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The contribution of phylogenetics to the study of ruminant evolutionary ecology

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Abstract

The increasing availability of published evolutionary trees and phylogenetic methods has changed the way we tackle the study of evolution. In this sense, ruminants have become one paradigmatic object of study due to their ecological variety and well-known evolutionary history. The last decades of ruminant research have benefited from diverse phylogenetic approaches, offering new perspectives on classic ideas and, sometimes, allowing to test previously untestable hypotheses. As a result, we now start to understand the complexity of the evolutionary responses of this clade to past global environmental changes. This is a brief review of some of the most outstanding and groundbreaking tree-based contributions to the research on the evolutionary ecology of this fascinating group of herbivorous macromammals.

Key words: Macroevolution, ruminants, Artiodactyla, community structure, phylogenetic comparative analysis, evolutionary models.

1. Introduction

Phylogenic trees represent evolutionary relationships among taxa. They are the synthesis of the work of taxonomists and systematists aiming to put the tree of life in order (Smith 1994; Bininda-Emonds et al. 2007, 2008; Jetz et al. 2012). However, whereas the resolution of evolutionary trees is the ultimate contribution of many academics, their precious work may be the starting point for the work of many other researchers, including (paleo)ecologists and evolutionary biologists. In fact, the boom of phylogenetic methods and the increasing availability of published evolutionary trees have changed the way in which we study and understand biology and evolution (Norell 1993; Mooers & Heard 2002; Ronquist 2004).

Ruminants are exceptional in this context. With over 200 living species, they are the most diverse clade of herbivorous macromammals and represent broad ecomorphological diversity (Vrba & Schaller 2000; Hernández Fernández & Vrba 2005; Wilson & Mittermeier 2011). They are distributed world-wide (naturally occurring in most continents; Cantalapiedra et al. 2014a), inhabit all of the world's terrestrial biomes (Vrba 1999; Cantalapiedra et al. 2011). The fossil record of ruminants is rich, complete and ubiquitous, spanning the last 50 Myr and including more than 400 genera and more than 1200 species (McKenna & Bell 1997; Cantalapiedra et al. 2013). Their extensive fossil record and habitat sensitivity make ruminants the ideal group for testing hypotheses about the role of ecology and climate in mammalian evolution. Their phylogenetic relationships have been explored for decades (see references in Hernández Fernández & Vrba 2005), and new phylogenetic hypothesis are presented almost every year (Hassanin et al. 2012; Bibi 2013). Here we provide an overview about how the combination of phylogenetic trees and diverse methods has contributed to broaden our perspective on the biology, evolution and biogeography of ruminants.

2. Statistics and evolutionary relationships among ecomorphological variables

Whether the length of their branches represents time or character change —chronograms or phylograms, respectively—, evolutionary trees hold in their structure a paramount certainty: all species are hierarchically related to each other. Closely related species will tend to be more similar just because their independent history is shorter. In ruminants, this "phylogenetic signal" is widespread and affects

