# Continental-scale variability in browser diversity is a major driver of diversity patterns in acacias across Africa

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## Summary

**1.** It has been proposed that, across broad spatial scales, climatic factors are the main drivers of ecological patterns, while biotic factors are mainly important at local spatial scales. However, few tests of the effect of biotic interactions on broad-scale patterns have been conducted; conclusions about the scale-dependence of the importance of biotic interactions thus seem premature.

**2.** We developed an extensive database of locality records of one of Africa's most conspicuous groups, the acacias (the genera *Senegalia* and *Vachellia*), and used species distribution models (SDMs) to estimate the distribution of all African acacias.

**3.** African acacias are particularly well adapted against mammalian herbivory; therefore, we hypothesized that browser diversity could be an important driver of acacia richness. Species richness maps for the two genera were created from SDM-generated maps. Ordinary least square (OLS) regressions and, to consider spatial autocorrelation, simultaneous autoregressive (SAR) analyses were used to model richness of the two genera in relation to mammalian browser richness, current environment (including climate), and climate history since the Last Glacial Maximum (LGM). We used variation partitioning to determine what percentage of variation could be explained by these three groups of factors.

**4.** Both genera showed centres of richness in East Africa and the Limpopo Basin of southern Africa. Browser richness was the best explanatory variable for richness of both genera. Environmental factors explained negligible variation in the richness of *Senegalia*, but some variation in *Vachellia*. For both genera, the residuals of the species richness model of one genus also explained

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much variation in the richness of the other genus, indicating that common factors not considered in the richness analyses here may additionally be driving the richness of both genera.

**5.** Mechanisms that could generate a correlation between browser and acacia richness are proposed, and differences in the determinants of richness patterns of *Senegalia* and *Vachellia* discussed in the light of the two genera's history of colonization of Africa.

**6.** *Synthesis.* This is the first study that demonstrates that consumer diversity can influence richness patterns at continental scales and demonstrates that biotic factors can drive richness even at broad spatial scales.

**Key-words:** diversity patterns, herbivory, plant–herbivore interactions, Quaternary climate change, resource–consumer relationships, savanna species, speciation

## Introduction

Broad-scale species richness patterns and their drivers have long fascinated scientists (Hawkins *et al.* 2003; Willig, Kaufman & Stevens 2003; Hawkins, Rodríguez & Weller 2011). A meta-analysis of the drivers that underlie such richness patterns has shown that water, energy or water-energy variables are often the best explanatory factors of species richness in both plant and animal taxa (Hawkins *et al.* 2003). Other evolutionary and environmental factors such as historical biogeography, palaeoclimate, environmental heterogeneity and edaphics have sometimes also been shown to be of importance, although usually less so, for richness patterns (see Field *et al.* 2009). How biotic interactions affect richness patterns is less well explored.

It has been suggested that, while climate is a major determinant of ecological patterns at broad scales, biotic interactions are of little importance at these scales (McGill 2010). However, others have argued that biotic interactions can play a more important role in macroecological processes than is widely thought, for example, as determinants of species distributions (Araújo & Luoto 2007). In species richness analyses, it has been shown that resource richness can successfully explain consumer richness patterns at broad spatial extent, including across continents (e.g. Kissling, Rahbek & Böhning-Gaese 2007; Qian *et al.* 2009; though see Jetz *et al.* 2009). However, whether consumers affect richness patterns of resource species has not previously been tested at continental scale, despite the well-known strong effects of consumers on local community structure and dynamics (Cumming 1982; du Toit & Cumming 1999).

We examine which factors determine species richness patterns of acacias, a group of mimosoid trees and shrubs (and more rarely lianas) that dominates much of the vegetation of the arid savannas of Africa (Huntley 1982), and can be locally common in other habitats from semi-desert conditions to montane forests. In Africa, acacias are represented by two genera, *Senegalia* Raf. and *Vachellia* Wight & Arn. While the first mimosoids were forest species, the ancestor of *Vachellia* originated in more arid open habitats in the early Miocene and experienced one colonization event into Africa, where it mainly diversified in open habitats (Bouchenak-Khelladi *et al.* 2010). In contrast, *Senegalia* originated in the closed forests of South America, and its presence in Africa can be attributed to at least

two cross-continental dispersal events in the late Miocene (Bouchenak-Khelladi *et al.* 2010). One of the resulting clades became adapted to and diversified in open habitats, while the other, smaller, clade remained in closed habitats. Therefore, although both genera possess some forest species, the majority of species are found in the more open habitats of African savannas (Bouchenak-Khelladi *et al.* 2010).

It is well-established that herbivores have a substantial effect on vegetation structure and plant species composition (Hester *et al.* 2002), particularly in African savannas, where large mammalian herbivores (particularly ungulates) persist, or have until very recently persisted, across vast areas. Here they are thought to act as ecosystem engineers and to have influenced the evolution and distribution of the savanna vegetation (Cumming 1982; Scholes & Walker 1993; du Toit & Cumming 1999). Various studies have also shown that plant species richness is affected by herbivore diversity (see Hester *et al.* 2002), although such tests have usually been conducted at local scales. Given the ubiquity of acacias in drier savannas across the African continent, they constitute an appropriate group to test whether biotic interactions, in the form of herbivory by browsers, affect plant diversity patterns. Acacia browse is favoured by many large herbivores (Timberlake, Fagg & Barnes 1999), and the variety of defence and tolerance traits that acacias have developed to deal with the impact of browsing (Ross 1979; Scholes & Walker 1993) indicates that the group has been evolving under strong selection by mammalian herbivores. Amongst these traits are thorns (spinescent stipules in *Vachellia* and prickles in *Senegalia*), which slow the browsing rate (Cooper & Owen-Smith 1986); chemical defences, which reduce leaf palatability (Cooper & Owen-Smith 1985); ant–acacia symbioses, where ants obtain housing and nectar from trees, and trees obtain herbivore protection in return (Palmer *et al.* 2008); and phenotypic plasticity of traits such as increasing thorn size (Milewski & Madden 2006) and spacing (Fornara & du Toit 2007), and increasing branch growth rates and denser branching patterns (Fornara & du Toit 2007), which also reduce browsing rates. Therefore, we predict that browser richness may affect acacia richness.

