The influence of climate on species distribution over time and space during the late Quaternary

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ABSTRACT

Understanding the effect of climate on the composition of communities and its change over time and space is one of the major aims in ecology and paleoecology. Herein, we tackled on this issue by studying late Quaternary large mammal paleocommunities of Eurasia. The late Quaternary was a period of strong environmental instability, especially characterized by the occurrence of the last glacial maximum (LGM). We used community phylogenetics and joint species distribution models in order to understand the factors determining paleocommunity composition in the late Quaternary. Our results support the existence of strong climatic selection operating on the LGM fauna, both through the disappearance of warm-adapted species such as *Elephas antiquus*, *Hippopothamus amphibious*, and *Stephanorhinus hemitoechus*, and by setting the stage for the existence of a community characterized by cold-adapted large mammals. Patterns of abundance in the fossil record, co-occurrence between species pairs, and the extent of climatic forcing on faunal composition, differ between paleocommunities, but not between extinct and extant species, which is consistent with the idea that climate change, rather than the presence of humans, exerted a major effect on the survival of the late Quaternary megafauna.

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1. Introduction

Understanding the influence that climate change has on the distribution of individual species and ecological communities over time and space is one major goal in ecology (Ovaskainen et al., 2013; Parmesan and Yohe, 2003; Walther et al., 2002). Many accounts focus on whether species with similar environmental tolerances react as an integrated community, or show individualistic responses either, to change (Burns et al., 1996; Lorenzen et al., 2011; Parmesan, 2006; Villalobos et al., 2016a). These approaches mostly focus on short-term species reactions. However, this could be misleading as deep time climatic events are known to have influenced the structuring of current communities (Davis and Shaw, 2001; Svenning et al., 2015; Valiente-Banuet et al., 2006). Hence, increasing attention is now being devoted to methods apt to integrate such deep time information in studies dealing with the ecological effects of climate change at the community level, either by explicitly modeling the paleobiogeography of the fossil record (Villalobos et al., 2016b), or by relying on the evidence stored in phylogenetic trees (Diniz-Filho and Bini, 2007; Diniz-Filho et al., 2013).

The paleoecological approach to the study of community composition and change over time (i.e. temporal turnover) is obviously marred by the issues of diachrony and the incompleteness of the fossil record (Alroy, 1998; Raia et al., 2009). Fortunately, several statistical methods are now able to account for these sampling biases (Fernández and Vrba, 2005; Raia et al., 2006; Wagner and Marcot, 2013), and to apply modern ecological tools to fossil communities (Barnosky, 2005; Blois et al., 2014; Cano et al., 2014; Cantalapiedra et al., 2011; Raia, 2010). As pertains to the influence of climate change on community composition and its evolution, several reports now clearly indicate that Quaternary fauna temporal turnover increased during periods of environmental turmoil (Barnosky, 2010; Blois et al., 2014; Blois and Hadly, 2009; Faith and Behrensmeyer, 2013; Prothero, 2012; Raia et al., 2005), suggesting that species co-occurring in time should also have comparable climatic tolerances (Burns et al., 1996; Raia, 2010; but see Villalobos et al., 2016b). Rates of speciation and extinction

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similarly affect community composition, and many studies link such rates to the climatic unrest that characterized the Quaternary period (Barnosky, 2005; Dynesius and Jansson, 2000; Kozak and Wiens, 2010; McPeek, 2008) still pointing to a large effect of climate on the identity of species within communities.

The late Quaternary was a period of extraordinarily intense environmental change (Dawson, 2013). By the end of this period, the last glacial maximum (LGM) marked one of Earth's most extreme moments of climatic variability (Clark et al., 2009). The intense, global sway in climate greatly affected terrestrial faunas, causing long-distance species movement (Raia et al., 2012), decreasing species endemism, and possibly increasing extinction rate in small-ranged species (Davis and Shaw, 2001; Sandel et al., 2011), and in small mammals (Blois et al., 2010). As for large mammals, LGM faunas in Eurasia were characterized by steppe specialists such as the woolly mammoth, saiga, woolly rhino, musk-ox and steppe bison, forming a no longer existent ecosystem known as the mammoth steppe (Dale Guthrie, 2001; Zimov et al., 2012). The demise of such ecosystem is usually viewed as part of the late Pleistocene megafaunal extinction (Koch and Barnosky, 2006), and attributed either directly to the effect of climate change (Grayson, 1977; Grayson and Meltzer, 2003; Lima-Ribeiro et al., 2014; Meltzer, 2015; Wroe et al., 2013), or to human overkill (Alroy, 2001; Brook and Bowman, 2005; Surovell et al., 2016). Although a number of warm-adapted, middle to late Pleistocene species went extinct before the LGM (e.g. hippopotamus, straight-tusked elephant, cave hyena) several components of the LGM steppe megafauna are still alive today (e.g. saiga antelope, musk-ox, reindeer). Other LGM species already occur in the warm last interglacial (LIG) preceding the LGM (e.g. woolly mammoth, steppe bison, woolly rhino). Finally, a number of species co-occurring geographically to the mammoth steppe megafauna, such as the Irish elk, red deer, and wolf, were not steppe specialists. Such idiosyncrasies suggest that neither the identity of the mammoth steppe megafauna, nor its demise were necessarily or solely controlled by the extraordinarily harsh LGM climate. Here, we ask whether climate change had any discernible effect on megafauna distribution over time and space, by using climate-explicit approaches to study species co-occurrence patterns in paleo-communities spanning in age from the last interglacial (LIG) to the beginning of the Holocene (thus encompassing the LGM). We tested whether climate shaped the composition and turnover of megafauna communities during LIG, LGM and Early Holocene discrete temporal intervals. This question also takes indirectly on the issue of whether humans, rather than climate, caused the extirpation of the megafauna at the end of the LGM. If humans had a major impact, we expect LGM faunal composition to bear little or no signature of climatic effects, since the incidence of species in the LGM fossil record would be more influenced by human hunting pressure than by the prevailing environmental conditions.

