

# Environmental heterogeneity predicts species richness of freshwater mollusks in sub-Saharan Africa

T. Hauffe · R. Schultheiß · B. Van Bocxlaer ·  
K. Prömmel · C. Albrecht

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**Abstract** Species diversity and how it is structured on a continental scale is influenced by stochastic, ecological, and evolutionary driving forces, but hypotheses on determining factors have been mainly examined for terrestrial and marine organisms. The extant diversity of African freshwater mollusks is in general well assessed to facilitate conservation strategies and because of the medical importance of several taxa as intermediate hosts for tropical parasites. This historical accumulation of knowledge has, however, not resulted in substantial macroecological studies on the spatial distribution of freshwater mollusks. Here, we use continental distribution data and a recently developed method of random and cohesive allocation of species

distribution ranges to test the relative importance of various factors in shaping species richness of Bivalvia and Gastropoda. We show that the mid-domain effect, that is, a hump-shaped richness gradient in a geographically bounded system despite the absence of environmental gradients, plays a minor role in determining species richness of freshwater mollusks in sub-Saharan Africa. The western branch of the East African Rift System was included as dispersal barrier in richness models, but these simulation results did not fit observed diversity patterns significantly better than models where this effect was not included, which suggests that the rift has played a more complex role in generating diversity patterns. Present-day precipitation and temperature explain richness patterns better than Eemian climatic condition. Therefore, the availability of water and energy for primary productivity during the past does not influence current species richness patterns much, and observed diversity patterns appear to be in equilibrium with contemporary climate. The availability of surface waters was the best predictor of bivalve and gastropod richness. Our data indicate that habitat diversity causes the observed species–area relationship, and hence, that environmental heterogeneity is a principal driver of freshwater mollusk richness on a continental scale.

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T. Hauffe (✉) · R. Schultheiß · B. Van Bocxlaer ·  
C. Albrecht (✉)

Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany  
e-mail: torsten.hauffe@gmail.com

C. Albrecht  
e-mail: christian.albrecht@allzool.bio.uni-giessen.de

R. Schultheiß  
Division of Genetics and Physiology, Department of Biology, University of Turku, 20014 Turku, Finland

B. Van Bocxlaer  
Research Unit Palaeontology, Department of Geology and Soil Science, Ghent University, Krijgslaan 281 (S8), 9000 Ghent, Belgium

K. Prömmel  
Institute of Meteorology, Freie Universität Berlin, Carl-Heinrich-Becker-Weg 6-10, 12165 Berlin, Germany

**Keywords** Diversity gradients · Climate simulations · Mid-domain effect · Species–area relationship · Dispersal barrier · East African Rift System (EARS)

## Introduction

Large-scale geographic variation in species richness and specifically, why diversity consistently peaks in the tropics and declines toward the poles, has been studied in many

taxonomic groups (Gaston 2000). Numerous hypotheses have been proposed to explain species richness and how it is determined by various ecological and evolutionary driving forces. So far, these hypotheses have been mainly tested for terrestrial and marine ecosystems (Beck et al. 2012), whereas freshwater habitats are still underexplored (but see Heino 2011; Wagner et al. 2014). Case studies across ecosystems have found that species richness patterns on a continental scale can be driven by productivity (Cardinale et al. 2009; Pinel-Alloul et al. 2013), evolutionary history (Tedesco et al. 2012; Hutter et al. 2013), and climate (Li et al. 2009; Levinsky et al. 2013), such as the contemporary availability of water and energy (Gaston 2000; Keil et al. 2008). The role of water and energy in generating species richness patterns has been mainly proposed for terrestrial systems (Whittaker et al. 2007), but they may also be of importance in marine and freshwater realms (Hawkins et al. 2003; Hurlbert and Stegen 2014). Moreover, dynamics of the past, such as the historical availability of water and energy, are believed to influence extant richness patterns drastically (Whittaker et al. 2007; Zagamajster et al. 2014). One proposed mechanism behind the water–energy hypothesis is that primary productivity is limited mainly by insolation and precipitation and that elevated plant biomass may allow higher animal diversity (reviewed in Hawkins et al. 2003). Habitat heterogeneity is also believed to increase species richness because more heterogeneous habitats provide more niche space, which may enable the coexistence of more species in a given area (Hortal et al. 2009).

Geography and geological processes also affect species richness patterns on various scales and via several processes, such as orogenesis (Cotterill and Wit 2011; Hoorn et al. 2013). Major tectonic events such as rift formation may have great effects on how species are distributed on a continental scale. Rifting causes substantial geological, ecological, and climatic changes, which ultimately affect regional biota by changing their habitats and by creating new corridors or barriers for dispersal (Danley et al. 2012) through the alteration of (paleo)drainages (Schwarzer et al. 2012). Under certain circumstances, these direct and indirect effects may promote isolation and a greater degree of endemism (Plumptre et al. 2007), as is observed related to lake-level changes in rift lakes (e.g., Schultheiß et al. 2009; Genner et al. 2010; Schultheiß et al. 2011, b). Arguably, the consequences of rifting are complex, but simulation studies have demonstrated that barriers for dispersal, as created by rifting, affect species richness patterns (Sizling et al. 2009).

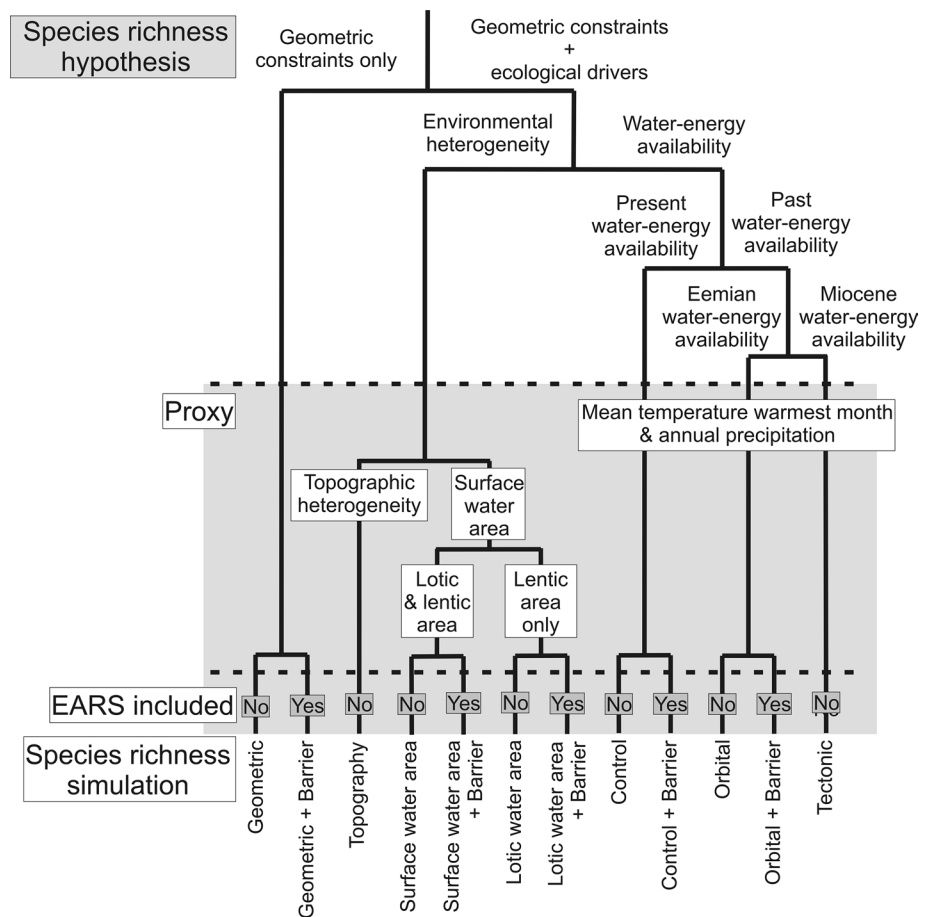
The East African Rift System (EARS) is a phenomenal setting to study the effects of geological processes on the freshwater fauna, and the ecological and biotic consequences of rifting, because global hotspots of freshwater biodiversity arose in this setting, as exemplified by the

extensive radiations of cichlid fishes (e.g., Danley et al. 2012; Salzburger et al. 2014). There is considerable debate about when rifting and the topographic uplift began (e.g., Bauer et al. 2010, 2012), but a recent study suggests that both branches of the EARS started developing synchronously from around 25 MYA (Roberts et al. 2012). The rifting process created tectonic basins, some of which are filled with lakes, and altered river catchments and hydrographic connections at various periods in the past (e.g., Beadle 1981; Goudie 2005; Stankiewicz and de Wit 2006). The effects of topographic changes on regional and continental climate during rift development have moreover been studied extensively in the EARS (e.g., Sommerfeld et al. 2014; Chakraborty et al. 2009; Kaspar et al. 2010; Prömmel et al. 2013). These studies demonstrated that topography affects atmospheric circulation and that before the uplift of East Africa, conditions were drier west of the western branch of the EARS and more humid east of it.

Beyond several ecological factors that are known to influence geographic patterns of species richness (see above), simulation studies have demonstrated that, even in the absence of environmental gradients, plotting diversity on geographic transects usually produces a hump-shaped curve (Colwell and Hurtt 1994). Hence, greater species richness in the tropics could have emerged simply from the assumption of a random association between the latitudinal range and the placement of this range along latitudes (Colwell and Hurtt 1994). In short, in a bounded geographic setting, higher richness is expected in the center, even if variation in fundamental biological processes (e.g., adaptation, speciation, extinction, and predation) is not structured along a geographic gradient (Colwell and Hurtt 1994). A hump-shaped distribution pattern that is simply caused by geometric constraints is known as the “mid-domain effect” (MDE). The MDE has been proposed as a model for testing the importance of ecological drivers in generating species richness patterns because it allows evaluating the degree to which observations can be explained by geometric constraints (Colwell and Lees 2000). Debate is ongoing about whether the MDE is a fully neutral model [i.e., all species sharing initially the same properties (dispersal, speciation, and extinction) *sensu* Gotelli and McGill 2006], a null model (i.e., pattern generated by randomization) against which potential ecological drivers of species richness have to be tested (McCain 2004), or whether geometric constraints are explanatory factors of equal validity to more biological drivers in explaining observed patterns of species richness (Colwell et al. 2009). In the following, we will use the term “geometric model” for species richness models that assume environmental gradients to be absent.

