

Bovoid locomotor functional trait distributions reflect land cover and annual precipitation in sub-Saharan Africa

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ABSTRACT

Background: Previous studies demonstrate that community-average mammalian hypsodonty is highly correlated with annual precipitation across geographic space and through evolutionary time. This approach of using community-level morphological traits to infer environmental parameters has been termed the ‘ecometric’ approach. The utility of this approach on narrower spatial and taxonomic scales is not well understood.

Questions: Do bovid (antelope) locomotor traits work well as ecometric traits? Do assemblage-average values of bovid locomotor traits reflect annual precipitation and vegetation cover within sub-Saharan Africa?

Data studied: I compiled five quantitative locomotor traits of the astragalus and five traits of the metatarsal for bovid species occurring across sub-Saharan Africa. I obtained estimates of annual precipitation and land cover for the corresponding locations.

Methods: General linear modelling to quantify the relationship of assemblage-average trait values to annual precipitation and land cover.

Conclusion: Astragalus and metatarsal traits explain major proportions of variation in annual precipitation and land cover ($R^2 > 0.6$). Because locomotor ecometric traits track vegetation cover and annual precipitation in modern assemblages, these traits may be useful for reconstructing environmental variables over evolutionary time based on the abundant bovid postcranial fossil record.

Keywords: Bovidae, ecometrics, ecomorphology, functional traits.

INTRODUCTION

Organisms interact with their environment by means of their phenotypic functional traits. The distribution of these functional traits across geographic space can reveal how community structure tracks environmental gradients (Vilà-Cabrera *et al.*, 2015) and shed light on the processes by which species communities are assembled (Kraft *et al.*, 2008). The relationship between functional trait distributions and environmental variables also offers a powerful

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tool for reconstructing past environments based on fossil assemblages (Andrews *et al.*, 1979; Reed, 1997, 1998; Fortelius *et al.*, 2002, 2016; Eronen *et al.*, 2010b).

Ecomorphology refers to the study of morphological variation that is related to the environment in which an organism lives (Ricklefs and Miles, 1994). Using principles of functional morphology, ecomorphic studies aim to link form with function to identify traits that impact an individual's fitness in a particular environmental context (Bock and von Wahlert, 1965). Thus, ecomorphology is often focused on traits of individuals, and the ways in which those traits are related to the environment. However, mapping individual phenotypes to ecology is not straightforward, as distinct phenotypes may correspond to overlapping ecological niches because of behavioural flexibility and individual functional performance (Ricklefs and Miles, 1994). Furthermore, species ranges encompass a diversity of environmental conditions, such that some individuals of a species will usually be occupying habitats to which they are sub-optimally adapted (Magurran and Henderson, 2003). Thus, linking individual functional traits with aspects of the environment involves a considerable amount of uncertainty.

When functional traits are analysed at the community level, individual- and species-level variation tends to be dampened, and thus community-level functional traits may track environmental gradients more closely than individual- or species-level traits (Polly, 2010). The study of community-level functional traits and their links with environmental parameters has been termed 'ecometrics' (Eronen *et al.*, 2010a; Lawing *et al.*, 2012; Polly *et al.*, 2015). Because ecometric traits can often be measured for both extant and fossil organisms, the ecometric approach provides an important tool for understanding trait–environment dynamics across geographic space and through evolutionary time (Polly *et al.*, 2011).

For example, average tooth crown height (i.e. the degree of hypsodonty) in mammalian communities is strongly correlated with annual precipitation. Individuals living in dry and dusty habitats experience high rates of tooth wear due to the ingestion of environmental grit, while individuals in moister habitats with less abrasive diets experience slower rates of wear (Damuth and Janis, 2011). Natural selection favours individuals with higher crowned teeth because higher crowned teeth have longer functional life spans (Janis and Fortelius, 1988). Tooth height is thus linked to precipitation levels through the relationship between precipitation and dietary abrasiveness. This selective pressure on individual tooth height scales up to the mammalian community level, and therefore average mammalian hypsodonty is strongly related to annual precipitation on a global scale (Eronen *et al.*, 2010c). This modern relationship apparently was active in the past, as changes in mammalian hypsodonty through the Miocene of Europe reflect changing precipitation regimes in response to physical and climatic drivers (Fortelius *et al.*, 2002; Eronen *et al.*, 2010b). The ecometric study of mammalian hypsodonty provides a powerful framework for understanding mammalian community responses to long-term climate change.

While hypsodonty is linked strongly to annual precipitation, other mammalian functional traits may be more directly related to vegetation structure, rather than to precipitation *per se*. Traits influencing how an organism moves through the environment should relate strongly to vegetation structure because different vegetation types present distinct locomotor challenges. Bovids (antelope and relatives) occupying different habitats are known to exhibit locomotor strategies related to habitat-specific predator-avoidance strategies (Jarman, 1974). Grassland bovids have adaptations for cursoriality that facilitate rapid flight from predators over open ground. Forest bovids have adaptations for crypsis and joint rotational mobility that facilitate locomotion over complex three-dimensional substrates. Many ecomorphic studies have identified links between bovid locomotor morphology and the

vegetation structure of preferred habitats (e.g. Scott, 1985; Kappelman, 1988, 1991; Plummer and Bishop, 1994; Scott *et al.*, 1999; DeGusta and Vrba, 2003; Kovarovic and Andrews, 2007; Plummer *et al.*, 2008; Barr, 2014; Scott and Barr, 2014). Bovids have been a common choice for ecomorphic study because they are very abundant in both modern and fossil African assemblages.

