Life tables and Leslie matrices for mammalian cohorts in different paleobiological contexts during the Pleistocene

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1 Principles and methods : establishing mortality profiles

For decades studying the Pleistocene human subsistence strategies has been a key area of research in archeology to address the ability or inability of human populations to exploit optimally their prey, and by extension, their environment. To answer this question the theoretical concept of attritional and catastrophic mortality have together emerged in paleontology and zooarchaeological literature, with methodological approaches to establish mortality curves. Some of them were directly rooted in ecological approaches, such as the introduction of life tables by Kurtén [1-5]. Since these pioneering works, new methods based on age-specific sequences of tooth eruption, tooth wear, and crown height now correspond to the main criteria used to assess mammalian mortality curves. As a matter of fact, fossil dental material is better preserved than bones and frequently identifiable to species. Consequently, teeth are very useful for estimating the minimum number of individuals and for constructing mortality curves in order to interpret the fossil demographic structures [6-13].

In zooarchaeology, the most common techniques to assign individual age are based on current tooth eruption and wear sequences, from which each stage is codified starting from known age individuals of domestic species [sheep/goat : 14, 15] or collected in the wild as for example in deer [16-18], Roe deer [19- 21], Ibex or Chamois [22-23] to men-

tion just a few. Unfortunately tooth eruption sequences do not allow distinguishing between adults and older individuals ; the distinction being only possible between juveniles and adults. Furthermore, the visual comparison may be difficult between current species wear sequences and fossil teeth with intermediate dental wear. The problem is more complicated when species are extinct : how to relate them to current representatives ?

Last but not least, the degree of hypsodonty is measured from the height of the crown, usually from the root to the occlusal surface of the tooth and regressed against age using animals of known age. Starting from the work of Kurtén this method was developed by Spinage [24-25] who focused on African taxa (bovids and equids). Similarly, the innovative quadratic method of Klein *et al.* [26], also called QHCM (Crown Heights Quadratic Method), provides a set of quadratic formulae for each tooth, according to his rank, that can be used to predict age-at-death from tooth crown height. QHCM has been applied to many Pleistocene deposits to interpret the exploitation of certain large ungulates by African Hominids [27-31]. However, the main bias of the QHCM is related to the non-linear wear of teeth from different ages [28, 32-35], and, more importantly, to the absence of average prediction error of the estimated age for each type of tooth [36]. This latter study by Fernandez & Legendre offers a model based on a regression analysis of curvilinear type, starting from both age and dental height intervals of known age individuals from the referential of Levine [37]. To each tooth position (*i.e.* P/2, M3/...) corresponds a polynomial equation whose parameters are estimated by bootstrap [38]. The randomisation makes possible to estimate the individual age of teeth and its standard deviation with median values of regression coefficients (slope, intercept, coefficient of determination) [36, tabl. 5, 39, fig. 1). This model was applied to different Pleistocene and Holocene equid populations [40-45].

We present here (Figure 1, A to D), a step-by-step procedure to estimate the age distribution from a hypothetical P4/ of fossil horse. This example clearly shows that the model resolution is based on a reliable prediction error of median age to derive appropriate age class intervals in order to properly distribute age frequencies. Indeed, it appears that no ageing method based on dental material allows obtaining exact absolute ages because individuals vary in the age of achievement of a given stage [46]. By ruling out the distribution information around the mean or median age, we gain a false sense of statistical power about statements based on absolute age. Consequently, it is crucial to reach a correct distribution of individual ages rather than focusing on an exact age [47].

Finally, it appears in all these approaches that the lifetime, the eruption and the tooth wear sequences can only be derived from current domesticated species or from wild representatives of fossil species. This analogy may lead to "mimicry age", where the estimated age structure partly resembles that of the reference population [48]. Moreover, it is always difficult to assess the degree of abrasion induced by the diet that determines tooth wear [49]. Nevertheless, dental meso-wear [50-51] or micro-wear analyses are highly relevant to determinate the proportion of grass, twigs, or fruit in the diet of extinct species [52-53]. Regardless of the ageing method, this approach is still underused although it recently provided information about changes in seasonal

equid diet and the presence of one or several horse cohorts through time in Schöningen 13 II-4 [54], both using isotopic analyses.

2 Attritional and catastrophic "models" : theoretical and practical limits

As mentioned before, theoretical mortality of mammalian population is often associated to two main models in zooarchaeology. Attritional model is characterized by a U-shaped profile because young and old animals die off more often than prime adults. From an ecological viewpoint, this is mostly explained by the occurrence of combined effects of neo-natal mortality, epizooty, human and carnivore predation or intraspecific competition for resources. The combination of all these factors affects the most vulnerable age groups through time.

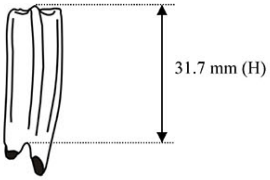
Conversely, the mass mortality also called "catastrophic", reflects the age distribution of the living "population" in which the frequency of individuals in each age group decreases regularly, exhibiting an L-shaped profile. Natural disasters such as floods [55], bush fires [56] or volcanic eruptions [57, 58] are natural events that characterize this punctual type of mortality.

However, fossil age structures mixed through time may result in different patterns than these two theoretical opposite types of mortality. Furthermore, different species can only be compared when age intervals are of similar duration and when lifespans are identical, which is rarely the case. That is why Kurtén [1, 2] in paleontology, Spinage [59] in ecology, and Klein [27] in zooarchaeology, were among the first in their field to standardize interval classes of ages of equal duration, each one representing a percentage of the maximum lifespan for a given species. Morever, in order to link fossil assemblage to attritional or catastrophic model, Klein & Cruz-Uribe [30] proposed to test frequencies (D Kolmogorov- Smirnov) of each age group with those of living species whose individual ages and type of death (natural or catastrophic) are known. This was validated starting from a cohort of known age wapiti after the volcanic eruption of the Mont St. Helens in 1980 [58]. Later on, Lyman, Byers & Hill [60], used Spearman's rank-order correlation coefficient to estimate the strength of the relationship between the observed dataset and the expected mortality under the model.

Many methods exist for constructing and comparing pleistocene mortality profiles ([reviewed in 39 and 61]). Greenfield [62-63] was the first to use triangular graph also called ternary diagram to understand better the variation in the frequencies of immatures, sub-adults, and adults in herd management for the Neolithic. As a result of the work carried out by Vigne & Helmer [64], culling profiles are now commonly represented by histograms in which the frequencies of each age class are proportional to the area of each bin (see discussion in Brochier [65]).

