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Before, during and after megafaunal extinctions: Human impact on Pleistocene-Holocene trophic networks in South Patagonia

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ABSTRACT

Worldwide extinctions of large terrestrial vertebrates in the late Pleistocene provide insight on how humans reshape ecological communities. Understanding the ecological causes and consequences of megafaunal extinctions requires integrating approaches to reconstruct the ecological communities from the past. Here, we combined archeological and paleontological evidence with network analyses to understand the changes in ecological communities from late Pleistocene to the Holocene in South Patagonia, the last continental region where the encounter between humans and extinct megafauna occurred. The zooarcheological record suggests humans would have interacted mainly with large-bodied species, which comprise a small subset of the available prey. Accordingly, using network reconstructions and structural analyses, we found that human arrival would have produced minor changes in the overall structure of trophic networks. However, those few novel interactions established by humans would have created multiple indirect paths among megafaunal species. Indirect paths are the route for indirect effects such as competition and increase the vulnerability of interaction networks to perturbations. After the extinctions of most of the megafauna, the impoverished network became structurally simpler and densely connected. Our reconstructions of past trophic networks show that multiple indirect effects, potentially contributing to extinctions, can emerge even from a limited number of novel interactions and illustrate how network organization can affect and be affected by extinctions events.

1. Introduction

The last spectacular change in faunal diversity took place during the Pleistocene (2.5–0.01 million years ago) when about two thirds of the megafauna (body mass > 44 kg *sensu* Martin, 1967, the most common definition; Elias and Schreve, 2020) and nearly all mammals larger than 1000 kg (i.e. megaherbivores *sensu* Owen-Smith, 1988), became extinct in Eurasia, Oceania and the Americas (Koch and Barnosky, 2006; Barnosky and Lindsey, 2010). The highest extinction rates were reached at the end of the Pleistocene, between 50,000 and 10,000 years ago, when about 97 genera of megafauna disappeared worldwide (Barnosky et al., 2004; Koch and Barnosky, 2006; Haynes, 2009; Cione et al., 2009). The specific causes of these global megafaunal extinctions, frequently referred to as late Quaternary extinctions, have been debated by researchers over decades (Martin and Klein, 1984; Stuart, 1991; Grayson and Meltzer, 2003; Koch and Barnosky, 2006). Although hypotheses of an expansion of a hyperdisease (MacPhee and Marx, 1997; Lyons et al., 2004) and of extraterrestrial impacts (Firestone et al., 2007; Pino et al., 2019) have been proposed, by far the most broadly accepted drivers of late Quaternary extinctions are climate change and human impacts, even though there is no consensus on the relative importance of each one (Mosimann and Martin, 1975; Cione et al., 2003; Barnosky et al., 2004; Lorenzen et al., 2011; Prescott et al., 2012; Lima-Ribeiro and Diniz-Filho, 2013; Johnson et al., 2013; Wroe et al., 2013; Sandom et al., 2014; Bartlett et al., 2016; Araujo et al., 2017; van der Kaars et al., 2017;

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Broughton and Weitzel, 2018; Andermann et al., 2020). In support of these last two hypotheses, there is evidence that this period was characterized simultaneously by severe climate changes and by the expansion of human populations in range and density around the globe (Henn et al., 2012; Prescott et al., 2012). As a consequence of the latter, the late Quaternary extinctions became a study system to understand the long-lasting impacts of human activities on biodiversity.

