Climatic Variables Alone do not Determine Ungulate Community Composition in the Afrotropics

Abstract

The relative importance of the different processes that determine the assembly of communities of species is a key question in ecology. The distribution of any individual species is affected by a wide range of environmental variables but potentially also by its interactions with surrounding species, with these distributions determining the overall community. A challenge in community ecology is that these interactions are often not directly measurable. Here, we used Hierarchical Modelling of Species Communities (HMSC), a recently developed framework for joint species distribution modelling, to estimate the role of biotic effects alongside environmental factors through the use of latent variables. We investigate the role of these factors in community assembly in ungulate communities in the Afrotropics, an area of peak ungulate species richness. We also calculate pairwise trait dissimilarity between ungulate species and investigate the relationship between dissimilarity and estimated residual co-occurrence in the model. We find that while ungulate communities appear to be predominantly determined by key climatic variables, such as precipitation, a proportion of the variance in ungulate species distributions can also be attributed to modelled latent variables. Although we only find a weak relationship between residual co-occurrence and trait dissimilarity, we suggest our results may show evidence that biotic interactions, likely influenced by historical barriers to species dispersal, are important in determining species communities on a continental scale. The HMSC framework shows great promise, not only for its potential to provide insight into factors affecting community assembly on a continental scale, but also for its ability to make more powerful predictions about future species distributions as we enter an era of increasing impacts from anthropogenic change.

Introduction

A central challenge in community ecology is understanding the factors that determine the assembly of species communities. A species community, here defined as the total assemblage of the species that co-occur at the same place at the same time (Krebs, 1972), is determined by the individual distributions of the species that comprise it. The factors that influence community assembly are varied, including phylogeographic effects (such as speciation, extinction and dispersal), environmental conditions and biotic interactions among species (Lawton, 1999; Hubell, 2001; Vellend, 2010; Stegen et al., 2013). In community ecology, these effects are often viewed as a series of filters (Zobel, 1997), with historical phylogeographic effects such speciation and dispersal acting as the first filter to create a regional pool of species that are theoretically able to be part of a community. Local environmental conditions act as a second filter to further limit the regional pool to the subset of species that are adapted to an area's climatic or geophysical conditions. Finally, interactions among species, such as plant-pollinator mutualisms or competition among ecologically similar species, can further affect community assembly by excluding species that would otherwise be able to persist in an area's environmental conditions. While these factors all influence community composition (Lortie et al., 2004; Sexton et al., 2009; Meier et al., 2010), their relative importance is often unclear.

The importance of biotic interactions in determining community composition has been a particular source of debate (Louthan et al., 2015; Pigot & Tobias, 2013; Wiens, 2011). Not only is it unclear to what extent biotic interactions might influence community compositions, it is also unclear at what scale such effects might be predicted to act. Some suggest that biotic interactions are typically likely to only be significant at highly local scales (i.e., $<10km^2$) rather than on ecoregion or biome-wide scales (Pearson & Dawson, 2003; Soberón & Nakamura, 2009). Others, however, stress the importance of biotic interactions at broader spatial extents (i.e., $>10km^2$; Wisz et al., 2013). Empirical evidence remains inconclusive, with some studies suggesting weaker but still present biotic effects at broader spatial scales (Bullock et al., 2000; Belmaker et al., 2015; Staniczenko et al., 2017; Mod et al., 2020), while others have suggested a key role for biotic

effects in determining range limits, especially at lower latitudes (Siren et al. 2021; Freeman et al. 2022), with competition in particular highlighted as the most important biotic effect in determining community composition (Staniczenko et al., 2018). Understanding how and at what scales biotic interactions affect community assembly remains a key goal in community ecology.

Joint species distribution models (JSDMs) offer a promising approach to investigating questions about the relative importance of environmental and biotic factors in community assembly, by allowing the responses of multiple species to their environment and to each other to be modelled simultaneously (Ovaskainen et al., 2017). These models use commonly collected and readily available ecological data, such as presence-absence data or count data. At a broad spatial scale, the former is widely available for many vertebrate species through the species geographic range polygons provided in the International Union for Conservation of Nature (IUCN) Red List (IUCN, 2023).

Although JSDMs are a powerful method for understanding community assembly, biotic effects can still only be inferred with the use of latent variables, rather than being directly measured (Warton et al., 2015). If it is the case that competition plays a meaningful role in ungulate community assembly, we would expect ecologically similar species to be less likely to occur together than expected from environmental conditions alone, as species with more similar functional traits are more likely to show niche overlap and therefore competitively exclude each other, limiting the overlap of distributions (Gause 1934; Hardin, 1960; Abrams, 1983; Booth & Murray, 2008). Therefore, as part of investigating the relative influence of biotic effects and abiotic effects on community composition, here, we assess the extent to which latent variables can be attributed to biotic effects by looking at how residual associations they capture correlate with trait dissimilarity.

We expect the residual associations between species (defined by the latent variables) to fall along roughly biogeographic boundaries as outlined by Lorenzen et al. (2012). These boundaries will

roughly reflect differences in communities due to both dispersal limitations imposed by geographical barriers and range limits due to biotic effects, therefore we predict that the model will reflect these after controlling for climate variables. Further, we predict that species with more similar traits are less likely to co-occur than would be expected from environmental conditions alone.

The Afrotropics are the most diverse region on Earth for ungulates (Du Toit & Cumming, 1999) with close to 30 species occurring in sympatry in areas of peak species richness (IUCN, 2022). The importance of biotic interactions among ungulate species in determining their distributions is unclear. Ungulates have a high degree of dietary overlap, typically having a predominantly or entirely herbivorous diet of fibrous plant material. This overlap suggests potentially high levels of competition among ecologically similar species. However, African ungulates show significant variation in morphology, both in body size, digestive system and dietary specialisation (i.e., browsing versus grazing), which may reduce interspecific competition (Veldhuis et al., 2019). Furthermore, in comparison to other mammalian clades, wild ungulates rarely exhibit direct interspecific interference (Ferretti & Mori, 2020); although we note that this is not the only mechanism by which competition can occur. One reason for the relatively limited evidence of competitive interference in ungulates may be due to predation pressure favouring the evolution of mutualistic antipredator strategies, such as herding, rather than competitive behaviour (Sinclair, 1985; Caro, 2005). It is therefore unclear the extent to which biotic interactions will affect range limits in ungulates. Understanding all relevant factors is crucial for predicting the impact of future changes in ungulate distributions resulting from climate change and anthropogenic pressure. This is especially pertinent, given the multiple ungulate species in Africa that are of conservation concern. For example, within antelopes, the largest grouping of ungulates, populations are decreasing in 61% of species (IUCN SSC Antelope Specialist Group, 2022). Furthermore, previous work has highlighted that already threatened ungulate species are likely to be disproportionately affected by climate change related range reductions (Payne & Bro-Jørgensen, 2016). Here, we use

107 species range data collected from the IUCN Red List together with publicly available climate data

108 to investigate the drivers of ungulate community composition on a continental scale using JSDMs.