For the Pleistocene assemblages, the ternary diagram was developed by Stiner [66]. Two major scenarios were related to a living/catastrophic age structure (the right-of-center portion of the graph) and to an attritional mortality (the left-of-center portion). The areas and limits of each have been reassessed, first by bootstrap resampling [67]

A. **Crown height measurement from the P4/ of a fossil horse**



B. **Median values of the regression coefficients for each tooth category. (a_0) = slope; (a_1, a_2, a_3) = intercept; (E) = mean prediction error; (R^2) = determination coefficient. From Fernandez & Legendre [36, Tab. 5].**

Teeth	a_0	a_1	a_2	a_3	E	R^2
P2/	28.290625	-1.028377	0.019429	-0.000141	0.544	0.986
P3/	33.658749	-1.041913	0.015383	-0.000087	0.257	0.993
P4/	40.593780	-1.318328	0.018488	-0.000096	0.494	0.986
P3-4/	25.617811	-0.406405	0.001078	0.000009	1.566	0.971
M1/	35.572249	-1.064404	0.013784	-0.000066	0.389	0.990
M2/	41.143669	-1.312885	0.018273	-0.000095	0.534	0.986
M3/	40.634788	-1.482155	0.023170	-0.000128	0.532	0.985
M1-2/	32.599580	-0.870571	0.010151	-0.000046	1.119	0.980
P/2	23.931106	-0.940985	0.020425	-0.000174	0.636	0.982
P/3	37.758397	-1.447331	0.024167	-0.000141	0.414	0.988
P/4	46.789425	-1.766535	0.027637	-0.000153	1.343	0.959
P/3-4	29.285176	-0.835852	0.011519	-0.000061	1.123	0.975
M/1	36.176726	-1.309214	0.020176	-0.000110	0.827	0.980
M/2	36.936030	-1.236690	0.018852	-0.000105	0.366	0.990
M/3	36.102387	-1.203143	0.018695	-0.000110	0.652	0.981
M/1-2	32.587336	-0.927905	0.011631	-0.000056	1.691	0.974

Given a crown height (H, in mm) the equation for age (in year) is: Age=$a_0+a_1H+a_2H^2+a_3H^3$

C. **Estimation of median, minimum and maximum age (year) from the P4/ with Height measurement (H)=31.7 mm**

Minimum age	Median age	Maximum age
14.32 – (2 x 0.494) = 13.33	$a_0 + a_1H + a_2H^2 + a_3H^3$ = 14.32	14.32 + (2 x 0.494) = 15.31

D. **Distribution of the age of P4/ in each age class**

			Age class in years					
Min. age	Med. age	Max. age	0-3	3-6	6-9	9-12	12-15	15-18
13.33	14.32	15.31					**0.84 (1)**	**0.16 (2)**

(1) = **1.67/1.98** that is to say **0.84**% into the age class of 12-15 years
(2) = **0.31/1.98** that is to say **0.16**% into the age class of 15-18 years

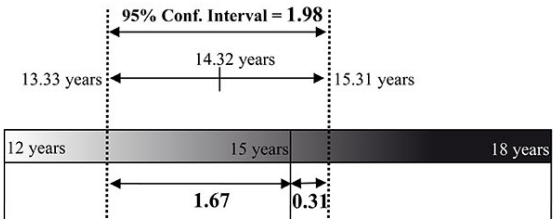


Figure 1 – Step-by-step procedure (A to D) to estimate the age distribution from a hypothetical P4/ of a fossil horse. Modified from Fernandez & Legendre [36, tabl. 5] and Fernandez [39, fig. 1]

and then by a likelihood approach that better takes into account when any of the age classes have counts of zero [68]. So far, ternary diagram remains very popular in Pleistocene zooarchaeological studies by allowing in a single graph, the comparison of multiple inter- or intra-specific age structures and to relate them to attritional and catastrophic mortality types. That's why recently Discamps & Costamagno [69] described four zones within the ternary diagram to interpret better the relative proportions of 7 common species.

Studies by Nimmo [70] and Lyman [57] put in light long ago the difficulty of interpreting specific human hunting strategies and natural mortality based on these two types of theoretical patterns. For example the minimum sample size required for a reliable detection of mortality patterns will depend on the life expectancy of the considered taxon [57]. More generaly, taphonomic processes often involve natural differential preservation of ageing elements that may lead to the misinterpretation of mortality curves and their related patterns. The frequency of ageing elements should be seen in light of their particular paleobiological contexts (open area, cave, den), their conditions of preservation (desertic : [71], periglacial : [72], temperate : [73]), human behavior (transport decision : [74-75], primary and secondary carnivores impact [76-77], as well as species ethology [37, 78-79].

In short, in zooarchaeological Pleistocene studies, mammal mortality curves are almost always established from dental material : the aim is to estimate the sum of individual ages to interpret them as an entire population. This raises the crucial issue of the multiple vs. unique time-deposit that corresponds to a strong assumption when interpreting the frequencies of dead animals. Considering the potential weakness of attritional or catastrophic mortality patterns and the fact that some current ecological models do allow taking into account multiple cohorts and/or single individuals over time, we present in the following a new approach using life tables and Leslie matrices to characterise stable age-structure of mammalian fossil populations.

3 Discussion : life tables and Leslie matrices

3.1 Presentation of life tables

Life tables were primarily introduced to biologists to determine the lifetime of insects [80]. They are constructed from observations of age structure of animals sampled as dead (d_x) in paleobiological contexts or/and as alive (l_x) in ecological field analyses. This approach was popularized to estimate age-specific survival rates of current mammal and bird populations by Deevey [81]. Two main models are employed according the sampling and the nature of the population : age-specific or dynamic (horizontal or longitudinal) ; static or time-specific (vertical or transversal).

The "dynamic" or "cohort" life tables consist in following all the individuals of a single cohort in a population from birth to death. The method depends on the recapture of marked individuals for mobile species and individuals should be monitored from birth to death. This "horizontal/longitudinal" life table technique is not well suited for the study of long-lived individuals and inappropriate with fossil samples. However the "static" or "time-specific" life tables are established from individuals of all ages

belonging to different cohorts. Then "vertical/transversal" life tables represent random samples of individuals and their distribution should reflect the whole population.

In this study we will focus on the latter that has been fully or partly used in both mammalian paleontological and archaeological contexts [1, 2, 5, 82-89, 36, 41, 43, 90-91].