Among the anthropogenic extinction models, the overkill hypothesis (Martin, 1973, 1984, 2005) may be considered as the most extreme model of extinction caused by the direct effect of human activities. However, an arriving predator, such as humans, may impact not only the populations of species with which it interacts directly, but also indirectly modify the dynamics of ecological communities by changing the way other species interact and influence each other (Pires et al., 2015). Indirect effects occur when the influence of one species is transmitted through one or several species to other species in the ecological community (Strauss, 1991; Abrams et al., 1996). Species interaction patterns in a community can be represented and examined using the network approach (Pascual and Dunne, 2006). Indirect relationships emerge from the paths that connect species indirectly to each other in such networks (Wootton, 1994). There is compelling evidence that these indirect paths can drive dynamics by providing multiple routes for cascading effects, and may even cause extinctions (Levin, 1999; Brook et al., 2008; Montoya, 2015; Pires et al., 2020). In this sense, indirect effects related to humans could have contributed to megafaunal extinction, especially where rapid overkill seems unlikely such as in South American Patagonia, where humans and megafauna coexisted for thousands of years (Borrero 2009; Villavicencio et al., 2016; Metcalf et al., 2016). Therefore, an important step in the study of late Pleistocene megafaunal extinctions is to understand how human arrival would have altered the organization of direct and indirect paths in interaction networks, contributing to shape extinction and post-extinction patterns.

Several lines of evidence indicate that human expansion through the Americas occurred in the late Pleistocene ca. 15,000–17,000 Cal. BP, preceding the changes in diversity and community composition at the Pleistocene-Holocene transition (Goebel et al., 2008; Haynes, 2009; Llamas et al., 2016; Perez et al., 2016; Politis et al., 2016; Moscardi et al., 2020; Prates et al., 2020). Archeological and molecular data show that the last continental region to be inhabited by humans was South Patagonia, peopled at least 14,000 Cal. years BP by small groups of hunter-gatherers (Raghavan et al., 2015; Villavicencio et al., 2016; Perez et al., 2016; Prates et al., 2020). The region had been colonized by the megafauna earlier, about 18,000 years ago, when the glacial retreat made it habitable (McCulloch et al., 2000; Tonni and Carlini, 2008; Metcalf et al., 2016; Villavicencio et al., 2016). Besides the rich fossil evidence documenting the changes of faunal assemblages, lithic technology of projectile points, stone balls, and the presence of large mammal fossils in Patagonian archeological sites suggest that humans exploited these species as food resource from the late Pleistocene to 400 Cal. years BP (Borrero, 1999, 2009; Miotti and Salemme, 1999; Miotti et al., 2018; Moscardi et al., 2020). Therefore, being the continental region where the encounter between the Pleistocene megafauna and humans occur for the last time and having an extremely rich archeological and paleontological record, South Patagonia has the elements for studying the potential role of humans in megafaunal extinctions and the consequences that these extinctions had for the composition and dynamics of ecological networks.

Here we combine paleontological and archeological data with models of ecological networks, to reconstruct the changes in the trophic network of South Patagonia and explore the potential direct and indirect role of humans in driving megafaunal extinctions. Specifically, we examine the zooarchaeological record of several sites from South Patagonia to assess how humans integrated these food webs. Then, using network models we investigate how changes in faunal composition altered the structure of trophic networks across the late Pleistocene-Holocene transition. We hypothesize that humans could have indirectly caused, or exacerbated, the megafaunal extinctions by changing the trophic network structure of South Patagonian late Pleistocene assemblages.

2. Materials and methods

2.1. Reconstruction of faunal diversity

We used the paleontological and archeological data from the literature to reconstruct the late Pleistocene (here ca. 18,000 to 14,000 Cal. years BP), the Pleistocene-Holocene transition (ca. 14,000 to 9500 Cal. years BP) and early-middle Holocene (ca. 9500 to 4000 Cal. years BP) assemblages of terrestrial vertebrates in the continental steppe environments that constitutes most of South Patagonia (Tonni and Carlini, 2008; Borrero, 2009; Prevosti and Martin, 2013; see Tables S1a, b and c for details about the studied species). The considered region includes Tierra del Fuego and covers continental Patagonia until the San Jorge Gulf basin (Fig. S1). The age of 14,000 Cal. years BP was established based on the first reliable evidence of human occupation (Perez et al., 2016; Borrero and Martin, 2017; Prates et al., 2020). In the archeological sample, only sites with a long sequence of occupation were included in the analyses (see below; Table S2a and b). We assume extant smaller-sized mammals were also part of past communities, since there is little evidence of major changes in distribution or extinctions of species weighting <10 kg.

