




RESEARCH PAPER

Reconstructing the climatic niche breadth of land use for animal production during the African Holocene

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Abstract

Aim: Domestic animals first appeared in the archaeological record in northern Africa c. 9000 years before present and subsequently spread southwards throughout the continent. This geographic expansion is well studied and can broadly be explained in terms of the movement of pastoralist populations due to climate change. However, no studies have explicitly evaluated changes in the climatic niche of these domesticates. A priori, one cannot assume a relationship between the geographic spread of animal production and changes in climatic niche breadth because their relationship is highly variable. Therefore, we investigated Holocene changes in the climatic niche of domestic animals (animal production) and compared these to changes in the climatic niche of hunted terrestrial ungulates.

Location: The African continent.

Time period: 9000–500 BP.

Major taxa studied: Domestic animals, hunted (wild) terrestrial ungulates.

Methods: For the first time, we applied methods from environmental niche dynamics to archaeological data to reconstruct and quantify changes in the climatic niche breadth of animal production during the African Holocene. We used faunal remains from archaeological assemblages and associated radiocarbon dates to estimate the proportion of the African climate space used for animal production and hunting at 500-year intervals.

Results: We found that the climatic niche of domestic species broadened significantly with the geographic spread, most notably during the termination of the African Humid Period, whilst no such broadening occurred for the climatic niche of hunted species.

Main conclusions: Our results provide a quantitative measure of the extent to which humans have constructed and adapted the climatic niche of animal production to manage their domestic animals across increasingly diverse ecological conditions. By incorporating ecological analysis into estimations of past land use, our methods have

the potential to improve reconstructions of land use change, and to provide a foundation on which further niche construction hypotheses may be tested.

KEYWORDS

animal production, anthropogenic land use change, climate change, global change, Holocene, human–environment interaction, niche breadth, niche construction, niche dynamics, pastoralism

1 | INTRODUCTION

The expansion of pasture and the effects of animal husbandry on Earth have received increased recognition over recent decades (Phelps & Kaplan, 2017; e.g. Asner, Elmore, Olander, Martin, & Harris, 2004, Foley et al., 2005, Vitousek, Mooney, Lubchenco, & Melillo, 1997). However, little attention has been given to the representation of prehistoric animal production in land use and land cover reconstructions, despite archaeological evidence that pastoralism was important and expansive throughout the Holocene (Figure 1, Supporting Information Figure S1). Relatively few anthropogenic land cover change datasets account for pasture or rangeland (e.g. Erb et al., 2007; Klein Goldewijk, Beusen, & Janssen, 2010), and those that do are often based on extrapolations of modern conditions or problematic assumptions about human land use (Phelps & Kaplan, 2017). As a result, existing estimates of prehistoric pasture (e.g. Klein Goldewijk et al., 2010) do not correspond well with animal production evidence, especially for the African continent (Figure 1, Supporting Information Figure S1). In recent years, studies have put more emphasis on land use (e.g. LandUse6k: Morrison, Gaillard, Madella, Whitehouse, & Hammer, 2016), and use of niche-based species distribution modelling (Guisan, Thuiller, & Zimmermann, 2017) in the archaeological context (e.g. Banks, 2017; Conolly, Manning, Colledge, Dobney, & Shennan, 2012; Lorenzen et al., 2011) has increased. Yet even in these efforts, analyses of land use ecology are rarely incorporated into spatial estimates of land use change, albeit see Manning and Timpson (2014) for demographic distributions.

Since the introduction of domestic animals on the African continent around 9000 years before present (BP), land use for animal production has changed dramatically in time and space (Figure 1, Supporting Information Figure S1). From c. 9000–7000 BP, during the African Humid Period (AHP), domestic animals spread throughout northern Africa (e.g. Kröpelin et al., 2008; Shanahan et al., 2015). By c. 5000 BP, the end of the AHP and aridification of the Sahara prompted a further southward spread. Over the following millennia the expansion of animal husbandry was patchy, occurring in mosaics (Crowther, Prendergast, Fuller, & Boivin, 2018) or multiple events (Fuller et al., 2011; Gifford-Gonzalez, 2000; Hanotte et al., 2002; Sadr, 2015) that often preceded the arrival of cultivation (Dunne et al., 2012; Lane, 2013; Marshall & Hildebrand, 2002; Prendergast, 2011). This latitudinal trend is well established, and thought to be driven by climatic changes or adaptation to disease (Kuper & Kröpelin, 2006; Manning & Timpson, 2014; Marshall,

2000), including trypanosomiasis (e.g. through dwarfing, tick resistance, and the development of grassy corridors; Chritz, Marshall, Esperanza Zagal, Kirera, & Cerling, 2015; Gifford-Gonzalez, 2000, 2017; Gifford-Gonzalez & Hanotte, 2013; Robinson & Rowan, 2017). Yet few publications have explicitly investigated the spatially extensive, underlying ecology of domestic animal expansion (di Lernia, 2013; Manning & Timpson, 2014).

In this paper we investigate prehistoric changes in the climatic niche of domestic animals as a means of advancing understanding of the relationship between changing land use strategies and the development of animal production in Africa. We used faunal remains to reconstruct changes in climatic niche breadth of animal production during the African Holocene. Faunal remains provide direct evidence of past animal production, and despite a number of potential taphonomic biases (e.g. Chang & Koster, 1986; Fauvelle-Aymar, Sadr, Bon, & Gronenborn, 2006), the basic presence and absence of species through time provides a powerful means of assessing changes in the exploitation of animals at archaeological sites. By comparing the climatic niche of domestic animals with that of hunted terrestrial ungulates (wild animals), differences in their development may be empirically investigated. Furthermore, we accounted for taphonomic and sampling biases in the archaeological record by utilizing both the proportion of domestic and wild animal remains at all sites as our primary data. We applied identical analysis methods to both data types, and assessed overall statistical significance with permutation tests. This aspect of our methods ensured that both data types were subject to the same archaeological biases and uncertainties, allowing us to draw confident inferences about the differences between wild and domestic climatic niches.