Most importantly, time specific model allows taking into account multiple fossil deposits through time. However, the validity of the life table analysis requires some strong assumptions to be fulfilled. For example, vertebrate population analyses have involved a female-dominant model, such that only demographic parameters of females are considered [92]. However it is widely accepted that male survival does not affect the population growth rate of most natural mammalian populations. Consequently the model can be used in a legitimate and appropriate manner assuming a balanced sex-ratio at birth and measuring the fecundity rate as the number of daughters per female as half the number of offspring produced alive at birth by a female of a given age. A stationary age structure through time is required except for the time-specific model, with constant survival and fecundity rates for the different cohorts [93-97]. It is also assumed that the age structure of the sample corresponds to a local population in the absence of immigration and emigration, that is to say that migration flows are random and did not modify the sample [98, 99]. We should keep in mind that in current ecological studies these strict assumptions are unlikely to be met in any population of wild mammals because opportunities to monitor entire cohorts for long periods of time are unlikely [100-102]. Time-specific life table and indices are explained below (see Table 1 for example) :

- (x) refers either to "age interval" or "age class" (in months, year or any time interval). There is often confusion between them. Let's retain that according to Caswell [103] the former begins at 0 and the latter at 1.
- (d_x) refers to the proportion of individuals of the whole cohort(s) dying between age x and $x+1$. This is typically the MNI. It can be derived from the variable (l_x) series by :

$$d_x = (l_x - l_{x+1})$$

- (l_x) refers to cumulated survivorship and corresponds to the fraction of a cohort that survives to an age interval x. The first value can be expressed per 1, 100 or 1000 :

$$l_{x+1} = (l_x - d_x)$$

In standardized life table with regular pooled age-class intervals (see example in Table 2) where d_x is not available the calculation by algebraic relation with (s_x) defined below in the text is simply :

$$l_{x+1} = s_x * l_x$$

As we can see in Figure 2, when l_x values are plotted on a logarithmic scale (y-axis) with standardized lifespan (x-axis), the survival curves obtained have the remarkable property of being similar for most mammal species despite the variation of their size

or their longevity [98]. This is also true for survival rates of other animal groups, which allows the identification of three main types of mortality. The comparison is then possible to a specific or an interspecific level. Type I, characteristic of most mammals, clearly shows that survivorship is relatively low in juveniles, becomes high and stable during adult primes, and then finally declined with a half-bell shape at old ages (senescent stage). Type II characterizes essentially small birds or raptors and is characterized by a quite constant survival over the lifetime. Type III is mainly associated with fish and marine vertebrates and shows survival rates that are low during early ages and prime ages, and then high throughout the rest of the lifetime, which generates an L-shape profile [93].

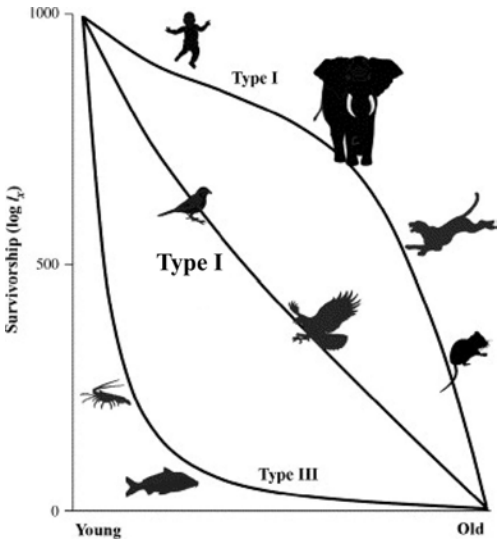


FIGURE 2 – Survivorship curves from stable populations (log l_x) according to the zoological group. Data are from Fernandez *et al.* [41] modified from Krebs [94] and Ricklefs [95].

- (q_x) indicates the mortality rates during the interval x to $x+1$. It is the ratio of d_x and l_x :

$$q_x = [d_x/(l_x)] * 100$$

- (s_x) refers to age-specific survival rate. Proportion of individuals surviving from age x to $x+1$:

$$s_x = [l_{x+1}/l_x] * 100$$

- (e_x) refers to life expectancy in each age class. Unlike the other columns, life expectancy deals with the intermediate calculation of T_x (total years lived for all individuals) and L_x (average individual number alive in age class) which are purely intermediate step without real biological meaning. Thus life expectancy is as follow :

$$e_x = T_x/l_x$$

where $T_x = \sum L_x$ and $L_x = (l_x + l_{x+1})/2$

- (k_x) also designated as killing power or killing factor is another measure of mortality between successive age class. By summing individual values $(\sum k_x)$, one obtains an additive index that indicates the "intensity" of mortality that may be generated by one or different factors (*g.* predation), calculation is as follows :

$$k_x = |\log_{10}(d_{x+1}) - \log_{10}(d_x)|$$

- (m_x) is the number of female offspring per female of age x (called fecundity rate).
- $(l_x m_x)$ is the contribution of a given age class to the population reproduction. It is simply the product of l_x and the m_x
- (R_0) is the net reproductive rate of the cohort. It corresponds to the mean lifetime reproductive success in the population. When $R_0 < 1$ the population is declining, meaning that animals of the cohorts are not replacing themselves. $R_0 > 1$ indicates an increasing population, while $R_0 = 1$ means a perfect stable stationary population :

$$R_0 = \sum l_x m_x$$

- The way to transform survival frequencies related to successive irregular age intervals and to distribute them into regular age class intervals is crucial and remains largely underused in zooarchaeological studies (see Caughley [98] for a full treatment of standardization). We present here how to pool age classes in regular intervals and calculate age-specific survival rates (s_x). Starting from an original life table data of fossil *H. refossa* (Geula, Israel, [90]), we detailed in the Table 2, a step-by-step example.

Table 1 – Example of time-specific life table based on the collection of dead animals with the key demographic parameters (see details for meaning and calculation in text).

Age class (x)	Frequency (d_x)	Survival rate (l_x)	Mortality rate (q_x)	Life expectancy				Killing power (k_x)	Fecundity rate	
				(s_x)	(e_x)	(L_x)	(T_x)		(m_x)	($l_x m_x$)
	$(l_x - l_{x+1})$	$l_{x+1} = (l_x - d_x)$	$d_x/(l_x)$	l_{x+1}/l_x	t_x/l_x	$(l_x + l_{x+1})/2$	$\sum L_x$	$\lvert \log_{10}(d_{x+1}) - \log_{10}(d_x) \rvert$		
0	45	100	0.450	0.550	1.870	77.5	187.0	0.653	0	0.000
1	10	55	0.181	0.818	1.991	50.0	109.5	0.096	1.2	0.660
2	8	45	0.177	0.822	1.322	41.0	59.5	0.204	0.9	0.405
3	5	37	0.135	-	0.500	18.5	18.5	(1.000)	-	-
4	-	-	-	-	-	-	-	-	-	-
								$\Sigma(k_x) = 0.954$	$R_0 = \Sigma(l_x m_x) = 1.065$	

Table 2 – Example of original life table of *Hystrix refossa* (A) and standardization with regular age classes intervals with calculation of survival rates. (Data from Monchot *et al.* [90].)

