

INVITED REVIEWS AND META-ANALYSES

Comparative phylogeography of African savannah ungulates¹

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Abstract

The savannah biome of sub-Saharan Africa harbours the highest diversity of ungulates (hoofed mammals) on Earth. In this review, we compile population genetic data from 19 codistributed ungulate taxa of the savannah biome and find striking concordance in the phylogeographic structuring of species. Data from across taxa reveal distinct regional lineages, which reflect the survival and divergence of populations in isolated savannah refugia during the climatic oscillations of the Pleistocene. Data from taxa across trophic levels suggest distinct savannah refugia were present in West, East, Southern and South-West Africa. Furthermore, differing Pleistocene evolutionary biogeographic scenarios are proposed for East and Southern Africa, supported by palaeoclimatic data and the fossil record. Environmental instability in East Africa facilitated several spatial and temporal refugia and is reflected in the high inter- and intraspecific diversity of the region. In contrast, phylogeographic data suggest a stable, long-standing savannah refuge in the south.

Keywords: comparative phylogeography, herbivores, regional structuring, savannah biome, Sub-Saharan Africa, ungulates

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Introduction

The African savannah biome harbours an ungulate (hoofed mammal, see Box 1) community of unique diversity. The diversity exceeds that of any other biogeographic region, even when accounting for the Late Pleistocene megafauna extinctions of Eurasia and America (Owen-Smith & Cumming 1993). The savannah biome spans the tropical grasslands, scrublands and

wooded savannahs of sub-Saharan Africa, encompassing the Sahel—the vast semi-arid region of North Africa south of the Sahara, the Rift Valley formation in equatorial East Africa and most of Southern Africa (Fig. 1) (Mayaux *et al.* 2004). It is punctuated by the extended tropical forests of Central and Western Africa and the fragmented coastal forests of Eastern Africa (Mayaux *et al.* 2004; de Vivo & Carmignotto 2004). The distribution and biomass density of ungulates is clearly associated with the distribution of savannah habitat (Fig. 2a) (du Toit & Cumming 1999), and many herbivores prefer areas of low tree density: a top-down response to minimize risks of predation (Riginos & Grace 2008).

Pleistocene climate

Around 80% of ungulates belong to the bovid family, which includes the true antelopes and buffalo (du Toit & Cumming 1999). The emergence and evolutionary success of the group is closely linked to the increased dominance of grassland formations on the African

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¹This manuscript is dedicated to our friend and colleague Peter Arcander, who retired from his position as professor at the Department of Biology, University of Copenhagen, in 2011. Peter initiated DNA laboratories in Copenhagen and at Makerere University, Uganda, which is still very active today. He pioneered phylogeographic research on African ungulates, devoting so much effort to developing the infrastructure necessary to achieve many of the studies that form the basis of this review; his major contributions to the field will be appreciated for many years.

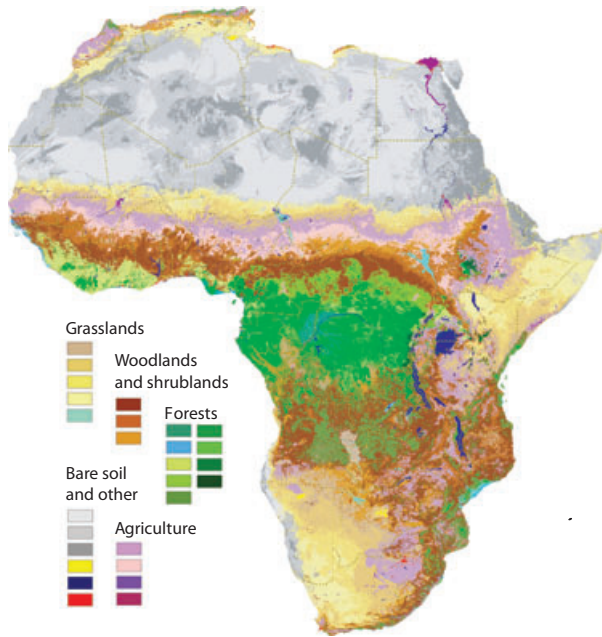


Fig. 1 Current distribution of African vegetation reconstructed from remotely sensed data; adapted from Mayaux *et al.* (2004).

continent (Kappelman *et al.* 1997; Bobe & Behrensmeyer 2004; Edwards *et al.* 2010). Data from marine records indicate that African climates shifted towards cooler temperatures and greater aridity at the onset of the Pleistocene *c.* 2.8 million years (Ma) ago (deMenocal 1995). Soil carbonate and n-alkane carbon isotopes document the progressive expansion of xeric vegetation around this time, including woodland and grassland savannahs (Feakins *et al.* 2005). The long-term increase in open habitats and arid-adapted C_4 plants facilitated the emergence of species with an associated diet

(deMenocal 2004), and many bovid taxa first appeared in the fossil record *c.* 2.8 Ma ago (Vrba 1995; Bobe *et al.* 2002; Bobe & Behrensmeyer 2004).

Owing to changes in the Earth's orbital forcing parameters, African climates became increasingly variable during the Pleistocene (deMenocal 1995; Maslin 2007; Trauth *et al.* 2009). Climate forcing mechanisms operated at both global scales—such as the glacial cycles of the northern hemisphere (deMenocal 1995)—and local scales, for example insolation-driven monsoons (Trauth *et al.* 2009) and the progressive formation of the Rift Valley in East Africa (Trauth *et al.* 2007).

The physiography of sub-Saharan Africa varies, but for convenience and as far as the distribution of wide-ranging species are concerned, the region can be divided into two major vegetation zones: savannah and tropical forests (Fig. 1; Lehmann *et al.* 2011). The distributional balance between the two is governed by precipitation (Lehmann *et al.* 2011; Staver *et al.* 2011). Climate variability in tropical Africa during the Pleistocene mainly resulted in changes in levels of precipitation, with oscillations between warm, wet periods (pluvials) and cooler periods of reduced humidity (interpluvials) (Dupont 2011). Pollen records from marine sediments covering several Pleistocene glacial–interglacial cycles indicate the repeated expansion and contraction of savannah and forests (Dupont 2011). During dry interpluvials, the decrease of CO_2 and precipitation facilitated an increase in savannah coverage; southern hemisphere grasslands shifted northward and West African savannahs expanded at the cost of lowland forests (Dupont 2011). During moist pluvials, the scenario reversed and grasslands were replaced by expanding tropical forests (Cowling *et al.* 2008).

