Journal of Human Evolution xxx (2018) 1–15

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Diversity analysis of Plio-Pleistocene large mammal communities in the Omo-Turkana Basin, eastern Africa

Andrew Du*, Zeresenay Alemseged

Department of Organismal Biology and Anatomy, The University of Chicago, 1027 E 57th St, Chicago, IL 60637, USA

ARTICLE INFO

Article history:
Received 5 October 2017
Accepted 16 July 2018
Available online xxx

Keywords:
Diversity
Rarefaction
Coverage
Habitat heterogeneity
Equilibrial dynamics
Omo-Turkana Basin

ABSTRACT

Knowing how the diversity of large mammal communities changes across space and time provides an important ecological framework for studying hominin evolution. However, diversity studies that apply methods currently used by neoecologists are rare in paleoanthropology and are also challenging due to diversity's unusual statistical properties. Here, we apply up-to-date analytical methods for understanding how species- and genus-level large mammalian diversity in the Omo-Turkana Basin changed through time and across space at multiple spatiotemporal scales (within each formation: 10^{2-3} km^2 and 10^{4-5} years; and within the basin as a whole: 10^3 km^2 and 10^5 years). We found that, on average, Koobi Fora's large mammal community was more diverse than Nachukui's, which in turn was more diverse than Shungura's. Diversity was stable through time within each of these formations (alpha diversity), as was diversity in the basin as a whole (gamma diversity). Compositional dissimilarity between these three formations (beta diversity) was relatively low through time, with a 0.6 average proportion of shared species, suggesting dispersal acted to homogenize the region. Though alpha and gamma diversity were fairly stable through time, we do observe several notable peaks: during the KBS Member in Koobi Fora (30% increase), the Lokalalei Member in Nachukui (120% increase), and at 1.7 Ma in the entire basin (100% increase). We conclude by (1) demonstrating that habitat heterogeneity was an important factor influencing alpha diversity within each of the three formations, and (2) hypothesizing that diversity stability may have been driven by equilibrial dynamics in which overall diversity was constrained by resource availability, implying biotic interactions were an important factor in structuring the communities that included hominins as members. Our findings demonstrate the need to quantify how large mammal diversity changes across time and space in order to further our understanding of hominin ecology and evolution.

1. Introduction

Understanding the larger ecological context of human evolution is a central goal in paleoanthropology, as hominin morphological and behavioral changes were by and large mediated by environmental changes and interactions with other organisms. Examples of key questions include: Why were hominins present or more abundant in some regions and sites but not others (Bunn, 1994; Su and Harrison, 2008)?; Why were hominins particularly speciose during certain time periods (Haile-Selassie et al., 2016; Wood and Boyle, 2016)?; How did climate change affect (or not) hominin biological and behavioral evolution (Potts, 1998; deMenocal, 2004; Maxwell et al., 2018)? One way to address these questions is by studying the larger mammalian communities of which hominins were a part. This has been done using a variety of approaches (Behrensmeyer et al., 2007; Reed et al., 2013), but an underutilized method within paleoanthropology is diversity analysis of mammalian communities.

Diversity is an information-rich concept that has been extensively studied in neoecology (i.e., the ecological study of extant organisms) (Rosenzweig, 1995; Magurran and McGill, 2011) and paleobiology (e.g., Sepkoski et al., 1981; Alroy, 2010a). While there is strong interest in hominin diversity itself (Leakey et al., 2001, 2012; White, 2003; Spoor et al., 2010; Haile-Selassie et al., 2016; Wood and Boyle, 2016; Maxwell et al., 2018), diversity of the larger mammalian community is often of secondary interest to paleoanthropologists, whereas the primary focus is on paleoenvironmental reconstruction (reviewed in Kingston, 2007). However, understanding how non-hominin, mammalian diversity changes across

* Corresponding author.
E-mail address: andrewdu@uchicago.edu (A. Du).

https://doi.org/10.1016/j.jhevol.2018.07.004
0047-2484/

Please cite this article in press as: Du, A., Alemseged, Z., Diversity analysis of Plio-Pleistocene large mammal communities in the Omo-Turkana Basin, eastern Africa, Journal of Human Evolution (2018), https://doi.org/10.1016/j.jhevol.2018.07.004

space and through time is crucial for understanding the ecological and evolutionary context of hominins.

For example, mammal diversity is correlated with primary productivity, a measure of the amount of energy entering an ecosystem (Badgley and Fox, 2000; Janis et al., 2004; Faith, 2013; Fritz et al., 2016), and habitat heterogeneity (Kerr and Packer, 1997; Stein et al., 2014), both of which may influence the ability of hominins to persist at a particular site. Diversity is also a product of diversification rates (i.e., origination minus extinction), which places the origin and maintenance of hominin species diversity in a broader community context. Beta diversity (explained below) enables quantification of community compositional (dis)similarity across space (or time) informing us about larger-scale environmental changes, dispersal, and vicariance (Vrba, 1999). And lastly, diversity is an intuitive way to distill a community into one number, thereby enabling statistical analyses of its drivers and correlates (e.g., climate).