Ecomorphic studies provide strong evidence that bovid locomotor traits are tightly linked to the vegetation structure of the habitats they occupy. It is likely that these same locomotor traits are also related to annual precipitation because of the relationship between vegetation structure and precipitation. While the growth of significant woody cover requires a baseline level of precipitation (Whittaker, 1975), woody cover is limited by (and increases linearly with) annual precipitation only up to ~650 mm per year (Sankaran *et al.*, 2005). Beyond this precipitation threshold, other factors such as fire, herbivory, precipitation seasonality, and soil characteristics heavily influence the percentage of woody cover (Bond, 2008; Good and Caylor, 2011). Thus, the vegetation structure in a given habitat is constrained by – but not determined by – annual precipitation levels. Therefore, bovid locomotor traits are expected to more closely track vegetation cover than precipitation values.

In general, previous ecomorphic studies have focused on linking morphology with habitat preference in individual bovid specimens and species. However, it is not clear the degree to which individual-level selective pressures scale up to the level of bovid species assemblages. Thus, while bovid species clearly exhibit habitat-specific locomotor adaptations, the degree to which species assemblage-level bovid locomotor traits are linked to environmental gradients is not well known. The ecometric approach offers a way to bridge the gap between individual traits and assemblage-level traits, and therefore to better understand how bovid species assemblages are structured with respect to their environment.

The aim of this study is to test the hypothesis that modern bovid locomotor trait distributions reflect annual precipitation and vegetation cover in sub-Saharan Africa. If assemblage-level postcranial traits co-vary strongly with environmental variables, this result would point to an important mechanism structuring bovid species assemblages, and would validate the use of bovid locomotor functional traits as ecometric traits. Postcranial ecometrics could provide a powerful framework for interpreting the abundant postcranial African fossil record which spans from the Miocene to the Holocene (Bibi *et al.*, 2009) and provide a means to use locomotor trait distributions in fossil assemblages to infer annual precipitation and vegetation cover of ancient landscapes.

MATERIALS AND METHODS

The approach taken in this study is to combine ecomorphic data with species range maps in order to calculate a single assemblage-average trait value for the species that occur at a particular location. These average values are then compared with estimates of annual precipitation and land cover classifications for the same locations to determine whether assemblage-level locomotor traits are correlated with the environmental variables. Ecomorphic traits were selected for analysis based on the results of prior studies that have indicated a functional link between individual trait values and habitat preference (Barr, 2014; Scott and Barr, 2014). In order to meaningfully compare the shape of bones from species of different overall body size, I divided each ecomorphic variable by a body-size proxy variable computed using a geometric mean (described more fully in the Appendix). I further scaled all ecomorphic variables to *z*-scores by subtracting the mean and dividing by the standard deviation (additional details in the Appendix).

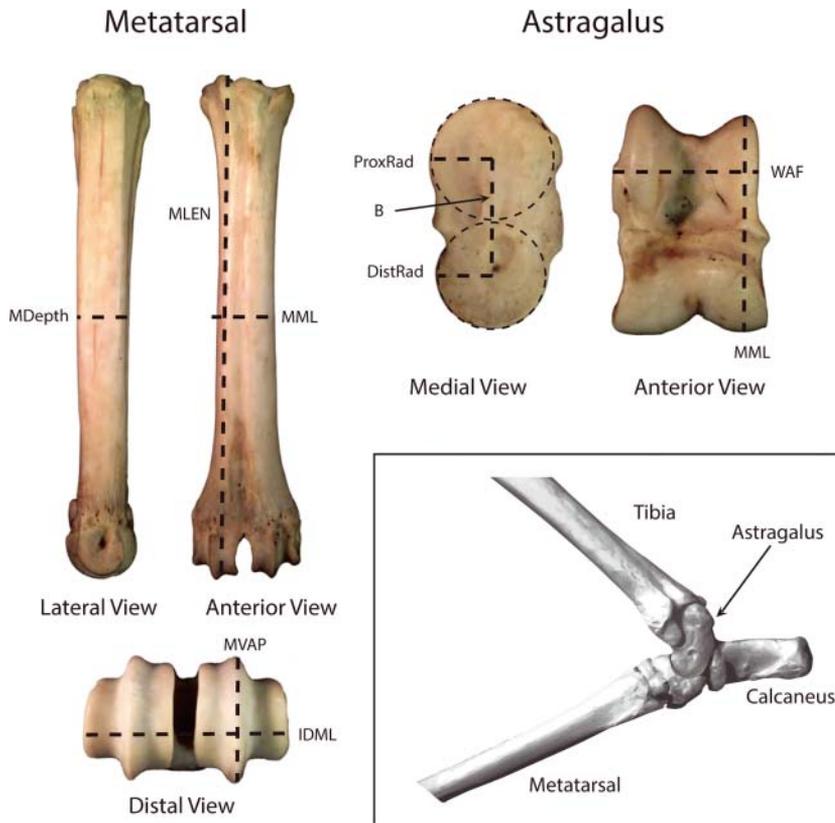


Fig. 1. Right metatarsal and astragalus of an *Ammotragus lervia* individual from the author's personal skeletal collection. The ecomorphic variables discussed in the text are indicated as dotted lines. *Note:* Figure is not to scale.

