



Effect of simulated faunal impoverishment and mixture on the ecological structure of modern mammal faunas: Implications for the reconstruction of Mio-Pliocene African palaeoenvironments

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ABSTRACT

The strong link between environment and the ecological diversity of communities is often used for drawing palaeoenvironmental inferences from fossil assemblages. Here we focus on the reliability of fossil samples in comparison to original communities when inferring palaeoenvironments from the ecological diversity of fossil mammal faunas. Taphonomic processes and sampling techniques generally introduce two kinds of biases in fossil samples: 1) the directional impoverishment of communities, i.e. the absence of some specific categories of bones, individuals or species; and 2) the mixture of several communities, temporally (time-averaging) and/or spatially (space-averaging). We explore the impact of such alterations on ecological diversity and taxonomic richness by simulating an impoverishment in small species (1–45 kg) and a mixture of communities on an original dataset of 50 modern African communities.

The progressive impoverishment in small species in a mammal community induces a relative enrichment in terrestrial and grazing species and a depletion (or even the disappearance) of several ecological categories (e.g., fossorial, arboreal, sub-arboreal, frugivorous, omnivorous and insectivorous species), thus leading to the ecological homogenisation of the altered communities. Other categories (carnivorous species, browsers, mixed feeders and sub-aquatic species) prove stable and seem to be good estimates for the relative abundances in the parent communities. Ideally, palaeoenvironmental inferences should be drawn from those ecological categories. For strong degrees of impoverishment, the discriminating power of the ecological diversity is reduced and other proxies should be used. Once the degree of impoverishment is assessed, it becomes possible to consider the condensation of several communities into a single fossil sample by comparing its taxonomic richness with those of modern communities, first impoverished to the same level. The mixture of communities tends to increase the taxonomic richness but does not significantly modify the overall ecological diversity.

As a case study, we applied this approach to 15 African mammal samples from the late Miocene–earliest Pliocene, a period of particular interest, as it saw the emergence of hominins, together with faunal turnovers, and major climatic and environmental changes. Most of our fossil samples, especially those that yielded early hominins, appear altered to different degrees by taphonomic processes and sampling techniques, meaning that their faunal structures may not be comparable and that their inferred palaeoenvironmental differences may not be genuine.

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1. Introduction

That the environment has a role in the evolution of mammal species is widely accepted, even if the specific mechanisms involved are still debated (e.g., Vrba, 1980; Vrba et al., 1989; Potts, 1996, 1998). It is

therefore crucial to reconstruct past environments, notably by using proxies such as sedimentological and geochemical evidences, plant items and animal remains. In particular, the ecological diversity of fossil assemblages has often and successfully been applied in that perspective, especially with mammals (e.g., Andrews and Nesbit Evans, 1979; Andrews et al., 1979; Andrews, 1980; Van Couvering, 1980; Nesbit Evans et al., 1981; Artemiou, 1983; Legendre et al., 1991; Damuth, 1992; Andrews, 1996; Gagnon, 1997; Reed, 1997; Rodríguez, 2001; Kovarovic et al., 2002; Pazoni, 2004; Rodríguez, 2004; Fara et al., 2005; Mendoza et al., 2005). In such reconstructions, the ecological diversity of fossil

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faunal assemblages is compared to that of modern communities for which the environmental context is well defined. However, in numerous studies on mammal faunas from different continents and at various periods (Artemiou, 1983; Rodríguez, 2001; Rodríguez et al., 2004; Soligo and Andrews, 2005; Koufos, 2006; Su and Harrison, 2007), the ecological diversities of fossil assemblages significantly depart from the range expressed by modern faunas.

The recurrence of that pattern of difference between ancient and modern faunas could indicate that no modern equivalent exists for these past communities, at least for their faunal and floral structures. However, that hypothesis necessitates the reassessment of the use of the actualistic principle in palaeoecological studies relying on mammals. Alternatively, Soligo and Andrews (2005) proposed that, in most cases, the absence of congruence between past and modern faunal structures results from taphonomic and/or methodological biases. Indeed, from the death of the animals to their sampling as fossils, several physical, chemical, and biological processes occur, altering the picture of the original community. These alterations happen first during the formation of the fossil assemblage, especially during the constitution of the death assemblage – passing from a living community to an accumulation of skeletal remains – and then at the time of the collection of fossil remains – passing from a fossil assemblage to a fossil sample (Etter, 1999; Western and Behrensmeyer, 2009). Resulting fossil samples only supply a partial picture of the living communities they represent.

To handle that issue in palaeoecological studies comparing modern and fossil faunas, some authors propose to exclude generally biased aspects of fossil assemblages. For instance, small species (e.g., Reed and Rector, 2007), micromammals only (e.g., Reed, 1997; Kovarovic et al., 2002), or some taxa considered as rare in the fossil record (e.g., Reed and Rector, 2007) are often excluded. That practice requires performing, beforehand, a careful taphonomic study in order to identify the biases present in the fossil samples. This is also essential to assessing the reliability of the resulting palaeoenvironmental inferences.

Is it possible to assess the nature and the extent of biases present in a fossil sample? Taphonomic processes that contribute to the formation of fossil assemblages, as well as sampling techniques, generally introduce two kinds of biases in fossil samples: 1) the impoverishment of communities, i.e. the lack of preservation or of collection of some bones, individuals, or species; and 2) the mixture of several communities, temporally (time- or analytical-averaging) and/or spatially (space-averaging). In this study, we will first artificially impoverish (i.e., deplete in species) and/or mix modern mammal communities in order to test the impact of these alterations on the ecological diversity and the taxonomic richness of faunas. Then, as a case study, we will focus on the determination of such biases in African faunas from the late Miocene–earliest Pliocene, a period of particular interest that saw the emergence of hominins (Haile-Selassie, 2001; Senut et al., 2001; Brunet et al., 2002, 2005; White et al., 2009), but also important global climatic, environmental and other faunal upheavals (Quade et al., 1989; Cerling et al., 1993; Molnar et al., 1993; Hill, 1995; Kennett, 1995; Quade and Cerling, 1995; Leakey et al., 1996; Cerling et al., 1997; Ségalen et al., 2007). This will ultimately help to understand the observed discrepancies between fossil samples and modern faunas.

2. Material and methods

Marine species, micromammals (body mass <1 kg) and bats are excluded from modern and fossil mammal faunas of the study, because they represent sub-communities with ecological specificities (Behrensmeyer et al., 1979). Bats and marine mammals are excluded because of their specific aerial and marine way of life, respectively. Micromammals are discarded owing to the smaller scale of the palaeoenvironmental signal they carry in comparison to larger

mammals. They remain, nevertheless, a useful tool for palaeoenvironmental and palaeoclimatic purposes (e.g., Montuire et al., 2006).

We assembled a set of 50 modern African mammal communities (Appendix 1 and 2), most of them from protected areas (national parks or faunal reserves) and coming from various environmental settings (tropical forest to semi-arid areas). These faunas illustrate the whole spectrum of modern African environments and, according to the actualistic principle, are supposed to provide good equivalents of Mio-Pliocene environments. Two kinds of alterations were applied on these modern faunas: 1) the impoverishment of communities, and 2) the mixture of several communities (Fig. 1).

