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The power of models: Mathematical approaches to the study of human–fauna interactions in the Pleistocene



Understanding the complexity and dynamics of biological or ecological systems requires the inclusion of an abstract representation of the phenomena in the focus of interest. Indeed, a model is an abstract and simplified representation of a complex system in form of a narrative, a graph, a physical object, or a mathematical development. Narratives, i.e. verbal models, are the first step towards abstraction, and they are profusely used in palaeontology and archaeology to explain complex phenomena like biological dispersions (e.g. Koenigswald, 1992; van der Made, 1992; Agustí et al., 2009; Carbonell et al., 2010; Made and Mateos, 2010; Moncel, 2010; Muttoni et al., 2010; O'Regan et al., 2011; Palombo, 2013; Muttoni et al., 2014), human survival strategies (v.g. Hill, 1982; Speth, 1989; Bunn and Ezzo, 1993; Bunn and Pickering, 2010; Speth, 2010; Pobiner, 2015), human evolution (e.g. d'Errico and Sánchez Goñi, 2003; Rosas, 2003; Finlayson et al., 2004, 2006; Foley and Gamble, 2009; Condemi and Weniger, 2011; Dennell et al., 2011; Bermúdez de Castro and Martínón-Torres, 2013), or ecosystem evolution and dynamics (e.g. Turner, 1992; Blumenschine et al., 1994; Brantingham and Kuhn, 2001; Van Valkenburgh and Sacco, 2002; Croitor and Brugal, 2010; Kahlke et al., 2011). Being useful as they are, verbal models have a number of disadvantages in comparison to formal models. Formal models usually go beyond questions that require only data interpretation and/or statistical analysis. They work in several situations, helping to evaluate empirical problems resulting from field or laboratory data and/or to propose theoretical settings based on initial assumptions (Jopp et al., 2011). Mathematical models are, indeed, formal models, and thus they are formally precise. As a result, any inconsistency in the formulation of processes is easily detected. They are also numerically accurate, producing quantitative predictions and simulations that are supposed to be tested against the observed data (Soetaert and Herman, 2009). Although mathematical representations and verbal descriptions are usually thought of as entirely different processes, in fact, both are components of the same epistemological system.

1. Getting started: what can models help us to do?

The importance of mathematical models has continuously been increasing during the last couple of decades. Mathematical modelling, indeed, has more and more revealed itself as an extremely helpful tool to describe complex systems dynamics (e.g. among several others Berliner, 1996; Hritonenko and Yatsenko, 1999; Willgoose, 2005; Hanzhong, 2009; Villa et al., 2009; Lane, 2010; Reitsma, 2010; Carloni et al., 2011; Jiangqi et al., 2011; Grinin

et al., 2014). Throughout time, statistical models have been used to describe the dynamics of complex systems in a number of disciplines, in particular to explore ecological theory. Moreover, some improvements in statistical modelling have also been attained based on ecological concepts. A growing literature deals with modern statistical methods for describing patterns in data, sometimes trying to link statistics with mathematical models able to depict multifaceted ecological dynamic scenarios (e.g. among several others Wangersky, 1978; Jørgensen, 1995; Hilborn and Mangel, 1997; Liu and Chen, 2003; Wikle, 2003; Peck, 2004; Grimm and Railsback, 2005; Katz et al., 2005; Soberon, 2005; Prokopkin et al., 2006; Gavrilets et al., 2007; Royle and Dorazio, 2008; Li et al., 2010; Wang et al., 2010; Zhao, 2010; Acharyulu and Ramacharyulu, 2011; Liu et al., 2011; Koch et al., 2012; Kranz, 2012; Hannon and Ruth, 2014; Feller et al., 2015; Henson, 2015; Poggiale et al., 2015; Sun, 2016).

Ecological modelling is founded on the knowledge of how organisms behave, how they move, disperse and interact with their environments. Models, and to a lesser extent datasets, for instance, embody sophisticated statements of environmental knowledge. The basic premise for modelling is to deepen our understanding of biological knowledge and to establish relations to its ecological background. Thus, the observable state of any ecological system depends, for instance, on historical contingencies, whose dynamics can be understood only if properly described analysing long-term variability, measuring abiotic features and deconstructing compound biological variables (e.g. species diversity and abundance, as well as the functioning of food webs, among others) by means of a multidisciplinary approach supported by basic to more sophisticated statistical tools. Significant aspects of a number of biological processes may be clarified by mathematical models that convert conceptually formulated models into mathematical ones by means of parameters that may be estimated considering the different levels of certainty regarding their own values.