Current insights into spatial variation in species richness of African freshwater biota are based on data from a limited set of habitat types and a restricted set of taxa (Wagner

**Fig. 1** Conceptual outline of hypothesized drivers of species richness and the simulations we performed to test how these drivers shape species richness in bivalves and gastropods. The explanatory power of geometric constraints, environmental heterogeneity, or climatological models related to water–energy availability in shaping species richness patterns was tested with simulations that use probability maps and random range allocations (see text). Furthermore, the influence of the East African Rift System (EARS) as a barrier for dispersal was included in our simulations, resulting in a total of 12 richness simulations



et al. 2012, 2014; but see Darwall et al. 2011). Invertebrates are particularly underrepresented in these studies, and mollusks have not been included (Graf et al. 2011; Seddon et al. 2011; see Collen et al. 2014), despite (1) being taxonomically well studied, (2) being a major component of macroinvertebrate communities, and (3) their considerable degree of species diversity (Mandahl-Barth 1988; Brown 1994; Daget 1998; Graf and Cummings 2011). The absence of freshwater mollusks from macroecological analyses of sub-Saharan Africa is unfortunate because current knowledge on taxonomy and distribution is considerably more advanced for mollusks than other freshwater invertebrates (Salzburger et al. 2014). Here, we try to address the above-mentioned knowledge gap for both classes of freshwater mollusks, Gastropoda and Bivalvia. They differ in their biology, ecology, and life-history parameters (e.g., Dillon 2000), and hence, these taxa may display different patterns of richness depending on environmental conditions (e.g., Davis 1982; Dillon 2000; Ponder and Colgan 2002).

In this paper, we investigate whether observed species richness patterns in African freshwater bivalves and gastropods are caused primarily by geometric constraints or whether a combination of geometric constraints and ecological drivers explains patterns better (Fig. 1). Through

the comparison of simulated and observed species richness patterns, we specifically tested the role of two ecological aspects for which strong impacts on species richness patterns have been proposed: environmental heterogeneity and the availability of water and energy for primary production. Because of the complexity of these ecological factors, we used several proxies to test their effects (Fig. 1), and we also examined whether species richness is better explained by past or contemporary patterns of water–energy availability by utilizing three climate models. In addition, we adapted our models to investigate whether inclusion of the EARS as a barrier for dispersal affects predicted species richness (Fig. 1).

## Materials and methods

This study treats continental sub-Saharan Africa as a biogeographic entity. There is some debate as to whether strict borders between zoogeographic regions exist and whether they are consistent among taxa (e.g., Krefl and Jetz 2010; Holt et al. 2013). However, for freshwater fauna, and particularly mollusks, the Sahara indeed delimits the Afrotropical zoogeographic region (Graf et al. 2011; Seddon et al.

2011). For all our analyses, we employed the Albers equal-area conic projection, with a grain size of  $100 \times 100$  km, which is a resolution that has typically been applied for studies on a continental scale (e.g., Beck et al. 2012).

#### Range maps, range-size frequency distribution, and species richness

We used distribution data of sub-Saharan freshwater mollusk species compiled during the freshwater biodiversity assessments of Africa by the International Union for Conservation of Nature (IUCN; Darwall et al. 2011). We excluded Malagasy species and island endemics, 30 brackish water species, and one questionable subfossil species (Table S1). Four range maps were adapted to include data from Brown (1994) (Table S1), e.g., by adding missing type localities. The resulting range maps for 82 bivalve and 318 gastropod species represent 70.1 and 86.8 %, respectively, of the known Afrotropical and Malagasy species richness in these classes (Strong et al. 2008; Bogan 2008). Range-size frequency distributions (RSFDs) were calculated for bivalves and gastropods separately. African freshwater mollusks have been intensively studied because of the medical importance of some gastropods that act as intermediate hosts for tropical parasites, and because of conservation concerns related to bivalves (Brown 1994; Daget 1998; Graf and Cummings 2011). After previous phases of splitting and lumping, the taxonomy is overall well resolved, but it is still not fully stable, and taxonomic uncertainty may influence estimates of species richness. Specifically, for some of the endemic lacustrine species flocks, such as that of *Lavigeria* in Lake Tanganyika, species diversity is uncertain, as more species may need to be described (West et al. 2003; Glaubrecht 2008; Schultheiß et al. 2009). To assess the robustness of our conclusions against taxonomic uncertainty, we repeated our calculations and simulations excluding all taxa that are endemic to rift lakes (Table S2; Supplementary material).

The IUCN initially mapped mollusk distributions to watersheds (Darwall et al. 2011), as delineated by the highest available resolution of the HYDRO1k Elevation Derivative Database (published by the US Geological Survey Earth Resources Observation and Science Center; Masutomi et al. 2009). Similar approaches have been used in other studies of species richness patterns (Markovic et al. 2014). Range maps were gridded onto the domain by rasterizing only those parts of the distribution that cover more than 50 % of one grid cell. However, in case a species displayed a fragmented distribution, single fragments smaller than the grain size were also gridded to preserve the signal of a scattered distribution within small watersheds. Species richness was calculated by summing the overlapping ranges in each grid cell. All calculations and richness simulations

were performed using the package raster version 2.2-31 (Hijmans 2014) in R version 3.0.1 (R Core Team 2014).

#### Species richness simulations

To evaluate the extent to which current species richness patterns are driven by geometric constraints, environmental heterogeneity, or water–energy availability, we performed richness simulations for each of these potential drivers, to subsequently estimate the correlation between simulated results and observed species richness. Specifically, we constructed four types of Monte Carlo models to simulate species richness under each of these potential drivers and performed 100 species richness simulations with each driver to create statistical populations of simulations that were used to test correlations with observed species richness.

#### Geometric constraints only

In general, two methods have been proposed to randomize range allocation for testing a two-dimensional MDE (Jetz and Rahbek 2001; VanDerWal et al. 2008). The latter one defines species ranges as rectangular units defined by the longitudinal and latitudinal extent of the species' observed range. The other approach focusses on the actual size of observed species ranges, and because it does not overestimate range sizes, we applied this approach. The way simulated species ranges are constructed with this second approach has been compared to “the spreading of dropped dye” (Jetz and Rahbek 2001): the first grid cell to be occupied is chosen randomly, and subsequent grid cells adjacent to already occupied cells are added randomly, until the observed range size has been reached. This mode of range allocations was performed for all species, each with its own observed range size, and the complete simulation was repeated 100 times for the entire dataset.

Because the western branch of the EARS appears to have acted as a dispersal barrier for many freshwater mollusks since the Pliocene (Schultheiß et al. 2014), with the result that many freshwater mollusk species occur only at one side of this rift branch, we repeated simulations of geometric constraints with the western branch of the EARS as a dispersal barrier for randomized range building. We defined this barrier by considering the cells along the western branch of the EARS as a hard boundary, so that when the boundary is reached, the chance of adding a grid cell at its other side is reduced to zero. Note, however, that spreading around the boundary is possible at its northern and southern end, so that this additional parameter does not prevent taxa with a wide range to occur at both sides of the western branch of the EARS, as was observed in nature for some taxa.

## Water–energy hypothesis and climate simulations

The random range allocation model that we used for testing the presence of geometric constraints can be altered to test hypotheses related to ecological drivers. The effects of ecological drivers can be simulated by replacing the assumption of an unstructured bounded lattice with a rugged surface, where the addition of grid cells to a range is more likely in one direction (i.e., more likely toward valleys in the rugged surface than toward peaks) (see Rahbek et al. 2007). The rugged surface can be modeled so that ruggedness reflects the environmental characteristics of a particular ecological factor and variation of that ecological factor on the grid. From this rugged surface, a probability map for spatial range expansion is created, and range allocation based on this probability map (i.e., the specific underlying environmental driver) can then be compared to observed species richness to investigate the effect of the driver beyond the effects of geometric constraints alone (Levinsky et al. 2013). In this modification, the first cell is chosen based on the ecological probability landscape, and subsequent cells are added adjacently to already occupied grid cells based on these probabilities as well.

The impact of the availability of water and energy for primary production has received substantial attention during the previous decade, but a consensus on relationships of these factors to species richness is still lacking (Levinsky et al. 2013). Different studies implemented a variety of different climate variables (e.g., Whittaker et al. 2007; Rahbek et al. 2007; Dias et al. 2014). Here, we follow the approach of Levinsky et al. (2013) and constructed a probability map using the first axis of a principle component analysis (PCA) that includes mean temperature of the warmest month and annual sum of precipitation. These variables are taken from the climate simulations of Prömmel et al. (2013), which were obtained using a non-hydrostatic regional climate model CCLM (COSMO model in CLimate Mode; Rockel et al. 2008). The original climate model covered the African continent almost entirely with a resolution of  $0.5 \times 0.5^\circ$ . All climatic variables were resampled to the approximately four times coarser resolution of  $100 \times 100$  km adopted in our study.

Three climate simulations from Prömmel et al. (2013) were used representing different forcing mechanisms as described by Kaspar et al. (2010) and with modifications by Prömmel et al. (2013). The first climate simulation was a pre-industrial control simulation with pre-industrial greenhouse gas concentrations, topography, and orbital parameters. The second represented Eemian climate conditions (i.e., 125,000 years BP) by changing the orbital parameters and greenhouse gas concentrations to values from that time but keeping the topography at pre-industrial conditions. The third simulation represented the effects of

tectonic forcing by reducing topography in Southern and Eastern Africa by 50 % whereas the orbital parameters and greenhouse gas concentrations were kept at pre-industrial levels. This model arguably is an oversimplification of the more complex rifting process, which began in the north and propagated to the south (Maslin and Christensen 2007), but changing topography alone may give a better insight into the explanatory power of this factor. Hence, this climate model does not represent a single moment in time, but rather, general Miocene conditions. The modeled topography probably represents Early to Middle Miocene conditions in the north and Middle to Late ones in the south (Prömmel et al. 2013). Systematic errors in climate models were corrected by comparison with gridded observation of temperature (ERA-Interim reanalysis; Dee et al. 2011) and precipitation (Global Precipitation Climatology Centre full data reanalysis product; Schneider et al. 2011; Rudolf and Schneider 2005).

## Environmental heterogeneity

As mentioned in the introduction, heterogeneity in habitats may have a strong effect on species richness. We incorporated this aspect in our analyses by taking topographic variability within grid cells as a proxy for habitat heterogeneity, which is an approach that has been utilized before (Rahbek et al. 2007). However, we modified the approach of former authors by including areas above the snowline because some African mollusks occur in ecosystems at greater altitudes (Mandahl-Barth 1988; Brown 1994; Bößneck 2012). For each 10,000-km<sup>2</sup> cell, we calculated the difference between maximum and minimum elevation as given by the GTOPO30 dataset with a spatial resolution of approximately 1 km at the equator. These differences in elevation were directly transformed into a probability map. Increased topographic variation also increases the habitable surface area; hence, the proxy we used to some extent also reflects available space, which may influence patterns of extant species richness (Rahbek et al. 2007).