To such aim, we applied joint species distribution models and community phylogenetics techniques. The former allow identifying the climatic conditions individual species lived in, and how much species with similar climatic requirements tend to co-occur in space. With this, it is possible to ascertain how large the effect of climate was on patterns of geographic co-occurrence (Hui et al., 2015; Pollock et al., 2014). Community phylogenetics offers the opportunity to understand the factors affecting community composition, telling the effects of competition apart from those of habitat filtering (Godoy et al., 2014; Kembel, 2009). Habitat filtering is commonly associated with phylogenetic clustering since closely related species tend to show similar climatic tolerances. Conversely, high levels of interspecific competition lead to phylogenetic overdispersion because niches of closely related species tend to overlap consistently, so that they settle apart from each other (in space) in

order to reduce interspecific competition. Under habitat filtering, evolutionary convergence originates phylogenetic overdispersion because species from different branches of the tree tend to converge on similar climatic tolerance. Finally, under intense competition and in the presence of convergence the community structure shows a random dispersion or phylogenetic clustering either (Cavender Bares et al., 2004; Cavender-Bares et al., 2009; Ndiribe et al., 2013; Swenson et al., 2006; Webb et al., 2002). Community phylogenetics was successfully extended to the study of fossil faunas (Raia, 2010). Herein, we statistically defined the paleocommunities first (Raia et al., 2009, 2006), then tested species co-occurrence patterns as explained by climate by using JSDMs (Hui et al., 2015; Pollock et al., 2014). Eventually, we applied community phylogenetics to test whether the paleocommunity composition was influenced by climate, or by ecological interactions either. Our goal was to compare LGM to pre- and post-LGM communities to understand the effect of climate change on patterns of co-occurrence in these fossil assemblages.

2. Material and methods

2.1. Setting the database of fossil occurrences and feeding categories

We prepared a database including 6462 Eutherian mammals fossil occurrences distributed over 947 fossil localities for 161 extinct and living species. This database geographically spans over Eurasia and ranges in age from 0.130 to 0.005 Mya. We collected the information about fossil localities and their faunal lists from the following databases: the paleobiodb database (https://paleobiodb.org/#/), the NOW database (http://www.helsinki.fi/science/now/) integrated to the databases provided in Raia et al. (2009) and Carotenuto et al. (2010, 2015). In order to assess the influence of species ecology on community composition, we assigned each species to distinct feeding categories after Price et al. (2012), Meloro et al. (2008) and Raia et al. (2010) (see Supplementary Table 1 for species attributions). When compiling the dataset, we discarded species with uncertain classification and fully revised them for synonyms. The dataset includes both biochronological and radiometric estimates as localities age. For localities with dubious estimates, we used the ages provided in Carotenuto et al. (2010), which were computed by using spectral ordering (Fortelius et al., 2006). Under this procedure, Fiedler eigenvector scores are computed in order to collate the fossil localities in time, depending on the similarity of their faunal lists. Then scores are regressed against radiometric age estimates to obtain the mathematical relationship between scores and ages. The formula is eventually applied to those localities which lack a reliable age estimate. With a very high R^2 (0.98) between Fiedler scores and localities with radiometric age estimation (Raia et al., 2009), this method proved to be very successful to obtain age references for fossil localities of uncertain age.

We divided the database into three temporal intervals, according to the most important climatic events of the Quaternary: from 0.130 to 0.115 Mya (a temporal range including the Last Interglacial, here LIG); from 0.022 to 0.0145 Mya focusing on LGM, and from 0.009 to 0.005 Mya (around the Holocene Climatic Optimum, here epitomized simply as "Holocene", HOL).

2.2. Identifying paleo-communities (PCOMs)

Paleo-communities (PCOMs sensu Raia et al., 2006) are statistically discrete groups of fossil localities (Raia et al., 2009, 2005). To identify LIG, LGM and HOL PCOMs we used bootstrapped cluster analyses (BCA), as in (Raia et al., 2009, 2005). BCA works by performing a single cluster analysis (the reference clusters) based on

the similarity between the faunal lists of the fossil localities, their geographic positions and age estimations, then it produces new random localities by mixing species and the other variables among the original fossil sites. After each mixing session, the random generated dataset is subjected to a new cluster analysis. This procedure was repeated 999 times. The frequency distribution of the new simulated clusters is used to assign a probability to each partition level of the reference cluster analysis. In order to have the finest resolution level at partitioning, we identified as stable groups (i.e. as PCOMs) the clusters corresponding to the level of partition of the reference analysis that had a probability just higher than the significance level ($\alpha = 0.05$), meaning that they do not appear random as compared to the simulated sample (Raia et al., 2009, 2005). In this study, we performed an improved bootstrap cluster analysis with a new method, which applies approximately unbiased (hereafter-denoted AU) p values for PCOMs identification (Shimodaira, 2004, 2002), using the package "pvclust" in R. This new method, known as "Multistep-multiscale bootstrap resampling" (Shimodaira, 2004) stands on the observation that bootstrap probabilities (BP) tends to be too much conservative (Hillis and Bull, 1993). This means that, by using BP, the probability of a wrong rejection is higher than the significance level (Shimodaira, 2002). The method proposed by Shimodaira (2004) is able to perform an unbiased computation of the p values for each partitioning level as it allows general smooth boundaries for the region of all reference clusters and performs simulations by using samples with variable sizes, thus computing a more accurate p value and preventing real groups from unjustified exclusion. For the sake of our study, we searched for the optimal distinction of three different PCOMs, temporally pertaining to the LIG, LGM, and HOL intervals, respectively. Faunal lists (at fossil localities) are potentially flawed by time-averaging and uncertain dating. Thus, clusters found by BCA may contain localities of different age (i.e. actually pertaining to different time periods). Hence, after finding the best partition levels via BCA, we took from the resulting clusters only the localities whose dating fall within the three intervals we were interested into. If two localities with similar ages (e.g. they both are "LIG" in age) belong to different clusters, we took within individual PCOMs only localities belonging to the same cluster, as to maintain faunal homogeneity. This conservative approach was meant to limit as much as possible the effect of temporal faunal mixing at fossil sites on the identity of species included in individual PCOMs.

2.3. Co-occurrence patterns within PCOMs

We used the joint–Species Distribution Models (JSDMs) approach proposed in (Pollock et al., 2014) and refined in Hui et al. (2015), to test whether the species co-occurrence patterns within each PCOM is a result of habitat filtering, species sorting or biotic interactions, either. The JSDMs method prescribes to model species co–occurrence using multivariate probit regression models (Agresti, 1996; McCullagh and Nelder, 1989), parameterized by a latent variable formulation. Model estimations are performed using Markov Chain Monte Carlo (MCMC) methods (for further details see Hui et al., 2015). As a result, this technique allows disentangling the amount of correlation between the occurrence of two species that can be explained ('environmental'), or not explained ('residual'), by similar/different environmental responses, usually interpreting the latter as an effect of ecological interactions (Pollock et al., 2014). To select the most appropriate number of latent variables to include in the within-PCOM co-occurrence pattern model, we compared models trained with four-to-two latent variables and performed an AIC-based (Akaike, 1971) selection of the final models (Hui et al., 2015). As an initial set of environmental predictors we considered the 19 bioclimatic variables derived from the

WORLDCLIM database, at a spatial resolution of five arc-minutes (~10 km) and for LIG, LGM and HOL time periods (Hijmans et al., 2005; Otto-Bliesner et al., 2006). Climate layers were converted into Lambert Azimuth Equal Area projection separately for each time interval. To take into account the pairwise correlation between the predictors, the final set of variables was sub-selected considering a variance inflation factor (VIF) ≤ 3 (Zuur et al., 2010) and included the following seven predictors: Mean Diurnal Range (BIO2), Temperature Seasonality (BIO4), Mean Temperature of Wettest Quarter (BIO8), Precipitation Seasonality (BIO15), Precipitation of Warmest Quarter (BIO18) and Precipitation of Coldest Quarter (BIO19). To prevent any bias in the results due to taphonomic effects and the inclusion of rare species, we performed the JSDMs by considering only species with at least 4 occurrences per PCOM and localities with at least 4 species. Then, we repeated the analysis by using the whole dataset, whose results are showed in the supplementary material.