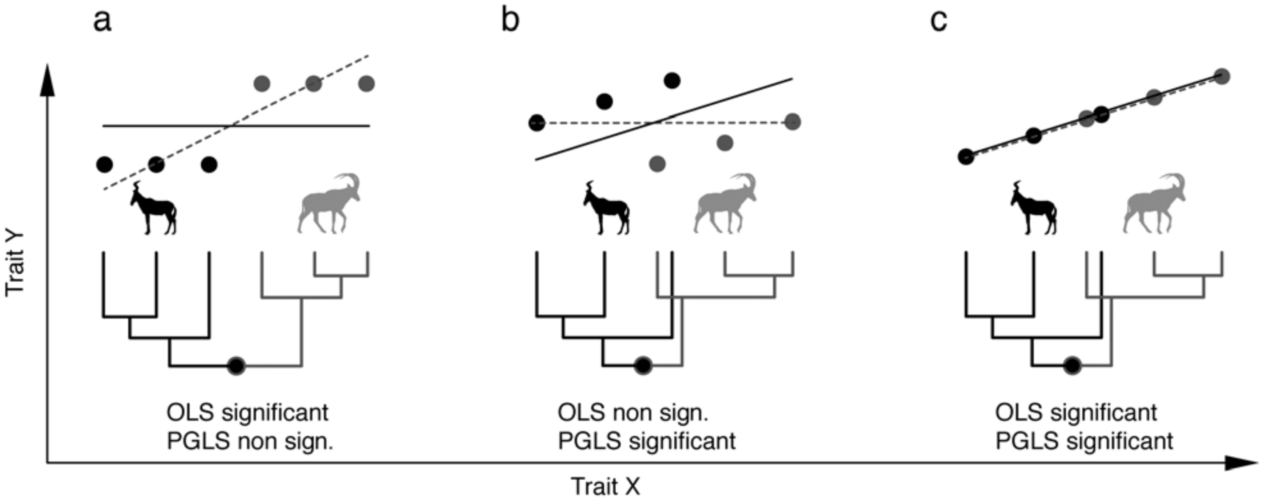

Figure 1: Schematic representation of some of the combinations of results from ordinary (OLS) and phylogeny-informed statistical analyses (PGLS). Two clades and their respective datasets (black and grey) are depicted. Dashed grey line, fitted OLS model. Black solid line, fitted PGLS model. In **(a)**, the relationship between X and Y exists at the scale of the whole tree, but does not apply within subclades (e.g. tribes), suggesting no convergence, as in Brashares et al. (2000). **(b)** Convergent evolution resulted in a within-subclade relationship that is not recognized by the OLS. Both PGLS and OLS may yield a significant result if only one subclade is analyzed, like in **(c)**, where the relationship arises both at the scale of the whole tree and within more closely related taxa. Illustration after the original figures by Clauss et al. (2013), who also provide more examples and an extensive interpretation of the potential results.

many traits of interest including morphology (e.g. oral traits; Pérez-Barbería & Gordon 2001), behavior (e.g. diet, gregariousness; Brashares et al. 2000) or ecology (e.g. habitat preference; Barr & Scott 2013).

Since species are non-independent elements with a shared history, the evolutionary information contained in evolutionary trees is of major importance for exploring trait evolution (Ronquist 2004) and trait-dependent diversification (FitzJohn 2010; Cantalapiedra et al. 2014b), modeling correlated evolution of traits (Pagel 1994), or removing phylogenetic effects on statistical tests (as exemplified in Fig. 1; Felsenstein 1985; Harvey & Pagel 1991). Studies on ruminant evolutionary ecology mainly fall in this last category, a body of research to which we will reserve most part of this article (a comparison of the results of various phylogenetically informed analyses applied to ruminant and ungulate diets can be found in Clauss et al. 2008a). The application of other methods to the study of ruminant ecology and evolution will be treated in a second section.

Different combinations of outcomes from ordinary and phylogenetically controlled tests can yield valuable information on the evolutionary processes after the observed trait distribution (see Fig. 1; Clauss et al. 2013; Clauss et al. 2014). In a very illustrative work, Brashares et al. (2000) revisited classic hypotheses linking diet, antipredatory behavior, body size and group size in the African antelope (Jarman 1974). They found that conventional analyses gave support to Jarman's conclusions, but phylogenetic analyses were less consistent with the classic ideas. In particular, their results show that the relationship found in ordinary approaches is a result of variation among tribes rather than within them (see Fig. 1a), suggesting that the ecological shorting observed is rendered by evolutionary processes that acted at the basal radiation of tribes. In fact, relationships among the other variables were very weak within tribes, reflecting the strong phylogenetic signal of these traits among the African antelope. Overall, this work provides a good example of how phylogenetic approaches can help us to improve our understanding of ruminant ecology.

For years, some ideas on ruminant and, more broadly, artiodactyl ecology based on ordinary methods have became a truism in the literature. Probably one of the most popular topics regards the study of oral morphology (e.g. hypsodonty or premaxillary shape) as a predictor of feeding mode (Janis & Ehrhardt 1988; Pérez-Barbería & Gordon 1999). This correlation is especially useful for academics aiming to infer the diet of fossil specimens and, in turn, past environmental conditions in which they lived (Solounias & Moelleken 1993). But, again, both diet-related morphology and feeding behavior show a marked phylogenetic signal (see below). Furthermore, some traits like the increase in hypsodonty, apart from showing a pronounced phylogenetic inertia, have been reported to be virtually non-reversible (Damuth & Janis 2011). This means that closely related species probably have a more similar hypsodonty degree than expected based only on their phylogenetic relationships because the evolution of this trait does not follow a random walk through lineages probably due to morphological constrains.