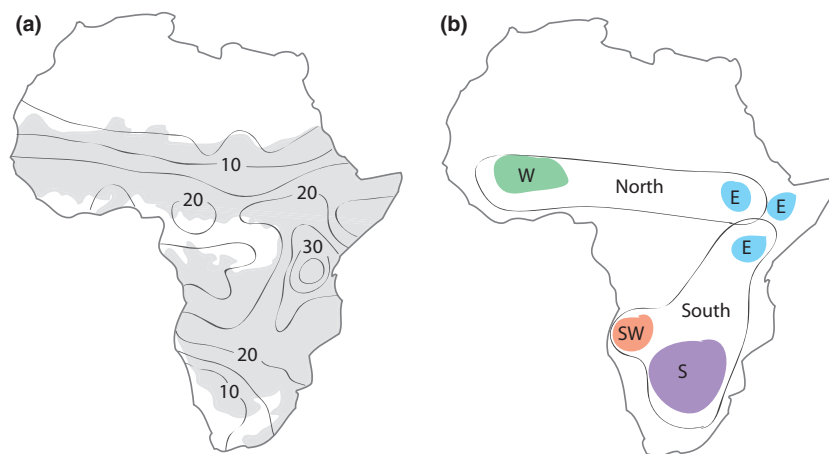


Fig. 2 Distribution, diversity and regional biogeography of ungulates across sub-Saharan Africa. (a) Isoclines of ungulate diversity across Africa, with the distribution of savannah in grey shading, redrawn from du Toit & Cumming (1999). (b) Biogeographic regions discussed throughout the text and in Box 2. Two continental areas on either side of the tropical forests of Central Africa (*north*, *south*) encompass four regions: west (W), east (E), south (S) and southwest (SW). In many taxa, East Africa harbours several endemic lineages, and in addition, the area represents a suture zone between lineages from other biogeographic regions.

Box 1 Ungulate Taxonomy

Although it bears no taxonomic significance, the term *ungulate* is used in a descriptive sense to refer to any mammal with hooves. The taxonomy of African ungulates has been a subject of intense debate (e.g. Simpson 1945; Gentry 1992; Fernández & Vrba 2005; Wilson & Reeder 2005), which is expected, given the unique diversity of the assemblage. Traditionally, species were identified and distinguished based on morphology (e.g. coat colour, size, craniometry), behaviour and ecology. This resulted in a very high number of described taxa (e.g. Christy 1924; Ruxton & Schwarz 1929), and as in other areas of systematics, the multitude of proposed species concepts has led to a dichotomy of the two polarized approaches to species delimitations: lumping and splitting.

With the advent of molecular genetics, the evolutionary relationships between populations within species have been investigated using genetic markers, and genetic data have been used to identify taxonomic units. In several cases, studies based on mtDNA and microsatellites have revealed a discrepancy between genetic diversity and morphological variation, for example kob (Lorenzen *et al.* 2007a), Grant's gazelle (Lorenzen *et al.* 2007b), and zebra (Lorenzen *et al.* 2008), suggesting that either method alone is a poor proxy for taxonomic inference.

The World Conservation Union (IUCN 2011) currently recognizes 92 antelope species worldwide. A recent review on ungulate taxonomy has increased this number substantially to 204 by lifting many local ecotypes and subspecies to full species status (Groves & Grubb 2011). For example, the Alcelaphine taxa included in our review have been split into several species: hartebeest into eight, wildebeest into four and topi into 11. While we do not discuss the validity of the approach used by Groves & Grubb (2011), where fixed differences in any character such as morphology, behaviour or genetic variation are used to define a species, we have not followed their species delimitations.

Rather, we have applied a pragmatic approach and have treated as species those taxa that were treated as such in the reviewed studies, unless subsequent genetic-based research has shown this to be erroneous. Some species complexes have therefore been lumped, for example Grant's gazelle and giraffe. Others such as bushbuck and African elephant, a dominant member of the herbivore assemblage, have been omitted, as the available phylogeographic studies on these taxa have in hindsight proven difficult to interpret. In the only phylogeographic study of bushbuck to date, it was treated as a monophyletic group (Moodley & Bruford 2007). However, it consists of two species, and perhaps even two species complexes, which are paraphyletic with respect to the other tragelaphines (Moodley *et al.* 2009). Recent genetic data have convincingly shown that African elephant consists of two distinct species: forest and savannah (Ishida *et al.* 2011). To date, there has been no phylogeographic study of savannah elephant—the species of relevance here—without the inclusion of its sister species, which complicates the inference of intraspecific diversity.

Ungulate population sizes are intrinsically linked with climate change over evolutionary timescales (Lorenzen *et al.* 2011), and the distributions of savannah herbivores would have shifted in accordance with vegetation change. When climates change and habitats are altered, species are forced to adapt, migrate or go extinct. The Pleistocene refuge theory (Haffer 1969) was originally conceptualized for Neotropical rain forests, but can equally be applied to the African savannahs. The maintenance of isolated grassland refugia—core areas of stable savannah habitat—during moist pluvials would have enabled the continued survival of savannah-adapted taxa. Over time, natural selection and genetic drift would promote the divergence of species genomes, ultimately shaping differences between populations in behaviour, morphology and ecology (Avice 2000).

Biogeographic insights from genetic data

Phylogeography is the study of the geographic distribution of genetic lineages (Avice 2000). In combination with population genetic inference, it provides a powerful approach to elucidating the evolutionary processes that have shaped present-day diversity within and

among species. Comparative phylogeography uses data from taxa with varying life history traits, habitat preferences and ecological requirements to elucidate the historical biogeography of a region (Moritz 1998). As hypothesized in models of environmentally driven evolution (Vrba 1995), congruent phylogeographic patterns across taxonomic groups and trophic levels suggest similar forces shaped species evolutionary histories.