In spite of their analytical and predictive value, mathematical models have been used only sporadically, although increasingly, in deconstructing causal factors driving the dynamics of palaeoecological and archaeological processes (see e.g. Birks, 1985; Flores, 1998, 2014; Brantingham and Kuhn, 2001; Banks et al., 2006, 2008; Holmes, 2007; Lycett and von Cramon-Taubadel, 2008; Steele, 2009; Griffith et al., 2010; Stiner et al., 2010; Barton et al., 2011; Sørensen, 2011; Rodríguez-Gómez et al., 2012, 2014; Wales, 2012; Romanowska, 2014; Frank et al., 2015; Peart, 2015; Yule et al., 2014; Romanowska et al., in press). This is in particular true with regard to dispersal, dispersion and settlement of hominin

populations in Eurasia throughout the Early and early Middle Pleistocene. It has been commonly accepted that animal resources and competition with large predators were among the crucial factors conditioning population dynamics and survival opportunities of hominins during the Pleistocene (see e.g. Turner, 1992; Arribas and Palmqvist, 1999; Dennell, 2003; but see also; Palombo, *in press*). Therefore, estimating the amount of resources that can be obtained from an ungulate population, evaluating the effect of human hunting on the extinction of some large mammal species, and measuring the intensity of competition within the carnivore guild are of unquestionable interest to better understand the role of humans in past food webs and properly delineate the viability and dispersion of early human populations from Africa towards and across Europe.

2. Getting on: diversity of approaches in modelling

The aforementioned research questions are amenable to quantitative analyses and most of them have been occasionally addressed using mathematical models. During the XVII International UISPP Congress (2014, Burgos, Spain) a session was devoted to discuss and promote the use of mathematical tools, mainly through mathematical modelling, for studies related to human evolution and human–ecosystem interactions. Some among the themes discussed during the session are presented in this volume aimed to illustrate to what extent various analytical approaches, conceptual models and mathematical modelling may contribute to examine complex human–fauna–ecosystem interactions. Papers have different levels of abstraction in the development of models, from a more concrete qualitative approach (Vinuesa et al., 2016), to the most complex level of abstraction (Hölzchen et al., 2016). All in all, they can be considered as examples of an increasing abstraction process, from describing the patterns observed in the fossil record, applying analytical approaches and explicative hypotheses to develop conceptual models incorporating causal mechanisms, to finally translating conceptual models into formal models suitable for statistical validation and/or able to produce predictions that may be contrasted with data.

Any increase of our knowledge on the autoecology and ethology of species provide valuable clues to the debate of the putative competition among large predators and humans during the Pleistocene. An example of this kind of analysis is provided by Vinuesa et al. (2016), who try to clarify the behaviour of fossil hyaenas by means of digital palaeoneurological techniques, analysing the brain morphology of the fossil Eurasian species *Crocota spelaea* and *Crocota ultima*. The results obtained suggests that extinct species of *Crocota* displayed less-developed social abilities and/or had a more restricted adaptability to new environments compared to extant ones. Behavioural differences may contribute to improve our understanding of the ecological roles played by humans and hyenas as well as the degree of competition in Pleistocene ecosystems.

Faunal dynamics in the past may also be studied at a low level of abstraction by collecting an extended data set and analysing it by means of innovative approaches that adapt methodologies used to study present communities to describe the ecological structure of past spatio-temporal metacommunities (*sensu* Palombo, 2007). The analysis of the Functional Diversity (FD) (i.e. the amount of inter-specific variation in functional traits in an ecological community) can provide information useful to quantify the functional aspect of biodiversity and to infer changes in ecosystem functioning and environmental constraints estimating the change in the amount of resource partitioning among species, humans included. The paper by Palombo (2016a) focuses on the trend of FD in SW Europe at the time of the Mid-Pleistocene Revolution (MPR). The

results support the hypothesis that the climate setting as well as environmental instability characterizing this interval may have supported the appearance of newcomers occupying different ecological niches in SW Europe. An important role in the success of human dispersal was possibly played by the functional change in the structure of large mammalian communities inhabiting a more arid and open environment where more flexible, opportunistic species, such as hominins, may have had higher chances to exploit a broader spectrum of resources, thereby avoiding or at least reducing competition with more specialised species.