First, the communities were impoverished according to body size. The general aim is to test for the impact of increasing depletion in small species on the ecological diversity of observed samples. The impoverishment was greater for small species and less for the largest. That choice is motivated by the finding that palaeocommunities are often size-biased against small species (e.g., Behrensmeyer et al., 1979). As a whole, the smaller a species, the more fragile its bones and the more likely that they will be destroyed by scavengers or weathering (Damuth, 1982; Lyman, 1984; Staff et al., 1985; Kidwell and Flessa, 1995; Conard et al., 2008). It is also more difficult to spot small fossil remains in the field, especially during surface sampling (Wolff, 1975; Soligo and Andrews, 2005). Thus, the probability of preserving and sampling a species generally tends to decrease with body size. For each of the 50 mammal communities, species are sampled without replacement, according to a probability assigned for their body mass. The resulting faunal assemblages constitute what we will call sub-communities. The absence of replacement in the sampling of species avoids the artificial enrichment in species of some ecological categories, i.e. no category contains more species than observed in the original community. For sampling probabilities, it was not possible to construct a distribution based on modern observations as very few studies compare mammal death assemblages with the corresponding parent communities (e.g., Behrensmeyer et al., 1979; Sept, 1994). Thus, five intuitive sets of probabilities were constructed, simulating different degrees of size-related impoverishments in fossil samples (Table 1). The less altering set of probabilities (“very weak”) corresponds to a monotonically decreasing curve, from the largest species to the smallest. The four other sets of probabilities follow sigmoid distributions. That kind of function enables to contrast the sampling probabilities between large and small species, the latter being associated with a lower sampling probability. That contrast increases with the degree of impoverishment. In order to integrate observations made on modern death assemblages (e.g., Behrensmeyer et al., 1979; Sept, 1994), the probabilities of species heavier than 100 kg are set to 1. Indeed, both studies showed that species heavier than 100 kg were systematically represented in the death assemblage (except the lion in the Virunga National Park). For each set of probabilities, sampling is iterated ten times for each of the 50 communities. All simulations were performed with the R version 2.12.1 software environment (2010). Importantly, these simulations do not take into account the complex macroecological relationship between abundance and body size. In living mammal communities, small species are usually represented by more individuals and have higher turnover rates than large ones (e.g., Damuth, 1981; Vermeij and Herbert, 2004; White et al., 2007). They are therefore expected to supply more bones to the death assemblage, which would counterbalance the effect of their greater vulnerability to destruction by physical and/or biological processes. However, this does not seem to be the case for most fossil assemblages, especially among late Miocene–earliest Pliocene sites (e.g., Senut and Pickford, 1994; Harrison, 1997a; Pickford and Senut, 2001; Vignaud et al., 2002; Leakey and Harris, 2003; Haile-Selassie et al., 2004; Fara et al., 2005; Le Fur et al., 2009), neither for modern mammalian death assemblages in the Amboseli National Park (Behrensmeyer et al., 1979). This suggests that high density is not sufficient to compensate for the potential taphonomic and/or sampling biases affecting small species. Because our study aims at mimicking observed fossil samples

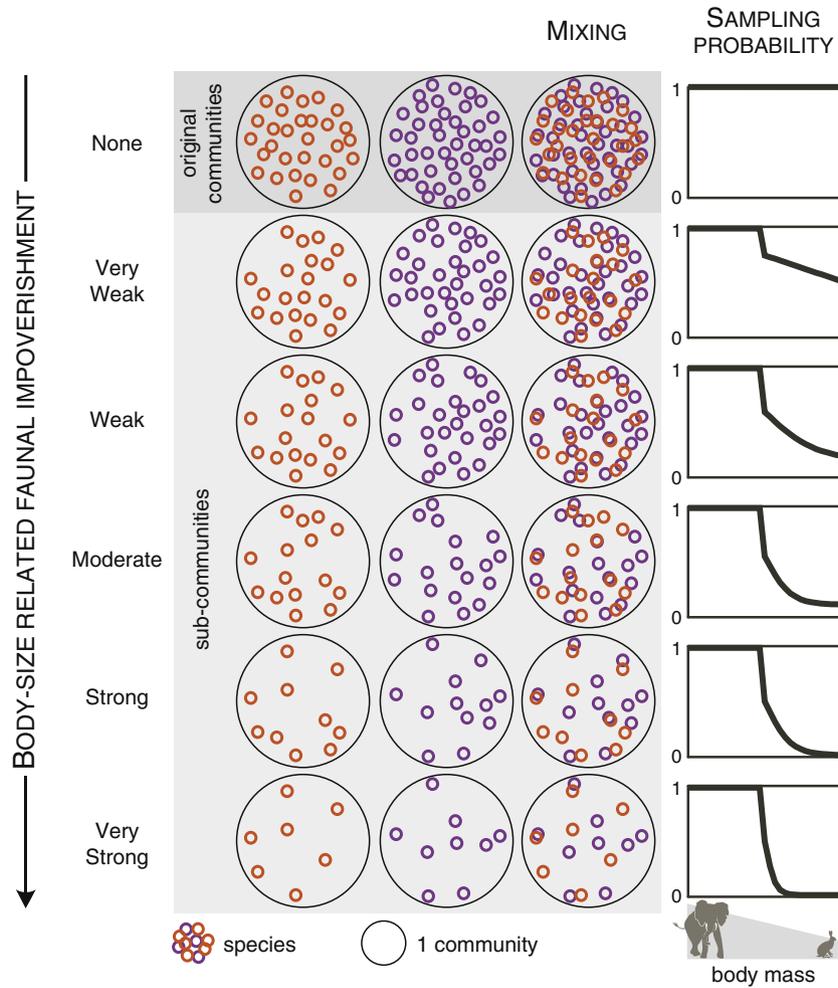


Fig. 1. Schematic representation of the protocol proposed to alter modern African communities by impoverishing communities of small species and/or mixing several communities.

by degrading extant communities, our simulations deliberately ignore what could have been the original abundance distributions.

Secondly, for each level of impoverishment, we constructed two sets of 500 sub-communities, corresponding to the mixing of two and three randomly drawn communities that have been first impoverished (Fig. 1). Draws of the same communities were evicted. That simulation mimics a space- and a time-averaging and the aim is to test the consequences of different degrees of averaging. Thus, even if it may not constitute the general rule, only sub-communities impoverished at the same degree were merged. Otherwise, the mixing of

faunas contributing in different proportions to the resulting faunal assemblage would introduce other sources of variation and confuse the interpretation of results. In that procedure, species shared by two sub-communities that are mixed are counted only once.

The first step is to study separately the impact of these two alterations on the ecological diversity and the taxonomic richness of modern sub-communities. Subsequently, we will use these two simulations to assess for the presence and consequences of such biases in late Miocene–earliest Pliocene fossil mammal faunas from Africa. While many fossil localities of that period have been discovered, only the most sampled and studied are used here. Table 2 lists the 15 fossil localities used in this study, among which three yielded hominin remains. The faunal lists were developed from published sources revised with recently published accounts on some taxa.

The ecological diversity of a mammal fauna, modern or fossil, is defined as the combination of three ecologically relevant variables: diet preferences, body mass, and locomotion of species (Table 3). These covariables are distributed over ecological categories which represent the optimum balance between the resolution possible with fossil material and that necessary to draw palaeoenvironmental inferences (e.g., Andrews et al., 1979; Artemiou, 1983; Damuth, 1992; Gagnon, 1997; Reed, 1997; Rodríguez, 2001; Kovarovic et al., 2002; Pazonyi, 2004; Fara et al., 2005; Mendoza et al., 2005). We use the proportion of ecological categories to construct the ecological profile for each faunal assemblage. The attribution of ecological categories to fossil taxa is based on several approaches (e.g., isotopes, ecomorphology, and dental microwear). When necessary, the ecological features

Table 1

The five sets of sampling probabilities used to alter modern communities according to the body size of species. When a species lies on two ranges of body mass, an intermediate sampling probability is assigned (↔).

Body mass ranges	Degree of impoverishment				
	Very weak	Weak	Moderate	Strong	Very strong
> 360 kg	1.00	1.00	1.00	1.00	1.00
180↔ > 360 kg	1.00	1.00	1.00	1.00	1.00
180–360 kg	1.00	1.00	1.00	1.00	1.00
90↔ 360 kg	1.00	1.00	1.00	1.00	1.00
90–180 kg	1.00	1.00	1.00	1.00	1.00
45↔ 180 kg	0.75	0.59	0.55	0.50	0.50
45–90 kg	0.70	0.46	0.31	0.23	0.05
10↔ 90 kg	0.65	0.35	0.17	0.08	0.00
10–45 kg	0.61	0.27	0.12	0.03	0.00
1↔ 45 kg	0.56	0.22	0.11	0.01	0.00
1–10 kg	0.51	0.19	0.10	0.00	0.00

Table 2
Late Miocene–earliest Pliocene African mammal localities. The ages are radiochronologically (r) or biochronologically (b) estimated and the areas that yielded early hominin remains are labelled (H). For faunal lists, only the main or most recent reference is given.

