat for extrapolation is that both, too coarse and too fine resolutions, could lead to substantial bias when 'characteristic scales' (i.e., scales at which the variables of interest interact most strongly) exist at an intermediate level of the scale range, resulting in humped scaling relations (Oksanen 1996; Chase & Leibold 2002). Indeed, characteristic scales have been observed in many ecological systems including biodiversity patterns (e.g., Schooley, 2006). In the context of this study, characteristic scales, if present, could be interpreted as typical grain sizes and spatial extents at which mammals perceive surrounding landscapes during their life history (for foraging, home range defense, and so forth). The optimal data resolutions should match characteristic scales, because if observed far away from characteristic scales,

the link between landscape attributes and species assemblage would become imprecise (too coarse) or dominated by noise (too fine). We speculate the highest explanatory power observed at 0.5 km spatial resolution of the standard land cover data for the African mammals (Fig. 2B and 4B) as an artefact (possibly from data quality), rather than a reflection of characteristic scale, because if the characteristic scale truly exists, it is expected to be detected with resampled data as well.

Clearly, our work based on correlative analyses have certain limitations. Multiple intertwined spatial processes often make it difficult to elucidate the role of landscape attributes with only few key variables, and difficult to distinguish between many inter-correlated landscape variables, as well as between landscape variables and other confounding factors such as climate (Xu et al., 2014). Even for a limited subset of landscape metrics we can observe substantially different scaling relations (Fig. S7-S10), suggesting that different local landscape processes can operate within distinct scale domains and thus vary in optimal data resolutions (characteristic scales). Further exploration may focus on whether and to what extent particular local landscape processes shape macroecological patterns. For example, testing the habitat amount hypothesis *sensu* Fahrig (2013) in this context can help to elucidate the relative importance of the sample area effect on species richness across scales.

As an important point, we note that while numerous, the existing landscape metrics may not always sufficiently represent complex, but relevant landscape attributes (Weyland, Baudry, & Ghersa, 2012). Our scaling analyses are far from exhaustive in terms of scale range and taxon (for example our results could be mammal-specific). In addition, time as an important dimension of scale has not been explored in our study due to data limitations. The role of temporal resolution would be essential for quantifying changes of biodiversity in relation to broad-scale landscape modifications, but remains unassessed so far.

Despite these limitations, our work contributes to highlight the importance of two dimensions of scale issue in macroecological studies. The first reflects how ecological interactions may come into effect crossing the hierarchical organization structure of ecological systems (e.g., from community and ecosystem scales to landscape and macroecological scales). Biotic interactions have served as a

strikingly counterintuitive example that smaller-scale processes are able to scale up onto a macroecological scale (Wisz et al., 2013). As a similar example, however, local landscape attributes remain largely overlooked to date. Revisiting the scale ladder (e.g., illustrated by Pearson & Dawson, 2003; McGill, 2010), there is a strong need to comprehensively assess whether other processes can pronounce cross-scale effects shaping macroecological patterns.

The second dimension is related with observational scale. Dependence of observational scale for quantifying macroscopic patterns is not new to macroecologists. For representing macroecological spatial patterns, a considerable proportion of studies have adopted grid cells as a basis, the size of which has been shown to be able to strongly influence the explanatory power and estimated driver relationships for the studied patterns (e.g., Rahbek & Graves, 2001). In these studies, observational scale corresponds with the size of grid cells that are used to partition the system. We addressed a different aspect of observational scale, i.e., the size of minimum identifiable (spatial/thematic) units for the within-grid-cell landscape attributes. In any case, scaling analysis is essential for understanding macroecological phenomena, because it is often impossible to a priori determine the optimal observational scales.