2.2. Estimation of human consumption

We used zooarchaeological data as the main source of information to investigate the direct trophic interactions of humans. We obtained data for each species from 51 assemblages in eleven archeological sites dated between 14,000 and 4000 Cal. years BP (Tables S2a, S2b and S3). The archeological sites where chosen attending the following criteria: all sites have an abundant faunal record and evidence of human consumption patterns in the zooarchaeological samples, are reliably dated, and comprise a long sequence of human occupation, beginning with the earliest peopling of the area (for further details for human consumption see Moscardi et al., 2020). The sample size of taxonomically determined specimens is 15,357. The dates of these data were calibrated (with the Calib 7.0.4 software and the calibration curve for the Southern Hemisphere SHCal13; Hogg et al., 2013; Stuiver et al., 2014), and divided according to the two periods posterior to human arrival Pleistocene-Holocene transition (ca. 14,000 to 9500 Cal. years BP) and early-middle Holocene (ca. 9500 to 4000 Cal. years BP). The first period covers the arrival of humans in the area, as well as the significant environmental modifications of the end of the late Pleistocene and the extinction of the Pleistocene megafauna. The second period represents the post-extinction communities and is linked to important changes in subsistence and technology, such as the emergence and increased frequency of stone balls and blades as well as a reduction in the size of projectile points (Cardich et al., 1973; Bird, 1988; Politis, 1991; Banegas et al., 2014).

We computed the frequency of occurrence (FO) of each taxon in the archeological record as the proportion of sites/assemblages in which the different taxa had been recorded. This metric can be interpreted as the likelihood that a particular taxon would have been used by humans in the past. To assess the relative contribution of each taxon to human populations we recorded the number of identified specimens (NISP; Lyman, 2008), which is the most frequently available metric in the literature reporting zooarcheological data, and transformed it to percent values (% NISP). We used the NISP values of the unequivocally consumed fauna, i.e. samples with cut and/or percussion marks and/or thermoalteration, which show very low weathering stages, as well as very low or null values of modifications made by carnivores, rodents and roots (see Moscardi et al., 2020 for taphonomic details of the selected samples; Table S2). Because NISP considers each bone or fragment as a unit, this measure is sensitive to fragmentation patterns within and between taxa, which may lead to an overestimation of the number of individuals. Therefore, we used this metric only to infer a rank of abundance in a given site. To confirm the main temporal trends, we also characterized the usage of the guanaco (*Lama guanicoe*), previously shown to be the most important prey for ancient human populations in Patagonia (Mengoni Goñalons, 1999; Rindel, 2017; Miotti et al., 2018), based on the minimal number of individuals represented in a given assemblage, MNI (Table S4). This metric is reported in a smaller subset of studies but has the advantage of being less sensitive to fragmentation patterns and thus more conservative than NISP (Grayson, 1984).

2.3. Reconstruction of trophic networks

In order to explore the direct and indirect effects of humans in the ecological networks, we first obtained body mass data for extinct and extant terrestrial vertebrates from published sources (Table S1). We consider only the mammalian fauna and the rheas since rheas are known to be consumed by large mammalian predators and early human populations in the region and have fossil preservation comparable to that of mammals. All carnivores and humans were considered as potential predators and herbivores as the potential prey. We excluded *Arctotherium* sp. from the reconstructed networks because morphometric analyses suggest most tremarctine bears were omnivores, consuming a high percentage of plant matter and eventually consuming carcasses (Figueiro and Soibelzon, 2010). Therefore, inferring diet for this species based on body size while assuming it was a carnivore would result in unrealistic links with large potential prey. Thus, the trophic networks analyzed here represent a subset of actual food webs but encompass the bulk of the trophic interactions of mammalian predators. We reconstructed predator-prey interaction networks representing each period using a probabilistic model (the log-ratio model) in which the probability of an interaction between predator species *i* and prey species *j* depends on the body-mass ratios between predators and prey (Rohr et al., 2010; Yeakel et al., 2014; Pires et al., 2015):

