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Evaluating Hominin Taxic Diversity in the African Middle Pleistocene With Evolutionary Quantitative Genetics

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ABSTRACT

The Middle Pleistocene (Chibanian) hominin fossil record is taxonomically diverse, with *Homo sapiens*, *Homo neanderthalesis*, *Homo naledi*, and *Homo erectus*, all existing at various times during this period. These species are generally recognized as valid, but there is also an ambiguous group consisting of individuals that are regionally, temporally, and morphologically variable and difficult to categorize. This 'Muddle in the Middle' has been at the heart of many debates in the paleoanthropological literature, with the main disagreement centered on how many species this group consists of. This disagreement has been further exacerbated given the difficulty of defining species in the fossil record using existing species concepts. While this is a challenge, some species concepts do include predictions that can be tested. One of these is Van Valen's Ecological Species Concept (ESC), which describes a species as a group that occupies an adaptive zone, with stabilizing selection acting to maintain its morphological stability.

In this study, an established approach derived from evolutionary quantitative genetics was used as a proof of concept to test whether the pattern of morphological variation among the crania of eight Middle Pleistocene hominin individuals from Africa (~ 600–150 ka) is more consistent with diversifying selection, stabilizing selection, or genetic drift. Results show that the vast majority of comparisons indicate a pattern of less between-group variation than expected, a pattern that may reflect stabilizing selection, which aligns with the definition of a species according to the ESC. Four comparisons involving the Bodo 1 cranium show possible evidence of diversifying selection, which may indicate some taxic diversity. In conclusion, most of the individuals in this study follow the expectation of a single ecological species lineage. This is the first study to use this approach for taxonomic purposes.

INTRODUCTION

The Middle Pleistocene, also known as the Chibanian geochronologic age, between 781 and 126 thousand years ago (ka) (Cohen et al. 2013, updated) is characterized by a regionally and morphologically diverse hominin fossil record. During this interval, we see the emergence of *Homo sapiens* at about 300 ka (Hublin et al. 2017; Schlebusch et al. 2017), the rise and fall of *Homo neanderthalensis* (Arsuaga et al. 2014; Higham et al. 2014), the continued existence of *Homo erectus*, evidence of *Homo naledi* in South Africa (Berger et al. 2015), as well as the presence of an enigmatic and variable group of large-brained and large-bodied individu-

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TABLE 1. COMMON SPECIES CONCEPTS.

Species concept	Description	Reference
Biological Species Concept	"Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups."	Mayr 1942: 120
Recognition Species Concept	"A species is the most inclusive population of individual biparental organisms which share a common fertilization system."	Paterson 1985: 25
Phylogenetic Species Concept	"A species is an irreducible cluster of organisms, diagnosably distinct from other such clusters and within which there is a parental pattern of ancestry and descent."	Cracraft 1989: 34–35
Evolutionary Species Concept	"A lineage (an ancestral-descendant sequence of populations) evolving separately from others, with its own unitary evolutionary role and tendencies."	Simpson 1961: 153
Cohesion Species Concept	"A species is the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms."	Templeton 1989: 12
Ecological Species Concept	"A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range."	Van Valen 1976: 233
Phenetic Species Concept	"We may regard as a species (a) the smallest (most homogeneous) cluster that can be recognized upon some given criterion as being distinct from other clusters, or (b) a phenetic group of a given diversity somewhat below the subgenus category."	Sokal and Crovello 1970; Sneath and Sokal 1973: 365

als that has been difficult to interpret taxonomically—the so-called "Muddle in the Middle" (Athreya and Hopkins 2021; Bae 2010; Bräuer 2008; Harvati and Reyes-Centeno 2022; Rightmire 1998, 2008; Roksandic et al. 2022; Stringer 2012). For decades, scholars have grappled with this taxonomic problem—exacerbated by the similarity, not difference, between this group and early *Homo sapiens*, including evidence of hybridization during this time period (Ackermann et al. 2019)—which has led to many disagreements and debates. While some of these debates have revolved around disagreements as to the most likely representatives of the ancestor of *Homo sapiens* and the region in which this ancestor would most likely be found (e.g., Bergström et al. 2021; Bermúdez de Castro and Carbonell 2022; Bermúdez de Castro and Martinon-Torres 2022; Mounier and Mirazón Lahr 2019; Stringer 2016; Wu 2004), most discussions have focused on the number of species or taxonomic units this group encompasses (see Rightmire 2008, 2013 for a review; Bräuer 1992, 2012; Groves and Lahr 1994; Ji et al. 2021; Mounier and Mirazón Lahr 2016; Ni et al. 2021; Roksandic et al. 2022; Stringer 2012). Given the range of analytical approaches and theoretical foundations used to understand and classify these individuals, together with the inherent subjectivity that underlies the taxonomic interpretation of morphological features in terms of importance (which has led to disagreements over "lumping" or "splitting"; see Tattersall 1986), it is no surprise that taxonomic decisions are difficult to make.

One important aspect of this discussion pertains to how species are defined and the various species concepts that have been developed for this purpose (Table 1; historical review in Wilkins 2009). It may be obvious that most species in the fossil record are determined almost exclusively via morphological comparisons. Sometimes this is an operationalization of Simpson's (1961) practical approach to grouping similar individuals whose variation does not exceed that of an extant model taxon with previously quantified variation; essentially a morphospecies or chronospecies. Sometimes this involves naming a new species based on stratigraphic gaps in the fossil record or regional differences, and other times it involves decisions about apomorphies (Kimbel and Rak 1993). But in all instances, the application of classic species concepts in paleoanthropology—such as the biological, cohesion, phenetic, phylogenetic, recognition, and evolutionary species concepts—is difficult to accomplish due to the sparsity of fossils, the uncertainty of extinct taxon variability, the lack of evidence of reproductive isolation (relevant for the biological species concept), the arbitrariness of dividing populations that may exist within a continuous lineage, and the indeterminate relationships between fossil groups, among many other issues (see Silcox 2014). It is clear then that this species concept problem poses an issue for interpreting the taxic diversity within Middle Pleistocene *Homo*. If species concepts are difficult to apply in paleoanthropology, and some are foregoing species concepts altogether by identifying morphospecies using a suite of different criteria, how can we determine taxonomic units in this group? One possible solution may be to use the theoretical underpinnings of species concepts as hypotheses to test.

Turning to Table 1, one species concept that seems to have a testable component for paleoanthropology is the ecological species concept (ESC; Van Valen 1976). According to this species concept, a species is defined as “a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range” (Van Valen 1976: 233). Essentially then, a species is defined based on the occupation of an ecological niche, where stabilizing selection works to maintain a stable species phenotype on an adaptive landscape (Mallet 2013; Simpson 1944, 1953). This is testable in the sense that if the morphological variation of a group of extinct individuals can be explained via a microevolutionary model of stabilizing selection, then that group of extinct individuals may represent an ecological species. But how can this be operationalized in paleoanthropology when morphological data are all we have to work with?

The field of evolutionary quantitative genetics, dealing with the evolution of continuous phenotypic traits (Falconer 1960), has a methodological framework that is applicable to this question. Essentially, this framework allows for the reconstruction of evolutionary processes—e.g., genetic drift, natural selection—underlying morphological traits. Theoretical and analytical advances in the field by Russell Lande in the 1970s, James Cheverud in the 1980s, and then Rebecca Ackermann in the 2000s have allowed for the application of this framework to fossil data (Ackermann and Cheverud 2002; Cheverud 1988; Lande 1976, 1979; see Schroeder and Ackermann 2023 for a review). Importantly, this has also provided an approach to the investigation of morphological divergence in fossils that is non-adaptationist (see Gould and Lewontin 1979; Schroeder and Ackermann 2023).

A summary of these advances is as follows. Through the incorporation of aspects of Motoo Kimura’s neutral theory (an explanation invoking genetic drift as the most common cause of evolutionary change; Kimura 1968, 1983), Lande developed the multivariate Breeder’s equation that presents the relationship between morphology, genetic variance-covariance, and selection pressure (Lande 1979; further extended to the phenotype in Lande and Arnold 1983). In addition, he developed an equation to represent the morphological divergence of populations under a null hypothesis of genetic drift as a function of genetic variance-covariance, time, and population size (Lande 1979). The expectation with this equation is that the morphological divergence between populations represented by the between-group variance is proportional to the genetic variance/covariance within the initial population under genetic drift (Lande 1979). Cheverud showed that, for most of the morphological traits relevant to evolutionary biology, phenotypic and genetic variance/covariance matrices are relatively proportional, thus allowing for the substitution of phenotypic data in place of genetic data (Cheverud 1988). This represented a significant advancement in exploring the evolution of extinct species within a quantitative genetic framework. Finally, Ackermann and Cheverud (2002) extended Lande’s work on the morphological divergence of populations, with the incorporation of Cheverud’s 1988 work, by developing a simple regression test of the proportionality of between-group and within-group variability under the null hypothesis of drift. If proportionality is not met, the examination of the slope of the regression can provide some insight into whether more or less between-group variance was detected, which is relevant to the assessment of stabilizing versus diversifying selection.

These methods have been widely applied in evolutionary biology in both extinct and extant taxa, which reflects their investigatory utility for helping us better understand the evolution of morphological traits (e.g., Assis et al. 2017; Lofsvold 1988; Machado et al. 2022; Marriog and Cheverud 2004; Rossoni et al. 2017; Schroeder et al. 2022; Schroeder and von Cramon-Taubadel 2017; Simon et al. 2016). In paleoanthropology, this approach has mainly focused on exploring evolutionary processes underlying morphological divergence in hominin taxa, including across the genus *Homo* (Baab 2018; Schroeder and Ackermann 2017), between Neanderthals and humans (Weaver et al. 2007), between *Australopithecus* and *Homo* (Ackermann and Cheverud 2004; Schroeder et al. 2014), and between *Homo erectus* and *Homo floresiensis* (Diniz-Filho and Raia 2017). However, as mentioned above, there is potential for aspects of this methodological framework to be applied to the classification of hominin species, but up to now, no study has utilized this approach for taxonomic purposes.