A second proxy of environmental heterogeneity in freshwater ecosystems is the availability of freshwater habitats within each grid cell. We assessed this aspect on a  $1 \times 1$  km scale using high-resolution data from [www.diva-gis.org](http://www.diva-gis.org) (accessed October 26, 2013). Specifically, we subdivided each 10,000-km<sup>2</sup> grid cell into 10,000 grid cells of 1 km<sup>2</sup>. For each of these small grid cells, we weighted water availability. If <50 % of the grid cell was occupied by surface water, the cell received a value of zero. If >50 % was occupied by surface water, the cell received a value of 1 or 2, depending on whether this surface water was ephemeral or perennial, respectively. Subsequently, we added the values obtained for all of the 1-km<sup>2</sup> cells within a 10,000-km<sup>2</sup> cell to obtain a summary value for water availability in each

of the large grid cells, which again was converted in a frequency density distribution and a probability map.

Because lotic systems are, on average, more stable and long-lived than lentic systems (Hof et al. 2008), we also calculated the availability of running water separately in exactly the same way as indicated above.

In summary, we ran simulations with three proxies of environmental heterogeneity, i.e., one representing topographic variability, one with general surface water area, and one characterizing the surface occupied by rivers (Fig. 1).

#### Statistical analyses

In total, 12 species richness simulations were outlined above accounting for various factors that may affect the distribution of mollusks in sub-Saharan Africa (Fig. 1). As mentioned, we ran 100 simulations for each of these scenarios and calculated summary statistics of predicted species richness. These statistics were used for Pearson's correlation analyses to test the extent to which the simulated and observed diversity patterns are correlated. Acknowledging that spatial autocorrelation overestimates the number of observations, we corrected *P*-values using Dutilleul's method as implemented in the R package SpatialPack version 0.2 (Osorio et al. 2012).

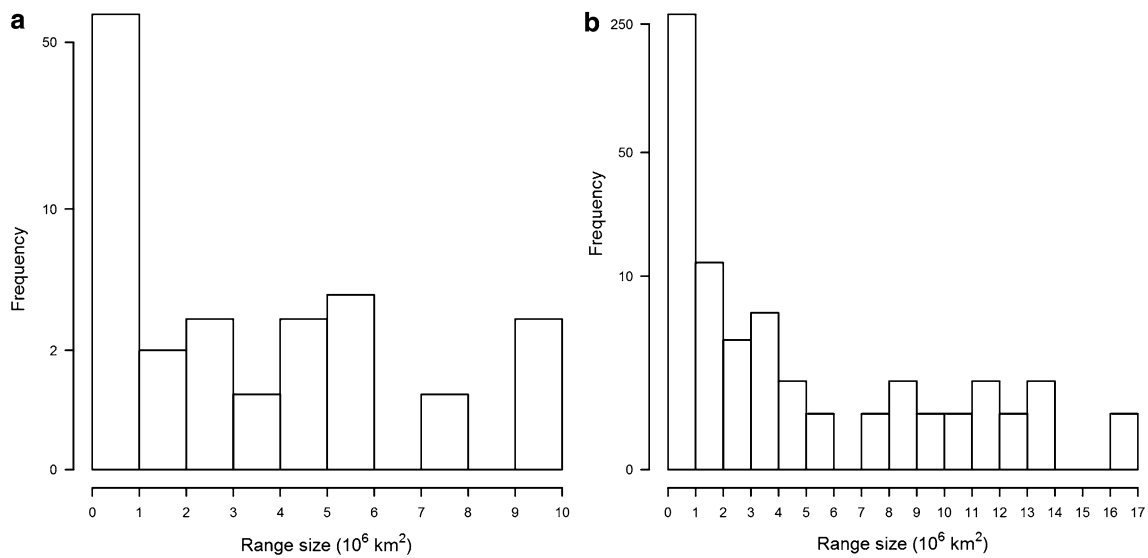
To test whether the 12 ways of simulating species richness (Fig. 1) differ in the way they predict observed richness patterns of African mollusks, we performed a Bayesian alternative of an Analysis of Variance (BANOVA) using all simulation runs. This method is capable of dealing with non-homogenous variances (Kruschke 2011), but also has several other advantages. First, the number of simulations is chosen arbitrarily, and even very small differences will yield significant results using traditional statistics if the number of individual observations (i.e., simulations) is greatly increased (White et al. 2014). In a Bayesian framework, the parameters of interest (here, the deflection of each model from the overall tendency and the differences among groups) are estimated directly by reallocating the coefficients across a set of possible candidates (i.e., the prior) during each Markov chain Monte Carlo run (MCMC), so that the number of simulations does not directly affect significance levels. Moreover, in contrast to traditional methods, no test statistic is required because the reliability of the parameter of interest is given by the 95 % highest density interval (HDI), which summarizes where the majority of reallocated coefficients falls (i.e., the posterior). The position of 95 % HDI in comparison with the overall mean resulting from all performed simulations forms the basis for evaluation. If the HDI does not include zero, that particular simulation differed substantially from the overall mean, and strong indications exist for a credible deflection of the particular simulation from this mean

(Kruschke 2013). The second reason for adopting a Bayesian framework is that we aim to test for pairwise differences between individual simulations and groups of simulations, e.g., groups including or excluding the EARS as dispersal barrier. Such correlations are in traditional statistics typically assessed with post-hoc testing after which the obtained *P*-values are corrected, to mitigate chances for false positives. Such corrections are not necessary in a Bayesian framework because differences between groups can be directly estimated from pairwise comparisons of the posterior distributions of each simulation (Kruschke 2011). The BANOVA was performed using package rjags version 3-11 (Plummer 2013) for R. Visual inspection of preliminary runs revealed substantial autocorrelation in posterior distributions. Therefore, after removing a burn-in of 10,000 generations, we sampled 10,000 runs for bivalves and gastropods at each 35 and 100th step, respectively.

#### Results

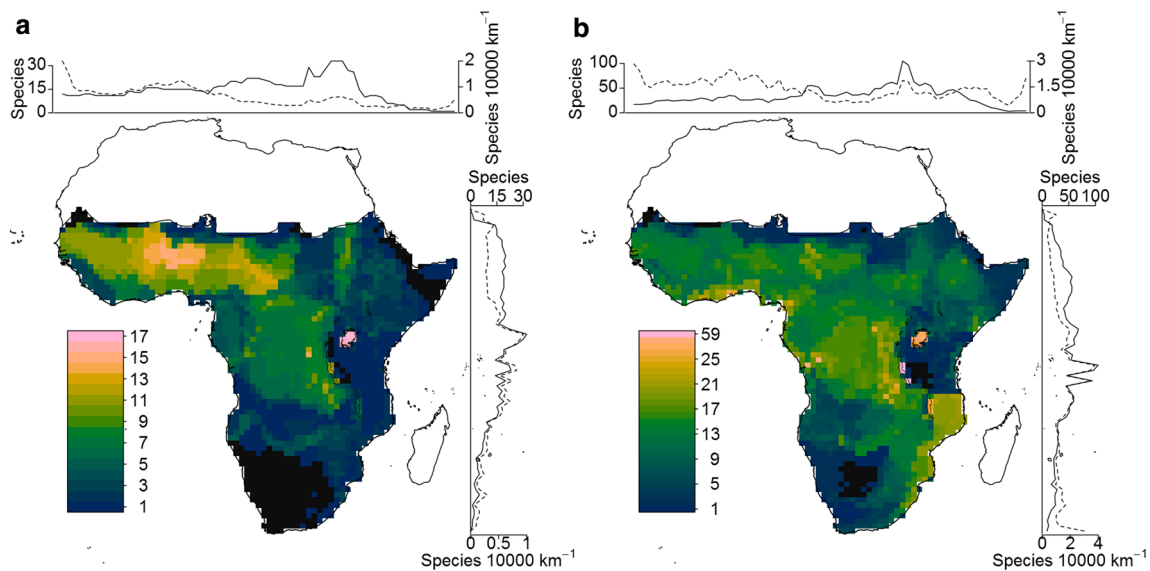
RSFDs of bivalves and gastropods were both left-skewed, indicating that most taxa have highly restricted distributions, whereas few occupy large geographic ranges (Fig. 2). In general, species richness maps of gastropods and bivalves showed greatly similar patterns in sub-Saharan Africa ( $r_{\text{Pearson}} = 0.49$   $DF = 152.3$   $P < 0.001$ ) with the highest richness in Lakes Malawi, Tanganyika, and Victoria (Fig. 3). Species richness peaked in longitudinal and latitudinal positions that correspond to the African Great Lakes (AGL), which testifies to the regional effects of rifting on species richness (Fig. 3, but see Fig S1 for a comparison without AGL endemic species). Despite great similarities, some differences exist between the overall distribution of bivalves and gastropods: bivalves reach relatively greater richness in forest-rivers of West Africa, and gastropod communities are more diverse in the East African coastal rivers and the Congo watershed.

Different random range allocation models showed various predictions of species richness (Fig. 4). The patterns revealed by various simulations were consistently similar for both classes. The two simulations relying purely on geometric constraints showed the typical pattern of a mid-domain effect, i.e., highest species richness in the center of the domain (Fig. 4). Generally, the distribution of species richness was rather homogenous for both classes: richness peaked at 7.02 and 14.78 species, for bivalves and gastropods, respectively, with minimal values of 1.51 and 3.52 at coastal grid cells. Whenever the EARS was included as a dispersal barrier in simulations, a higher richness peak was produced and this peak shifted toward the northwest in comparison with the peaks in simulations based solely on geographic constraints (Fig. 4). Climate-driven richness



**Fig. 2** Frequency distribution of range sizes of (a) 82 bivalve and (b) 318 gastropod species on a semi-logarithmic scale (actual frequency numbers are indicated). Range maps on which these frequency dis-

tributions are based were first compiled during the IUCN freshwater biodiversity assessments of Africa (Darwall et al. 2011) and were modified to include data from Brown (1994) and other resources

