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## Exploring Diversity of Hunter-Gatherer Behaviour in the European Mid-Upper Palaeolithic:

### The Gravettian Assemblages of Willendorf II and Mitoc-Malu Galben as Case Studies

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#### Résumé

#### Exploration de la diversité du comportement des chasseurs-cueilleurs au Paléolithique moyen-supérieur européen : les assemblages gravettiens de Willendorf II et Mitoc-Malu Galben comme études de cas

Cet article explore la variabilité dans les assemblages lithiques et fauniques au Gravettien. En nous appuyant sur l'utilisation d'indices et de ratios de diversité d'assemblage, nous examinons quels sont les facteurs importants de variabilité dans la culture matérielle. Traditionnellement, le Gravettien est divisé en Gravettien ancien, moyen et récent. Ici, nous considérons le Gravettien dans son ensemble afin d'étudier les changements dans la composition lithique et faunique à partir de deux sites à plusieurs niveaux d'occupation, Willendorf II (Europe centrale) et Mitoc-Malu Galben (Europe orientale). Sur les deux sites, il n'existe aucune tendance générale importante au cours du temps dans la composition lithique ou faunique, et ce, que ce soit d'un point de vue strictement chronologique, ce qui pourrait correspondre à des changements dans les conditions environnementales, ou que ce soit entre les différentes sous-phases définies technologiquement au sein du Gravettien (*i.e.* Gravettien ancien, moyen ou récent). Au contraire, les différences dans la composition lithique ou faunique sont principalement liées à la localisation du site dans le paysage en termes de, par exemple, la qualité de la matière première locale ou le type de terrains de chasse à proximité. Les stratégies d'exploitation de la faune sur les deux sites n'ont pas changé de façon drastique tout au long du Gravettien. De même, il y a peu de changements dans les gisements de matière première localement disponibles. Nous en concluons donc que les changements observés dans l'outillage lithique entre le Gravettien ancien, moyen et récent reflètent des traditions transmises plutôt que des adaptations fonctionnelles. Les deux sites ont été le lieu d'activités spécifiques et il semble probable que celles-ci ont formé la base des différences dans le matériel archéologique retrouvé sur les deux sites. Willendorf II et Mitoc-Malu Galben faisaient probablement partie de systèmes d'occupation plus larges caractérisés par une grande mobilité et des processus de fission / fusion au cours des cycles saisonniers. Le caractère rare et très fragmenté des données archéologiques pour ces chasseurs-cueilleurs gravettiens suggère une grande flexibilité dans le comportement de ces groupes.

Mots-clés : Paléolithique supérieur, Gravettien, Danube moyen, Est des Carpates, diversité comportementale, exploitation de la faune, organisation de la technologie lithique.

#### Abstract

This paper explores variability in Gravettian lithic and faunal assemblages. Using ratios and indices of assemblage diversity we investigate what are the important factors driving variability in material culture. Traditionally the Gravettian is divided in an Early, Middle and Late Gravettian. Here we consider the Gravettian as a whole to investigate changes in lithic and faunal composition drawing on two multi-layered sites, namely Willendorf II in Central Europe and Mitoc-Malu Galben in Eastern Europe. We found that, in our two case-study sites, there are no major trends in either lithic or faunal composition through time or by technologically defined sub-phases of the Gravettian (*i.e.*, Early, Middle and Late Gravettian). Instead, our results suggest differences in lithic and faunal composition are mainly driven by the location of the site in the landscape in terms of *e.g.* the quality of local raw material and the type of adjacent hunting grounds. Faunal exploitation patterns at both sites did not change drastically throughout the Gravettian. Nor did the locally available raw-material out-crops. We, therefore, propose that the observed changes in lithic toolkits between the Early, Middle, and Late Gravettian at Willendorf II and Mitoc-Malu Galben reflect learned traditions or changes in style rather than functional

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adaptations. Both sites were targeted for specific activities and it seems likely that these formed the underpinnings of the differences in archaeological remains recovered at both sites. Willendorf II and Mitoc-Malu Galben were likely part of larger forager settlement systems characterised by high mobility and fission/fusion processes throughout the seasonal cycles. The sparse, highly fragmented character of the Gravettian archaeological record suggests these hunter-gatherers were highly flexible foragers.

Keywords: Upper Palaeolithic, Gravettian, Middle Danube, East Carpathians, behavioural diversity, faunal exploitation, lithic technological organisation.

## 1. Introduction

Studies on variability in hunter-gatherer behaviour are often viewed from chronological and/or geographical phases (e.g. Svoboda *et al.*, 1996; 1999; Klaric, 2007; Moreau, 2012). For example, the Gravettian is usually divided into an Early, Middle, and, Late Gravettian on the basis of lithic and organic typological markers such as flechettes, gravette and microgravette points, Kostenki knives, and organic technology. There also exist stone tool industries that are more restricted in their geographic range or even limited to one or only a handful of sites, as for example the Maisirian in Belgium (de Heinzelin, 1973; Campbell, 1980), the Pavlovian in Moravia (e.g. Svoboda *et al.*, 1996), or even subdivisions of the Pavlovian (e.g. Polanská *et al.*, 2014). Nearly all of those taxonomic units are defined based on typological features (either lithic and organic tool types or types of reduction sequences), and might constitute cultural changes between phases or taxonomic units and as such should inform us about past hunter-gatherer behaviours. While some or all of these features are probably related to human behaviour, their typological nature makes comparisons difficult, because the units of analysis are changing between the named stone tool industries. Here, we take another approach using quantitative measures of past hunter-gatherer behaviour focusing on prey acquisition choices, technological organisation and landscape use (for similar approaches see, e.g. Kelly, 1988; Kuhn, 1991; 1995; Stiner *et al.*, 1992; Roth *et al.*, 1998; Blades, 1999; Blades, 2001; Beck, 2008; Verpoorte, 2009; Surovell, 2012; Moreau *et al.*, 2016; Clark *et al.*, 2017; Barton *et al.*, 2018; Cascalheira *et al.*, 2018). We employ a set of diversity measures to quantify taxonomic heterogeneity and taxonomic dominance in lithic and faunal datasets as well as ratios of cores, blanks, and tools to quantify reduction and retouch intensity. A basic assumption of our study is that prey acquisition choices and landscape use both will have an effect on lithic technology and lithic assemblage structure. Thus we should be able to use the latter two to test hypotheses about prey acquisition choices and landscape use.

Hunter-gatherer mobility influences how humans (or hominins) organise themselves and their activities across time and space, as has been shown by ethnoarchaeological studies in dramatically different environments (e.g. Binford, 1980; Kelly, 1983; Kelly, 1992; Grove, 2009; 2010). In this way mobility affects the organisation of technology and how it structures the archaeological record. There are a number of studies discussing the effects of mobility and landscape-use on specifically lithic technological organisation and the implications for the archaeological record (e.g. Binford, 1980; Kuhn, 1991; 1992; 1995; Surovell, 2012; Kuhn *et al.*, 2016).

Lithic technology and prey acquisition techniques both come with costs and benefits. With regard to lithic technology, the costs are related to procuring, making, using, and maintaining/resharpening lithic objects, but also transporting lithics has costs that might outweigh the benefits of transporting them. These costs will create variation in lithic archaeological datasets. Similarly, prey acquisition strategies have costs and the adapted strategy—regardless if it involves optimisation in caloric or nutritional return or any other currency (e.g. secondary products like antler, hides, etc.)—will shape the composition of faunal datasets and introduce variation in the archaeological record.

In this study, which we consider as a pilot study showcasing the approach on a limited dataset, we conduct our analyses on nine assemblages originating from two sites that cover the duration of the Gravettian technocomplex, namely Willendorf II in Central Europe and Mitoc-Malu Galben in Eastern Europe (fig. 1a). The two sites, located in the Middle Danube region (Willendorf II) and the East Carpathian region (Mitoc-Malu Galben), were selected because they are multi-layered sites with high-resolution stratigraphic and archaeological records and each of them has at least four archaeological horizons and as such spanning a large proportion of the Gravettian as a whole (fig. 1b and 1c). Both sites are in bottom slope positions and similar sedimentary dynamics were at work during their formation, thus keeping the sedimentary context and deposition of the archaeology at the two sites quite similar as opposed to when comparing, e.g.

with cave sites. In addition, from both sites detailed studies on both fauna and lithics are fully published, and, thus, make the data necessary for our case study available and accessible (fauna: Thenius, 1959; López Bayón et Gautier, 2007; Noiret, 2009; lithics: Felgenhauer, 1959; Otte, 1981; 1990; Otte *et al.*, 2007; Moreau, 2009; 2010; 2012; Noiret, 2009; Moreau *et al.*, 2016).