Most comparative phylogeographic studies have been focused on northern temperate zones, owing to the accumulation of data from especially Europe and North America (see references in Shafer *et al.* 2010). There have been few comparative works from the southern hemisphere and tropical regions. Within the past two decades, phylogeographic studies have been published on two-dozen ungulate taxa from sub-Saharan Africa. With the rapid accumulation of data from large-scale studies, the time is ripe to synthesize the work and summarize the overall findings.

In this review, we explore data from 19 ungulate taxa for which region- and continent-wide data exist. The taxa are ecologically associated with savannah ecosystems, although each has unique habitat preferences and life history traits (Estes 1991). Most of the taxa included are medium-sized and large bovids, reflecting the pre-

Table 1 Overview of the 19 ungulate taxa included in this review. We have included information on biogeographic regions inferred from phylogeographic data (west (W), east (E), south (S), southwest (SW); Fig. 3, Box 2), the presence of several lineages and/or a suture zone in East Africa, genetic markers used, level of differentiation among regions (Φ_{CT}/θ_{CT}) and study references.

No	Common name	Family	Subfamily	Scientific name	Regional hierarchy	Multiple east	Suture zone	Control region			Cyt b		Microsatellites			Reference
								bp	n	Φ_{CT}	bp	n	# loci	n	θ_{CT}	
1	Impala	Bovidae	Aepycerotinae	<i>Aepyceros melampus</i>	E-S, SW			c. 400	155	0.34*	364	27	8	162	0.19*	Nersting & Arcander (2001); Lorenzen & Siegmund (2004); Lorenzen <i>et al.</i> (2006a)*
2	Hartebeest	Bovidae	Alcelaphinae	<i>Alcelaphus buselaphus</i>	W, E, S	x	x	486	170	0.68†	417	11				Arcander <i>et al.</i> (1999)†; Flagstad <i>et al.</i> (2001)
3	Wildebeest	Bovidae	Alcelaphinae	<i>Connochaetes taurinus</i>	E, S			388	123	0.54						Arcander <i>et al.</i> (1999)
4	Topi	Bovidae	Alcelaphinae	<i>Damaliscus lunatus</i>	E, S			370	64	0.70						Arcander <i>et al.</i> (1999)
5	Grant's gazelle	Bovidae	Antilopinae	<i>Nanger granti</i>	E	x		375	177	0.74						Lorenzen <i>et al.</i> (2007b)
6	Buffalo	Bovidae	Bovinae	<i>Syncerus caffer</i>	W-E, E-S		x	358	766	0.42			17	209	NA	Van Hooft <i>et al.</i> (2000, 2002); Smits <i>et al.</i> (in press)†
7	Common eland	Bovidae	Bovinae	<i>Taurotragus oryx</i>	E, S		x	414	122	0.52						Lorenzen <i>et al.</i> (2010)
8	Greater kudu	Bovidae	Bovinae	<i>Tragelaphus strepsiceros</i>	E-S, SW			c. 400	90	0.40						Nersting & Arcander (2001)
9	Roan	Bovidae	Hippotraginae	<i>Hippotragus equinus</i>	W, E-S			401	137	0.49			8	137	0.26	Mathee & Robinson (1999); Alpers <i>et al.</i> (2004)†
10	Sable	Bovidae	Hippotraginae	<i>Hippotragus niger</i>	E, S, SW	x	x	496	106	0.82†	343	40				Mathee & Robinson (1999)†; Pitra <i>et al.</i> (2002, 2006)
11	Beisa oryx	Bovidae	Hippotraginae	<i>Oryx beisa</i>	E	x		423	58	0.55	666	19				Masembe <i>et al.</i> 2006

Table 1 Continued

No	Common name	Family	Subfamily	Scientific name	Regional hierarchy	Multiple east	Suture zone	Control region			Cyt b		Microsatellites			Reference
								bp	n	Φ_{CT}	bp	n	# loci	n	θ_{CT}	
12	Gemsbok	Bovidae	Hippotraginae	<i>Oryx gazella</i>	S			530	75			10	75	–	Osmers <i>et al.</i> 2011	
13	Waterbuck	Bovidae	Reduncinae	<i>Kobus ellipsiprymnus</i>	W-E, E-S		x	478	173	0.19		14	116	0.14	Lorenzen <i>et al.</i> 2006b	
14	Kob	Bovidae	Reduncinae	<i>Kobus kob</i>	W-E, E		x	357	187	0.53		7	151	0.11	Birungi & Arcander (2000); Lorenzen <i>et al.</i> (2007a) [†]	
15	Giraffe	Giraffidae	–	<i>Giraffa camelopardalis</i>	W, E, S, SW	x	x	1765 [§]	654	0.75		14	381	0.22	Brown <i>et al.</i> (2007)	
16	Hippopotamus	Hippopotamidae	–	<i>Hippopotamus amphibius</i>	E-S			400	109	0.10 [†]					Okello <i>et al.</i> (2005)	
17	Common warthog	Suidae	–	<i>Phacochoerus africanus</i>	W, E, S		x	c. 370	181	0.69		6	143	0.07	Muwanika <i>et al.</i> (2003)	
18	Plains zebra	Equidae	–	<i>Equus quagga</i>	E-S			309	204	0.06 [†]		7	80	0.03 [†]	Lorenzen <i>et al.</i> (2008)	
19	Mountain zebra	Equidae	–	<i>Equus zebra</i>	SW			445	77	–		15	291	–	Moodley & Harley (2005)	

NA Data not available.

[†] Φ_{CT}/θ_{CT} value among three regions: E, S and SW.[‡] Φ_{CT} value between two regions: E and S.[§]Reference for Φ_{CT}/θ_{CT} values.[¶]Sequence includes cyt b, tRNA and control region.

dominance of the group within the herbivore guild. We focus on major biogeographic signals within each taxon and evaluate community-wide patterns in the context of Pleistocene climate change.

Methods

Literature review

We compiled published studies on wild, free-ranging and widely distributed savannah ungulates. Works on captive or translocated populations were omitted, for example white rhinoceros, the global population of which is derived from a single bottlenecked population of c. 20–50 individuals (Emslie & Brooks 2002). Because we are interested in broad-scale, continental-level phylogeographic patterns, we did not include studies covering only a limited area, such as one or a few localities, and therefore omitted data on, for example, puku, black rhinoceros and Grevy's zebra.