A peculiar aspect of the structure of a mammalian community, but central in analysing human–fauna relationships, is the degree of competition for food resources shared with carnivores. The study presented by Volmer and Hertler (2016) aims to develop a model for quantifying competitive relations within extant and fossil carnivore guilds based on the theory of competition-free carrying capacity (CFCC). The CFCC value represents the maximum population size under the assumption that the guild member would exploit its essential resources in absence of competitors, and the loss of CFCC to other guild members may quantify the competition effect. Results obtained by applying the model to the large carnivore guilds from the Serengeti (Tanzania) and the Kruger (South Africa) National Parks underline that the method may be successfully transferred to analyse the structure of past guilds of large carnivores.

Nonetheless, knowledge on the structure of past carnivore guilds, although important, is just one aspect of the trophic interaction among species. Food webs are also addressed by analysing the network of direct and indirect interactions among diverse primary and secondary consumers in detail. Lozano et al. (2016) analysed the palaeo-food webs in the European Early and Middle Pleistocene with the aim of improving our understanding of the changes as a response to interactions among large mammals in this period. This study sheds some light on the influence of those changes on *Homo* species, and vice versa, how the presence of hominids shifted the structure of the food web. The results indicate, on the one hand, that the Pleistocene food webs shared basic features with the modern ones, although a marked shift in the networks occurred during the MPR. On the other hand, they underline that hominins by channeling energy fluxes occupied a central position in the trophic web.

The entity of energy fluxes and availability of resources, which constrain the competition among secondary consumers, may be estimated by measuring the intra-guild competition in faunal assemblages and in turn comparing the characteristic of the environment inhabited by a palaeocommunity. A standard method to measure competition intensity and resource availability in different assemblages is proposed by Rodríguez-Gómez et al. (2016). The authors present different indices to measure the intensity of competition in the secondary consumer guild combining a standard approach with a mathematical model based on Leslie Matrices. In particular, the mathematical model provides the expected density for each secondary consumer species by taking into account available prey and existing competitors, and estimating them from allometric equations. Rodríguez-Gómez et al. (2016) base their analysis on the available biomass of secondary consumers and their sustainable biomass. These indices are applied to different recent and Pleistocene faunal assemblages to identify their respective potential. Results obtained indicate that the six indices developed by Rodríguez-Gómez et al. (2016) provide valuable information for the analysis of competition intensity between secondary consumers, in particular with regard to their proportions and the biome type of the area. Furthermore, the values obtained for palaeocommunities fall within the range observed in recent faunal assemblages and show a pattern of variation between prey-predator ratios similar to that observed in other Pleistocene

Mediterranean faunal assemblages. Although both Volmer and Hertler (2016) and Rodríguez-Gómez et al. (2016) models are aimed to measure intra-guild competition, they differ in the data that are used as input and in focussing on diverse aspects of the trophic dynamics. Carnivore species density is the output obtained in Rodríguez-Gómez et al.'s (2016) model, while Volmer and Hertler (2016) use the number of identified specimens, a proxy for relative densities, as input. Moreover, Rodríguez-Gómez et al. (2016) model uses prey species densities estimated from allometric equations as input data. The model predicts stable population structures and mortality patterns for each prey population. Thus, both models are based on different assumptions and may be applied as complementary tools to study competition and trophic dynamics in past communities.

The age structure of fossil populations in a local faunal assemblage is an additional characteristic that may help to understand the structure of a past community and/or the behaviour of a predator. A parametrical model aimed to describe a stable and stationary age structure in a focal population was proposed by Martín-González et al. (2016), based on the Weibull model, a distribution-free survival model which distribution is simultaneously both proportional and accelerated (Carroll, 2003), combined with a model for population dynamics based on the Leslie Matrix. The values obtained represent the survival and mortality profiles for an ecologically stable population. The methodological approach proposed by Martín-González et al. (2016), answers the question of whether an observed mortality profile might correspond to a natural mortality pattern, and may provide some clues on the factors pertaining to the stability of a population through time.

Beyond the study of individual guilds, faunal assemblages, or palaeo-communities some models addressed the evolutionary dynamics of entire ecosystems. Various models are devised to unravel the intricate interactions among many biotic and environmental variables. Agent-based modelling is an innovative tool to deal with highly complex systems. Agent-based modelling permits to examine how agents behave in a non-reductive way and without inappropriate simplification. Agent-based modelling, indeed, permits to model various agents with different features and behaviours. These agents may interact and these interactions have in turn an impact on their behaviour. Such a methodological approach is used by Hölzchen et al. (2016) to show how the predictions of the main “Out of Africa 1 and 2” hypotheses may be evaluated. Each hypothesis suggests different causal factors such as climate, geography, vegetation, demography, competition, ecology and cognition. The most common Out of Africa hypotheses are reviewed, analysed and systematically formalized within an agent-based modelling framework. Results obtained show that the most common

hypotheses can be attributed to four different scenarios, i.e. environmental, demographic, resource driven, as well as ecology and cognition based scenarios. On one hand, the study by Hölzchen et al. (2016) provides a framework that helps designing integrative agent based models for the dispersal of early hominins out of the African continent, on the other hand it supports comparisons of the performance of individual hypotheses.