In summary, our modelling results provide a clear demonstration that local landscape attributes can play an important role in shaping macroscopic biodiversity patterns in the studied systems. While it is challenging to disentangle the effect of climate vs. landscape attributes, we confirm that landscape determinants are unneglectable for shaping species diversity at macroecological scales. As a primary finding, the shaping role of landscape attributes has a strong resolution sensitivity, suggesting that their strength can be overlooked if assessments are based on coarse resolutions of land cover data. Our results thus support the speculation that resolution (of land cover data) dependence is a plausible explanation to the contradictory findings on the role landscape attributes in shaping macroecological patterns, and imply that finer spatial and thematic resolutions could better reflect their shaping role. However, a caveat should be taken that the linear scaling relation cannot be extrapolated beyond the studied scale domains due to the complexity of scale issue. Understanding macroecological systems that contains complex hierarchical structures (e.g. see Guisan & Rahbek, 2011) must account for multiple facets of

scale. We expect that scaling analyses can be routinely adopted to systematically examine cross-scale effects in shaping macroecological patterns. Our work also calls attention to potential sensitivity of observational scales in relevant macroecological approaches involving land cover data.

Data availability:

The African mammal data from the African Mammal Databank (AMD) were available from <https://portals.iucn.org/library/node/23725>. The Chinese mammal data were available from the China Species Information Service (CSIS, www.baohu.org; the gridded species richness data used in this study is available upon request). The climate data are available from <http://www.worldclim.org/>. The land cover data were available from http://due.esrin.esa.int/page_globcover.php (GlobCover); <https://globalmaps.github.io/glcnm.html#use> (GLCNMO); <http://www.landcover.org/data/lc/> (GLCF).

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Figures

Figure 1. Species richness of terrestrial mammals per 50×50 km grid cell in the two study regions (i.e., sub-Saharan Africa and continental China, indicated by the black polygons). Species with average body mass <2 kg are excluded.

Figure 2. Explanatory power (adjusted R^2 , %) of the ordinary least square (OLS) models relating local landscape attributes and species richness patterns of terrestrial mammals in sub-Saharan Africa (A-B) and continental China (C - D), for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled (A, C) and standard (B, D) land cover data. Grey lines as a reference indicate the collective explanatory power of macro-climate variables based on the OLS models.

Figure 3. Explanatory power (pseudo R^2 , %) of the non-spatial component of simultaneous autoregressive models (SAR) relating local landscape attributes to species richness of terrestrial mammals in sub-Saharan Africa (A - B) and continental China (C - D), for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled (A, C) and standard (B, D) land cover data. Grey lines as a reference indicate the collective explanatory power of macro-climate variables based on the SAR models.

Figure 4. Explanatory power (pseudo R^2 , %) of the random forest models (RF) relating local landscape attributes to species richness of terrestrial mammals in sub-Saharan Africa (A-B) and continental China (C - D), for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled (A, C) and standard (B, D) land cover data. Grey lines as a reference indicate the collective explanatory power of macro-climate variables based on the RF models.

Supporting Information

The resolution-dependent role of landscape attributes in shaping macro-scale biodiversity patterns

Fig S1. An illustration of spatial and thematic analyses based on one single 50 × 50 km grid cell (left panel). For the spatial scaling analysis (upper right panel, note that in this example the thematic resolution is fixed at 3 land cover classes), land cover data at the spatial resolutions of 0.3, 0.5, 1.0 and 9.0 km are generated using the ‘resampled’ data (with the 0.3 km Globcover data as a basis) and the ‘standard’ data (adopted directly from ready-made remote sensing products). For the thematic scaling analysis (lower right panel, note that in this example the spatial resolution is fixed at 0.3 km), the land cover data at the thematic resolutions of 2, 3 and 5 land cover classes are generated. In our study we conducted analyses for all combinations, i.e., 3 thematic resolutions × 4 spatial resolutions × 2 spatial scaling approaches (standard and resampled data).

Table S1a. Classification scheme representing different thematic scales for the GlobCover data.