2.4. Phylogenetic tree preparation

We used the phylogenetic tree provided in Villalobos et al. (Villalobos et al., 2016a), which includes 126 species of the orders Carnivora, Cetartiodactyla, Perissodactyla and Proboscidea, pruned down to all of the species occurring in the detected PCOMs (Fig. 1). Overall, the tree includes 59 species. The tree topology follows (Raia et al., 2013). For the extinct species tips are placed at the last known appearance date of the species in the fossil record. Species first appearance records in the NOW and paleobiology databases were used to calculate branch lengths (Finarelli and Flynn, 2006; Meloro et al., 2008; Raia et al., 2010).

2.5. Community phylogenetics

In order to compute community phylogenetics metrics, for each PCOM we converted the phylogeny into a phylogenetic distance matrix (the variance-covariance matrix of the tree in Fig. 1). A second matrix was composed using the list of the species that show up in the three communities (i.e. a presence-absence matrix) having species as columns and PCOMs as rows. We quantified phylogenetic dispersion as the net relatedness index (NRI) and net taxon index (NTI) per PCOM. These are two of the most common metrics to achieve a realistic estimation of phylogenetic distance between taxa in a community (Vamosi et al., 2009). NRI is based on the mean pairwise distance (MPD), that is the mean distance between each taxon and any other tip in the tree. NTI is based on the mean nearest taxon distance (MNTD), namely the distance between each taxon and its closest relative in the tree (Vamosi et al., 2009). NRI and NTI are computed as the standardized values of MPD/MNTD by comparing the observed values against values obtained from 10.000 random draws. We estimated NRI and NTI with the R package picante (Kembel et al., 2010).

Community structure may be influenced by phenotypic evolution, as traits determine species environmental tolerance or might evolve to reduce interspecific competition (Ackerly, 2003; Cavender Bares et al., 2004; Webb et al., 2002). With the aim to understand how trophic requirements (feeding category) influenced the identity of species within PCOMs, we also performed a trophic dispersion analysis by using species feeding categories and abundances (i.e. number of occurrence in the fossil sites per PCOM) as entries. We first calculated a dissimilarity matrix of feeding categories per PCOM using Gower's index, and then computed a similarity matrix between PCOMs using species occupancies (fossil abundances) as entries. The latter matrix is based on the Euclidean distance. In this analysis, the dissimilarity matrix of feeding categories replaces the phylogenetic variance-covariance matrix in the
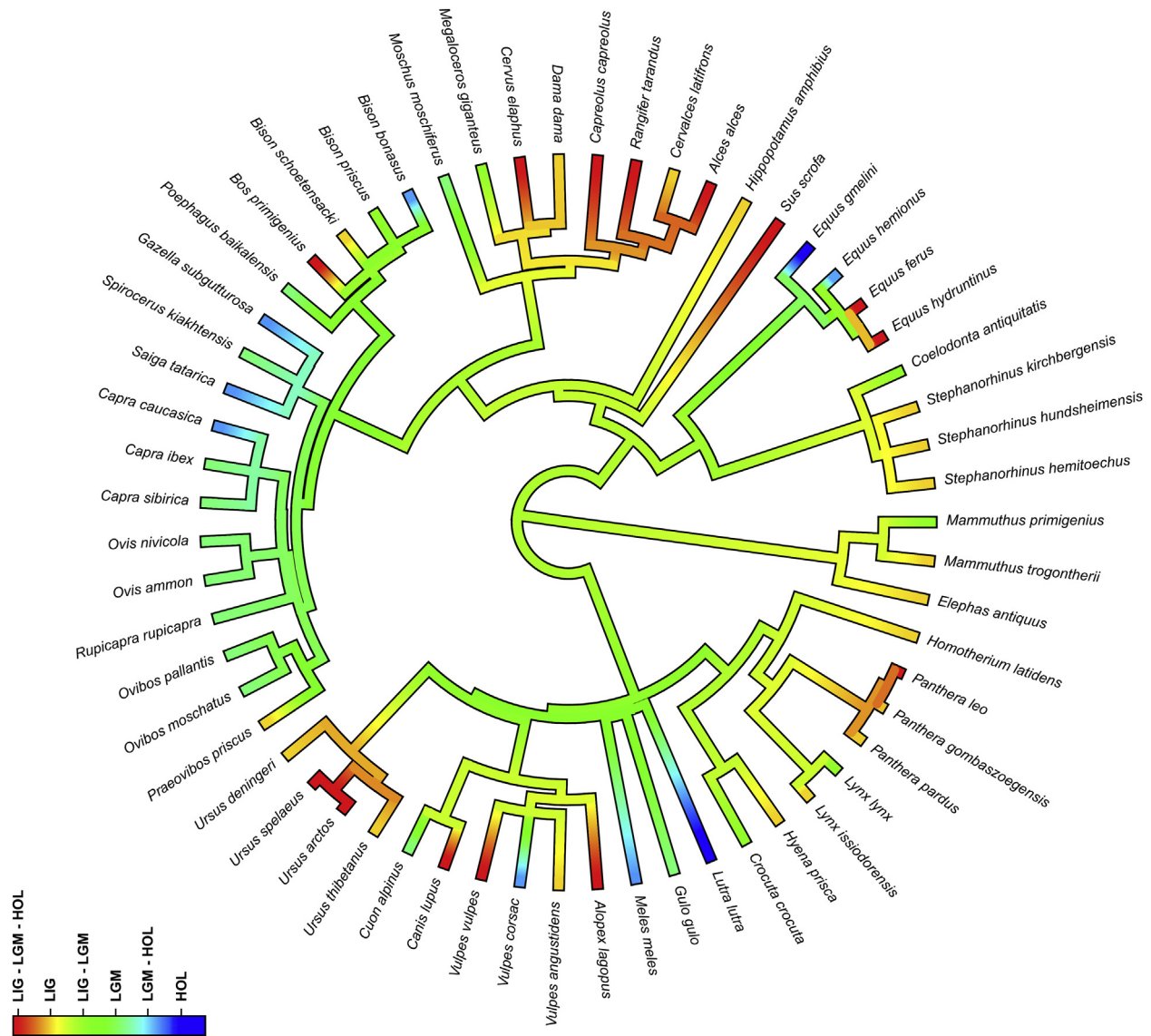
Fig. 1. The phylogenetic tree of the species included in this study. The branch colors are indicative of species age, from the Last Interglacial (red) to the Holocene (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

phylogenetic dispersion analysis described above, whereas the similarity matrix of fossil abundances replaces the presence absence matrix. We decided to use abundances rather than presence absence data in the trophic category analysis, because different environmental conditions impact on the abundance of individual species, rather than their presence (e.g. grazer populations are abundant in open habitats irrespective of whether browsing species are present). NRI and NTI can be computed to estimate trophic dispersion as they are for phylogenetic dispersion. Only the metric of distance differs between the two analyses. Matrices were computed with the packages StatMatch (D'Orazio, 2014) in R.