Specifically, we aim to explore the following questions:

- In what ways are lithic and faunal diversity measures different between Willendorf II and Mitoc-Malu Galben?
- Are changes in lithic and fauna diversity related to relative assemblage age?
- Are lithic and fauna diversity changing between Early, Middle, and Late Gravettian? If yes, in what ways are they different?
- What are the implications for our understanding of Late Pleistocene forager land-use and settlement systems?

Pursuing these research questions requires datasets on lithic and faunal collections of Willendorf II and Mitoc-Malu Galben. We used fully published datasets (tbl. 1) from both sites and, therefore, focus this study on the earlier excavations at both sites, as not all materials from the most recent excavations (*e.g.* Nigst *et al.*, 2014; 2021; Noiret *et al.*, 2016) are available for analysis.

At the outset of this study we should highlight that the research presented here is part of a larger project and should be considered a pilot study exploring the approach on a small dataset. As such, the research has limitations that we want to briefly mention here—we discuss them in more detail in the following sections. One of the biggest limitations is that our nine assemblages originate from only two sites. They might have been used in similar ways, and, hence, limiting our sampling of and inferences about Mid-Upper Palaeolithic forager land-use and settlement systems as well as prey acquisition strategies.

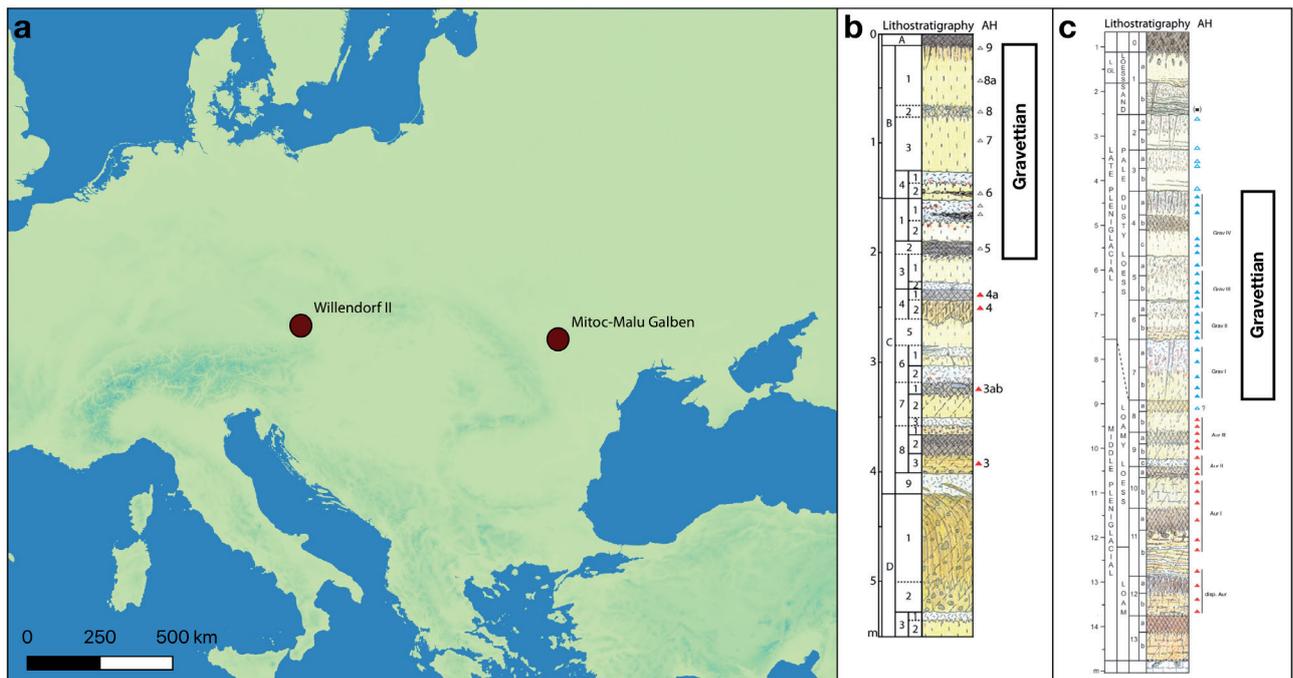


Fig. 1 – a: Map showing the location of Willendorf II and Mitoc-Malu Galben. Base map using GTOPO30 HYDRO1K dataset provided by U.S. Geological Survey’s Center for Earth Resources Observation and Science.  
 b: Stratigraphic log of the Willendorf II sequence (drawing: P. Haesaerts, modified after Nigst *et al.*, 2014): The Gravettian part of the sequence is highlighted.  
 c: Stratigraphic log of the Mitoc-Malu Galben sequence (drawing: P. Haesaerts, modified after Haesaerts *et al.*, 2009): The Gravettian part of the sequence is highlighted.

Site	AH	Culture	Relative age information from	Lithic data from	Fauna data from
Mitoc-Malu Galben	Grav I	Middle Gravettian	Haesaerts, 2007; Haesaerts <i>et al.</i> , 2010	Otte <i>et al.</i> , 2007	López Bayón and Gautier 2007
Mitoc-Malu Galben	Grav II	Middle Gravettian	Haesaerts, 2007; Haesaerts <i>et al.</i> , 2010	Otte <i>et al.</i> , 2007	López Bayón and Gautier 2007
Mitoc-Malu Galben	Grav III	Middle Gravettian	Haesaerts, 2007; Haesaerts <i>et al.</i> , 2010	Otte <i>et al.</i> , 2007	López Bayón and Gautier 2007
Mitoc-Malu Galben	Grav IV	Late Gravettian	Haesaerts, 2007; Haesaerts <i>et al.</i> , 2010	Otte <i>et al.</i> , 2007	López Bayón and Gautier 2007
Willendorf II	AH 5	Early Gravettian	Haesaerts <i>et al.</i> , 1996; Nigst <i>et al.</i> , 2014	Otte, 1981	Thenius, 1959
Willendorf II	AH 5+box	Early Gravettian	Haesaerts <i>et al.</i> , 1996; Nigst <i>et al.</i> , 2014	Moreau <i>et al.</i> , 2016	-
Willendorf II	AH 6	Middle Gravettian	Haesaerts <i>et al.</i> , 1996; Nigst <i>et al.</i> , 2014	Otte, 1981	Thenius, 1959
Willendorf II	AH 7	Middle Gravettian	Haesaerts <i>et al.</i> , 1996; Nigst <i>et al.</i> , 2014	Otte, 1981	Thenius, 1959
Willendorf II	AH 8	Middle Gravettian	Haesaerts <i>et al.</i> , 1996; Nigst <i>et al.</i> , 2014	Otte, 1981	Thenius, 1959
Willendorf II	AH 9	Late Gravettian	Haesaerts <i>et al.</i> , 1996; Nigst <i>et al.</i> , 2014	Otte, 1981	Thenius, 1959

Table 1 – List of assemblages analysed with references. Abbreviations: AH: Archaeological horizon.

## 2. Sites and Materials

### 2.1. Site backgrounds

Willendorf II (WII; 48° 19' 23.50" N, 15° 24' 15.20" E) is an open-air site located on the left bank of the Middle Danube river. Embedded in a ~6m deep loess-palaeosol sequence (fig. 1b) are at least 11 archaeological horizons (AH), including Early and Mid-Upper Palaeolithic assemblages (Haesaerts *et al.*, 1996; Nigst *et al.*, 2014). Most of the site was excavated in several phases between 1908 and 1955. Later, in the 1980s and 1990s, fieldwork was focused on stratigraphy and environmental context of the archaeology (Haesaerts, 1990; Haesaerts *et al.*, 1996). New fieldwork has been undertaken between 2006 and 2011 (Nigst *et al.*, 2007; 2008a; 2008b; 2008c; 2011a; 2011b; 2012; 2014). The chronostratigraphic framework of the site rests on a detailed stratigraphic sequence and more than 50 radiocarbon dates produced on charcoal samples dated by the Groningen and Oxford radiocarbon laboratories, placing the sequence between 48 ka and 25 ka BP (~55–29 ka cal BP) (Nigst *et al.*, 2014).

For this study the upper part of the sequence including AH 5 to AH 9, dated to between 30,5 ka and 25 ka BP (~35,5–29 ka cal BP), is of interest (fig. 1b). The assemblages of AH 5 to AH 9 are attributed to

the Mid Upper Palaeolithic, the Gravettian, including with AH 5 an Early Gravettian, with AH 6 to AH 8 Middle Gravettian, and with AH 9 a late Gravettian.

