

# Living with the elephant in the room: Top-down control in Eurasian large mammal diversity over the last 22 million years



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## ABSTRACT

Mammalian megaherbivores are an essential component of modern day ecosystems. They control a large share of primary productivity, modify habitats by clearing dense vegetation, and keep other herbivores populations small. When rare, small herbivores additionally suffer increased extinction risk by predation. Since megaherbivores are almost immune to predation, it was suggested that the detrimental effect of megaherbivores on smaller competitors has the additional consequence to reduce the prey biomass available to predatory species, thereby increasing their extinction risk. This form of indirect competition between guilds of species is known as apparent competition. These mechanisms are all forms of top-down control on ecosystem functioning, whereby species up on the food chain control diversity at lower levels. We tested these competing hypotheses on a large compilation of Neogene to Recent Old World mammals.

We found evidence in favor of apparent competition. However, direct competition effects by both megaherbivores and carnivores on small prey are even more pervasive. Our results suggest that megaherbivores have been a dominant component of the mammal diversity over time and space during the last 22 million years in Eurasia.

## 1. Introduction

Megaherbivore mammals are traditionally defined as species above 1000 kg (Fritz et al., 2011; Terborgh et al., 2010; du Toit and Owen-Smith, 1989) although alternative 'limits' were suggested to occur (e.g. 450 kg in Fritz et al., 2002). In modern-day ecosystems, the category just includes few species such as rhinos, elephants, the hippopotamus, gaur, yak, and the giraffe, and it is geographically restricted to sub-Saharan Africa and Asia. However, megaherbivores were much more diverse in the recent past. Mastodonts, mammoths, ground sloths, giant armadillos, a number of notoungulates, very large bovids, deer, and camels, plus giant kangaroos and other marsupials (e.g. *Diprotodon*) made the list just a few kilo years ago (Koch and Barnosky, 2006; Sandom et al., 2014). The present-day paucity of megaherbivores is the result of a massive extinction crisis they underwent through the end of the Pleistocene (Koch and Barnosky, 2006; Sandom et al., 2014; Smith et al., 2016).

Extant megaherbivores play a pivotal role in controlling ecosystem functioning and diversity at different trophic levels (Fritz et al., 2002; Fritz et al., 2011; Terborgh et al., 2010; du Toit and Owen-Smith,

1989). By virtue of their body size, megaherbivores control a large share of primary productivity, may exclude smaller species from accessing limiting resources (such as water at ponds during the dry season), and expose them to increased predation risk by clearing thickets of vegetation they use to hide from predators (Fritz et al., 2002; Tambling et al., 2013; Terborgh et al., 2010). All of this translates into negative effects on smaller prey population viability (Burney and Flannery, 2005; du Toit and Yetman, 2004).

Since megaherbivores are almost immune to predation as adults (Fritz et al., 2011; Terborgh et al., 2010; du Toit and Owen-Smith, 1989), predators are expected to suffer from reduced prey availability where megaherbivores are abundant (Hummel and Clauss, 2008). This classical mechanism, known as apparent competition (Holt, 1977) describes competition of a species (or guild of species) upon another through indirect effects. Evidence in favor of apparent competition was advanced for Pleistocene mammal communities (Meloro et al., 2007; Raia et al., 2007; Rodríguez et al., 2012). Crucially, it was demonstrated to negatively affect carnivore diversity in the long term in Pliocene-Pleistocene large mammal communities in Europe (Meloro et al., 2007; Raia et al., 2007; Rodríguez et al., 2012).

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These forms of top-down control on ecosystem functioning were demonstrated to apply in modern African savannah environment (Fritz et al., 2011; Terborgh et al., 2010; du Toit and Owen-Smith, 1989), and are well-recognized mechanisms of diversity regulation in present-day food webs (Pasanen-Mortensen et al., 2017).

We tested the idea that apparent competition of megaherbivores on carnivores applies to Neogene to Recent large mammals at large geographic and temporal scales. To this aim, we used the Eurasian large mammals record to compute the predator-to-prey ratio (PPR), and regressed PPR against the number of megaherbivores per time interval, while accounting for spatial autocorrelation. Apparent competition would imply a negative regression slope between megaherbivores species richness and carnivore species richness over time, whereas a negative slope should apply to megaherbivore species richness and small herbivore richness because of direct competition (Meloro et al., 2007; Raia et al., 2007; Rodríguez et al., 2012).