3. Results

3.1. The paleocommunities

Cluster analysis of fossil faunas performed via the approximately unbiased bootstrap resampling (Shimodaira, 2004, 2002) produced

an initial partitioning level with two large groups, denoted as G1 and G2. These groups include 82 and 96 fossil localities, respectively. The partition of the clusters is obviously not the same as the temporal interval we are interested into (LIG, LGM and HOL). Thus, we further applied approximately unbiased BCA on G1 and G2 separately detecting two additional subgroups for both clusters, which we named G1.1 (including 31 localities), G1.2 (51 localities), G2.1 (2 localities) and G2.2 (94 localities). The G1.1 cluster was mainly composed by LIG and LGM localities with very few Holocene ones (13, 15 and 3 localities, respectively), whereas the G1.2 group was mainly composed by localities belonging to the LIG temporal interval (number of localities per bin: LIG = 26; LGM = 18; Holocene = 7). We considered eligible as the oldest PCOM (PCOM LIG) unambiguously pertaining to LIG, localities belonging to the G1.2 cluster with LIG age. By our procedure, this PCOM fully corresponds to the Eemian, and genuinely includes a statistically distinct fauna ranging in age from 0.130 to 0.116 Mya, with the oldest locality being Taubach-Weimar Ehringsdorf layer 1 in Germany and the youngest being Koneprusy C718 bei Karlstejn located

in Czec Republic (Supplementary Table 1). The G2.1 group included only two localities, whereas G2.2 cluster was mainly composed by localities belonging to the LGM temporal interval (number of localities per bin: LIG = 4; LGM = 72; Holocene = 20). We further partitioned the G2.2 group but results did not provide statistically discrete subgroups. Thus, we chronologically partitioned this group into a LGM assemblage of fossil localities (PCOM LGM, 71 localities), and a Holocene (PCOM HOL, 17 localities) assemblage of localities. The PCOM LGM ranges in time from 0.022 to 0.0147 Mya, with the oldest locality being Gura Cheii-Rasnov (Romania) and Chulatovo layer 1 in Ukraine being the youngest one (Supplementary Table 1). The PCOM HOL covers the temporal interval from 0.0061 to 0.005 Mya, within Lisia (Poland), and Sevan lake (Armenia) as the oldest and youngest locality, respectively (Supplementary Table 1).

3.2. The geographical distribution and taxonomical composition of PCOMs

The PCOM LIG is geographically distributed over the Central and Central-East Europe (Fig. 2). Its faunal assemblage has some important warm-adapted species like *Panthera leo*, *P. pardus* and *Hippopotamus amphibious* (the latter being very abundant even in Central Europe). The PCOM LGM occurs over most of the Eurasian territory, ranging from the Central-East Europe to the Eastern Russia (Fig. 2).

The most representative species of this group are still living like *Rangifer tarandus*, *Cervus elaphus*, *Canis lupus*, *Ursus arctos*, *Capreolus capreolus* and *Saiga tatarica*, along with other extinct species like *Bison priscus*, *Mammuthus primigenius*, *Coelodonta antiquitatis* and *Ursus spelaeus*. The PCOM HOL covers the geographical territories belonging to the Eastern Europe at middle latitudes (Fig. 2). The PCOM HOL fauna is almost entirely inclusive of extant species like *Cervus elaphus*, *Sus scrofa*, *Capreolus capreolus*, *Equus ferus*, *Vulpes vulpes*, *Ursus arctos*, *Canis lupus*, with the only exception of the recently extinct auroch *Bos primigenius*.

3.3. Joint species distribution models

The PCOM LIG includes 24 species. Of the 276 possible pairwise species comparisons, 155 are significant (56.2%), and are explained by climate or by individual species ecology by almost equal proportions. In particular, the pattern of ecological control on species co-occurrences is stronger for this PCOM than for the others (Table 1).

For the PCOM LGM, JSDMs retrieved 33.7% significant associations (101 out of 300 possible pairwise combinations of 25 the species included in this PCOM, Supplementary Table 2A,B). The total number of significant pairwise associations explained by climate (75), though, is almost as much as with PCOM LIG (79, Table 1), pointing to a stronger climatic forcing on species co-occurrences within this PCOM than for PCOM LIG.

Finally, for PCOM HOL, the percentage of significant co-occurrences is 29.1%, almost entirely explained by climatic effects (93.8%).

Throughout the study period, a few species always co-occur with the same set of species. For instance, mammoth, woolly rhino, and reindeer show significant climatic association to each other in both LIG and LGM (Figs. 3 and 4). Conversely, there are a number of species showing little patterns of significant climatic associations to any other species (Supplementary Table 2A,B). For instance, only 7 out of 58 (12.1%) pairwise co-occurrences for the red deer, the most abundant species in the fossil record, gave a significant climatic association to any other species (Table 2). For the wolf, the lion, and the auroch, the corresponding figure is even lower (wolf: 8.8%, lion: 8.5%, auroch: 10.5%; Table 2). These species

acted as climatic generalists, a notion which is further confirmed by their huge geographic ranges, which trespass the limits of the Eurasian continent (the red deer and the wolf occur in North America even today, the lion occurred in North America during the late Pleistocene). In contrast, the climatic signature on co-occurrences of mammoth, reindeer and woolly rhino is impressive (as high as 46.2%, Table 2). The residual (non-climatic) variation in significant species co-occurrences is usually explained as an effect of ecological interactions (Pollock et al., 2014). These ecological interactions matter to steppe bison (40.4% of the significant pairwise co-occurrences, Table 2), roe deer *Capreolus capreolus* (31.6%) and Merck's rhino *Stephanorhinus kirchnergensis* (30.4%). Conversely, ecological interactions explain less than 5% of the significant co-occurrences for a number of species, including the Arctic fox *Alopex lagopus*, onager *Equus hemionus*, fallow deer *Dama dama*, Irish elk *Megaloceros giganteus*, saiga antelope *Saiga tatarica*, and the lion (Table 2 and Supplementary Table 2A). These species are either ecological specialists, restricted to a particular environment, or the largest representatives of their guilds (lion).