Mitoc-Malu Galben (MMG; 48° 05' 52" N, 27° 01' 23" E) is also an open-air site with a long loess-palaeosol sequence. It is situated in the Prut valley in north-eastern Romania. Within the ~14m deep sequence (fig. 1c), a multitude of archaeological horizons has been documented (Haesaerts, 2007), grouped by the initial excavators into 9 layers or phases. Most of the site was excavated between 1978 and 1990 by V. Chirica with additional fieldwork carried out between 1991 and 1995 by a Romanian-Belgian team (Chirica, 2001; Otte *et al.*, 2007). More recently, fieldwork at Mitoc-Malu Galben has been conducted between 2013 and 2016 by a Romanian-Belgian-British team (Chirica *et al.*, 2014; 2015; 2016; Noiret *et al.*, 2016; Libois *et al.*, 2017; 2018; Nigst *et al.*, 2021). The chronostratigraphy of the sequence is based on the stratigraphic record and more than 40 radiocarbon dates (Haesaerts, 2007).

Here, the Gravettian phases in the upper part of the sequence are included in our study (fig. 1c), namely the phases Grav I to Grav IV. Grav I to Grav III represent Middle Gravettian, while Grav IV is classified as Late Gravettian (Otte *et al.*, 2007).

## 2.2. Materials

The assemblages of MMG and WII used in this study are from the earlier excavations at the two sites. The five WII assemblages used here were excavated between 1908 and 1955. Already during the 1908 and 1909 excavations the materials were curated by archaeological horizon (Felgenhauer, 1959; Haesaerts *et al.*, 1996; Antl-Weiser, 2008; Nigst, 2012; Moreau *et al.*, 2016). The four MMG assemblages utilized in our research were excavated between 1978 and 1995. They have been mostly recorded by depth and assigned to stratigraphic units based on the 1991-1995 stratigraphic work (Haesaerts, 2007). We collected the data from Otte *et al.* (2007) and used the archaeological layers (*i.e.*, Grav I to Grav IV) defined by the excavators (Otte *et al.*, 2007). Some of these layers span more than one stratigraphic unit.

WII AH 5 is attributed to the Early Gravettian and comprises ~700 lithics and 42 fauna specimens (tabl. 2 and 3). AH 6 to AH 8 are Middle Gravettian with similar lithic and bone recovery. The Late Gravettian AH 9 has provided ~2580 lithics and 195 fauna specimens. Detailed descriptions of the lithic tool types, technological sequences, and fauna are fully published (fauna: Thenius, 1959; lithics: Felgenhauer, 1959; Otte, 1981; Otte, 1990; Moreau, 2009; 2010; 2012; Moreau *et al.*, 2016). In MMG

there is no Early Gravettian present, Layers Grav I to Grav III are attributed to the Middle Gravettian. The lithic datasets of those layers comprise between ~2200 and ~2900 pieces and the Number of Identified Specimens (NISP) of all fauna ranges from 11 to 74. Layer Grav IV is a Late Gravettian with ~11,450 lithics and, with regard of the fauna, a NISP of 139 (tabl. 2 and 3). The faunal and lithic datasets are fully described and published (fauna: López Bayón *et al.*, 2007; Noiret, 2009; lithics: Otte *et al.*, 2007; Noiret, 2009). Fauna is poorly preserved at both WII and MMG, but the material was kept and studied in detail.

Assemblage	n lithics	n cores	n blanks	n tools
MMG-Grav I	2263	57	2170	36
MMG-Grav II	3756	42	3633	81
MMG-Grav III	2922	67	2814	41
MMG-Grav IV	11469	295	11064	110
WII-AH5	706	23	556	127
WII-AH5+box	2308	66	1970	272
WII-AH6	310	24	221	65
WII-AH7	488	30	318	140
WII-AH8	1425	78	915	432
WII-AH9	2586	75	1715	796

Table 2 – Lithic raw data used in the analysis.  
Abbreviations: AH: Archaeological horizon, WII: Willendorf II, MMG: Mitoc-Malu Galben.

## 3. Methods

Differences in taphonomic history between sites and individual archaeological horizons may have resulted in differential faunal preservation which would indicate a post-depositional preservation bias in the faunal material that may have affected lithics as well. Before comparing assemblages statistically, it first has to be established if these potential differences could significantly influence the results (Grayson, 1984).

To this end we tested the relation between NISP and Minimum Number of Individuals (MNI) carrying out a best-fit regression analysis between logNISP to logMNI using Pearson's correlation coefficient (as the values are not ranked). A significant correlation suggests a similar taphonomic history for all assemblages, which, in turn, would warrant comparison.

The approach applied in this study quantifies variation in lithic and faunal datasets by using a number of diversity indices and ratios. With regard of faunal exploitation strategies, we employ diversity indices on the total faunal assemblage as well as on subsets such as taxa exploited for subsistence purposes (*e.g.* horse, bison, rhinoceros, mammoth, red

deer, reindeer, roe deer, and ibex), or for their fur (*e.g.* bear, wolf, arctic and red fox and hare). In the analysis of lithic artefacts, we look at the diversity of basic lithic categories (cores, blanks, and tools), lithic reduction intensity and retouch intensity.

In our analysis of faunal assemblage composition and diversity, we use taxonomic heterogeneity (H; Shannon/Shannon-Wiener index of diversity; Shannon, 1948; Spellerberg *et al.*, 2003; Magurran, 2004; Lyman, 2008) and taxonomic dominance (1/D; inverse Simpson index of diversity; Simpson, 1949; Magurran, 2004; Lyman, 2008). Both indices describe assemblage composition, but with subtle differences. The Shannon index focusses on the evenness in the distribution of all taxa, while inverse Simpson's index places emphasis on frequently exploited taxa (Lyman, 2008). The larger the value of H, the greater is the taxonomic heterogeneity. The higher the 1/D value the more evenly species are distributed, whereas low values signify dominance by one or few species.

Lithic diversity here is used to describe the composition of the assemblages with regard of the major, basic lithic categories, *i.e.*, cores, blanks, and tools (Glauberman, 2016). As with faunal diversity we use

H and 1/D to explore lithic diversity. As with ratios of reduction intensity, these diversity indices quantify assemblage composition which to a large degree is related to landscape use and technological organisation. Core reduction intensity is analysed utilising blank/core ratio and tool/core ratio, while retouch intensity is assessed using tool/blank ratio and tool/core ratio (e.g. Kuhn, 1991; 1992; 1995; Stiner et Kuhn, 1992; Blades, 1999; 2001).

All statistical analysis has been conducted in R 3.5.3 (R Core Team, 2019). For bootstrapping we used the R package boot (Davison et Hinkley, 1997; Canto et Ripley, 2017), graphics were produced using the R packages ggplot2 (Wickham, 2016) and cowplot (Wilke, 2019). Diversity indices were calculated using the R package vegan (Oksanen *et al.*, 2019).

As test for normality we employed Shapiro-Wilk test (Royston, 1982a; 1982b; 1995). Correlation between the used variables and sample size was tested employing Pearson's correlation coefficient

(Hollander et Wolfe, 1973; Lyman, 2008; Kloke et Mckean, 2015). As a number of our ratios/indices were not normally distributed, we used bootstrapping (Davison and Hinkley, 1997) to calculate nonparametric confidence intervals (adjusted bootstrap percentile (BCa) intervals (Carpenter et Bithell, 2000)) for Pearson's correlation coefficient. For testing correlation between ratios/indices and ranked data (like the relative chronological position), we used Spearman's rank correlation coefficient (Hollander *et al.*, 2014; Kloke et Mckean, 2015). To compare continuous variables of two samples we used Wilcoxon (Mann-Whitney U) test and of three or more samples Kruskal-Wallis test (Hollander et Wolfe, 1973; Kloke et Mckean, 2015). For our analysis of lithic and faunal diversity indices and ratios we also employed general linear models with one or more fixed effects (Chambers, 1992; Gelman et Hill, 2007).