The relationship between climate and the spread of domestic animals on the African continent has been widely discussed (e.g. Kuper & Kröpelin, 2006; Marshall & Hildebrand, 2002; Smith, 1992). However, no studies have explicitly or quantitatively investigated temporal changes in the climatic space used for Holocene animal production. Whilst it is well established that domestic animals expanded geographically on the African continent, it cannot be assumed that the range of climatic conditions used for animal production, that is, climatic niche breadth, expanded proportionally. Climatic niche expansion has rarely been found for non-native invasive plant species (Petitpierre et al., 2012), even when species have expanded into a new geographic area. The relationship between geographic range and climatic niche breadth is highly variable, with studies showing that both positive and negative correlations are possible (Gregory

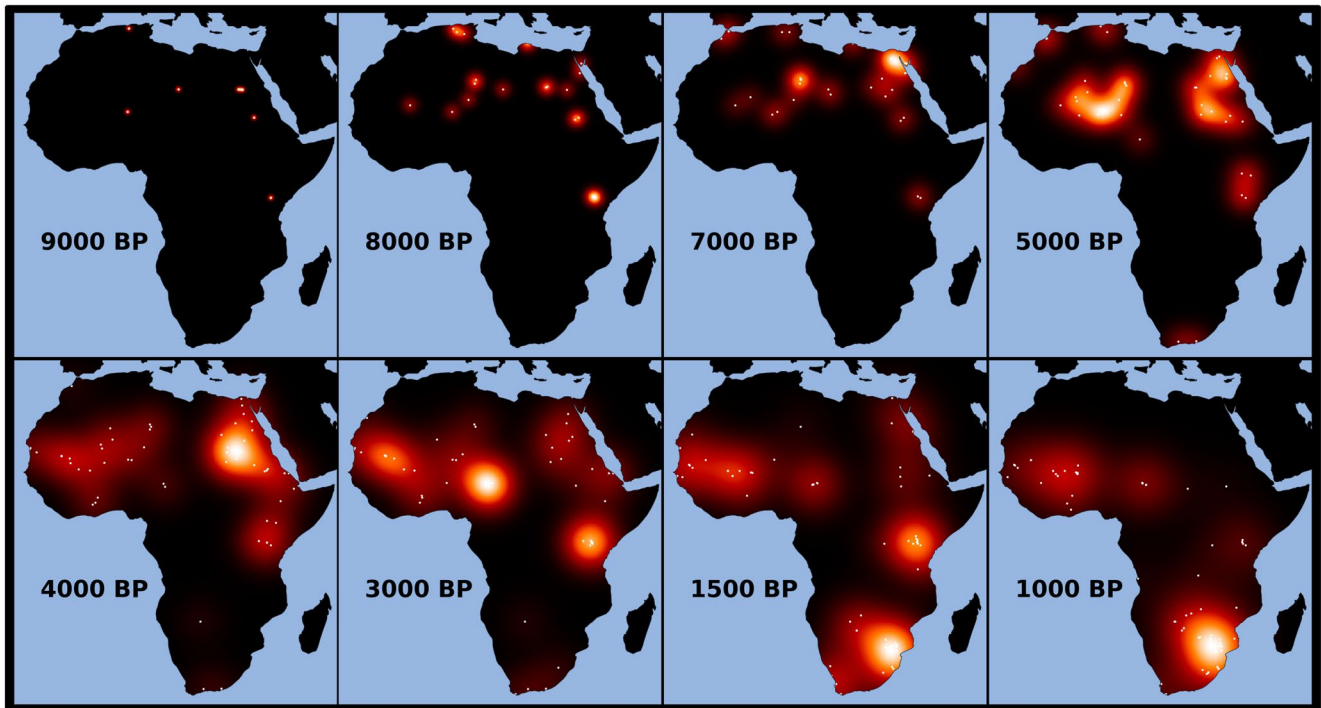


FIGURE 1 Faunal assemblages utilized in this study, generated with kernel density estimation of the number of identified specimens and chronological uncertainties. Individual sites are indicated by a small white dot. Outliers were not excluded. These illustrations are not intended to depict the distribution of land use in space and time (also see Supporting Information Figure S1 and Movies S1, S2) [Colour figure can be viewed at wileyonlinelibrary.com]

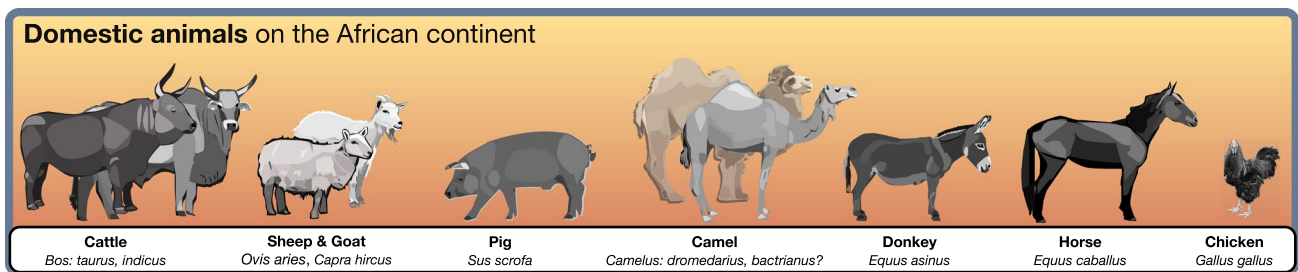


FIGURE 2 Domestic animals on the African continent (illustrations are not intended to represent animal breeds). For more detail, see Supporting Information (section: “Domestic animals in Africa”) [Colour figure can be viewed at wileyonlinelibrary.com]

& Gaston, 2000; Reif et al., 2006; Slatyer, Hirst, & Sexton, 2013). It is thus crucial to consider geographic and climatic space separately (Colwell & Rangel, 2009). Furthermore, quantitative estimates of climatic niche change require consistent comparison between time periods. For the first time, we therefore apply climatic niche modelling methods to archaeological data to reconstruct and statistically test whether the climatic niches of domestic and wild animals changed during the African Holocene (Figure 2).