Methods

Data collection

We included all ungulate species (orders *Artiodactyla* and *Perissodactyla*) that had at least some of their native range in continental Africa (n = 98). In addition to ungulates, we included both species of African elephant (*Loxodonta cyloctis* and *Loxodonta africana*) because, although not closely related to other species in the model, as mega-herbivores they are plausible candidates for competition with predominantly herbivorous ungulates (Ferry et al., 2016). We excluded both African rhino species (*Diceros bicornis*, *Ceratotherium simum*) as the IUCN range maps for these only show countries where these species are present rather than exact distributions due to risks from poachers. Shapefiles for all species ranges were taken from the IUCN Red List (IUCN, 2018), selecting only shapefiles for parts of the range where the species was both extant and native. These shapefiles were converted into a presence-absence matrix with a resolution of 10 arcminutes using the R package letsR (Vilela & Villalobos, 2015). To focus exclusively on the Afrotropics, we selected only points south of 15°N.

We note that using IUCN range data places some limitations on this work. The IUCN range for a species indicates that the species likely occurs within these limits, but does not imply it is distributed evenly across that range or that it occurs at all points within it, and this is particularly problematic at finer spatial scales (IUCN SSC Red List Technical Working Group, 2021). Using IUCN range data also means we can only consider presence/absence in species distributions rather than abundance, which may vary substantially across a specie's range, particularly at range limits (Yancovitch Shalom et al., 2020). Both of these factors mean that negative associations among species may be underestimated by our models, as we do not have information on how competition among species can impact abundance and we may miss finer-scale spatial segregation between species that may occur even if their ranges overlap at coarser scales. Despite these limitations, we consider the IUCN range data to be the best source currently available for ungulate ranges in the Afrotropics as it is available for all species and all areas of the

region, in contrast to other sources that are biased towards the Global North (e.g. Global Biodiversity Information Facility; GBIF).

To control for the effect of human activities on ungulate distributions, we selected only points that fell within highly protected areas, reasoning that these areas were most likely to have "natural" ungulate communities, with community composition relatively unaffected by human activity. We downloaded shapefiles for African protected areas from the World Database on Protected Areas (WDPA; UNEP-WCMC & IUCN). These were filtered to select only IUCN category Ia (Strict Nature Reserve), Ib (Wilderness Area) and II (National Park) protected areas. Data on the IUCN category was not available for all protected areas in WDPA. Therefore, we also selected protected areas with the self-described designation "national park". To further control for the effect of human influence, we used the FAO's Global Land Cover-SHARE database (Latham et al., 2014) to remove points where the dominant land cover was cropland or urban surface, and removed points where land cover was not recorded or where the dominant cover was open water, i.e. lakes.

All bioclimatic variables were taken from WorldClim (Fick & Hijmans, 2017). We used annual mean temperature (°C), annual precipitation (mm), mean diurnal range (°C) and precipitation seasonality (coefficient of variation) (mm). We calculated the variance inflation factor for each of these variables; all were between 1 and 1.2, indicating no multicollinearity in the model.

At a simplified level, the Afrotropics can be divided into two broad vegetation zones, open grasslands and tropical rainforests (Lorenzen et al., 2012), with the difference between the two largely determined by level of precipitation and wildfire (Staver et al., 2011). We reasoned that biotic interactions would be especially prominent in determining the distribution of species within a biome, rather than between biomes (as here the climatic differences between the highly different habitats would be expected to be pre-eminent in determining the distributions). Therefore, for the JSDMs (see below), we fitted models for different Afrotropical biomes separately, fitting two models. One used only points from within the Tropical & Subtropical Moist Broadleaf Forests biome (hereafter, the Tropical Forests model), including 45 species, and one that contained all points **not**

in this biome, covering a range of open and semi-open habitats (hereafter, the Open Habitats

model), which included 46 species. We obtained data on biomes using shapefiles taken from the

RESOLVE Ecoregions map (Dinerstein et al., 2017).

Trait data for body mass and body length were taken from COMBINE, a database of intrinsic and

extrinsic mammalian traits (Soria et al., 2021). This database did not recognise the African forest

elephant (*Loxodonta cyclotis*) as a distinct species from the African bush elephant (*Loxodonta

africana*), so this species was excluded from dissimilarity analyses (see below). Data on diet for

most species was taken from Gagnon & Chew (2000). From this paper, we recorded the proportion

of fruit, dicotelydon plants, and monocotyledon plants in the diets of all extant African Bovidae

(aside from Caprinae), which made up the majority of species in our models. We also recorded

whether diet showed seasonal and/or geographic variability (a binary Yes/No). For species not

covered by Gagnon & Chew (2000), i.e. all odd-toed ungulates, the African bush elephant and

even-toed ungulates outside of Bovidae, we estimated these variables with reference to Schlitter et

al (2014). Finally, for all species, we recorded the digestive system (i.e. monogastric, ruminant or

pseudoruminant). Overall, for the Open Habitats model we were able to record complete trait data

for all 46 species included in the model and for the Tropical Forests model, we had complete trait

data for 44 out of 45 (i.e., all except African forest elephant).

Analyses

All analyses used R version 4.1.1 (2021-08-10) (R Core Team 2023). All R code is available on

GitHub at *removed to anonymise manuscript for peer review* [Zenodo DOI to be added after

acceptance]. The core analyses in HMSC (see below) were conducted using a modified version of

the HMSC pipeline made publicly available by the package authors and available at

https://www.helsinki.fi/en/researchgroups/statistical-ecology/software/hmsc.

Joint species distribution models

We used joint species distribution models (JDSMs) to evaluate the relative impact of biotic and abiotic factors on ungulate species distributions, specifically using the Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017) approach. We chose HMSC due to its relative ease of use and excellent predictive power in comparison to other comparable methods (Norberg et al., 2019). HMSC uses generalised linear mixed models (GLMMs), fitted using Bayesian inference, where latent variables are estimated to explain the residual variation in species' occurrences, i.e., the variation not explained by the fixed effects of the model (Tikhonov et al., 2020). Typically, these fixed effects are directly measurable environmental variables, while the latent variables may estimate variables that are difficult or impossible to measure directly, such as biotic factors like competition or facilitation among species. However, it is important to note that these latent factors may also capture unexplained environmental variation and it is not possible to interpret them as representing a specific variable with 100% confidence.