We also tested the competing idea that the diversity of megaherbivores positively affected the diversity of sabertoothed cats. Such species were deemed to have specialized, to some extent, on large sized species as prey. Positive association between sabertooths like *Homotherium*, *Smilodon* and *Barbourofelis* and megaherbivore fossil remains further supports this idea (Raia et al., 2007; Rawn-Schatzinger, 1992; Van Valkenburgh et al., 2016), to the extent sabertoothness is thought to have evolved for killing the largest prey, and sabertooths are said to have gone extinct once their favoured prey vanished by the end of the Pleistocene (Antón and Turner, 1998; Koch and Barnosky, 2006). Such preference of sabertooths for megaherbivores is often reported in literature (Palmqvist et al., 1996; Randau et al., 2013; Van Valkenburgh et al., 2016), despite counteracting evidence coming from studies of their enamel isotopic composition (Feranec, 2005), long-term analysis of their prey consumption style (DeSantis et al., 2012), modelling of prey selection in extinct guilds of carnivores (Randau et al., 2013; Van Valkenburgh et al., 2016), and biomechanical modelling (Andersson et al., 2011; McHenry et al., 2007; Piras et al., 2013). A further reason to test for the association between megaherbivores and sabertooths diversity is that the latter are hypercarnivorous predators by definition. Van Valkenburgh et al. (2016) surveyed the ecological literature on current ecosystems to find that the diversity of large hypercarnivores and megaherbivore species (there defined as animals > 800 kg in body size) are positively associated, which indicates that the presence of very large herbivores promotes coexistence among large predators, possibly via predation on juvenile megaherbivore individuals. Specialization to feed on megaherbivores by sabertooths would imply a positive relationship between the diversity (species richness) of the two categories, regardless of the actual prey spectrum of individual species (Ives et al., 2004). In other words, sabertooths are expected to have been more abundant and diverse where and when megaherbivores were (Palmqvist et al., 1996; Randau et al., 2013; Van Valkenburgh et al., 2016). Van Valkenburgh et al. (2016) further noted that the large carnivore trophic category also includes non-sabertooth species, such as North American lion *Panthera atrox*, which they deem could limit the populations of megaherbivores by preying upon their juveniles. We consistently tested this notion by regressing the number of megaherbivores against the number of megacarnivores (i.e. carnivore species above 100 kg in body mass, Van Valkenburgh et al., 2016) over time, regardless of whether they were or not sabertooths. A positive regression slope is expected to apply if top predators used megaherbivore calves for their subsistence.

## 2. Materials and methods

We downloaded from the Paleobiology Database ([www.paleodb.org](http://www.paleodb.org)), NOW Database (<http://www.helsinki.fi/science/now>) and Pangea Database ([www.pangea.de](http://www.pangea.de)) Neogene fossil occurrences of mammals belonging to Artiodactyla, Perissodactyla, Proboscidea, Carnivora and Creodonta. We supplemented these data with occurrence records from

Raia et al. (2009) and other published sources (Appendix S1). For each species, age estimates and geographical paleocoordinates of individual occurrences at fossil sites were recorded. Latitude and longitude information from the NOW database are not rotated to their past position on Earth, and were therefore converted in paleolatitude and paleo-longitude coordinates by using the software Point Tracker 2.0d ([www.scotese.com](http://www.scotese.com)). Overall, the occurrences dataset includes 655 artiodactyls, 114 carnivores, 4 creodonts, 163 perissodactyls, 67 proboscideans, for a total of 1003 species spanning from the earliest Miocene (21.9 Ma, *Cainotherium commune*) to the Holocene, distributed over 3021 fossil localities. For each species, we compiled body size estimates from different databases (Appendix S2). We were unable to find estimates for 31.2% of the species (313 taxa). In these cases, we used the mean body size estimate per genus. The use of genus means is certainly less precise than species-level estimates. Yet, given we were interested in distinguishing among meso- and megaherbivores, and among meso- and megacarnivores, genus means are perfectly feasible, given body size tends to be very similar among phylogenetically close species (Blomberg et al., 2003).