1.1 | Applying climatic niche modelling methods to land use

The climatic niche is a term commonly used in ecology and biogeography, referring to the set of climatic conditions where a species can occur. Here we refer specifically to the realized climatic niche,

which is traditionally inferred from field observations (Holt, 2009) and represents the portion of the climatic fundamental niche that is occupied at a given time (e.g. Maiorano et al., 2013). Whilst the fundamental niche is defined by the set of theoretical environmental conditions where a species can occur, the realized climatic niche implicitly incorporates further restrictions by including biotic (e.g. competition, carrying capacity) and dispersal limitations in the real world (Soberón, 2007). In addition, changing ecological conditions or evolutionary processes can modify the realized climatic niche through time. The fact that the ecological and evolutionary causes of climatic niche change cannot be discerned from field observations (Maiorano et al., 2013; Pearman, Guisan, Broennimann, & Randin, 2008) has been widely acknowledged and addressed (e.g. Espíndola et al., 2012; Maiorano et al., 2013; Veloz, Williams, Blois, Otto-Bliesner, & Liu, 2012).

We adapt methods from niche dynamics (see Broennimann et al., 2012; Guisan, 2014; Petitpierre et al., 2012) to quantify changes in the climatic niche breadth of domestic animals (the climatic niche of animal production: Figure 2). Such niche dynamic metrics provide tools for estimating climatic niche change in space (e.g. of non-native invasive species) and time (e.g. species' response to climate change: Broennimann et al., 2012; Guisan et al., 2014; Nogues-Bravo, 2009; Petitpierre et al., 2012; Tingley, Vallinoto, Sequeira, & Kearney, 2014). Traditional species distribution models (SDMs), which are typically calibrated with modern data and projected into space or time (Guisan et al., 2017: chapters 1 & 5), can lead to significant inaccuracies when applied to a species with a labile realized niche (Broennimann et al., 2007; Holt, 2009). This bias has been consistently observed for hindcasted mammalian niches, for example (Davis, McGuire, & Orcutt, 2014). Because one expects the human–environment relationship to change through time, standard methods are unsuitable for the land use context. For this reason, we chose to apply a suite of methods from niche dynamics, and to reconstruct the climatic land use niche at 500-year intervals.

Changes in the climatic niche of domestic animals shed light on niche construction processes in prehistory. Niche construction (sometimes referred to as ecosystem engineering) is the process whereby organisms modify their own and each other's niches, and although niche constructors include any species with the capacity to make these modifications, humans are the most prominent (Laland & O'Brien, 2011; Odling-Smee, Laland, & Feldman, 2003; Smith, 2007). Niche construction theory connects evolutionary processes to environmental and social factors (Kendal, Tehrani, & Odling-Smee, 2011; Laland, Odling-Smee, Feldman, & Kendal, 2009; Odling-Smee, 1988). It is often used to explain domestication processes (O'Brien & Laland, 2012; Rowley-Conwy & Layton, 2011; Smith, 2011) and even the onset of the Anthropocene (Smith & Zeder, 2013). A number of studies have used archaeological and palaeoecological data to demonstrate anthropogenic niche construction processes (Boivin et al., 2016). For example, extensive research documents genetic and genomic variations associated with the spread of domestic species on the African continent (e.g. Hanotte et al., 2002; MacHugh, Shriver, Loftus, Cunningham, & Bradley, 1997; Pereira et al., 2009; Pérez-Pardal et al., 2010), including the development of lactase persistence (e.g. Gerbault et al., 2011; Ranciaro et al., 2014).

The effects of these niche construction processes on the climatic niche of domestic animals have yet to be explicitly investigated, however. Here we reconstruct temporal changes in the climatic breadth occupied by domestic and wild animals. We do not aim to provide a dynamic model of land use change that addresses every component of niche construction theory, but we reconstruct temporal changes in the climatic extent of animal production, which broadened as a result of niche construction processes.

2 | METHODS

We derived domestic and wild animal occurrence records from dated faunal remains in the archaeological record from 9000 to 500

BP (Phelps et al., 2019: <https://doi.pangaea.de/10.1594/PANGAEA.904942>; Supporting Information Figure S2; data sources are listed in the Appendix), and sorted them into three animal groups: domestic species (see Figure 2); hunted species from the families Bovidae, Equidae, Suidae, Cervidae and Giraffidae (wild terrestrial ungulates); and the triad of cattle, sheep and goats. We included only wild terrestrial ungulates in the hunted group because these provide the closest comparison with domestic ungulates (as in Rowan, Kamilar, Beaudrot, & Reed, 2016). Aquatic species and cane rats would also have provided valuable contributions to livelihood strategies, but we do not include these animals. We used the group of cattle, sheep and goats as a control, to test whether the introduction of new domestic animal species had a significant impact on climatic niche development, as these three animals were present throughout the entire study period. We excluded remains that could not be identified as wild or domestic, for example, where the species of *Bos* and *Equus* and the genera of *Caprinae* and *Suidae* were not indicated.