I characterized bovid species in sub-Saharan Africa using ten ecomorphic variables (Fig. 1 and Table 1). Five of the variables relate to the functional anatomy of the astragalus, a bone of the hock (ankle) that acts as a double-pulley during locomotion in artiodactyls (Schaeffer, 1947). The ecomorphology of bovid astragali has been well studied (DeGusta and Vrba, 2003; Plummer *et al.*, 2008; Barr, 2014, 2015). Bovids occupying grasslands are characterized by shorter, wider astragali. This morphology reduces the force arm for the ankle plantarflexors and increases the range of motion and speed of the foot during locomotion. Forest bovids are characterized by longer, narrower astragali, which results in longer lever arms for the ankle plantarflexors by increasing the effective length of the calcaneus (Barr, 2014). Species-mean values of the astragalus variables in Table 1 were compiled for each of 46 sub-Saharan African bovid species using published data (Barr, 2014). Note that in this dataset as well as the metatarsal dataset, I only included species for which range map data were available, which slightly reduced the species coverage compared with previous studies using the ecomorphic dataset. The ecomorphic dataset used in this study is available on the github code-sharing website (<https://github.com/wabarr/bovid-locomotor-ecometrics/>).

Five variables describing the functional morphology of the metatarsals were also investigated. The functional anatomy of metatarsals has previously been shown to relate

Table 1. The ten ecomorphic variables examined in this study

Variable	Element	Description	Reference
MMLa	Astragalus	Maximum medial length	DeGusta and Vrba (2003), Plummer <i>et al.</i> (2008)
B	Astragalus	Functional length	Barr (2014)
WAF	Astragalus	Width at level of flange on lateral surface	Barr (2014)
DistRad	Astragalus	Radius of circle fit to the margin of the distal trochlea	Barr (2014)
ProxRad	Astragalus	Radius of circle fit to the margin of the proximal trochlea	Barr (2014)
MMLm	Metatarsal	Relative mediolateral width at midshaft	Scott and Barr (2014)
MLEN	Metatarsal	Relative metatarsal length	Scott and Barr (2014)
MDepth*	Metatarsal	Relative anteroposterior depth at midshaft	Scott and Barr (2014)
MVAP	Metatarsal	Relative height of medial verticilli	Scott and Barr (2014)
IDML	Metatarsal	Mediolateral width of distal articular surface	Scott and Barr (2014)

Note: To control for the effects of isometric size, all variables were divided by a geometric mean size proxy as described in Barr (2014) and Scott and Barr (2014) (see details in the Appendix). Variables were scaled to *z*-scores (see Appendix) before use in GLM. *Referred to as MAP in Scott and Barr (2014).

to habitat. Grassland taxa are characterized by relatively long metatarsals that are medio-laterally narrow at the midshaft (Scott, 1985). This morphology reflects longer stride lengths and more stereotypical bone loading during locomotion. Taxa occupying more closed environments have significantly shorter and wider metatarsals (Scott, 2004; Scott and Barr, 2014) relative to body size, which reflects more varied loading patterns. Grassland species also possess higher (more ‘railed’) medial verticilli and a broader distal articular surface (Kohler, 1993). Species-mean data on the five metatarsal variables were compiled for 49 species of sub-Saharan African bovinds (Scott and Barr, 2014).

The astragalus and metatarsal ecomorphic datasets sample 83–89% of the 55 species of bovid that occur in sub-Saharan Africa. Species that are not represented in the ecomorphic datasets tend to have small geographic ranges and to be poorly represented in osteological museum collections.

I obtained species range maps from the IUCN Red List of Threatened Species™ website (IUCN, 2015). I obtained annual precipitation raster data from WORLDCLIM (Hijmans *et al.*, 2005), and land cover classification raster data from Broxton *et al.* (2014). The land cover dataset comprises a categorical variable derived from remote sensing data, with full details of this classification scheme available elsewhere (Friedl *et al.*, 2010). I simplified the land cover variable to include only land cover classes that are well represented in sub-Saharan Africa. The simplified set of land cover classes used is summarized in Table 2.

All spatial and statistical analyses were performed using R v.3.2.2 (R Development Core Team, 2015). The *raster* package v.2.5-2 (Hijmans, 2015) and *maptools* v.0.8-37 (Bivand and Lewin-Koh, 2015) were used to project raster data to a common extent and resolution, and to perform spatial joins. All datasets were projected to the Eckert IV equal area projection using the WGS84 geodetic datum prior to analysis.

Table 2. Land cover classes with codes and descriptions following Friedl *et al.* (2010)

Code	Description	Number of pixels in raster
2	Evergreen broadleaf forest	932
7	Open shrublands	906
8	Woody savannahs	1567
9	Savannahs	1705
10	Grasslands	860
11	Permanent wetland	59
16	Barren or sparsely vegetated	366

Note: Only land cover classes analysed in this study are included in the table.

I created a 50×50 km spatial grid over sub-Saharan Africa. I calculated the mean annual precipitation and the modal land cover category for each grid cell. I determined which species ranges intersected each grid cell. Using this list of species, I computed a grid cell average for each ecomorphic trait.

An ordinary least-squares general linear model (GLM) was used to test the relationship between the grid cell ecomorphic variables and the annual precipitation and land cover variables. Annual precipitation values were strongly non-normal and therefore were square-root transformed to improve normality to meet assumptions of GLM. Analyses were repeated using a coarser 75×75 km spatial grain, but the results were extremely similar to those discussed below and are not presented.