The retrieved studies were qualitatively assessed based on sampling coverage, data quality and reported genetic pattern, and are listed in Table 1. Of the 19 ungulate taxa included in this review, 14 are bovids. To assess whether major biogeographic patterns were found in other taxonomic groups and trophic levels, we include a discussion of comparable large-scale data sets of other widely distributed savannah taxa where appropriate.

Sampling varied greatly among studies, which is inevitable given the extensive logistical challenges associated with obtaining samples, and the varied scope of the studies. The best-sampled regions are Eastern and Southern Africa. Although half the species included in this review are found across the Sahel, genetic data from central Sahel are limited. Because we are focusing on the sub-Saharan savannah biome, we did not include data from Africa north of the Sahara and the Arabian Peninsula.

Data analysis also differed considerably among studies, reflecting that publications span 15 years of population genetic research. Variations included (i) the use of different genetic distance measures, (ii) presence or absence of internal support for regional clades and (iii) varied approaches to assessing the robustness of results. All studies used mitochondrial DNA (mtDNA) sequences, and about one-third included nuclear data in the form of microsatellites. For each paper that was specifically compliant with the goals of this review, we recorded sample size, the genetic marker(s) used and major observed phylogeographic patterns (Table 1, Box 2).

To investigate the mechanisms behind present-day ungulate diversity and elucidate the impact of past environmental change on populations and species, we relate overall phylogeographic patterns to information

on past climates and environments, including pollen records, dust deposition and stable isotope data, and to the fossil record. Other biotic and abiotic factors, such as humans, pathogens and interspecific competition, may also have impacted the historical biogeography of savannah species, although we do not explicitly consider them here.

Dating of phylogeographic events

By dating phylogeographic splits, divergence events can be directly associated with the timing of known biotic or abiotic changes such as climatic shifts or anthropogenic events (Ramakrishnan & Hadly 2009). However, identifying reliable calibrations for intraspecific analyses remains challenging. The association between genetic divergence and population divergence is not always clear because of factors such as incomplete lineage sorting (Edwards & Beerli 2000). The fossil record is usually uninformative with regard to the timing of intraspecific divergences, and local replacement events over shorter timescales of hundreds or thousands of years may pass unnoticed. Furthermore, fossil calibrations are less than optimal for intraspecific analyses owing to the effects of saturation, purifying selection and other factors (Ho & Larson 2006; Ho *et al.* 2008).

It is therefore preferable to employ calibrations within the intraspecific genealogy, using DNA sequences from dated material sampled at various points in time (Rambaut 2000). However, because there are so few ancient DNA analyses of fossil samples from sub-Saharan Africa, in part because DNA survives poorly in tropical deposits (Smith *et al.* 2003), such time-stamped data are not available for the species included in this review. Few of the reviewed studies have attempted to date the major phylogeographic splits between regions, and those that did used very different methods for the estimation of mutation rates (Flagstad *et al.* 2001; Brown *et al.* 2007; Lorenzen *et al.* 2010). Consequently, we are not able to assess the temporal fit between community-wide patterns of vicariance and driving factors. Although outside the scope of this review, estimating the timing of phylogeographic events among codistributed species may be accomplished if data sets are reanalysed using reliable mutation rates and the incorporation of environmental data, providing a promising venue for future research.

Discussion

Major biogeographic patterns

Across species, one major genetic signal has emerged: the phylogeographic structuring of regional populations