A. Original life table with raw data (in months)

Age interval (x) in months	l_x	s_x	
0	1.000	**0.690**	if $S_{0\text{-}5}$ = **0.690**
5	0.690	**0.825**	and $S_{5\text{-}8}$ = **0.825** thus we easily get $S_{0\text{-}8}$ = **0.690*0.825** = 0.56925.
8	0.569	**0.818**	We also know $S_{8\text{-}18}$ = **0.818** and we have to consider an interval of 10 months to get $\sqrt[10]{0.818}$ = 0.9801112
18	0.466	0.815	Then $S_{8\text{-}12} = (0.9801112)^4 = 0.9227869$.
30	0.379	0.545	
48	0.207	0.000	
144	0.000	0.000	

B. Standardized life table (in years)

Age interval (x) in years	l_x	s_x	
0	1.000	**0.525**	Thus in standardized life table (B) we find $S_{0\text{-}1}$ year = 0.56925*0.9227869 = **0.525**. So on, to find subsquent values.
1	0.525	0.800	To estimate the fraction of the cohort surviving (l_x) during age interval x to $x+1$, the calculation is simply $l_{x+1} = s_x \times l_x$
2	0.420	0.737	
3	0.310	0.667	
4	0.206	0.667	
5	0.138	0.667	
6	0.092	0.667	
7	0.061	0.667	
8	0.041	0.667	
9	0.027	0.667	
10	0.018	0.667	
11	0.012	0.667	
12	0.008	0.667	

3.2 Presentation of Leslie matrices

In paleobiological contexts, Leslie matrices have only been used or even mentioned until recently in a very few works ([43], [90], [104-108]). However, they have become a standard in population ecology ([103], [109]) due to their long-established use since the works of Bernardelli [110], Lewis [111] and the most accomplished studies of age-structured model of population growth by Leslie [112, 113]. Later on, Lefkovitch [114] introduced developmental stages rather than ages and Usher [115] developed a size-structured model. We present here the simplest matrix projection model also called Lewis-Leslie :

$$\underbrace{\begin{pmatrix} m_0 & m_1 & m_2 & \cdots & m_{12} \\ S_0 & 0 & 0 & \cdots & 0 \\ 0 & S_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & 0 \\ 0 & 0 & 0 & S_{11} & 0 \end{pmatrix}}_{A} * \underbrace{\begin{pmatrix} n_0(t) \\ n_1(t) \\ n_2(t) \\ \vdots \\ n_{12}(t) \end{pmatrix}}_{n(t)} = \underbrace{\begin{pmatrix} n_0(t+1) \\ n_1(t+1) \\ n_2(t+1) \\ \vdots \\ n_{12}(t+1) \end{pmatrix}}_{n(t+1)}$$

Matrix A is constructed with the same age-specific fecundity rates (m_0, $m_1 \ldots$) as in the life tables. The diagonal of the matrix contains age-specific survival rate (S_0, $S_1 \ldots$) corresponding to the values of s_x in our life tables. The state vector $n(t)$ is derived from the (l_x) as the fraction of the total number of individuals. The projection of the matrix, with the state vector $n(t)$ gives a new vector $n(t+1)$, which is simply the new number of individuals in each age interval at the next succeeding census of the projection interval such as : $An(t) = n(t+1)$

In addition to the above, the model is based on three strong assumptions :

- age is a discrete variable where the first value is 0, is divided into age classes numbered from 1 to n ;
- the time is regarded as a discrete variable. The time is denoted t, and the time step projection is $t+1$;
- the time step projection is strictly equal to the duration of each age class interval. This implies that from t to $t+1$ all surviving individuals move to the next age class.

Let's give an example of this theoretical model starting from the demographic parameters of *E. achenheimensis* recovered on the natural middle Pleistocene swallow-hole of Romain-la-Roche (Doubs, France) [43]. Using the software PopTools developed by Hood [116], we first entered data into a pre-breeding [1] Leslie matrix [102]. In the Figure 3-A, the first line of our matrix contains the fecundity rates multiplied by juvenile survival (*i.e.* S_0), and the survival rates from S_1 onward are entered on the sub-diagonal in order to be multiplied by the state vector. The matrix returns the dominant eigenvalue (λ) also known as the asymptotic growth rate (λ) and r, the exponential or continuous growth rate, which is simply the natural logarithm of λ, in

1. This is the basic model used for mammals where cohorts are censuse just before they breed as opposed to post-breeding model (see details in Caswell [103]).

our example $r = \ln(0.9869) = -0.013$ [2]. Decreasing populations are characterized by negative values of r, corresponding to lambda values less than 1. Conversely, increasing populations have positive r-values, and asymptotic growth rate greater than 1 (see details in [94]). In our example, considering $\lambda = 0.9869$ and $r = -0.013$, the horse population of Romain-la-Roche was likely going extinct (less than 2 individuals at t_{297}) (Figure 3-B). In our projections, if we divide the entire population distribution (n) at time t_{+1} by the members of the preceding age-class, we obtain quotients that converge to the dominant eigenvalue of the matrix, which is 0.9869. The lambda is the ratio of the population size in one year relative to that in the preceding year [97]. In our example, population changes in number by a factor of $\lambda = 0.9869$ (98.69%) from one year to the next. In other words, the entire population will decrease by more than 1% per year (0.0131%). Works on different current populations of wild Equids indicate that when they evolve in optimal conditions the λ is comprised between 1.21 and 1.26 [117-118 with $\lambda = 1.21$]; [119 with $\lambda = 1.26$]; [120-121 where $\lambda = 1.22$]. We should note that the early fluctuations of λ, the so-called transient dynamics, are due to initial conditions of the demographic parameters of the age distribution. For instance, in going from time t_3 to t_4, the projection of the cohorts is of 0.9884%. If we look now to t_{19} including the following years, the lambda is stabilized to the dominant eigenvalue of the matrix. The damping ratio [3] ($\rho = \lambda_1/|\lambda_2|$) describes how quickly the transient dynamics is stabilized after perturbation around the asymptotic growth rate regardless of population structure; the larger the ρ (always more than 1), the quicker the population converges [102]. Surprisingly, in our example $\rho = 1.245$ is not very much larger than 1 suggesting that the stable size distribution is not reached very quickly.