Species	Type	MMG				WII				
		Grav I	Grav II	Grav III	Grav IV	AH5	AH6	AH7	AH8	AH9
<i>Mammuthus primigenius</i>	meat	0	5	1	2	2	0	3	1	6
<i>Coelodonta antiquitatis</i>	meat	0	0	0	4	0	0	0	0	0
<i>Equus sp.</i>	meat	7	23	40	64	0	0	0	4	9
<i>Bos taurus/Bison priscus</i>	meat	2	3	24	48	0	0	2	0	2
<i>Capra ibex</i>	meat	0	0	0	0	11	2	0	20	51
<i>Ovicaprid</i>	meat	0	0	0	0	0	0	0	0	1
<i>Megaloceros giganteus</i>	meat	0	0	1	1	0	0	0	0	0
<i>Cervus elaphus</i>	meat	0	0	0	0	2	0	0	2	8
<i>Rangifer tarandus</i>	meat	2	10	8	20	18	4	4	3	15
<i>Lepus sp.</i>	fur	0	0	0	0	3	0	0	1	0
<i>Aves</i>	-	0	0	0	0	0	0	0	0	2
<i>Ursus arctos</i>	fur	0	0	0	0	2	1	1	0	3
<i>Panthera spelaea</i>	fur	0	0	0	0	1	1	0	4	2
<i>Canis lupus</i>	fur	0	0	0	0	1	1	1	1	10
<i>Vulpes vulpes</i>	fur	0	0	0	0	2	0	1	1	38
<i>Vulpes alopex</i>	fur	0	0	0	0	0	0	0	0	46
<i>Gulo gulo</i>	fur	0	0	0	0	0	0	0	0	2
MNI total	-	5	11	18	30	14	5	8	11	52
NISP total	-	11	41	74	139	42	9	12	37	195
NISP fur	-	0	0	0	0	9	3	3	7	101
NISP meat	-	11	41	74	139	33	6	9	30	92

Table 3 – Faunal raw data used in the analysis. Number of Identified Specimens (NISP) of the individual species and animals exploited for meat and fur as well as Minimum Number of Individuals (MNI) and NISP for all species. Abbreviations: AH: Archaeological horizon, WII: Willendorf II, MMG: Mitoc-Malu Galben.

Assemblage	blank/core ratio	tool/blank ratio	tool/core ratio	H lithics	1/D lithics	H fauna	1/D fauna	H meat	1/D meat
MMG-Grav I	38,070	0,017	0,632	0,199	1,087	0,908	2,123	0,908	2,123
MMG-Grav II	86,500	0,022	1,929	0,165	1,068	1,116	2,535	1,116	2,535
MMG-Grav III	42,000	0,015	0,612	0,183	1,077	1,055	2,442	1,055	2,442
MMG-Grav IV	37,505	0,010	0,373	0,173	1,074	1,202	2,833	1,202	2,833
WII-AH5	24,174	0,228	5,522	0,608	1,530	1,660	3,737	1,037	2,404
WII-AH5+box	29,848	0,138	4,121	0,489	1,345	-	-	-	-
WII-AH6	9,208	0,294	2,708	0,767	1,792	1,427	3,522	0,637	1,800
WII-AH7	10,600	0,440	4,667	0,809	1,958	1,633	4,500	1,061	2,793
WII-AH8	11,731	0,472	5,538	0,805	1,972	1,565	3,049	1,063	2,093
WII-AH9	22,867	0,464	10,613	0,738	1,868	2,019	5,681	1,373	2,810

Table 4 – Shannon (H) and inverse Simpson (1/D) indices and ratios used in the analysis. Abbreviations: AH: Archaeological horizon, WII: Willendorf II, MMG: Mitoc-Malu Galben.

#### 4. Results and Discussion

Table 4 presents the calculated ratios and diversity indices for faunal and lithic datasets.

##### 4.1. Exploring potential bias through excavation and preservation

We identified three possible sources of bias for the assemblages under study namely a potential lack of sieving leading to underrepresentation of smaller specimens, collection bias during excavation/curation leading to overrepresentation of identifiable/characteristic specimens, and difference in taphonomic history of the assemblages that might hamper comparability of (especially faunal) assemblages.

##### 4.1.1. Underrepresentation of small fraction

While WII—compared to MMG—is the older excavation (the sample used here originates in its vast majority from the 1908 and 1909 excavations) and, therefore, often by default assumed to be missing smaller elements (size-bias), records in the Natural History Museum Vienna show that during the 1908 and 1909 excavations sometime sieving was employed, sometimes not (Antl-Weiser, 2008). Interestingly, Moreau (2009) argues based on a comparison of the size distribution of projectiles from WII AH 5 and Geissenklösterle AH I, where excavations employed sieving throughout, that the relatively high proportion of small projectiles at WII AH 5 is a good indicator for sieving during the excavation of AH 5. In sum, this suggests that some of the assemblages are probably biased by an underrepresentation of smaller specimens, but the question is to what degree, as for example it is unknown whether specific archaeological horizons were sieved while others were not.

On the other hand, neither the 1978-1990 excavations nor the 1991-1995 excavations at MMG employed sieving (Otte *et al.*, 2007), and, hence, are both biased against the small fraction. However, the presence of some small lithic objects, including fragments of microgravettes and backed bladelets, in both the WII and MMG collections (WII: Felgenhauer, 1959; Otte, 1981; Moreau, 2009; MMG: Otte *et al.*, 2007) suggests the excavation methods were similarly thorough and the bias in small material recovery was potentially comparable for both sites.

##### 4.1.2. Overrepresentation of tools and cores (or ‘interesting’ pieces)

The WII assemblages of AH 5 to AH 9 described by Otte (1981) comprise a curated selection of the entire excavated material by the original excavators in 1908 and 1909. About twenty years after Otte’s publication, boxes with additional, typologically less interesting lithic materials were located in the storage of the Natural History Museum in Vienna (Nigst, 2004; 2012; Antl-Weiser, 2008; Nigst *et al.*, 2014; Moreau *et al.*, 2016). Moreau *et al.* (2016) re-analysed AH 5 including the additional material from the box (hereafter AH 5+box). To test the extent of curatorial bias, we compare all the ratios and indices used in this paper between the AH 5 and AH 5+box assemblages (tabl. 4 and fig. 2). There is a substantial difference in the blank/core ratio between AH 5 and AH 5+box, where the latter has more blanks per core (tabl. 4 and fig. 2e). The tool/blank ratio (tabl. 4 and fig. 2d) also shows substantial difference between AH 5 and AH 5+box, including the lithics from the storage box results in fewer tools per blank. In both cases the WII AH 5+box values are in the range of the other WII values. The same is true for the H and 1/D values (tabl. 4 and fig. 2a and 2b).

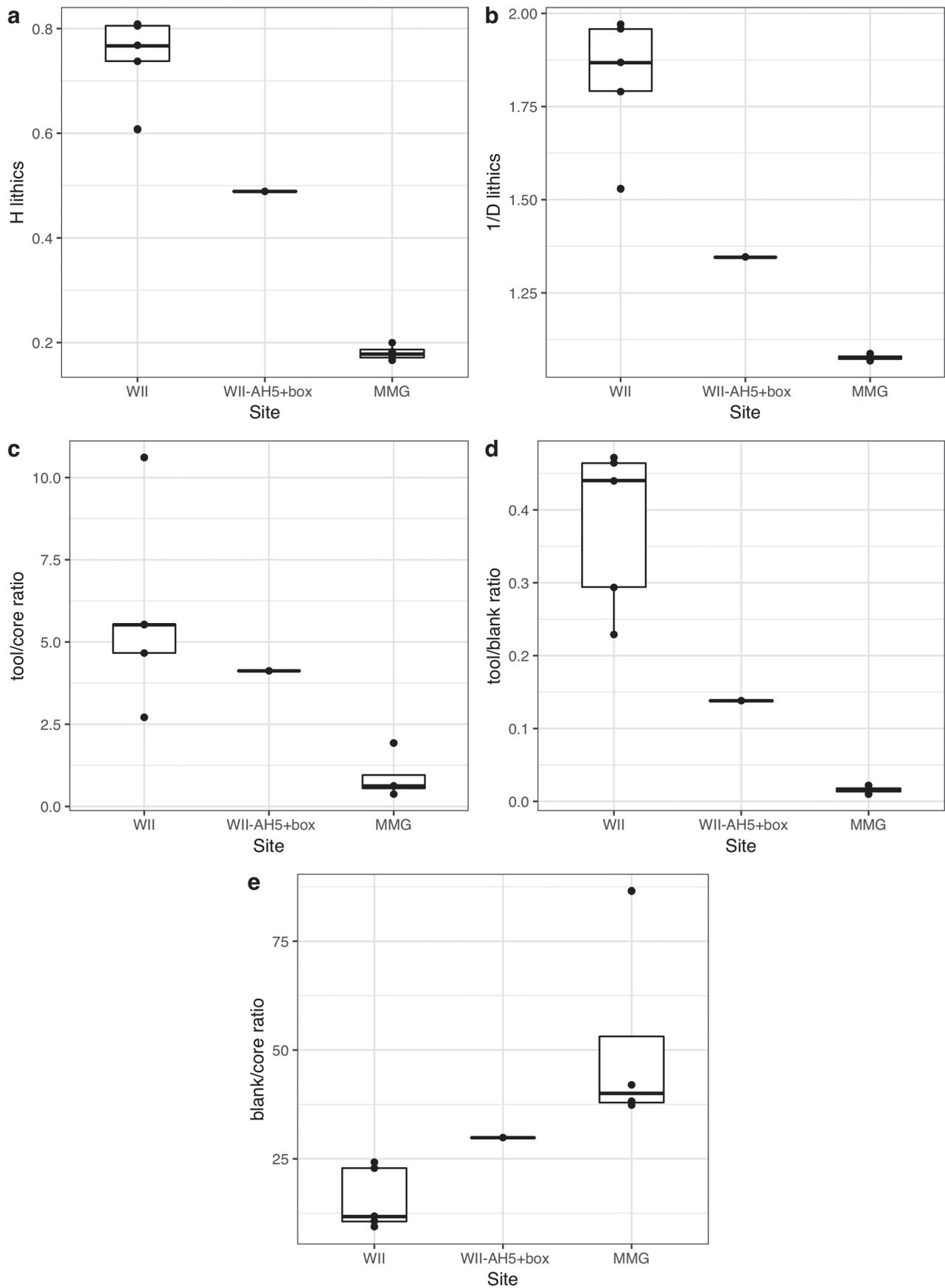


Fig. 2 – Comparison of lithic diversity indices (a-b) and ratios (c-e) between the assemblages of Willendorf II (WII), of Mitoc-Malu Galben (MMG), and the enlarged Willendorf II- AH 5+box assemblage (WII-AH5+box).  
Abbreviations: H: Shannon index of diversity, 1/D: inverse Simpson index of diversity.