Using HMSC, we fitted a probit model to estimate the probability of presence for each species at each point in our dataset. Each model used a random sample of 300 points per model from our overall dataset to make running the models computationally feasible. The models that we used failed to accurately explain the distribution of very rare species. Therefore, for each model, we included only species that had a prevalence of at least 5% in the sample of data used. We note that for the Tropical Forests model, this prevalence threshold meant that a significant number of species typically regarded as savannah or open habitat specialists, ended up being included in the model, i.e. Common Eland (*Tragelaphus oryx*). This is likely due to the low spatial resolution of both the IUCN and RESOLVE Ecoregions map. Low resolution, or coarseness, likely leads to a higher degree of overlap of these savannah species' ranges with the Tropical & Subtropical Moist Broadleaf Forests biome than is truly representative of these species' habitat preferences. However, we chose to proceed with this threshold as setting it any lower in an effort to remove all savannah/open habitat species would lead to also removing tropical forest species of interest, such

as Jentink's Duiker (*Cephalophus jentinki*) and Zebra Duiker (*Cephalophus zebra*), which have very limited ranges.

In addition to our fixed environmental variables, we used spatially explicit latent variables in an attempt to model the residual associations between ungulate species. HMSC uses a Markov chain Monte Carlo (MCMC) approach to sample the posterior distribution for each parameter estimated by the model. For our models, we used four chains, and each was run for 37,500 iterations. We discarded the first 12,500 iterations as burn-in and then thinned by 100 to yield 250 posterior samples for each chain. We checked MCMC convergence for each model using a potential scale reduction factor. In each model for each parameter inspected, this factor was close to 1 and MCMC convergence was deemed to be satisfactory.

We evaluated model fit for each species in the model using root mean squared error (RMSE), and Tjur's R^2 (for both explanatory and predictive power). We estimated predictive power using two-fold cross-validation in the HMSC R package. After running the models, we estimated the relative importance of environmental versus biotic factors in determining species distributions by partitioning the variance explained by each of the fixed effects and the latent variables. We also examined the residual associations among ungulate species captured by the latent variables, plotting these as a correlation matrix using the gplots package (Warnes et al. 2009), with positive values indicating a higher degree of co-occurrence than would be expected from environmental conditions alone (and vice versa), with only values with over 95% support deemed statistically significant.

Trait dissimilarity Analysis

We calculated pairwise dissimilarity in our chosen traits between species using Gower's distance (Gower, 1971), implemented in R through the package "gower" (van der Loo, 2022). This gives a value of 1 for species that had maximally dissimilar traits and 0 for species where the traits were

identical. We then took the omega values estimated by HMSC; these are pairwise estimates of the

residual association between species, i.e. the extent to which species are expected to co-occur

after controlling for the fixed effects. We excluded omega values with less than 95% support and

then fitted a linear regression of pairwise Gower's distance against omega. Higher omega indicates

high association between species, so if our hypothesis that more dissimilar species were more

likely to associate with each other was true, we expect to find a positive correlation between

omega and Gower's distance.

Results

Joint species distribution models

Both the explanatory and predictive power of both models was relatively high (Open Habitats: RMSE = 0.20, mean Tjur's R^2 = 0.67, mean Tjur's R^2 with cross-validation = 0.59; Tropical Forests: RMSE = 0.14, mean Tjur's R^2 = 0.73, mean Tjur's R^2 with cross-validation = 0.63) although this varied significantly across species; for example, in the Open Habitats model, Tjur's R^2 ranged from 0.20 for the hippopotamus (*Hippopotamus amphibius*) to 0.95 for the East African oryx (*Oryx beisa*). There was no relationship between extent of occupancy and Tjur's R^2 in either model (Open Habitats: R^2 = 0.0053, $F_{1,44}$ = 0.23, p = 0.632; Tropical Forests: R^2 = 0.063, $F_{1,43}$ = 2.89, p = 0.096).

In both models, the majority of the explained variance was attributable to the climatic fixed effects. In the Open Habitats model, 69% was explained by the climate factors versus 31% by spatial random effect, while in the Tropical Forests model, the proportion was 70% to 30%. Again, in both models there was a great deal of variation across species (Figure 1), with some species in some models having the majority of their explained variance attributed to the spatial random effect, for example, the impala (*Aepyceros melampus*) in the Open Habitats model.

The residual associations among species were plotted in a correlation plot for all models (Figure 2). The Open Habitats model had five clusters (plus five species that did not appear to belong to any cluster). The first consisted largely of species with most of their distribution occurring in West Africa, such as the kob (*Kobus kob*) and the red-flanked duiker (*Cephalophus rufilatus*). The second, largest, cluster, consisted of species typical of southern and eastern African savannas, such as the greater kudu (*Tragelaphus strepsiceros*) and the plains zebra (*Equus quagga*). The third cluster consisted largely of species with most of their distribution occurring in arid regions of the Horn of Africa (Ethiopia, Somalia, north-east Kenya), such as Günther's dik-dik (*Madoqua guentheri*), and East African oryx (*Oryx beisa*). Finally, two small clusters were also present. The

first consisted largely of species that have the bulk of their range in the tropical forest biome, that nonetheless had a high enough occupancy to be included in the Open Habitats models, such as yellow-backed duiker (*Cephalophus silvicultor*) and blue duiker (*Philantomba monticola*). Finally, there was a small cluster of four species (hippopotamus, puku, roan antelope, and southern reedbuck); the distributions of these species show limited similarity, leaving this last cluster harder to explain.

In the Tropical Forests model there were three clusters (plus four species that did not appear to cluster with any other). The first cluster consisted largely of species with most of their distribution occurring in the Congolian rainforest region, such as Peters' duiker (*Cephalophus callipygus*). The second consisted largely of species with most of their distribution occurring in the Guinean forests of West Africa, such as Jentink's duiker (*Cephalophus jentinki*) and Maxwell's duiker (*Philantomba maxwellii*). Finally, the third cluster appeared to mostly contain the typical savannah species (such as African bush elephant) which fell into this model due to reaching the 5% prevalence threshold (see Methods). However, it also contained species with most of their distribution occurring in the East African montane or coastal tropical forests, such as Harvey's duiker (*Cephalophus harveyi*) and the suni (*Nesotragus moschatus*).

We plotted the values of the latent variables at each point in the model, with Kriging interpolation to more easily visualise gradients over the entire biome. Each model estimated a total of five latent variables to explain the residual variation in species occupancy; however, in both the Open Habitats and the Tropical Forests model, only the first two latent variables made a substantial contribution to the model. Therefore, only these variables are discussed here (Figures 4 and 5).

In the Open Habitats model, the first latent variable (Figure 4A) shows that the main axis of difference was between the West African and the Southern and Eastern African savannahs. The second latent variable (Figure 4B) shows the secondary axis of difference was between the Horn

307 of Africa and Southern and Eastern African savannahs. Taken together, this suggests that these

308 three regions all have differences in ungulate community composition not explained by climate

309 effects alone.