3.4. Community phylogenetics

For the net relatedness index (NRI), we found that the observe MPD is significantly lower than standardized MPD (p = 0.004) in the PCOM LGM (Table 3). The net taxon index (NTI) indicates that MNTD is lower than random for the PCOM LIG.

The analysis of trophic dispersion (which takes into account the abundance of species belonging to different feeding categories) indicates that the differences in observed and standardized MPD for NRI are not significant for the three communities. Yet, we found that observed MNTD in PCOM LGM is significantly lower than standardized MNTD (p = 0.044, Table 3). In both cases, the evidence points to phylogenetic clustering.

4. Discussion

The last interglacial fauna was characterized by climatic-generalist species like *Cervus elaphus*, *Canis lupus*, and *Equus ferus*, whose presence is pervasive in this faunal assemblage and well documented in the fossil record. Despite in the bootstrapping procedure we deliberately restricted LIG attribution to localities belonging to a single cluster of faunas (rather than including all fossil localities dating to LIG or localities dated as LGM and Holocene but classified as LIG), joint species distribution models point to a strong, climate-driven pattern of co-occurrence between warm-loving, forested taxa such as roe and red deer, wild boar, and straight-tusked elephant on the one side, and species preferring colder environments such as the elk, steppe rhino, reindeer and horses on the other (Fig. 3).

This means this PCOM shows a heterogeneous asset of species, which includes both open-habitat grazers (e.g. *Stephanorhinus hemitoechus*, *Bison priscus*) and closed (forested) habitat browsers (e.g. *C. capreolus*, *S. scrofa*). In keeping with this, the percentage of significant species pairs co-occurrences explained by climate (51%) is comparable to purely "ecological" associations (49%, see Table 1 and Fig. 3). Although we found evidence for phylogenetic structuring for the PCOM LIG, no trophic structuring was found for this community, which is expected given the variable environmental preferences of the species it includes. It is interesting to note how this fauna changes into the next, PCOM LGM. The bulk of LGM paleocommunity is made of typically tundra/steppe species, like reindeer, saiga antelope, woolly mammoth, steppe bison and woolly rhino. Although more climatically tolerant species (*C. elaphus*, *C. lupus*, *Sus scrofa*, *Ursus arctos*) are still present and lively during this period, it shows little co-occurrence pattern
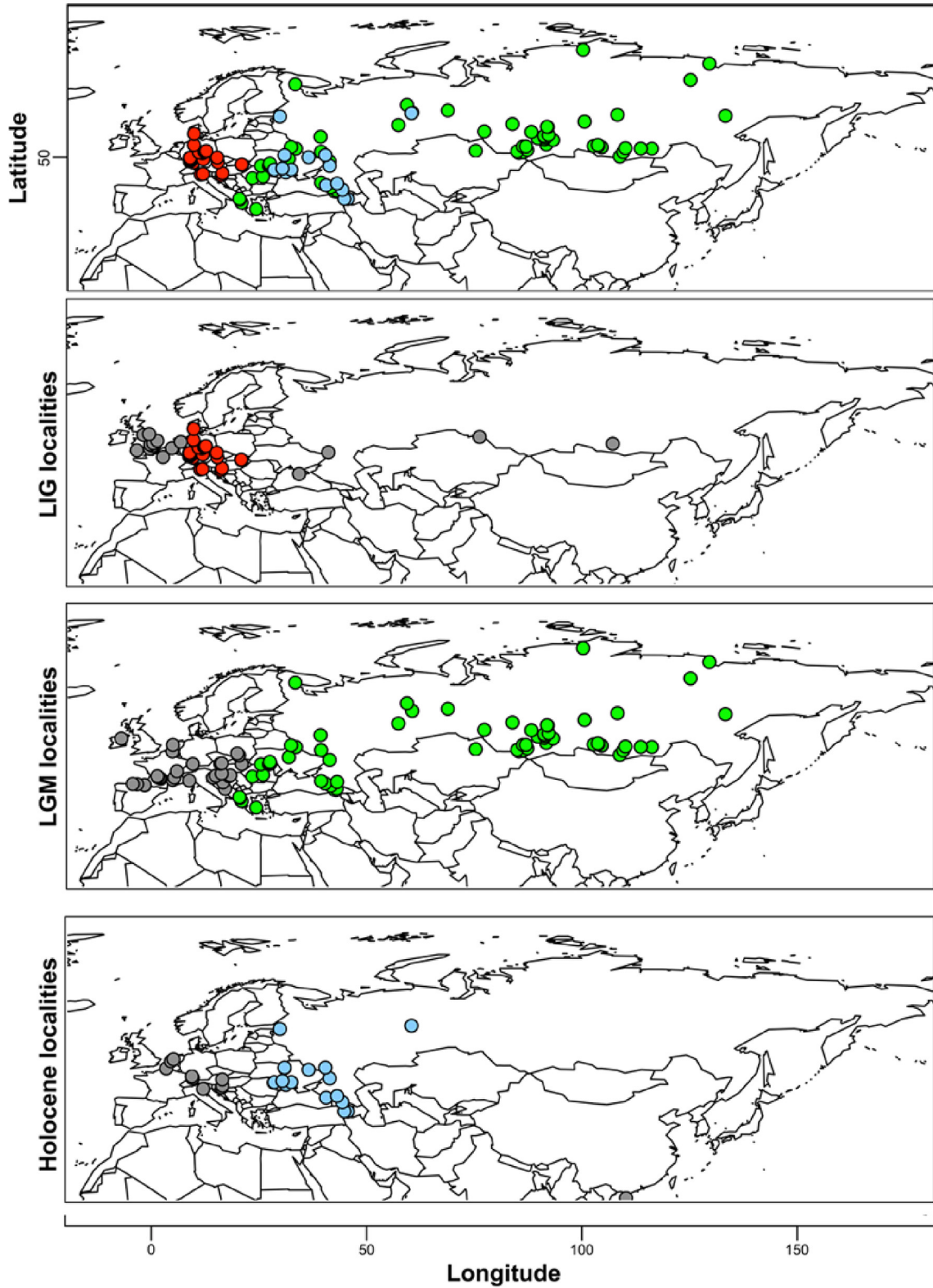
Fig. 2. The geographic distribution of the fossil localities falling within the three paleocommunities (PCOMs) we identified: last interglacial (LIG, red dots); last glacial maximum (LGM, green dots); Holocene (HOL, light blue dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Summary results of Joint Species Distribution Models (JSDMs) analysis per PCOM. The absolute number and percentages of significant co-occurrences between species pairs as explained by climatic (upper half) or ecological (lower half) factors, per time period. Significant co-occurrences are further divided into positive, and negative statistically significant associations.