Species were divided in four ecological categories based on both diet and estimated body mass: Megaherbivores (Mega), Herbivores (Herb), Carnivores (Carn) and Sabertooths (Sab). The megaherbivore (Mega) category includes species with body mass estimates over 900 kg (Owen-Smith, 1988). The limit between herbivores and megaherbivores is traditionally set at 1000 kg. Given uncertainty in body mass estimates and the presence of sexual size dimorphism in most large herbivore species, we preferred to use a 10% lower limit to be conservative. Species belonging to Machairodontinae, Barbourofelidae, Nimravidae, and Hyperailurictinae clades fall under the sabertooth category. Although not all of them were actually equipped with very long upper canines, and there are felids belonging to the Felinae and Pantherinae families which are considered to be morphologically convergent on sabertooths (i.e. the clouded leopard *Neofelis*, Christiansen, 2008; Therrien, 2005) we preferred maintaining ecomorphologic homogeneity within the sabertooth clades, because carnivores tend to form close knit ecological guilds of closely related species (Dayan and Simberloff, 2005), and presumed sabertooth-like *Neofelis* canines are not laterally flattened (Meachen Samuels and Van Valkenburgh, 2009). In addition, this way we avoided our own choices to influence the data composition. The carnivore (Carn) category only includes species larger than 21 kg in body size. This is because at that size threshold carnivores start feeding on prey larger than themselves by energetic constraints (Carbone et al., 1999). Hence, including smaller species is unfeasible without considering the diversity of small prey such as rodents and lagomorphs.

We first divided the record in 2-million-year-long temporal intervals. This is close to average duration of mammalian species (2.6 myr according to Alroy, 2000; and 2.3 myr according to Marshall, 2017). This way we minimized the temporal autocorrelation between the compositions of subsequent intervals while maintaining a reasonably dense record per interval. For each species and within each time bin, we constructed minimum convex polygons (MCP, Carotenuto et al., 2010; Lyons and Smith, 2010, Supplementary Fig. S1) starting from its fossil occurrences. We overlaid a 500 × 500 km grid cell resolution on each projected continent, sampling regions in an equal area context. To maintain accuracy in spatial sampling, under the equal-area design we used the Mollweide projection for Eurasia, and the Lambert Equal Area projection for Africa. The use of polygons overcomes problems generated by sampling inequality per species and geographic area, by adding cells to the species presence where no fossil occurrence is indeed present, but still within the minimal range of species geographic extent (Supplementary Fig. S2). Similarly, by using a geographic grid all the fossil localities falling within a given cell (i.e. within an area of 25,000 km<sup>2</sup>) in a given time intervals are collapsed in a single faunal list (counting replicated species occurrences as one). In this way, the effect of unequal sampling and taphonomic effects across fossil sites is

leveled off. We performed all analyses twice, both by using the raw fossil occurrence (henceforth “occurrence record”), and by using MCP polygons to attribute species to cells (henceforth “polygon record”). At this stage, for each cell and time bin, we had the species composition, species ecological categories and their body size estimates. Cells with < 5 species overall, or lacking any predator or prey, either, were removed from the analyses.

In order to calculate the predator-to-prey ratio (PPR), we additionally classified Carnivores plus Sabertooths within the “Predators” category ( $Pr = Carn + Sab$ ) and Meso- and Megaherbivores as “Prey” ( $Py = Herb + Mega$ ). For each geographic cell within a given time bin, PPR was computed as the number of predatory species divided by the number of prey ( $Pr / Py$ ). We also computed the body size range of “Predators” (i.e. the difference between  $min\_Pr$  = the size of the smallest predator and  $max\_Pr$  = the size of the largest predator) and “Prey” ( $max\_Py - min\_Py$ ) for each cell within each time bin. We computed degree of overlap between Predators and Prey body masses (PPR-Overlap). When the smallest Predators ( $Pr$ ) body mass was lower than the smallest Prey ( $Py$ ), PPR-Overlap was calculated as the ratio between  $(max\_Pr - min\_Py)$  and  $(max\_Py - min\_Pr)$ . When  $min\_Py$  is lower than  $min\_Pr$ , it means that the body mass range of Predators is included in body mass range of Prey. In this case, Mass Overlap was calculated as the ratio between  $(max\_Pr - min\_Pr)$  and  $(max\_Py - min\_Py)$ .