2 Classes	3 Classes	5 Classes	Original Data
Vegetated	Forests	Forests	Closed to open (>15%) broadleaved evergreen or semi-deciduous forest (>5m)
			Closed (>40%) broadleaved deciduous forest (>5m)
			Open (15-40%) broadleaved deciduous forest/woodland (>5m)
			Closed (>40%) needleleaved evergreen forest (>5m)
			Open (15-40%) needleleaved deciduous or evergreen forest (>5m)
			Closed to open (>15%) mixed broadleaved and needleleaved forest (>5m)
			Mosaic forest or shrubland (50-70%) / grassland (20-50%)
			Closed to open (>15%) broadleaved forest regularly flooded (semi-permanently or temporarily) - Fresh or brackish water
			Closed (>40%) broadleaved forest or shrubland permanently flooded - Saline or brackish water
	Lower-statured vegetation	Croplands	Post-flooding or irrigated croplands (or aquatic)
			Rainfed croplands
			Mosaic cropland (50-70%) / vegetation (grassland/shrubland/forest) (20-50%)
			Mosaic vegetation (grassland/shrubland/forest) (50-70%) / cropland (20-50%)
		Grasslands / Shrublands	Mosaic grassland (50-70%) / forest or shrubland (20-50%)
			Closed to open (>15%) (broadleaved or needleleaved, evergreen or deciduous) shrubland (<5m)
			Closed to open (>15%) herbaceous vegetation (grassland, savannas or lichens/mosses)
			Closed to open (>15%) grassland or woody vegetation on regularly flooded or waterlogged soil - Fresh, brackish or saline water

Non- Vegetated	Non- Vegetated	Bareland	Sparse (<15%) vegetation
			Artificial surfaces and associated areas (Urban areas >50%)
			Bare areas
			Permanent snow and ice
		Water Bodies	Water bodies

Table S1b. Classification Basis of different thematic resolutions – GLCNMO.

2 Classes	3 Classes	5 Classes	Original Data
Vegetated	Forests	Forests	Broadleaf Evergreen Forest
			Broadleaf Deciduous Forest
			Needleleaf Evergreen Forest
			Needleleaf Deciduous Forest
			Mixed Forest
			Tree Open
			Mangrove
	Lower-statured vegetation	Croplands	Cropland
			Paddy Field
			Cropland / Other Vegetation Mosaic
		Grasslands / Shrublands	Shrub
			Herbaceous
			Herbaceous With Sparse Tree / Shrub
			Wetland
Non-Vegetated	Non-Vegetated	Bareland	Sparse Vegetation
			Bare Area, Consolidated (Gravel, Rock)
			Bare Area, Unconsolidated (Sand)
			Urban
			Snow / Ice
		Water Bodies	Water Bodies

Table S1c. Classification Basis of different thematic resolutions – GLCF.

2 Classes	3 Classes	5 Classes	Original Data
Vegetated	Forests	Forests	Evergreen needleleaf forest
			Evergreen broadleaf forest
			Deciduous needleleaf forest
			Deciduous broadleaf forest
			Mixed forest
	Lower-statured vegetation	Croplands	Croplands
			Cropland and natural vegetation mosaic
		Grasslands / Shrublands	Closed shrublands
			Open shrublands
			Woody savannas
			Savannas
			Grasslands
			Permanent wetlands
Non-Vegetated	Non-Vegetated	Bareland	Urban and built-up
			Snow and ice
			Barren or sparsely vegetated
		Water Bodies	Water

Table S2. Landscape metrics used to quantify landscape attributes

Landscape metrics	Abbreviation	Level
Class area	CA	Class
Number of patches	NP	Class/Landscape
Mean patch size	MPS	Class/Landscape
Patch size standard deviation	PSSD	Class/Landscape
Patch size coefficient of variation	PSCV	Class/Landscape
Total edge	TE	Class/Landscape
Mean patch edge	MPE	Class/Landscape
Largest patch index	LPI	Class/Landscape
Landscape shape index	LSI	Class/Landscape
Mean shape index	MSI	Class/Landscape
Area-weighted mean shape index	AWMSI	Class/Landscape
Mean patch fractal dimension	MPFD	Class/Landscape
Area-weighted mean patch fractal dimension	AWMPFD	Class/Landscape
Double log fractal dimension	DLFD	Class
Mean Euclidean nearest neighbor distance	MENND	Class/Landscape
Mean proximity index	MPI	Class/Landscape
Interspersion & juxtaposition index	IJI	Class/Landscape
Total core area	TCA	Class/Landscape
Mean core area	MCA	Class/Landscape
Number of disjunct core areas	NCA	Class/Landscape
Mean core area index	MCAI	Class/Landscape
Core area standard deviation	CASD	Class/Landscape
Total core area index	TCAI	Class/Landscape
Core area percentage of landscape	CPLAND	Class/Landscape
Mean core area per patch	MCAP	Class/Landscape
Core area coefficient of variation	CACV	Class/Landscape
Patch core area standard deviation	PCASD	Class/Landscape
Patch core area coefficient of variation	PCASV	Class/Landscape

Table S3. Climate variables and data sourced used in this study.