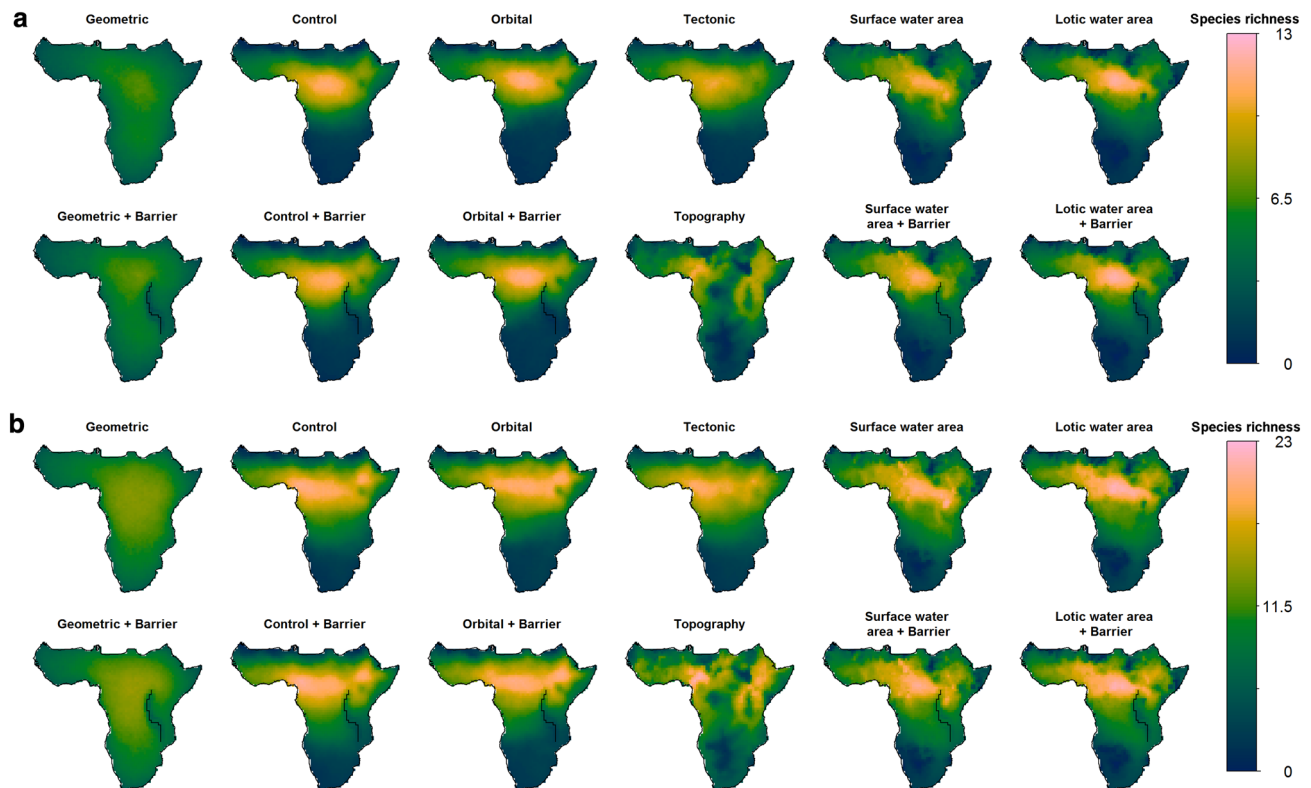


**Fig. 3** Extant species richness patterns in sub-Saharan Africa in 10,000-km<sup>2</sup> grid cells for (a) Bivalvia and (b) Gastropoda. All maps use Albers equal-area projection. The legend for the gastropod dataset has been truncated at its top end because the high diversity in Lake Tanganyika would otherwise obscure patterns elsewhere in Africa. Black areas indicate regions that are not occupied by any of the mol-

lusk species assessed by the IUCN (Darwall et al. 2011). Summarily latitudinal and longitudinal richness gradient are indicated at the top and right side: Solid lines show species richness per 100-km-wide latitudinal and longitudinal sector, respectively, and dashed lines illustrate richness gradients corrected for the number of grid cells sampled per sector

simulations, which were based on a probability map that reflects precipitation and temperature, resulted consistently in more pronounced richness peaks in northern sub-Saharan Africa. Simulations guided by the grid cell probabilities based on topographic heterogeneity showed highest species richness along the rift shoulders and at the Gulf of Guinea

(Fig. 4). Simulations that used surface area of inland waters as proxy of environmental heterogeneity revealed a broader richness peak than the one obtained for climate-driven simulations and the peak extended more toward the south-east. Comparisons of simulated and observed species richness patterns resulted in significant results only for the four



**Fig. 4** Averaged patterns of species richness obtained from 100 simulations for each of the different range cohesion methods that were implemented (see Fig. 1) for (a) Bivalvia and (b) Gastropoda. The

superimposed line is showing the western branch of the East African Rift System (EARS), which was included in the respective simulations as barrier for the allocation of species ranges

**Table 1** Pearson correlation coefficients between observed and simulated species richness using different range cohesion methods

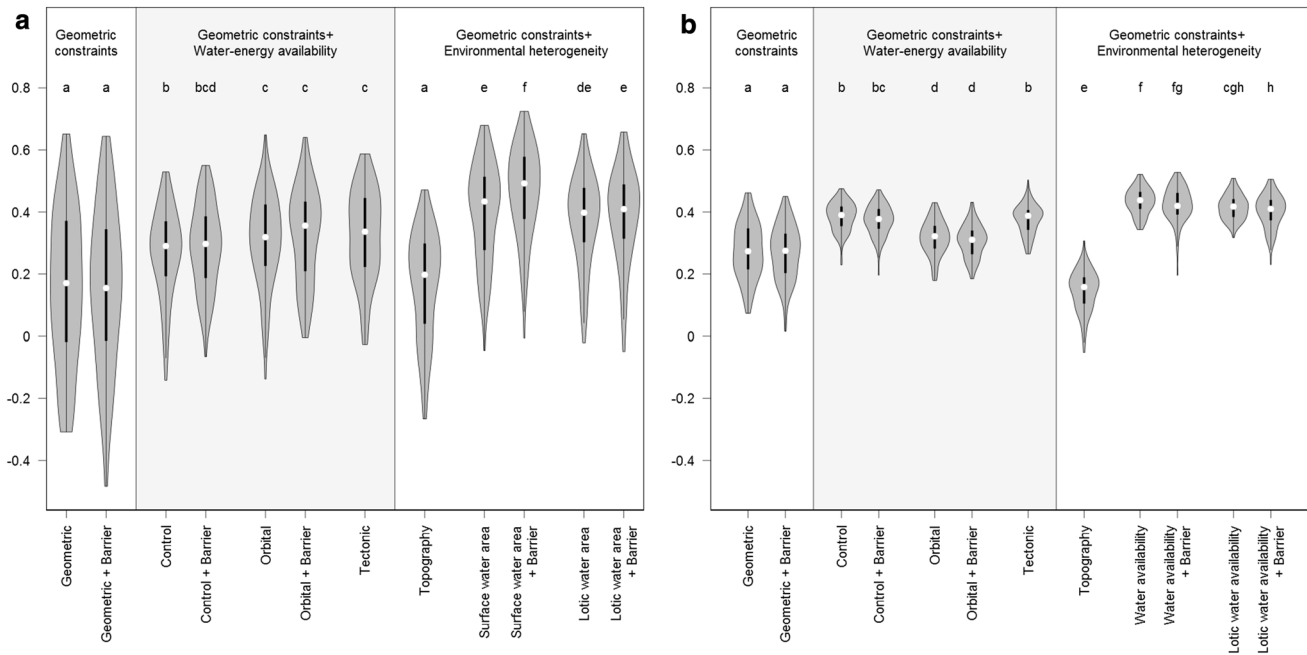
Model	Bivalvia		Gastropoda	
	$r_{\text{Pearson}}$	$P$ -value	$r_{\text{Pearson}}$	$P$ -value
<i>Hypothesis of geometric constraints only</i>				
Geometric	0.319	0.120	0.339	0.154
Geometric + barrier	0.340	0.111	0.333	0.135
<i>Hypothesis of geometric constraints + water–energy relationship</i>				
Control	0.462	0.080	0.413	0.069
Control + barrier	0.470	0.081	0.408	0.066
Orbital	0.481	0.095	0.340	0.150
Orbital + barrier	0.493	0.089	0.342	0.135
Tectonic	0.516	0.067	0.411	0.072
<i>Hypothesis of geometric constraints + environmental heterogeneity</i>				
Topography	0.325	0.177	0.211	0.247
Surface water area	<b>0.578</b>	<b>0.022</b>	<b>0.464</b>	<b>0.028</b>
Surface water area + barrier	<b>0.632</b>	<b>0.019</b>	<b>0.466</b>	<b>0.026</b>
Lotic water area	<b>0.539</b>	<b>0.033</b>	<b>0.446</b>	<b>0.034</b>
Lotic water area + barrier	<b>0.551</b>	<b>0.034</b>	<b>0.443</b>	<b>0.030</b>

Due to spatial autocorrelation, all  $P$ -values have been calculated with reduced degrees of freedom. Significant correlations ( $\alpha \leq 0.05$ ) are highlighted in bold

models of environmental heterogeneity that deal with the availability of surface water. Pearson's correlation coefficients for these models are consistently higher than those of other models in both classes; they range between 0.54 and 0.63 for bivalves and between 0.44 and 0.47 for gastropods (Table 1).

Pearson's correlation coefficients between simulated and observed species richness showed overall higher values and more variability for bivalves than for gastropods, testifying to the differences in sample sizes (i.e., total species diversity; Fig. 5). The BANOVA indicated that many simulations for both bivalves and gastropods displayed credible deflections from the common mean of all models (Table 2). The Bayesian test of pairwise differences between simulations revealed that the geometric constraints model resulted in significantly lower correlation coefficients (see lower case letters in Fig. 5) than the other models (with a mean difference between two models of up to  $\Delta r_{\text{Pearson}} = 0.3$ ; Table S3). Climate models including water–energy availability predicted species richness better than the models of geometric constraints. However, the pattern differs somewhat between bivalves and gastropods: Simulations using pre-industrial climatic proxies for these resources correlated better with observed species richness





**Fig. 5** Violin plots showing populations of Pearson's correlation coefficients obtained from observed species richness and individual runs (100 in total) of simulated species richness with each of the range cohesion methods for (a) Bivalvia and (b) Gastropoda (see Fig. 1). Letters above the plots indicate statistic similarity or dif-

ferences. Models with the same letter are not significantly different from one another, whereas those with different letters are. These differences were inferred from a Bayesian alternative for ANOVA with post-hoc testing (see text for details)

for gastropods (mean  $\Delta r_{\text{Pearson}} = 0.069$ ; HDI = 0.044:0.084; Table S3) than did models of orbital forcing conditions from the past. But these pre-industrial models performed equally well as models employing tectonically forced climate (mean  $\Delta r_{\text{Pearson}} = 0.009$ ; HDI = 0.004:0.023; Table S3). For bivalves, the differences between climatic models are smaller, with a maximum of  $\Delta r_{\text{Pearson}} = 0.055$  (Table S3). Models of current climate and Eemian climate conditions both correlated in a very similar way with extant species richness (Table 2). Inclusion of the rift as dispersal barrier increased the correlations somewhat, though not significantly (Fig. 5). The tectonic model performed well for both bivalves and gastropods (Table 2, Fig. 2). Models including surface water area as proxy of environmental heterogeneity yielded the best correlations with observed species richness (Table 2); correlation coefficients for these models are consistently higher than those of other simulations (see lower case letters in Fig. 5). An overall comparison of models that included the rift as barrier did not correlate better with observed species richness than models without rift: The BANOVA results showed that the mean of these two groups of simulations are likely equivalent because the posterior distribution of pairwise differences includes zero in both taxa (Bivalvia: mean  $\Delta r_{\text{Pearson}} = 0.011$ , HDI =  $-0.001:0.024$ ; Gastropoda: mean  $\Delta r_{\text{Pearson}} = -0.004$ , HDI =  $-0.008:0.001$ ).