Spatial autocorrelation is a potential concern in this type of analysis. Spatial autocorrelation increases the risk of Type I errors, which renders GLM *P*-values on spatially autocorrelated data suspect. However, GLM effects sizes are unbiased estimators (Dormann *et al.*, 2007) of their ‘true’ value (value after correction for autocorrelation) (Fig. 2). In the

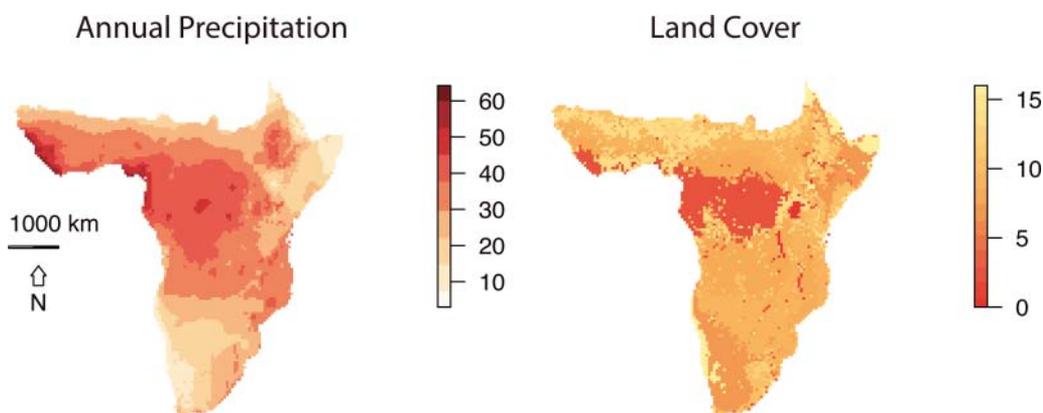


Fig. 2. Maps showing annual precipitation and land cover rasters for sub-Saharan Africa. See Table 2 for land cover class codes. Units for annual precipitation are in millimetres after square root transformation.

results below, I do not report *P*-values. I rely on standardized slope estimates as a measure of the strength of the relationship between the ecometric variables and the environmental variables, and on coefficients of determination (R^2) as a measure of goodness-of-fit.

RESULTS

The spatial distributions of species assemblage-average values for each of the ten ecomorphic variables are illustrated in Fig. 3. The results of the GLM for each ecometric variable against annual precipitation are presented in Fig. 4 and Table 3. Of the five ecomorphic variables pertaining to the metatarsal, midshaft mediolateral width (MMLm: slope = 0.09, $R^2 = 0.67$) and the height of the medial verticilli (MVAP: slope = -0.08, $R^2 = 0.60$) have the strongest effect sizes and explain the most variation in annual precipitation. Metatarsal length (MLEN) explains a moderate amount of variation in annual precipitation (slope = 0.07, $R^2 = 0.42$), while metatarsal depth (MDepth: slope = -0.04, $R^2 = 0.17$) and distal mediolateral width (IDML: slope = -0.03, $R^2 = 0.06$) explain minimal variation in annual precipitation. Among the five variables pertaining to the astragalus, the radius of the distal articular end (DistRad: slope = -0.07, $R^2 = 0.45$) and the width at the level of the flange (WAF: slope = -0.07, $R^2 = 0.39$) explain a modest amount of variation, while the remaining variables explain even less variation in annual precipitation (slope ≤ 0.06 , $R^2 \leq 0.3$).

The results of the GLM for each ecometric variable against the land cover categorical variable are presented in Fig. 5 and Table 4. For the metatarsal variables, a similar pattern is observed in the relative performance of the variables in the land cover analysis as in that for annual precipitation. However, the R^2 values are uniformly higher in the land cover GLMs compared with the annual precipitation GLMs. Midshaft mediolateral width (MMLm: $R^2 = 0.70$) and height of the medial verticilli (MVAP: $R^2 = 0.64$) explain the most variation in land cover, with metatarsal length (MLEN) also performing reasonably well ($R^2 = 0.47$). Metatarsal depth (MDepth) and distal mediolateral width (IDML) do not explain much

Table 3. GLM results for the ten variables (scaled) against annual precipitation

	Intercept	SE intercept	Slope	SE slope	R^2
Astralagus					
MMLa	-1.63	0.04	0.05	< 0.01	0.24
B	-1.80	0.03	0.06	< 0.01	0.30
WAF	2.05	0.03	-0.07	< 0.01	0.39
DistRad	2.21	0.03	-0.07	< 0.01	0.45
ProxRad	-1.71	0.03	0.06	< 0.01	0.27
Metatarsal					
MMLm	-2.56	0.02	0.09	< 0.01	0.67
MLEN	2.03	0.03	-0.07	< 0.01	0.42
MDepth	1.30	0.03	-0.04	< 0.01	0.17
MVAP	2.42	0.02	-0.08	< 0.01	0.60
IDML	0.76	0.04	-0.03	< 0.01	0.06

Note: R^2 values are reported.