Formation	Member / level	Sector	Country	Age (Ma)	Faunal list ref.	
Nawata	Upper Lower	Nup Nlo	Lothagam Kenya	5–6.54 ^r (McDougal and Feibel, 2003) 6.54–7.44 ^r	(Leakey and Harris, 2003)	
Lemudong'o	Speckled Tuff Lower Sandstone	LemST LemLS	Narok Kenya	6.084 ± 0.018 ^r (Ambrose et al., 2003)	(Ambrose et al., 2007)	
Nkondo		Nko	Kaiso-Nkondo	Ouganda-DRC	5–6 ^b (Pickford et al., 1993)	(Senut and Pickford, 1994)
Adu Asa ^H	Asa Koma	Asa	Middle Awash (Afar)	Ethiopia	5.54–5.77 ^r (WoldeGabriel et al., 2001)	(Haile-Selassie et al., 2004)
Varswater	Pelletal Phosphate*	PPMn PPMs	Langebaanweg (Cap Province)	S. Africa	~5 ^b (Hendey, 1981)	(Hendey, 1981)
Manonga	Quartzose Sand	QSM				
Ibole		Man	Manonga Valley	Tanzania	~5–5.5 ^b (Harrison, 1997a)	(Harrison, 1997a)
Sahabi	U1	Sah	Syrte Basin	Libya	7–6.5 ^b (Bernor et al., 2008; Boaz et al., 2008; Sanders, 2008)	(Boaz et al., 2008)
Baynunah	Upper Lower	Bay	Abu Dhabi	United Arab Emirates	6–8 ^b (Whybrow and Hill, 1999) ~6.5 ^b (Bibi et al., 2006)	(Whybrow and Hill, 1999)
Lukeino ^H	Kapcheberek Kapsomin Kapgoywa	Luk	Tugen Hills	Kenya	5.7–6 ^r (Sawada et al., 2002)	(Pickford and Senut, 2001)
Anthracotheriid Unit ^H	TM266 locality	TM	Toros-Menalla	Chad	ca 7 ^r , ^b (Lebatard et al., 2008; Vignaud et al., 2002)	(Le Fur et al., 2009)
Kossom Bougoudi	KB03 locality	KB	Kossom Bougoudi	Chad	ca 5.26 ^r , ^b (Brunet et al., 2000; Lebatard et al., 2008)	(Fara et al., 2005)

* That member is divided in two beds (3aN and 3aS) separated by 0.5 Ma, 3aS being older (Ungar et al., 2007).

of the closest modern relatives of fossil taxa are used as ecological analogues. The differences between the ecological diversities of mammal faunas are expressed by the chi-square distance (Lebart and Fénelon, 1971), and compared through a correspondence analysis (Fisher, 1940; Benzecri, 1973). The analysis was first done on the 50 living communities. The sub-communities and the fossil samples were then interpolated in the analysis so that they did not influence the construction of the correspondence axes.

Taxonomic richness represents the minimum number of species recorded in a faunal assemblage, whether modern or fossil. The distribution of these taxa is compared for various degrees of impoverishment and mixing levels.

Because the data are not normally distributed, we use non-parametric descriptors and tests (median, percentiles and Mann–Whitney *U* test) instead of their parametric equivalent.

3. Results

3.1. Effect of body size-related impoverishment on the ecological structure of faunas

First, a correspondence analysis was conducted on the ecological diversity of the 50 modern mammal communities in order to

determine the ecological categories that mainly drive the distribution of these faunas in the multivariate space. The three first axes express 80% of the variation in the data. The first axis is weighted by large species (90–180 kg), grazers, and mixed feeders toward the positive values, and by frugivorous and arboreal species toward the negative values (Fig. 2a). The second axis is dominated by very large species (>360 kg) toward the negative values and by insectivorous and fossorial species toward the positive values (Fig. 2a). The third axis is weighted by sub-aquatic species (not represented). As the degree of impoverishment increases, the data sets of altered sub-communities migrate toward the positive values along the first axis, and the negative ones along the second axis (Fig. 2b–f). No such migration is observed along the third axis, which thus will not be discussed hereafter. Impoverishment therefore leads toward a relative enrichment of the assemblages in large species, which was expected, and also in mixed feeders and grazing species. Actually these diet categories are partly correlated with large species as 75% of large species (90–180 kg) and 75% of very large species (>180 kg) in the modern data set of this study are grazers or mixed feeders.

Focusing on the consequences of impoverishment among covariables, Fig. 3 displays progressive change of the median relative abundance of each ecological category with increasing faunal impoverishment. Relative abundance of body mass categories

Table 3
Ecological categories used for assessing the ecological diversity of mammal communities.

Body mass	Diet preferences	Locomotor adaptations
C 1–10 kg (e.g. Cape hare)	BG Mixed feeder grass and browse (e.g. sable antelope)	Aq Sub-aquatic spend 50% of the time in water (e.g. hippopotamus)
D 10–45 kg (e.g. steenbok)	Ca Carnivorous meat, bones and fishes (e.g. leopard)	Ar Arboreal cannot survive without tree (e.g. red colobus)
E 45–90 kg (e.g. aardvark)	Fr Frugivorous fruits, gums, seeds (e.g. mangabey)	Fo Fossorial dig or modify burrows, use forelimbs to find food in the soil (e.g. aardwolf)
F 90–180 kg (e.g. Southern reedbuck)	Hb Browser browse, bark (e.g. giraffe)	T Terrestrial (e.g. buffalo)
G 180–360 kg (e.g. Burchell's zebra)	Hg Grazer grass, roots, bulbs (e.g. waterbuck)	T-Ar Sub-arboreal often at earth, nest and eat in trees (e.g. chimpanzee)
H > 360 kg (e.g. African elephant)	I Insectivorous insects and other invertebrates (e.g. ground pangolin)	
	O Omnivorous at least 3 kinds of food categories (e.g. bush pig)	

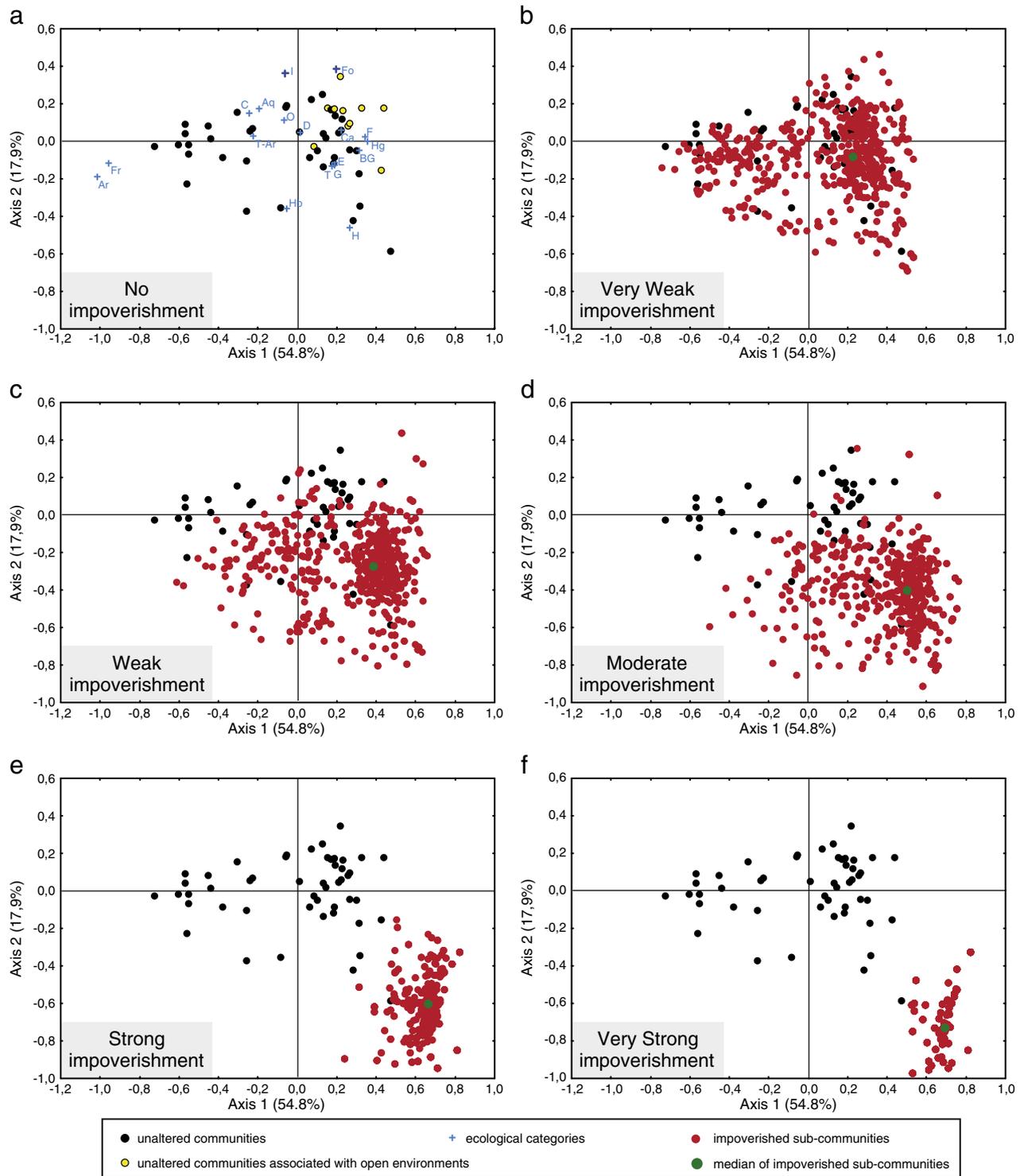


Fig. 2. Correspondence analysis carried out on the ecological structure of modern African communities (open landscapes are spotted in yellow in the first graphic). Ecological categories are classified under three ecological variables: body mass, locomotion and diet preferences (see Table 3 for abbreviations). Modern impoverished sub-communities are reported. The points migrate toward the lower right hand of the graphic as the impoverishment in small species increases.

undergoes drastic changes (Fig. 3a). The proportions of small species (<45 kg) decrease, whereas those of species larger than 90 kg increase. These changes were expected considering the sampling probabilities attributed to each body mass range. The behaviour of the medium-sized species (45–90 kg) is not linear as their relative abundance remains fairly stable with even a strong degree of impoverishment, but fall to zero for a very strong impoverishment.