310

311 In the Tropical Forests model, the first latent variable (Figure 5A) shows that the main axes of

312 difference was between the East African coastal rainforests and all other areas of the biome, while

313 the second latent variable (Figure 5B) shows the secondary axes of difference was between the

314 Guinean rainforest and all other areas. As in the Open Habitats model, this overall indicates that

315 the three main areas of rainforest (the Western Guinean forests, the central Congolian rainforest,

316 and the eastern coastal forests) all have distinct ungulate communities not explained by climate
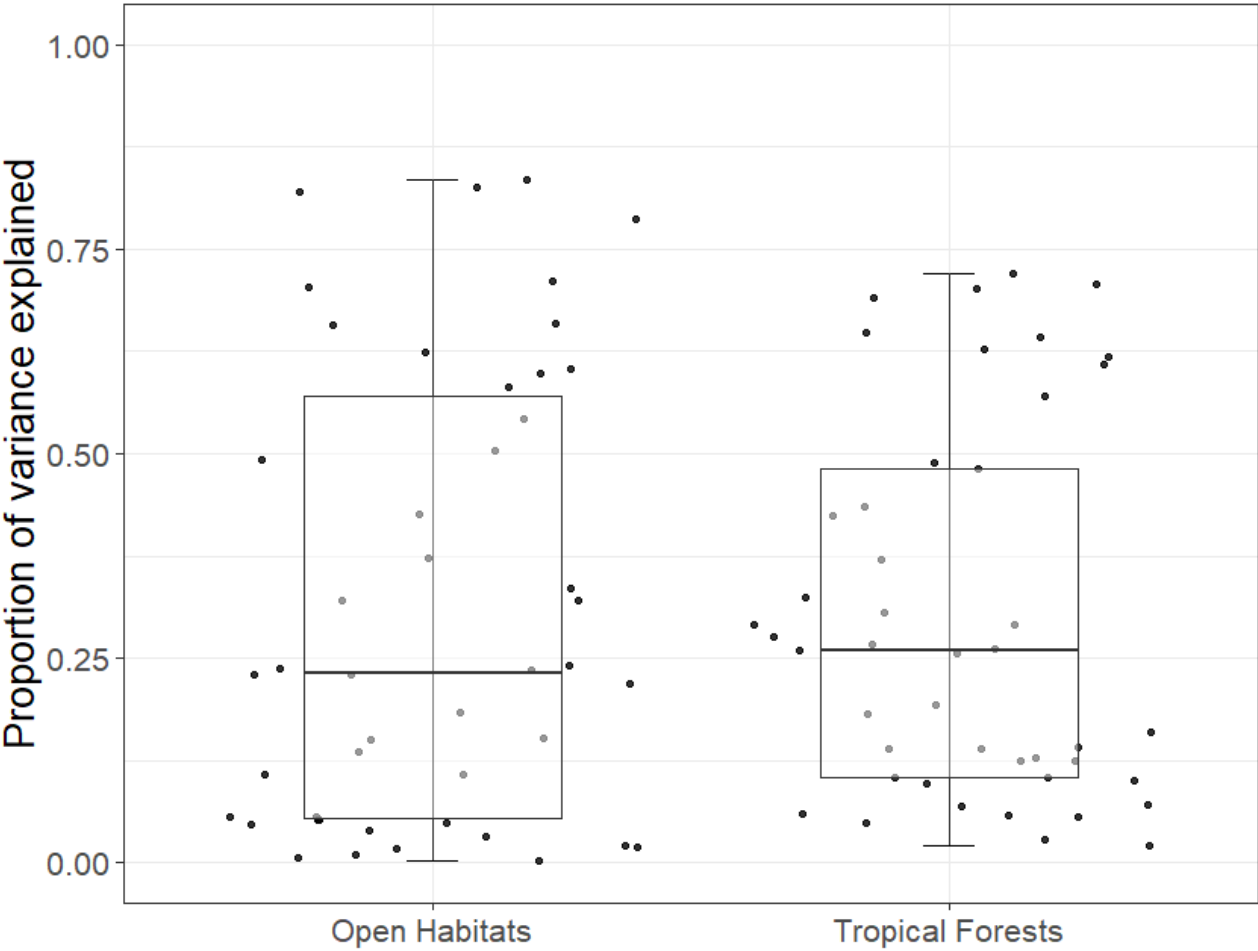
317 effects alone.

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Figure 1: Proportion of explained variance in species presence/absence attributed to the random effect (latent variables) in the Open Habitats model and Tropical Forests model.

Trait dissimilarity analysis

There was a extremely weak but significant negative relationship between pairwise trait dissimilarity (measured using Gower's Distance) and residual association (measured using the omega parameter estimated in HMSC) in both the Open Habitats model (R^2 = 0.0244, $F_{1,520}$ = 13, p < 0.001) and the Tropical Forests model (R^2 = 0.0450, $F_{1,500}$ = 23.55, p < 0.001), indicating that, contrary to our hypothesis, more dissimilar species were less likely to co-occur with each other.