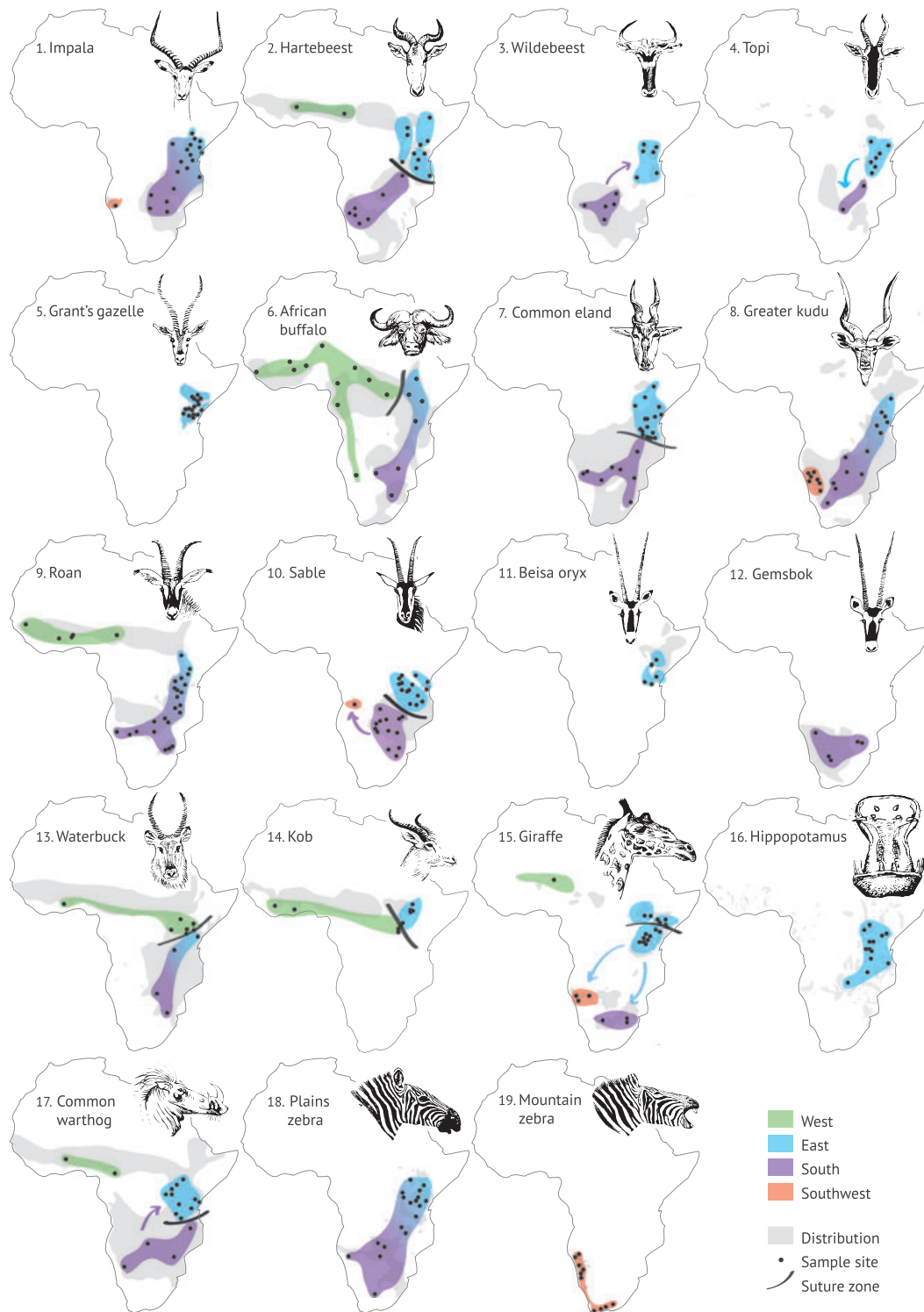


Fig. 3 Major biogeographic patterns of the 19 ungulate taxa included in this review inferred from phylogeographic data (further information in Box 2). Current species distributions based on the IUCN red list (IUCN 2011) are shaded in grey; dots indicate DNA sampling localities from the studies listed in Table 1. Owing to the large number of localities sampled in buffalo, only the mid-point of each sampled country is shown. The four biogeographic regions correspond to those shown in Fig. 2b: west (green), east (blue), south (purple), southwest (red). Arrows depict colonization between regions, where this has been inferred from genetic data; the colour and direction of the arrow indicates the source area. Thick black lines indicate the locality of the East African suture zone, where biogeographic lineages meet. Ungulate illustrations by Jon Fjeldså.

(Fig. 3, Box 2). As shown in Fig. 2b, we have defined two overall areas, *north* and *south*, indicating their periodic separation by an equatorial forest belt during moist pluvials. *North* represents the Sahel and encompasses biogeographic regions in the west and east. *South* includes Southern Africa and is split into regions in the east, south and southwest. During dry interpluvials, *south* joins and overlaps with *north* in East Africa, which therefore represents a melting pot of long-diverged lineages across many taxa.

Although the level and pattern of differentiation and diversity vary among taxa, and sample localities and sample sizes differ, most show significant structuring between at least two biogeographic regions (Fig. 3, Table 1, Box 2). Differences among taxa reflect unique evolutionary trajectories, including taxon-specific responses to common biotic and abiotic factors and the distinct demographic history of each individual population.

Divergence driven by environmental change

Phylogeographic data from Western Africa are available from seven of the nine focal species found in the region (Fig. 3, Table 1, Box 2). For those species whose ranges extend into Southern Africa, all but buffalo are structured north and south of the equatorial forest belt. In waterbuck, the distribution and nuclear differentiation of two phenotypically distinct subspecies mirrors the areas of *north* and *south* (Fig. 2b), and ranges overlap in the east (Lorenzen *et al.* 2006b). In hartebeest, roan and giraffe, *north/south* mitochondrial lineages are reciprocally monophyletic (Arctander *et al.* 1999; Alpers *et al.* 2004; Brown *et al.* 2007). A *north/south* split is also observed at the interspecific level, with the allopatric distribution of sister taxa such as kob in the Sahel and puku in Southern Africa, and of giant eland in West Africa and common eland across East/Southern Africa (Kingdon 1997).

Similar *north/south* structuring is observed in species from other taxonomic groups, indicating common cause. These include ostrich (Miller *et al.* 2010) and white-tailed mongoose (Dehghani *et al.* 2008), both of which are widely distributed across sub-Saharan African savannahs. The phylogeographic signal further permeates trophic levels and is reported in apex predators whose distributions are determined by prey abundance, including lion (Barnett *et al.* 2006) and spotted hyena (Rohland *et al.* 2005).

We attribute the pronounced *north/south* split to the periodic confinement of populations to the two continental areas. An increase in tropical forest across Central Africa during pluvials would present an impenetrable barrier to gene flow between populations

of savannah taxa isolated on either side. The Pleistocene included at least five full pluvial cycles (Szabo *et al.* 1995), and the repeated shifts of the two major vegetation zones facilitated the emergence and evolution of many bovid taxa (Vrba 1995; Bobe *et al.* 2002; Bobe & Behrensmeyer 2004).

In ungulates with additional phylogeographic structuring, the differentiation between populations north and south of the equatorial forest belt remains the most pronounced, suggesting several vicariance events (Flagstad *et al.* 2001; Muwanika *et al.* 2003; Brown *et al.* 2007). In hartebeest, buffalo, kob and giraffe, Sahelian populations are split into clades in the west and east (Fig. 3; in wart-hog, the east was colonized from the southern clade). In buffalo, the predominance of the west–east Sahelian divide is distinct among the reviewed species, as the western clade includes populations from the southwest (Fig. 3) (Van Hooft *et al.* 2002; Smitz *et al.* in press). A west–east divide is also found in several other savannah taxa, including red duiker (Van Vuuren & Robinson 2001), white-tailed mongoose (Dehghani *et al.* 2008), Guinea multimammate mouse (Brouat *et al.* 2009), African common toad (Vasconcelos *et al.* 2010) and ostrich (Miller *et al.* 2010). Similarities across taxonomic groups indicate common cause and suggest ecologically driven divergence within the Sahel; a divergence that is nested within the higher-level split of *north* and *south* in many taxa.

Ecologically driven divergence is supported by indirect data from the first tropic level. The maize stalk borer *Busseola fusca* is a pathogen of domesticated C₄ plants and shows similar phylogeographic structuring of west and east (Sezonlin *et al.* 2006). Although currently associated with cultivated plants, the biogeographic history of the stalk borer mirrors that of its wild C₄ host(s) before domestication, as the organisms coevolved over evolutionary timescales.