Among the substrate adaptations, only the proportion of terrestrial species increases, since 90% of species from the data set heavier than 90 kg are terrestrial. This change is the most significant among locomotion categories (Fig. 3b), whereas the drop of the other categories is less spectacular considering their low initial values (they range between 5% and 18%). Arboreal species rapidly fall to zero whereas the sub-arboreal and the fossorial species slowly decrease

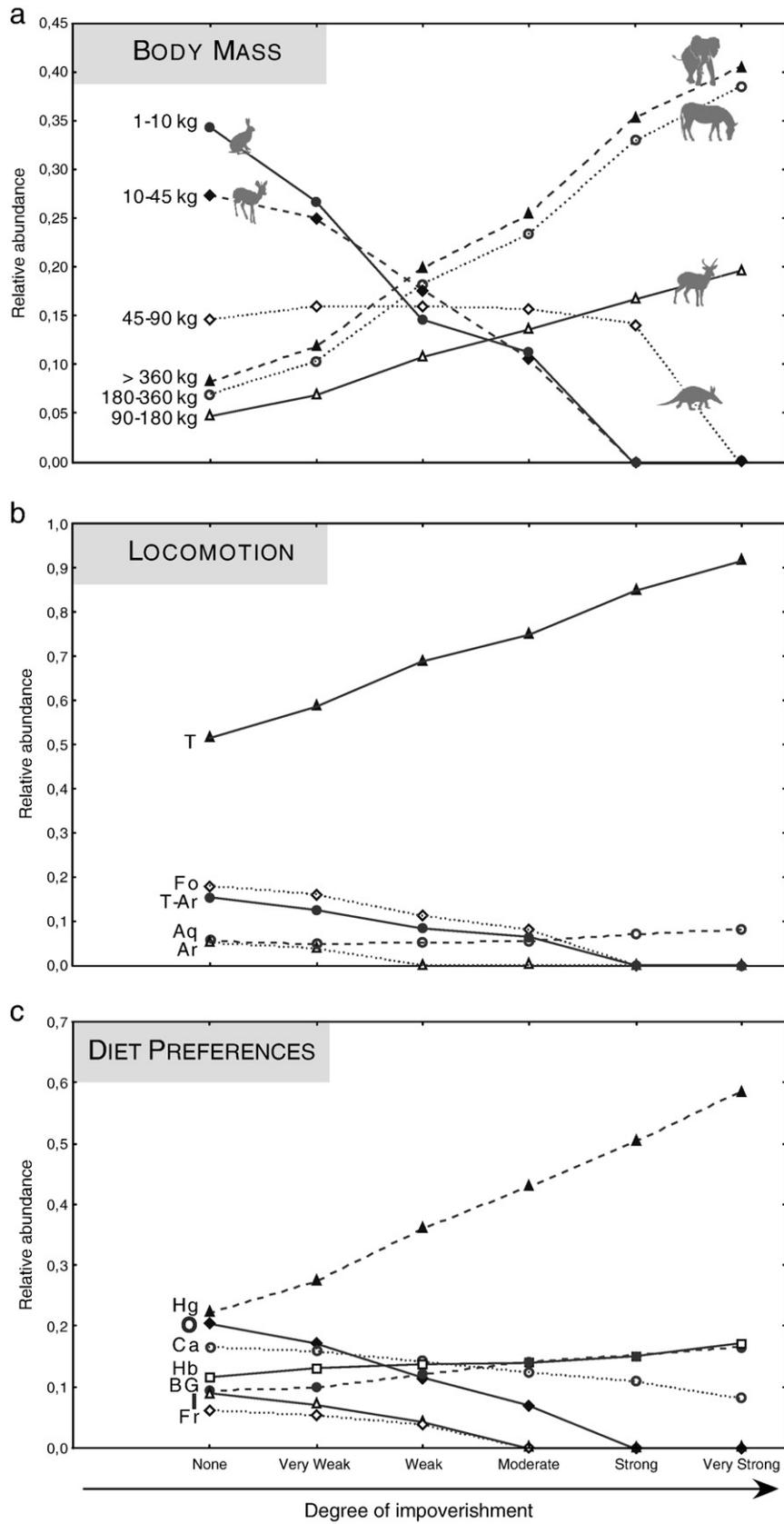


Fig. 3. Evolution of median relative abundances of ecological categories following increasing impoverishment of small species (see Table 3 for abbreviations).

until reaching a null value for a strong impoverishment. These three locomotor adaptations are largely dominated by small species (1–45 kg), ranging from 82% for fossorial to 100% for arboreal species.

Finally, the proportion of sub-aquatic species shows little variation as the impoverishment increases and remains relatively representative of its initial median proportion.

The trophic diversity of communities suffers important disturbances as the impoverishment becomes harsher. The proportion of grazing species records the greatest changes (Fig. 3c), which explains the deviation of sub-communities toward that category along the first correspondence axis (Fig. 2). Insectivorous, omnivorous and frugivorous species are also affected as they reach a null value with a moderate or a strong degree of impoverishment (Fig. 3c). More than 90% of species in these categories weigh less than 45 kg. Remaining categories are little affected by the size-related impoverishment: the proportion of carnivorous species tends to decrease whereas browsers and mixed feeders slightly increase.

The medians of the six runs of modern communities and altered sub-communities clearly migrate toward the positive values of the first axis and the negative values of the second (Fig. 2). However, the scattered points show considerable overlap, in spite of significant differences computed between any two consecutive treatments (Mann–Whitney U test: $p < 0.01$ along the two first axes). The ecological profiles of sub-communities are also significantly different. As a consequence, it is hazardous to attribute a fossil fauna interpolated onto this figure to one or another run. This overlap results from the relatively large dispersion of points within each run. Nevertheless, we notice a reduction in the dispersion as the faunal impoverishment increases (Figs. 2 and 4). This decrease is especially important along the first axis (Fig. 4) for which the dispersion of runs was compared. For each treatment, we thus computed the distances between the median and each individual point of the corresponding treatment. The six resulting sets of distances were then compared by mean of a Mann–Whitney U test. The two less impoverished runs (weak and very weak) show dispersion similar to the parent communities ($p > 0.05$). For a moderate degree of impoverishment, the dispersion of sub-communities becomes significantly less than that of the original data ($p < 0.05$), but remains similar to that of a weak impoverishment ($p > 0.05$). Finally, the two most impoverished sets of sub-communities (strong and very strong) have similar dispersions, being significantly smaller than less impoverished runs ($p < 0.01$) (Fig. 4). This result reveals that a strong impoverishment in small species tends to homogenise ecological diversities of communities. Thus, the data sets of strongly impoverished sub-communities distinguish from less impoverished sub-communities.