In addition to large herbivores, richness patterns of acacias are likely to be influenced by factors that are recognized as richness drivers for broader groups of organisms such as trees in general, namely current climate and habitat heterogeneity

(e.g. O'Brien, Field & Whittaker 2000). While we expect that habitat heterogeneity should have a positive effect on acacia richness, acacias' tendency to predominate in drier environments (Bouchenak-Khelladi *et al.* 2010) suggests that their richness may peak not at high, but rather at intermediate productivity (medium precipitation, high precipitation seasonality). A further general driver of diversity is climatic stability through geological time, which should reduce extinction rates, while increasing speciation rates, thereby promoting higher species richness (McGlone 1996). In Africa, this has frequently been discussed, often from a phylogenetic viewpoint, and usually in the context of African rain forests, where it has been proposed that areas that remained relatively stable during past climatic changes retained higher diversity (e.g. Lovett *et al.* 2005). The effects of long-term climate stability on richness patterns have been less considered for savanna systems (but see Schidelko, Stiels & Rödder 2011). We use a recently developed variable, climate-change velocity, which measures how fast organisms have had to migrate to successfully track historical climate shifts (Sandel *et al.* 2011). Low climate-change velocity was expected to promote higher richness in acacias, as it would represent conditions conducive for long-term local survival as well as diversification.

We developed a large database of acacia (*Senegalia* and *Vachellia*) locality records that we used to obtain distribution maps for all African acacia species using SDMs. These maps were overlaid to obtain species richness maps, and the factors influencing species richness of the two genera were subsequently assessed; we specifically gauged the relative importance of two sets of general richness determinants, namely current environment (current climate and habitat heterogeneity) and climatic stability through geological time, relative to large-browser diversity as specific potential biotic drivers of acacia richness.

## Materials and methods

The genus *Acacia* Miller was recently shown to be paraphyletic (Maslin, Miller & Seigler 2003). For the purpose of this study, we will use the umbrella-term acacia to refer to both newly defined genera that occur in Africa and use the naming convention used by Maslin, Miller & Seigler (2003) to discuss the genera individually: *Senegalia* (previously *Acacia* subg. *Aculeiferum*) and *Vachellia* (previously *Acacia* subg. *Acacia*).

### SPECIES DISTRIBUTION MODELLING

An extensive database of African acacias was collated (M. Greve, A.M. Lykke, C.W. Fagg, R.E. Gereau, G.P. Lewis, R. Marchant, A.R. Marshall, J. Ndayishimiye, J. Bogaert and J.-C. Svenning, unpublished data) using the free BRAHMS databasing system for botanical data (www.brahmsonline.com/). Database records mainly originated from herbarium data, though some, particularly North African, records are field observations. Data were obtained from various herbarium and personal databases (see Acknowledgements) and georeferenced (Appendix S1A, Table S1 in Supporting Information). Over the years, several acacia species have been renamed, split or lumped; therefore, we used the naming convention of the African Plant Database website (Klopper *et al.* 2007). Specimens were

excluded if uncertainties in plant identity existed because of nomenclatural issues.

We modelled the distribution of acacia species with presences in ten or more grid cells. Forty-three of 49 *Senegalia* and 49 of 74 *Vachellia* species had sufficient data to be modelled (Table S1). Modelling was conducted at quarter-degree grid resolution (Appendix S1B) using environmental and spatial variables in Maxent v. 3.3.3e (Phillips, Anderson & Schapire 2006), one of the best-performing SDMs for modelling species using presence-only data (Elith & Leathwick 2007). Nine environmental variables were used to calibrate SDMs. Climatic variables (from Hijmans *et al.* 2005) that are thought to influence the distribution of plants, and particularly those in savannas (Huntley 1982; Scholes 1997), were selected: annual mean temperature, maximum temperature of the warmest month, mean temperature of the driest quarter, precipitation of the coldest quarter, annual precipitation, precipitation seasonality and precipitation of the driest quarter. In addition, because it has been shown at regional scales that the distributions of acacias are influenced by soil fertility (Scholes & Walker 1993), soil pH (FAO *et al.* 2009) was included as a further predictor variable. Finally, trees in savanna systems may be limited by fire (Staver *et al.* 2009); therefore, a fire intensity index (see Greve *et al.* 2011), calculated as the number of fire events between 2000 and 2007 (Tansey *et al.* 2008), was also included as a predictor. All variables were correlated with each other by $r^2 < 0.7$.

Species distributions are not only limited by environmental factors; they may be constrained by factors such as the history of the landscape, biotic interactions or organisms' dispersal abilities (Gaston 2009). For SDMs, spatial filters have been shown to be particularly effective at representing non-environmental constraints across large geographic distances (Blach-Overgaard *et al.* 2010). Therefore, we also included ten spatial filters in the SDMs (Appendix S1C). The filters were created using SAM v. 4.0 (Rangel, Diniz-Filho & Bini 2010).

Maxent models were run with presence localities and 10 000 background localities from across the African continent. Default Maxent settings were used. The equal training sensitivity and specificity threshold was used to create presence–absence maps for each of the species. This threshold has been shown to perform well (Liu *et al.* 2005). Although it may result in over-predictions for smaller-ranged species (Freeman & Moisen 2008), we used presence–absence maps produced with this threshold to produce species richness maps (see below) throughout to remain objective. To evaluate predictive performance of the Maxent models, each species was re-modelled using the same settings, but with fivefold cross-validations (Elith *et al.* 2011). For the cross-validations, only 5000 background points were used.