Analyses excluding lacustrine endemic faunas of the EARS to investigate whether taxonomic uncertainty affects correlations between observed and simulated species richness patterns (Fig. S1) resulted often in slightly higher Pearson's correlation coefficients than those obtained when these endemics are included (Table S4). A significant, but nevertheless minor improvement (mean  $\Delta r_{\text{Pearson}} = 0.015$ ; HDI = 0.013:0.018), was only achieved for gastropods, which arguably have larger species flocks in the EARS than bivalves (Fig. S2). Like for analyses utilizing all species, simulations based on surface water area yielded the best resemblance to extant species richness for the pruned dataset (Table S4; Fig. S2).

## Discussion

### Range-size determination in freshwater mollusks

On a continental scale, the relative importance of geometric constraints and ecological drivers on extant species richness depends somewhat on the frequency distribution of range sizes (Colwell and Lees 2000). If many of the studied species have large range sizes, richness pattern will be predominantly determined by geometric constraints, whereas

**Table 2** Deflection of simulation models from the overall mean, resulting from all performed simulations, and their 95 % HDI as estimated by the Bayesian alternative of an ANOVA

	Bivalvia	Gastropoda
Hypothesis of geometric constraints only		
Geometric	<b>-0.069</b>	<b>-0.139</b>
	<b>-0.085:-0.053</b>	<b>-0.183:-0.097</b>
Geometric + Barrier	<b>-0.074</b>	<b>-0.140</b>
	<b>-0.09:-0.059</b>	<b>-0.185:-0.097</b>
Hypothesis of water-energy relationship		
Control	<b>0.041</b>	<b>-0.033</b>
	<b>0.032:0.051</b>	<b>-0.060:-0.005</b>
Control + Barrier	<b>0.029</b>	-0.015
	<b>0.019:0.038</b>	-0.04:0.014
Orbital	<b>-0.027</b>	0.008
	<b>-0.038:-0.017</b>	-0.020:0.037
Orbital + Barrier	<b>-0.037</b>	0.021
	<b>-0.046:-0.026</b>	-0.008:0.050
Tectonic	<b>0.032</b>	0.021
	<b>0.022:0.041</b>	-0.007:0.049
Hypothesis of environmental heterogeneity		
Topography	<b>-0.197</b>	<b>-0.132</b>
	<b>-0.209:-0.185</b>	<b>-0.163:-0.100</b>
Surface water area availability	<b>0.090</b>	<b>0.096</b>
	<b>0.081:0.098</b>	<b>0.066:0.124</b>
Surface water area + Barrier	<b>0.081</b>	<b>0.160</b>
	<b>0.070:0.091</b>	<b>0.132:0.189</b>
Lotic water area	<b>0.072</b>	<b>0.070</b>
	<b>0.064:0.08</b>	<b>0.042:0.097</b>
Lotic water area + Barrier	<b>0.059</b>	<b>0.083</b>
	<b>0.048:0.069</b>	<b>0.054:0.111</b>

Departures where the 95 % HDI does not include zero indicate credible differences from the overall tendency and are highlighted in bold

environmental constraints are usually more important if many species have small range sizes. Bivalves and gastropods both show similar RSFD with few widely and many narrowly distributed species (Fig. 2), despite differences in their biology (e.g., mode of reproduction, feeding strategy, substrate preference, and dispersal capacity). Such left-skewed RSFDs are characteristic for most taxa (Lomolino 2010). Observed range sizes are influenced by both biotic and abiotic factors, and the range of a species is often set by dispersal limitation (for recent reviews, see, e.g., Cahill et al. 2014; Hargreaves et al. 2014). Some closely related taxa have massively different range sizes, which suggests that intrinsic properties at the class level are no major determinant of differences in range size and thus regional species richness patterns in freshwater mollusks.

#### Species richness patterns in Africa

Upon testing for the first time the role of various factors in shaping mollusk richness distributions on a continental scale, we found great similarity between richness patterns of bivalves and gastropods (Fig. 3). The latitudinal diversity gradient constructed here resembles earlier, more general descriptions of diversity distributions (Brown 1994; Graf

and Cummings 2011). The fine-scaled diversity patterns revealed here clearly testify to the role of rifting in generating diversity in African freshwater mollusks, because species richness peaked within the EARS for both bivalves and gastropods. In general, diversity patterns of African freshwater mollusks seem to match recently compiled richness patterns for other African freshwater taxa that were included in a global diversity dataset (Collen et al. 2014).

The various simulations ultimately did not differ much between bivalves and gastropods in generated species richness patterns (Fig. 4), which is a consequence of these taxa's similar RSFD (Colwell and Lees 2000). Our two-dimensional geometric models resulted in a central richness peak (Fig. 4), which matches the MDE observed in birds (Jetz and Rahbek 2001). Most other studies that have investigated two-dimensional geometric models (e.g., Jetz and Rahbek 2001; Murphy et al. 2011 and others, summarized in Colwell et al. 2004), obtained similar correlation values between observed and simulated species richness to ours (converted to  $r_{\text{Pearson}}$  between 0.00 and 0.45). The correlation between patterns of observed species richness and those simulated with models of geometric constraints indicate that the distribution of mollusk richness is driven partly by the shape of sub-Saharan Africa.

Nevertheless, the limited strength of the correlation suggests that environmental gradients and evolutionary history play major roles in structuring biodiversity spatially. Indeed, ecological models that incorporated spatial heterogeneity and climatological information predicted observed species richness better than models of geometric constraints alone. Our findings hence corroborate the patterns observed in two similar studies dealing with the species richness of South American birds (Rahbek et al. 2007) and of North American trees (Murphy et al. 2011). Species richness in both of these studies is explained best by water–energy dynamics and hence climatological factors. Noteworthy is that these studies used a highly similar approach to the one adopted here and that many of the models tested in the first study, like some of ours, were also on the edge of reaching significance. Our results document a strong and significant correlation of extant mollusk richness with models that incorporate the area of available water bodies. These models did not produce the most complex patterns of species richness; our simulations with topographic data simulated species richness distributions with peripheral richness peaks and cratered rings (Fig. 4). This complex spatial structuring resembles observed species richness patterns of African birds (Jetz and Rahbek 2001), but not of bivalves and gastropods.

Simulations with a dataset that excluded all species endemic to rift lakes from the analyses indicated that our analyses are robust against taxonomic uncertainty. These additional analyses did not generate large differences, and our models still ranked the same in explaining observed species richness (Fig. S2). This observed robustness against different taxonomic scenarios for rift–endemic taxa is likely due to the limited influence of a few grid cells with spectacular species richness on correlation analyses with continent-wide data (<10 % of >2,000 grid cells).

Below, we will try to use our insights into correlations between observed and simulated richness patterns to explore the mechanisms that may be responsible for generating and maintaining species richness patterns, which is a much needed insight (e.g., Hawkins et al. 2003; Cahill et al. 2014).

#### The EARS as dispersal barrier

Results of simulations that included the EARS as an impermeable barrier for organismal dispersal did not improve the fit with observed species diversity much beyond the fit of the same model without inclusion of this barrier (Fig. 5). This result was somewhat surprising, given that observed species distributions suggest a limited degree of trans-rift dispersal. Only two bivalve and 21 gastropod species (out of 82 and 318, respectively, so <10 %) occur at both sides of the rift. We had expected that the inclusion of the rift as

a dispersal barrier would result in a westward shift of the richness peak toward the Congo Basin, which would have resembled empirical species richness better, at least for gastropods, than the results of simulations based on geometric constraints alone (Fig. 4). Nevertheless, our observed species richness patterns (Fig. 3) indicate great diversity within the rift, which suggests that the EARS played an important role in generating and structuring species richness. Hence, the rift had a more complex influence on species diversity than was accounted for in our models. However, the effect of the EARS on continental species richness patterns remains overall rather limited, which could be contributed to the fact that the EARS represents <10 % of >2,000 grid cells. The regional effect of the EARS was exemplified in our analyses that excluded all species endemic to the rift lakes: Limited differences were observed from those that included the large species flocks of the EARS, and the ranking of our models in explaining observed species richness stayed the same (Fig. S2).

Mountain ranges, like the Tibetan Plateau, have been shown to act as strong dispersal barriers for freshwater gastropods (e.g., von Oheimb et al. 2013), but this is not the primary role the EARS played in generating macroecological patterns. Perhaps the limited effect is due to the fact that the EARS is not a homogenous mountainous structure and that climate and topography may have interacted strongly with another in generating and obliterating dispersal corridors through time (e.g., Van Bocxlaer et al. 2008; Day et al. 2013; Schultheiß et al. 2014). Beyond the diversity in the AGLs (e.g., Darwall et al. 2011; Salzburger et al. 2014; Schultheiß et al. 2014), the uplift of the rift shoulders also promoted the evolution of mollusks endemic to high altitudes (Bößneck 2012). In conclusion, our study does not indicate that the western branch of the EARS impacted species richness in mollusks strongly, at least not as a potential dispersal barrier between regions more to the east and west. However, in mollusks and in some vertebrates, it may have caused a high turnover in species composition at both sides of the Albertine rift (Leprieur et al. 2011; Schultheiß et al. 2011a; Linder et al. 2012), and at least for fishes, differences in species richness were observed as well (Leprieur et al. 2011).

#### Past and present water–energy availability and its impact on species richness

As mentioned several times above, the EARS may have influenced present-day species richness patterns of freshwater mollusks in sub-Saharan Africa through its impact on African climate (Trauth et al. 2005, 2009; Donges et al. 2011; Prömmel et al. 2013). This impact includes changes in the distribution of precipitation and energy for primary productivity over the continent through time, and hence, the effects of the EARS on species richness may be largely

indirect. The rift–climate interaction has been outlined in several studies (e.g., Danley et al. 2012), and the major impact of climate on distribution patterns on a continental scale has been demonstrated for many taxa, both terrestrial (e.g., Levinsky et al. 2013) and freshwater (e.g., Van Bocxlaer et al. 2008; Damm et al. 2010; Dias et al. 2014). Moreover, a recent meta-analysis highlighted a greater influence of climate- and productivity-related parameters on species richness than that of factors related to other aspects of habitat heterogeneity (Field et al. 2009).