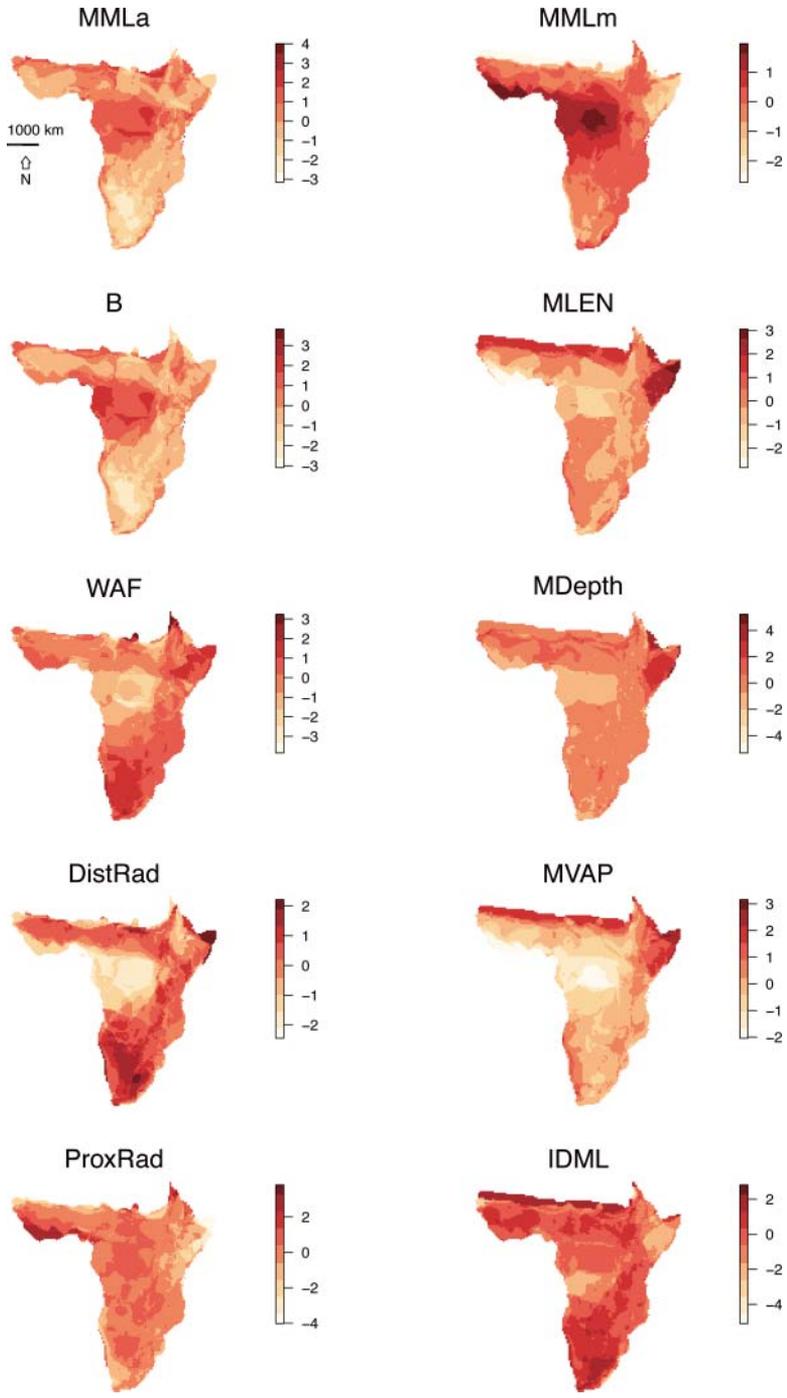


Fig. 3. Rasters showing the spatial distribution of assemblage-average ecometric values for the ten variables.

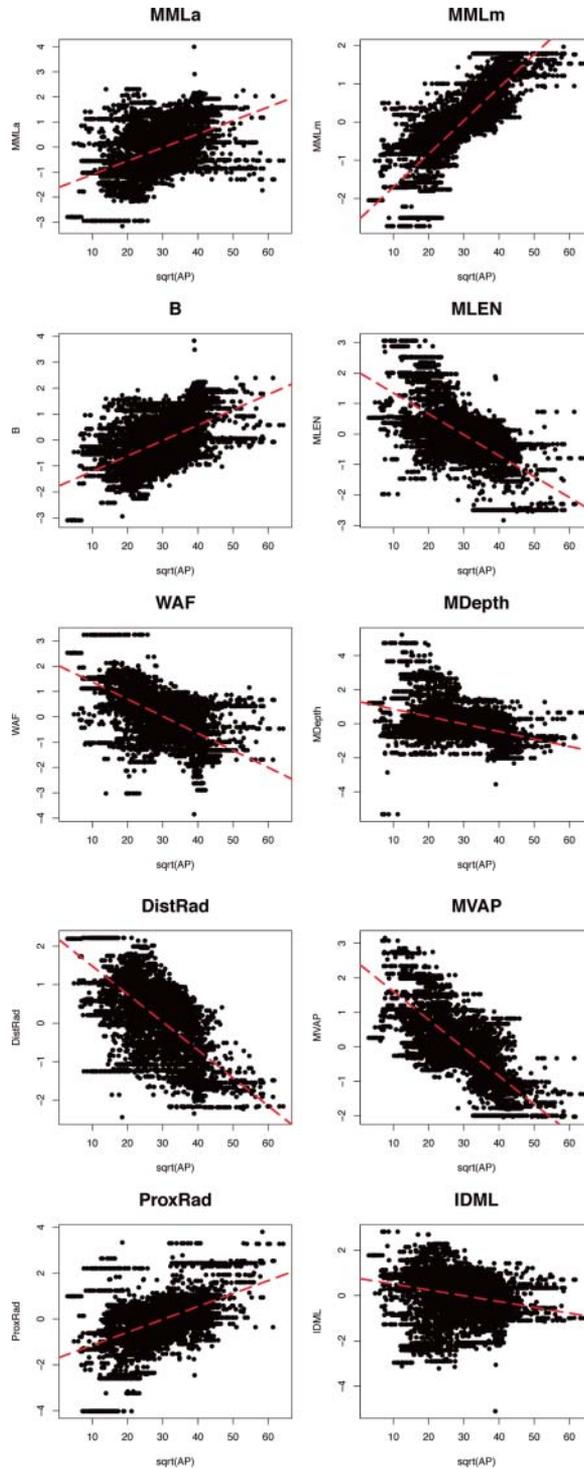


Fig. 4. Scatterplots showing the relationship between annual precipitation (AP) and the ten scaled ecomorphic variables.