Because diversity is an underexplored topic within paleoanthropology, in the next section, we first review what diversity is and the challenges involved with its quantification. We then briefly summarize the few studies which have looked at mammal diversity in the Plio-Pleistocene of eastern Africa. We finally end the section with our research goals, which include investigating how diversity within the Omo-Turkana Basin changes through time at different spatiotemporal scales, i.e., within each of the three main formations (Shungura, Koobi Fora, and Nachukui) and in the basin as a whole. We also examine how taxonomically similar these three formations are to each other during a given time period and how this changes through time.

2. Diversity in neo- and paleoecology

2.1. Three kinds of diversity: alpha, beta, and gamma

In ecology, the concept of diversity is actually an amalgam measure of richness and evenness (Table 1; Magurran, 2004), though it is often informally equated with richness (Spellerberg and Fedor, 2003). Richness is defined as the number of taxa in a community, and evenness describes how uniformly abundances are distributed across those taxa (a perfectly even community has its abundances divided equally among all taxa) (Table 1; Faith and Du, 2017). We adopt these definitions here and will use all three terms, which are not interchangeable.

Diversity is conventionally described at three progressively larger scales: alpha, beta, and gamma (Whittaker, 1960, 1972). Alpha diversity measures diversity within a single community, which is traditionally defined as a group of taxa co-occurring at a given place and time (Table 1). This concept has proven difficult to operationalize, however, and we follow other researchers in asserting that the delineation of a community is somewhat arbitrary and ultimately depends on the spatiotemporal scale of one's research question (Vellend, 2016; Leibold and Chase, 2017). Therefore, we use “fossil community” here in the broadest sense to characterize fossil assemblages that may range from collecting localities all the way up to depositional basins. Gamma diversity is defined as the total combined diversity across multiple communities, so it is always greater than or equal to alpha diversity (Table 1; Fig. 1). Gamma and alpha diversity will only be equal if all communities have identical species composition, and the difference between the two measures will be maximized if no species are shared between communities (Fig. 1). Therefore, the excess of gamma diversity over alpha diversity quantifies the degree of compositional differentiation among communities, and this is known as beta diversity (Table 1; Fig. 1). Beta diversity was originally defined in a multiplicative framework, where beta equals gamma divided by the mean of alpha across communities (Whittaker, 1960, 1972), but since then a number of related indices have been adopted to measure beta diversity on a scale from 0 to 1 (Jost et al., 2011).

2.2. Challenges with measuring diversity

It is well established in neoecology (Sanders, 1968; Gotelli and Colwell, 2001), and in zooarchaeology (Grayson, 1984; Cruz-Uribe, 1988; Lyman, 2008), that an assemblage's richness is correlated with sampling effort and number of individuals (see also Fig. 2A and B). For fossil assemblages, richness is also affected by how fossiliferous a site is, differential time-averaging, collecting biases, and other taphonomic processes. Therefore, comparing the richness of two communities with different sampling intensities and/or taphonomic histories is likely to result in erroneous ecological conclusions. It is often assumed that the biases affecting fossil assemblages are all mediated through the number of collected individuals (e.g., taphonomic processes decrease richness by deleting fossil individuals, time-averaging increases richness by increasing the number of preserved individuals), with the idea that these issues can be addressed by standardizing diversity by the number of individuals in one's sample (e.g., Alroy, 2010a). This is a less than straightforward endeavor, however, for two reasons, which we lay out in the following two paragraphs.

Diversity is not a simple linear function of number of individuals (i.e., an “extensive variable” in statistical mechanics) (Fig. 2A), nor is

Table 1
Glossary of ecological concepts discussed in this article, generally in the order in which they appear.

Community	A group of taxa co-occurring in a given place and time period. Any limits on space and time are somewhat arbitrary and should be tailored to the scale of the researcher's question and the processes of interest (Vellend, 2016; Leibold and Chase, 2017).
Richness	Total number of taxa in a community.
Evenness	How equally individuals are distributed among taxa within a community. More equitable abundance distributions mean higher evenness.
Diversity	Though sometimes used synonymously with richness, diversity typically measures both richness and evenness (Magurran, 2004). Various diversity indices exist which give different weights to each component.
Alpha diversity	Total diversity measured within a community.
Gamma diversity	Total diversity summed across multiple communities. Thus, gamma diversity must be equal to or greater than alpha diversity.
Beta diversity	Can be thought of as diversity found among communities, i.e., how much compositional variation exists among communities. Originally defined as gamma divided by mean alpha (Whittaker, 1960, 1972).
Rarefaction	A method of interpolating richness for a selected sample size (either number of individuals or coverage [see below]). Rarefaction provides a way to estimate richness while standardizing sampling effort among communities. This is necessary because richness is strongly correlated with sampling effort.
Species abundance distribution	A description of how number of individuals are divided among species.
Coverage	The proportion of total number of individuals in a community that belongs to the species represented in one's sample (Chao and Jost, 2012).
Dynamic equilibrium	Where diversity exists at a steady state, but species composition is constantly changing due to extinctions being offset by immigration and/or speciation.

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