From an entirely theoretical point of view, and following Karplus (1983) and Haefner (2009), three different applications of models may be distinguished in science according to the type of problem they address: synthesis, analysis and instrumentation. Moreover, any model consists of three components (the input, the system, and the output) and models aimed to solve different types of problems focus on different components (Fig. 1). Models emphasizing synthesis tend to focus on the system itself and try to understand its functioning inferred from input and output components. Models aimed to compare different hypotheses about “Out of Africa” events, as presented by Hölzchen et al. (2016), belong to this category. The study of trophic food webs presented by Lozano et al. (2016) also embarks on this philosophy. Analytical models, on the other hand, simulate the functioning of the system in order to infer an output from a known input. In this sense, most of the approaches presented in this volume represent analytical models (Martín-González et al., 2016; Rodríguez-Gómez et al., 2016; Volmer and Hertler, 2016). The third type of problem, instrumentation, finally implies designing and manipulating a system such that a specified output is the result of an input which is unknown. This last approach has been used, for instance, to study the reliability of the overkill hypothesis as an explanation for the megafauna extinction in Australia at the end of the Pleistocene (Brook and Johnson, 2006), but it is absent from the array of quantitative studies presented here. The studies presented in this volume should encourage researchers to apply quantitative analyses and mathematical modelling approaches to the study of human evolution and dispersals in the frame of the dynamics of terrestrial ecosystems during the Pleistocene. As exemplified by the review of Hölzchen et al. (2016), the plethora of conceptual models formulated to explain the dynamics of early human dispersal towards and across Eurasia, may be converted into mathematical models. However, any model should be based on robust databases provided by multidisciplinary synergic researches. Modellers should realize that the quality of their results or the reliability of their models to represent a process of interest rely on the quality of the input datasets. Aims of modellers on one hand and empirical scientists on the other are not always convergent, sometimes not even commensurable.

As a conclusion, quantitative approaches, and mathematical models in particular, represent a powerful tool to deconstruct the

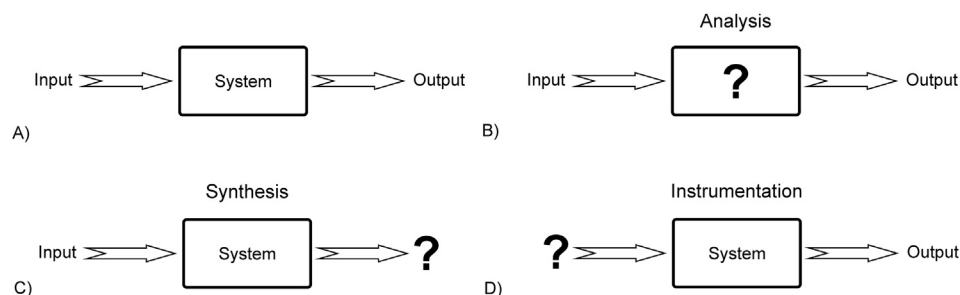


Fig. 1. A model is composed of three elements (A): the input, the system and the output. According to the purpose for which the model was designed we may distinguish three cases. In B) the model is used for analytical purposes, the focus is on the system and the input and output are given. In C) the model is used for synthesis, the focus is on predicting the output, and both the system and the input are given. The model in D) has been designed for instrumentation, the system is manipulated and constrained in order to obtain a given result. Modified from Haefner (2009).

complex network driving the human–fauna–environment interactions during the Pleistocene, a tool able to provide explicative hypotheses based on multidimensional datasets.

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Jesus Rodríguez*, Ana Mateos
National Research Center on Human Evolution (CENIEH),
Paseo Sierra de Atapuerca, 3, 09002 Burgos, Spain

Christine Hertler
The Role of Culture in Early Expansions of Humans (ROCEEH),
Senckenberg Forschungsinstitut, Senckenberganlage 25, 60325
Frankfurt/M, Germany

Maria Rita Palombo
Dipartimento di Scienze della Terra, Sapienza Università di Roma,
Piazzale A. Moro, 5, I-00185 Roma, Italy

* Corresponding author.
E-mail address: jesus.rodriguez@cenieh.es (J. Rodríguez).