Table 4. GLM results for the ten variables (scaled) against the land cover categorical variable

	Coefficients							R^2
	Forest (intercept)	Wetland	Woody savannah	Savannah	Open shrubland	Grassland	Barren	
Astragalus								
MMLa	1.16	-1.17	-1.09	-1.54	-0.49	-2.09	-1.93	0.39
B	1.44	-1.50	-1.34	-2.00	-0.55	-2.19	-2.22	0.50
WAF	-1.26	1.44	1.04	1.57	0.37	2.37	2.32	0.49
DistRad	-1.54	1.86	1.36	2.07	0.52	2.36	2.49	0.60
ProxRad	0.71	-1.38	-0.42	-0.67	-0.05	-1.34	-1.65	0.25
Metatarsal								
MMLm	1.41	-2.52	-0.92	-1.40	-0.48	-2.14	-2.96	0.70
MLEN	-1.01	2.00	0.68	0.75	0.50	1.55	2.33	0.46
MDepth	-1.25	1.51	1.12	1.32	0.76	1.81	1.86	0.29
MVAP	-1.37	2.38	0.97	1.28	0.43	2.05	2.97	0.64
IDML	-0.46	0.78	0.22	0.84	0.02	0.56	0.80	0.10

Note: The first level of the categorical variable is taken as the baseline (intercept), so the reported intercept is the mean of the forest group. All other coefficients are expressed as the difference between that group's mean and the baseline mean.

variation in land cover ($R^2 < 0.3$). Among the astragalus variables, the R^2 values were higher for land cover than for annual precipitation for all variables except for the radius of the proximal articular end (ProxRad). The radius of the distal articular end (DistRad: $R^2 = 0.60$) was strongly correlated with land cover, while the functional length (B: $R^2 = 0.50$) and the width at the level of the flange (WAF: $R^2 = 0.49$) were moderately correlated. The medial length of the astragalus (MMLa: $R^2 = 0.39$) and the radius of the proximal articular end (ProxRad: $R^2 = 0.25$) were weakly related to land cover.

DISCUSSION

The results of this study demonstrate that locomotor traits computed at the level of bovid species assemblages are closely linked to environmental parameters, in particular to vegetation structure. These results provide strong support for the use of metatarsal and astragalus ecomorphic variables as ecometric variables. Variables relating to both anatomical elements explain major proportions of the variance in one or both of the environmental variables. The ecomorphic variables are more closely linked with land cover than with annual precipitation, as reflected by the higher proportion of variance explained in the land cover GLM analyses. This result can be interpreted in light of the fact that these variables were selected based on their established relationship with species habitat preference. Habitat preference has a more direct link with land cover than with precipitation, and this link is reflected in the greater proportion of land cover variance explained. Nonetheless, due to the (albeit complex) relationship between annual precipitation and land cover, the ecomorphic variables do explain a meaningful proportion of variance in annual precipitation.