In this case study, we use the regression test of the proportionality of between versus within-group variation (Ackermann and Cheverud 2002) to determine whether the pattern of morphological variation among the crania of eight Middle Pleistocene hominin individuals from Africa (dated between 600 ka and 150 ka) is more consistent with diversifying selection, stabilizing selection, or genetic drift. The African Middle Pleistocene hominin fossil re-

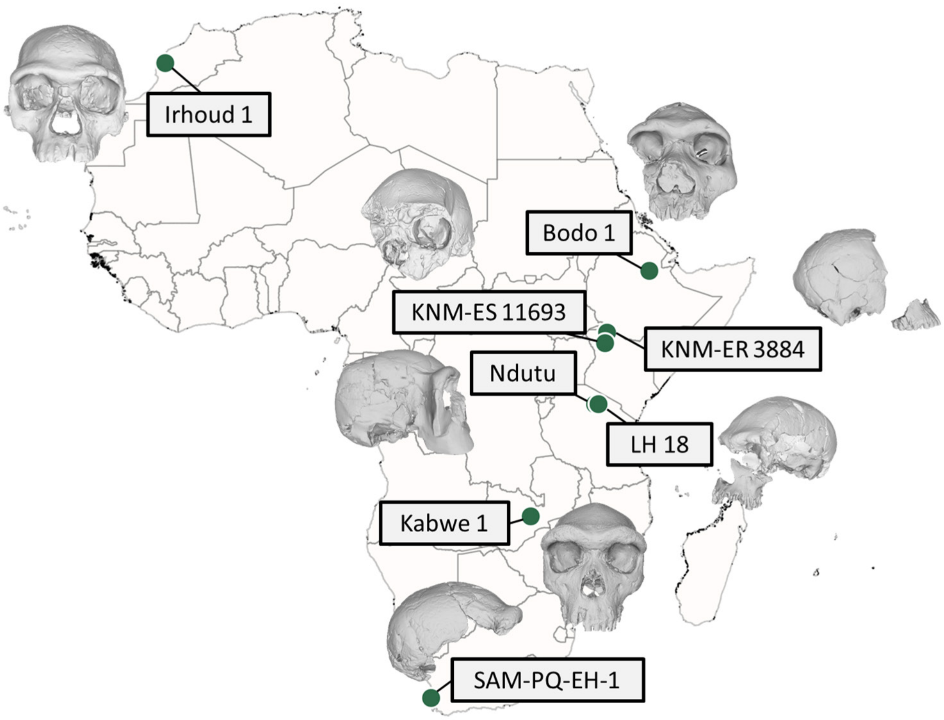


Figure 1. Localities of Middle Pleistocene hominin individuals utilized in this study.

cord is morphologically diverse (e.g., Harvati and Reyes-Centeno 2022; Mbua and Bräuer 2008; Rightmire 2008). In the earlier phases (before 300 ka), this diversity has been interpreted by most as representative of a single variable species lineage (e.g., Rightmire 2008; Roksandic et al. 2022). In the later phases (after 400 ka), this diversity has been interpreted as evidence for multiple morphotypes and/or species (e.g., Foley and Lahr 2003; Mounier and Mirazón Lahr 2019). In addition, *H. sapiens* emerged during the Middle Pleistocene, and some early *H. sapiens*-like individuals exhibit both derived and ancestral traits that has made their classification difficult (Hublin et al. 2017; Rightmire 2008). Therefore, taxonomic interpretations of this group can benefit from another approach. A widespread signal of stabilizing selection across this group may be indicative of a single species lineage according to the ESC (Van Valen 1976), as crania are useful for taxonomic classification in paleoanthropology. If this is not the case, and diversifying selection is detected, then the sample of African Middle Pleistocene individuals in this study may be characterized by more than one taxon according to this particular species concept. While this paper is not advocating for the use and superiority of the ESC out of all other species concepts, it recognizes its value for hypothesis testing within this quantitative genetic framework.

MATERIALS

The 3D surface scans of eight Middle Pleistocene hominin crania were utilized in this study (Figure 1). These include the Ndutu cranium from the lake margin of Lake Ndutu, Tanzania (450±40 ka; Manega 1993; Mturi 1976), KNM-ER 3884 from Ileret, Kenya (270 ka; Bräuer et al. 1997; 1992), KNM-ES 11693 from beach deposits at Eliye Springs, Kenya (200–300 ka; Bräuer and Leakey 1986; Bräuer et al. 2003), SAM-PQ-EH-1 from Elandsfontein near Hopefield, South Africa (~600 ka; Drennan 1953; Klein et al. 2007), Bodo 1 from Bodo D'ar, Middle Awash, Ethiopia (640±30 ka; Clark et al. 1994; Conroy et al. 1978), LH 18 from the Ngaloba Beds at Laetoli, Tanzania (200–300 ka; Day et al. 1980; Manega 1993), Irhoud 1 from Irhoud, Morocco (315±34 ka; Hublin et al. 2017; Richter et al. 2017), and Kabwe 1 from Kabwe, Zambia (299±25 ka; Grün et al. 2020; Woodward 1921). The 3D scans of Ndutu, KNM-ER 3884, KNM-ES 11693, SAM-PQ-EH-1, and LH 18 crania were collected on the original specimens using a NextEngine surface laser scanner by one of the authors (LS). LH 18 is curated in three pieces, and KNM-ER 3884 is curated in two pieces. The 3D scans of Irhoud 1 and Bodo 1 are surface scans of high-quality, first-generation casts. The 3D surface scan of Irhoud 1 was obtained from K. Bergstrom. The 3D model of Kabwe 1 was generated from a CT scan (~120μ resolution) of the original specimen obtained from B. Viola. These eight individuals have been variously referred to as *Homo heidelbergensis*, *Homo rhodesiensis*, *H. sapiens*, or sometimes as "archaic" *H. sapiens*. One of these individuals has been classified as an early representative of the *H. sapiens* clade (Irhoud 1, Richter et al. 2017), while others represent holotypes for different species (Bodo 1 – *Homo bodoensis*, Roksandic et al. 2022; Kabwe 1 – *H. rhodesiensis*, Woodward 1921; SAM-PQ-EH-1 – *Homo saldanensis*, Drennen 1955).

A comparative sample comprising NextEngine-generated surface scans taken from previous studies (Schroeder

2015; Schroeder and Ackermann 2017) of recent *H. sapiens* from the Raymond A. Dart Collection at the University of the Witwatersrand (n=51) and the Iziko Museums of South Africa (n=49) was also included with roughly equal numbers of males and females (Supplementary Information Table S1). This sample was used in this study to model the limits of within-species phenotypic variation given that the estimation of phenotypic variance-covariance matrices, which is central to the regression tests, requires large sample sizes above n=40 (Cheverud 1988). The use of an extant model of variation to assess evolutionary processes in extinct taxa has been used in previous research (e.g., Ackermann and Cheverud 2004; Schroeder and Ackermann 2017) and is justified through studies that have shown a similar—although not the same (see Ackermann 2003)—within-group phenotypic covariance structure across closely related hominoid species (Ackermann 2002).

Contingent upon the preservation status of each cranium, a maximum of 30 landmarks were placed on these scans using Meshlab v2021.05 (Cignoni et al. 2008) according to the landmark protocol in Schroeder (2015). Landmark definitions are provided in Table 2 and landmarks are visualized in Figure 2. A series of interlandmark distances (traits) were then extracted from these landmarks for use in each subsequent analysis (list of traits given in Table 2; n=91). These traits were chosen to maximize the amount of morphologically relevant data captured and to minimize the amount of data redundancy. Traits were extracted from the left side for the recent *H. sapiens* comparative sample, and from both sides for the fossils. If traits on both sides were present, the average value was calculated. All traits and landmarks for the fossils are provided in a Supplementary Information Dataset (see Data Availability).

METHODS

As mentioned above, according to Lande (1979), under a neutral model of evolution (evolution under genetic drift and mutation), between-group phenotypic variation is a function of genetic variance-covariance, time, and population size, and is described by the following equation:

$$E(B_t) = G(\frac{t}{N_e})$$

where $E(B_t)$ is the expected between-group variance-covariance matrix, t is the time since divergence between the groups being compared, N_e is the effective population size and G is the additive genetic variance-covariance matrix of the source population. Following Cheverud (1988), we substitute the phenotypic variance-covariance matrix P in place of G as these have been shown to be relatively proportional to each other (Cheverud 1988; Roff 1995; Sodini et al. 2018). Additionally, as P cannot be robustly estimated from small sample sizes (n needs to be 40 or higher; Cheverud 1988), a covariance matrix calculated from our full recent *H. sapiens* comparative sample was used to model the phenotypic variance-covariance matrix P of our fossil groups. Although this substitution may affect the results of our analyses, it has been shown that the covariance matrices of closely related hominoid species are similar (Ackermann 2002; Jung et al. 2023), and therefore this assumption has some support.

Ackermann and Cheverud's (2002) regression test, which is an extension of the Lande (1979) equation above, was then used to assess the proportionality of B and P under a model of neutral evolution. To do this, P was first decomposed into its principal components (PCs) via a principal component analysis, then B was calculated as the product of the variance among these principal components and the group trait means of the groups being compared. Next, B was log-transformed and regressed on the log-transformed eigenvalues of P. Slopes that do not deviate significantly from 1.0 using a t-test means that the null hypothesis of neutrality cannot be rejected. Slopes that deviate significantly from 1.0 indicate that a model of neutrality can be rejected, pointing to the possibility of natural selection underlying the divergence between the groups being compared. It is important to note that these tests have low power when few groups are being compared, so this study will focus on the pattern of results.

Furthermore, as established in Ackermann and Cheverud (2002), the slope of the regression line can be examined to provide further insight into the observed patterns. A regression slope that is greater than 1.0 indicates more between-group variation than expected under conditions of genetic drift, which can reflect diversifying selection in the major PCs (those that account for most of the morphological variation between groups) and/or stabilizing selection in the minor PCs (those that account for the least of the morphological variation between groups). On the other hand, a regression slope that is less than 1.0 demonstrates less between-group variation than expected under neutral conditions, which can reflect stabilizing selection in the major PCs and/or diversifying selection in the minor PCs.

In this study, individual fossil crania are assumed to represent the group means of eight different populations. Pairwise regression tests were then performed between these hypothetical populations. As these regression tests are most commonly applied in studies that include more than two populations, we also assess whether the number of groups compared had an effect on the type I error rate of the test. This was carried out through a simulation study of 1000 repeats, with a sample size of n=40 per group of k=10 traits each. The number of groups ranged between 2 and 60. For this simulation, random positive definite covariance matrices were simulated from a random normal distribution, and random group means were generated from a multivariate normal distribution under the null hypothesis. The rate of p-values less than the significance level was then recorded for each number of groups.

Analyses were also performed across more than two hypothetical populations when there were a number of shared traits between fossils. Table 3 lists each analysis performed, the traits included in each analysis, and the sample size of the comparative sample used, which reflects the maximum number of individuals with shared traits. All tests were conducted in R version 4.1.0 using the package *evolqg* (Melo et al. 2016; R Core Team 2021). The significance

TABLE 2. CRANIAL LANDMARKS UTILIZED IN THIS STUDY[a, b].