We found that pre-industrial, recent climate explains observed species richness in gastropods better than Eemian climate conditions (Table 1). This result indicates that contemporary water–energy availability structures species richness and that the imprint of past climate on current species distributions is limited, despite the effects it had on generating and obliterating species in the past (e.g., Van Damme and Pickford 2003; Van Bocxlaer et al. 2008; Levinsky et al. 2013). These studies and our results suggest that species richness patterns may be very dynamic.

#### Environmental heterogeneity as drivers of species richness

Upon investigating environmental heterogeneity with models accounting for topographic variation, no significant correlation between observed and simulated species richness patterns was obtained (Table 1). This result suggests that temperature and other factors related to heterogeneity in elevation do not play a major role in structuring species richness geographically.

Models using available surface water area overall performed best in explaining observed bivalve and gastropod richness patterns in sub-Saharan Africa. At least in the case of gastropods, the correlation of observed and simulated richness patterns was significantly better if lotic and lentic habitats were considered, than when only lotic waters were included ( $\Delta r_{\text{Pearson}} = 0.018$ ; Table S3; Fig. 5).

The area of surface waters has been suggested to be a critical determinant of distribution patterns of freshwater organisms including mollusks on regional and continental scales (Aho 1978; Dehling et al. 2010). Although species–area relationships are often observed, like in our study, debate continues as to the mechanisms responsible for it (e.g., Lomolino 2010; Triantis et al. 2012). In the case of freshwater mollusks, habitat availability and diversity likely drive this correlation, as has been proposed for other taxa as well (Scheiner 2003). Future analyses may examine this issue by including more complex classifications of freshwater environments (and how environments have changed over time), as more ecological data on mollusk habitat preferences become available. Lotic–lentic water availability and differences in the habitats they provide were shown to be determinants of species range sizes

in aquatic Coleoptera: Running-water (lotic) beetle species have much smaller distributions than those occurring in standing water (Ribera and Vogler 2000), but more work on mollusks is required to document whether types of inhabited water bodies are correlated with species range size. Our result that surface water area is the main predictor of species richness patterns in sub-Saharan Africa contrasts some of the results other workers obtained using similar methods (Rahbek et al. 2007). These authors and others (summarized in Field et al. 2009) investigated environmental heterogeneity as a driver of terrestrial species richness on a continental scale, but found that climate factors and productivity explain observed species richness better. Surprisingly, similar results were also obtained for some freshwater animals, including mollusks, in Europe (Field et al. 2009; Dehling et al. 2010).

We expected strong correlations between observed patterns and those simulated with climate models because sub-Saharan Africa in general and East Africa in particular have experienced pronounced moisture–drought cycles (Trauth et al. 2005, 2009, 2010; Donges et al. 2011). However, our results demonstrate that the availability of surface waters has a stronger effect than climate stress. Perhaps the differences between species richness patterns in Europe and Africa relate to an on average higher degree of instability of surface waters in Africa, and the greater limitations of energy at higher latitudes (Hawkins et al. 2003; Whittaker et al. 2007). Global richness patterns of freshwater fish are also more influenced by environmental heterogeneity than by climate and productivity (Oberdorff et al. 2011), but the impact of climate may differ greatly between zoogeographic regions (Dias et al. 2014).

Interestingly, environmental heterogeneity had been proposed as one of the main drivers of species richness where and when climatic conditions (water–energy hypothesis) are not limiting (Stein et al. 2014). Overall, our results indicate that factors like the availability of climatic water and energy do not currently structure mollusk species richness in most regions of sub-Saharan Africa, but drastic changes in climate parameters may have occurred in the past. Our study hence confirms that, in the absence of precipitation and insolation as limiting factors, the heterogeneity of freshwater environments in sub-Saharan Africa shapes species richness patterns in bivalves and gastropods in highly similar ways.

#### Conclusions and future directions

Comparisons of observed and simulated species richness indicate that environmental heterogeneity and geometric constraints together shape bivalve and gastropod richness in sub-Saharan Africa, which has not been demonstrated on a continental scale. Our understanding of contemporary

geographic patterns of species richness in Africa could be further enhanced by more in-depth studies. Whereas all of our models are influenced by geometric constraints, future models should incorporate the fact that many mollusks have limited dispersal capabilities in the absence of hydrographic connections, which may have contributed to the restricted occurrence of most species (left-skewed RSFD). Hence, species distribution patterns in the past and historic biogeography may have strongly influenced current species richness patterns, which could be investigated by implementing detailed information on species niches and phylogeny. Ideally, future studies that aim to model species richness could also embed changes in paleohydrographic connections (e.g., Dias et al. 2014).

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## References

- Aho J (1978) Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. *Ann Zool Fenn* 15:146–154
- Bauer FU, Glasmacher UA, Ring U, Schumann A, Nagudi B (2010) Thermal and exhumation history of the central Rwenzori Mountains, Western Rift of the East African Rift System, Uganda. *Int J Earth Sci* 99:1575–1597. doi:10.1007/s00531-010-0549-7
- Bauer FU, Karl M, Glasmacher UA, Nagudi B, Schumann A, Mroszewski L (2012) The Rwenzori Mountains of western Uganda: aspects on the evolution of their remarkable morphology within the Albertine Rift. *J Afr Earth Sci* 73–74:44–56. doi:10.1016/j.jafrearsci.2012.07.001
- Beadle L (1981) The inland waters of tropical Africa—An introduction to tropical limnology, 2nd edn. Longman, London
- Beck J, Ballesteros-Mejia L, Buchmann CM, Dengler J, Fritz SA, Gruber B, Hof C, Jansen F, Knapp S, Kreft H, Schneider A-K, Winter M, Dormann CF (2012) What's on the horizon for macroecology? *Ecography* 35:673–683. doi:10.1111/j.1600-0587.2012.07364.x
- Bogan AE (2008) Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. In: Balian EV, Lévêque C, Segers H, Martens K (eds) *freshw. Anim. Divers. Assess*, Springer, pp 139–147
- Bößneck U (2012) Leben am Limit: Besiedlung von Süßwasser-Habitaten extremer Hochlagen Asiens, Amerikas und Afrikas durch Mollusken (Mollusca: Bivalvia & Gastropoda). In: Hartmann M, Weipert J (eds) *Biodiversität Naturlandschaft Im Himalaya IV - Biodivers. Nat. Herit. Himalaya IV*. Verein der Freunde & Förderer des Naturkundemuseums Erfurt e.V., Erfurt, pp 103–106
- Brown DS (1994) *Freshwater snails of Africa and their medical importance*. Taylor & Francis, UK
- Cahill AE, Aiello-Lammens ME, Caitlin Fisher-Reid M, Hua X, Karanewsky CJ, Ryu HY, Sbeglia GC, Spagnolo F, Waldron JB, Wiens JJ (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. *J Biogeogr* 41:429–442. doi:10.1111/jbi.12231
- Cardinale BJ, Bennett DM, Nelson CE, Gross K (2009) Does productivity drive diversity or vice versa? A test of the multivariate productivity-diversity hypothesis in streams. *Ecology* 90:1227–1241. doi:10.1890/08-1038.1
- Chakraborty A, Nanjundiah RS, Srinivasan J (2009) Impact of African orography and the Indian summer monsoon on the low-level Somali jet. *Int J Climatol* 29:983–992. doi:10.1002/joc.1720
- Collen B, Whitton F, Dyer EE, Baillie JEM, Cumberlidge N, Darwall WRT, Pollock C, Richman NI, Soulsby A-M, Böhm M (2014) Global patterns of freshwater species diversity, threat and endemism. *Glob Ecol Biogeogr* 23:40–51. doi:10.1111/geb.12096
- Colwell RK, Hurtt GC (1994) Nonbiological gradients in species richness and a spurious Rapoport Effect. *Am Nat* 144:570–595
- Colwell RK, Lees DC (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends Ecol Evol* 15:70–76. doi:10.1016/S0169-5347(99)01767-X
- Colwell RK, Rahbek C, Gotelli NJ (2004) The mid-domain effect and species richness patterns: what have we learned so far? *Am Nat* 163:E1–E23. doi:10.1086/382056
- Colwell RK, Gotelli NJ, Rahbek C, Entsminger GL, Farrell C, Graves GR (2009) Peaks, plateaus, canyons, and craters: the complex geometry of simple mid-domain effect models. *Evol Ecol Res* 11:355–370
- Cotterill FPD, Wit MJD (2011) Geocodynamics and the Kalahari epeirogeny: linking its genomic record, tree of life and palimpsest into a unified narrative of landscape evolution. *South Afr J Geol* 114:489–514. doi:10.2113/gssajg.114.3-4.489
- Daget J (1998) *Catalogue raisonné des mollusques bivalves d'eau douce africains*. Blackhuys Publishers and ORSTOM, Leiden and Paris
- Damm S, Dijkstra K-DB, Hadrys H (2010) Red drifters and dark residents: the phylogeny and ecology of a Plio-Pleistocene dragonfly radiation reflects Africa's changing environment (Odonata, Libellulidae, *Trithemis*). *Mol Phylogenet Evol* 54:870–882. doi:10.1016/j.ympev.2009.12.006
- Danley PD, Husemann M, Ding B, DiPietro LM, Beverly EJ, Peppe DJ (2012) The impact of the geologic history and paleoclimate on the diversification of East African cichlids. *Int J Evol Biol* 2012:1–20. doi:10.1155/2012/574851
- Darwall WRT, Smith KG, Allen DJ, Holland RA, Harrison IJ, Brooks EGE (2011) The diversity of life in African freshwaters: under water, under threat. An analysis of the status and distribution of freshwater species throughout mainland Africa. IUCN, Gland, Switzerland; Cambridge
- Davis GM (1982) Historical and ecological factors in the evolution, adaptive radiation, and biogeography of freshwater mollusks. *Am Zool* 22:375–395. doi:10.1093/icb/22.2.375
- Day JJ, Peart CR, Brown KJ, Friel JP, Bills R, Moritz T (2013) Continental diversification of an African catfish radiation (Mochokidae: *Synodontis*). *Syst Biol* 62:351–365. doi:10.1093/sysbio/syt001
- Dee DP, Uppala SM, Simmons AJ, Berrisford P, Poli P, Kobayashi S, Andrae U, Balmaseda MA, Balsamo G, Bauer P, Bechtold P, Beljaars ACM, van de Berg L, Bidlot J, Bormann N, Delsol C, Dragani R, Fuentes M, Geer AJ, Haimberger L, Healy SB, Hersbach H, Hólm EV, Isaksen I, Kållberg P, Köhler M, Matricardi M, McNally AP, Monge-Sanz BM, Morcrette J-J, Park B-K, Peubey C, de Rosnay P, Tavolato C, Thépaut J-N, Vitart F (2011) The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Q J R Meteorol Soc* 137:553–597. doi:10.1002/qj.828
- Dehling DM, Hof C, Brändle M, Brandl R (2010) Habitat availability does not explain the species richness patterns of European