$$P_{ij} = \frac{e^{\alpha+\beta log\left(\frac{m}{M}\right)+\gamma log^2\left(\frac{m}{M}\right)}}{1+\ e^{\alpha+\beta log\left(\frac{m}{M}\right)+\gamma log^2\left(\frac{m}{M}\right)}} \tag{1}$$

In this model m represents the body mass of prey species j, M represents the body mass of predator species i, and α, β, and γ are parameters that determine how body mass ratios affect interaction probability. This model has been shown to adequately reproduce interaction networks between mammals, while incorporating the uncertainty inherent to depicting interactions from the past (Yeakel et al., 2014; Pires et al., 2015). To obtain realistic parameters for Patagonian species we first compiled data on prey use by extant predator species (*Puma concolor*, *Leopardus geoffroyi*, *Lycalopex culpaeus*, *Lycalopex griseus*) in Patagonia (Table S5). Then, using the information on the mean frequency of use of each prey (the proportion of fecal samples containing a given prey species) across these studies, and body mass estimates of predators and their prey, we fitted the model to data corresponding to each predator. The models were able to explain on average about 70% of variation in prey use for the different predators (Fig. S2).

Next, to obtain interaction probabilities for the extant and extinct species in the past, we parameterized eq. (1) with the values estimated from data. To encompass the variation across predator species, we drew parameter values randomly from a uniform distribution with ranges determined by the smallest and largest values obtained for either canids or felids (Fig S2). Using this parameterization, the model generates realistic interaction patterns where canids and small felids are expected to have fed mainly on rodents and other small-sized mammals, whereas the large felid predators are hypercarnivores expected to have interacted mainly with medium and large-sized prey (Carbone et al., 1999; Prevosti and Vizcaíno, 2006; Prevosti and Martin, 2013).

We add humans to the network assuming the probability of preying upon each herbivore species is proportional to the frequency of occurrence of each potential prey in the zooarcheological record, i.e. the proportion of assemblages where each species has been registered. Because the zooarcheological record may be biased towards certain species, this inserts a new source of variation that does not apply to other carnivores, whose interaction probabilities are modeled according to body size. Thus, we performed sensitivity analyses in which interactions of humans were also assigned based on body-size relationships. We tested two scenarios: in the first, human trophic interactions are constrained by the actual human mean body size (65 kg); in the second, we assign interaction probabilities for humans similar to those of *S. populator*, the largest predator in Pleistocene communities, thus assuming humans were able to prey upon species larger than expected by body mass (Pires et al., 2015) due to behavioral aspects such as communal hunting and tool use.

From each probabilistic network obtained from the model we generated weighted networks by sampling interactions according to the pairwise interaction probabilities. Each resulting network can be depicted as a matrix $\mathbf{W}$ where columns represent predators, rows represent prey, and each matrix element w_{ij} represents the expected frequency of interactions given a certain number of sampled interactions. We set a fixed number of sampled interactions, E, according to the number of species in each time period so that E = number of prey × number of predators × 2. Because we adopt a probabilistic approach, instead of assuming one fixed network topology, we generate an ensemble of 1000 potential networks for each time period and analyze the structure of each generated network.