Landmark abbreviation	Landmark	Landmark definition
ANS	Anterior nasal spine	The most anterior point on the maxilla.
PRO	Prosthion	The most anterior point in the midline of the maxillary alveolar process.
IOF	Infraorbital foramen	The most inferior lateral point on the border of the infraorbital foramen.
ALR	Alare	The most lateral point on the nasal aperture.
OR	Orbitale	The most inferior point on the midpoint of the lower edge of the orbit.
SON	Supraorbital notches	The most lateral point on the supraorbital notch.
DAC	Dacryon	The point of intersection of the frontolacrimal and lacrimomaxillary sutures.
NA	Nasion	The point at the intersection of the nasofrontal suture and the midsagittal plane.
FMT	Frontomalare temporale	The most lateral point on the frontozygomatic suture.
ZMI	Zygomaxillare inferior	The most inferior point on the zygomaxillary suture.
AP	Anterior pterion	The most anterior point on the sphenoparietal suture/the intersection of the parietal, sphenoid, and frontal bones.
POR	Porion	The most superior point on the margin of the external auditory meatus.
EMI	External auditory meatus inferior	The most inferior point on the margin of the external auditory meatus.
MAS	Mastoidale	The most inferolateral point on the mastoid process.
MT	Maxillary tuberosity	The most distal point on the maxillary alveolar process.
AST	Asterion	The junction of the lambdoid, parietomastoid, and occipitomastoid sutures.
LA	Lambda	The midline junction of the sagittal and lambdoid sutures, taken in the midline.
BR	Bregma	The midline junction of the coronal and sagittal sutures.
IN	Inferior Nuchal	The most inferior midpoint on the inferior nuchal line.
OP	Opisthion	The midpoint on the posterior border of the foramen magnum.
BA	Basion	The midpoint on the anterior border of the foramen magnum.
FML	Foramen magnum lateral	The most lateral point on the margin of the foramen magnum, posterior to occipital condyle.
OCA	Occipitocondyle anterior	The most anteroinferior point on the occipital condyle.
HOR	Hormion	The midpoint junction of the posterior aspect of the vomer and sphenoid bone.
PNS	Posterior nasal spine	The midpoint projection formed by the union of the posterior processes of the palatine bones.

TABLE 2. CRANIAL LANDMARKS UTILIZED IN THIS STUDY[a, b] (continued).

Landmark abbreviation	Landmark	Landmark definition
GPF	Greater palatine foramen	The most posterolateral point on the border of the greater palatine foramen.
INC	Incisivon	The most posteroinferior point on the border of the incisive foramen.
ALV	Alveolare	The most anterior point on the alveolus of the M1.
MFL	Lateral mandibular fossa	The most lateral point on the mandibular fossa.
MFM	Medial mandibular fossa	The most medial point on the mandibular fossa.

[a] Landmark protocol from Schroeder (2015).

[b] Interlandmark distances were extracted from this list as follows: NA-ANS, ANS-PRO, ALR-ALR, IOF-IOF, FMT-FMT, DAC-DAC, ALV-ALV, PRO-NA, NA-BA, PRO-IOF, ANS-IOF, DAC-ALR, ZMI-IOF, DAC-ANS, OR-SON, OR-PRO, OR-ZMI, ALV-IOF, ALV-PRO, FMT-MT, DAC-FMT, NA-FMT, ZMF-NA, ZMI-MT, ZMI-ANS, ZMI-FMT, ALV-ZMI, SON-FMT, FMT-ZMF, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, MT-MT, PRO-PNS, INC-PNS, PRO-INC, GPF-PNS, MT-GPF, INC-GPF, INC-MT, PRO-GPF, PNS-MT, ALV-GPF, ALV-MT, ALV-INC, IN-OP, OP-BA, OCA-OCA, BA-PNS, BA-HOR, HOR-PNS, AST-AST, LA-OP, HOR-MFL, OCA-BA, FML-BA, AST-BA, IN-MAS, IN-AST, EMI-OCA, MFM-EMI, MT-HOR, MT-OCA, FML-OCA, EMI-HOR, EMI-POR, MFL-MFM, MAS-AST, MFL-MAS, AST-MFM, MFL-EMI, POR-MFL, POR-MFM, AST-POR, EMI-MAS, POR-MAS, MFL-AST, BR-LA, BR-NA, IN-LA, NA-LA, AST-LA, AP-BR, AP-POR, AP-LA, BR-POR, BR-AST, MFL-BR, SON-AST, SON-BR.

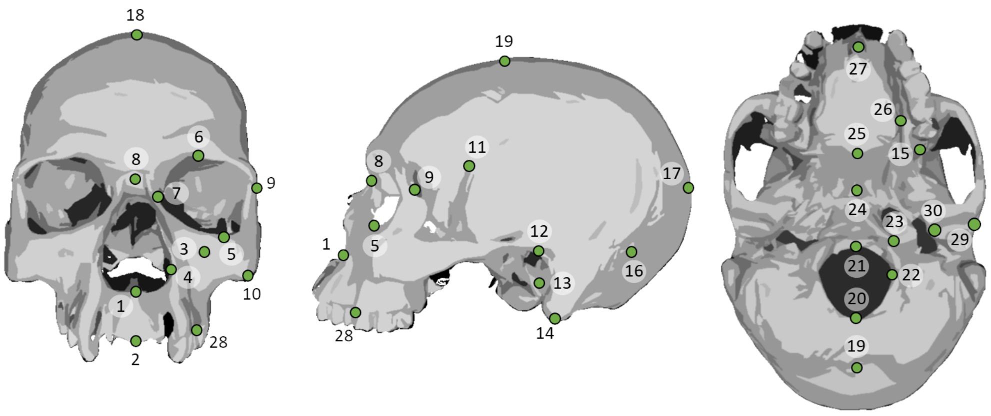
of each *t*-test was assessed using a significance level (α) of 0.05.

RESULTS

The simulation of the type I error rate across the number of groups compared shows general stability around 5% (Supplementary Information Figure S1), which is the expected rate.

The results of the 27 regressions of logged between-group variation against logged within-group variation are given in Table 4. The regression plots are provided in the Supplementary Information (Figures S2–S8). Out of the 25 pairwise analyses performed, the null hypothesis of genetic drift was rejected eight times. Four of these rejections involved Kabwe 1, three involved Irhoud 1, three involved Ndutu, and the rest are varied. Of the two analyses that comprised more than two specimens, one produced a rejection of the null hypothesis. Overall, these rejections of the null hypothesis indicate that, for these comparisons, variation is greater than or lesser than expected under a model of genetic drift, and non-neutral processes such as natural selection may be responsible for the divergence of these groups.

All nine analyses with rejections of the null hypothesis were associated with slopes less than 1.0 (see Table 4), meaning that variation was less than expected under a model of neutrality. The vast majority of the remaining regression tests that were not associated with a rejection of the null



1. ANS 2. PRO 3. IOF 4. ALR 5. OR 6. SON 7. DAC 8. NA 9. FMT 10. ZMI 11. AP 12. POR 13. EMI
14. MAS 15. MT 16. AST 17. LA 18. BR 19. IN 20. OP 21. BA 22. FML 23. OCA 24. HOR
25. PNS 26. GPF 27. INC 28. ALV 29. MFL 30. MFM

Figure 2. Cranial landmarks used in this study. Landmark definitions are provided in Table 2.

TABLE 3. ANALYSIS COMPOSITION[a].

Analysis	n traits	Extant model n	Traits
Bodo 1 & KNM-ES 11693	13	94	DAC-DAC, ANS-IOF, DAC-ALR, ZMI-IOF, DAC-ANS, OR-ZMI, DAC-FMT, ZMI-ANS, ZMI-FMT, ALR-ANS, ALR-IOF, BA-HOR, POR-MFM
Bodo 1 & LH 18	9	92	ANS-PRO, ALR-ALR, PRO-IOF, ANS-IOF, ALV-IOF, ALV-PRO, ALR-ANS, ALR-IOF, POR-MFM
Bodo 1 & Ndutu	16	93	NA-ANS, ALR-ALR, DAC-DAC, NA-BA, ANS-IOF, DAC-ALR, DAC-ANS, OR-SON, DAC-FMT, NA-FMT, SON-FMT, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, POR-MFM
Bodo & KNM-ER 3884	6	92	ANS-PRO, ALR-ALR, ALV-PRO, ALR-ANS, PRO-INC, ALV-INC
Bodo 1 & Irhoud 1	30	83	NA-ANS, ANS-PRO, ALR-ALR, DAC-DAC, PRO-NA, PRO-IOF, ANS-IOF, DAC-ALR, ZMI-IOF, DAC-ANS, OR-SON, OR-PRO, OR-ZMI, ALV-IOF, ALV-PRO, DAC-FMT, NA-FMT, ZMI-ANS, ZMI-FMT, ALV-ZMI, SON-FMT, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, PRO-PNS, INC-PNS, PRO-INC, ALV-INC, POR-MFM
Bodo 1 & Kabwe 1	32	82	NA-ANS, ANS-PRO, ALR-ALR, DAC-DAC, PRO-NA, NA-BA, PRO-IOF, ANS-IOF, DAC-ALR, ZMI-IOF, DAC-ANS, OR-SON, OR-PRO, OR-ZMI, ALV-IOF, ALV-PRO, DAC-FMT, NA-FMT, ZMI-ANS, ZMI-FMT, ALV-ZMI, SON-FMT, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, PRO-PNS, INC-PNS, PRO-INC, ALV-INC, BA-PNS, BA-HOR
Irhoud 1 & KNM-ER 3884	12	90	ANS-PRO, ALR-ALR, ALV-ALV, ALV-PRO, ALR-ANS, PRO-INC, ALV-INC, AST-AST, MAS-AST, AST-POR, POR-MAS, AST-LA
Irhoud 1 & KNM-ES 11693	32	89	DAC-DAC, ANS-IOF, DAC-ALR, ZMI-IOF, DAC-ANS, OR-ZMI, FMT-MT, DAC-FMT, ZMI-MT, ZMI-ANS, ZMI-FMT, ALR-ANS, ALR-IOF, MT-GPF, AST-AST, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, BR-LA, AST-LA, AP-BR, AP-POR, AP-LA, BR-POR, BR-AST, MFL-BR
Irhoud 1 & LH 18	17	88	ANS-PRO, ALR-ALR, ALV-PRO, ALR-ANS, AST-AST, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, NA-LA, AST-LA, SON-AST

TABLE 3. ANALYSIS COMPOSITION[a] (continued).