Many studies based on traditional approaches have found a strong correlation between oral morphology and dietary behavior. For instance, based on traditional discriminant analyses (whose suitability is discussed in Barr & Scott 2013), Mendoza et al. (2002) obtained a 100% of correct reclassifications of bovid diets based on their morphology due to the strong correlation of their variables (similar results are reported here: Mendoza & Palmqvist 2006a; Mendoza & Palmqvist 2006b, 2008). However, in a study encompassing ungulates, Pérez-Barbería and Gordon (2001) reported that, whereas all the nine morphological variables included in their study — including muzzle width and dental height and volume, among others — correlated with diet in an ordinary analysis, only two of them — molar-row volume and M_3 height — remained explicative after controlling for phylogenetic relationships and body size as a covariable. In fact, these authors found that body size alone provided a better prediction of feeding modes than any of the other seven morphological variables (Pérez-Barbería & Gordon 1999). Although the taxonomic scale of the two studies is not directly comparable (Clauss et al. 2008a), their results highlight the need to incorporate the phylogeny to avoid misleading conclusions on the adaptive role of morphology (Barr & Scott 2013). The relation between teeth features — hypsodonty, mesowear and enamel ridges— and dietary preferences in ungulates and ruminants has been also reconsidered using phylogenetic-informative tests (Kaiser et al. 2010; Kaiser et al. 2013).

The interest for diet-related anatomical traits extends further, and tests accounting for phylogenetic linkage have revealed strong associations between soft tissue anatomy and the percentage of grass intake in ruminants and other herbivorous macromammals (Clauss et al. 2006; Clauss et al. 2008b; Hofmann et al. 2008; Clauss et al. 2009; Clauss et al. 2010). Studies like these highlight the importance of phylogenetic methods to reinforce classic evolutionary scenarios. In fact, they signify the strong and complex relation between the multiple organs of the digestive tract and species ecology. Therefore, we envision future integrative studies, which will take a holistic approach in order to model the way in which these relationships shaped ruminant evolution.

Phylogenetic comparative methods have also been broadly applied in order to address questions regarding diverse ecomorphological parameters as well as social and behavioral ecology of ruminants. Bro-Jørgesen (2008) used bovids as study group to support the maneuverability hypothesis, which predicts that dense habitats select for smaller sizes. His study also revealed the connections of diet, latitude and sexual dimorphism with the maneuverability hypothesis. The same author has applied the phylogenetic comparative method to prove the connection between sociality and longevity as well as the significant effect of predation on the increasing sprint speed in bovids (Bro-Jørgensen 2012, 2013). Mysterud et al. (2001) found support for a general correlation between home range size and body mass in ruminants, although they also reported peculiarities under different feeding styles. Müller et al. (2013) questioned the extent to which digesta retention increases with body size among large herbivores, as posed by classic hypotheses. Using a 110 ruminant species dataset, Zerbe et al. (2012) explored the causes of seasonal patterns of reproduction and proved they are connected to the latitude of the geographical range and were independent of body mass. They also reported that the gestation period is limited as an adaptation to ensure favorable conditions.

The use of the comparative method also encompasses many other interests. As two recent examples, it has been applied to construct model equations that predict body mass of fossil bovid species using several body measures (De Esteban-Trivigno & Köhler 2011), or to identify preservation biases in the fossil record derived from differences in ecomorphological variables (Cantalapiedra et al. 2012).

3. Biogeography, community ecology and evolutionary models

Although phylogenetic information in ruminant and ungulate research has mostly been applied in phylogenetically controlled correlations, its application extends far beyond. One of the most promising fields in community ecology regards the phylogenetic structure of species assemblages. This approach is based on asking whether the species that we found in a given place are more or less phylogenetically related than expected by chance, or whether they represent a random subset of a regional species pool (Vamosi et al. 2009), yielding valuable information on ecological and evolutionary perspectives behind assembly processes. Furthermore, combining phylogenetic structure metrics with multi-scalar perspectives can yield valuable insights into macroevolutionary and macroecological processes (Cardillo 2011). Research tackling the phylogenetic structure of mammalian communities has usually been limited to tropical and subtropical clades (Heard & Cox 2007; Cardillo et al. 2008). Nevertheless, in a recent contribution, Cantalapiedra et al. (2014a) assessed the signal of past evolutionary events — e.g. biogeography, adaptive radiations — in living ruminant communities worldwide. Significantly, the study encompassed all the diverse biomes inhabited by ruminants: from the equatorial rainforest to the tundra. Their results proved that the phylogenetic structure of ruminant communities is highly influenced by within-biogeographic realm radiations. Only assemblages located in extremely arid deserts harbor closely related species due to local habitat selection and within-habitat radiations.