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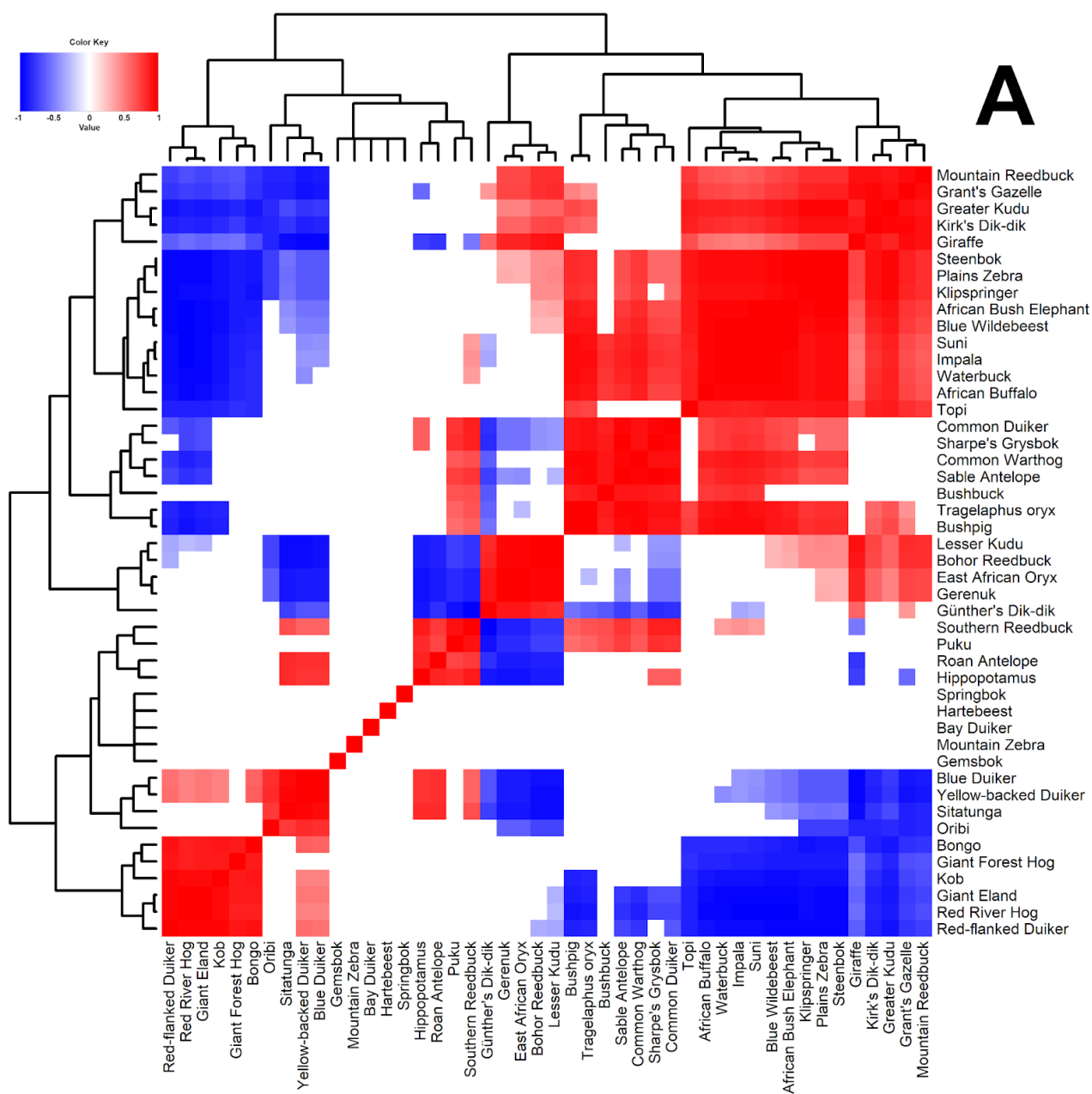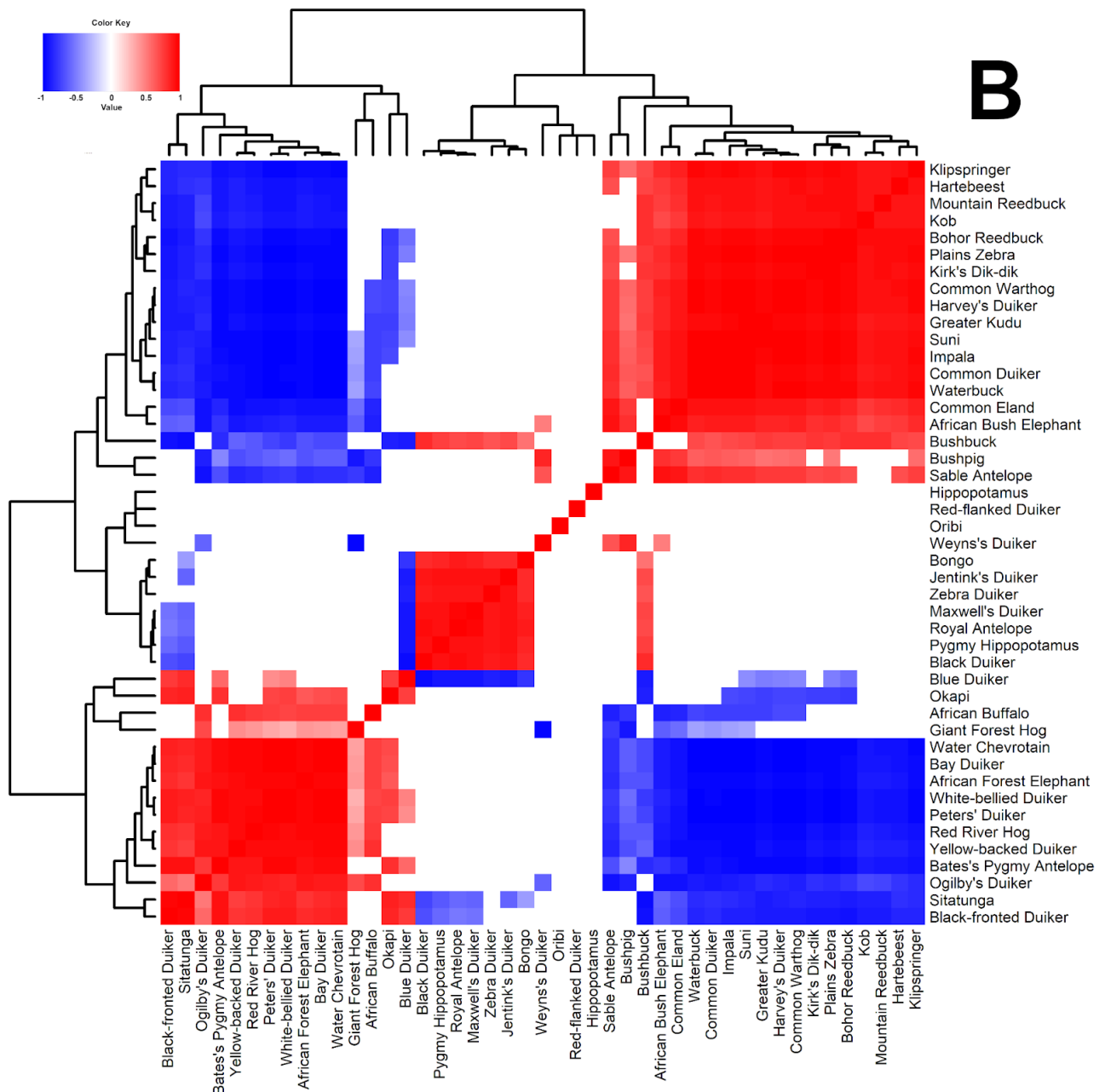
Figure 3. Correlation plots showing residual associations between species in the Open Habitats model (A) and Tropical Forests model (B). Red indicates that the residual association between two species is significant and positive, i.e. species are more likely to co-occur than would be expected from the environmental factors included as fixed effects in the model. Blue indicates the reverse, i.e. species are less likely to co-occur than would be expected from the