With these variables, we performed six different regressions using the number of species in each category and their estimated body sizes per cell, and separately per time bin. The regression (1) of PPR against the number of Megaherbivores (Mega) was calculated to test for the effect of apparent competition of the latter on Predators. Predators ( $Pr$ ) were regressed (2) against Herbivores (Herb) to verify for the relationship between the richness of predators and non-megaherbivore prey. The regression (3) between Mega and Herb was computed to test for competition between species belonging to these categories, to test the idea that megaherbivores did control the diversity of Herb. The richness of Sabertooths ( $Sab$ ) was regressed (4) against Mega in order to test the idea that sabertooths preferentially preyed upon megaherbivores. Similarly, the diversity of large carnivores ( $Pr > 100$ ) was regressed against Mega (5). Eventually, we regressed (6) PPR against Overlap in order to verify if an increment in degree of overlap is correlated to a higher chance of predation on megaherbivores, under the observation that larger predator might tackle down comparatively larger prey (Van Valkenburgh et al., 2016).

All of the six regressions were controlled for spatial autocorrelation by using GLS models. In details, we fitted the related empirical semi-variograms with 4 models (Gaussian, Spherical, Rational Quadratic, Exponential) and then updated an OLS regression by these 4 spatial correlation structures. The outcomes of these five models (OLS and the 4 spatially structured) were then compared by means of ANOVA. The spatial neighboring was drawn by using the “spdep” package (Bivand and Piras, 2015), whereas the spatially structured regressions were computed by means of the R package “nlme” (Pinheiro et al., 2014). The six regression models were performed by using cell species richness as a covariate, in order to account for uneven sampling across cells, time bins, or trophic category. In addition, we repeated each regression model, with both cutoff values for the size of megaherbivores (i.e. either 900 kg or 400 kg), by dividing the record in 1 myr long temporal intervals (see Appendices S3–S6 for results).

Consecutive intervals within the same geographical place share a number of species. This means that the data could be temporally autocorrelated, thereby originating spurious associations between the variables. To address the issue of temporal autocorrelation, we used the autoregressive integrated moving average (ARIMA) model. ARIMA works by regressing a variable point value on previous (older) data-points, at some (fitted) distance (i.e. lag). The best lag between variables was estimated via cross-correlation, and the existence (and removal thereof) of temporal autocorrelation was assessed by means of

Breusch-Godfrey test (McMurry and Politis, 2015). To produce ARIMA models, we used the polygons record to maximize the number of datapoints. However, rather than using the 500 km wide cells we opted for  $2000 \times 2000$  km cells and selected only cells possessing at least 10 species and at least one carnivore species per time bin, for at least 6 time bins. These criteria are quite stringent, because the mammal fossil record is rarely continuous (Behrensmeyer et al., 2000). Yet, they were necessary to ensure the variables were properly autoregressed, avoiding using loose time series. We performed the ARIMA regressions of PPR against Mega,  $Pr$  against Herb, Mega against Herb, and  $Pr > 100$  against Mega. All the variables but PPR were standardized by dividing per cell species richness before regression. We only ran ARIMA models on the 2 myr long time bins version of the record, because by using bins 1 myr long species will typically appear over consecutive intervals, since the average duration in mammal species is slightly above 2 myr (Alroy, 2000; Marshall, 2017). ARIMA models were produced by using the R package “forecast” (Hyndman, 2015).

### 3. Results

The results were qualitatively very similar using either the polygon or occurrence record. The polygon record is much more dense and less affected by sampling issues, and was therefore used to perform ARIMAs. We present the results obtained by using the polygon record, yet the results relative to both versions of the data are available as Supplementary material.

The Neogene large mammal fossil record we sampled includes 1003 species distributed over 14,399 fossil occurrences (Table 1, Appendices S1–S2). Recent intervals are much better sampled than others. Overall, the most recent interval (the last 2 million years) accounts for 58.5% of the species, and 65.8% of the fossil occurrences. The number of valid cells is 74 by using raw occurrences, and 380 by using species polygons (Table 1).