Assigning a date range to each archaeological assemblage required the incorporation of substantial chronological uncertainty. We first constructed a date probability distribution for each archaeological assemblage: where radiocarbon dates were available we generated a summed probability distribution (SPD: Rick, 1987; Shennan et al., 2013). Calibrations were performed with the 'Bchron' package in R using either *intcal13* or *shcal13* depending on the hemispheric location of each site (Haslett & Parnell, 2008; R Core Team, 2018). For assemblages associated with a clear date range but devoid of radiocarbon data, we generated a uniform probability date distribution between the specified typological or cultural start and end dates. In either case we used these probabilistic date distributions to update an empirical prior date distribution, which was an SPD constructed from all radiocarbon dates from all sites. This prior had a deliberately conservative effect of widening each assemblage's date distribution, particularly where typological date ranges were narrow, or only a few radiocarbon dates were available for a particular assemblage. Finally, for each assemblage we summarized start and end dates using the 99.9% range of the date distribution. Therefore, an assemblage date range (start and end) typically spans several of our 500-year time slices, and can be assigned to either a single (mean date) time slice, or to several time slices by weighting accordingly.

We took an inclusive approach to the available radiocarbon and faunal data in order to investigate the most probable changes in the climatic niche of animal production; therefore, we have not attempted to exclude outliers or radiocarbon dates with large uncertainties. This means that some occurrence records are likely to appear earlier than they would have actually arrived, for example, the few domestic records appearing in east Africa before 5000 BP (Figure 1, Supporting Information Figure S1), as a result of errors in dating, sampling, or species identification. Although our reconstructions do not precisely reflect the first securely dated geographic arrivals of domestic animals, the goal of this study is to predict broad-scale changes in the climatic niche of domestic animals. Therefore, these methods are most suitable because they maximize the use of all available data, and are unlikely to be strongly affected

by outliers because they are density-based. In this sense, we also avoid interpretation bias and can challenge existing notions about arrival times of domesticates where there is substantial evidence. Nonetheless, we consider the effects of potentially intrusive faunal remains in Supporting Information Table S4, and acknowledge that analyses could be refined in the future with improved radiocarbon dating.

We tested three versions of occurrence records. Version one, '1occ', is unweighted and includes only one occurrence record per assemblage for each time interval. Version two, 'date', is weighted by the probability of occurrence in each time interval. We repeated each occurrence record 100 times, and distributed replications on the basis of the probability that they occurred within each time interval. For example, if an assemblage had a .3 probability of occurrence between 5500 and 5000 BP and a .7 probability of occurrence between 5000 and 4500 BP, we repeated it 30 and 70 times, respectively, and zero times for all other time slices. Version three, 'taxa', is weighted by the number of taxa present at a given site and time interval, effectively weighting occurrence records on the basis of taxonomic diversity. Our analysis of the three animal groups and versions of occurrence records described above is a form of sensitivity testing.

Our data requires analysis in time bins. Initial exploratory tests to assess the influence of bin width on the noise to signal trade-off established that the exact bin width had a negligible effect on our results and did not change the overall inferences. Bin widths in the order of a few centuries provided stable and consistent results, and we arbitrarily settled on 500-year bins as a sensible balance between the number of bins and the sample sizes in each bin. We therefore generated palaeoclimate variables from 9000 to 500 BP to match these bins, with 500-year averages centred on the turn of each half-millennia, e.g. 500 BP \pm 250, at 2.5×2.5 spatial resolution.

We obtained nine annual climate variables (Supporting Information Figure S3a) from the TraCE-21ka simulation of the Community Climate System Model (version 3: Liu et al., 2009) with PALEOVIEW (Fordham et al., 2017). Although these variables are correlated (Supporting Information Table S1), our methods are based on principal component analysis and therefore are not sensitive to multicollinearity. However, the TraCE-21ka simulation and the latest PMIP3 (The Palaeoclimate Modelling Intercomparison Project) / CMIP5 (Coupled Model Intercomparison Project) models are unable to simulate all of the observed precipitation anomalies during the AHP, typically underestimating the northward extent of the African monsoon during the mid-Holocene (Harrison et al., 2015; Perez-Sanz, Li, González-Sampériz, & Harrison, 2014; Shanahan et al., 2015).

For supplementary analysis, we tested whether similar trends could be obtained after assuming a stable climate gradient through time, using climate data with a higher spatial resolution, and including more climatic variables in the analysis. To do this, we obtained 19 present-day WorldClim variables at 10-min resolution (Fick & Hijmans, 2017: see Supporting Information Table S2). Absolute *D* values cannot be compared when climate data have different spatial resolution. To ensure that climate gradients were comparable between WorldClim data

and TraCE21-ka information, we calculated the correlation between the nine corresponding present-day WorldClim variables (upscaled to 2.5×2.5) and TraCE-21ka variables at AD 1970 (bias corrected). To validate our results, we also obtained palaeoclimate information at 10-min resolution for nine additional general circulation models at 6000 BP [upscaled to 2.5×2.5 , Supporting Information Figure S4a (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005)].

2.1 | Quantifying trends in the climatic land use niche

To quantify temporal changes in our climatic land use niches, we adapted methods from niche dynamics (Broennimann, Mráz, Petitpierre, Guisan, & Müller-Schärer, 2014; Di Cola et al., 2017). This approach accounts for niche fluctuations (i.e. shifts, contractions, or expansions), and can be used to track changes in the realized climatic niche through time. Additionally, niche dynamic methods can accommodate incomplete spatial coverage, which is a significant limitation of the archaeological record, especially on the African continent.

First, we defined a reduced climate space with a principal components analysis (PCA), calibrated with the climate space of the entire study area (background climate: Broennimann et al., 2012), pooled across all 18 time periods. Second, for each time interval, we calculated the scores of the corresponding faunal occurrences and their density of occurrence, weighted by the climate availability in PCA space (modified from PCA-env in Broennimann et al., 2012). Third, we used niche dynamics metrics (*Db* and *Dd*, which are based on Schoener's *D*) to measure the overlap between climatic land use niches at each 500-year interval and their corresponding background climates (i.e. the portion of the African climate in which the animals occurred), and the overlap between the domestic and hunted (wild) animal niches (e.g. see Broennimann et al., 2012).