East Africa: a cradle of diversity

The highest diversity of African ungulates is in East Africa (Fig. 2a) (du Toit & Cumming 1999) and many of the reviewed species have endemic sister taxa in the region, including lesser kudu, desert warthog and Grevy's zebra (Kingdon 1997; IUCN 2011). Several divergent lineages are also present within taxa (Fig. 3): in hartebeest, sable and giraffe (Arctander *et al.* 1999; Flagstad *et al.* 2001; Pitra *et al.* 2002; Brown *et al.* 2007), and in the endemic beisa oryx and Grant's gazelle (Masembe *et al.* 2006; Lorenzen *et al.* 2007b). In addition, genetically distinct impala and kudu are found in northern Kenya, suggesting several clades within these species as well (Nersting & Arctander 2001; Lorenzen *et al.* 2006a). The limited range of the East African lineages indicates local divergence, and phylogeographic

Box 2 Species summaries

The following data summaries are intended as an extended figure legend for the biogeographic maps presented in Fig. 3, where we outline major phylogeographic patterns within each of the 19 reviewed taxa (Fig. Box 2). Details of the genetic markers used and references are listed in Table 1.

Below, we have indicated current range distributions in parentheses () after the taxon name, corresponding to the grey shading in Fig. 3. Nonsampled regions are indicated with []. For example, hippopotamus is found across sub-Saharan Africa, but genetic data are only available from East and Southern Africa, and hence its distribution is denoted ([W]-E-S-[SW]). The biogeographic regions of *north*, *south*, W, E, S and SW discussed below correspond to the areas indicated in Fig. 2b.

1. **Impala** (E-S-SW) Control region, cytochrome b and microsatellites distinguish the phenotypically distinct and geographically isolated black-faced impala in the SW. There is no phylogeographic structuring of East and Southern Africa, although microsatellites suggest isolation by distance along the east-to-south gradient. The population in Samburu, Kenya, is genetically distinct, suggesting several lineages in the E.

2. **Hartebeest** (W-E-S) The species shows high levels of morphological variation, and control region sequences indicate pronounced differentiation between *north* and *south*. Further phylogeographic structuring is found within each area, indicating several vicariance events. *North* is split into a W and E clade; with additional structuring within the latter. There is a suture zone in East Africa, and control region sequences and microsatellites suggest gene flow or incomplete lineage sorting between two of the eastern groups. Genetic variation is highest within populations in East Africa, and sequences are central in haplotype networks, suggesting an eastern origin of extant lineages and one or more eastern refugia. Most recognized subspecies are reciprocally monophyletic.

3. **Wilbebeest** (E-S-SW) Control region sequences from the south are paraphyletic, and an E clade groups within them. Branches in the S are longer, and nucleotide diversity progressively declines towards the east, suggesting a pattern of colonization from south to east.

4. **Topi** ([W]-E-S) Control region sequences from East Africa are paraphyletic and the southern clade groups within them, suggesting a pattern of colonization from E to S.

5. **Grant's gazelle(s)** (E) Three reciprocally monophyletic control region lineages. Lineages are parapatric with limited distributions, indicating local divergence and several refugia in East Africa. Although based on mtDNA only, there is no evidence of interbreeding among lineages in areas of contact, suggesting reproductive isolation.

6. **African buffalo** (W-E-S-SW) Control region sequences show clear divergence between two groups within *north*, which are recognized as distinct subspecies. The W group includes the SW, which is not seen in other taxa. The E group includes populations from the S, which was colonized relatively recently.

7. **Common eland** (E-S) Control region sequences show a strong phylogeographic signal between E and S, which overlap in the East African suture zone. The eastern lineage is more structured and has lower overall nucleotide diversity and a more recent common ancestor, suggesting differing evolutionary scenarios in east and south and a younger origin of eastern populations.

8. **Greater kudu** (E-S-SW) Control region sequences distinguish Namibian populations in the SW from the rest. Kudu show decreasing nucleotide diversities along the east-to-south gradient, suggesting an origin in Southern Africa. One northern Kenyan sample is genetically distinct, which may suggest several lineages in the E.

9. **Roan** (W-E-S-SW) Control region sequences and microsatellites indicate phylogeographic structuring between W and the sampled populations in E, S and SW. There is no phylogeographic structuring within the latter clade.

10. **Sable** (E-S-SW) Strong phylogeographic structuring among three control region lineages. Two lineages are limited to the E, indicating several vicariance events in the region. The third lineage includes all southern localities, and branch lengths decrease from south to east, suggesting a southern origin and a suture zone in East Africa. A genetically distinct SW population, represented by the giant sable in Angola, is nested within the S lineage.

11. **Beisa oryx** (E) Control region and cytochrome b data reveal three distinct clades, suggesting several vicariance events in the E. Two clades are found in the same localities in central Kenya, and the third clade is found primarily in south Kenya/north Tanzania.

12. **Gemsbok** (S) No phylogeographic structuring among control region haplotypes, although microsatellites distinguish between two differentiated populations in the northern and southern part of its range.

13. **Waterbuck** (W-E-S) Distribution of phenotypically and geographically distinct subspecies corresponds to *north* and *south*. Subspecies are clearly distinguished by microsatellites, but not by mtDNA, and form a tight parapatric boundary in the East African suture zone, with limited introgression.

14. **Kob** (W-E) Two well-diverged control region lineages: one encompasses mostly West African and Ugandan localities, and the other includes Ugandan localities and white-eared kob, a phenotypically, behaviourally and genetically distinct subspecies from Sudan and Ethiopia. A tight parapatric suture zone is present in East Africa, with introgressive hybridization from white-eared to Uganda kob.

15. **Giraffe** (W-E-S-SW) Mitochondrial DNA and microsatellites show significant divergence among six clades. The strongest split is between *north* and *south*; additional phylogeographic structuring is found within each group, indicating several vicariance events. The *north* group includes a W lineage and two E lineages. The *south* group includes distinct lineages in E, S and SW. Genetic data suggest a suture zone in East Africa with introgression between lineages.