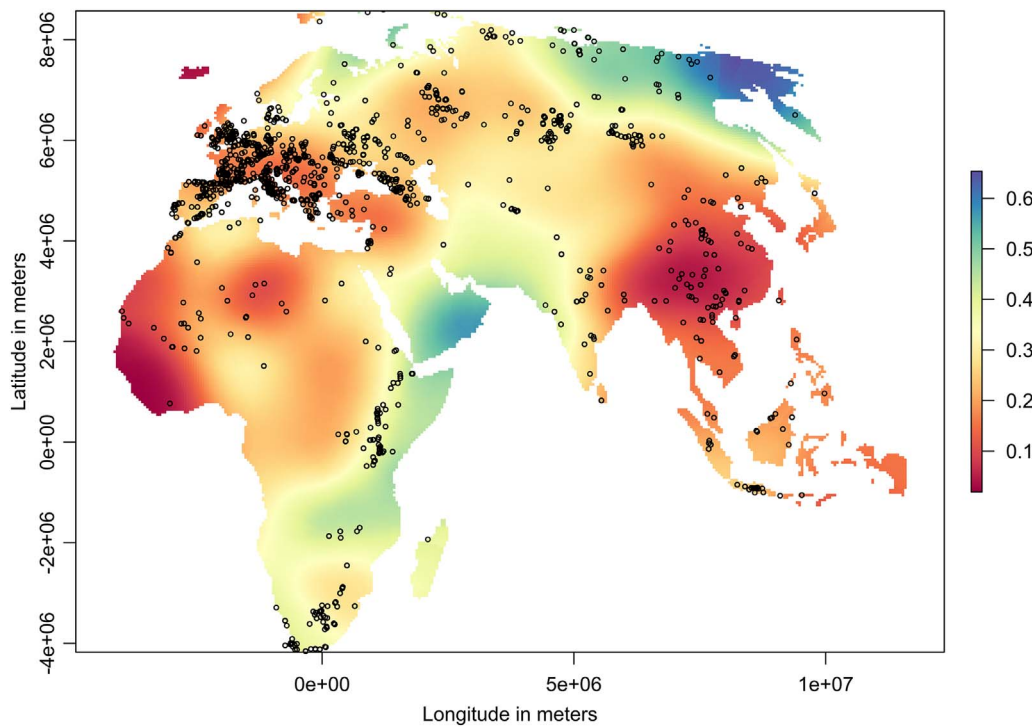
For this reason, while presenting the results obtained for all intervals, we pay special attention to the most recent interval. In addition, to better interpret PPR global dynamics, for this interval only we tested for geographical autocorrelation in PPR (Fig. 1).

The results of the regressions are summarized in Table 2. The predator to prey ratio (PPR) is significantly and negatively correlated to the number of megaherbivores in one fourth of the intervals. No positive relationship applies. The number of predators ( $Pr$ ) is negatively and significantly related to the number of mesoherbivores (Herb) in 6 out of 8 intervals (75%). Nearly two-thirds of the times (5 times in 8 intervals, 62.5%) the richness of megaherbivores (Mega) is inversely and significantly related to Herb. There is no positive relationship between the

**Table 1**  
Summary statistics of the distribution of fossil occurrences per cell and time bin.

Interval (Ma)	Raw occurrences	Polygons	Number of species	Total number of fossil occurrences
	Number of valid cells	Number of valid cells		
2–0	74	380	587	9465
4–2	22	54	180	984
6–4	5	14	54	160
8–6	23	74	160	1153
10–8	20	54	165	758
12–10	11	21	140	719
14–12	6	15	76	299
16–14	2	2	45	109
18–16	11	21	96	623
20–18	4	4	39	92
22–20	2	2	15	37

The number of “valid” cells (with species richness > 5 and at least one carnivore species being represented) is reported when using both raw occurrences and after producing the geographic polygon of each species per time bin.



**Fig. 1.** Interpolated values of the predator to prey ratio (PPR) calculated over a grid of 500 km × 500 km wide geographic cells in the Old World during the last 2 million years. The colour gradient indicates high (blue) to low (red) PPR values. Map portrayed in Mollweide equal area projection. The circles represent the distribution of fossil localities aged in between 2 and 0 million years ago. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**  
Summary statistics for the regressions of the number of species within ecological categories per cell.