The *Dd* metric—the classic *D* metric (Broennimann et al., 2012; Warren, Glor, & Turelli, 2008)—is based on the ratio of occurrence density to the density of available environmental conditions. Therefore, *Dd* is highly dependent on how the background climate is defined, or the extent of the background climate. Conversely, *Db*, a modified *D* metric, is based on binary representation of niches [i.e. pixels take value of 0 if the density of occurrence is 0, or the value of 1 if the density is higher; see 'niche stability' calculations (Di Cola et al., 2017; Guisan et al., 2014)] and is independent of the background extent, meaning that information about occurrence densities is lost, and all parts of the niche have equal weight. For this reason, *Db* measurements may be more likely to reflect errors in the archaeological record. In the majority of our analyses, *Dd* and *Db* niche metrics provide two ways of measuring the portion of the African climate that is occupied by domestic or wild animals at each time interval (Figure 3a). This aspect of our methods differs from typical applications of niche dynamic metrics, where two niches are compared. We also compared the domestic and wild climatic niches directly (Figure 3b).

After calculating *Dd* and *Db* values, we tested whether the observed broadening of the climatic niche of domestic animals was statistically significant through time (Figure 3), and whether it could

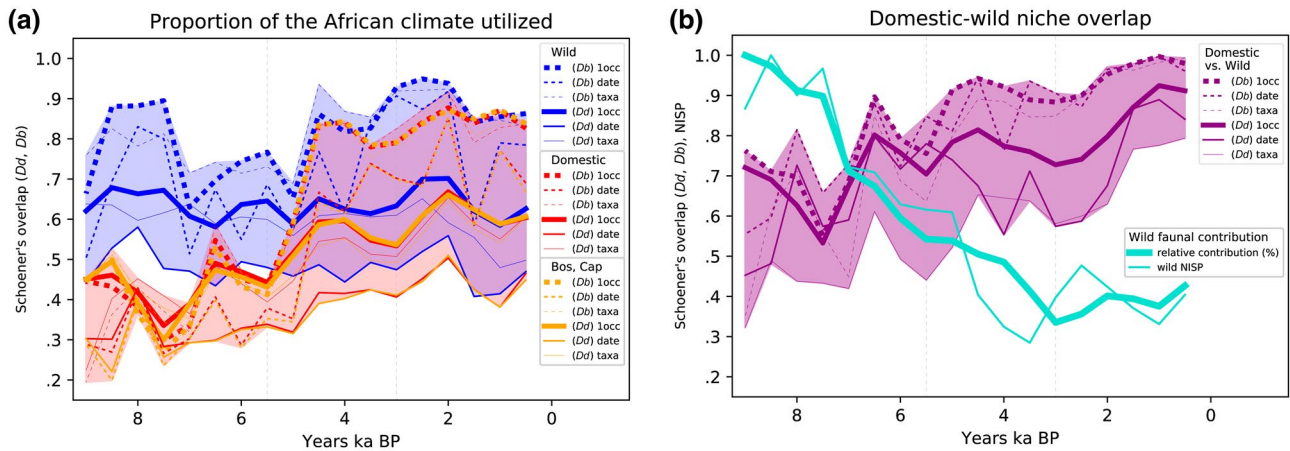


FIGURE 3 Quantification of climatic niche breadth for domestic (animal production), domestic *Bos* and *Caprinae* only (*Bos*, *Cap*), and wild (hunted terrestrial ungulates) animals during the African Holocene. For each niche, three versions of occurrence records were analysed: one occurrence record per assemblage for each time interval (1occ), the number of taxa present at a given site and time interval (taxa), and the probability of occurrence in each interval (date). *D* values (*Dd*: density-based niche metric, *Dd*: binary niche metric) quantify the degree of overlap between the animal niche and the African background climate. (a) Degree of overlap among three groups: domestic (red), wild (blue), and cattle, sheep and goats (orange). (b) Overlap between climatic niches of domestic and wild animals (purple), relative contribution of wild and domestic remains, and total number of wild remains (rescaled 0–1), based on assemblage-averaged number of individual specimens present (NISP) where available (turquoise). Vertical, dashed lines indicate the termination of the African Humid Period [c. 5500–3000 years before present (BP)]. See Supporting Information for *D* values (Table S3), further comparison against other climate models at 6000 BP (Figure S4), and principle components analysis of pooled occurrence records (PCA-occ) with TraCE-21ka and repeated WorldClim data (Figure S5) [Colour figure can be viewed at wileyonlinelibrary.com]

be explained by other factors such as sampling, taphonomic or methodological artefacts. We used a permutation test to randomly shuffle (5,000 times) the climatic niche metrics calculated for domestic animals at each of the 18 time slices, while retaining all other structure in the data. For each shuffle, we calculated the correlation between time and *D* values with Pearson's *R*, which formed a null distribution of test statistics (histograms: Supporting Information Figure S6). We calculated the same test statistic once for the observed data (unshuffled), and calculated a two-tailed *p*-value as the proportion of the null distribution that is greater or equal to the observed test statistic. We then performed the same permutation test on the wild species group.

We performed niche dynamic analyses with the 'ecospat' package in R (Di Cola et al., 2017; R Core Team, 2018), and plotted metrics with Python (Python Software Foundation, 2018). To test the robustness of our results, we performed supplementary analyses using principal components analysis of occurrence records (PCA-occ; see Broennimann et al., 2012), where *D* values were calculated as the proportion of the pooled animal niche rather than the proportion of the background climate information (PCA-env). We also performed supplementary analyses with a stable climate gradient (modern-day WorldClim data: Supporting Information Figure S4). To independently test whether the relative importance of hunting and animal husbandry changed through time, we separately calculated the relative mean contribution of wild and domestic faunal remains for each time interval on the basis of the number of individual specimens (Figure 3b, turquoise line), and the mean absolute number of wild remains. Additionally, we tested the effects of excluding assemblages with potentially intrusive faunal remains (Supporting Information Table S4).