Box 2 Continued

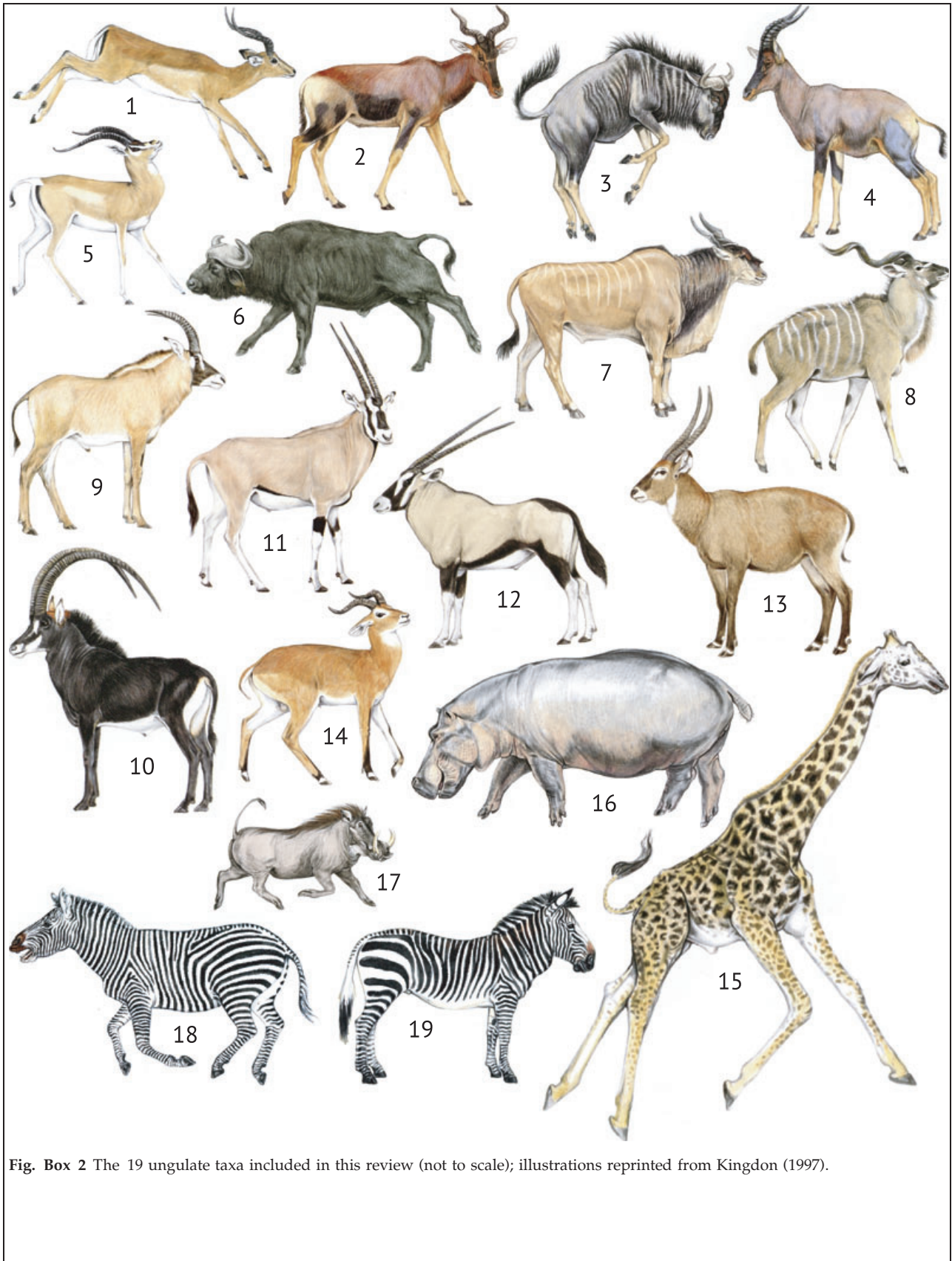


Fig. Box 2 The 19 ungulate taxa included in this review (not to scale); illustrations reprinted from Kingdon (1997).

16. **Hippopotamus** ([W]-E-S-[SW]) Control region sequences show no phylogeographic structuring. Sequences show a signal of expansion and suggest the (sampled) populations originated in the east.

17. **Common warthog** (W-E-S-SW) Control region sequences distinguish among three regional lineages in W, E and S, a signal also found in microsatellites. The S sequences are paraphyletic and basal to the W and E lineages, both of which are reciprocally monophyletic, suggesting an origin in the south.

18. **Plains zebra** (E-S-SW) An absence of any phylogeographic signal, despite significant variation in size, coat colour and pattern from Kenya in the north to the extinct quagga in the south. Significant levels of gene flow may have masked a past vicariance event, as two widely distributed lineages are differentiated by three substitutions. Microsatellites reveal a clinal pattern of genetic variation along the east-to-south gradient, concordant with morphological diversity.

19. **Mountain zebra** (SW) No phylogeographic structuring, although the two recognized subspecies harbour private microsatellite alleles.

clades appear to be maintained despite the lack of contemporary barriers to gene flow (Flagstad *et al.* 2001; Masembe *et al.* 2006; Lorenzen *et al.* 2007b).

High spatial heterogeneity in both quantity and quality of food resources has been invoked as one of the main drivers of ungulate diversity (du Toit & Cumming 1999). In addition, we argue that the high levels of temporal heterogeneity unique to East Africa have shaped the exceptional diversity of this region. East Africa has been characterized by highly interchangeable environments over the past 2 Ma (Maslin 2007); local environments have been affected by the volcanism and tectonism associated with the uplift of the Rift Valley, and global climates contrasting between very dry and very wet have caused the periodic disappearance and reappearance of the large deep lakes in the East African Rift valley (Trauth *et al.* 2007).

Environmental instability would facilitate evolutionary innovation and change, as natural selection acted in concert with genetic drift on isolated populations (deMenocal 2004; Maslin 2007). However, there would also be a greater risk of local extirpation (Reynolds 2007). For example, ecological instability in the form of drought is the single most important cause of ungulate mortality in East African parks (i.e. Ogutu *et al.* 2008), and African buffalo and savannah elephant declined dramatically during the mid-Holocene aridification (Heller *et al.* 2008; Okello *et al.* 2008). In addition, the demographic signal of population expansion observed in hippopotamus—an amphibious species wholly dependent on water for survival (Estes 1991)—may reflect its recovery from a recent drought-induced environmental bottleneck (Okello *et al.* 2005).