Regression model (y-x)	Significant		Non-significant
	Positive	Negative	
PPR-Mega	0	2	7
Pr-Herb	0	6	2
Mega-Herb	0	5	3
Sab-Mega	0	1	7
Pr > 100-Mega	0	1	7
PPR-Overlap	6	1	2
PPR-Mega	0.00%	22.22%	77.78%
Pr-Herb	0.00%	75.00%	25.00%
Mega-Herb	0.00%	62.50%	37.50%
Sab-Mega	0.00%	12.50%	87.50%
Pr > 100-Mega	0.00%	12.50%	87.50%
PPR-Overlap	66.67%	11.11%	22.22%

For each regression model, we reported the number of significant (at  $\alpha = 0.05$ ) regression slopes, and the percentage of significant regression slopes for both negative (slope significantly lower than 0) and positive (slope significantly larger than 0) relationship.

diversity of sabertooths (Sab) and Mega. We found a significant and negative relationship in the first interval only (the last 2 myr, see Table 2 and Supplementary material). The richness of large predators (species > 100 kg in body size) is negatively and significantly associated to the number of megaherbivores in 1 interval, and not significant in 7 others. Again, for the intensely-sampled first interval, the regression between Mega and Pr > 100 is significant and negative.

Finally, the degree of overlap between the body size distribution of predators and prey is positively and significantly related to PPR six times (66.7%, Table 2). A significant and negative relationship occurs once. As regards the first (most recent) interval, all the regression results are consistent with the apparent competition theory (Appendices S3–S6). Changing the body size threshold for megaherbivores from 1000 to 450 kg (which actually is from 900 to 400 kg to accommodate estimate uncertainties) does not change the results. Similarly, by using the 1 myr long time bins, all of the results remain qualitatively the same (Appendices S3–S6). The spatial distribution of PPR in the Old World

**Table 3**  
Spatial autoregression of PPR in the Old World during the last 2 million years.

A					
	Slope	Std.Error	t value	p	
Longitude	− 8.095E − 09	3.769E − 09	− 2.148	0.032	
Latitude	− 8.872E − 09	4.703E − 09	− 1.977	0.020	
Interaction (lat * long)	2.723E − 15	8.856E − 16	3.074	0.002	
B					
	df	AIC	logLik	L.Ratio	p
no_structure	5	− 95.87341	52.937	1	0.954
cor_gauss	7	− 91.87341	52.937	0.6	1
cor_ratio	7	− 253.64891	133.825	161.1	0.000
cor_spher	7	− 91.87341	52.937	146.7	1
cor_exp	7	− 91.87341	52.937	0.6	1

For the best model (no structure) we reported in A the slope estimate (slope), the standard error of the estimate (Std.Error), the t-value (t.value), and the probability that the slope differs from zero (p) of the regression of PPR against latitude, longitude, and their interaction term. In B, for each autoregressive model we reported the model Akaike Information Criterion (AIC), likelihood (logLik), likelihood ratio to the best model (L.Ratio) and the significance of the likelihood ratio test (p). The fitted spatial autoregressive (SAR) are simple linear model = no\_structure; Gaussian = cor\_gauss; Exponential = cor\_exp; Rational Quadratic = cor\_ratio; Spherical = cor\_spher.

during the last interval (i.e. almost coinciding to the Quaternary) shows no significant spatial autoregression (Table 3). Yet, we found significant geographical trends in PPR (Table 3). In general, PPR was low in the deserts and at high latitudes (Fig. 1).

The results of ARIMA regressions confirm the existence of a negative relationship between the number of predators (Pr) and mesoherbivores (Herb) in four out of five valid cells (Table 4). The number of megaherbivores is negatively associated to the number of mesoherbivores (Mega-Herb) in three cells out of four. PPR is always negatively associated to Mega. Finally, the number of megacarnivores (i.e. predators above 100 kg in body mass) is negatively associated to the number of megaherbivores twice, and positively associated as many times.