Demographic rates in paleobiological contexts are inferred from current species, then it is of great interest to generate noise in the matrix or to explore different hypotheses by changing values such as m_0, m_1, S_0, S_1... In other words, how much would λ respond to a 10 or 20% change in survival or in fecundity rates? Elasticity [4] or sensitivity analyses answer this question since they have become a standard practice in population dynamics [122-123]. Elasticity is a normalized dimensionless sensitivity as a response to a proportional perturbation. We will focus here on the former, which is easier to interpret because it is scaled to 1.

2. Then $P{=}P_0 e^{rt}$, where P_0 is the initial population, r is the continuous growth rate, and t is time. In our example :
$P = P_0(0.9869)^t = P_0 e^{rt}$
$(0.9869)^t = e^{rt} = (e^r)^t$
$0.9869 = e^r$

3. The calculation was made with R version 3.2.3 with package "popdemo". Theoretical details of the calculation of the damping ratio with the subdominant eigenvalue $_2$ go well beyond our paper (for details see Caswell [103, p. 95]).

4. We will not delve into matrix formulations in detail here (see Caswell [103, Chapter 9]) and we will only focus in this study on elasticity that can be formalized such as :
$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial \log \lambda}{\partial \log a_{ij}}$ where e_{ij} is just the slope of log λ plotted against log a_{ij}.

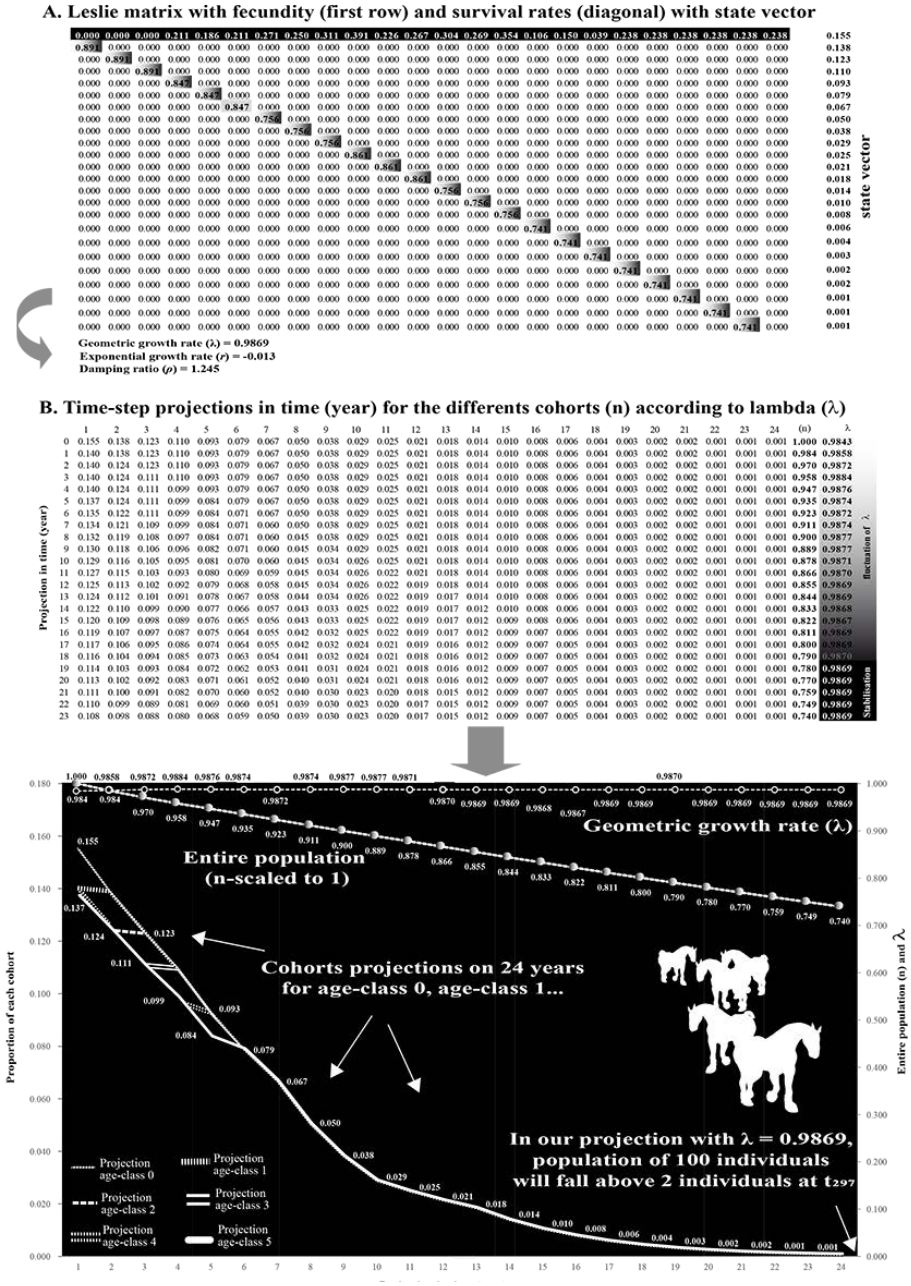


FIGURE 3 – Leslie matrix with survival from 1 year of age (values in diagonal) and fecundity rates times juvenile survival (value in the first row) with the state vector (value on the right) of *Equus achenheimensis* (A). Time-step projections of the population with the geometric growth rate (B) and their graphical overview. (Data from Fernandez & Boulbes [43], Table 3.)

A. Leslie matrix with fecundity and survival rates of *Hystrix refossa*. Data from Monchot *et al.* [124]

0.000	**0.250**	**0.563**	**0.693**	**0.693**	**0.693**	**0.693**	**0.693**	**0.693**	**0.693**	**0.693**	**0.693**	**0.693**
0.525	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	**0.800**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	**0.737**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	**0.667**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	**0.667**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	**0.667**	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	**0.667**	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.667**	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.667**	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.667**	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.667**	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.667**	0.000

Changing vital rates...

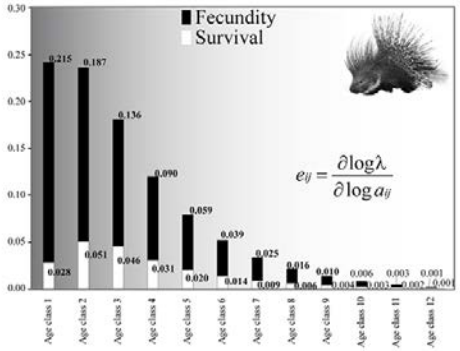
Original Geometric growth rate (λ) = 1.0001.
If we increase by 20% the first year survivorship [0.525 becomes now 0.630], therefore new λ = 1.0391. However an increase of 20% of the first fecundity rate [0.250 becomes 0.300] gives λ = 1.0333 (see explanations in the text)

B. Elasticity matrix with 1% perturbation

0.000	**0.228**	**0.051**	**0.046**	**0.031**	**0.020**	**0.014**	**0.009**	**0.006**	**0.004**	**0.003**	**0.002**	**0.001**
0.215	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	**0.187**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	**0.136**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	**0.090**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	**0.059**	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	**0.039**	0.000	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	**0.025**	0.000	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.016**	0.000	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.010**	0.000	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.006**	0.000	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.003**	0.000	0.000
0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	**0.001**	0.000

Perturbation analysis...