### SPECIES RICHNESS ANALYSES

Species richness analyses were conducted at $55 \times 55$ km (approx. 30 min) resolution using Lambert Azimuthal equal-area grids to remove possible effects of area on richness (Whittaker, Willis & Field 2001). Environmental layers were resampled to 55-km resolution using bilinear resampling. Resampling species presence–absence maps (of acacias and browsers) to a coarser resolution could result in distortions in species occurrences (e.g. individual presence cells could be classified as absences because reclassification is carried out on the basis of the majority classification in the new cell). Therefore, each 55-km cell was classified as a presence if at least one finer resolution cell within it contained the species. For the species that could not be modelled, distribution maps were created simply by marking the grid

cells in which they were recorded as presences. These presence–absence maps were overlain to produce species richness maps for *Senegalia* and *Vachellia*. Species richness analyses were conducted separately for the two genera.

Variation partitioning (Legendre & Legendre 1998) was used to evaluate how the species richness patterns of *Senegalia* and *Vachellia* are affected by (i) browser richness (BROWSERS), (ii) current environment (ENVIRONMENT), and (iii) climate-change velocity (STABILITY). The species richness of large mammals ($\geq 10$ kg) which have browse as a significant component ($>30\%$) of their diet was calculated for Africa (Fig. 2a) based on IUCN distribution maps (IUCN 2009). (See Appendix S1D for more details and a list of browsers.) Distribution maps of the individual species were resampled to 55 km resolution, as described for acacia richness above.

Climatic factors and habitat heterogeneity were used to represent ENVIRONMENT. Climatic factors, and water and water–energy factors particularly, have consistently been shown to be important predictors of species richness patterns (Hawkins *et al.* 2003). We therefore initially considered potential evapotranspiration (PET; Ahn & Tateishi 1994), minimum temperature of the coldest month, annual precipitation and precipitation seasonality (Hijmans *et al.* 2005) as potential predictors. The interaction between PET and annual precipitation was also included in analyses to represent the interaction between water and energy factors (Appendix S1E). Finally, habitat heterogeneity has been shown to influence the diversity of organisms by creating several environmental niches allowing greater numbers of species to coexist in geographic space (e.g. Thuiller *et al.* 2006). Therefore, the standard deviation of elevation (The CGIAR Consortium for Spatial Information 2008) within the 55-km grid cells was calculated in ArcGIS to represent habitat variation across the elevation gradient. The elevation data set had a resolution of 1 km.

Climate-change velocity describes the displacement rate of a climate condition over the Earth's surface (Loarie *et al.* 2009). It is influenced by the rate of change through time and the magnitude of local spatial climate gradients. We calculated velocity (STABILITY) measures for mean annual temperature and mean annual precipitation since the LGM. Palaeoclimate data were obtained from the Paleoclimate Modeling Intercomparison Project Phase II (PMIP-2, Braconnot *et al.* 2007) (Appendix S1F). The 2.5′ resolution Worldclim data (Hijmans *et al.* 2005) provided estimates of modern mean annual temperature and precipitation. We calculated the spatial climate gradient by taking the slope of these modern climate surfaces. The final products of these calculations were two climate velocity maps (temperature velocity and precipitation velocity).

Soil characteristics have also been proposed to be drivers of species richness (Cowling, Procheş & Partridge 2009), and acacias are generally thought to favour nutrient-rich soils (Timberlake, Fagg & Barnes 1999). Therefore, the effect of soil pH (FAO *et al.* 2009) on species richness was also assessed. However, for both genera, this variable was poorly correlated with species richness ($r^2 < 0.03$), and it was therefore not considered in the final analyses.

In analyses conducted across spatial surfaces, spatial autocorrelation may violate the assumption of independence of data points and result in Type I errors (Dormann *et al.* 2007). Because the richness maps are spatially interpolated, resulting in strong spatial autocorrelation, we subsampled species localities from the species richness grid using a checkerboard-like pattern (Fig. S1). This still left us with a large sample size for both genera ($n = 1426$ for *Senegalia* and $n = 1322$ for *Vachellia*). The reason for the subsampling was (i) to ensure that the non-spatial results were less "distorted" by spatial autocorrelation and (ii) to prevent having to use excessively high α

values in the inverse-distance weighted matrix in the models that took spatial autocorrelation into account (see below).

The contribution of each of the above groups of factors (BROWSERS, ENVIRONMENT and STABILITY) to the species richness patterns of African acacias was assessed using multiple linear regressions (OLS). Separate models were constructed for *Senegalia* and *Vachellia* to assess the effects of each of the three groups of factors on species richness. Initially, three models of species richness against each of the groups of factors (BROWSERS, ENVIRONMENT, STABILITY) were created. For example, species richness was modelled against the five ENVIRONMENT variables. Quadratic relationships were considered and some predictors required transformation (Appendix S1G). Tolerance values for all predictors were $>0.1$, indicating limited collinearity between variables (Quinn & Keough 2002). A backward selection procedure which relied on model performance statistics and the distribution of residuals (Appendix S1G) was employed (Zuur *et al.* 2009).

The above models were also used to conduct variation partitioning (Legendre & Legendre 1998). In variation partitioning, the unique variation explained by a group of factors and the variation that can be attributed to the combined effect of two or more groups of factors can be separated (Legendre & Legendre 1998). Here, variation partitioning was thus used to establish how much variation could be explained by each of the following groups of factors: the unique contributions of pure BROWSERS, pure ENVIRONMENT and pure STABILITY; and the shared contributions of BROWSERS-ENVIRONMENT, BROWSERS-STABILITY, ENVIRONMENT-STABILITY, and BROWSERS-ENVIRONMENT-STABILITY (see Lobo, Castro & Moreno 2001 for more details). Partial $R^2$-values representing the above contributions were obtained by subtracting the $R^2$-values of models containing one or two of the groups of factors from the $R^2$-value of the model containing all three groups of factors, following Heikkinen *et al.* (2005).