environmental factors included as fixed effects in the model. Only significant values are shown, white indicates non-significant values. The dendrograms on the top and left axes show clustering of species with similar values, i.e. species that are broadly associated with each other.
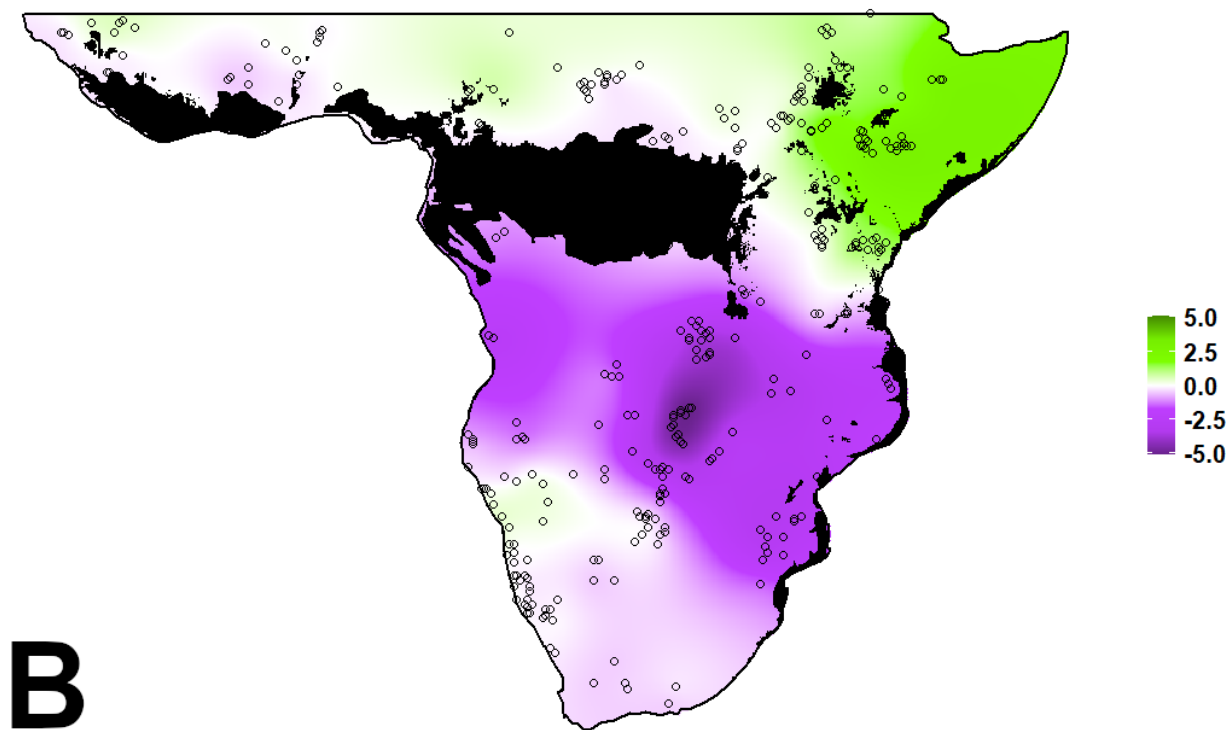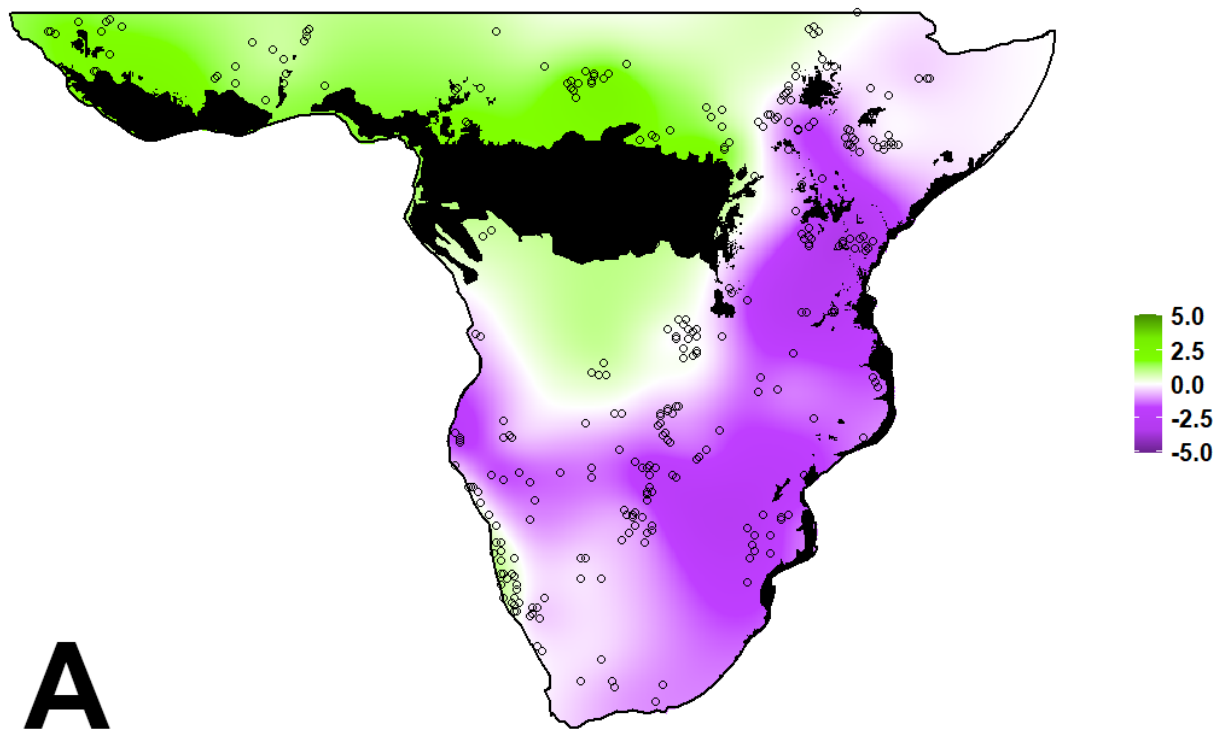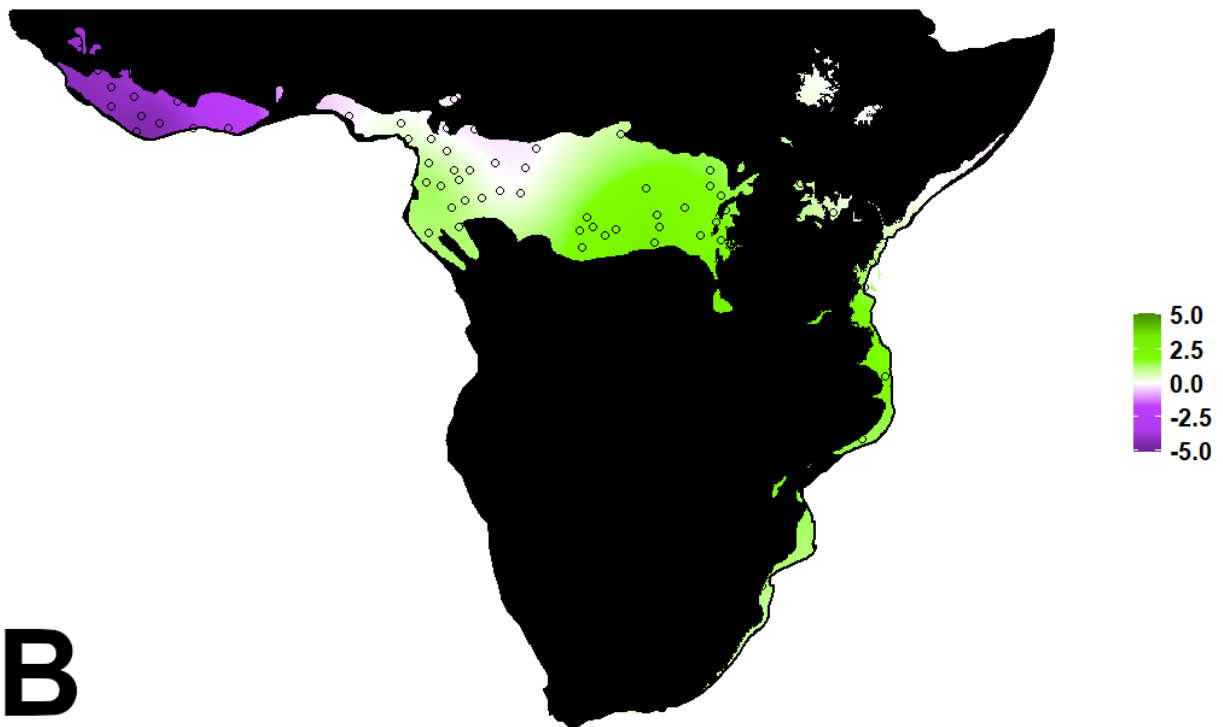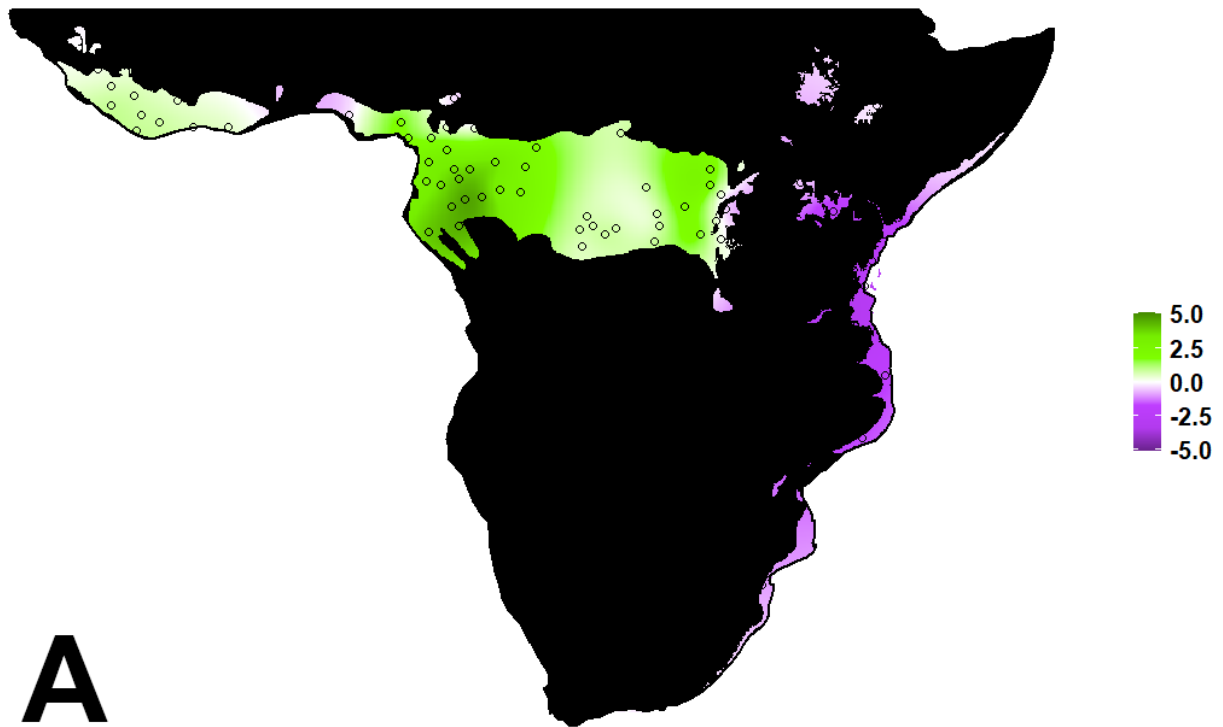
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345 Figure 4. The site loadings values of the first (A) and second (B) latent variable from the Open