Suture zone in East Africa

A suture zone is an area where lineages that have diverged in allopatry come into secondary contact (Remington 1968). East Africa represents such a zone, where major biogeographic lineages from different regions meet and overlap. The extent and form of con-

tact varies across taxa—ranging from admixture to speciation—and is exemplified by a narrow hybrid zone in eland (Lorenzen *et al.* 2010), limited hybridization across a tight parapatric boundary in waterbuck (Lorenzen *et al.* 2006b), pronounced one-way introgression in kob (Lorenzen *et al.* 2007a) and reproductive isolation in giraffe (Brown *et al.* 2007).

The location of the contact zone varies, depending on the geographic origin of lineages (Fig. 3). In kob and buffalo, Sahelian lineages from west and east meet in Uganda (Lorenzen *et al.* 2007a; Smitz *et al.* in press). Distinct ecotypes of other taxa also overlap here, including forest and savannah elephant (Ishida *et al.* 2011). In hartebeest, waterbuck and giraffe, where lineages diverged north and south of the Central African forests, the suture zone is located in Kenya and Tanzania (Flagstad *et al.* 2001; Lorenzen *et al.* 2006b; Brown *et al.* 2007; Ouma *et al.* 2010). Ostrich shows a similar pattern (Miller *et al.* 2010), and plains zebra and Grevy's zebra also overlap in Kenya, producing fertile offspring (Cordingley *et al.* 2009). In eland and sable, whose allopatric lineages from East and Southern Africa meet, the contact zone is shifted to central Tanzania (Pitra *et al.* 2002; Lorenzen *et al.* 2010). In warthog, which shows similar regional structuring, the zone is found yet further south (Muwanika *et al.* 2003).

Differing evolutionary scenarios in east and south

Most of the reviewed species are distributed across East and Southern Africa, and many show phylogeographic structuring (Fig. 3). In most cases, the divergence follows the east–south axis of open formations in Southern Africa (Kingdon 1997). The level of differentiation varies from clinal variation in plains zebra (Lorenzen *et al.* 2008) to reciprocal monophyly between eland populations in east and south (Lorenzen *et al.* 2010). Divergence is most pronounced between beisa oryx and gemsbok, where mitochondrial control region lineages differ by 40% (Osmers *et al.* 2011). Considered conspecific until recently (Estes 1991), these allopatric sister

taxa are endemic to Eastern and Southern Africa, respectively. A similar regional divide is reported across many diverse savannah species including ostrich (Miller *et al.* 2010), fiscal shrike (Fuchs *et al.* 2011), four-striped grass rat (Castiglia *et al.* 2012), cheetah (Charreau & Fernandes 2011) and wild dog (Marsden *et al.* 2012).

In several species, genetic data from East Africa suggest the region was colonized from the south. This may reflect the replacement of populations following local extirpation. Such complex evolutionary dynamics, with frequent loss and replacement of populations and lineages over evolutionary timescales, has been well documented in northern hemisphere ungulates by ancient DNA analysis (e.g. Debruyne *et al.* 2008; Campos *et al.* 2010).

In wildebeest and warthog, the eastern lineage falls within the diversity of the southern clade (Arctander *et al.* 1999; Muwanika *et al.* 2003), a pattern also observed in ostrich (Miller *et al.* 2010). In eland, eastern populations have shorter branch lengths and show higher levels of among-population structuring, and differences in genetic variability and coalescence times between east and south suggest the more recent ancestry of populations in the east (Lorenzen *et al.* 2010). A younger origin of eastern populations is also supported by the longer branch lengths of wildebeest from the south (Arctander *et al.* 1999), and in impala and kudu, nucleotide diversities decrease from south to east (Nersting & Arctander 2001; Lorenzen *et al.* 2006a). In impala, the (re)colonization of East Africa is supported by shifts in morphological variation between Plio-Pleistocene and modern populations from the two regions (Reynolds 2007, 2010).

Across taxa, less pronounced phylogeographic structuring and higher levels of genetic variation in Southern Africa suggest a large, long-standing population in the region, in contrast to the mosaic of refugial populations in the east (Lorenzen *et al.* 2010). This is supported by palaeoclimate proxies, which indicate stable levels of moisture throughout the Pleistocene and greater environmental stability in the south (deMenocal 2004; Quinn *et al.* 2007; Trauth *et al.* 2007; Maslin *et al.* 2012). A continuous Southern African refuge area would act as a museum, conserving populations and species over evolutionary timescales (Reynolds 2007). However, the local loss of populations in Southern Africa and subsequent colonization from the east is suggested by some taxa. Hartebeest, topi, buffalo and giraffe show a reversed phylogeographic pattern, where the southern clade is derived from the east, suggesting the biogeographic history of Southern Africa has also been dynamic (Arctander *et al.* 1999; Pitra *et al.* 2002; Brown *et al.* 2007; Smitz *et al.* in press).

Location of Pleistocene refugia

Although species distributions change through time owing to local extirpations, replacements and the colonization of new areas, we can use the current distribution of genetic lineages to infer the putative geographic location of past refugia. The concordance among phylogeographic patterns observed across the ungulate assemblage strongly suggests the presence of Pleistocene refugia in West and Southern Africa and a mosaic of refugia in East Africa (Fig. 2b). Genetic data from four of the reviewed species (Fig. 3, Table 1) indicate an additional refuge area in the southwest (Nersting & Arctander 2001; Lorenzen & Siegmund 2004; Pitra *et al.* 2006; Brown *et al.* 2007). This hyper-arid region is characterized by high floral endemism (Maggs *et al.* 1998) and also harbours the endemic mountain zebra, a sister species of plains zebra (Wichman *et al.* 1991).

Conclusions

Evaluating two decades of published studies, we conclude that codistributed ungulate taxa show a striking level of phylogeographic concordance, a pattern mirrored in species from other assemblages and trophic levels. We present evidence that ecological shifts associated with Pleistocene climate change shaped taxonomic diversity. Oscillations between warm, wet and cool, dry climates facilitated several divergence events. During moist pluvials, forests displaced savannahs, isolating populations of arid-adapted species. In turn, savannahs expanded at the expense of forests during dry interpluvials, enabling secondary contact among diverged lineages. The signal of regional structuring across taxa indicates that Pleistocene savannah refugia were located in West, Southern and South-West Africa, with a mosaic of spatial and temporal refugia in East Africa.

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