**Table 4**  
ARIMA regression statistics for six different cells of 2000 km side.

Cell	Slope	p	p.bg	lag
<b>Pr-Herb</b>				
eu9	−1.105	0.003	0.233	2
eu7	−1.036	0.002	0.897	2
eu18	−0.404	0.001	0.313	2
eu15	−0.601	0.059	0.257	3
eu11	0.756	0.035	0.401	2
<b>Mega-Herb</b>				
eu9	−1.077	0.000	0.232	2
eu7	−1.023	0.000	0.938	2
eu15	−0.755	0.001	0.303	2
eu14	1.824	0.000	0.706	2
<b>PPR-Mega</b>				
eu9	−0.003	0.004	0.521	2
eu8	−0.001	0.032	0.737	2
eu7	−0.004	0.011	0.306	1
eu15	−0.002	0.026	0.764	1
<b>Pr &gt; 100-Mega</b>				
eu8	−1.408	0.023	0.154	2
eu18	2.348	0.001	0.477	3
eu15	−1.657	0.034	0.732	3
eu14	0.902	0.035	0.316	3

The slope, p-value, p-value for the Breusch–Godfrey test after correcting for temporal autocorrelation (p.bg) and lag (expressed as the number of 2 myr long time bin), for individual regression models and cells were selected.

Cross-correlation applied to the residuals consistently shows a lag of 1 to 3 intervals, and mostly of 2 (i.e. 4 myr) between herbivores and predators and megaherbivores respectively, meaning that Pr and Mega negatively affected the diversity of mesoherbivores in successive temporal intervals. In several cases the lags are too large to be meaningful (up to 4 lags, that is 8 myr which is well beyond the average species duration for mammals) and were therefore omitted.

#### 4. Discussion

Predator-to-prey ratios tend to be negatively, and significantly related to megaherbivore richness more often than not. The same tendency applies to the relationship between sabertooths and megaherbivores, and between the latter and large hypercarnivorous taxa. It still holds when temporal autocorrelation is taken into account. This is true regardless of the fact that we found strong confirmation for the notion that large predators hunted down large prey. These results indicate that large carnivores paid a price to the ecological dominance of megaherbivores, rather than the other way around (Van Valkenburgh et al., 2016). As megaherbivores diversified, the biomass available to carnivores reduced, exactly because megaherbivores are hard to kill, and smaller herbivores were significantly outcompeted (and their population size thereby decreased) by the larger herbivores. In fact, rather than the apparent competition of megaherbivores on carnivores, the most robust generalizations we derive from this study is that the diversity of mesoherbivores is negatively affected by the diversity of both carnivores and megaherbivores, which means predation and direct competition increases extinction probability in small herbivores, as often suggested to occur for living prey species (Fritz et al., 2002; Malhi et al., 2016).

Some sabertooths, and other large sized carnivores such as North American lion *Panthera atrox*, or short faced bear *Arctodus simus*, were probably able to dispatch juveniles of very large prey species such as mammoths or ground sloths. This was suggested to exercise a top-down control on megaherbivores (Van Valkenburgh et al., 2016). While killing juvenile megaherbivore is perfectly feasible for a top predator, and not contradicted by our data, we suggest these were probably not their most profitable prey, and more importantly, megaherbivores

diversity did not sustain higher carnivore diversity.

During the last 2 million years, the PPR varied geographically, being larger outside the tropics, and presumably species poor areas (Fig. 1). Since the tropics harbour more species (Rosenzweig, 1995), this means predator diversity grows more slowly than herbivores' as species richness increases (Trebilco et al., 2013). This pattern is consistent with ecological theory, and since it reverses today, it provides evidence that carnivores were even more affected than herbivores by late Quaternary megafauna extinction outside the tropics (Malhi et al., 2016). A brief review of the fossil records concurs on this. During the Quaternary, temperate Eurasian faunas housed a large number of predators (several species of hyenas, pantherine cats, Eurasian cheetah, cave bears, sabertooths) that went extinct by the end of the Pleistocene, while the herbivore fauna maintained many species of deer, the feral horse, large bovids, rhinos, and the Asian elephant (Sandom et al., 2014). The results we obtained for the last two million years are much more clear than for older temporal intervals (Appendices S3–S6). It is hard to judge to what extent could uneven sampling produce this pattern, yet it is clear that the geographic cells of older time periods are much less dense with fossil localities than in younger intervals, which probably means actual species richness becomes less and less well represented as one moves towards the past (Table 1). The last two million years is when *Homo* colonised the Old World. The effect of *Homo* on the mammalian fauna, though, is not apparent in our data. By using 1 myr-long time bins, regression slopes and signs for the interval spanning from 2 to 1 Ma are almost the same as with the last interval (from 1 Ma to the Recent). Considering that hunting ability in *Homo* just became significant from the Middle Pleistocene onwards (Carotenuto et al., 2016; Rodríguez et al., 2012; Stiner and Kuhn, 2006), this implies the effect of *Homo* observed at this scale is marginal at best.