- lentic and lotic freshwater animals. *J Biogeogr* 37:1919–1926. doi:[10.1111/j.1365-2699.2010.02347.x](https://doi.org/10.1111/j.1365-2699.2010.02347.x)
- Dias MS, Oberdorff T, Huguény B, Leprieur F, Jézéquel C, Cornu J-F, Brosse S, Grenouillet G, Tedesco PA (2014) Global imprint of historical connectivity on freshwater fish biodiversity. *Ecol Lett* 17:1130–1140. doi:[10.1111/ele.12319](https://doi.org/10.1111/ele.12319)
- Dillon RT (2000) The ecology of freshwater molluscs. Cambridge University Press, Cambridge
- Donges JF, Donner RV, Trauth MH, Marwan N, Schellnhuber H-J, Kurths J (2011) Nonlinear detection of paleoclimate-variability transitions possibly related to human evolution. *Proc Natl Acad Sci* 108:20422–20427. doi:[10.1073/pnas.1117052108](https://doi.org/10.1073/pnas.1117052108)
- Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Turner JRG (2009) Spatial species-richness gradients across scales: a meta-analysis. *J Biogeogr* 36:132–147. doi:[10.1111/j.1365-2699.2008.01963.x](https://doi.org/10.1111/j.1365-2699.2008.01963.x)
- Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405:220–227. doi:[10.1038/35012228](https://doi.org/10.1038/35012228)
- Genner MJ, Knight ME, Haesler MP, Turner GF (2010) Establishment and expansion of Lake Malawi rock fish populations after a dramatic Late Pleistocene lake level rise. *Mol Ecol* 19:170–182. doi:[10.1111/j.1365-294X.2009.04434.x](https://doi.org/10.1111/j.1365-294X.2009.04434.x)
- Glaubrecht M (2008) Adaptive radiation of thalassoid gastropods in Lake Tanganyika, East Africa: morphology and systematization of a paludomid species flock in an ancient lake. *Zoosystematics Evol* 84:71–122. doi:[10.1002/zoos.200700016](https://doi.org/10.1002/zoos.200700016)
- Gotelli NJ, McGill BJ (2006) Null versus neutral models: what's the difference? *Ecography* 29:793–800. doi:[10.1111/j.2006.0906-7590.04714.x](https://doi.org/10.1111/j.2006.0906-7590.04714.x)
- Goudie AS (2005) The drainage of Africa since the Cretaceous. *Geomorphology* 67:437–456. doi:[10.1016/j.geomorph.2004.11.008](https://doi.org/10.1016/j.geomorph.2004.11.008)
- Graf DL, Cummings KS (2011) Freshwater mussel (Bivalvia: Unionoidea) richness and endemism in the ecoregions of Africa and Madagascar based on comprehensive museum sampling. *Hydrobiologia* 678:17–36. doi:[10.1007/s10750-011-0810-5](https://doi.org/10.1007/s10750-011-0810-5)
- Graf D, Jørgensen A, Van Damme D, Kristensen TK (2011) The status and distribution of freshwater molluscs (Mollusca). The Status and Distribution of Freshwater Biodiversity in Central Africa. Cambridge, UK and Gland, Switzerland IUCN, pp 48–61
- Hargreaves AL, Samis KE, Eckert CG (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am Nat* 183:157–173. doi:[10.1086/674525](https://doi.org/10.1086/674525)
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117. doi:[10.1890/03-8006](https://doi.org/10.1890/03-8006)
- Heino J (2011) A macroecological perspective of diversity patterns in the freshwater realm. *Freshw Biol* 56:1703–1722. doi:[10.1111/j.1365-2427.2011.02610.x](https://doi.org/10.1111/j.1365-2427.2011.02610.x)
- Hijmans RJ (2014) raster: geographic data analysis and modeling. R package version 2.2-31. <http://CRAN.R-project.org/package=raster>
- Hof C, Brändle M, Brandl R (2008) Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. *Glob Ecol Biogeogr* 17:539–546. doi:[10.1111/j.1466-8238.2008.00394.x](https://doi.org/10.1111/j.1466-8238.2008.00394.x)
- Holt BG, Lessard J-P, Borregaard MK, Fritz SA, Araújo MB, Dimitrov D, Fabre P-H, Graham CH, Graves GR, Jönsson KA, Nogués-Bravo D, Wang Z, Whittaker RJ, Fjeldså J, Rahbek C (2013) An update of Wallace's zoogeographic regions of the world. *Science* 339:74–78. doi:[10.1126/science.1228282](https://doi.org/10.1126/science.1228282)
- Horn C, Mosbrugger V, Mulch A, Antonelli A (2013) Biodiversity from mountain building. *Nat Geosci* 6:154. doi:[10.1038/ngeo1742](https://doi.org/10.1038/ngeo1742)
- Hortal J, Triantis KA, Meiri S, Thébaud E, Sfenthourakis S (2009) Island species richness increases with habitat diversity. *Am Nat* 174:E205–E217. doi:[10.1086/645085](https://doi.org/10.1086/645085)
- Hurlbert AH, Stegen JC (2014) When should species richness be energy limited, and how would we know? *Ecol Lett* 17:401–413. doi:[10.1111/ele.12240](https://doi.org/10.1111/ele.12240)
- Hutter CR, Guayasamin JM, Wiens JJ (2013) Explaining Andean megadiversity: the evolutionary and ecological causes of glass-frog elevational richness patterns. *Ecol Lett* 16:1135–1144. doi:[10.1111/ele.12148](https://doi.org/10.1111/ele.12148)
- Jetz W, Rahbek C (2001) Geometric constraints explain much of the species richness pattern in African birds. *Proc Natl Acad Sci* 98:5661–5666. doi:[10.1073/pnas.091100998](https://doi.org/10.1073/pnas.091100998)
- Kaspar F, Prömmel K, Cubasch U (2010) Impacts of tectonic and orbital forcing on East African climate: a comparison based on global climate model simulations. *Int J Earth Sci* 99:1677–1686. doi:[10.1007/s00531-010-0538-x](https://doi.org/10.1007/s00531-010-0538-x)
- Keil P, Simova I, Hawkins BA (2008) Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata). *Insect Conserv Divers* 1:142–150. doi:[10.1111/j.1752-4598.2008.00019.x](https://doi.org/10.1111/j.1752-4598.2008.00019.x)
- Kreft H, Jetz W (2010) A framework for delineating biogeographical regions based on species distributions. *J Biogeogr* 37:2029–2053. doi:[10.1111/j.1365-2699.2010.02375.x](https://doi.org/10.1111/j.1365-2699.2010.02375.x)
- Kruschke JK (2011) Doing Bayesian data analysis: a tutorial with R and BUGS. Academic Press, Burlington
- Kruschke JK (2013) Bayesian estimation supersedes the t test. *J Exp Psychol Gen* 142:573–603. doi:[10.1037/a0029146](https://doi.org/10.1037/a0029146)
- Leprieur F, Tedesco PA, Huguény B, Beauchard O, Dürr HH, Brosse S, Oberdorff T (2011) Partitioning global patterns of freshwater fish beta diversity reveals contrasting signatures of past climate changes. *Ecol Lett* 14:325–334. doi:[10.1111/j.1461-0248.2011.01589.x](https://doi.org/10.1111/j.1461-0248.2011.01589.x)
- Levinsky I, Araújo MB, Nogués-Bravo D, Haywood AM, Valdes PJ, Rahbek C (2013) Climate envelope models suggest spatio-temporal co-occurrence of refugia of African birds and mammals. *Glob Ecol Biogeogr* 22:351–363. doi:[10.1111/geb.12045](https://doi.org/10.1111/geb.12045)
- Li J, He Q, Hua X, Zhou J, Xu H, Chen J, Fu C (2009) Climate and history explain the species richness peak at mid-elevation for *Schizothorax* fishes (Cypriniformes: Cyprinidae) distributed in the Tibetan Plateau and its adjacent regions. *Glob Ecol Biogeogr* 18:264–272. doi:[10.1111/j.1466-8238.2008.00430.x](https://doi.org/10.1111/j.1466-8238.2008.00430.x)
- Linder HP, de Klerk HM, Born J, Burgess ND, Fjeldså J, Rahbek C (2012) The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *J Biogeogr* 39:1189–1205. doi:[10.1111/j.1365-2699.2012.02728.x](https://doi.org/10.1111/j.1365-2699.2012.02728.x)
- Lomolino MV (2010) Biogeography, 4th edn. Sinauer Associates, Inc., Sunderland
- Mandahl-Barth G (1988) Studies on African freshwater bivalves. Danish Bilharziasis Laboratory
- Markovic D, Carrizo S, Freyhof J, Cid N, Lengyel S, Scholz M, Kasperdus H, Darwall W (2014) Europe's freshwater biodiversity under climate change: distribution shifts and conservation needs. *Divers Distrib* 20:1097–1107. doi:[10.1111/ddi.12232](https://doi.org/10.1111/ddi.12232)
- Maslin MA, Christensen B (2007) Tectonics, orbital forcing, global climate change, and human evolution in Africa: introduction to the African paleoclimate special volume. *J Hum Evol* 53:443–464. doi:[10.1016/j.jhev.2007.06.005](https://doi.org/10.1016/j.jhev.2007.06.005)
- Masutomi Y, Inui Y, Takahashi K, Matsuoka Y (2009) Development of highly accurate global polygonal drainage basin data. *Hydrol Process* 23:572–584. doi:[10.1002/hyp.7186](https://doi.org/10.1002/hyp.7186)
- McCain CM (2004) The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *J Biogeogr* 31:19–31. doi:[10.1046/j.0305-0270.2003.00992.x](https://doi.org/10.1046/j.0305-0270.2003.00992.x)
- Murphy HT, VanDerWal J, Lovett-Doust J (2011) One, two and three-dimensional geometric constraints and climatic correlates of