Overall, the patterns described suggest that there is some bias in the WII assemblages not including the storage box materials. Because the boxes of AH 6 to AH 9 are not analysed yet, we need to limit our study to the assemblages without the storage box materials.

With regard of the tool/core ratio, there is a difference between AH 5 and AH 5+box, but the AH 5+box value remains within the range of the other WII tool/core ratios. Therefore, despite the fact that the WII materials used here originate from the old excavations and we, in turn, might expect an over-representation of tools and cores (curatorial bias), we can—based on the above described patterns—assume that the tool/core ratio is least affected by the curatorial bias.

#### 4.1.3. Comparability of assemblages using faunal data

Faunal preservation at both sites leaves a lot to be desired. Differences in taphonomic history between sites and individual archaeological horizons may have resulted in differential preservation rendering them unsuitable for comparative purposes. Faunal remains, which are of course more prone to diagenetic biases than stone tools, are ideally suited to identify such differences in preservation and assess compatibility of assemblages. The significant correlation between logNISP and logMNI across all MMG and WII faunal assemblages ( $r=0.985$ ,  $t=5.03$ ,  $df=7$ ,  $p<0.01$ ) suggests that they are interrelated in a consistently similar way and can therefore be compared.

#### 4.2. Sample size effects

In order to test whether ratios and diversity indices are driven by sample size, we investigated whether they are correlated to the total number of lithics or

fauna using Pearson’s correlation coefficient. The total number of lithics ( $n$  lithics), all lithic diversity indices and all ratios except the tool/core ratio are not normally distributed (tabl. 5), therefore we used bootstrapping to calculate nonparametric confidence intervals (adjusted bootstrap percentile (BCa) intervals) for Pearson’s correlation coefficient to test the correlation between sample size and the ratios and indices. None of the diversity indices and ratios are significantly correlated to sample size ( $n$  lithics) (tabl. 6). The diversity indices for overall fauna and the subset of meat-based exploitation are normally distributed, while  $n$  fauna is not normally distributed (tabl. 5). Bootstrapped confidence intervals for Pearson’s correlation coefficient suggest that none of the diversity indices are significantly correlated to sample size ( $n$  fauna) (tabl. 6). The above warrants comparison of assemblages.

variable	W	p
n lithics	0,710	<b>0,002</b>
H lithics	0,764	<b>0,008</b>
1/D lithics	0,793	<b>0,017</b>
tool/blank ratio	0,809	<b>0,026</b>
blank/core ratio	0,831	<b>0,046</b>
tool/core ratio	0,876	0,143
n fauna	0,809	<b>0,026</b>
H fauna	0,961	0,812
1/D fauna	0,914	0,347
n meat	0,873	0,133
H meat	0,920	0,393
1/D meat	0,921	0,400

Table 5 – Results of tests for normality (Shapiro-Wilk test [W]). Significant p-values (<0.05) are in bold. Abbreviations: H: Shannon index of diversity, 1/D: inverse Simpson index of diversity.

variable	r	t	df	p	CI 95% BCa
H lithics	-0,612	-2,046	7	0,079	-0.822, 0.181
1/D lithics	-0,573	-1,849	7	0,107	-0.776, 0.403
tool/blank ratio	-0,533	-1,667	7	0,139	-0.735, 0.685
blank/core ratio	0,378	1,081	7	0,316	-0.538, 0.841
tool/core ratio	-0,401	-1,157	7	0,285	-0.739, 0.624
H fauna	0,391	1,122	7	0,299	-0.601, 0.889
1/D fauna	0,466	1,395	7	0,206	-0.630, 0.935
H meat	0,690	2,522	7	0,040	-0.022, 0.836
1/D meat	0,637	2,184	7	0,065	-0.301, 0.923

Table 6 – Results of tests whether Shannon (H) and inverse Simpson (1/D) indices and ratios are correlated to sample size (Pearson’s Correlation Coefficient (r), bootstrapped 95% confidence intervals using adjusted bootstrap percentile intervals [CI 95% BCa]). Abbreviations: df: degrees of freedom, t: t-test statistic value.

#### 4.3. Trends through time

We do not expect the behaviour tracked with the variables analysed here to vary just because of passage of time, but rather that relative assemblage age—or increasing assemblage age—represents other trends, *e.g.* environmental and climatic change during the general climatic downturn towards the Last Glacial Maximum (especially increased aridity). Under this assumption, we would expect responses and adaptations by Pleistocene hunter-gatherers to changing, *i.e.* deteriorating, environmental and climatic conditions, which can be measured by comparing behavioural variables to relative assemblage age. This might include changes in mobility, settlement systems and landscape use as well as changes in prey acquisition strategies, which are all creating variation in the archaeological record.

To explore whether there are any trends in lithic and faunal diversity through time, we ordered the assemblages according to their chronostratigraphic position (WII: Haesaerts *et al.*, 1996; Nigst *et al.*, 2014; MMG: Otte *et al.*, 2007), both within the individual sites as well as between the two sites. For the latter we used the chronostratigraphic correlation for the Middle and Late Pleniglacial after Haesaerts *et al.* (2004; 2009; 2010).

Analysis including both WII and MMG lithic assemblages does not show any trend in time, nor do investigations of the sites separately (tabl. 7). Equally, none of the faunal diversity indices show any chronological trend, with the exception of animals that were primarily exploited for their meat. In the latter instance, H but not 1/D is correlated with relative chronological position of our entire dataset, *i.e.*, the nine Gravettian assemblages of WII and MMG. This might indicate that over time the composition of prey taxa primarily hunted for subsistence purposes became more even (less specialised), but the distribution of frequently exploited taxa (*i.e.*, the number of preferred prey species) did not significantly change. This change in species composition may point to a weak increase in exploitation pressure, which could be caused by the deteriorating climatic conditions towards the LGM, or simply signify a shift towards a moderately more opportunistic hunting strategy. However, it is more likely that the shift in meat exploitation represents behavioural variability rather than an adaptation to the climatic downturn towards the LGM, because the taxonomic evenness and dominance of the total faunal spectrum (meat and fur exploitation) do not change significantly over time.

Variable	WII + MMG		WII		MMG	
	S	p	S	p	S	p
H lithics	156	0,437	14	0,683	14	0,750
1/D lithics	140	0,678	6	0,233	14	0,750
tool/blank ratio	140	0,678	2	0,083	18	0,333
blank/core ratio	88	0,493	20	1,000	14	0,750
tool/core ratio	144	0,613	6	0,233	18	0,333
H fauna	126	0,912	14	0,683	2	0,333
1/D fauna	128	0,880	14	0,683	2	0,333
H meat	22	<b>0,011</b>	2	0,083	2	0,333
1/D meat	40	0,059	10	0,450	2	0,333

Table 7 – Results of Spearman's rank order correlation (S) of Willendorf II (WII) and Mitoc-Malu Galben (MMG) to test whether Shannon (H) and inverse Simpson (1/D) indices and ratios are related to relative assemblage age. Significant p-values (<0.05) are in bold.

#### 4.4. Changes between Early, Middle, and Late Gravettian

We also explored whether we can identify any significant differences in the studied variables between Early, Middle and Late Gravettian assemblages. There could be cultural differences, changes in landscape-use, mobility and/or the duration of site occupation.