Apparent competition was common both temporally and geographically. One of our main arguments is that megaherbivore diversity influenced negatively the diversity of predators. This happens to be the case because megaherbivores control a large amount of the primary productivity (Fritz et al., 2011; Terborgh et al., 2010; du Toit and Owen-Smith, 1989) limiting prey populations (Hummel and Clauss, 2008; Owen-Smith and Mills, 2008). We found evidence that, in the long run, such pervasive dominance of megaherbivores translates into higher extinction rate upon (primarily) small prey and (secondarily) predatory species, thereby altering predator to prey ratios (Melo and Clauss, 2012; Raia et al., 2007; Rodríguez et al., 2012), which is further conceivable considering that small prey populations tend to be limited by predation, while larger species are mainly controlled by resources (Terborgh et al., 2010).

It must be noted that very large predators and sabertooths were much less influenced by the diversity of megaherbivores than mesoherbivores. Together with the quite consistent, positive relationship between body size overlap (between trophic guilds) and PPR, this indicates that very large carnivores did actually go for larger prey than other carnivores on average. However, this is also consistent with their larger average body size, and not just with any preference for megaherbivores. Indeed, large predators do not specialize on the larger prey, they just exploit a wider prey spectrum (Radloff and du Toit, 2004).

Sabertooths were formidable predators. They were large by carnivore standards, and had large and muscular forelimbs which helped pinning down the prey during the kill (Akersten, 1985; Antón et al., 2005; Meachen-Samuels, 2012). Sabertooths, but not pantherines, could inflict terrible wounds to the soft tissues of even formidable prey (Meachen Samuels and Van Valkenburgh, 2009) and were designed to go for the bulk of prey muscles, rather than for extracting any bit of energy from the carcasses of their kills, as modern large carnivores do. All big cats tend to prey upon herbivores larger than themselves (Carbone et al., 2007). Sabertooths, though, had one additional weapon to exploit. Their canines were so long that they could effectively reach internal organs and major blood vessels to make the prey bleed to death. Skin thickness has positive scaling to body mass in mammals. As

the body size doubles, skin thickness increases by some 33% (Prothero, 2015), which implies it takes quite long canines to pierce dermis up to 4 cm thick in very large prey. Internal organs and major vessels are further away from the prey skin surface, which means reaching such vital organs is a task hard to accomplish for the 8 cm long upper canines of lions or tigers, but not, perhaps, for the exceptional, some 20 cm long *Smilodon* or *Barbourofelis* sabres. Given most sabertooths were large, possibly social (McCall et al., 2003), and bore exceedingly long canines designed for slicing, it comes natural to think they adapted to feed on larger animals than pantherines (the conical toothed big cats). While all of this is indicative that sabertooths were probably more efficient than conical toothed cats at killing large prey, our data indicate their survival was not conditioned by the presence of megaherbivores. Conversely, our results are consistent with the idea that megaherbivores did exert a strong top-down control on the ecosystems, affecting the diversity of prey, predators, and of vegetation structure (Gill, 2014; Gill et al., 2012; Olf et al., 2002; Sankaran et al., 2008). Rather than specialized on killing larger prey than conical toothed cats, we argue sabertooths did exploit the large end of the prey spectrum, as compared to similar sized pantherines. This might help explaining why sabertooths tend to be associated to large prey in the fossil record, and why there is no sabertooth alive today.

## 5. Conclusions

In keeping with previous studies, we found strong evidence for top-down control exerted by megaherbivores on both carnivores and smaller prey. This control resulted in the preferential extinction of carnivores and small herbivores where megaherbivores diversity thrived, and points to the large, extensive effect megaherbivory had on the control of trophic relationships in mammalian ecosystems. A number of very large predators, and most prominently so sabertooths, possibly escaped the negative influence of megaherbivores on their coexistence, possibly by intraguild dominance on smaller carnivores. Predators, as a whole, limited the diversity of mesoherbivores, which is further evidence for top-down regulation of ecosystem functioning in large mammal faunas of Eurasia during the last 22 million years.

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