Analysis	n traits	Extant model n	Traits
Irhoud 1 & Ndutu	29	89	NA-ANS, ALR-ALR, DAC-DAC, ANS-IOF, DAC-ALR, DAC-ANS, OR-SON, DAC-FMT, NA-FMT, SON-FMT, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, AST-AST, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, NA-LA, AST-LA, AP-POR, AP-LA, SON-AST
Irhoud 1 & SAM-PQ-EH-1	9	95	SON-FMT, AST-AST, BR-LA, BR-SON, AST-LA, AP-BR, AP-LA, BR-AST, SON-AST
Kabwe 1 & Irhoud 1	60	76	NA-ANS, ANS-PRO, ALR-ALR, IOF-IOF, FMT-FMT, DAC-DAC, ALV-ALV, PRO-NA, PRO-IOF, ANS-IOF, DAC-ALR, DAC-ANS, OR-SON, OR-PRO, OR-ZMI, ALV-PRO, FMT-MT, DAC-FMT, NA-FMT, ZMI-MT, ZMI-ANS, ZMI-FMT, SON-FMT, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, PRO-PNS, INC-PNS, PRO-INC, GPF-PNS, MT-GPF, INC-GPF, INC-MT, PRO-GPF, PNS-MT, ALV-GPF, ALV-MT, ALV-INC, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, BR-LA, BR-NA, NA-LA, BR-SON, AST-LA, AP-BR, AP-POR, AP-LA, BR-POR, BR-AST, MFL-BR, SON-AST
Kabwe 1 & KNM-ER 3884	15	87	ANS-PRO, ALR-ALR, ALV-ALV, ALV-PRO, ALR-ANS, PRO-INC, ALV-INC, FML-BA, AST-BA, MAS-AST, EMI-POR, AST-POR, EMI-MAS, POR-MAS, AST-LA
Kabwe 1 & KNM-ES 11693	43	84	DAC-DAC, ANS-IOF, DAC-ALR, ZMI-IOF, DAC-ANS, OR-ZMI, FMT-MT, DAC-FMT, ZMI-MT, ZMI-ANS, ZMI-FMT, ALR-ANS, ALR-IOF, MT-GPF, BA-HOR, HOR-MFL, OCA-BA, AST-BA, EMI-OCA, MFM-EMI, MT-HOR, MT-OCA, MAS-AST, EMI-HOR, EMI-POR, MFL-MFM, MFL-MAS, AST-MFM, MFL-EMI, POR-MFL, POR-MFM, AST-POR, EMI-MAS, POR-MAS, MFL-AST, BR-LA, AST-LA, AP-BR, AP-POR, AP-LA, BR-POR, BR-AST, MFL-BR
Kabwe 1 & LH 18	21	86	ANS-PRO, ALR-ALR, ALV-ALV, ALV-PRO, ALR-ANS, MFM-EMI, MAS-AST, EMI-POR, MFL-MFM, MFL-MAS, AST-MFM, MFL-EMI, POR-MFL, POR-MFM, AST-POR, EMI-MAS, POR-MAS, MFL-AST, NA-LA, AST-LA, SON-AST
Kabwe 1 & Ndutu	33	84	NA-ANS, ALR-ALR, DAC-DAC, NA-BA, ANS-IOF, DAC-ALR, DAC-ANS, OR-SON, DAC-FMT, NA-FMT, SON-FMT, SON-DAC, DAC-NA, ALR-ANS, ALR-IOF, OCA-BA, FML-BA, AST-BA, MAS-AST, FML-OCA, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, NA-LA, AST-LA, AP-POR, AP-LA, SON-AST

TABLE 3. ANALYSIS COMPOSITION[a] (continued).

Analysis	n traits	Extant model n	Traits
Kabwe 1 & SAM-PQ-EH-1	8	95	SON-FMT, BR-LA, BR-SON, AST-LA, AP-BR, AP-LA, BR-AST, SON-AST
KNM-ER 3884 & KNM-ES 11693	14	97	IN-OP, OP-BA, AST-AST, LA-OP, AST-BA, IN-MAS, IN-AST, MAS-AST, EMI-POR, AST-POR, EMI-MAS, POR-MAS, IN-LA, AST-LA
KNM-ER 3884 & LH 18	15	89	ANS-PRO, ALR-ALR, ALV-ALV, ALV-PRO, ALR-ANS, AST-AST, IN-MAS, IN-AST, MAS-AST, EMI-POR, AST-POR, EMI-MAS, POR-MAS, IN-LA, AST-LA
KNM-ER 3884 & Ndutu	11	92	ALR-ALR, ALR-ANS, OP-BA, AST-AST, LA-OP, FML-BA, AST-BA, MAS-AST, AST-POR, POR-MAS, AST-LA
KNM-ES 11693 & LH 18	19	94	ALR-ANS, AST-AST, IN-MAS, IN-AST, MFM-EMI, MAS-AST, EMI-POR, MFL-MFM, MFL-MAS, AST-MFM, MFL-EMI, POR-MFL, POR-MFM, AST-POR, EMI-MAS, POR-MAS, MFL-AST, IN-LA, AST-LA
KNM-ES 11693 & Ndutu	25	86	DAC-DAC, ANS-IOF, DAC-ALR, DAC-ANS, DAC-FMT, ALR-ANS, ALR-IOF, OP-BA, OCA-OCA, AST-AST, LA-OP, OCA-BA, AST-BA, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, AST-LA, AP-POR, AP-LA
KNM-ES 11693 & SAM-PQ-EH-1	6	95	AST-AST, BR-LA, AST-LA, AP-BR, AP-LA, BR-AST
LH 18 & Ndutu	15	92	ALR-ALR, ALR-ANS, AST-AST, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST, NA-LA, AST-LA, SON-AST
Ndutu & SAM-PQ-EH-1	5	96	SON-FMT, AST-AST, AST-LA, AP-LA, SON-AST
Within Middle Pleistocene *Homo* (KNM-ES 11693, KNM-ER 3884, Ndutu, LH 18, Irhoud 1, Kabwe 1)	10	97	ALR-ANS, MAS-AST, MFL-MFM, MFL-MAS, AST-MFM, POR-MFL, POR-MFM, AST-POR, POR-MAS, MFL-AST
Within Middle Pleistocene *Homo* (KNM-ES 11693, Bodo 1, Ndutu, Irhoud 1, Kabwe 1)	8	95	DAC-DAC, ANS-IOF, DAC-ALR, DAC-ANS, DAC-FMT, ALR-ANS, ALR-IOF, POR-MFM

[a] Pairwise comparisons between KNM-ER 3884 and SAM-PQ-EH-1, LH 18 and SAM-PQ-EH-1, as well as Bodo 1 and SAM-PQ-EH-1 could not be carried out due to very low trait overlap of four or fewer traits.

TABLE 4. RESULTS OF REGRESSION ANALYSIS OF BETWEEN- VERSUS WITHIN-GROUP VARIATION AS A TEST OF THE NULL HYPOTHESIS OF GENETIC DRIFT.*

Analysis	Rejection of the null hypothesis?	Slope	*t*-statistic	*p*-value	r^2
Bodo 1 & KNM-ES 11693	No	1.145	0.712	0.491	0.741
Bodo 1 & LH 18	No	1.804	1.117	0.345	0.677
Bodo 1 & Ndutu	No	1.084	0.300	0.769	0.517
Bodo & KNM-ER 3884	No	1.810	1.072	0.344	0.589
Bodo 1 & Jebel Irhoud 1	No	0.822	1.046	0.304	0.456
Bodo 1 & Kabwe 1	Yes	0.416	2.836	**0.008**	0.120
Jebel Irhoud 1 & KNM-ER 3884	No	0.006	1.777	0.106	0.000
Jebel Irhoud 1 & KNM-ES 11693	Yes	0.594	2.053	**0.049**	0.232
Jebel Irhoud 1 & LH 18	Yes	0.427	2.593	**0.020**	0.199
Jebel Irhoud 1 & Ndutu	Yes	0.441	4.053	**0.000**	0.275
Jebel Irhoud 1 & SAM-PQ-EH-1	No	0.488	1.297	0.236	0.179
Kabwe 1 & Jebel Irhoud 1	Yes	0.422	5.145	**0.000**	0.196
Kabwe 1 & KNM-ER 3884	No	0.629	0.758	0.462	0.113
Kabwe 1 & KNM-ES 11693	Yes	0.673	2.773	**0.008**	0.444
Kabwe 1 & LH 18	No	0.871	0.607	0.551	0.471
Kabwe 1 & Ndutu	Yes	0.518	2.854	**0.008**	0.233
Kabwe 1 & SAM-PQ-EH-1	No	0.566	0.947	0.380	0.203
KNM-ER 3884 & KNM-ES 11693	No	0.674	1.047	0.316	0.282
KNM-ER 3884 & LH 18	No	0.998	0.005	0.996	0.284
KNM-ER 3884 & Ndutu	No	0.216	1.852	0.097	0.028
KNM-ES 11693 & LH 18	No	0.598	1.569	0.135	0.243
KNM-ES 11693 & Ndutu	No	0.796	1.456	0.159	0.584
KNM-ES 11693 & SAM-PQ-EH-1	No	0.922	0.200	0.851	0.581
LH 18 & Ndutu	Yes	0.619	2.170	**0.049**	0.490
Ndutu & SAM-PQ-EH-1	No	-0.926	2.726	0.072	0.364
Within Middle Pleistocene *Homo* (KNM-ES 11693, Ndutu, LH 18, Jebel Irhoud 1, Kabwe 1)	Yes	0.489	3.030	**0.016**	0.513
Within Middle Pleistocene *Homo* (KNM-ES 11693, Bodo 1, Ndutu, Jebel Irhoud 1, Kabwe 1)	No	0.725	2.070	0.084	0.832

*Slope values highlighted in light grey indicate slopes greater than 1.0 and slope values highlighted in green indicate slopes less than 1.0. Bolded *p*-values indicate statistical significance ($p<0.05$).

hypothesis (18 analyses in total), were also associated with slopes less than 1.0. Only four tests produced slopes greater than 1.0, and all are comparisons that involve the Bodo 1 cranium. These regressions, however, do not indicate a deviation from the neutral model of evolution. Altogether, 23 out of the 27 analyses performed exhibited slopes less than 1.0 (85%).

Because these slope estimations are also influenced by the r^2 values in each analysis that describes the scatter around the line, it is important to include an interpretation of these with the results. As shown in Table 4 and visualized in Supplementary Information Figures S2–S8, r^2 values range from 0.0 to 0.832. If we only concentrate on comparisons with r^2 values above the mean r^2 of 0.365, then eight out of 23 comparisons with slopes below 1.0, and all four comparisons with slopes above 1.0 satisfy this condition. This means that even when a conservative approach is taken, the majority of slopes remain less than 1.0.

DISCUSSION

There is extensive paleoanthropological literature that has focused on characterizing the morphological diversity within and between Middle Pleistocene hominins, with a particular emphasis on those large-brained, large-bodied individuals often referred to collectively as the ambiguous "Muddle in the Middle" (e.g., Athreya and Hopkins 2021; Bae 2010; Bräuer 2008; Harvati and Reyes-Centeno 2022; Rightmire 1998, 2008; Roksandic et al. 2022; Stringer 2012). These previous studies have mostly used traditional qualitative and quantitative methods for assessing this morphological variation, however, debates and disagreements related to how many species are represented are still evident. In this context, this study utilized a novel quantitative genetic approach in an attempt to contribute to our understanding of hominin taxic diversity in the African Middle Pleistocene. This represents the first use of this method for taxonomic purposes, and thus, this study serves as a proof of concept.

The slope results of the regression analyses conducted indicate that for the majority of comparisons, slopes are less than 1.0, implying that morphological divergence follows a pattern of less between-group variation than expected, a possible indication of stabilizing selection (see Table 4). Although most regression tests did not produce rejections of the null hypothesis of genetic drift, those that did were all associated with slopes less than 1.0, which indicates that morphology between groups is significantly less variable than what is expected under a model of neutral evolution. According to the ESC, this may define a single ecological species lineage. This is consistent with previous studies that classify all early large-brained African Middle Pleistocene hominins (excluding *H. sapiens*-like individuals) into a single species (e.g., Rightmire 1996, 2008; Roksandic et al. 2022; Stringer 2012). Interestingly, in this study, the Jebel Irhoud 1 cranium is included, which could suggest that this single species lineage includes early members of *H. sapiens*, or that the transition to *H. sapiens* was not marked by an abrupt speciation event characterized by diversifying selection.