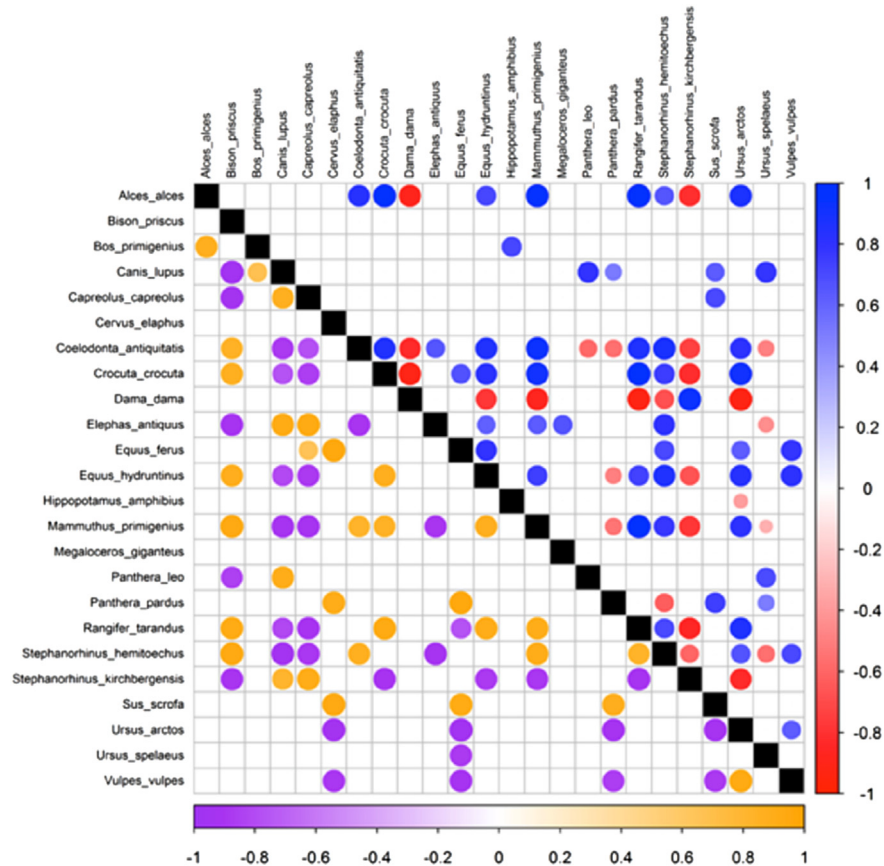| Factor		LIG	LGM	HOL
Climate	Positive	51	51	8
	Negative	28	24	7
	% Climate	51.0%	74.3%	93.8%
Ecological interactions	Positive	32	11	0
	Negative	44	15	1
	% Ecological	49.0%	25.7%	6.3%

Fig. 3. Joint species distribution models for PCOM LIG. Significant correlations between species pairs are represented by circles. Blue circle: positive and significant relationship driven by climate. Red circle: negative and significant relationship driven by climate. Orange circle: positive and significant relationship not driven by climate. Purple circle: negative and significant relationship not driven by climate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

within its constituent species (Fig. 4). As compared to the PCOM LIG, co-occurrences between species pairs are now dominated by climate-driven effects (74.3%) being much larger than residual, ecological effects (25.7%, see Table 1 and Fig. 4).

The best explanation for this stands in the strong climatic selection this fauna underwent, which is further testified by the significant pattern of phylogenetic clustering it exhibits in terms of both composition and feeding categories (Table 1). Importantly, this equally applies to both extinct, and extant cold-adapted megafauna. In fact, holdovers from warmer climates that were still abundant during the Eemian times, disappear before the onset of the LGM. The straight-tusked elephant *Elephas antiquus*, hippo, and narrow-nosed rhino *Stephanorhinus hemitoechus* are all representative of the late Pleistocene fauna that disappeared before the advent of the coldest phase of the last glaciation (Lister and Stuart, 2013; Stuart, 2015). Patterns of abundance at fossil sites (i.e. species

occupancy (Carotenuto et al., 2010) support the notion for strong climatic selection operating on PCOM LGM fauna (Table 4), with typical mammoth steppe inhabitants showing disproportionately more occurrences during this time period. Again, it is important to notice this is true of both extinct (mammoth, wooly rhino) and extant (onager, reindeer) species.

Over 70% of the total fossil occurrences for mammoth, woolly rhino, steppe bison, reindeer, musk-ox, argali *Ovis ammon*, and goitered gazelle *Gazella subgutturosa* fall in this PCOM. This percentage falls to some 50% for the two most abundant species in our data, red deer and wolf, to 35% for roe deer, the fifth most abundant species, to only 19% for the wild boar (which is the eighth most abundant species overall, Table 4). These results point to strong climatic filtering operating on the PCOM LGM community composition. Still, patterns of pairwise species co-occurrence invariably indicate that reindeer, mammoth, and woolly rhino at least, co-
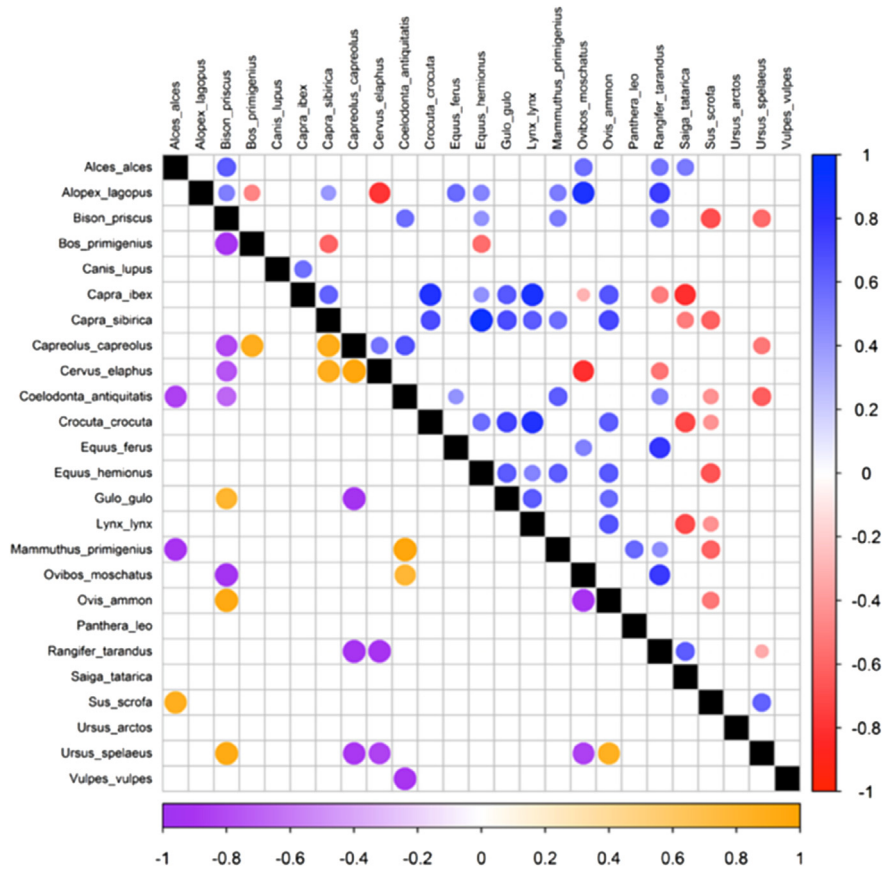
Fig. 4. Joint species distribution models for PCOM LGM. Significant correlations between species pairs are represented by circles. Blue circle: positive and significant relationship driven by climate. Red circle: negative and significant relationship driven by climate. Orange circle: positive and significant relationship not driven by climate. Purple circle: negative and significant relationship not driven by climate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Number of significant co-occurrences explained by climate, ecology, their percentages, according to JSDMs analysis. The total number of possible co-occurrences per species is indicated as #co-occ. The table includes species with at least 10 occurrences in the fossil record.

