Palaeogeography, Palaeoclimatology, Palaeoecology 471 (2017) 15–30

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

Allometric models in paleoecology: Trophic relationships among Pleistocene mammals

Mariana Di Giacomo *,[1], Richard A. Fariña

Departamento de Paleontología, Facultad de Ciencias, Universidad de la República, Iguá 4225, Montevideo 11400, Uruguay

ARTICLE INFO

Article history:
Received 15 July 2016
Received in revised form 25 January 2017
Accepted 29 January 2017
Available online 2 February 2017

Keywords:
Allometry
Pleistocene
Mammalian faunas
Trophic relationships
Paleoecology

ABSTRACT

Paleoecology is a discipline within paleontology that has grown enormously but still remains relatively new. The paleoecology of South American Pleistocene mammals has been a point of major debate since the mid-1990s. This debate focuses mainly on the discussion of the existence of an ecological imbalance between the energetic requirements of the carnivores and the amount of energy provided by the herbivores, and the possibility of using allometric models when studying fossil faunas. The aim of this work was to study the Pleistocene mammalian faunas as a whole and to contribute to such debate. A total of 107 Pleistocene faunas was selected and studied with four thermodynamically based trophic models. Two other faunas were included in the study, Serengeti (modern) and Santa Cruz (Miocene) because they would contribute to the discussion of the relevance of allometric models used in paleoecology. Although this approach may produce results with errors, currently it is among the best tools to be employed in studying paleontology since they can predict characteristics of species, communities or environments with small amounts of data. The models behaved differently in each territory and none of them could explain on its own the paleoecology of the Pleistocene mammalian faunas. The Productivity models are the ones that better explain the paleoecology of several faunas and show the absence of imbalance in the modern Serengeti fauna. Further refinement of these models will make it possible to better understand Pleistocene mammal communities around the world and to analyze vertebrate faunas from other times in the fossil record.

1. Introduction

Paleoecology is a discipline within paleontology that has grown enormously since the seminal work by Dodd and Stanton (1990). It differs from ecology, according to these authors, in three main aspects. The first one is that ecologists use the environment in order to determine the characteristics of the organisms living in it, while this is the opposite in paleontology, fossil organisms help make inferences about the environment in which they lived. The second one is that the fossil record is incomplete, so it is not possible for those studying the discipline to have all the same type of information that is available to ecologists that study modern ecosystems. And the third one is the time scales used in ecology and paleoecology are very different; ecologists can study processes that may take ten years to occur, while paleoecologists study processes that take place in periods lasting thousands or even millions of years.

It is for this reason that studies in paleoecology are relatively new, since new technologies and approaches constantly provide new ways to extract information from the fossil record. It is in this context that mathematical tools such as allometric models come into play, being constantly tested for their predictive powers (Brown et al., 2004, Marquet et al., 2005). Moreover, body size of vertebrates (expressed as their mass) is a most important variable that determines many aspects of the biology and ecology of animals (Brown et al., 2004) and one that can be calculated for paleontological studies. Given the importance of this subject, it becomes a critical factor to utilize, and serves as a starting point in many paleoecological models involving such organisms.

The paleoecology of South American Pleistocene mammals has been a point of major debate since the mid-1990s. This debate focuses mainly on the discussion of the existence of an ecological imbalance (between the energetic requirements of the carnivores and the amount of energy provided by the herbivores) in the South American faunas and the possibility of using allometric models, and their implications when studying fossil faunas.

Fariña (1996) proposed a model for the study of the ecology of fossil faunas in which he related the mass of organisms with their population densities (Damuth, 1981) and metabolic rates (Peters, 1983). His work

* Corresponding author.
E-mail addresses: marudigi@udel.edu (M. Di Giacomo), dogor@netgate.com.uy (R.A. Fariña).
[1] Present address: Department of Art Conservation, University of Delaware, 303 Old College, Newark, Delaware 19716, U.S.A.

http://dx.doi.org/10.1016/j.palaeo.2017.01.040
0031-0182/

mainly focused on the Luján Local Fauna (defined by Tonni et al., 1985), a South American Pleistocene fauna with a high proportion of megamammals. His results suggested this fauna was unbalanced in terms of the numbers of species of primary and secondary consumers compared to modern mammalian faunas, as there were more herbivores than predicted by the inferred primary productivity and too few carnivores for the number of herbivorous species. This model has been used not only in the aforementioned fauna, but also has been applied to other South American and European faunas from the Plio-Pleistocene and Miocene (Fariña, 1996; Palmqvist et al., 2003; Vizcaíno et al., 2004; Vizcaíno et al., 2010). The results of those analyses were mixed, and identified both balanced and imbalanced faunas.

In 2006, Prevosti and Vizcaíno conducted another analysis and suggested that an imbalance did not occur in the Pleistocene community analyzed by Fariña (1996). This study alleged that Fariña's (1996) model is not sufficient for predicting the density of carnivores based on their mass, since the correction factors used for the regression were higher than accepted, causing it to lose its predictive power (Prevosti and Vizcaíno, 2006). They also discussed the relevance of allometric models to study the ecology of carnivores, since it is affected by factors outside the organisms, such as diseases, prey abundance and climate, among others (Prevosti and Vizcaíno, 2006).