Deviations from this pattern were detected in some analyses involving the Bodo 1 cranium, with four comparisons producing slopes greater than 1.0 (see Table 4). This suggests that for these comparisons, between-group variation is greater than expected under a model of neutral evolution and therefore morphological divergence could be consistent with a pattern of diversifying selection. This could indicate species-level differences according to the ESC.

In terms of morphology, the Bodo 1 cranium from the Middle Awash in Ethiopia exhibits many features that are similar to other Middle Pleistocene hominins such as large brain size, extent of its cranial robusticity, and signs of parietal bossing, but it also shares some morphological features with *H. erectus* including large brow ridges, frontal keeling, and thick cranial vault bones (Adefris 1992; Rightmire 1996). Even though Bodo 1 exhibits this so-called "intermediate" anatomy (Rightmire 1996) and represents the oldest known well-preserved large-brained African Middle Pleistocene individual, dated to ~600 ka (Clark et al. 1994), most scholars have grouped it with other large-brained Middle Pleistocene African hominins such as Kabwe 1 based on qualitative and quantitative analyses (e.g., Freidline et al. 2012; Harvati et al. 2010; Mbua and Bräuer 2008; Mounier and Mirazón Lahr 2016; Rightmire 1996, 2008; Roksandic et al. 2022). Yet, there are still some morphological differences detected between Bodo 1 and other individuals, particularly related to its large face, and questions about how much of its facial form reflects sexual dimorphism versus taxonomic differentiation have been discussed (Stringer 2016). Phenotypic plasticity could also be a factor contributing to these differences as the face has been shown to present higher degrees of plasticity compared to other cranial regions (but this is not necessarily a problem for reconstructing phylogenetic relationships, e.g., von Cramon-Taubadel 2009a). Nevertheless, the present study does suggest that some of these differences may be taxonomically significant in that they could be the result of diversifying selection. Alternatively, it could be indicative of an end-stage speciation event where we see the transition from diversifying selection to stabilizing selection reflected in morphology. It is also important to note that none of these comparisons with slopes greater than 1.0 resulted in a rejection of the null hypothesis of genetic drift, so it could be that neutral processes can explain the morphological divergence in these cases.

One question that arises when discussing the results of this study is how these slopes compare with slopes generated in previous quantitative genetic analyses of fossil hominins. Even though this approach has not been used for taxonomic purposes before, it is useful to assess whether taxic diversity across known hominin groups is reflected in these regression slopes. Schroeder and Ackermann (2017) provide an opportunity for this comparison. In this study, evolutionary processes across the *Homo* lineage were explored, which included comparisons between *Homo habilis*, *Homo rudolfensis*, *H. erectus*, Middle Pleistocene *Homo*, and *H. sapiens*. Results show that there is a more widespread pattern of diversifying selection within early *Homo*, and from early to later *Homo* in the face (45/76 [59%] comparisons with slopes greater than 1.0; Schroeder and Ackermann 2017: Table S1), whereas the neurocranium has more of a pattern of stabilizing selection (29/88 [33%] slopes greater than 1.0). While this is not a straightforward pattern and includes different cranial traits in smaller subsets than the current analysis, it does follow the typical taxonomic understanding of the genus *Homo*, where there are a number of species represented early in the *Homo* lineage (most slopes greater than 1.0 were related to this group), with more stabilizing selection detected later on. When interpreted through the ESC, this indicates more adaptive divergence associated with different ecological niches in early *Homo* (see Antón et al. 2014). The different results obtained for the neurocranium and face point to the differential effects of evolutionary processes on different skeletal regions, and the taxonomic efficacy of each of these (see von Cramon-Taubadel 2009b). This cross-comparison suggests that the approach in the current paper may be more useful for assessing large-scale patterns when more traits are available.

Overall, this study finds that most morphological divergence between African Middle Pleistocene *Homo* crania follows a pattern where between-group variation is less than expected, reflective of possible stabilizing selection, which is consistent with a single species under the ESC. However, there are multiple shortcomings of this approach that need to be noted. First, we do not know the extent of morphological variation across Middle Pleistocene *Homo*. This issue extends to the estimation of within-group variation that is central to these methods but can only be calculated using large sample sizes. A recent human sample was used in the current study, but it is unclear if this sample is the most appropriate, especially as it has been shown that the extent of cranial variation in Middle Pleistocene *Homo* generally exceeded that of recent *H. sapiens* (Rightmire 2008). However, as mentioned, there is evidence that supports similar patterns of cranial covariance across hominoids (e.g., Ackermann 2002; Jung et al. 2023). Second, as the $r2$ values indicate in Table 4, there is a high scatter about the regression line (see Supplementary Information Figures S1–S8), reflecting the low power of these tests. Even though this study focused on the pattern of results and slopes, not statistical significance, it is worth mentioning that there could be instances where one or two PCs are influencing the slope in the positive or negative direction. For future studies, an alternative measure, Lande's Generalized Genetic Distance, could be used to calculate rates of evolution to assess whether divergence is fast, slow, or neutral, which can indicate directional selection, stabilizing selection, or genetic drift, respectively (Lande 1979).

Finally, while this study does not advocate for the use of only the ESC to categorize species, it does suggest that this species concept has a prediction that is testable within a quantitative genetic hypothesis-testing framework. In this context, this approach adds to the analytical resources available for assessing taxic diversity in the Middle Pleistocene, and when combined with other more traditional quantitative and qualitative methods, it could be used to shed light on inter- or intraspecific variation in other regions.

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DATA AVAILABILITY

The fossil data that support the findings of this study are available in the Supplementary Information Dataset (https://doi.org/10.17605/OSF.IO/F3S8U). The human comparative data used in this study are available on request from the relevant repositories in accordance with their policies on the distribution of data for third party use.

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Special Issue: What's in a Name?
Late Middle and Early Late Pleistocene Hominin Systematics

Evaluating Hominin Taxic Diversity in the African Middle Pleistocene With Evolutionary Quantitative Genetics

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SUPPLEMENT 1

This supplement includes: supplementary material table S1 and supplementary material figures S1–S8. The Supplementary dataset is available at: https://doi.org/10.17605/OSF.IO/F3S8U.

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Table S1. Description of comparative sample (from Schroeder 2015).

Repository number	Age	Sex	Population group
RDC-A22	30	Female	Xhosa
RDC-A80	38	Male	Zulu
RDC-A96	75	Female	Sotho
RDC-A182	32	Female	Tswana
RDC-A244	39	Male	Tswana
RDC-A250	43	Male	Zulu
RDC-A252	30	Male	Xhosa
RDC-A263	30	Female	Shana
RDC-A267	50	Male	Sotho
RDC-A381	29	Female	Zulu
RDC-A395	Adult	Male	Zulu
RDC-A396	60	Male	Xhosa
RDC-A399	39	Male	Zulu
RDC-A400	36	Male	Xhosa
RDC-A437	68	Male	Zulu
RDC-A465	30	Male	Zulu
RDC-A591	28	Male	Xhosa
RDC-A700	45	Female	Sotho
RDC-A702	25	Male	Ndabele
RDC-A740	25	Female	Sotho
RDC-A761	37	Female	Xhosa
RDC-A787	22	Female	Xhosa
RDC-A799	54	Female	Zulu
RDC-A863	20	Female	Xhosa
RDC-A865	49	Male	Sotho
RDC-A866	30	Female	Sotho
RDC-A883	27	Female	Sotho
RDC-A900	26	Female	Swazi
RDC-A1228	62	Female	Zulu
RDC-A1256	32	Female	Zulu
RDC-A1276	39	Male	Xhosa
RDC-A1324	58	Male	Zulu
RDC-A1338	39	Male	Tswana
RDC-A1370	52	Female	Xhosa
RDC-A1423	40	Male	Zulu
RDC-A1429	49	Female	Zulu
RDC-A1451	39	Female	Zulu

RDC-A1464	25	Male	Xhosa
RDC-A1532	69	Female	Ndabele
RDC-A1549	28	Female	Ndabele
RDC-A1551	51	Male	Xhosa
RDC-A1653	29	Female	Venda
RDC-A1937	50	Male	Xhosa
RDC-A2058	50	Male	Xhosa
RDC-A2183	25	Female	Sotho
RDC-A2221	44	Female	Zulu
RDC-A2248	48	Male	Sotho
RDC-A2307	60	Female	Sotho
RDC-A2359	30	Female	Zulu
RDC-A3151	59	Male	Zulu
RDC-A3582	28	Male	Xhosa
SAM-AP 1	Adult	Indeterminate	No Data
SAM-AP 17	Adult	Male	Khoesan
SAM-AP 27	Adult	Male	Khoesan
SAM-AP 278g	Adult	Male	Khoesan
SAM-AP 1145	Adult	Female	Khoesan
SAM-AP 1146	Adult	Female	Khoesan
SAM-AP 1247a	Adult	Female	Khoesan
SAM-AP 1254	Adult	Indeterminate	No Data
SAM-AP 1268	Adult	Indeterminate	Khoesan
SAM-AP 1276	Adult	Indeterminate	No Data
SAM-AP 1278	Adult	Indeterminate	No Data
SAM-AP 1440	Adult	Male	Khoesan
SAM-AP 1441	Adult	Male	Khoesan
SAM-AP 1473	Adult	Male	Khoesan
SAM-AP 1871	Adult	Male	Khoesan
SAM-AP 1877	Adult	Male	Khoesan
SAM-AP 1878a	Adult	Male	Khoesan
SAM-AP 1879	Adult	Male	Khoesan
SAM-AP 3692	Adult	Indeterminate	No Data
SAM-AP 3700	Adult	Female	Khoesan
SAM-AP 4188	Adult	Male	Khoesan
SAM-AP 4300	Adult	Female	Khoesan
SAM-AP 4312	Adult	Female	Khoesan
SAM-AP 4314	Adult	Female	Khoesan
SAM-AP 4507	Adult	Female	No Data
SAM-AP 4520	Adult	Male	No Data

SAM-AP 4521	Adult	Female	No Data
SAM-AP 4666	Adult	Indeterminate	No Data
SAM-AP 4756	Adult	Indeterminate	No Data
SAM-AP 4782	Adult	Indeterminate	No Data
SAM-AP 4790	Adult	Male	Khoesan
SAM-AP 4838	Adult	Female	Khoesan
SAM-AP 4840	Adult	Female	Khoesan
SAM-AP 4844	Adult	Female	Khoesan
SAM-AP 4867	Adult	Male	Khoesan
SAM-AP 4874	Adult	Male	Khoesan
SAM-AP 4920a	Adult	Male	Khoesan
SAM-AP 4942	Adult	Male	Khoesan
SAM-AP 5035a	Adult	Male	Khoesan
SAM-AP 5048	Adult	Female	Khoesan
SAM-AP 5050	Adult	Female	Khoesan
SAM-AP 5069	Adult	Female	Khoesan
SAM-AP 5083	Adult	Female	Khoesan
SAM-AP 6044	Adult	Female	Khoesan
SAM-AP 6074	Adult	Female	Khoesan
SAM-AP 6252a	Adult	Female	Khoesan
SAM-AP 6260a	Adult	Female	Khoesan
SAM-AP 6319	Adult	Female	Khoesan
SAM-AP 6331	Adult	Female	Khoesan