- North American tree species richness. *Ecography* 34:267–275. doi:10.1111/j.1600-0587.2010.06395.x
- Oberdorff T, Tedesco PA, Hugueny B, Leprieur F, Beauchard O, Brosse S, Dürr HH (2011) Global and regional patterns in riverine fish species richness: a review. *Int J Ecol* 2011:e967631. doi:10.1155/2011/967631
- von Oheimb PV, Albrecht C, Riedel F, Bössneck U, Zhang H, Wilke T (2013) Testing the role of the Himalaya Mountains as a dispersal barrier in freshwater gastropods (*Gyraulus* spp.). *Biol J Linn Soc* 109:526–534. doi:10.1111/bij.12068
- Osorio F, Vallejos R, Cuevas F (2012) SpatialPack: Package for analysis of spatial data. R package version 0.2. <http://CRAN.R-project.org/package=SpatialPack>
- Pinel-Alloul B, André A, Legendre P, Cardille JA, Patalas K, Salki A (2013) Large-scale geographic patterns of diversity and community structure of pelagic crustacean zooplankton in Canadian lakes. *Glob Ecol Biogeogr* 22:784–795. doi:10.1111/geb.12041
- Plummer M (2013) rjags: bayesian graphical models using MCMC. R package version 3-11. <http://CRAN.R-project.org/package=rjags>
- Plumptre AJ, Davenport TRB, Behangana M, Kityo R, Eilu G, Ssegawa P, Ewango C, Meirte D, Kahindo C, Herremans M, Peterhans JK, Pilgrim JD, Wilson M, Languy M, Moyer D (2007) The biodiversity of the Albertine Rift. *Biol Conserv* 134:178–194. doi:10.1016/j.biocon.2006.08.021
- Ponder WF, Colgan DJ (2002) What makes a narrow-range taxon? Insights from Australian freshwater snails. *Invertebr Syst* 16:571–582
- Prömmel K, Cubasch U, Kaspar F (2013) A regional climate model study of the impact of tectonic and orbital forcing on African precipitation and vegetation. *Palaeogeogr Palaeoclimatol Palaeoecol* 369:154–162. doi:10.1016/j.palaeo.2012.10.015
- R Core Team (2014) R: a language and environment for statistical computing, version 3.0.1. R Foundation for Statistical Computing, Austria, Vienna
- Rahbek C, Gotelli NJ, Colwell RK, Entsminger GL, Rangel TFLVB, Graves GR (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proc R Soc B Biol Sci* 274:165–174. doi:10.1098/rspb.2006.3700
- Ribera I, Vogler AP (2000) Habitat type as a determinant of species range sizes: the example of lotic–lentic differences in aquatic Coleoptera. *Biol J Linn Soc* 71:33–52. doi:10.1111/j.1095-8312.2000.tb01240.x
- Roberts EM, Stevens NJ, O'Connor PM, Dirks PHGM, Gottfried MD, Clyde WC, Armstrong RA, Kemp AIS, Hemming S (2012) Initiation of the western branch of the East African Rift coeval with the eastern branch. *Nat Geosci* 5:289–294. doi:10.1038/ngeo1432
- Rockel B, Will A, Hense A (2008) The regional climate model COSMO-CLM (CCLM). *Meteorol Z* 17:347–348. doi:10.1127/0941-2948/2008/0309
- Rudolf B, Schneider U (2005) Calculation of gridded precipitation data for the global land-surface using in situ gauge observations. *Proc Second Int Precip Work Group IPWG Monterey Oct 2004 EUMETSAT ISBN92-9110-070-6 231–247 (ISSN1727-432X)*
- Salzburger W, Bocxlaer BV, Cohen AS (2014) The ecology and evolution of the African Great Lakes and their faunas. *Annu Rev Ecol Evol Syst* 45:519–545. doi:10.1146/annurev-ecolsys-120213-091804
- Scheiner SM (2003) Six types of species-area curves. *Glob Ecol Biogeogr* 12:441–447. doi:10.1046/j.1466-822X.2003.00061.x
- Schneider U, Becker A, Meyer-Christopher A, Ziese M, Rudolf B (2011) Global precipitation analysis products of the GPCC. Global Precipitation Climatology Centre (GPCC), Deutscher Wetterdienst, Offenbach a. M., Germany, Dec. 2011:1–13
- Schultheiß R, Bocxlaer BV, Wilke T, Albrecht C (2009) Old fossils–young species: evolutionary history of an endemic gastropod assemblage in Lake Malawi. *Proc R Soc B Biol Sci* 276:2837–2846. doi:10.1098/rspb.2009.0467
- Schultheiß R, Ndeo OW, Malikwisha M, Marek C, Bößneck U, Albrecht C (2011a) Freshwater molluscs of the Eastern Congo: notes on taxonomy, biogeography and conservation. *Afr Invertebr* 52:265–284. doi:10.5733/afn.052.0204
- Schultheiß R, Wilke T, Jørgensen A, Albrecht C (2011b) The birth of an endemic species flock: demographic history of the *Bellamyia* group (Gastropoda, Viviparidae) in Lake Malawi. *Biol J Linn Soc* 102:130–143. doi:10.1111/j.1095-8312.2010.01574.x
- Schultheiß R, Van Bocxlaer B, Riedel F, von Rintelen T, Albrecht C (2014) Disjunct distributions of freshwater snails testify to a central role of the Congo system in shaping biogeographical patterns in Africa. *BMC Evol Biol* 14:42. doi:10.1186/1471-2148-14-42
- Schwarzer J, Swartz ER, Vreven E, Snoeks J, Cotterill FPD, Misof B, Schliwen UK (2012) Repeated trans-watershed hybridization among haplochromine cichlids (Cichlidae) was triggered by Neogene landscape evolution. *Proc R Soc B Biol Sci* 279:4389–4398. doi:10.1098/rspb.2012.1667
- Seddon M, Appleton C, Van Damme D, Graf D (2011) Freshwater molluscs of Africa: diversity, distribution, and conservation. *Divers Life Afr Freshw Water Threat Anal Status Distrib Freshw Species Mainl Afr IUCN Camb UK Gland Switz* 92–125
- Šizling AL, Storch D, Keil P (2009) Rapoport's rule, species tolerances, and the latitudinal diversity gradient: geometric considerations. *Ecology* 90:3575–3586. doi:10.1890/08-1129.1
- Sommerfeld A, Prömmel K, Cubasch U (2014) The East African Rift System and the impact of orographic changes on regional climate and the resulting aridification. *Int J Earth Sci (Geol Rundsch)* 1–16. doi:10.1007/s00531-014-1102-x
- Stankiewicz J, de Wit MJ (2006) A proposed drainage evolution model for Central Africa—did the Congo flow east? *J Afr Earth Sci* 44:75–84. doi:10.1016/j.jafrearsci.2005.11.008
- Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecol Lett* 17:866–880. doi:10.1111/ele.12277
- Strong EE, Gargominy O, Ponder WF, Bouchet P (2008) Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. In: Balian EV, Lévêque C, Segers H, Martens K (eds) *Freshw. Anim Divers Assess* Springer Netherlands, Dordrecht, pp 149–166
- Tedesco PA, Leprieur F, Hugueny B, Brosse S, Dürr HH, Beauchard O, Busson F, Oberdorff T (2012) Patterns and processes of global riverine fish endemism. *Glob Ecol Biogeogr* 21:977–987. doi:10.1111/j.1466-8238.2011.00749.x
- Trauth MH, Maslin MA, Deino A, Strecker MR (2005) Late Cenozoic moisture history of East Africa. *Science* 309:2051–2053. doi:10.1126/science.1112964
- Trauth MH, Larrasoña JC, Mudelsee M (2009) Trends, rhythms and events in Plio-Pleistocene African climate. *Quat Sci Rev* 28:399–411. doi:10.1016/j.quascirev.2008.11.003
- Trauth MH, Maslin MA, Deino AL, Junginger A, Lesoloyia M, Odada EO, Olago DO, Olaka LA, Strecker MR, Tiedemann R (2010) Human evolution in a variable environment: the amplifier lakes of Eastern Africa. *Quat Sci Rev* 29:2981–2988. doi:10.1016/j.quascirev.2010.07.007
- Triantis KA, Guilhaumon F, Whittaker RJ (2012) The island species–area relationship: biology and statistics. *J Biogeogr* 39:215–231. doi:10.1111/j.1365-2699.2011.02652.x
- Van Bocxlaer B, Damme DV, Feibel CS (2008) Gradual versus punctuated equilibrium evolution in the Turkana Basin molluscs: evolutionary events or biological invasions? *Evolution* 62:511–520. doi:10.1111/j.1558-5646.2007.00296.x

- Van Damme D, Pickford M (2003) The late Cenozoic Thiaridae (Mollusca, Gastropoda, Cerithioidea) of the Albertine Rift Valley (Uganda-Congo) and their bearing on the origin and evolution of the Tanganyikan thalassoid malacofauna. *Hydrobiologia* 498:1–83. doi:[10.1023/A:1026298512117](https://doi.org/10.1023/A:1026298512117)
- VanDerWal J, Murphy HT, Lovett-Doust J (2008) Three-dimensional mid-domain predictions: geometric constraints in North American amphibian, bird, mammal and tree species richness patterns. *Ecography* 31:435–449. doi:[10.1111/j.0906-7590.2008.05396.x](https://doi.org/10.1111/j.0906-7590.2008.05396.x)
- Wagner CE, Harmon LJ, Seehausen O (2012) Ecological opportunity and sexual selection together predict adaptive radiation. *Nature*. doi:[10.1038/nature11144](https://doi.org/10.1038/nature11144)
- Wagner CE, Harmon LJ, Seehausen O (2014) Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecol Lett* 17:583–592. doi:[10.1111/ele.12260](https://doi.org/10.1111/ele.12260)
- West KA, Michel E, Todd JA, Brown DS, Clabaugh J (2003) The gastropods of Lake Tanganyika: diagnostic key and taxonomic classification with notes on the fauna. *Int Association Theor Appl Limnol SIL Occas Publ* 2:1–132
- White JW, Rassweiler A, Samhuri JF, Stier AC, White C (2014) Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* 123:385–388. doi:[10.1111/j.1600-0706.2013.01073.x](https://doi.org/10.1111/j.1600-0706.2013.01073.x)
- Whittaker RJ, Nogués-Bravo D, Araújo MB et al (2007) Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins et al. (2003) using European data for five taxa. *Glob Ecol Biogeogr* 16:76–89. doi:[10.1111/j.1466-8238.2006.00268.x](https://doi.org/10.1111/j.1466-8238.2006.00268.x)
- Zagmajster M, Eme D, Fišer C, Galassi D, Marmonier P, Stoch F, Cornu J-F, Malard F (2014) Geographic variation in range size and beta diversity of groundwater crustaceans: insights from habitats with low thermal seasonality. *Glob Ecol Biogeogr* 23:1135–1145. doi:[10.1111/geb.12200](https://doi.org/10.1111/geb.12200)