Models of the effects of each of the three groups of factors, and of all factors, on the species richness patterns of the two genera were re-run with SAR$_{error}$ models (Kissling & Carl 2008) in the software SAM v. 4.0 (Rangel, Diniz-Filho & Bini 2010) to incorporate spatial autocorrelation (Appendix S1H). A backward selection was again used to select variables for the final model, and variation partitioning employed to test how much variation is explained by BROWSERS, ENVIRONMENT and STABILITY factors after the effects of space were removed (Appendix S1H).

Finally, we tested how much of the variation in richness of the two genera could be attributable to factors that drive species richness of both genera, but were not incorporated in the above models. The residuals of the OLS of species richness against the final set of variables selected in the SAR models were extracted for each genus. These residuals were then included as an additional predictor in the whole model SAR analysis of the other genus to represent such 'unknown' factors (cf. Tuomisto, Ruokolainen & Yli-Halla 2003). The residuals were taken from OLS rather than the SAR model, because in the SAR model the spatial structure is incorporated into the residuals to remove spatial autocorrelation (Tognelli & Kelt 2004). Since these analyses required using only data points where both genera had occurrences, the sample size for these analyses was somewhat less than that of the other models ($n = 1095$ for both genera). Variation partitioning was again conducted on these data to assess what contribution BROWSERS, ENVIRONMENT and STABILITY factors vs. the residuals of the other genus made in explaining the diversity of the genera (Tuomisto, Ruokolainen & Yli-Halla 2003). Again, the $R^2$-values for the effect of non-spatial factors after the effect of space had been removed from the SAR models were used for variation

partitioning. For this purpose, we constructed a model of richness against the variables of the whole model (as defined in Table 1), against *Vachellia* residuals alone (for *Senegalia*) or *Senegalia* residuals alone (for *Vachellia*), and against the combined whole model variables and residuals. Note that the results for the 'whole model' here differed somewhat from those in Table 1 because a smaller data set, which contains only localities where both *Senegalia* and *Vachellia* are present (see above), was used for variation partitioning.

Variables were centred and scaled by one standard deviation for OLS and SAR analyses, so that the magnitude of the coefficients could be compared (Schielzeth 2010). Although we report both AIC and *P*-values for richness models, we focus on the results of model selection using AIC rather than *P*-values when considering which variables have an effect on species richness (Burnham & Anderson 1998).

All GIS analyses were conducted in ArcGIS v. 10 (except the analyses with Hawth's Tools [Appendix S1B], which were run in ArcGIS v. 9.2). The SAR models were run in SAM v. 4.0 (Rangel, Diniz-Filho & Bini 2010), and any other analyses in R v. 2.12.1 (R Development Core Team 2008).

## Results

The AUC values of SDM models (obtained from fivefold cross-validations) were all above 0.8, and mostly > 0.9 (Table S1), indicating that the models performed well.

Species richness maps (Fig. 1) indicate that the two genera have a similar centre of high species richness in the Limpopo Basin, which straddles the borders between Mozambique, South Africa and Zimbabwe. Both genera also show high richness centres in East Africa (see also Marshall *et al.* in press), though *Vachellia* species are concentrated along the Eastern Rift of the East African rift system, from where they extend along the eastern edge of the East African plateau. *Senegalia*'s East African centre of richness is located further south-east, extending from Lake Victoria south-east towards the central coastline of Tanzania. Other areas of high species richness for both genera include the Horn of Africa and northern Namibia/southern Angola, and, for *Senegalia*, possibly eastern Burkina Faso and the regions east thereof. *Senegalia* also extends into the African wet tropics, which *Vachellia* does not.

When considering the results of the non-spatial OLS models (Table S2), all three groups of potential drivers (BROWSERS, ENVIRONMENT and STABILITY) contributed to the species richness patterns of both genera. The SAR models (Table 1), which accounted for spatial autocorrelation, indicated that several of the variables that were included in final OLS models actually did not significantly explain acacia richness and that more than half of the variation in richness of both genera was explained by spatial effects. We thus focus on the results of SAR models.

For *Senegalia*, all three groups of potential drivers contributed to its richness pattern, though the effect of STABILITY was weak (Table 1a). The BROWSERS model alone explained a large fraction of the variation after spatial effects had been factored out – even more than the final model including BROWSERS, ENVIRONMENT and STABILITY effects (Table 1a). (The $R^2$-value considered here represents

only the variation after space has been removed, which is why the whole model $R^2$ is lower than that of the BROWSERS model.) Browser diversity was positively related to richness (Table 1a, Fig. 2b), while amongst the environmental variables, PET and habitat heterogeneity were positively related to richness, and the minimum temperature of the coldest month was negatively related to richness (Table 1a). However, the amount of variation explained by ENVIRONMENT was negligible. Precipitation velocity was negatively related to richness (Table 1a).

Both BROWSERS and ENVIRONMENT models explained significant variation in *Vachellia* richness, though BROWSERS explained more than twice the variation of ENVIRONMENT (Table 1b). Browser richness was positively related to *Vachellia* richness (Fig. 2b). Annual precipitation was related to richness with a hump-shaped quadratic relationship, though the effect of precipitation also interacted with PET, while minimum temperature of the coldest month was again negatively related to richness (Table 1b). The richness of *Vachellia* was not affected by STABILITY in the final model (Table 1b).

Variation partitioning indicated that for *Senegalia*, the unique contribution of browser diversity was the greatest contributor to the variation in species richness – both for non-spatial and spatial models (Table 2a). As already mentioned above, environmental variables considered here explained virtually no variation in the richness of *Senegalia* – the contribution of predictors to richness was less for the full model than for the model of browser diversity only in the spatial models (hence the negative values in Table 2a). The contribution of STABILITY to *Senegalia* richness was also small. In contrast, the unique contribution of environmental factors to *Vachellia* richness was bigger, though less in the spatial than the non-spatial models. However, the unique contribution of browser diversity still contributed most to the *Vachellia* model.