We projected the climatic land use niches of domestic and wild animals into geographic space on the basis of the relative density of

occurrence records, providing maps of climate suitability for both animal husbandry and hunting at 500-year intervals (Figure 4). We do not intend these maps to represent past domestic animal densities, although they are likely correlated.

3 | RESULTS

D values increased from past to present for the climatic niche of domestic animals, unlike that of wild animals (Figure 3a, Supporting Information Table S3), indicating that the climatic space used for animal production widened significantly through time with a concomitant increase in domestic–wild climatic niche overlap (Figure 3b, Supporting Information Figure S3). Around 4500 BP, *D* values of the domestic climatic niche increased most obviously (> 7%) across all versions of occurrence records (Supporting Information Table S3). The niche for wild animals, meanwhile, increased much less, and was accompanied by a significant decrease (–20.5%) in the number of individual specimens of wild animals. Trends in the climatic niche of cattle, sheep and goats were nearly identical to that of domestic animals.

Permutation tests (Supporting Information Figure S6) indicated that the widening of the climatic niche of domestic animals was strongly and significantly time dependent (*R* values = .744 to .903, *p* values < .001), whereas that of wild animals did not have a consistent trend (*R* values = –.624 to .56, *p* values = .021 to .802). Sensitivity tests were also included in our analyses, contributing to methodological development and showing that our results were robust: first, we demonstrated that similar trends were produced by two different PCA analyses (PCA-env: Figure 3, PCA-occ: Supporting Information

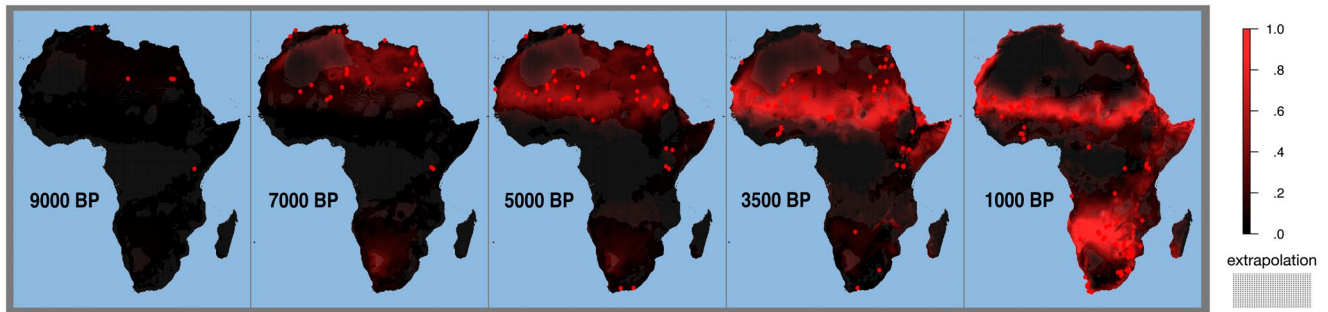


FIGURE 4 Climatic land use niches for domestic animals projected into geographic space with present-day WorldClim data. Reconstructions are based on the relative density of occurrence records in climate space (rescaled from 0 to 1, relative to the maximum density of all time periods), weighted by the probability of radiocarbon date occurrence. Values near zero indicate that the niche is not well established, whereas values near one indicate that the niche is well established, although the niche may not be realized in geographic space for ecological, social or cultural reasons. Domestic occurrence records are plotted (red circles), and grey cross-hatching indicates niche extrapolation (calculated with multivariate environment similarity surface, MESS), that is, the climatic space outside of the sampled area in this study. See Supporting Information for 500-year intervals of domestic and hunted niches using present-day WorldClim data (Figure S7.1, Movie S3) and TraCE-21ka climate information (Figure S7.2, Movie S4) [Colour figure can be viewed at wileyonlinelibrary.com]

Figure S4), three types of occurrence records (Figure 3a) and a stable climate gradient through time (Supporting Information Figure S4; although PCA-env and Dd values are less reliable because of their sensitivity to changes in the climate gradient). In comparisons of our results with nine additional climate models at 6000 BP, the wild climatic niche always produced higher D values than that of domestic animals (Supporting Information Figure S4a). Analysis of the control group of cattle, sheep and goats suggested that the introduction of new domestic species was not responsible for the temporal expansion of the domestic niche. Our empirical and quantitative results imply that continental-scale climatic niche construction was prominent throughout the Holocene, and that extensive land use change is not a recent phenomenon. Our work yielded spatially continuous maps of the suitable climatic space for both animal husbandry and hunting on the basis of the density of occurrence records in climatic space (Figure 4, Supporting Information Figures S7.1, S7.2). Results derived from PCA-occ, repeated modern-day WorldClim data, and other climate models are in Supporting Information Figure S4.

3.1 | Background climate space

In analyses performed with TraCE-21ka climate information, 83.4% of variance in the PCA of pooled background climate was explained by the first two principal component axes (PC1 = 62.1%, PC2 = 21.3%; Supporting Information Figure S3). These two axes provided the climatic space within which niches were plotted, measured and compared. Temperature seasonality and isothermality explain the vast majority of both pooled and individual time period variance, although these variables are highly correlated with each other (Supporting Information Tables S1, S2) and with precipitation variables, which are underrepresented in the TraCE-21ka simulation. For analyses performed with WorldClim data, 69.5% of the background climate variance was explained (PC1 = 46.1%, PC2 = 23.4%), and the nine TraCE-21ka variables (bias corrected) agreed well with corresponding WorldClim data for 1970 AD (Supporting Information Figure S5).