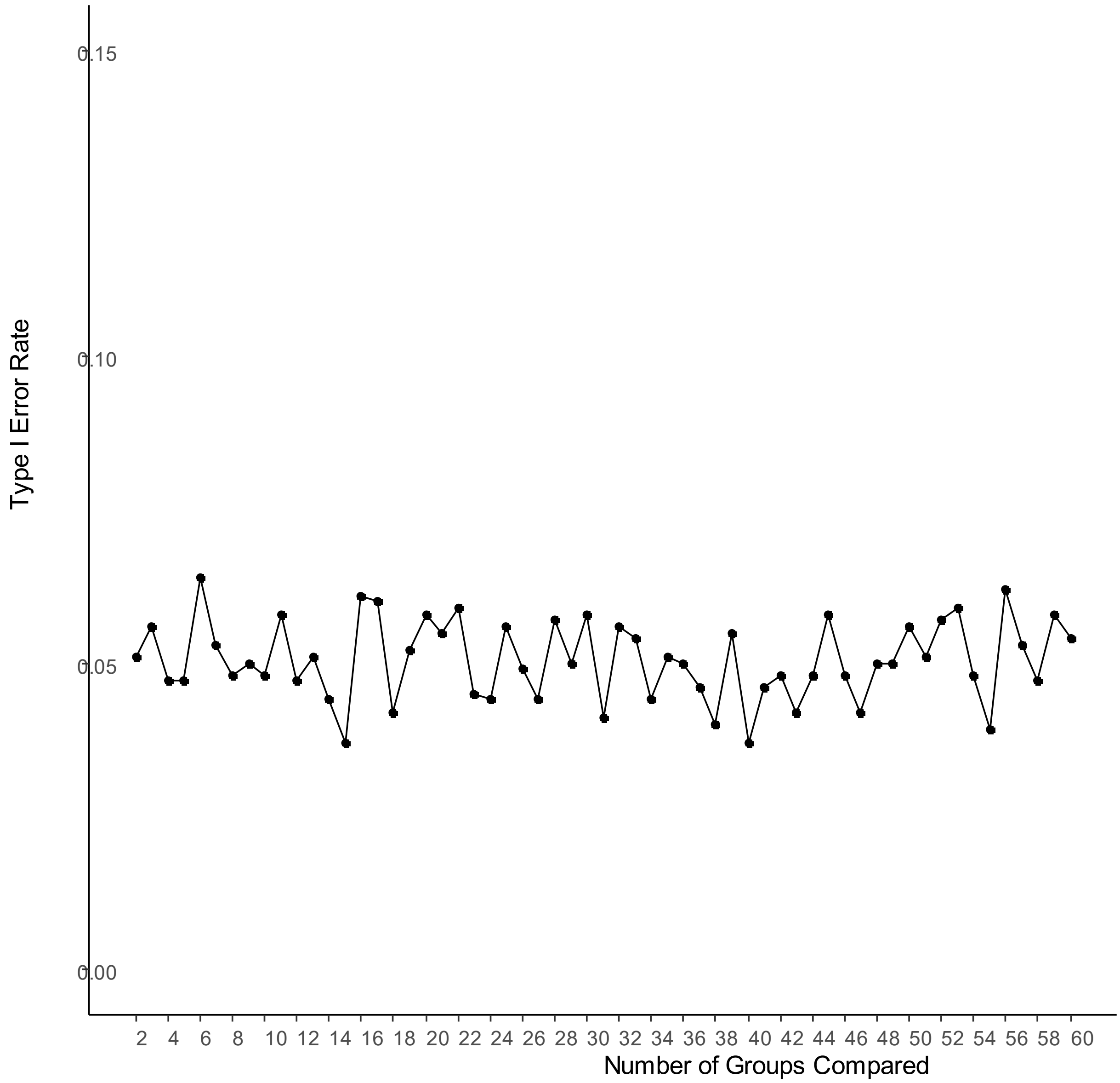

Figure S1. Type I error rate according to the number of groups compared.

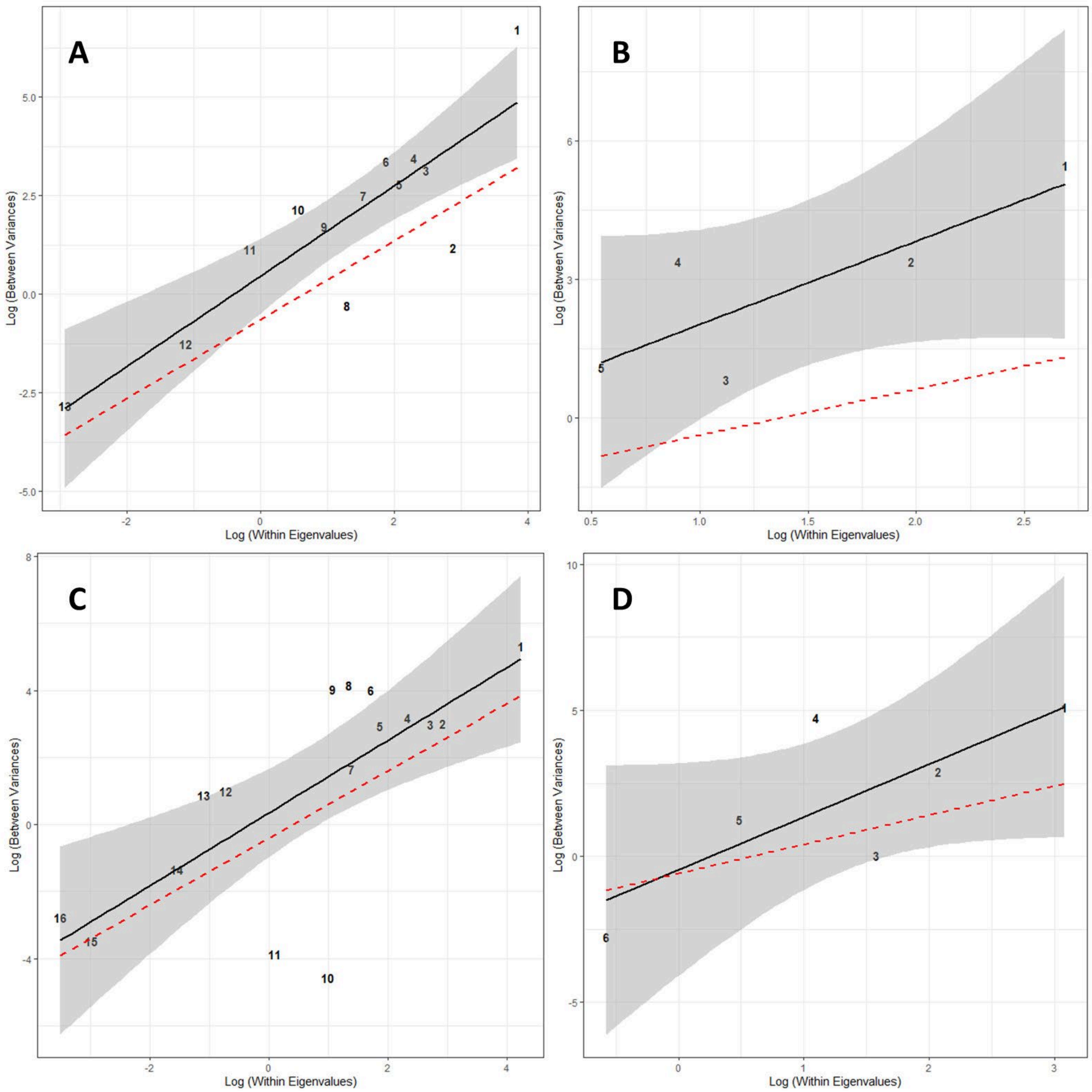

Figure S2. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) Bodo 1 & KNM-ES 11693; B) Bodo 1 & LH 18; C) Bodo 1 & Ndutu; D) Bodo 1 & KNM-ER 3884.

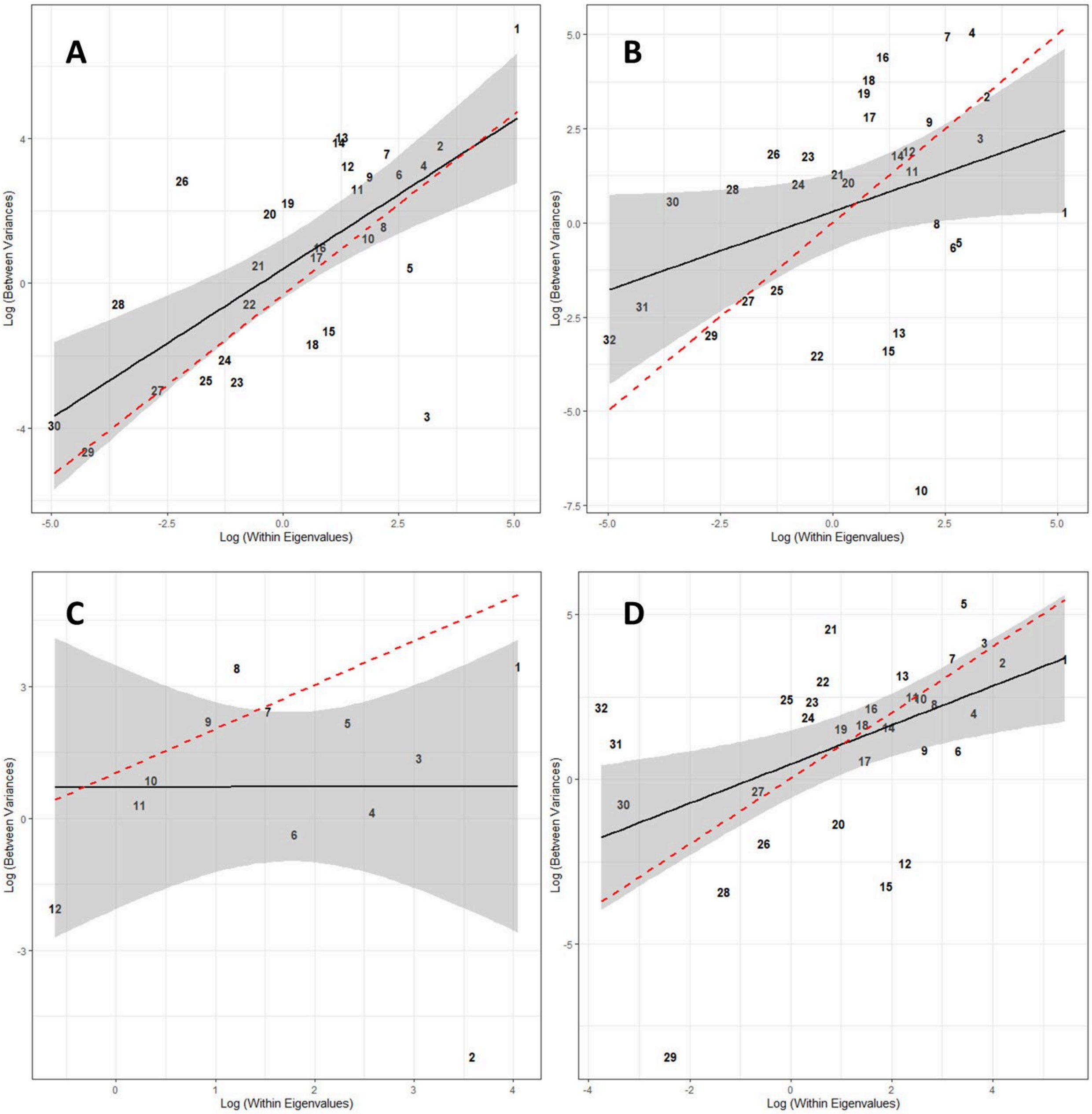

Figure S3. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) Bodo 1 & Irhoud 1; B) Bodo 1 & Kabwe 1; C) Irhoud 1 & KNM-ER 3884; D) Irhoud 1 & KNM-ES 11693.