These typologically grouped comparisons are hampered by the fact that there is only one Early Gravettian assemblage and only two Late Gravettian assemblages in our dataset. As a result, no site based analyses could not be conducted. However, analysis of WII and MMG assemblages together suggests no significant differences between Early, Middle, and Late Gravettian (tabl. 8 and fig. 3). This suggests

that faunal exploitation did not change between the Gravettian phases, nor did lithic reduction or retouch intensity. One could argue that at WII and MMG there are no apparent changes in landscape-use and, therefore, we propose that the changes in toolkit morphology, on which the Gravettian phases are based, could reflect different learned traditions. In other words, changes in lithic toolkit morphology and the related production technology signify innovations providing new solutions to existing tasks rather than adaptations to changing conditions. This will have to be evaluated against a larger dataset in the future.

variable	Chi <sup>2</sup>	df	p
H lithics	0,356	2	0,837
1/D lithics	0,089	2	0,957
tool/blank ratio	0,089	2	0,957
blank/core ratio	0,000	2	1,000
tool/core ratio	0,622	2	0,733
H fauna	2,600	2	0,273
1/D fauna	1,689	2	0,430
H meat	4,356	2	0,113
1/D meat	4,200	2	0,123

Table 8 – Results of Kruskal-Wallis test to compare Shannon (H) and inverse Simpson (1/D) indices and ratios between Early, Middle and Late Gravettian. Significant p-values (<0.05) are in bold. Abbreviations: df: degrees of freedom.

4.5. Differences between sites

There are substantial differences in the lithic indices and ratios between WII and MMG assemblages. As shown in Table 9 and Figures 4a to 4e, comparison between the MMG and WII assemblages shows significantly higher diversity in all WII assemblages. Moreover, all diversity indices show a broader range of variation among WII assemblages, whereas the studied MMG assemblages cluster tighter together. The more evenly distributed lithic assemblages at WII may relate to lower blank frequencies, which in turn might reflect a curatorial bias (see discussion above), and/or relate to lower rates of retouched pieces at MMG.

The tool/blank and tool/core ratios are significantly higher at WII, suggesting higher rates of retouch, both when comparing the number of retouched pieces to blanks and to cores, than at MMG (tabl. 9 and fig. 4c and 4d). Conversely, the blank/core ratio is significantly higher at MMG (tabl. 9 and fig. 4e), which indicates that reduction intensity of cores,

*i.e.* the number of blanks produced from one core is significantly higher at MMG. The latter may be explained by the proximity of MMG to high-quality raw-material, whereas a large portion of raw-material at WII constitutes local, low-quality Danube gravels.

In terms of fauna diversity, H and 1/D show more specialised faunal exploitation, *i.e.*, dominated by fewer taxa (tabl. 9 and fig. 4f and 4g), at MMG. WII, which exhibits more even faunal exploitation, is situated in the Wachau valley where the Danube cuts through the foothills of the Bohemian Massif. The small river plain is surrounded by rocky, in part forested slopes. On the contrary, MMG lies on the flat to hilly but open plain of the Prut. In fact, faunal exploitation patterns at both sites are clearly embedded in the habitats surrounding the sites. At MMG steppe animals such as horse and to a lesser extent bison were primarily targeted (López Bayón et Gautier, 2007; Noiret, 2009), while at WII there is a wider range of rocky terrain (*e.g.* ibex), forest (*e.g.* red deer, fox, glutton), and floodplain or more open terrain (*e.g.* mammoth, horse) species (Thenius, 1959).

Contrary to the above mentioned trend through time to broader dietary faunal exploitation (H meat), the diversity of species exploited for meat does not differ between the two sites (tabl. 9 and fig. 4h and i). Hence, the significant difference in overall faunal composition rests on secondary (*e.g.* fur, ivory, antler, etc.) rather than primary exploitation for meat consumption.

variable	W	p
H lithics	20	<b>0,016</b>
1/D lithics	20	<b>0,016</b>
tool/blank ratio	20	<b>0,016</b>
blank/core ratio	0	<b>0,016</b>
tool/core ratio	20	<b>0,016</b>
H fauna	20	<b>0,016</b>
1/D fauna	20	<b>0,016</b>
H meat	9	0,905
1/D meat	7	0,556

Table 9 – Results of Wilcoxon test (W) to compare Shannon (H) and inverse Simpson (1/D) indices and ratios between Willendorf II and Mitoc-Malu Galben. Significant p-values (<0.05) are in bold.

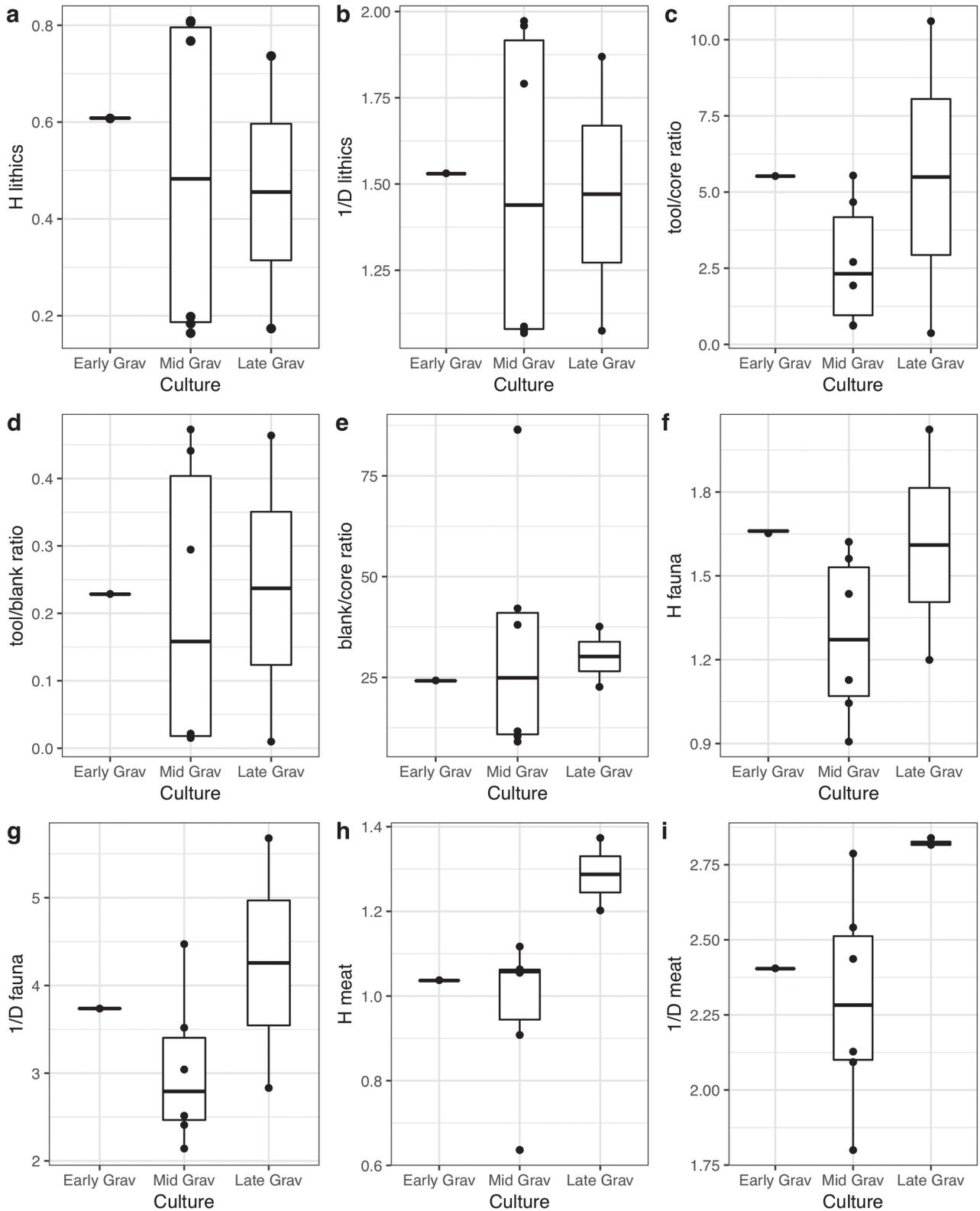


Fig. 3 – Comparison of diversity indices and ratios between Early, Middle, and Late Gravettian. Abbreviations: H: Shannon index of diversity, 1/D: inverse Simpson index of diversity, Grav: Gravettian.