4 | DISCUSSION

4.1 | The expanding climatic niche and niche construction processes

We distinguish the broadening of the climatic niche of animal production, which has never been explicitly analysed, from the time transgressive geographic spread of domestic animals in Africa, which is already well established (e.g. Crowther et al., 2018; Fuller et al., 2011; Gifford-Gonzalez, 2000; Hanotte et al., 2002). For the first time, we quantitatively demonstrate that the climatic niche of African animal production (domestic animals) expanded significantly during the Holocene, whereas that of hunted (wild) terrestrial ungulates did not. This broadening of the domestic animal climatic niche co-occurred with the geographic spread of domestic animals, a relationship that could not be assumed a priori, indicating continental-scale climatic niche construction as a result of land use change. Our findings indicate that novel environments were increasingly incorporated into animal husbandry practices, likely through inceptive relocation or exposure to novel selective environments. Other forms of climatic niche construction likely occurred, for example, counteractive relocation or inceptive perturbation, but we do not explicitly address these (Laland & O'Brien, 2010; O'Brien & Laland, 2012). For further discussion of our methods, see Supporting Information (section: "Methodological contributions to the land use niche").

It seems clear that climatic niche expansion did not result from the addition of new domestic species (e.g. horse, camel, pig, chicken), given that trends in the climatic niche of cattle, sheep and goats were similar to trends observed in the climatic niche of domestic animals. In the case of African animal production, this climatic niche construction likely occurred by two means: first, the physical expansion of animal husbandry into novel climatic environments, and second, in situ adaptation of animal production strategies to novel climates as a result of climate change. The extent to which climate directly (e.g. through thermoregulatory constraints) or indirectly (e.g. through food and water

availability) affected niche change is unclear, however. The observed changes in the climatic niche of animal production reflect the development of different production systems (see Phelps & Kaplan, 2017) and their environmental interactions over the past 9000 years.

Our results indicate that climate change was a key driver in broadening the climatic niche of domestic animals, particularly during periods of increasing aridification. For example, the most obvious increase in the domestic animal climatic niche (c. 4500 BP) occurred during the end of the AHP (e.g. Shanahan et al., 2015), when both a strong reduction in the cover of tropical trees and Sahelian grassland cover and spatially extensive dust mobilization occurred (Kröpelin et al., 2008). At this point, animal production began to spread substantially into sub-Saharan Africa. This inference is consistent with observations that mobile pastoralism is resilient to variable contemporary rainfall, especially in arid and semi-arid ecosystems (e.g. Ellis & Swift, 1988; Homewood, 2008; Niamir-Fuller, 1999; Vetter, 2005). However, our findings suggest that pastoralism was advantageous during this long period of increasing aridification, with implications for land use planning today. The precise causal relationships between these past land use and land cover changes remain unclear, however.

The evolutionary processes leading to the expansion of the animal production climatic niche are suggested by declines in wild cattle (*Bos primigenius*) around the end of the AHP, whereas domestic cattle (*Bos taurus*), which either bred with or were domesticated from wild African cattle (Pérez-Pardal et al., 2010), expanded southwards into sub-Saharan Africa. Similarly, a hunted and potentially managed wild caprine [Barbary sheep (*Ammotragus lervia*)] remained confined to northern Africa throughout the entire study period, while both domestic sheep and goats expanded southward (i.e. divergence of close relatives: see Supporting Information Figure S8). Regardless of whether domesticates appeared on the African continent through indigenous development or importation, domestication is acknowledged as part of a continuous, coevolutionary process (e.g. Gifford-Gonzalez & Hanotte, 2011). For example, several studies demonstrated the correlated spread of cattle and lactase persistence in humans (Gerbault et al., 2011; Macholdt et al., 2014; Ranciaro et al., 2014; Tishkoff et al., 2007); Pérez-Pardal et al. (2010) demonstrated that sub-Saharan cattle are genetically distinct from other domestic populations; and there is a possible but unproven relationship between dwarfism and trypanotolerance (e.g. Gifford-Gonzalez & Hanotte, 2011; Linseele, 2013). In addition, breed diversification has been a major factor in the zoogeography of African livestock, enabling domesticates to live in a wide variety of modern ecological zones (Bahbahani et al., 2018; Murray & Trail, 1984; Mwai, Hanotte, Kwon, & Cho, 2015; Wang, Dzama, Rees, & Muchadeyi, 2015). Thus, the broadening of the animal production climatic niche is associated with evolutionary trends, and it is highly likely that these were the mechanism for expansion of the climatic land use niche for domestic animals that we observed. We therefore suggest that ecological and evolutionary factors drove the observed geographic expansion of animal husbandry.

In contrast to the animal production climatic niche, and despite a proportional increase in the number of domestic and hunted

assemblages through time (Supporting Information Figure S9), we did not find a consistent temporal trend in the climatic niche of hunted animals (Figure 3). This suggests that expansion of the climatic niche of domestic animals is not an artefact of sampling or taxonomic bias in the archaeological record (Supporting Information Figure S6). Our results indicate that spatially, animal production did not replace hunting, but rather moved into the same climatic areas. The apparent spread of domestic animals is associated with a decline in human reliance on absolute numbers of wild taxa [based on average number of individual specimens present (NISP): see Supporting Information Table S5], which was most pronounced around 4500 BP, when the domestic climatic niche expanded substantially and population declined substantially as a result of the end of the AHP. Again, this demonstrates the adaptive advantage that domestic animals likely provided during the end of the AHP, and that expansion of the climatic niche of domestic animals was closely associated with changes in other forms of human subsistence.