Adding the *Vachellia* or *Senegalia* model residuals to the species richness model of the other genus indicated that factors not considered in the analyses could also be affecting the richness patterns of African acacias. For both *Senegalia* and *Vachellia*, including the other genus' OLS residuals in the equation resulted in a substantial increase in the $R^2$-values of the non-spatial component of the model (Tables 1 and 2b). The $R^2$-value of the whole model with *Vachellia* or *Senegalia* residuals was greater than the sum of the $R^2$-values of the whole model without the residuals and the model containing only the residuals. This explains the negative $V_{FR}$ values in Table 2b and indicates that the effect of these other factors (i.e. the factors represented by the other genus' residuals) was dependent on the other predictors considered in the model. Noteworthy is, however, that even when these residuals were entered into the analyses, browser diversity still emerged as an important predictor of richness (Table 1).

For both genera, much of the variation in richness appeared to be explained by spatial signal alone. The $R^2$-values representing only the contribution of the predictors after the effect of space has been removed were less than half (and sometimes

**Table 1.** Simultaneous autoregressive (SAR) modelling of the effects of browser richness (BROWSERS), current environment (ENVIRON) and climate-change velocity (STABILITY) on the species richness of (a) *Senegalia* and (b) *Vachellia* across Africa separately and in a combined (whole) model

(a) *Senegalia*

| | Browser | PET | PET$^2$ | PrecSeas | MinTemp | ElevStd | PrecVel | *Vachellia* res | F | $R^2$ preds | $R^2$ preds + space | AIC preds | AIC preds + space |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BROWSERS | 0.210*** | | | | | | | | 315*** | 0.181 | 0.807 | 6711 | 4646 |
| ENVIRON | | 0.057* | −0.026ns | −0.144** | −0.179*** | 0.124*** | | | 0.03ns | $<1.0 \times 10^{-3}$ | 0.833 | 7005 | 4451 |
| STABILITY | | | | | | | −0.054*** | | 52*** | 0.035 | 0.812 | 6946 | 4610 |
| Whole Model | 0.162*** | 0.058* | −0.029ns | −0.100* | −0.168*** | 0.107*** | −0.031ns | | 38*** | 0.157 | 0.828 | 6765 | 4499 |
| + *Vachellia* res | 0.425*** | 0.089*** | −0.008ns | −0.015ns | −0.109*** | 0.057* | −0.01ns | 0.283*** | 99*** | 0.421 | 0.718 | 4894 (310) | 4105 (227) |

(b) *Vachellia*

| | Browser | Prec | Prec$^2$ | PET | PET*Prec | MinTemp | *Senegalia* res | F | $R^2$ preds | $R^2$ preds + space | AIC preds | AIC preds + space |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| BROWSERS | 0.253*** | | | | | | | 497*** | 0.274 | 0.880 | 6934 | 4548 |
| ENVIRON | 0.023ns | −0.187*** | <0.001ns | −0.056ns | −0.094 | −0.085* | | 40*** | 0.132 | 0.952 | 7177 | 3348 |
| Whole Model | 0.202*** | −0.014ns | −0.149*** | 0.002ns | −0.064* | | | 105*** | 0.323 | 0.954 | 6851 | 3298 |
| + *Senegalia* res | 0.296*** | −0.151*** | −0.121*** | 0.003ns | −0.070** | −0.082*** | 0.222*** | 115*** | 0.425 | 0.695 | 5526 (251) | 4833 (110) |

The last row of each table contains the results of adding the residuals of the Whole Model ordinary least square regression (OLS) of the other genus to the Whole Model of the genus in question. The latter models were built with fewer data points than the other models (see text), and thus, AIC-values are not comparable with other models. Therefore, the difference in AIC-values of a model built on this reduced data set with the Whole Model predictors and the '+ residuals' model is indicated in brackets. The standardized coefficients are shown in the left part of the table, and overall model statistics on the right side. The $R^2$- and AIC-values for the model explained by the predictors alone after the effect of space has been removed (preds) and the values for the models including both predictors and space (preds + space) are shown. For *Vachellia*, the effects of STABILITY are not shown because they did not improve model performance. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ns, non-significant.