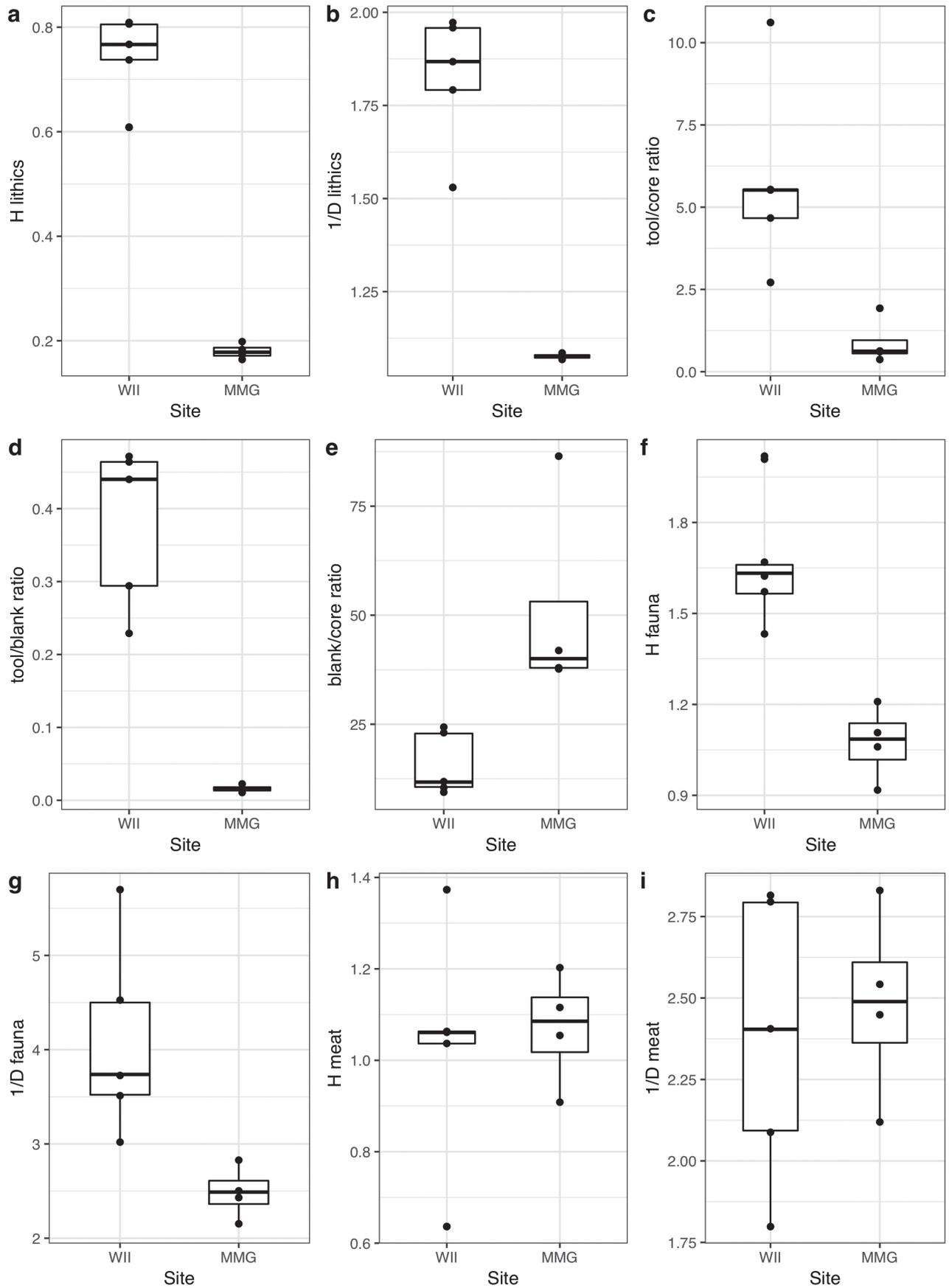


Fig. 4 – Comparison of diversity indices and ratios between the assemblages of Willendorf II (WII) and Mitoc-Malu Galben (MMG). Abbreviations: H: Shannon index of diversity, 1/D: inverse Simpson index of diversity.

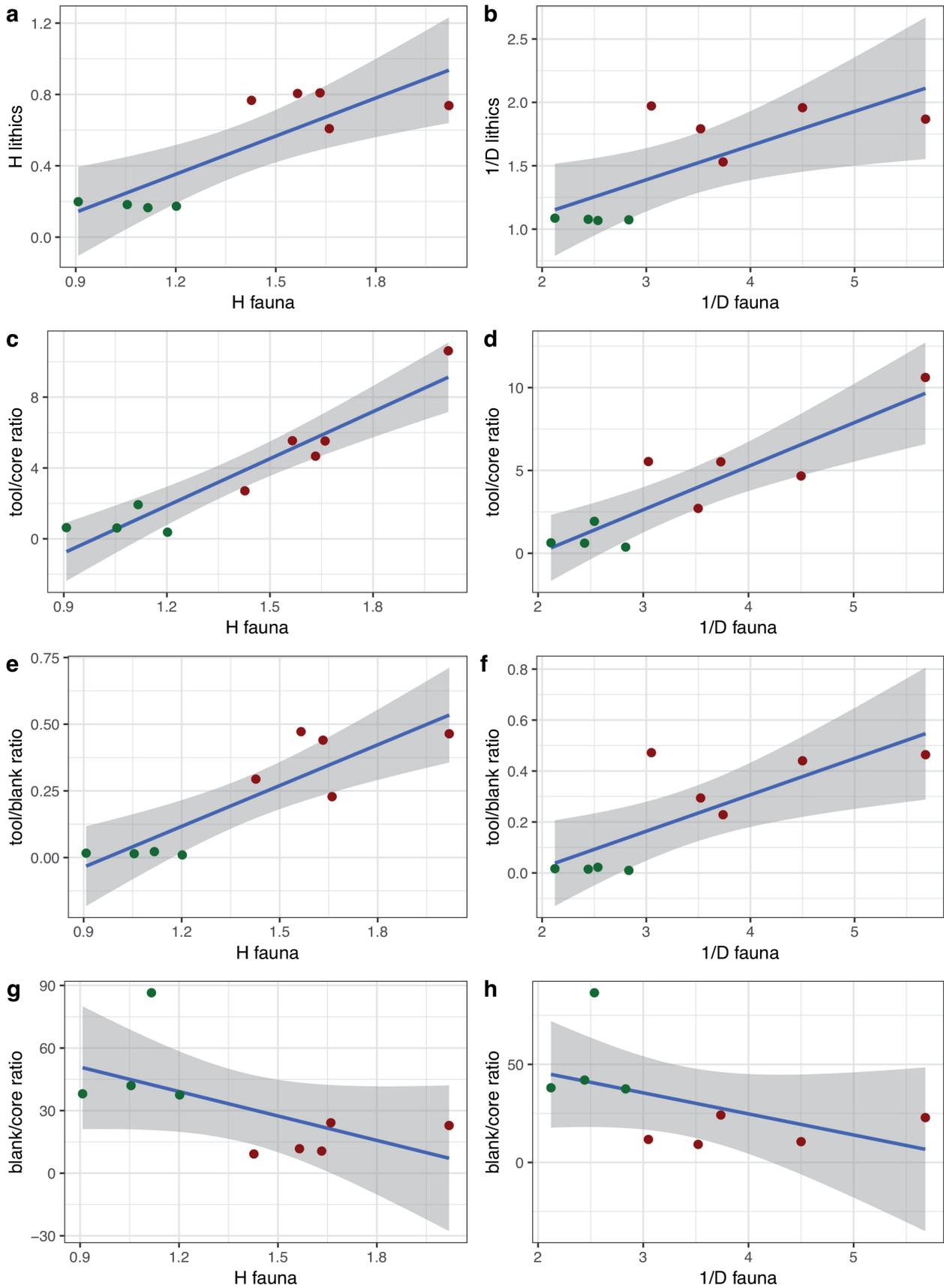


Fig. 5 – Scatterplots showing the correlation of lithic diversity indices/ratios and faunal diversity. Green: Mitoc-Malu Galben assemblages. Red: Willendorf II assemblages. Regression lines based on linear regression are shown in blue, 95% confidence intervals in grey. Abbreviations: H: Shannon index of diversity, 1/D: inverse Simpson index of diversity.