Species	Climate	Ecology	% Climate	% Ecology	% Sig. Co-occs	# Co-occ.
Cervus elaphus	7	10	12.3%	17.5%	29.8%	57
Canis lupus	5	13	8.8%	22.8%	31.6%	57
Bison priscus	8	19	17.0%	40.4%	57.4%	47
Rangifer tarandus	20	11	42.6%	23.4%	66.0%	47
Capreolus capreolus	7	18	12.3%	31.6%	43.9%	57
Ursus arctos	15	5	26.3%	8.8%	35.1%	57
Mammuthus primigenius	20	12	42.6%	25.5%	68.1%	47
Sus scrofa	16	6	28.1%	10.5%	38.6%	57
Coelodonta antiquitatis	20	11	42.6%	23.4%	66.0%	47
Equus ferus	13	8	22.8%	14.0%	36.8%	57
Bos primigenius	6	5	10.5%	8.8%	19.3%	57
Alces alces	16	4	28.1%	7.0%	35.1%	57
Vulpes vulpes	7	6	12.3%	10.5%	22.8%	57
Panthera leo	4	2	8.5%	4.3%	12.8%	47
Ursus spelaeus	12	6	25.5%	12.8%	38.3%	47
Megaloceros giganteus	1	0	4.3%	0.0%	4.3%	23
Stephanorhinus kirchbergensis	9	7	39.1%	30.4%	69.6%	23
Saiga tatarica	10	0	29.4%	0.0%	29.4%	34
Equus hemionus	12	0	35.3%	0.0%	35.3%	34
Elephas antiquus	6	6	26.1%	26.1%	52.2%	23
Crocuta crocuta	18	7	38.3%	14.9%	53.2%	47
Dama dama	9	0	39.1%	0.0%	39.1%	23
Ovis ammon	7	3	29.2%	12.5%	41.7%	24
Alopex lagopus	9	0	37.5%	0.0%	37.5%	24

Table 3
Phylogenetic dispersion and trophic dispersion analysis per PCOM. LIG indicates the last interglacial PCOM, LGM the last glacial maximum PCOM, and HOL the Holocene community. ntaxa is the number of taxa occurred in the communities; mpd.obs and mntd.obs are the real (observed) MPD/MNTD; mpd/mntd.rand.mean are the means of MPD and MNTD in null (random) communities, respectively; mpd/mntd.rand.sd are the standard deviation values of MPD and MNTD in null communities; mpd and mntd.obs.rank are the ranks of observed MPD and MNTD compared to null communities values; mpd/mntd.obs.z represent the standardized effect size of MPD and MNTD compared to null communities values (= (mntd.obs - mntd.rand.mean)/mntd.rand.sd, equivalent to -NTI); mpd/mntd.obs.p are *P*-value of observed MPD/MNTD compared to null communities. Runs is the number of randomizations used to establish significance by producing null communities.

Phylogenetic dispersion
NRI

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p
lig	38	159.776	153.363	3.284	987	1.953	0.987
lgm	39	144.342	153.441	3.125	4	−2.912	0.004
hol	23	149.342	152.749	4.299	262	−0.792	0.262

NTI

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p
lig	38	35.502	42.038	3.728	28	−1.753	0.028
lgm	39	47.312	41.571	3.679	937	1.561	0.937
hol	23	47.099	49.339	5.854	364	−0.383	0.364

Trophic Dispersion
NRI

	ntaxa	mpd.obs	mpd.rand.mean	mpd.rand.sd	mpd.obs.rank	mpd.obs.z	mpd.obs.p
lig	38	0.728	0.69	0.055	744	0.695	0.744
lgm	39	0.669	0.678	0.065	401	−0.138	0.401
hol	23	0.727	0.652	0.096	764	0.783	0.764

NTI

	ntaxa	mntd.obs	mntd.rand.mean	mntd.rand.sd	mntd.obs.rank	mntd.obs.z	mntd.obs.p
lig	38	0.011	0.038	0.031	288	−0.863	0.288
lgm	39	0	0.038	0.037	44	−1.022	0.044
hol	23	0	0.064	0.065	81	−0.994	0.081

Table 4
Species occupancy. Total number of occurrences in the fossil record, first column (the second column contains the species common names), and the percentage of such occurrences falling in the PCOM LGM, third column. The species are the same as in Table 2.

Species	Common name	# Occurrences	% Of LGM occurrences
Cervus elaphus	red deer	67	0.46
Canis lupus	wolf	53	0.55
Bison priscus	steppe bison	51	0.73
Rangifer tarandus	reindeer	45	0.8
Capreolus capreolus	roe deer	43	0.35
Ursus arctos	brown bear	39	0.49
Mammuthus primigenius	woolly mammoth	38	0.71
Sus scrofa	wild boar	36	0.19
Coelodonta antiquitatis	woolly rhino	32	0.81
Equus ferus	horse	28	0.32
Bos primigenius	auroch	28	0.21
Alces alces	elk	27	0.33
Vulpes vulpes	red fox	27	0.3
Panthera leo	lion	24	0.42
Ursus spelaeus	cave bear	23	0.52
Megaloceros giganteus	irish elk	18	0.06
Stephanorhinus kirchbergensis	merck's rhino	17	0
Saiga tatarica	saiga	15	0.73
Equus hemionus	onager	15	0.67
Elephas antiquus	straight-tusked elephant	14	0
Crocuta crocuta	spotted hyena	13	0.38
Dama dama	fallow deer	11	0
Ovis ammon	argali	10	1
Alopex lagopus	arctic fox	10	0.8

occur together according to the prevailing climatic conditions. Steppe bison significantly co-occur, and becomes much more abundant, with these species during LGM.