Browser, browser richness; ElevStd, standard deviation of elevation; MinTemp, Minimum temperature of the coldest month; PET, Potential Evapotranspiration; Prec, Annual Precipitation; Prec-Seas, Precipitation seasonality; PrecVel, Precipitation velocity; res, OLS model residuals.
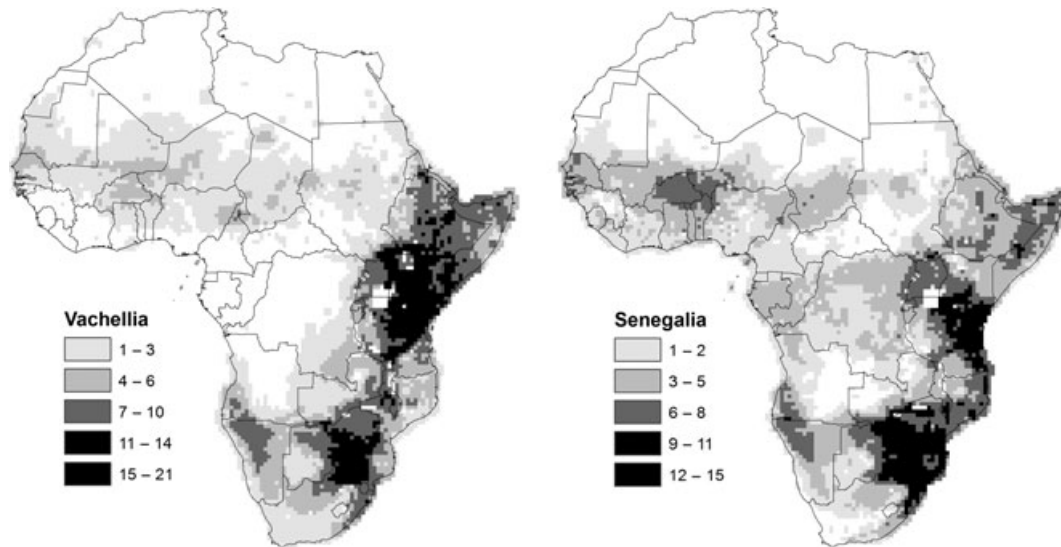
**Fig. 1.** Species richness maps of *Senegalia* and *Vachellia* in Africa.
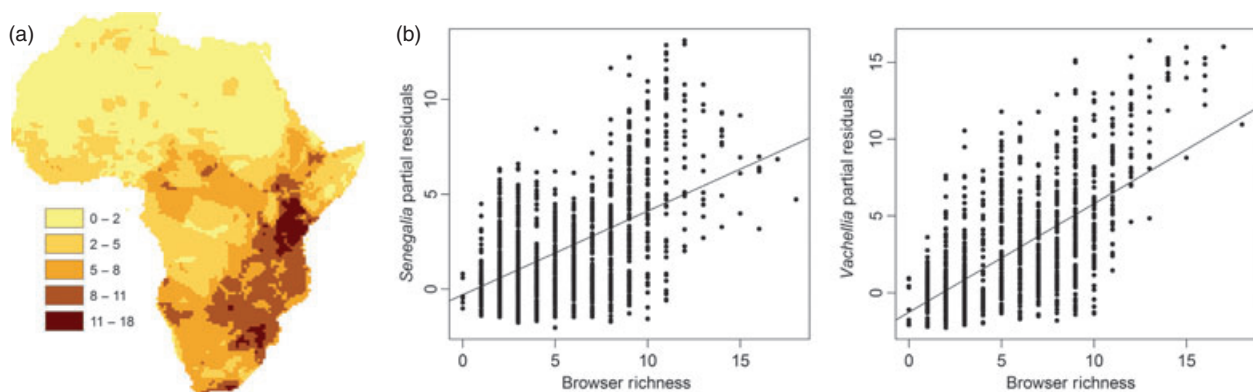


**Fig. 2.** (a) Map of large (≥ 10 kg) mammalian browser species richness across Africa, compiled from the list of browsers in Appendix S1D. (b) Partial residual plots showing the effect of browser diversity on the species richness of *Senegalia* and V*achellia* after controlling for the effects of the other variables in multiple linear regressions.

less than a third) of the contribution of the combined ecological and spatial effects (Table 2a). Thus, combined ecological and spatial effects were particularly successful at predicting the richness patterns of the two genera, with $R^2$-values exceeding 0.8 (Table 1).

## Discussion

The effect of biotic influences on species richness patterns have been poorly assessed at large spatial scales. Here, we used distribution modelling to map the distribution of *Senegalia* and *Vachellia* species, and the species richness patterns for these two genera, across the African continent. For these genera, factors that usually best explain species richness patterns have less explanatory power than factors seldom considered in richness analyses. Most significantly, we show – for the first time to our knowledge – that consumer diversity may be a key driver of richness at macroecological scale.

*Senegalia* and *Vachellia* possess two main, and similar, centres of diversity (Fig. 1). Across Africa, *Senegalia* is more widely distributed than *Vachellia*, and their richness patterns differ to such an extent that the factors that best explain the two genera's distributions differ considerably. Only browser diversity is a common explanatory variable to both models. In addition, the amount of variation explained by the three groups of factors (ENVIRONMENT, BROWSERS and STABILITY) differs between the genera. *Senegalia*'s wider distribution across Africa, particularly into the wet tropics, may be ascribed to the fact that the genus' presence in Africa is attributable to at least two immigration events to the continent, with one clade diversifying in open environments, and the other, smaller, clade in the moister forested parts of the continent (Bouchenak-Khelladi *et al.* 2010). In Africa, the forest-adapted clade within *Senegalia* is relatively species-poor (maximally 13 species, Ross 1979; Bouchenak-Khelladi *et al.* 2010; the lack of an updated phylogeny makes it difficult to

**Table 2.** (a) Partitioning of the amount of variation in species richness of *Senegalia* and *Vachellia* that can be attributed to pure browser richness ($V_B$), current environment ($V_E$), climate velocity ($V_V$), and the combined effects of browser richness and current environment ($V_{BE}$), browser richness and climate velocity ($V_{BV}$), current environment and climate velocity ($V_{EV}$), and browser richness, current environment and climate velocity ($V_{EBV}$). Variation partitioning results are shown for ordinary least square (OLS) models, which assume independence of all data points regardless of their spatial position, and for the environmental contribution of simultaneous autoregression (SAR) models after the effect of space on the models has been factored out ($R^2$ preds in Table 1). The best SAR model for *Vachellia* excluded climate velocity variables; therefore, only the contribution of the other two sets of variables is shown. (b) The amount of variation in species richness of *Senegalia* and *Vachellia* that can be attributed to the variables of the 'Whole Model' in (a) ($V_W$), to the residuals of the whole model OLS of the other genus ($V_R$), and to the combined contribution of the two ($V_{WR}$). For both (a) and (b), total variation explained by all variables considered is given by $R_{TOT}$

(a)

| Genus | Model | $V_B$ | $V_E$ | $V_V$ | $V_{BE}$ | $V_{BV}$ | $V_{EV}$ | $V_{EBV}$ | $R_{TOT}$ |
|---|---|---|---|---|---|---|---|---|---|
| *Senegalia* | OLS | 0.142 | 0.066 | 0.023 | 0.068 | 0.027 | 0.030 | 0.050 | 0.407 |
|  | SAR | 0.148 | −0.047 | 0.020 | 0.021 | −0.011 | 0.003 | 0.023 | 0.157 |
| *Vachellia* | OLS | 0.192 | 0.170 | 0.012 | 0.106 | 0.011 | 0.031 | 0.136 | 0.659 |
|  | SAR | 0.191 | 0.049 | 0.083 | 0.323 |  |  |  |  |