Climate metrics	Abbreviation	Source*
Mean annual temperature	MAT	WorldClim
Maximum temperature of the warmest month	MTWM	WorldClim
Minimum temperature of the coldest month	MTCM	WorldClim
Mean temperature of the coldest quarter	MTCQ	WorldClim
Mean temperature of the warmest quarter	MTAQ	WorldClim
Mean temperature of the wettest quarter	MTWQ	WorldClim
Mean temperature of the driest quarter	MTDQ	WorldClim
Annual potential evapotranspiration	PET	GEWB
Mean annual precipitation	MAP	WorldClim
Precipitation of the wettest month	PWM	WorldClim
Precipitation of the driest month	PDM	WorldClim
Precipitation of the wettest quarter	PWQ	WorldClim
Precipitation of the driest quarter	PDQ	WorldClim
Precipitation of the warmest quarter	PAQ	WorldClim
Precipitation of the coldest quarter	PCQ	WorldClim
Annual actual evapotranspiration	AET	GEWB
Temperature diurnal range	TDR	WorldClim
Temperature annual range	TAR	WorldClim
Temperature seasonality	TSN	WorldClim
Precipitation seasonality	PSN	WorldClim

*WorldClim (<http://www.worldclim.org>); GEWB, Global Evapotranspiration and Water Balance Data Sets (Tateishi & Ahn, 1996, <http://www.grid.unep.ch>)

Reference:

Tateishi, R., & Ahn, C. (1996). Mapping evapotranspiration and water balance for global land surfaces. *ISPRS Journal of Photogrammetry and Remote Sensing*, 51(4), 209-215.

Fig S2. Moran's I coefficients of the residuals of OLS and SAR models at 20 distance units at the grain size of 50 km for the Sub-Saharan Africa mammals.

Fig S3. Moran's I coefficients of the residuals of OLS and SAR models at 20 distance units at the grain size of 50 km for the continental China mammals.

Fig S4. Root mean square error (RMSE) of the ordinary least square (OLS) models relating local landscape attributes and species richness patterns of terrestrial mammals in sub-Saharan Africa (upper panels) and continental China (lower panels), for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled (left panels) and standard (right panels) land cover data. Grey lines as a reference indicate the collective explanatory power of macro-climate variables based on the OLS models.

Fig S5. Root mean square error (RMSE) of the non-spatial component of simultaneous autoregressive models (SAR) relating local landscape attributes and species richness patterns of terrestrial mammals in sub-Saharan Africa (upper panels) and continental China (lower panels), for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled (left panels) and standard (right panels) land cover data. Grey lines as a reference indicate the collective explanatory power of macro-climate variables based on the SAR models.

Fig S6. Root mean square error (RMSE) of the random forest models (RF) relating local landscape attributes and species richness patterns of terrestrial mammals in sub-Saharan Africa (upper panels) and continental China (lower panels), for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled (left panels) and standard (right panels) land cover data. Grey lines as a reference indicate the collective explanatory power of macro-climate variables based on the RF models.

Fig S7. Pearson's correlation coefficient between the four selected landscape-level metrics and species richness of terrestrial mammals in sub-Saharan Africa and continental China, for different thematic (2 - 5 land cover classes), and spatial resolutions (0.3 - 9.0 km), using resampled and standard land cover data. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig S8. Relative importance of the four selected landscape-level metrics based on the ordinary least square (OLS) models.

Fig S9. Relative importance of the four selected landscape-level metrics based on the non-spatial component of simultaneous autoregressive models (SAR).

Fig S10. Relative importance of the four selected landscape-level metrics based on the random forest models (RF).