Finally, these authors argued that the low metabolism proposed for mylodontids (Vizcaíno et al., 2006) suggests that they would not have been so abundant and would not need as much food as suggested by Fariña (1996) (see 4. Discussion).

Another review of the model proposed by Fariña (1996) was recently published (Fariña et al., 2014). In this work, the authors apply the model to 15 South American faunas, including the Local Fauna of Luján but find that none of the faunas are balanced. Other models are applied as well (see 2. Methods); one of the models used (the Carnivore density model) was applied given the importance Prevosti and Vizcaíno (2006) had given to the population density of carnivores. This model not only did not show any positive results but made the difference between secondary productivity and the requirements of the carnivores the greatest obtained with any of the models applied. The Productivity models showed better results, although more studies are required in South American faunas, given the little data available at the moment.

More recently, Prevosti and Pereira (2014) made a revision of the paleoecological scenario in South America in which they state (rather erroneously – see 4. Discussion) that neither the conclusions in Vizcaíno et al. (2010) nor in Fariña et al. (2014) may be reliable since they did not address the issues pointed out by Prevosti and Vizcaíno (2006).

Unlike previous studies, this work introduces the use of data from local faunas worldwide, further expanding the work by Fariña (1996) and addressing some of the issues presented by Prevosti and Vizcaíno (2006) and Prevosti and Pereira (2014). Moreover, the fact that it includes faunas from all continents and during the same time, makes it advantageous as it eliminates the biases associated with geographical areas or age (although a present day fauna and an older fauna were included for comparison purposes – see below). Working with multiple databases (see 2. Methods), additionally provides a vast amount of information that would not be possible to collect working with individual sites. The only disadvantage is the inability to verify all the species present in each database, as these might not be up to date. The database used in this work seeks to bring together all existing information on the fossil record and has the advantage of being developed, revised and updated by paleontologists from around the world, so that the information provided is of high quality.

1.1. Allometric equations

As addressed above, more and more researchers apply models based on body mass to study vertebrate paleoecology, which involves allometric equations to predict various characteristics of biological species (West and West, 2012). These equations relate the mass of an individual with another of its features and usually have the form $Y = aM^b$, where M is the body mass of the taxon. If an animal is built identical to another but on a different scale, then several of the features of the original model scale should be modified to generate a functional animal (Peters, 1983). Thus, a single model can be applied to phylogenetically different organisms in which their primary difference is in body mass.

These models have been refined in recent years and this is the reason why they are preferred by many ecologists. In paleontology this is relatively new, and there is still a debate about whether they should or not be used (Prevosti and Vizcaíno, 2006). We recognize that a fossil deposit is only a portion of the ancient ecosystem, and therefore such models may underestimate some attributes and overestimate others.

In this paper these models are used because we judge them to provide more advantages than disadvantages. One of these advantages is that these models are independent of the scale, i.e., they are suited to study ecological systems that show variability on time, spatial and organizational scales (Marquet et al., 2005). In paleontology this is the rule, not the exception, as there often exist sites with large time averaging, as is possibly the case of the Luján Local Fauna (Fariña, 1996).

While some of the criticism toward the use of these models relies on the fact that they do not consider many factors that could be critical in the ecology of the different species (Prevosti and Vizcaíno, 2006), some authors propose allometric studies linking other ecologically important variables for those individuals whose results deviate because of them (Carbone and Gittleman, 2002) and others include both deterministic and statistical aspects using the probability calculus in allometric relations (West and West, 2012).

1.2. Pleistocene paleoecology

While the model by Fariña (1996) has been tested in various faunas, these are not sufficient to determine whether it should be used as a general model for mammalian fossil faunas. In addition, the model has always been applied in specific cases, i.e., analyzing individual faunas, but it has never been used globally to identify paleoecological patterns within Pleistocene mammalian faunas other than those from South America dealt with in Fariña et al. (2014). Moreover, with the exception of Venta Micena in Europe and Rancho La Brea in North America, this model has only been applied to South American faunas.

Fossil mammalian local faunas from around the world are numerous and the vast majority of them have been studied only within the context of their discovery or for the descriptions of the taxa present. Only a few have been studied from a paleoecological point of view but usually have not been compared to other faunas. Rather, the focus was to understand the characteristics of the site and the geological events involved in their formation (Palmqvist et al., 2003; Vizcaíno et al., 2004).

In summary, the aim of this work is to contribute to the study of the paleoecology of Pleistocene mammals on multiple continents from an energetic point of view and to see whether any of these faunas have an energy imbalance as proposed by Fariña (1996) or to determine if this perceived imbalance is the result of the ecological model employed for their analysis. It also intends to contribute to the discussion on scaling equations and the pertinence of their use in paleontology. The importance of this work is that it aims to conduct a study that encompasses a diversity of Pleistocene faunas as a whole, looking for a model that can explain the dynamics of mammals from any site on the planet.

2. Methods

2.1. Database

The Paleobiology Database (fossilworks.org) was employed as the main source of the faunas studied here, which were selected from four continents: North America, Europe, Asia and Africa. The browser was