(b)

| Genus | Model | $V_W$ | $V_R$ | $V_{WR}$ | $R_{TOT}$ |
|---|---|---|---|---|---|
| *Senegalia* | SAR | 0.316 | 0.191 | −0.086 | 0.421 |
| *Vachellia* | SAR | 0.348 | 0.150 | −0.073 | 0.425 |

quantify the exact number of species in the clade) compared with the open-environment clade within *Senegalia*. The two independent colonization events into Africa of *Senegalia* clades adapted to different environments may at least partly explain why ENVIRONMENT explains virtually no variation in the richness of the genus. In contrast to *Senegalia*, the African *Vachellia* are thought to originate from a single open-environment African ancestor (Bouchenak-Khelladi *et al.* 2010). One could thus expect that, if environmental preferences are heritable (for which Bouchenak-Khelladi *et al.* 2010 provide evidence), *Vachellia* richness should be considerably better predicted by the environment, which is what we find here (Table 1).

That herbivory has significant effects on African acacias is well-established (references in Introduction). However, it is noteworthy that plant species richness could be so well predicted by browser diversity, which emerges as the strongest predictor of richness for both acacia genera. Previous tests on the effects of herbivore species richness on plants have mainly been considered at community level and shown contradictory results (reviewed in Hester *et al.* 2002).

How browsers may facilitate higher acacia species richness at continental scale is difficult to elucidate (Kissling, Rahbek & Böhning-Gaese 2007). It is known that plant–insect herbivore interactions frequently result in evolutionary arms races, which are thought to be behind the frequently highly concordant richness of both insects and plant species (Futuyma & Agrawal 2009). However, mammalian herbivores, which have probably exerted the greatest herbivory pressure on acacias over evolutionary time (Maclean *et al.* 2011), tend to have more generalist food requirements than insects, and evolutionary arms races may thus be weaker in plant–large mammal herbivore interactions than in plant–insect interactions (Prins *et al.* 2006; Futuyma & Agrawal 2009). Therefore, plant–consumer

associations between individual acacia species and browser species may not directly drive concordant richness of the two groups.

Decreased fitness of acacias because of browsing could be an alternative mechanism governing the genera's richness patterns. While acacias are well adapted to herbivory, herbivory defence and tolerance come at a cost to the plants: their reproductive output directly decreases through reduced or non-existent fruit production (Fornara & du Toit 2007; Staver *et al.* 2009), seedling survival (Maclean *et al.* 2011) and adult survival and growth (Maclean *et al.* 2011), which leads to decreased tree densities (Staver *et al.* 2009). The fact that several phenotypic responses to browsing are less pronounced under low browsing pressure (Fornara & du Toit 2007) further indicates that these responses are initiated at a cost to the plant. The competitive ability and fitness of acacias exposed to high herbivory may thus be reduced (assuming that high browser diversity is also related to high herbivory pressure), resulting in fewer offspring and less gene flow. This may diminish competition and facilitate coexistence of closely related species, though mainly if herbivore pressure affects dominant rather than inferior species (Hulme 1996). Therefore, species which evolved allopatrically may come to coexist because of secondary dispersal (e.g. Gehrke & Linder 2011). Alternatively, this could promote habitat specialization or genetic drift because the gene pool across the range of a species is not swamped by dominant genes (Fine *et al.* 2006), which may eventually culminate in speciation (McPeek 1996). In support of this, many widespread African acacias show much trait variation across their range, so that individuals from two distributional extremes appear to be different species, but are classified as a single species because intermediate forms exist (e.g. *Acacia senegal* and *Acacia oliveri*; Thulin 1993). In addition, amongst coexisting acacias, some species may be more palatable than others,

resulting in lower recruitment of the more palatable than the less palatable species (Bond, Smythe & Balfour 2001). The trade-off between investments in growth (of more palatable species) vs. defence (of less palatable species) could thus favour coexistence under higher browsing pressure.

As already mentioned, current environment alone predicts a significant amount of variation in *Vachellia's* richness. This, together with the fact that the effects of environment on *Vachellia* richness were not as substantial as they often are in other groups (Hawkins *et al.* 2003; Field *et al.* 2009), suggests that, while most acacias have a preference for more arid environments (Bouchenak-Khelladi *et al.* 2010), environmental preferences may not be strongly conserved within this range of climatic conditions, that is, the group may display a lack of niche conservatism (with 'niche' in this context denoting the environmental niche). Otherwise, the effects of current environment on *Vachellia* richness are as expected. Annual precipitation is quadratically related to richness, although its influence is dependent on PET, indicating that productivity (encompassing both energy and water dynamics) affects the richness of the group. In addition, richness decreases with minimum temperature of the coldest quarter, showing that acacia richness may be restricted by cold temperatures.

Climate-change velocity is only a weak predictor of *Senegalia* richness, with stability (low velocity) in precipitation predicting higher species richness. Various other studies have found that climate stability promotes species diversity (e.g. Jansson 2003; Sandel *et al.* 2011). Because acacias are adapted to drier and seasonal environments, glacial periods that were characterized by even drier and more seasonal environments may have had relatively little effect on the diversity of the group. Importantly, African savannas were more extensive during the long-lived glacial periods than they are at present (Morley 2000), suggesting that today's savannas may, at least partly, be 'remnants' of the savannas that reached maximum extent during the LGM. Therefore, if range shifts of acacias did occur because of post-LGM warming, they may well have involved extinctions from areas where the group no longer occurs, rather than recolonizations of previously unfavourable areas by secondary dispersal from areas where species persisted. In addition, climate-change velocity represents the difference between current and LGM climates while taking topography into account, but ignores climate oscillations between the LGM and the present, and late Tertiary climate changes, the period during which much of the diversification of the two genera occurred (Bouchenak-Khelladi *et al.* 2010).