C. Elasticity values (*eij*) of fecundity and survival rates



The sum of the elasticities (*eij*) is 1

FIGURE 4 – (A) changing vital rates from the original Leslie matrix of *Hystrix refossa* ; (B) perturbation analysis with elasticity Matrix ; (C) proportional effect of changes on survival and fecundity rates (see explanation in text ; data from Monchot *et al.* [90])

Let's take the matrix of the fossil porcupine *H. refossa* (Figure 4-A) from the natural shelter of Geula cave (Mount Carmel, Israel) [124]. The dominant eigenvalue of the matrix is $\lambda = 1.0001$ showing a perfect stability through the deposits of the different cohorts of porcupines and suggesting a non-impacted population. Suppose that we increase by 20% the first survival rate S_0=0.525 being now 0.630, then new growth rate is 1.0391 (increased by 3.9%). Let's do the same with the original fecundity rate $m_1 = 0.250$ being now 0.300 corresponding to new $\lambda = 1.0333$ (increased by 3.3%). It appears that the population lambda is more sensitive to changes in the first year survivorship than to changes of fecundity rate from the first reproduction. In our example it is possible to display elasticity values in a new matrix to each of the matrix entry (Figure 4-B). The results clearly show that a given change in young

and adult survival would have a greater effect on λ than fecundity (Figure 4-C). This perturbation analysis indicates that a 1% increase in the survivorship of the first age class leads to increase the lambda by 0.21%, ten times more than the corresponding fecundity that would lead to increase the λ by 0.02%. In our field, it is not trivial to consider this approach because it gives trends on how λ evolves for different species.

To summarise, and as if we were in the cave counting the last individual, elasticity of *H. refossa* indicates that the most critical vital rate to impact the age structure was the survivorship of young and adults. This is also the case in modern populations of large herbivores [125]. Elasticity analysises are consequently very powerful in wildlife management to identify what demographic rates are the most inferential in the population dynamics and the evolution of life histories (see for example r or K selection theory : [126-127]).

4 Conclusion

Giving step-by-step examples we showed that estimating dental individual ages, and then, establishing their distribution in appropriate age class intervals according to prediction error of median age provide an efficient way to construct mortality curves. We questioned the two dominant theoretical types of mortality, attritional *vs* catastrophic that are usually considered as key components to describe fossil age structures in zooarchaeological literature. With minor exceptions, and whatever the methodological approach, all fossil age structures are submitted to taphonomic biases (*s.l.* natural, anthropic or carnivore modifications) so that only a fraction of the original paleontological or archaeological assemblage is recovered. Furthermore if the deposit conditions (*i.e.* unique or multiple assemblage) are not known precisely, then U- and L-shape mortality and especially intermediate patterns cannot accurately be associated to specific human/carnivore food behaviour tactics. For example does it make sense to interpret different fossil age structures mixed through time that are not consequently related to one single population of predators ? We examined in detail how the use of time specific model provided standard demographic parameters to assess mammalian mortality.

The remarkable properties of life table components (see above l_x, q_x, s_x, e_x, k_x, R_0, etc.) offer multiple possibilities to compare fossil age structures between species from different zoological groups and contexts. Moreover, current mammal life tables whose causes of death are known as well as demographic parameters may help control for some biases in the fossil assemblages. Finally, on the basis of different case studies we presented a simple Leslie matrix model that admit multiple cohorts and allow to answer central issues such as is the sum of their different age structures reflect a stationary and stable population at a given time ? Which demographic parameters are the most sensitive to the final state of the population ? This prerequisite is essential in natural paleontological contexts (carnivore dens, pitfall/aven, etc.) as well as in anthropic sites. We showed that Leslie matrices gave both the picture of the initial fossil sample and the projection of the entire population according to original demographic parameters. This may seem counterintuitive in our field but this is the way

to characterize the state of a population and its viability in a population dynamics context.

Finally, we showed that the model could provide suppleness by performing perturbation analysis (*e.g.* sensitivity/elasticity) in order to identify in each age class which demographic component (survivorship, fecundity) was potentially the most sensitive to influence the population growth.

To conclude, the review of methodological different approaches in zooarchaeological studies indicates that our community failed to normalize mortality patterns for Pleistocene mammal species. It appeared that all paleobiological contexts are submitted to multiple taphonomical biases including natural or animal modifications that affect original samples size. With few exceptions with clear evidence of unique deposit and contemporaneity of all individuals, assumption of different cohorts/individuals through time should be made to interpret mammalian age structures. In this way current ecological models such as life table and Leslie matrices are appropriate to estimate crucial demographic parameters of fossil age structures.

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Encart 10. – Improving eco-cultural niche estimations : the potential of archaeological faunal remains for taking biotic interactions into consideration

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1 Introduction

Since cultures operate within an environmental context, it is important to understand the range of environmental conditions they habitually, or could potentially, exploit —*i.e.*, their ecological niche— when examining and interpreting the diversity and complexity of material cultural assemblages, as well as settlement and subsistence systems. In doing so, it becomes possible to better understand culture-environment relationships, begin disentangling the constellations of factors and processes at work behind them, and comprehend how they influenced documented cultural trajectories. When studying prehistoric cultures that lived during periods marked by rapid and dramatic climatic, and thus environmental, change (*e.g.*, Marine Isotope Stages 4-2) and whose behaviors are only attested to by the archaeological record, our ability to reliably estimate the ecological niches that they potentially exploited —termed an 'eco-cultural niche'— becomes even more critical.

A number of studies have examined archaeological data in the context of climatic variability to infer how shifting environmental frameworks may have influenced Paleolithic cultural adaptations and demography [1-11]. Despite the variety of approaches taken, no real consensus has emerged as to how best to evaluate and interpret adaptive changes documented in the archaeological record, and this is due in large part from a lack of focus on how culture-environment relationships might be intertwined with ecological niche dynamics.

Eco-cultural niche modeling (ECNM), an heuristic approach that integrates archaeological, chronological, and paleoclimatic data, via predictive algorithms developed within the ecological and biodiversity sciences, provides a means to estimate the ecological conditions exploited by culturally cohesive populations and evaluate their potential variability through time—*i.e.*, evaluate potential ecological niche dynamics [12, 13]. By characterizing estimated eco-cultural niches and evaluating them against quantified material culture variability and inferred adaptive shifts, ECNM makes it possible to tease apart the various mechanisms (*i.e.*, suites of factors and their processes of interaction) [14], be they cultural or

ecological, implicated in past culture-environment relationships and understand how they influenced cultural trajectories.