Eventually, the passage to the last PCOM HOL fauna is marked by the lack of cold adapted, steppe specialists like *M. primigenius*, *C. antiquitatis*, and *Bison priscus*. Within this PCOM, the prevalent species are climatically tolerant, abundant taxa such as the red deer, wolf, and wild boar (Fig. 5) and climatic effects on species co-occurrences are overtly important (Table 1). One of the main reasons for such prevalence of climatic control is that megafauna extinction in Eurasia could have been partly determined by climatic

change (Abramson et al., in press; Bartlett et al., 2015; Prescott et al., 2012; Pushkina and Raia, 2008). Hence, besides climate, the end Pleistocene extinction crisis (Barnosky, 2004; Koch and Barnosky, 2006) certainly contributed to forming the PCOM HOL. Although its fauna is too much reduced in diversity (11 species) and distribution to advance any strong explanation for its composition, the percentage of significant co-occurrences explained by ecological factors is the lowest in this PCOM (6.3%, Table 1), which suggests that end-Pleistocene extinction disrupted ecosystem functioning to some extent during the Early Holocene (Malhi et al., 2016).

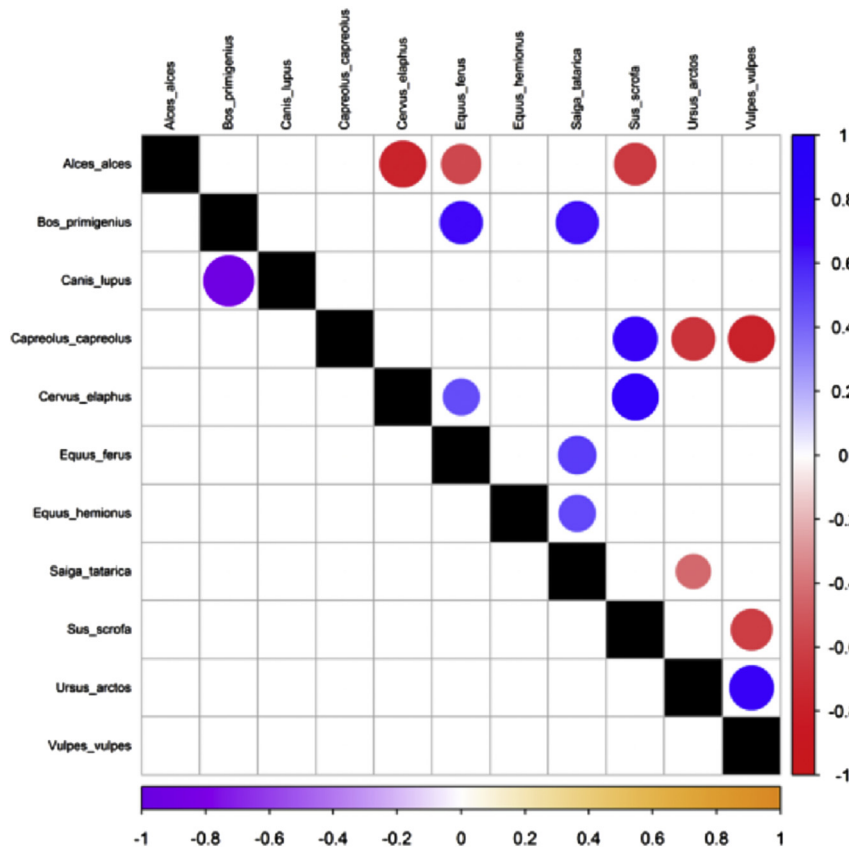In this paper we asked whether late Pleistocene large mammal

Fig. 5. Joint species distribution models for PCOM HOL. Significant correlations between species pairs are represented by circles. Blue circle: positive and significant relationship driven by climate. Red circle: negative and significant relationship driven by climate. Orange circle: positive and significant relationship not driven by climate. Purple circle: negative and significant relationship not driven by climate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

fauna of Europe behaved individualistically or in a coordinated fashion according to the intense climatic changes that characterized this period. Our data point to the latter, with climatic forcing controlling the onset, composition and possibly the demise of PCOM LGM. Not only its constituent species (both living and extinct) rose and fell in abundance together, and present a climate-driven co-occurrence pattern (which implies they were geographically associated over time and space), they also vanished in the same place and time. Woolly rhino, mammoth, and steppe bison, for example, all made for Northern and Eastern Siberia in the wake of LGM, where they eventually disappeared (Stuart, 2015). Importantly, the fact that these species tend to co-occur with each other both temporally and geographically, and under the same environmental conditions, is evidence that, at the very least, humans did not alter the spatial distribution, or the abundance either, of those of them which are now extinct.

Although the evidence for coordinated patterns of abundance and co-occurrence is not nearly as evident for the warm adapted fauna typical of the other two PCOMs, such concerted changes could be partly true for these species as well. The straight-tusked elephant and narrow-nosed rhino co-occur significantly depending on climate, went extinct at roughly the same age, and were both very abundant during the warm stadials. The hydruntine horse *Equus hydruntinus* made for southern Europe during its last stands (at roughly the same time when mammoth and wooly rhino got extinct in the far North), the same applies to cave bear (Crees and Turvey, 2014; Pacher and Stuart, 2009). Eventually, the very patterns of climate driven co-occurrence during PCOM LIG point to the

existence of a warm adapted, together with a coeval, cold-adapted ensemble of species (Fig. 4). This suggests either that the existence and extension of refugia (Hewitt, 2000; Sommer and Nadachowski, 2006) were at least as important during LIG as they were during LGM, or that the geographic species turnover during LIG was more important than during LGM. The great geographic extension of the PCOM LGM (Fig. 2) and of its dominant biome, the mammoth steppe (Dale Guthrie, 2001; Zimov et al., 2012) points to the latter. The reduced geographic extension of PCOM LIG further complies with this. Fossil sites of LIG age are geographically much more widespread than the geographic distribution of PCOM LIG itself would suggest (Fig. 2). This means that the spatial turnover (beta diversity) in LIG faunas was much higher than during the LGM. In keeping with this, significant associations between species pairs in PCOM LIG are much more often explained by species ecology than with the other PCOMs (Table 1).

The main conclusion of this study is that climate forcing determined the onset, composition and occurrence of large mammals during the last glacial maximum. Climatic settings preceding the LGM, are instead more consistent with uncoordinated responses at the community level, probably because of higher spatial habitat variability. Finally, ecological instability seems to have characterized Early Holocene faunas. Abundance in the fossil record, which is a very good proxy for ecological commonness (Meloro et al., 2007) unsurprisingly indicates that cold-adapted species were extremely common during the LGM. Yet, this is true of both extinct and extant cold-adapted species. Therefore, we found no evident effect of human presence on LGM faunal composition, abundance, and co-

occurrence patterns, which suggests climate change was probably more important than human hunting activities in causing the extinction of the megafauna in Eurasia.

Author contribution

PR, FC, MDF, and AL conceived the paper. All authors contributed to collect the data, to perform the analyses and to the writing of the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2016.07.036.

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