346 Habitats model for all points in the model interpolated across the Afrotropics (aside from tropical

347 forests areas) using Kriging interpolation. These site loadings show differences in ungulate

348 communities after controlling for climate differences included in the fixed effects of the model.

349 Areas with positive values have more different communities compared to areas with negative

350 values than expected for climate alone. Sample sites in the model are shown by the hollow circles.

351 Areas in black indicate areas belonging to the Moist Tropical Forest biome which were not included

352 in this model and hence not interpolated over. Site loadings values plotted without interpolation, are

353 in the supplementary materials (Supplementary Materials: Figure S1).

354

357 Figure 5. The site loadings values of the first (A) and second (B) latent variable from the Tropical

358 Forests model for all points in the model interpolated across the entire moist tropical forest biome

359 in the Afrotropics, using Kriging interpolation. These site loadings show differences in ungulate

communities after controlling for climate differences included in the fixed effects of the model. Areas with positive values have more different communities compared to areas with negative values than expected for climate alone. Sample sites from the model used to produce this interpolation are shown by the hollow circles; note that to successfully interpolate, these points required thinning as some were very close together and therefore only 71 of the 300 used in the JSDM were used for Kriging interpolation. Areas in black indicate areas that do not belong to the moist tropical forest biome which were not included in this model and hence were not interpolated over. Site loadings values plotted without interpolation are in the supplementary materials (Supplementary Materials: Figure S2).

Discussion

HMSC successfully detects biogeographic patterns

Our results indicate that while climate is the primary determiner of ungulate distribution in the Afrotropics (after controlling for the influence of human activity), it is not the only important factor with the latent variables revealing significant differences in ungulate community composition even after controlling for climatic conditions. Contrary to our expectations however, there was only a very weak (Open Habitats model: R^2 = 0.0244; Tropical Forests model: R^2 = 0.0450), but significant, negative relationship between residual association and trait dissimilarity, with more dissimilar species being marginally less likely to be significantly associated after controlling for the environment.