3.2. Effect of community mixture on the ecological structure of sub-communities

The scatter of points corresponding to the mixture of two or three unaltered communities are included into the range defined by that of the parent communities, mixed communities being nevertheless more bunched (Fig. 5a). With increasing degrees of impoverishment, mixed sub-communities migrate toward the positive values of the first axis and the negative values of the second one. This is as observed

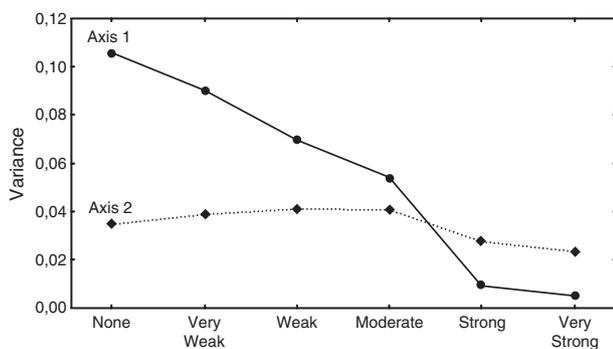


Fig. 4. Change in the variance of the data sets of sub-communities along the two correspondence axes. The dispersion of the faunas decreases as the impoverishment in small species increases, especially along the first axis.

for sub-communities merely impoverished. The shift on axes 1 and 2 is thus induced by the impoverishment in small species and not by the mixture of communities. Thus, we conclude that the mixture of two or three communities does not affect the ecological diversity of sub-communities. Further, as for the single community treatments, the dispersion within the data decreases as the degree of impoverishment rises, especially along the first axis (Fig. 6). The mixture of communities nevertheless acts in reducing the dispersion of the points for same degrees of impoverishment (Fig. 6). This is even more emphasised when mixing three communities. This condensation of the scatter of points comes about because the mixing of several communities is equivalent to averaging the ecological structures of the communities included, which reduces the influence of outlying communities.

3.3. Effect of faunal impoverishment and community mixture on the taxonomic richness of faunal assemblages

The impoverishment in small species naturally tends to decrease the species richness of mammal communities (Fig. 7). However, for the same level of impoverishment, mixture of communities tends to increase the species richness of the resulting sub-communities. These results appear trivial but potentially may reveal the presence of several communities within a fossil sample, at least for fossil assemblages that have been impoverished. This is illustrated in the following section for late Miocene–earliest Pliocene African mammal faunas.

3.4. Assessment of the degree of alteration of the late Miocene–earliest Pliocene African mammal assemblages

The fossil samples can be interpolated along the first and the second correspondence axes constructed from the ecological diversity of modern communities (Fig. 8a). The median, the 5th and the 95th percentiles of impoverished modern sub-communities are also shown on this figure. The fossil assemblages are not only spread along the gradient displayed by the altered sub-communities, but also are concentrated in the lower right-hand corner. This suggests that the impoverishment in small species can explain, by itself, the difference between the ecological structures of fossil and modern communities. Impoverishments of similar intensities, in terms of number of species lost, but independent from the body-size of species (i.e., a random sampling) has also been done and does not show any pattern of migration as displayed by the impoverishment in small species. This supports the interpretation that the migration of sub-communities is clearly due to the depletion in small species and not to the mere decrease in species richness. Also, it seems improbable that past environments systematically favoured a higher proportion of large species than that observed in modern environments (see Section 4.2).

From Fig. 8a, we can therefore estimate the potential degree of impoverishment undergone by a fossil sample. A fossil assemblage can be assigned to a kind of treatment if it overlaps the rectangular area delineated by the 5th–95th percentiles of the corresponding impoverished data set (Fig. 8a). Considering the overlapping of the different runs, a fossil sample can be attributed to several runs. For instance, the Manonga assemblage is included in the 5th–95th percentile ranges displayed by sub-communities with a strong to very strong degree of impoverishment, which constitutes a potential degree in the depletion in small species. Fig. 8b summarises the extent of the impoverishment degree estimated for each fossil assemblage from the correspondence analysis.

Given an estimate of the degree of impoverishment in small species undergone by a fossil sample, it is possible to infer the presence of a faunal mixture in the fossil assemblage. In Fig. 9, the taxonomic richness of each fossil sample is compared to that observed in modern sub-communities impoverished to the same degree(s), as

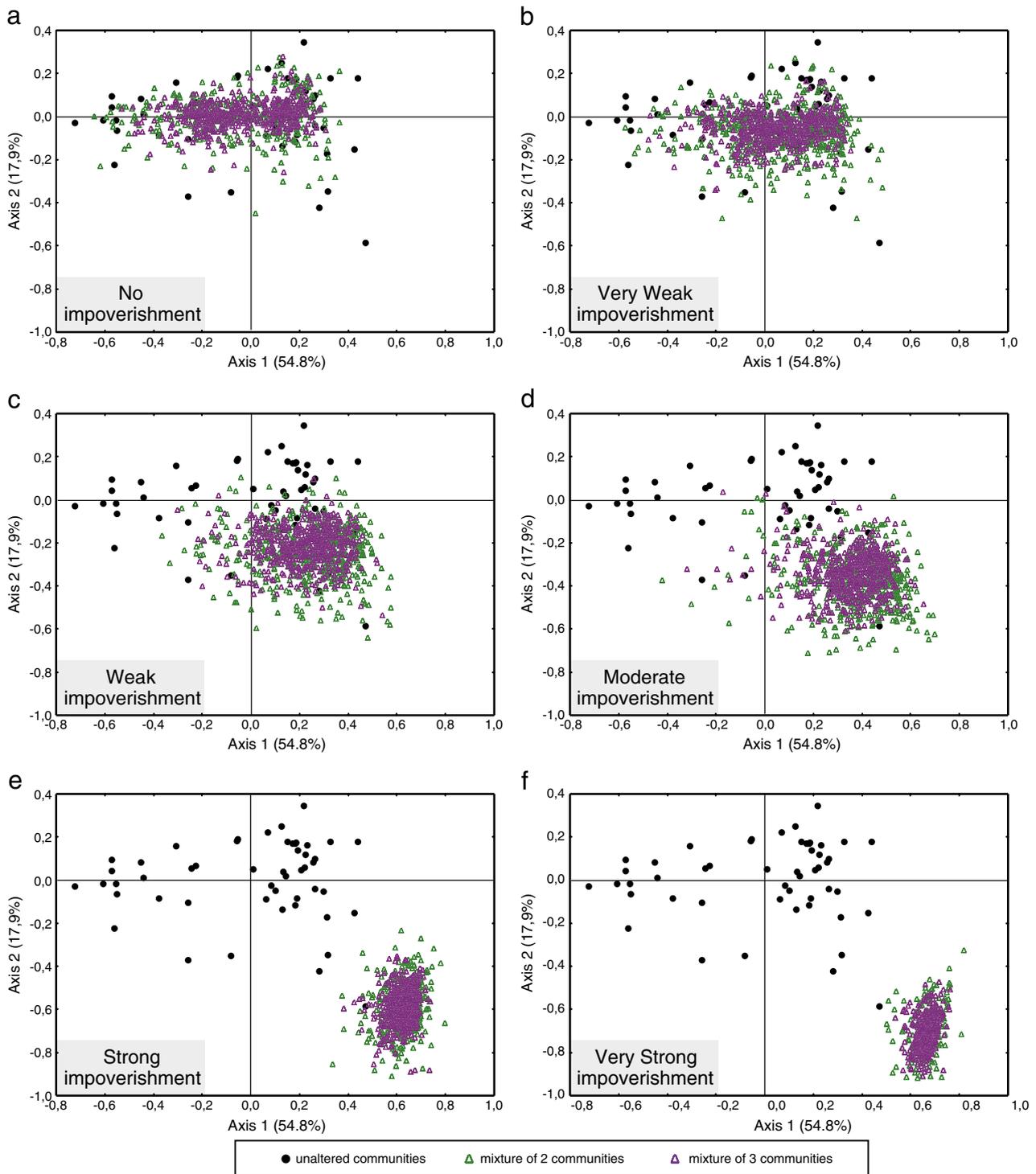


Fig. 5. Correspondence analysis carried out on the ecological structure of modern African mammal communities. The unaltered communities are figures by black dots and the ecological structures of mixed composite communities are shown by purple and green symbols. The points migrate toward the lower right hand of the graphic as the impoverishment in small species increases. The mixture of several communities does not influence the position of the composite communities.

assessed from the correspondence analysis (Fig. 8). If the fossil sample shows a higher taxonomic diversity than any modern sub-community, it would suggest the contribution of several communities to the formation of that fossil sample. By this reasoning, it is highly probable that the fossil samples from the Lower and Upper Nawata members, PPMs, Sahabi and Nkondo correspond to a mixture of several communities and probably a sampling of several environments (Fig. 9). The reverse of this reasoning, however, cannot be applied. When the taxonomic richness of an assemblage lies within the range of those obtained for impoverished

sub-communities, it does not imply the absence of mixture in that assemblage. Any taxonomic richness can also result from a mixture of several communities impoverished at different levels. For instance, if we mix the two Lemudong'o samples, we obtain a potential impoverishment extending from none to weak and a richness of 28 taxa. That value lies within the range of sub-communities impoverished at the same level (Fig. 9) and yet corresponds to the mixture of at least two communities. Thus, the presence of several communities in a fossil sample cannot be ruled out.