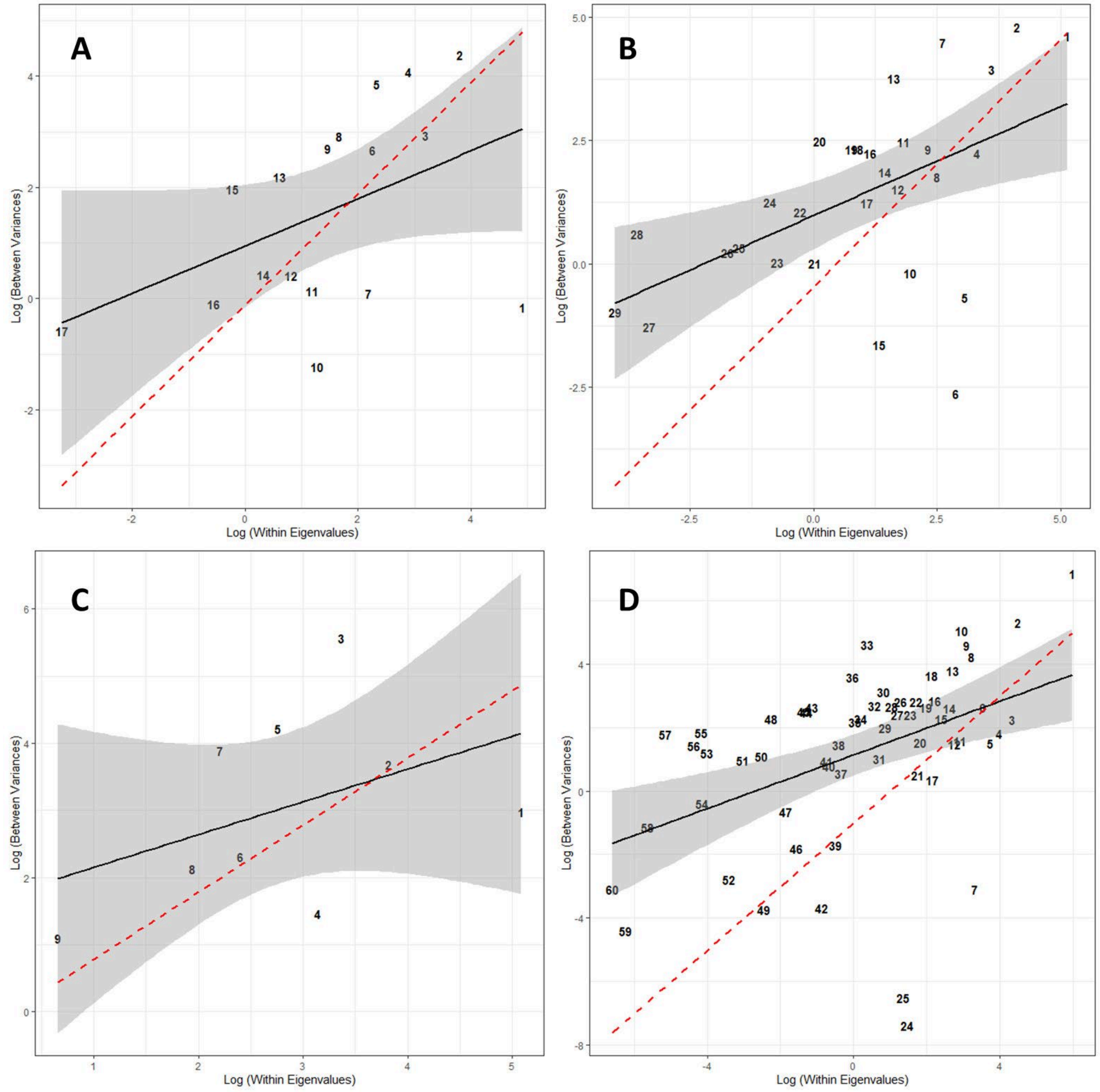

Figure S4. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) Irhoud 1 & LH 18; B) Irhoud 1 & Ndutu; C) Irhoud 1 & SAM-PQ-EH-1; D) Kabwe 1 & Irhoud 1.

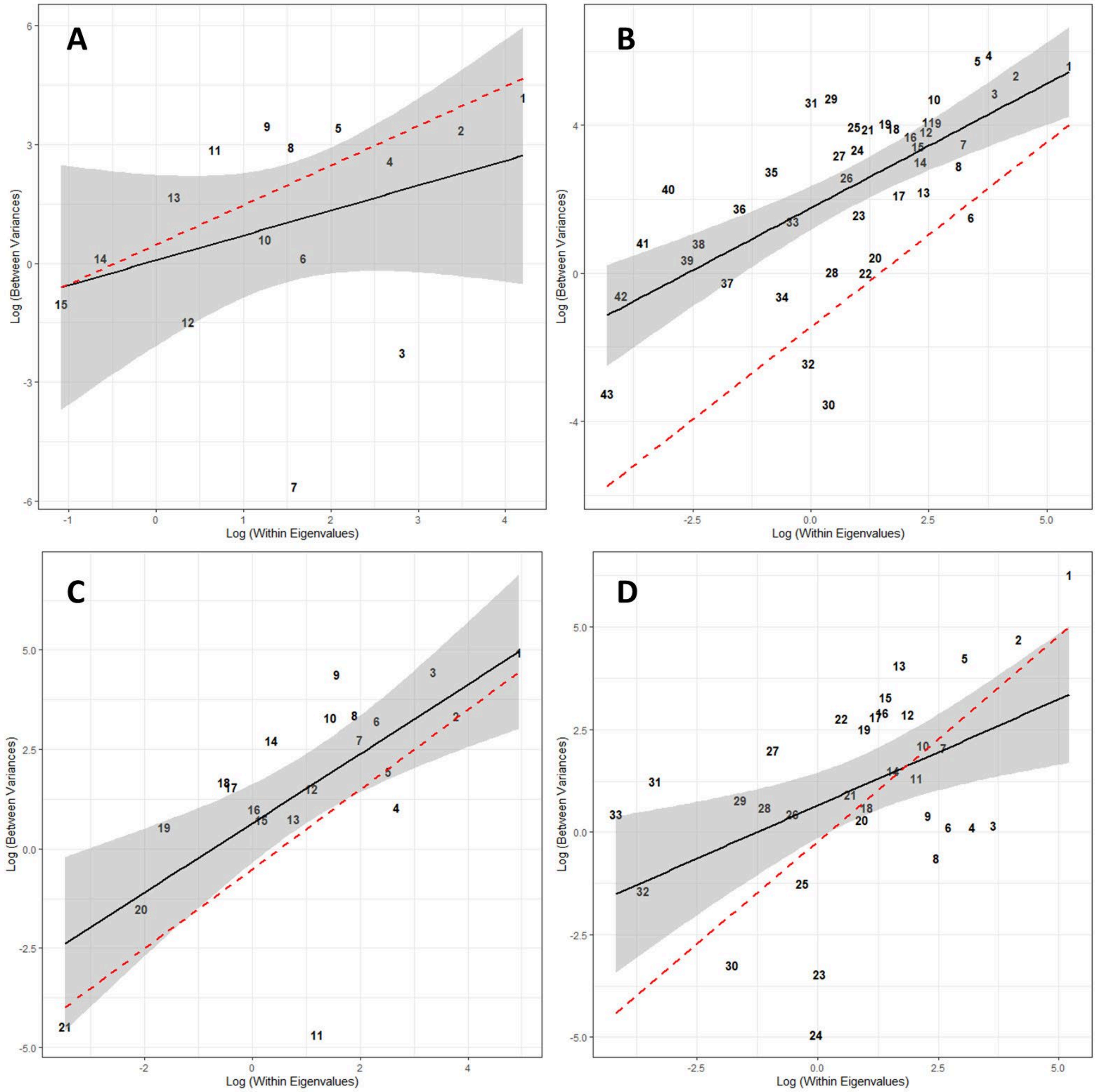

Figure S5. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) Kabwe 1 & KNM-ER 3884; B) Kabwe 1 & KNM-ES 11693; C) Kabwe 1 & LH 18; D) Kabwe 1 & Ndutu.