In the Tropical Forests model, significant differences exist between ungulate communities in the Congolian rainforests and the Western Guinean and Eastern African montane and coastal rainforests. This result was not unexpected as the African tropical rainforest biome is noncontiguous, with the areas of tropical grassland potentially acting as barriers between areas of rainforest, such as the Dahomey Gap between the Western Guinean region and the Congolian region (Salzmann & Hoelzmann, 2005). It is likely that the latent variables in our model are capturing these barriers to dispersal that result in differences in community composition even after controlling for climate. These barriers have not been stable over evolutionary history; pollen records indicate that the Dahomey Gap, for example, has fluctuated in size over the last 150,000 years, including disappearing completely during periods of maximum forest expansion (Dupont & Weinelt, 1996). Furthermore, multiple lines of evidence suggest expansion of open savannah grasslands, and corresponding contraction of wooded habitats, in East Africa over the last 10 million years (Cerling et al., 1997; Bobe et al., 2002; Cerling et al., 2011; Uno et al., 2016). These fluctuations in forest cover, and the expansion and contraction of barriers of unsuitable habitat have likely led to some community differences between regions while still allowing some admixture, with species such as the bay duiker (*Cephalophus dorsalis*) distributed across both the Congolian and Guinean forests. Genetic differentiation in other taxa, such as coffee (Gomez et al.,

2009; Labouisse et al, 2020), supports the idea that the Dahomey Gap acts as a biogeographic barrier to dispersal and gene flow. Similar differentiation can be seen in primates between populations in Congolian forests and in Kenyan and Tanzanian coastal rainforests (McDonald et al., 2022).

Historical biogeographic barriers may offer a similar explanation for the results seen in our Open Habitats model. Correlation plots and the site loadings from the latent variables suggest differences in community composition between West African savannahs and East Africa, and differences between the Horn of Africa and the rest of the continent. The Great Rift Valley (GRV) lies perpendicular to the main gradient in the first latent variable from the Open Habitats model (Figure 4). The GRV acts as both a topographical and climatic barrier for some highland specialist species in Ethiopia (Evans et al., 2011; Freilich et al., 2016) and a mosquito species in Kenya (Lehmann et al., 1999). However, the extent to which it has posed a barrier to ungulate populations over evolutionary history requires more research.

In addition to the GRV, historical vegetation barriers may explain the results seen in this model. As described above, extent of tropical forests in sub-Saharan Africa has fluctuated significantly, with alternating periods of relative dryness and relatively high precipitation (Dupont, 2011), with climate modelling suggesting that in wet periods, tropical forest may have expanded to cover most of central Africa in a continuous belt from the west to east coasts (Cowling et al., 2008). This would have prevented species dispersal between remaining areas of savannah habitat in West Africa and the Horn of Africa with savannah habitats in Southern Africa.

The boundary between these regions appears to match closely the proposed boundaries between Sudanian, Somalian, and Zambesian biogeographic regions proposed by Linder et al., (2012; see their Figure 2). As well as representing boundaries between areas with distinct ungulate community composition, these boundaries reflect genetic differences within species that range

across these zones which have been shown to have genetic differentiation between populations in West Africa and South/East Africa, i.e., the common warthog (*Phacochoerus africanus*; Lorenzen et al., 2012). Similar genetic differentiation is seen in savannah species other than ungulates, such as ostriches (Miller et al. 2010) and lions (Barnett et al., 2006).

Do biotic effects influence ungulate communities?

Taking the above context into account, we conclude the latent variables estimated by HMSC are likely capturing a combination of dispersal limitations due to present-day biogeographic boundaries and biotic effects. Under this interpretation, historically these barriers will have prevented population movement and gene flow between areas of contiguous suitable habitat. This would enable genetic differentiation and allopatric speciation. In the present day, these biogeographic barriers appear to have partially disappeared (in the context of the Open Habitats model) but our model suggests that differences in community are maintained by biotic effects and differences in climate. It is important to reiterate that the latent variables cannot be assumed to automatically reflect either biotic effects or dispersal limitations as they estimate all variation not explained by the fixed effects in the model. Therefore, they could equally represent unexplained environmental variation not captured by the fixed effects. Our trait dissimilarity analysis found only a very negative weak relationship between residual association and ecological trait similarity in both models, so we have no direct additional evidence that would support the interpretation of these latent variables as biotic effects specifically. Indeed, a negative relationship may suggest that the latent variables are at least partly capturing environmental variation. This would explain why species with more similar traits are marginally more likely to co-occur after controlling for the environment. However, the overall relationship between trait similarity and association was so weak that arguably no meaningful interpretation can be drawn from it. This may indicate that dispersal limitations are the dominant underlying driver of these latent variables, especially in the Tropical Forests model. A bigger role for dispersal limitations in the Tropical Forests model would make sense, as the areas of moist tropical forest are highly fragmented in the Afrotropics (as previously discussed) whereas open habitats are broadly contiguous, with limited evidence existing for the effect of potential barriers such as the GRV on ungulate dispersal.

An alternative explanation for the unexpected relationship between residual association and similarity may be a function of how HMSC estimates values for residual association. As discussed above, HMSC does not estimate the residual association between each individual species pair, as in large species communities, this would lead to an enormous number of parameters being estimated. Instead, HMSC uses latent variables which model residual associations for all species pairs simultaneously, effectively summarising the main axes of residual variation. This greatly reduces the number of parameters needed to be estimated for the model but it introduces the limitation of necessarily simplifying the covariance matrix between all species in the model (Warton et al. 2015). This reduction in the number of parameters may introduce bias into the estimates of covariance between species by unintentionally forcing spurious associations between species whilst trying to approximate the overall structure of associations with fewer parameters than there are species pairs (Pichler & Hartig, 2021). This appears to lead to clustering of species that may show limited co-occurrence in reality, which in turn will introduce noise that may explain why the relationships between association and similarity are so weak and not in the direction we predicted. For example, in both models, we see species with little or no overlap in their ranges, such as the Kob and Harvey's Duiker in the Tropical Forests model (found in West African Savannah habitats and East African coastal forests respectively), have a high omega value, indicating higher than expected residual association, despite no actual association in the data. This is because the residual association in this model is dominated by two latent variables; the first shows a gradient between Congolian rainforest and all other areas of the biome (Figure 5A), and second shows a gradient between Guinean rainforest and all other areas of the biome (Figure 5B), effectively inducing residual associations among species that do not fall within either of these two regions, even if they have very different ranges.

Conclusions

We found that climatic conditions were the primary driver of community assembly in Afrotropical ungulate communities, while dispersal and biotic effects (as interpreted from the latent variables estimated by HMSC) played a secondary role. These latter effects led to differences in community structure that closely match the conclusions of previous studies around the phylogeographic

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structure of African ungulates (Lorenzen et al. 2012). In addition to offering an insight into the factors

determining ungulate community composition, joint species distribution models such as the one

presented here may be used to predict how those communities are likely to respond to anthropogenic

climate change. HMSC compares very favourably both to SDMs and other JSDMs in terms of

predictive power (Norberg et al., 2019). Moreover, our results show that the predictive power

(measured with Tjur's R^2) of both our models is relatively high; 0.62 for the Tropical Forests model

and 0.59 for the Open Habitats model. The latent variable approach implemented in HMSC

therefore offers potential insights into factors affecting community assembly and exciting

possibilities for making more powerful predictions about future distributions than we can from

climatic effects alone. This is crucial at a time when anthropogenic effects are increasingly

threatening ungulate populations across the African continent.

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