Ecological niche modeling methods [15], from which ECNM is derived, are effective for estimating a species' or population's environmental requirements and associated potential geographic distribution, as well as anticipating likely geographic range shifts in the context of climate change. There remain uncertainties, however, concerning how the interplay between abiotic and biotic factors influence a species' ecological niche and potential distribution, and this despite a hierarchical view of these factors' relations. This view, termed the Eltonian Noise Hypothesis (ENH) [16] posits that inter-species interactions and resource distributions (*i.e.*, biotic factors) are important at reduced spatial scales, whereas coarse-scale environmental (*i.e.*, abiotic) factors are more influential on species distributions at broader scales and at these larger scales the influence of biotic factors is difficult to discern statistically [17]. A massive literature supports the general expectations of the ENH (*i.e.*, distributions can be predicted rather well from abiotic conditions only), although some studies' findings do not [18-20]; the latter are likely a result of biotic interactions that operate across relatively homogenous regions that are abiotically suitable for a species [15]. The degree to which ENH may hold true for human hunter-gatherer populations and estimations of the geographic distributions of their respective eco-cultural niches remains an open research question. This paper argues that archaeologists possess a unique class of data —the presence of faunal remains representing animal species hunted by human groups— that can and should be used to attempt to capture biotic interactions, thereby potentially improving the robustness and accuracy of eco-cultural niche estimations and allowing the relevance of the ENH to past hunter-gatherer populations to be evaluated.

2 Placing archaeological cultures in an environmental context

When the goal is to examine whether cultural shifts documented in the archaeological record may correlate to rapid-scale climate change, the ability to accurately determine with which climatic episode(s) a given archaeological culture was associated is critical. A little more than two decades ago paleoclimatologists discovered that the Late Pleistocene (ca. 120-11k cal BP) in the northern Hemisphere was characterized by abrupt and pronounced climatic fluctuations that occurred on millennial and sub-millennial time scales [21-23]. Temporal resolution of this Dansgaard-Oeschger (D-O) variability has continually increased [24, 25], however completely deciphering the complexity of these events and the mechanisms behind them remains problematic [26-30]. Detailed analyses of marine and terrestrial climatic archives, along with paleoclimatic simulation studies, have allowed detailed reconstructions of climatic and environmental conditions across Europe during the Last Glacial period [31-33]. Tephra signatures suggest that D-O events were largely synchronous across the North Atlantic and Europe [34, 35], although marine and terrestrial archives demonstrate that their regio-

nal expressions differed [31, 36-38]. As it concerns the late Middle Paleolithic and Upper Paleolithic, improvements in radiocarbon dating methods [39, 40], calibration curves [41, 42], in conjunction with Bayesian age-modeling methods and readily available software packages (*e.g.*, OxCal, ChronoModel) [43-46] have allowed researchers to better constrain the chronological limits of archaeological cultures and thus more accurately correlate them with specific climatic events and corresponding environmental frameworks [12, 47].

Bayesian age-modeling methods are especially valuable for time periods approaching the chronological limits of 14C dating (*i.e.*, ca. 40-50k cal BP) since their incorporation of stratigraphic or contextual priors can help reduce the statistical noise due to the relatively large errors of radiocarbon ages associated with late Middle Paleolithic and early Upper Paleolithic archaeological levels. One must be extremely cognizant of contextual and taphonomic issues, however, when compiling and evaluating radiometric data to be analyzed with such methods [48]. Most Middle and Upper Paleolithic archaeological sites, and their associated cultural levels, have been subjected to some degree of post-depositional modification in addition to the fact that many cultural levels represent palimpsests of cultural activity or occupations. If such factors are not taken into account, then the validity of age model results may be compromised, so it is paramount that all chronological data be adequately evaluated and vetted prior to running and interpreting Bayesian age models.

3 Potential cultural responses to environmental change

From an ecological perspective, when faced with rapid-scale climatic change and subsequent reorganization of environments, hunter-gatherers can respond in a number of ways. First, groups may maintain existing settlement, subsistence, and technological systems, conserve the ecological niche they exploit, and simply track its shifting geographic footprint. In another scenario, environmental changes could negatively impact demography and social networks, thereby preventing the maintenance of cultural traditions [49]. This effect could lead to loss of certain technological and social adaptations and ultimately niche contraction such that the population would only make use of a subset of the environmental conditions that it used previously. Inversely, periods of climatic amelioration can result in a lowering of ecological risk levels such that a human population may, with the same or similar cultural adaptations, shrink their realized ecological niche by only focusing on certain subsets of the niche exploited previously. Such situations may be characterized by the regionalization of hunter-gatherer populations and cultural drift between macro regions—a situation hypothesized to have occurred between the Middle and Upper Solutrean in Western Europe [13].

It follows, thus, that the fact that culture allows for rapid adjustments and adaptations to changing climatic conditions and new environments must also be considered [50, 51]. This behavioral flexibility among hunter-gatherers may be recognized archaeologically by technological changes (bone and lithic tool-

kits), shifts in subsistence and settlement systems (mobility structure, geographic ranges, etc.), and shifts in social network structures (inferred from shared material culture styles). As a result, in some instances, cultural adaptations allow for the potential expansion of the exploited ecological niche as a means of adjusting to abrupt restructuring of environments. An examination of archaeological cultures for early AMH populations in Europe found that the Early Aurignacian cultural technocomplex expanded its niche significantly during a period of marked climatic deterioration [12]. This study demonstrated that the tendency towards niche conservatism generally observed among plant and animal taxa [52-54] does not necessarily apply to human hunter-gatherer populations. Therefore, an important question is, what are the mechanisms (involving ecological or cultural factors, or both) involved in determining whether an archaeological culture conserves, contracts, or expands its exploited niche, with respect to a previous culture, in response to climate change ? It is only by reliably and accurately estimating past ecological (eco-cultural) niches, and therefore by attempting to take into consideration all relevant factors that serve to influence an ecological niche (discussed below), that this question can be answered.

4 The ecological niche

The *realized ecological niche*, represents the environments associated with the intersection (G_0) of three broad factors : environmental conditions (A), biotic interactions (B), and geographic regions potentially accessible to the target population (M), as depicted by the BAM diagram [15, 55] (Figure 1). With respect to human populations, one can substitute the term *eco-cultural niche*. The overlap between A and M is termed the *existing fundamental niche* ; because biotic interactions [18, 56, 57] are difficult to quantify and incorporate into predictive architectures, many modeling efforts neglect such interactions and allow them either to represent noise in the system or to manifest via correlations with A or M. However, the Eltonian Noise Hypothesis (ENH) [16] suggests that biotic interactions are only influential at finer spatial scales and will rarely be manifested in geographic effects.