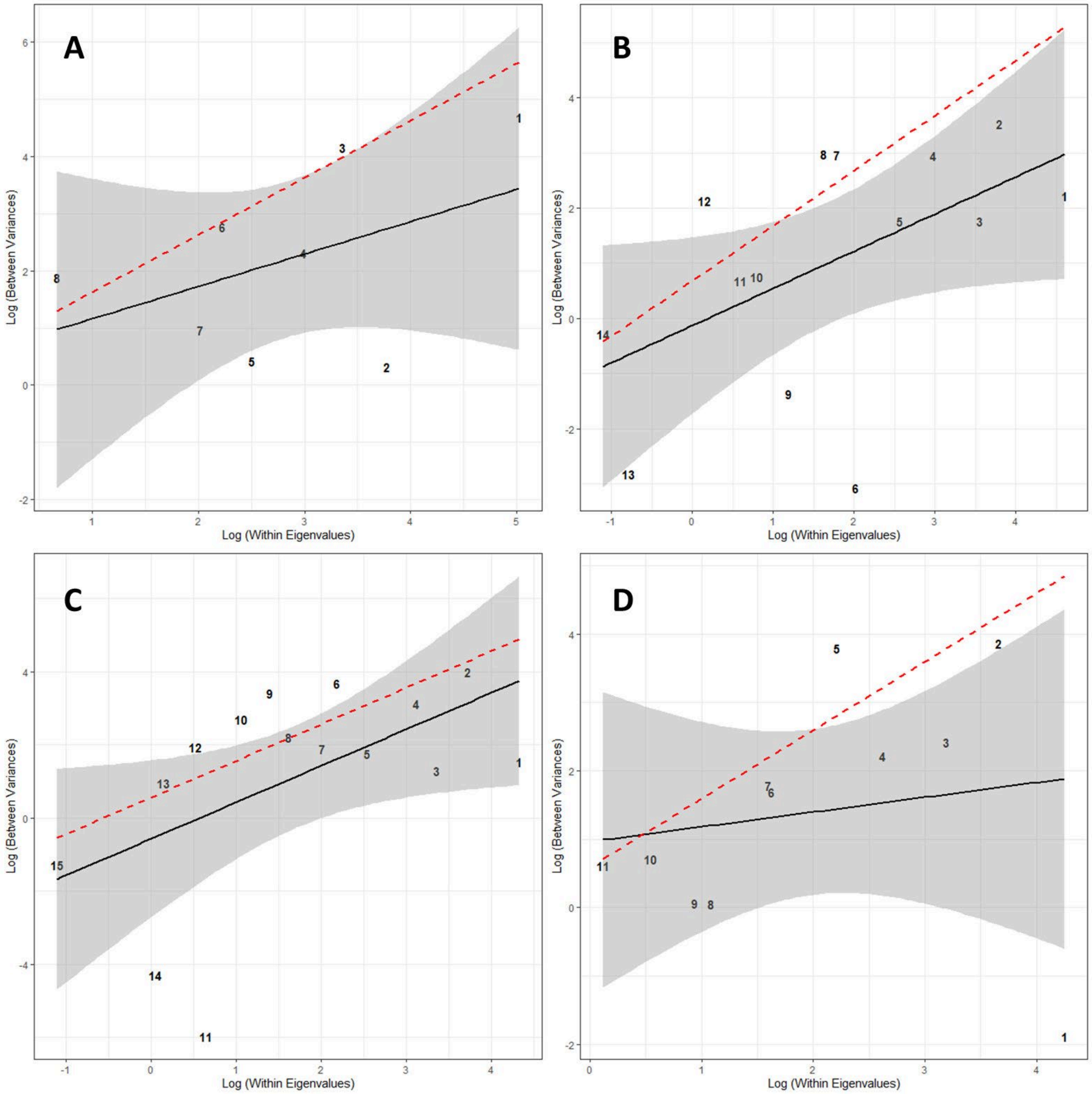

Figure S6. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) Kabwe 1 & SAM-PQ-EH-1; B) KNM-ER 3884 & KNM-ES 11693; C) KNM-ER 3884 & LH 18; D) KNM-ER 3884 & Ndutu.

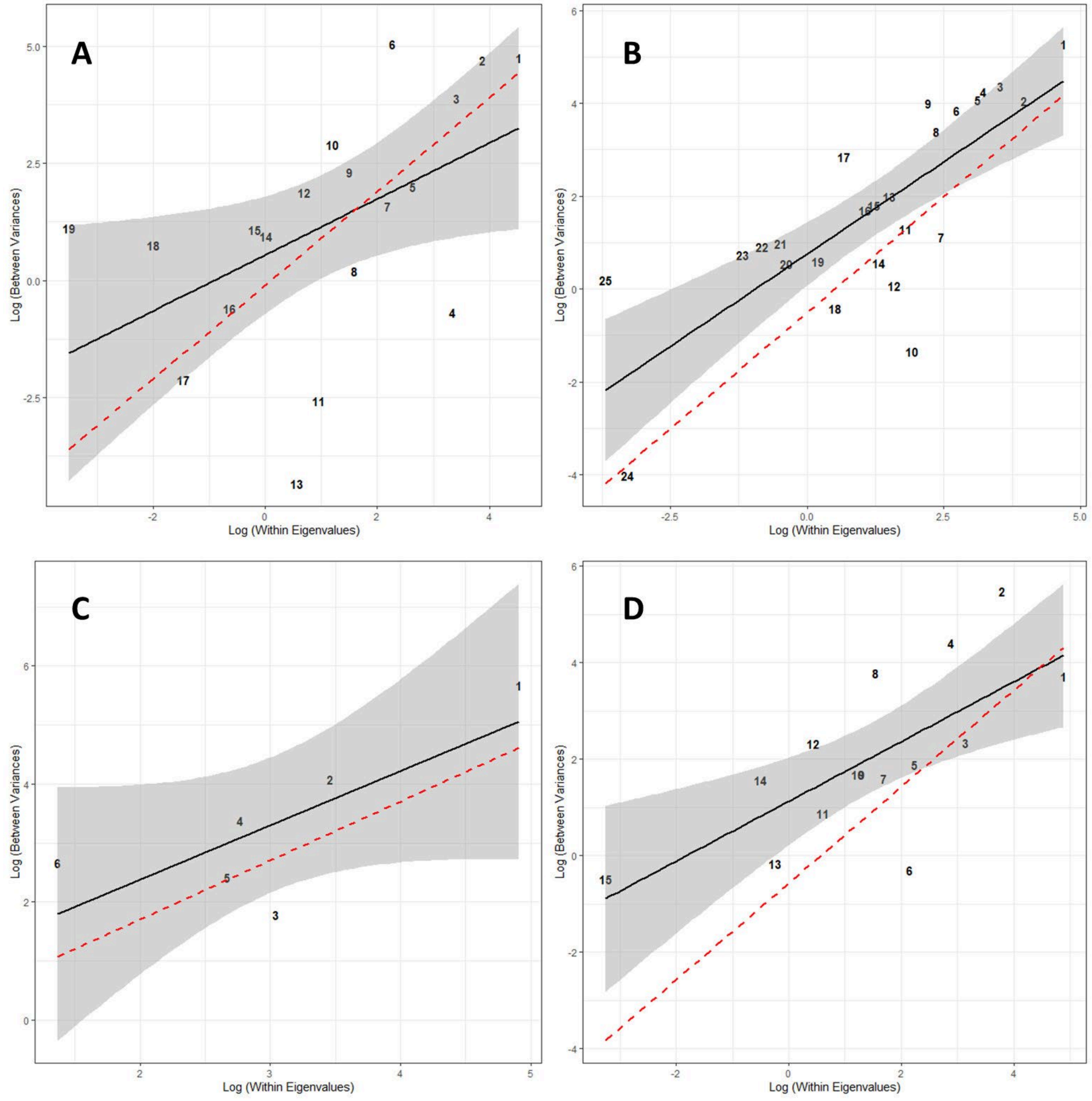

Figure S7. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) KNM-ES 11693 & LH 18; B) KNM-ES 11693 & Ndutu; C) KNM-ES 11693 & SAM-PQ-EH-1; D) LH 18 & Ndutu.

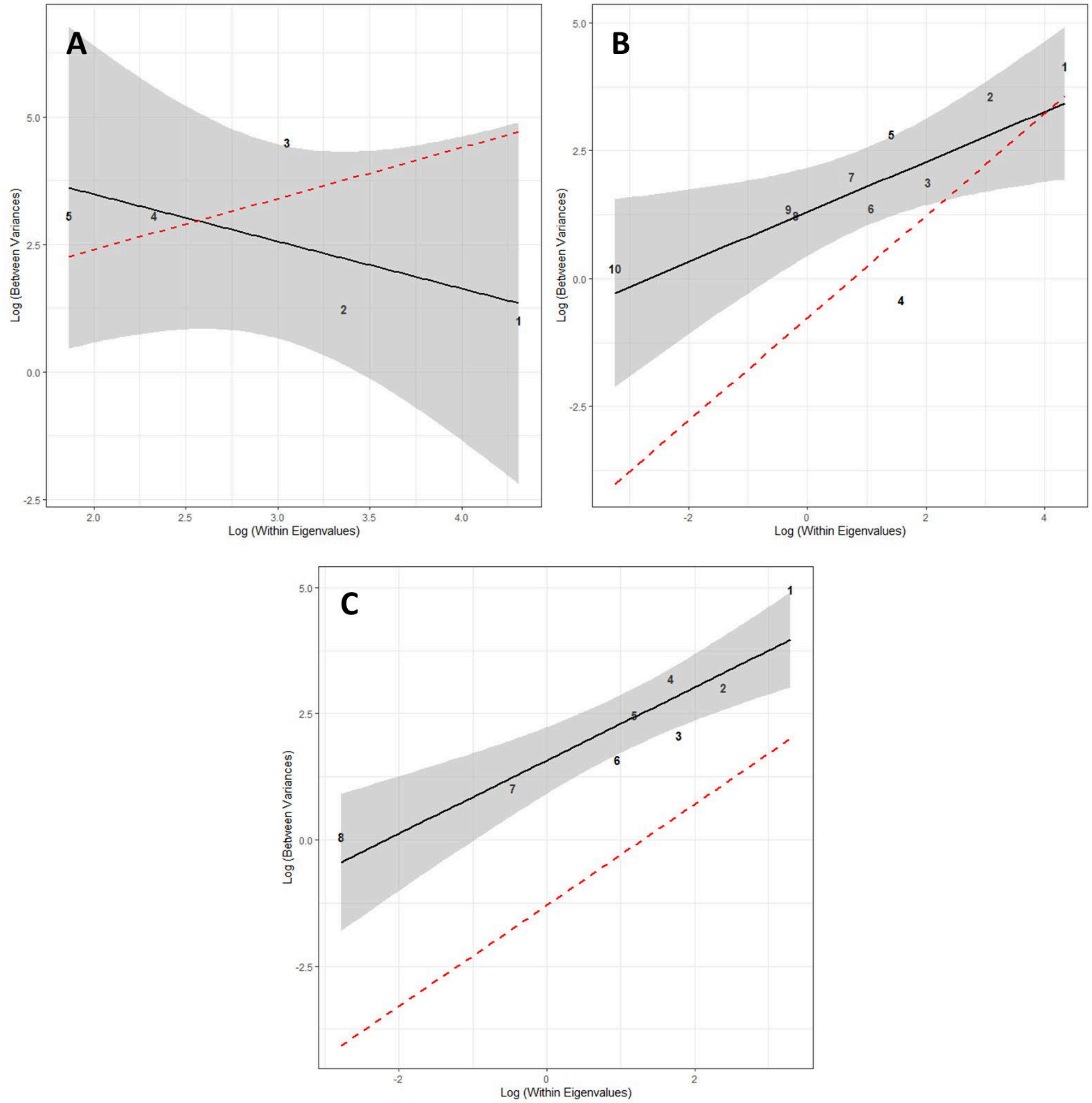

Figure S8. Regression plots of between versus within-group variation. Red dashed line indicates line with slope = 1. A) Ndutu & SAM-PQ-EH-1; B) Within Middle Pleistocene *Homo* (KNM-ES 11693, KNM-ER 3884, Ndutu, LH 18, Irhoud 1, Kabwe 1); C) Within Middle Pleistocene *Homo* (KNM-ES 11693, Bodo 1, Ndutu, Irhoud 1, Kabwe 1).