Ruminant research has also drawn from evolutionary models (based on maximum likelihood; Pagel 1994) to test the coevolution of traits. This method simulates the evolution of two traits and generates two models where the traits evolve dependently and independently from each other. The best-fit model is selected based on the maximum likelihood scores (Pagel 1994). In a pioneer study, Pérez-Barbería et al. (Pérez-Barbería et al. 2001) tested the coevolution of feeding strategies — browser, mixed-feeder and grazer — and the occupancy of different habitats — close, mixed and open habitats — in artiodactyls. According to their results, mixed diets evolved before lineages occupied open habitats, which were inhabited occupied by artiodactyls before a pure grazer diet appeared. They also found that habitat use was more flexible than feeding style.

Pagel's method has been recently used in combination with exhaustive phylogenetic and ecological data to test hypotheses linking habitat occupancy and locomotor adaptations in ruminant lineages (Alcalde et al. 2013). In some cases both ordinary and phylogenetic approaches found support for classic associations like the coevolution of gallop with open landscapes — e.g. savannahs or deserts — or between zigzagging (sensu Caro et al. 2004) and dense forests. In others, the phylogenetic analyses challenged classic correlations, like the association of stotting to the occupation of savannas and open woodlands. This indicates that, although savanna ruminants perform stotting, its adaptive value is not well defined — there is no convergence — because stotting species inhabiting savanna only evolved once.

Eventually, in the last few years, evolutionary biologists have drawn from novel phylogenetic approaches to investigate the signals of evolutionary processes — i.e. speciation and extinction — in calibrated phylogenies (Morlon 2014). Such methods can be especially useful when studying the evolutionary history of groups lacking a well known fossil record (Fordyce 2010), but also to explore the influence of a trait of interest in the diversification pattern of a group when that trait is only known for the living species of the clade — e.g. behavioral traits. This is achievable by fitting new evolutionary models — based on Pagel's — that now allow to add differential diversification rates to lineages with different states of a given trait (Maddison et al. 2007; FitzJohn 2012). For example, the combination of novel phylogenetic methods, an extensive dataset of dietary preferences and a paleoclimate proxy provides a useful framework testing the connections among climate, feeding behavior and diversification rates in ruminants (see Cantalapiedra et al. 2014b). The results of this work pointed out that the appearance of mixed diets — i.e. eating both browse and grass — spurred the diversification of ruminants during the Oligocene-Miocene transition, concomitant with high global temperature. The appearance of graze diets could have taken place along the late middle Miocene. Also, both grazer and mixed feeder lineages underwent higher diversification than browsers, although their diversification rates slowed down as temperature dropped towards the late Miocene. Interestingly, this view challenges the classic perspective, based in raw diversity patterns, that the great radiation of ruminants affected grazing forms and was rendered by the global cooling and aridification of the late Miocene (Cantalapiedra et al. 2014b).

Today, we perceive the evolution of ruminants as an integrated process in which global climate changes modified the environments inhabited by ruminant assemblages, triggering various evolutionary responses (Cantalapiedra et al. 2011). During the last 30 million years, different ruminant lineages have modified their behavior and the complex associated ecophysiology (i.e. diet, locomotion, social behavior) as a way to adapt to new environmental conditions (Cantalapiedra et al. 2014b; DeMiguel et al. in press.). Finally, this intricate process of adaptation has been modulated by biogeography and historical factors that in turn influenced the raw material — species pools — on which macroevolutionary processes acted (Cantalapiedra et al. 2011; Cantalapiedra et al. 2014a).

4. Conclusions

During the last decades, diverse analytical methods based on phylogenetics have brought a deep time perspective to the macroevolutionary research in ruminant biology. They have allowed researchers to test hypotheses that were virtually untestable in a straightforward way. Also, taking evolutionary relationships into account has helped to rule out certain ideas that were based on the study of species as if they were independent results of evolution. The current view in which the interplay of climatic shifts, biogeography, historical contingency and ecology have driven ruminant — and mammalian — evolution has been strengthened to a large extent due to contributions based on phylogenetic approaches.

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