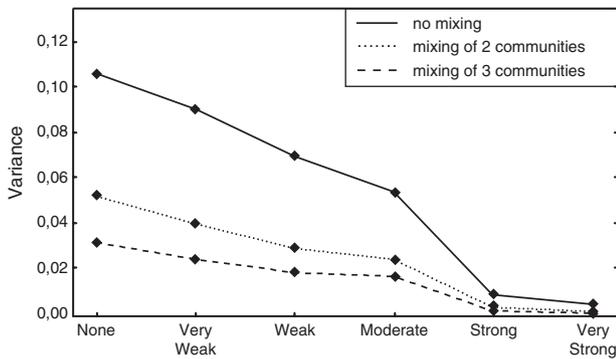


Fig. 6. Change in the variance of the data sets of sub-communities along the first axis, for different degrees of impoverishment and three levels of mixture. The mixture of communities tends to decrease the dispersion of the scattered points along the first axis.

4. Discussion

4.1. To what extent does faunal impoverishment in small species affect the ecological diversity in faunal assemblage?

The impoverishment in small species induces important perturbations in the ecological signal of communities by significantly modifying its ecological structure and homogenising ecological diversity. However, all ecological categories are not affected to the same degree. The greatest changes are recorded for terrestrial species and grazers whose relative abundances are over-estimated in impoverished communities (Fig. 3a, c). The large proportion of terrestrial and grazing species in comparison to modern communities has already been documented in other African Cenozoic mammal assemblages (e.g., Kovarovic et al., 2002; Sandrock et al., 2007; Su and Harrison, 2007) and could ultimately be explained by impoverishment in small species. Note also that high values in these two ecological categories, especially in grazing species, are traditionally

associated with open habitats. The living communities inhabiting more open habitats are located on the right of the scatter plot, toward the positive values of the first axis (Fig. 2). Thus, the migration of the impoverished sub-communities along this axis is comparable to an opening of the landscape. The use of the proportions of terrestrial and grazing species as proxies to discriminate modern environments and subsequently assess palaeoenvironments (e.g., Reed, 1997; Harris et al., 2003) may not be justified if we have no knowledge of the extent of biases associated with each fossil sample. Such proxies may falsely imply more open landscapes for strongly impoverished fossil mammal assemblages.

Some other categories (insectivorous, frugivorous, omnivorous species, and arboreal, sub-arboreal and fossorial species), generally less abundant in the parent communities than terrestrial or grazing species, undergo important changes in species relative abundances, reaching a null value in strongly impoverished sub-communities (Fig. 3). The loss of these categories corresponds in proportion to habitat loss and explains the homogenisation of the ecological structure of faunas as the impoverishment increases. Likewise, such categories should not be used for palaeoenvironmental reconstructions, unless one carefully assesses the degree of alteration undergone by fossil samples.

The remaining categories (sub-aquatic species, browsers, mixed feeders and carnivorous species) appear to offer more reliable relative abundances, whatever the degree of impoverishment in small species. Two options could then be favoured: 1) one might restrict the comparisons with modern communities to the ecological categories whose proportions suffer less from impoverishment in small species (sub-aquatic species, browsers, carnivorous or mixed feeders); or 2) in order to benefit from the environmental signal carried by the most discriminating ecological categories (e.g., arboreal, terrestrial, grazers, etc.), one could compare fossil samples with modern faunas impoverished to a similar degree, as assessed by the approach proposed here. This will certainly lead to a loss in the resolution of environmental discrimination, because the impoverishment in small species tends to homogenise ecological diversities. In turn, it will limit

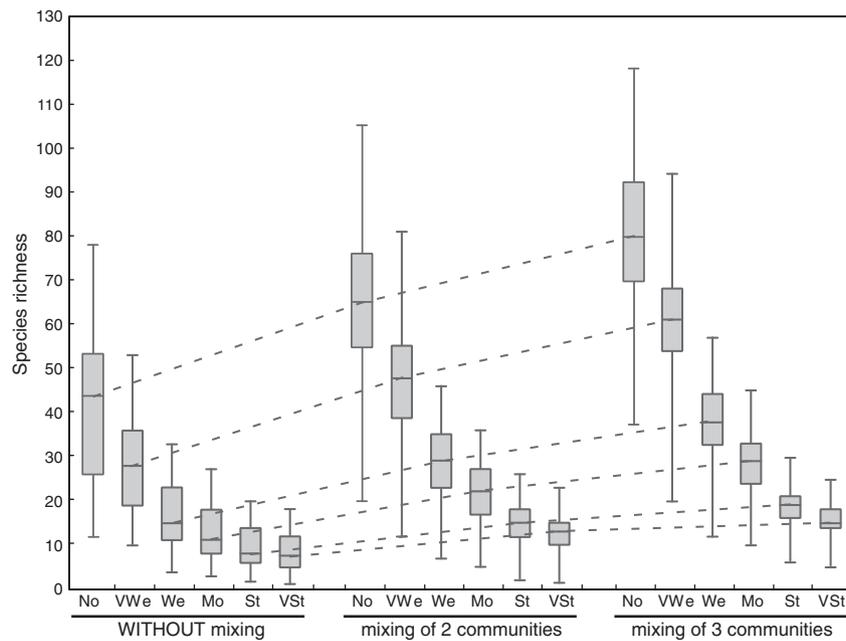


Fig. 7. Species richness of modern communities after impoverishments in small species at various degrees and/or mixture of several communities. Each boxplot shows median (horizontal line), 25th and 75th percentiles (box including 50% of the values) and range (vertical line). Impoverishment: none (No), very weak (VWe), weak (We), moderate (Mo), strong (St) and very strong (VSt). Unsurprisingly, the impoverishment in small species decreases the species richness of faunal assemblages, whereas the mixture of communities increases it.