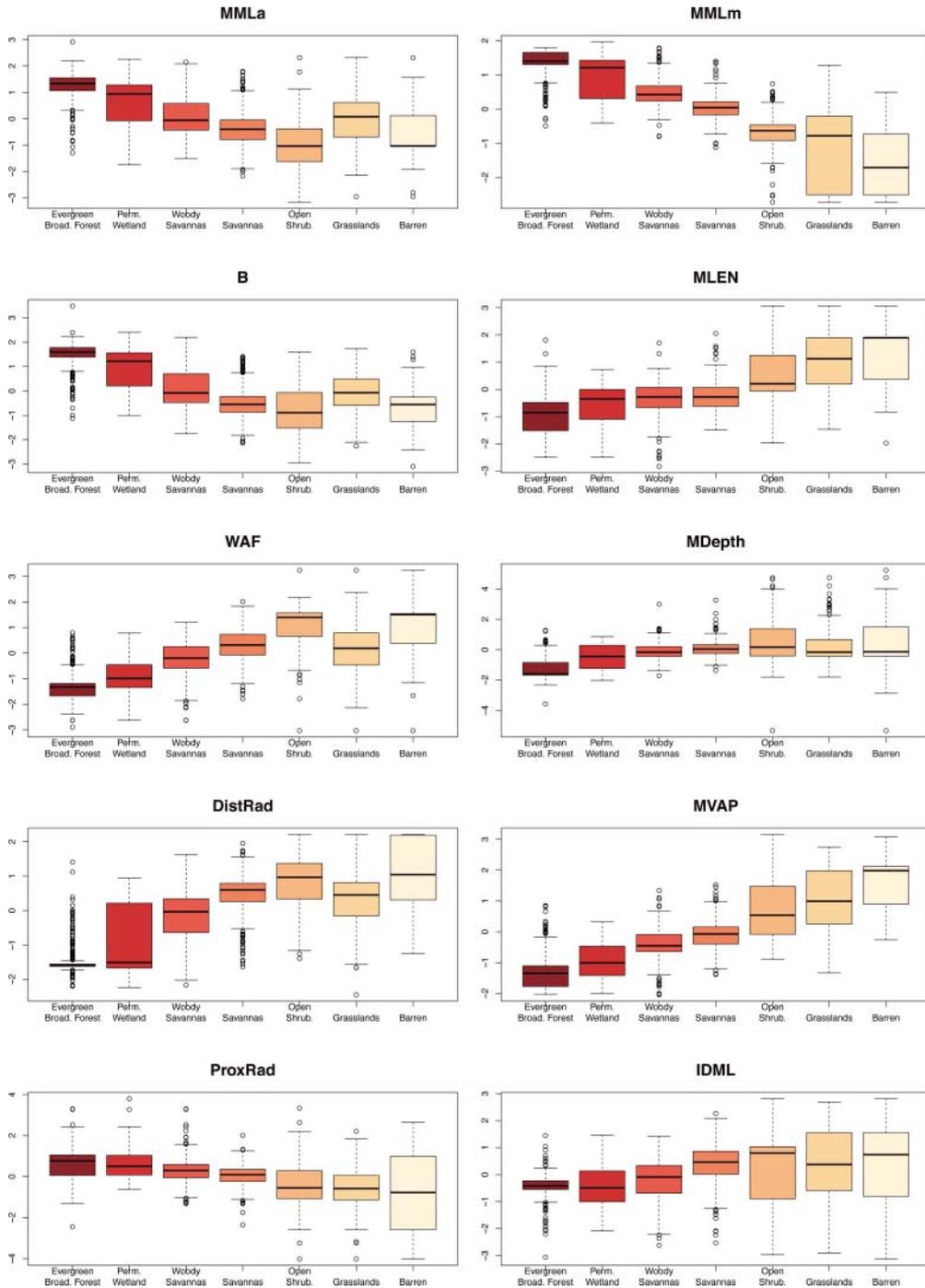


Fig. 5. Boxplots showing the distribution of the assemblage-average values of the ten variables among the different land cover classes. Forest = evergreen broadleaf forest, Wetland = permanent wetland, WS = woody savannahs, Savan. = savannahs, Shrub = open shrublands, Grass = grasslands, Barren = barren or sparsely vegetated.

Overall, the results accord well with previous work on the ecomorphology of the astragalus and metatarsal. In general, the variables that have been shown in previous work to have the strongest relationship to individual habitat preference are the same variables that perform best as ecometric variables.

Metatarsal width (MMLm) explained more variance in both annual precipitation and land cover than any other ecometric variable examined. Metatarsal width reflects the relative width of the metatarsal in the medio-lateral direction at midshaft. Relative metatarsal width is greatest in taxa that experience pronounced medio-lateral bending moments on complex substrates (Scott and Barr, 2014), which are more common in vegetatively closed or moist habitats. Taxa in drier and more open habitats likely experience more stereotyped antero-posterior bending moments during fast running on relatively flat and open substrates (Kappelman, 1988). Thus, taxa adapted to open habitats have medio-laterally narrower metatarsals (Scott, 2004; Scott and Maga, 2005). As shown in Fig. 5, land cover classes corresponding to dense woody vegetation (e.g. evergreen forest and woody savannah) show the highest mean values of MMLm, while land cover classes representing open habitats have the lowest MMLm values. Furthermore, there is a strong positive correlation between MMLm values and annual precipitation (Fig. 4). These results support prior functional interpretations suggesting a strong link between MMLm and habitat preference.

The height of the medial verticilli (MVAP) has also previously been shown to have a strong link with species habitat preference (Scott and Barr, 2014). The height of the verticilli is related to the mobility of the metatarsal-phalangeal joint and reflects the ability of the toes to 'splay' laterally (Kohler, 1993). High values of MVAP reflect highly 'railed' articulations that fit tightly with the proximal phalanges to prevent joint dislocation and restrict the ability of the toes to splay. Lower values of MVAP reflect less restricted mobility and a greater ability of the toes to splay laterally. Phalangeal splay, as indicated by MVAP, is thought to be advantageous in negotiating complex or moist substrates (Kohler, 1993; Scott and Barr, 2014). This link to habitat is reflected in the strong ecometric performance of MVAP in both the annual precipitation and land cover GLM analyses. As seen in Figs. 4 and 5, the highest average values of MVAP (reflecting joint stability and lack of phalangeal splay) are found in the driest and most open environments, while lower values of MVAP (reflecting greater ability for phalangeal splay) are found in the moistest and most densely vegetated habitats.

Among the astragalus variables, the radius of the distal articular end (DistRad) explained the most variance in both annual precipitation and land cover. The functional length of the astragalus (B) also explained a major proportion of variance in land cover. These two variables have previously been shown to relate to species habitat preference (Barr, 2014). The relative dimensions of the astragalus are related to the range of motion possible at the ankle joint, as well as the mechanical advantage of the ankle plantarflexors during locomotion. Open-adapted highly cursorial forms tend to possess astragali with a short functional length, and a broad distal articular end. This morphology emphasizes range of motion in the sagittal plane, and emphasizes speed of limb movement during plantarflexion (Barr, 2014). Taxa that are adapted to closed and moist habitats exhibit longer functional lengths and smaller distal articular ends, which emphasizes power in plantarflexion at the expense of speed (Barr, 2014). These interpretations are supported by the ecometric results showing the largest DistRad values in open habitats, and the largest B values in closed habitats (Fig. 5).

The results of the present study build upon existing scholarship documenting a link between bovid species-assemblage composition and habitat. For example, assemblages dominated by Antilopini (gazelles and allies) and Alcelaphini (wildebeest and allies) are

commonly considered indicative of open and arid habitats (Vrba, 1975, 1980), and these groups have had a long evolutionary history of association with open environments. At the other extreme, species assemblages dominated by Cephalophini (duikers) and/or Tragelaphini (bushbuck, bongo, eland, etc.) are often interpreted as indicative of habitats with more woody cover (Shipman and Harris, 1988; White *et al.*, 2009). Differences in locomotor morphology among bovids on these extremes of the habitat continuum are pronounced and well documented (Gentry, 1970; Kappelman, 1988, 1991). Therefore, it is perhaps unsurprising that species assemblages vary systematically in locomotor traits, and that this variation is strongly related to land cover.