When the ENH hold true, the effects of biotic interactions are essentially averaged out over broad geographic scales, thereby making $A = B$ (Figure 1), and when M has been incorporated into niche modeling process, then resulting niche predictions could be considered to estimate, at a minimum, the intersection of the existing ecological niche with geographically accessible regions. On the other hand, in situations where the ENH does not hold true for examined hunter-gatherer populations, resulting predictions may overestimate the fundamental niche (A). This has important implications especially when trying to identify the factors that may have resulted in an archaeological culture having an observed distribution that differs significantly from that predicted with the eco-cultural niche modeling approach. In other words, one should consider the possibility that a large divergene between observed distributions and the estimated niche may be a product of the non-inclusion of biotic factors rather than cultural or

adaptive factors. The validity of the ENH with respect to prehistoric hunter-gatherer populations and estimations of their ecological niches has not yet been formally evaluated. The archaeological community, however, is in a unique position to test its validity by incorporating archaeological faunal data into the niche estimation process.

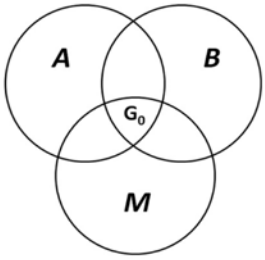


FIGURE 1 – BAM scheme for understanding species' distributions. A – environmental conditions (the fundamental ecological niche) ; B – biotic interactions (the interaction niche) ; M – the geographic region(s) accessible to a species. The 'realized niche' is the intersection of environments associated with these three factors, indicated by G_0. (Adapted from [55].)

4.1 Eco-cultural niche modeling

Before discussing the incorporation of faunal data into the niche estimation process, it is necessary to briefly outline how ECNM works. As pointed out above, this analytical approach, which examines archaeological data, in conjunction with chronological and paleoenvironmental data and via predictive algorithms, allows questions related to the diverse nature of culture-environment relationships to be addressed.

Once an archaeological culture, or a distinct regional variant of a larger techno-complex, has been placed in its correct chronological, and thus, paleoenvironmental framework, appropriate paleoenvironmental rasterized data layers (climatic and vegetation) are selected along with the geographic coordinates of archaeological sites assigned to the culture being examined. With the above data as inputs, a number of statistical and mathematical predictive algorithms that work with presence-only data can be used to estimate past ecological niches and population distributions (*e.g.*, envelope models, genetic algorithms, and maximum entropy methods). Because no single predictive algorithm will be the best performer under all circumstances, the ecological community agrees that a combination of algorithms should be used [58-60] and the best single or few should be used in a given situation [61].

While each predictive algorithm functions differently, at a general level they identify environmental characteristics of known locations (geographic coordinates) of where the population being studied has been observed, create and test rules that define these parameters' relationships, and in effect estimate an ecological niche and its geographic distribution. ECNM thus reconstructs or estimates a past

ecological niche exploited by an archaeological culture, or regional variant of a broader technocomplex, and the geographic expression of this estimated niche.

4.2 Niche estimations that include faunal data

With the approach described above, which relies on paleoclimatic and vegetation variables as environmental data inputs, it is not entirely evident whether the produced niche estimation represents the realized ecological niche (G_0) or if the results depict the existing fundamental niche, which is represented by the intersection of A and M ($A \cap M$) (Figure 1), thereby overestimating G_0. As pointed out earlier, if the ENH holds true for the archaeological human population under investigation, then G_0 is in fact equivalent to $A \cap M$. If the ENH is not valid in a given situation, then it is important to find a means of capturing biotic interactions (B) so that one can attempt to approach G_0 with any produced niche estimations.

I propose that archaeological faunal remains represent an ideal class of data with which to conduct such evaluations of the ENH and to potentially improve our ability to accurately reconstruct the realized ecological niches of past hunter-gatherer populations. Past hunter-gatherer populations' subsistence strategies included the hunting of large herbivores and the evidence of interactions with these mammal species are attested to by the presence of their skeletal remains in archaeological cultural levels. While their subsistence regimes were not entirely dependent on the exploitation of large mammals, in most periods of the Paleolithic, large mammals represented a significant portion of their animal-based diet, and it has been demonstrated that in many instances human mobility and settlement systems were strongly influenced by the presence or seasonal presence of such game. Therefore, by taking large mammal faunal remains into consideration in the niche estimation process, one can, at least in part, capture biotic interactions. In other words, the presence and distribution of prey species could have played a role in defining a hunter-gatherer population's realized eco-cultural niche. By including these data in the estimations of past eco-cultural niches, one can evaluate whether or not the use of detailed climatic data is indirectly capturing the presence of such species, thereby supporting the ENH, or whether the inclusion of faunal data can add additional details or resolution to estimated niches and should, therefore, be included in all eco-cultural niche estimation studies.

To do this, one can document the presence of particular large mammal species recovered from sites with cultural levels associated with the archaeological culture(s) being investigated. The geographic coordinates of these faunal being sites can be used to create ecological niche estimations for each species (*e.g.*, reindeer, bison, horse, etc.). These faunal niche predictions will be in the form of rasterized geographic distributions where the potential presence and absence of each species is indicated, and these raster data can be included as individual environmental data layers that the predictive algorithms will take into consideration when estimating an eco-cultural niche. Thus, the resulting eco-cultural niche es-

timation will have a higher likelihood of capturing a hunter-gatherer population's realized ecological niche.

5 Conclusions

The advantages of the approach outlined above are two-fold. First, it provides archaeologists with the ability to evaluate the validity of the Eltonian Noise Hypothesis with respect to past hunter-gatherer populations in situations where multiple, high-resolution environmental variables are used to estimate eco-cultural niches. Most eco-cultural niche studies to-date have focused on large geographic scales, and based on the substantial literature demonstrating that the ENH hold true for most biological taxa at such scales, it is natural to assume that the same holds true for human populations. Nevertheless, such an assumption must be validated, and if it does not hold true, it is important to understand why and if such situations have a common denominator. Secondly, since one of the principal goals of eco-cultural niche modeling analyses is to identify the mechanisms that operated behind past culture-environment relationships, including the distributions of large mammal prey species in the eco-cultural niche estimation process should allow us to better capture the factors that potentially shaped the niche exploited by past hunter-gatherers and trace the influence of such factors through time and across cultural trajectories.

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