Trends in the taxa version of occurrence records for hunted animals suggest that people hunted an increasing variety of terrestrial ungulates in novel climates (Supporting Information Figure S6: Db R value = .56, p = .021), but that people also became less reliant on these diversified hunting assemblages through time (Dd R value = -.624, p = .035). Increasing Db values suggest that a greater diversity in terrestrial ungulates became available in novel climate spaces, or that the hunting of diverse terrestrial ungulates was an adaptive strategy that spread into novel climates. Conversely, decreasing Dd values and the overall decline in the wild NISP suggest a gradual transition from hunting to animal production at a continental scale. Further insight on subsistence change could be gained through the inclusion of genetic data that address changes in effective population sizes and admixture of some pygmy hunter-gatherer populations (Verdu et al., 2009) associated with the expansion of Bantu-speaking agriculturalists during the end of the AHP (Batini et al., 2011; Gignoux, Henn, & Mountain, 2011; Patin et al., 2013). Higher resolution analyses with spatial and temporal continuity could also help to clarify land use change during specific time periods, especially via regional and local investigation of changes in livelihood strategies (Phelps & Kaplan, 2017).

The fact that terrestrial ungulates occupied a relatively large portion of the African climate space across our study period (Figure 3a) is consistent with the conclusions of Rowan et al. (2016) that ungulates are ecologically resilient due to their large body sizes and the wide distribution of their food sources, and are strongly influenced by palaeoclimatic adaptations that began during the Last Glacial Maximum, prior to our study period. In this sense, terrestrial ungulates may be ideal species for domestication, but we find it remarkable that anthropogenic niche construction processes facilitated the expansion of the climatic niches of cattle, sheep and goats to the same extent as those of all hunted African ungulates (>90 species). We did not address the fact that the climatic niches of wild terrestrial taxa or hunting strategies may respond to climate change individually. In addition, our analyses were not intended to reflect the distribution of all wild terrestrial ungulates in Africa, but only those that were hunted and appeared in archaeological records.

4.2 | Assumptions, limitations and future work

One limitation of our approach is its reliance on climate models. For example, our results could be altered if the representation of precipitation variables was improved (see Shanahan et al., 2015 for discussion of TraCE-21ka). For this reason, and given errors and patchy spatial coverage of faunal remains, we focused on 500-year continental-scale intervals, performed several sensitivity analyses, and focused on niche changes >7% of the entire African climate space and where similar results were produced across analyses. Further interpretation of regional or local trends requires data that are of higher resolution and more complete. Additionally, although temperature seasonality and isothermality are highly correlated with mean precipitation, precipitation likely contributed more to the past distribution of domestic animals than is reflected in our analyses.

We assumed that the presence of domestic or wild animal remains equates with the location of land use. However, grazing, browsing and foraging are likely to have extended well beyond the archaeological site, or may not have occurred where remains were found. For this reason, we directly compared the climatic niches of domestic and wild ungulates. Because our analyses focused on faunal remains, we did not address the presence of animal production systems that did not yield this kind of data. Examples of pastoralist evidence that we do not consider here include rock art, which has indicated the presence of herding in the central Sahara during past periods of desertification (e.g. Guagnin, 2015), animal daybeds, trampled areas, tracks, and trails (Zerboni & Nicoll, 2019). Furthermore, where pastoralists are highly mobile and rely more on drought adapted species, such as *Camelus dromedarius*, remains may be less likely to appear in faunal assemblages. Therefore, the absence of evidence in our study is not evidence of pastoralist absence.

Investigative power can always be increased by analysing a more complete fossil record at higher temporal resolution, incorporating a wider variety of land use evidence, and making continental comparisons. This type of data-driven approach only recently became possible with the collation of continental databases like that of Jousse (2017) for Africa, or those for Europe (Manning, 2016; Manning, Colledge, Crema, Shennan, & Timpson, 2016). Our methods could be enhanced through the generation of temporally continuous niches rather than discrete time intervals. Radiocarbon date distributions and finer resolution land use changes could be better represented, and comparison with other types of evidence would be simpler. Additionally, land use representation may be enhanced by integrating process-based models (Tingley et al., 2014; Zurell et al., 2016) and geospatial approaches, and by including more types of evidence, such as archaeobotanical and fossil pollen remains; species-specific morphometric, genotypic and genomic faunal data (e.g. Hanotte et al., 2002; Pérez-Pardal et al., 2010), especially for highly mobile species with few faunal remains (Almathen et al., 2016); evidence of aquatic resource exploitation; rock art (e.g. Gallinaro, 2013; Guagnin, 2015); and geomorphic and ethnoarchaeological evidence of herding (e.g. Biagetti, 2014; Zerboni & Nicoll, 2019). The expansion of pastoralist systems likely was associated with cultural adaptations that relate to mobility, territory size, and social networks; further

investigation into material culture from associated archaeological records may provide relevant insight. With these types of improvements, understanding of land use extent and intensity can be enhanced, and further niche construction hypotheses may be tested.

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DATA AVAILABILITY STATEMENT

The archaeological data utilized in this study are available at <https://doi.pangaea.de/10.1594/PANGAEA.904942> (Phelps et al., 2019). Data sources are listed in the Appendix.

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BIOSKETCH

The research of the lead author, **Leanne Phelps**, focuses on the ecological intersection between land use and land cover change, across broad spatial and temporal scales. Her primary research interests lie in improving our understanding of human–environment relationships, in order to inform sustainable conservation and land use planning.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX: DATA SOURCES 1

The archaeological data analysed in this study were modified from Jousse, 2017 and associated datasets (see Phelps et al., 2019: <https://doi.pangaea.de/10.1594/PANGAEA.904942>). Taxonomy updates were made with reference to Kingdon et al. (2013) and Bibi (2013).

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