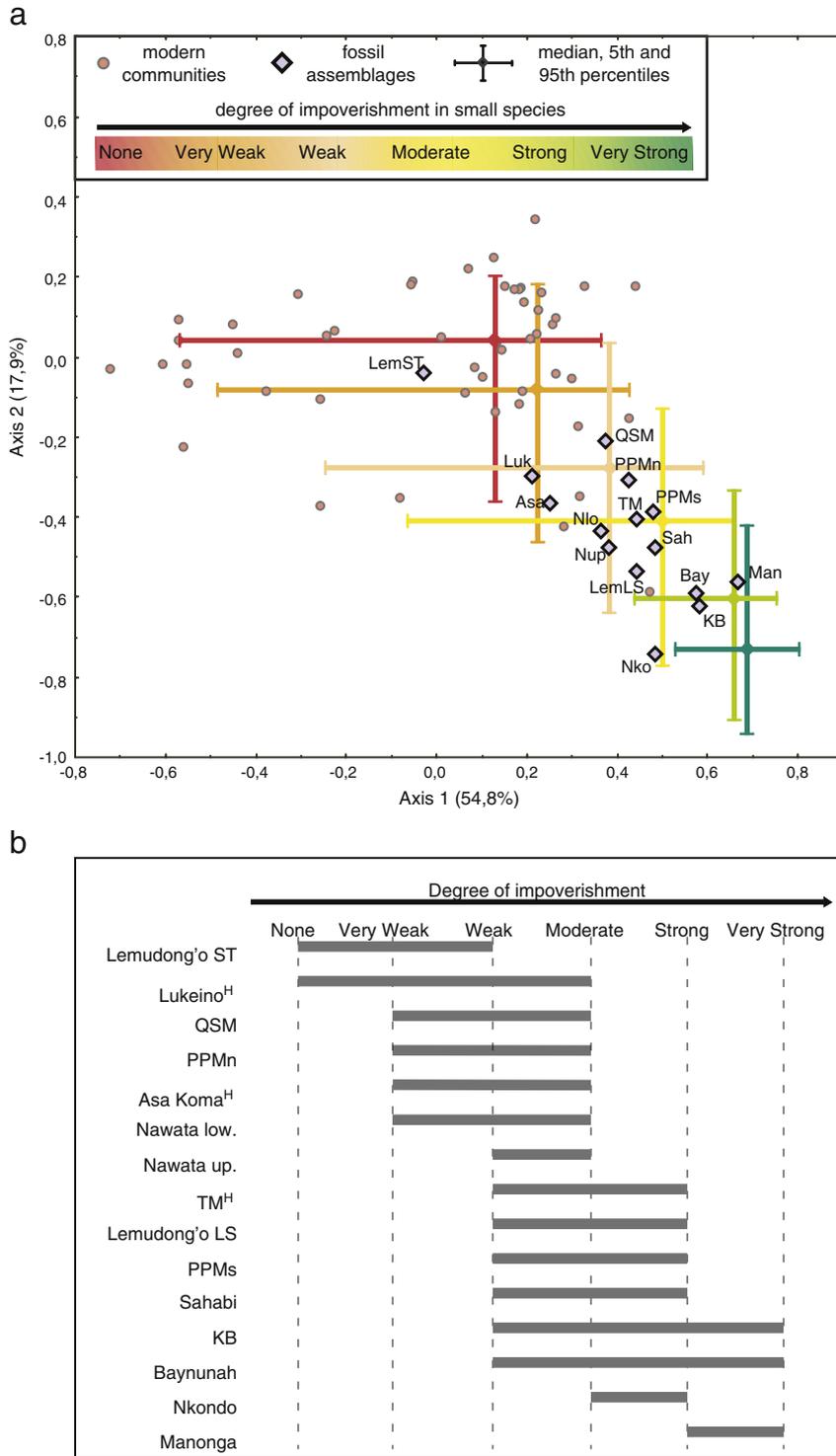


Fig. 8. Correspondence analysis carried on the ecological diversity of modern communities (a). The late Miocene–earliest Pliocene fossil samples and the 5th and 95th percentiles of the impoverished sub-communities are reported. The 5th and 95th percentiles define an interval including 90% of the values. The percentile ranges in which a fossil sample is included determine the most probable degree of impoverishment undergone, and are reported in the second panel (b). Samples that yielded early hominins are labelled with (H). For abbreviations, see Table 2.

the risk of incorrect palaeoenvironmental reconstructions. For the strongest impoverished fossil assemblages, the ecological structures of faunas from different environments become more similar and the environmental signature tends to disappear. When such cases are suspected, other proxies should be used.

Finally, although recognising the presence of two or more communities in a fossil assemblage first necessitates determining

the degree of impoverishment, these two biases remain independent. Indeed, whatever the number of modern communities/sub-communities that are mixed, their ecological structures overlap for the same degrees of impoverishment. Besides, a sample that is poorly diversified ecologically can nevertheless be taxonomically rich (e.g., Nkondo). The limit of our approach appears when several communities, having suffered from different degrees of impoverishment in

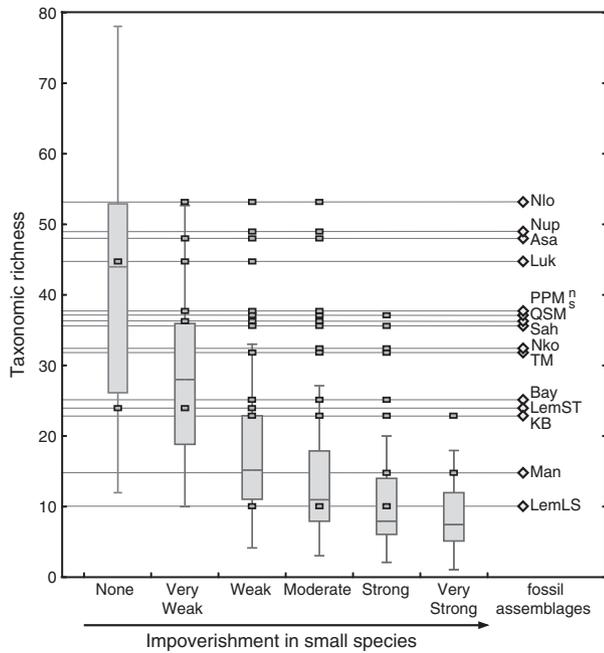


Fig. 9. Comparison of taxonomic richness of fossil assemblages with those of modern communities and impoverished sub-communities, considering the degree of impoverishment assessed for each fossil sample. The boxplots represent the median (horizontal line), 25th and 75th percentiles (box) and range (vertical line). The mixing of several communities/sub-communities in the formation of a fossil sample is highly likely for those with higher taxonomic richness than modern faunas. For abbreviations, see Table 2.

small species, form a single fossil sample. Thus, mixture can be detected with confidence only for samples that show higher taxonomic richness than modern communities impoverished at the same level.

4.2. Can biases assessed for the late Miocene–earliest Pliocene samples be correlated with their taphonomic and sedimentological context?

Mixing of several communities seems probable for the samples of Sahabi, Nawata members, PPM 3aS bed (PPMs) and Nkondo. All but the last assemblages are associated with fluvial depositional environments, which favour for the input of allochthonous and/or reworked material. Reworking has already been evoked for the PPMs bed and the Upper Nawata member, having reworked material from the QSM (Hendey, 1981) and the Lower Nawata members (Feibel, 2003) respectively. Little has been published about the sedimentological and the taphonomic context of Nkondo, but its fossil remains are associated with lacustrine deposits (clays and silts), revealing the presence of a 100 m deep lake (Pickford et al., 1993). Only a taphonomic study might reveal whether part of the material has been transported over long distances.

The approach proposed here helps to detect the presence of mixed communities for some assemblages, information that is not always available from sedimentological evidence alone. Whether it is due to time- or a space-averaging is not determinable with our technique, which should be complementarily performed with other investigations.

Different degrees of impoverishment have been assessed from the present study for late Miocene–earliest Pliocene African mammal assemblages. The least impoverished is probably the sample collected from the Lemudong'o speckled tuff (Fig. 8b). Fossils are well preserved but have been fragmented by post-depositional processes (Ambrose et al., 2003). The remains might have accumulated along lake margins and have been rapidly buried since the majority of bones are unweathered and unpatinated (Ambrose et al., 2007). All conditions are present for good preservation of the living community.

The degree of impoverishment assessed for this assemblage is in agreement with these observations. However, small to medium-sized carnivores might have significantly participated in the formation of the assemblage, potentially leading to a relative enrichment in small species (Ambrose et al., 2007).

Lukeino belongs to a set of unaltered to moderately impoverished communities, a result in agreement with the hypothesis that fossils have gathered along a shallow lacustrine margin (Sawada et al., 2002).

The samples from two levels of the Varswater formation (QSM and PPMn) are here estimated to have undergone very weak to moderate impoverishment, whereas PPMs could be more impoverished (Fig. 8b). The two beds of PPM illustrate similar depositional environments, reconstructed as river channels and banks, with marshes and ponds in PPMn (Hendey, 1981). Fluvial transport occurred but appears limited as no trace of high-energy alluvial transport or other post-depositional processes is recorded in the PPM's beds (Matthews et al., 2007). The faunal differences noted between these two beds might have been ecological: the landscape recorded by PPM 3aN would have been more open than that associated with PPM 3aS (Ungar et al., 2007). Otherwise, the presence of marshes and ponds would have contributed to better preserved individuals from the living community in the PPMn bed. QSM corresponds to an estuarine and terrestrial complex (floodplains, swamps and sub-aerial deposits), associated with channels of medium to weak energy that probably involved negligible transport (bones show little evidence of transport) and a rapid burial (Matthews et al., 2007). Fluvial transport may not have been sufficient to impoverish the fossil assemblages from these three levels of the Varswater formation. On the other hand in both members all the fossils were collected from the surface (Matthews et al., 2007). The relative impoverishment in small species may thus be related to sampling.

The fossil samples from Asa Koma and Lower Nawata appear very weakly to moderately impoverished, whereas the Upper Nawata sample is restricted to a weak or a moderate impoverishment. The bones from these three assemblages were deposited in fluvial systems (Feibel, 2003; Haile-Selassie et al., 2004), associated with swamps, floodplains and well-oxygenated freshwater bays for the Nawata members. These systems should have limited the impoverishment of the original communities. Indeed, the fluvial system associated with the Nawata members seems to have been large, sustainable and with limited energy (Feibel, 2003). For Asa Koma, micromammals and primates represent a high proportion of the assemblage (WoldeGabriel et al., 1994), suggesting that the size-related bias against small mammals was limited. On the contrary, large mammals are rare (WoldeGabriel et al., 1994), a pattern resulting either from a selective process of small species (e.g., the action of small to medium-sized predators) or from the initial structure of the community. Scarcity of large mammals is observed in some modern dense African rainforests (e.g., Ituri and Seredou forests, Curry-Lindahl, 1956; Roche, 1971).