There were strong patterns in acacia richness that were neither explained by browser richness, current environment nor long-term climate stability. Notably, the species richness of one genus (even after accounting for its correlations to browser richness, current environment, and climate stability) explained important amounts of variation in the species richness of the other genus (60% and 40% of the variation explained by the other three groups of factors for *Senegalia* and *Vachellia*, respectively). This suggests that some variable(s) not considered here have consistently affected the diversity pattern of both

plant genera (cf. Tuomisto, Ruokolainen & Yli-Halla 2003), although what precisely these might be is impossible to elucidate here. They could, for example, be factors that have an effect at finer scales than have been measured here, occurred locally (e.g. what allowed both genera to reach such diversity within the Limpopo Basin?), or be factors that have not been accurately mapped, such as soils and geology, fire, pollinator availability or diversity, seed dispersers, or even aspects of long-term faunal dynamics not captured by current patterns of browser richness (Martin 1966; Faith *et al.* 2011).

Even when accounting for the species richness of the other genus, there are unexplained spatial patterns in the richness of both acacia genera. Whatever drives these patterns must represent factors which affect the two genera differently. For example, some *Vachellia* species form symbiotic relationships with ants, with ants providing varying degrees of defence against herbivory to trees, and trees providing nests for the ants (Ross 1979; Palmer *et al.* 2008). This three-way biotic interaction may thus have affected distribution and diversity patterns of *Vachellia*. Furthermore, information on the evolutionary relationships between species and ages of the taxa in the two genera (information which is currently not available for most acacias, Bouchenak-Khelladi *et al.* 2010) could shed light on the role of historical factors on the diversification of the two genera (e.g. Gehrke & Linder 2011).

### LIMITATIONS AND CONSIDERATIONS

Several sources of error could have arisen in the analyses here. First, although SDMs performed relatively well in predicting the distributions of most species, inaccuracies in the maps will have arisen due to various factors. Some regions have been under-collected, resulting in potential distribution biases. Moreover, factors such as historical biogeography, dispersal barriers, and speciation because of range fragmentation would not have been entirely represented in SDMs. Finally, imprecisions in the projections of SDMs would have resulted in over- or underpredictions of some distributions and thus also inaccuracies and interpolation of the species richness maps.

The taxonomy of some acacias may also need revising. In the age of molecular phylogenetics, African acacias have received little attention and some of the subspecies and varieties might, for example, have to be elevated to species level. This might affect the delimitations of species distribution, although richness maps might not have been affected much, as many of the subspecies and varieties are allopatric.

Finally, a correlation between plant richness and other factors, for example, browser diversity, does not necessarily mean that one drives the other. Correlations could also be due to a third factor influencing the diversity of both factors. When including a range of environmental variables in models, browser diversity alone explained most of the non-spatial variation in the richness of both plant genera (Tables 1 and S2); therefore, we have confidence that browsers really do affect acacia richness to some extent. Other authors have argued that woody plant diversity drives mammal and bird diversity (Kissling, Rahbek & Böhning-Gaese 2007; Qian *et al.* 2009),

whereas we argue that browser diversity could drive variation in the diversity of plants. We believe that, in this case, the reverse argument – that the species richness of acacias alone should be able to predict much of the richness patterns of large herbivores – is less likely. For one, this would imply that individual plant genera drove the diversification of African browsers. Given the often patchy nature of savannas (du Toit & Cumming 1999), the fact that savannas support many woody species other than acacias, and the tendency for browsers to have generalist dietary requirements (e.g. Prins *et al.* 2006), this scenario seems less likely. In addition, modern African bovids, which constitute a significant proportion of browsers, diversified during the middle-late Miocene (Janis 1993), which is prior to the origin of many acacia species (Bouchenak-Khelladi *et al.* 2010) (though there would be turnover of browser assemblages with climate changes through subsequent periods of climate change, Janis 1993). Finally, the range of adaptations of acacias to herbivory by large herbivores is extensive, indicating that much of the evolution of the group has been driven by mammalian herbivory.

## Conclusion

The effects of different factors on species richness patterns may depend on the spatial scale and extent of the study being conducted (Willig, Kaufman & Stevens 2003; Field *et al.* 2009), the functional characteristics of the organisms (Hawkins, Rodríguez & Weller 2011) and habitat (Field *et al.* 2009). Here, we find that the factors that often correlate highly with species richness of clades at higher taxonomic levels do not explain most of the variation in acacia richness in Africa; yet consumer diversity, a factor otherwise seldom considered in richness analyses, explains much of the variation of the group. This 'anomaly' may be related to the functional characteristics (adaptations to herbivory) of the genera (Hawkins, Rodríguez & Weller 2011). Biotic factors have not often been considered in examining the drivers of richness patterns: besides tests of the congruence of resource–consumer diversity patterns, with resources and consumers usually comprising plants and animals, respectively (Kissling, Rahbek & Böhning-Gaese 2007; Qian *et al.* 2009), it has also been suggested that the discrepancy between 'fundamental' (the number of species predicted by abiotic factors) and 'realized' (the observed) species richness may be a result of biotic interactions (Violle *et al.* 2011).

Africa is unique in that large mammal species have mainly continued to coexist with humans over the last millennia (Owen-Smith 1989). However, large herbivore populations have declined, or been locally exterminated, across extensive regions of the continent in the last century, and the biotic interactions between herbivores and vegetation will therefore have been altered, or even disappeared (Spinage 1973; Owen-Smith 1989). Herbivory, previously a main agent in the evolution of acacias, may thus cease to act as a major adaptive pressure in such landscapes (although in some regions, e.g., goats and sheep may assume the ecological role of browsers, Groen *et al.* 2011). The retention of large herbivores is thus not only essential for retaining ecological (Marchant 2010), but also evolutionary functionality in African savannas.

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## Supporting Information

Additional supporting information may be found in the online version of this article:

**Figure S1.** Checkerboard-like grid.

**Table S1.** List of acacia species.

**Table S2.** Results from ordinary least square regressions modelling the determinants of acacia species richness.

**Appendix S1.** Supplementary methods.

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