The significance of the ecometric results presented here lies in the quantitative formalization of the relationship between assemblage-level locomotor traits and environmental variables. This study thus provides a bridge between species-level adaptations and higher-order trait patterns at the level of the species assemblage. This bridge in analytical scale makes it possible to use assemblage-level traits to infer broad-scale phenomena (i.e. the land cover and precipitation of a particular area). Thus, by demonstrating that assemblage-average postcranial traits are predictably related to environmental variables, this study provides a framework for interpreting assemblages of individual specimens – including fossils – in terms of important environmental variables.

Due to interest in understanding the context of human evolution, the African bovid fossil record has been well studied, particularly with regard to understanding the habitat preferences of fossil taxa (e.g. Vrba, 1975, 1980; Gentry, 1985; Haile-Selassie *et al.*, 2004; Geraads *et al.*, 2012; Bibi and Kiessling, 2015). The postcranial ecometric approach described here complements this body of work by shifting the analytical focus to the assemblage level, which creates opportunities to infer environmental parameters from fossil assemblage trait distributions.

Obstacles remain to the direct application of this method to postcranial fossil assemblages. The main issue is that identifying species based on fossil postcranial remains is extremely difficult. When faced with an assemblage of hundreds of astragali, for example, it may not be possible to group specimens by species. This means that it is difficult to estimate exactly the same ecometric variables (i.e. assemblage averages of species means) for fossil assemblages as for modern assemblages. Overcoming this difficulty requires reliable estimates of modern abundance data for bovids at the species level, which could then be used to weight species averages based on species relative abundance. Such weighted average of species means would be more directly comparable to fossil assemblage averages. However, reliable bovid census data are available from a relatively small number of game reserves and parks. The geographic distribution of these parks does not necessarily reflect the full extent of suitable habitat for bovid species, which is more fully captured in species distribution maps.

Finally, although rules of community assembly were not the focus of this study, this work has implications for understanding how bovid communities are assembled. Community assembly is often discussed in terms of three processes: habitat filtering, dispersal limitation, and competition (Blois *et al.*, 2014). Habitat filtering describes a process in which assemblages are sorted based on species' environmental tolerances. Habitat filtering is expected to produce assemblages in which the constituent species share similar functional traits. Species assemblages in different habitats would be expected to diverge in their functional traits. The results presented here clearly demonstrate that distinct habitat types support bovid species assemblages that differ systematically in their locomotor functional traits. While the study design does not allow for a potential role for competition and dispersal limitation to

be ruled out, the results of this study are consistent with habitat filtering as a strong force shaping bovid community assembly.

CONCLUSIONS

1. Bovid species assemblages differ systematically in their average locomotor trait distributions across environmental gradients.
2. Assemblage-average ecometrics of both the metatarsal and astragalus explain a large proportion of variation in annual precipitation and land cover.
3. Bovid locomotor ecometrics are more tightly linked to land cover than to annual precipitation.
4. Future work on bovid postcranial ecomorphology should focus on inferring environmental variables using assemblage-level ecometrics.

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APPENDIX: DATA TRANSFORMATIONS

Prior to analysis, all variables were size-standardized by dividing by a geometric mean size proxy computed for that anatomical element. Geometric means for the astragalus variables were computed using the following equation:

$$\text{geo-astragalus} = (\text{MML} * \text{WAF} * \text{ProxRad} * \text{DistRad} * \text{B})^{(1/5)}$$

For the metatarsal, the size correction procedure described in Scott and Barr (2014) was applied. This size proxy includes a carefully selected set of measurements and excludes length measurements from the calculation of the geometric mean. The reader is referred to Scott and Barr (2014) for additional details.

The use of these size correction procedures results in shape variables expressed as a proportion of the geomean size variable, and allows for meaningful shape comparisons between species of different overall body sizes (Jungers *et al.*, 1995).

As an example, consider the calculation of the size-adjusted value of the functional length of the astragalus (B) for the species *Hippotragus equinus*. Species means for the astragalus variables in *H. equinus* are as follows: B = 23.07, DistRad = 15.90, ProxRad = 17.77, MML = 56.50, WAF = 36.32. The geometric mean of these measurements is $(23.07 * 15.90 * 17.77 * 56.50 * 36.32)^{(1/5)} = 26.62$. The value of B for this species is divided by this geometric mean to produce the size-adjusted value of B: $23.07/26.62 = 0.867$.

In order to compare the effect sizes of different variables in GLM, these size-corrected variables were further transformed to z-scores by subtracting the mean and dividing by the standard deviation of each variable using the `base::scale()` function in R. For example, consider five hypothetical species with size-adjusted values of B as follows: species A = 0.85, species B = 0.84, species C = 0.95, species D = 0.81, species E = 0.90. The mean of these measurements is 0.87, and the standard deviation is 0.055. The mean is subtracted from each value, which results in the following numbers: species A = -0.02, species B = -0.03, species C = 0.08, species D = -0.06, species E = 0.03. Finally, each measurement is divided by the standard deviation, which results in the final scaled variables: species A = -0.36, species B = -0.54, species C = 1.45, species D = -1.09, species E = 0.54. These measurements reflect how far each measurement is from the mean of the distribution, in standard deviation units. This procedure is applied to all variables, and these scaled variables are used in the GLM analyses as described in the main text.