The fossil samples from Sahabi, Lemudong'o LS and TM appear to be weakly to strongly impoverished. The two first are associated with fluvial depositional environments which could have favoured such alteration: littoral channels for Sahabi (de Heinzelin and El-Arnauti, 1987; Muftah et al., 2008) and ephemeral channels for Lemudong'o LS (Bernor, 2007). At Sahabi, pre-depositional disarticulation and transport (Boaz, 1987) should have contributed to the weathering and the scattering of skeletal remains. Moreover, the surface collecting practiced in that area reduced the probability of sampling small bones as they are less easily spotted and more sensitive to modern aeolian deflation (Boaz, 1987). At Lemudong'o LS, the fossils are rolled, abraded and hardly identifiable (Ambrose et al., 2007). Presence of fluvial transport is expected for that assemblage which would have induced a preferential preservation of large species (Ambrose et al., 2007), especially equids (Bernor, 2007). The fossil

sample collected from TM266 is associated with an aeolian–lacustrine facies, corresponding to either a lateral variation or the alternation of humid/arid phases (Schuster, 2002; Vignaud et al., 2002). This depositional environment appears relatively quiet (fossils well preserved and no evidence of transport) and seems adequate to preserve most of the initial community. However, this sample comes in part from surface collecting.

The fossil assemblages of Baynunah and KB potentially correspond to various degrees of impoverishment (lying from a weak to a very strong intensity). Fossils from Baynunah are associated with a braided shallow fluvial system (Whybrow et al., 1999). They are found in lenses of conglomerates and are often covered by bar deposits (Bibi et al., 2006). Flooding would have been generally brief but of high energy, responsible for the transport and the erosion of sediments (Friend, 1999), and probably for depletion of small carnivores (Barry, 1999). Fossils from KB are associated with fluvio–lacustrine sandstones interspersed by diatomitic and clayey levels. These sediments represent flooding deposits alternating with periods of emersion of several years, as attested by the mud cracks and the high density of roots and bioturbations (Brunet et al., 1997, 2000; Durringer et al., 2000; Schuster et al., 2000). The absence of cross stratification and the good state of preservation of fossils and sand grains testify to a quiet sedimentary environment with limited transport of material (Brunet et al., 1997). However, surface sampling could again have been responsible for the degree of impoverishment assessed for that fossil sample. All the taphonomic and sedimentological features associated with these samples are consistent with the results obtained in the present study.

On the contrary, a lack of congruence is observed for the fossil sample of Manonga, which would have suffered from a strong to very strong impoverishment. It is associated with a shallow and oxygenated lacustrine depositional environment (Harrison, 1997b), punctuated in the upper part of the member by some short periods of recession with formation of palaeosols under a seasonal climate (Verniers, 1997). Moreover, there is no evidence for transport or for the involvement of carnivores in the formation of the assemblage (Harrison, 1997b). The short emersions might have accelerated the weathering and the destruction of the most delicate remains.

The fossil sample from Nkondo appears to be moderately to strongly impoverished. The amazing richness of large mammals (at least 13 species heavier than 360 kg on a total of 32 mammal species), including several species of proboscideans, hippos and rhinos, may be primarily responsible for its position in the multivariate space in comparison to modern communities. However, even if we re-analyse the fossil and modern faunas excluding the very large species (>360 kg), Nkondo still falls within the range of strongly impoverished faunas. The fluvial systems draining the hypothetical paleolake may have contributed to the depletion of that assemblage in small species by the destruction of small remains deposited upstream the paleolake.

Such a diversity of large species at Nkondo, never found in modern African mammal faunas, can result either from time-averaging of several communities, as suggested by the present model, or from a real ecological signal. Certainly, the diversity of the Mio-Pliocene megafauna is higher than the extant one in Africa (Artemiou, 1983; Rodríguez et al., 2004; Fara et al., 2005), and increased from the beginning of the Cenozoic to the Pliocene (Alroy, 1999), when giant mammals prospered (Bakker, 1980; Wing and Tiffney, 1987). In addition to modern groups already present at this time (rhinocerotids, elephantids, giraffids and hippos), several now extinct taxa were still present (sivatheres, chalicotheres, gomphotheres, deinotheres, *Stegotetralodon*, etc.) and others are no longer present on the African continent (e.g., ursids). The co-occurrence of such a large number of very large species would imply unusual environmental conditions. For instance, higher atmospheric CO₂ pressure would have favoured a greater vegetal productivity (Janis et al., 2002), which could have

supplied enough resources for such a herbivorous biomass (Artemiou, 1983). Besides, seasonality characterised by long wet periods could allow the increase of leaf productivity at the expense of fruit productivity (Foley, 1987), thus favouring the expansion of browsing species. At a larger scale, the steadiness of environments should also be considered because large species survive better than smaller species in fluctuating environments as they spend less energy per mass unit (Rodríguez et al., 2004). Further work is needed to eventually link the number of large mammal species with climatic factors. However, even if this high diversity is not an artefact, all these species did not necessarily co-inhabit the same place and/or at the same time. In the present study, those samples for which the presence of mixture is highly probable are also those that yielded the largest numbers of very large mammals, ranging from 8 species (PPMs) up to 14 species (Nkondo). Asa Koma and Lukeino areas also yielded a high number of species heavier than 360 kg (11 and 12 respectively), but no mixture of communities was evidenced from the analyses. In order to test the effect of that body mass range on the migration of altered sub-communities along the two correspondence axes and the position of fossil assemblages, we performed a second simulated depletion in small mammals excluding beforehand very large species (>360 kg) from modern and fossil faunas. The results were very similar to those obtained earlier with all the species heavier than 1 kg. The fossil assemblages still depart from the range expressed by modern faunas and the progressively impoverished sub-communities migrate toward a pole rich in terrestrial and in grazing species, the scattered points of each run being nevertheless more stretched. Thus, high diversity in very large species could result either from mixture of several communities or from particular environmental settings. However, these eventual environmental specificities cannot explain by themselves the pattern of deviation of fossil assemblages which would result from taphonomic factors.

Our results call for a critical review of some palaeoenvironmental reconstructions, especially for the samples associated with high degrees of impoverishment (e.g., Baynunah, Manonga, KB, etc.). These assemblages may indicate more closed environments than previously thought. Interestingly, the fossil assemblages that yielded hominin remains are associated with different degrees of impoverishment. Even if the ranges of impoverishment assessed for these three fossil samples overlap, the Lukeino sample appears less impoverished than Asa Koma, being itself less impoverished than Toros-Menalla. Therefore, their faunal structures may not be comparable and the inferred palaeoenvironmental differences could in part result from taphonomic processes and sampling techniques. Moreover, these palaeoenvironments could have been more closed than previously assessed from their associated faunal structure.

5. Conclusions

We have quantified the potential impact of taphonomic and sampling biases upon the reconstruction of palaeoenvironments using the faunal structure of mammal assemblages. Our probabilistic model helps to explain the frequent incongruence between the ecological diversity of fossil and modern African mammal faunas. The progressive impoverishment of modern faunas in small species (1–45 kg) leads to an over representation of terrestrial and grazing species and to a depletion or even the disappearance of several ecological categories (e.g., insectivorous, arboreal and semi-arboreal species, fossorial species, frugivorous and omnivorous species). These changes in the proportions of ecological categories are sufficient to lead to the exclusion of fossil assemblages from the ecological space defined by modern faunas.

In addition, impoverishment in small species leads to the homogenisation of the ecological diversity of faunas and subsequently to weaker palaeoenvironmental discrimination. This underlines the importance of small species (1–45 kg) in palaeoenvironmental

reconstructions and it would be of interest to clarify the palaeoenvironmental signal carried by that range of species. Thus, for the most impoverished fossil faunas, it seems necessary to restrain the comparisons to some robust ecological categories (browsers, mixed feeders, carnivorous or sub-aquatic species) or to compare them with modern communities first impoverished to a similar degree. Once the degree of impoverishment is evaluated, it becomes possible to assess the probability of faunal mixture.

Thus, we strongly recommend exploring the presence of faunal impoverishment and mixture of communities before reconstructing palaeoenvironments with mammal assemblages in order to reduce the probability of misleading palaeoenvironmental inferences. For instance, in light of these results, the palaeoenvironment associated with some early hominins (e.g., *Sahelanthropus tchadensis*, *Toros-Menalla*) could have been more closed than previously assessed.

Finally, the use of this tool would also be pertinent for palaeobiogeographical studies that rely on taxonomic comparisons through time and space (e.g., Bobé, 2006; Maridet et al., 2007; Werdelin, 2008). For instance, the differing taphonomic contexts and sampling strategies of fossil samples, resulting in different degrees of mixture and impoverishment, could lead toward altered estimates of similarity between samples.

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Appendix A. Supplementary data

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