response variable	fixed effect 1	fixed effect 2	response ~ fixed effect 1		response ~ fixed effect 1 + fixed effect 2		
			lm(response ~ fixed effect 1)	lm(response ~ fixed effect 1 + fixed effect 2)	correlation fixed effect 1	correlation fixed effect 2	correlation fixed effect 2
H lithics	H fauna	site	adj.R2=0.654, F(1,7)=16.1, <b>p=0.005</b>	adj.R2=953, F(2,6)=82.43, <b>p&lt;0.001</b>	t=-0.619, p=0.559	t=-6.766, <b>p=0.001</b>	
1/D lithics	1/D fauna	site	adj.R2=0.479, F(1,7)=8.363, <b>p=0.023</b>	adj.R2=0.876, F(2,6)=29.21, <b>p&lt;0.001</b>	t=0.285, p=0.785	t=-4.832, <b>p=0.003</b>	
tool/core ratio	H fauna	site	adj.R2=0.875, F(1,7)=57, <b>p&lt;0.001</b>	adj.R2=0.868, F(2,6)=27.29, <b>p&lt;0.001</b>	t=4.257, <b>p=0.005</b>	t=0.792, p=0.459	
tool/blank ratio	H fauna	site	adj.R2=0.732, F(1,7)=22.9, <b>p=0.002</b>	adj.R2=0.833, F(2,6)=20.89, <b>p=0.002</b>	t=0.945, p=0.381	t=-2.277, p=0.063	
blank/core ratio	H fauna	-	adj.R2=0.236, F(1,7)=3.475, p=0.105	-	-	-	
tool/core ratio	1/D fauna	site	adj.R2=0.760, F(1,7)=26.35, <b>p=0.001</b>	adj.R2=0.756, F(2,6)=13.4, <b>p=0.006</b>	t=2.658, <b>p=0.038</b>	t=-0.940, p=0.383	
tool/blank ratio	1/D fauna	site	adj.R2=0.554, F(1,7)=10.95, <b>p=0.013</b>	adj.R2=0.831, F(2,6)=20.61, <b>p=0.002</b>	t=0.902, p=0.402	t=-3.523, <b>p=0.013</b>	
blank/core ratio	1/D fauna	-	adj.R2=0.147, F(1,7)=2.381, p=0.167	-	-	-	
H lithics	H meat	-	adj.R2=-0.127, F(1,7)=0.100, p=0.761	-	-	-	
1/D lithics	1/D meat	-	adj.R2=-0.129, F(1,7)=0.087, p=0.777	-	-	-	
tool/core ratio	H meat	-	adj.R2=0.095, F(1,7)=1.837, p=0.218	-	-	-	
tool/blank ratio	H meat	-	adj.R2=-0.129, F(1,7)=0.086, p=0.778	-	-	-	
blank/core ratio	H meat	-	adj.R2=-0.071, F(1,7)=0.467, p=0.517	-	-	-	
tool/core ratio	1/D meat	-	adj.R2=-0.078, F(1,7)=0.420, p=0.538	-	-	-	
tool/blank ratio	1/D meat	-	adj.R2=-0.143, F(1,7)=0.001, p=0.984	-	-	-	
blank/core ratio	1/D meat	-	adj.R2=-0.081, F(1,7)=0.402, p=0.546	-	-	-	

Table 10 – Linear Models to study Shannon (H) and inverse Simpson (1/D) indices of lithic diversity and lithic ratios as a function of Shannon (H) and inverse Simpson (1/D) indices of fauna diversity [lm(response ~ fixed effect 1)] and as a function of fauna diversity plus site [lm(response ~ fixed effect 1 + fixed effect 2)]. Significant p-values (<0.05) are in bold.

#### 4.6. Comparison of lithic and faunal diversity indices and ratios

Up to now we have analysed lithic and faunal diversity indices and ratios separately, and we have shown that most of them are not driven by relative assemblage age or cultural attribution (*i.e.*, Early, Middle and Late Gravettian), but seem to be influenced primarily by differences between the two case-study sites.

Below, we compare lithic and faunal diversity indices with each other because one would expect that prey acquisition (measured here through composition and diversity of the faunal assemblages) influences lithic assemblage composition and diversity. Equally, both may be driven by other factors such as climate or the site's role in a forager settlement system.

To explore what drives lithic variability we used linear models with one or two fixed effects (tabl. 10 and fig. 5). We constructed a linear model of H lithics as a function of H fauna. This model was significant ( $F(1,7) = 16.1$ ,  $p = 0.005$ ) (tabl. 10 and fig. 5a). To evaluate the impact of site on our model, to account for the significant differences when comparing the diversity indices between WII and MMG, we included it as a second fixed effect. The resulting model was again significant ( $F(2,6) = 82.43$ ,  $p < 0.001$ ), while the coefficients for each effect clearly show that the model is driven by site ( $p = 0.001$ ) rather than H fauna ( $p = 0.559$ ) (tabl. 10). The same pattern emerges when testing the correlation of 1/D lithics to 1/D fauna, as well as the correlation of tool/blank ratio to faunal diversity (both H and 1/D) (tabl. 10 and fig. 5b, 5e, and 5f).

The two linear models for blank/core ratio as a function of either H or 1/D of fauna are not significant (tabl. 10 and fig. 5g and 5h). However, when we investigate the tool/core ratio as a function of either H or 1/D of fauna, both models are significant (tabl. 10 and fig. 5c and 5d). When site is added as a second fixed effect the latter two models are still significant and driven by faunal diversity. Interesting in this context is also our suggestion that tool/core ratio is among the least biased in old collections as tools and cores were collected in larger percentages even in old excavations, which normally are biased against blanks (especially flakes and cortical elements) as well as smaller lithic fractions. The patterns described for the tool/core ratio suggest that the more even the faunal assemblage is, the more tools are produced per core, *i.e.*, the more curated or more reduced the assemblage is.

While it is possible that the faunal composition drives the tool/core ratio, it is also possible that both

are connected to other hunter-gatherer behaviours that influence both variables, which do not differ significantly between the two sites. For example, longer occupation duration and re-occupation or palimpsest of occupations, both leading to more tools per core and a more even faunal distribution. Another option is highly residentially mobile groups also leading to more curated lithic assemblages (many tools and few cores, partly as transport of cores has higher costs) and more even assemblages.

Overall, our analysis of the nine Gravettian assemblages from WII and MMG suggests that site is a driving factor in most the ratios and indices. Our variable 'site' captures the location of the site in the landscape, *e.g.* in terms of access to high vs. low quality lithic raw materials and access to animal resources through the type of adjacent hunting grounds, and its role in the forager settlement system.

#### 5. Concluding remarks

This paper investigated the underpinnings of diversity in material culture of the Gravettian at Willendorf II and Mitoc-Malu Galben. Specifically, we explored the differences in lithic and faunal composition both from a temporal and cultural perspective and discuss implications for our understanding of Late Pleistocene forager land-use and settlement systems.

While the individual variables used in this study are not driven by sample size, we are aware that due to the focus on nine assemblages we have a rather low number of assemblages in our analyses. Also the fact that these nine assemblages come from only two case study sites might bias our results. Future studies of the questions raised here will have to be pursued including more assemblages from more sites, and will need to evaluate the reproducibility of the patterns described.

MMG is close to high-quality raw-material resources and as a result the blank to core ratio is higher than at WII where high-quality raw material outcrops are far away (min. 80km) and a large part of the raw material constitute locally available (secondary source < 1km distance from site), rather low-quality Danube gravels. Furthermore, WII is located on the west bank of the Danube overseeing the narrow river plain and is surrounded by rugged, mountainous terrain, which explains the focus on ibex exploitation and the frequency of small and larger carnivores (Thenius, 1959). MMG in the Prut valley on the flat to hilly but open east Carpathian plain facilitated hunting of horse and bison (Noiret, 2009).

Through linear modelling we assessed how faunal diversity influences lithic diversity. Faunal diversity is significantly positively correlated with the tool/core ratio. In other words, the more even or heterogenic the faunal composition is, the more tools were produced per core. Or the fewer tools were made per core, the more selective the faunal assemblage.

Coming back to our case-study sites, MMG can from a faunal point of view be characterised as short-term (1-6 weeks) occupations in which few activities (e.g. organic tool production [from reindeer antlers], butchery of large mammals, specifically horses and bison killed close to the site) repeatedly took place (López Bayón et Gautier, 2007; Noiret, 2009). Moreover, from the lithics perspective MMG can be seen as a residential camp close to a high-quality raw material outcrop with high levels of blank production and core reduction, but only a few tools per core or per blank. For WII we know little about the duration of site-occupation although Felgenhauer (1959) mentions the presence of lenses dense in material remains. Nevertheless, there is a broader set of activities recorded at WII, namely lithic knapping, exploitation for subsistence purposes of medium-sizes ungulates e.g. ibex and reindeer, but also larger mammals including mammoth, organic tool production (antler and perhaps ivory), production of figurative art (ivory and stone), and exploitation of furbearing animals from hare to foxes, wolves, and bears (Thenius, 1959).

Clearly, MMG and WII were targeted for specific activities and it seems likely that these formed the underpinnings of the differences in the archaeological remains recovered at both sites. The multitude of activities conducted at WII, which are reflected in the faunal composition, may well explain the lithic diversity.

In sum, with the archaeological assemblages of WII and MMG we probably have repeated samples of forager settlement systems that are characterised by high mobility and probably fission/fusion processes throughout the seasonal cycles at two different locations, both in terms of season and space. The sparse, highly fragmented character of the Gravettian archaeological record of these hunter-gatherers suggests highly flexible foragers exploiting their landscapes to the full.

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Author contributions: Both authors designed the research, collected and analysed data, and wrote the paper.

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