2.4. Structure of trophic networks

The dynamics of an ecological community are affected by the way ecological interactions are organized (Rooney and McCann, 2012). To investigate how network structure would have changed over time, we characterized structure by measuring network-level properties that are related to how perturbations spread across networks. We measured the degree to which the network is organized in modules, sets of species that are more densely connected to each other than to the rest of the network (Montoya et al., 2015), using the modularity metric Q (Newman and Girvan., 2004). To test the significance of the modularity degree we used a null model approach. We generated random versions of the analyzed networks where interactions are equiprobable while keeping the same number of sampled interactions, computed modularity for each of these networks, and then calculated the probability of obtaining the observed Q for the random set. Interaction diversity was computed as e^H, where H is the Shannon diversity index computed from interaction frequencies. To measure how closely connected species in the network are, we computed the average length of shortest paths (L) weighted by interaction frequencies (Opsahl et al., 2010). Small values of L mean most species in a network are strongly connected to each other directly or are connected via short indirect paths.

All metrics above are based on how direct pairwise interactions are organized. Yet, these direct interactions give rise to multiple indirect paths between species (Pires et al., 2020). We thus quantify how the number of indirect paths connecting species change across periods. The number of indirect paths of a given length l can be computed as $N_l = \sum_i \sum_j a_{ij}^l$ where a_{ij}^l is an element of the matrix $\mathbf{A}^l$, the adjacency binary matrix $\mathbf{A}$ depicting presence and absence of interactions multiplied by itself l times (Borrett and Patten., 2003) We focus on paths of lengths $l = 2$ and $l = 3$ as these represent indirect effects such as competition and indirect interference that are easier to interpret (Wootton, 1994). Considering the evidence that the guanaco (*L. guanicoe*) was the main prey used by humans, we examined how the human-guanaco interaction could have mediated indirect effects of human arrival. To do that we measured the proportion of all paths involving humans that also involved the guanaco by removing the interaction between humans and guanacos and estimating the change in the number of paths of length 2 and 3 that are lost when this interaction is absent. We also examined how species roles in network structure changed across time periods by measuring species strengths, the sum of the proportional contribution of species i to each of the other species' interaction set (Bascompte et al., 2006). Because we generated an ensemble of possible networks for each time period, structure was characterized not by single values representing structural metrics, but by distributions representing several potential networks. We performed all analyses using packages bipartite (Dormann et al., 2008) or tnet (Opsahl, 2009) in R (R Core Team, 2019).

3. Results

3.1. Changes in faunal diversity

During the late Pleistocene (here represented by sites dating ca. 18,000–14,000 Cal. years BP) the South Patagonian assemblages of large terrestrial vertebrates included nine species of large herbivores and six species of large carnivores (Table S1). According to paleontological data the most frequent herbivores were the ground sloth *Mylodon darwini*, the equid *Hippidion saldiasi* and the guanaco (*Lama guanicoe*), while the most frequent carnivores were the patagonian panther (*Panthera onca mesembrina*) and the canid *Dusicyon avus* (Miotti and Salemme, 1999; Borrero, 2009; Prevosti and Martin, 2013). Towards the Pleistocene-Holocene transition (ca. 14,000–9500 Cal. years BP) this assemblage underwent two main changes, the extinction of a large herbivore, *Macrauchenia patachonica*, and the arrival of a new predator: humans (Table S1). Finally, by the early-middle Holocene (ca. 9500–4000 Cal. years BP) the diversity of the mammalian fauna had already collapsed and the only large-bodied species that survived were the guanaco, Darwin's or lesser rhea (*Rhea pennata*), the puma (*Puma concolor*), *D. avus*, and *Homo sapiens* (Table S1) in addition to the extant small-sized species. Overall, of the 15 species larger than 10 kg that comprised the late Pleistocene ecological communities, only 5 remained in the early-middle Holocene, and of the 10 species that became extinct, 9 can be labeled as megafauna (Table S2).

3.2. Human trophic relationships

The zooarcheological record show that human populations of South Patagonia have exploited large vertebrates, particularly camelids, whose usage continued after the megafaunal extinctions. Although multiple megafauna species are present across sites, the extinct megafauna represents less than 10 percent (approximately 7.4%) of the total NISP within zooarchaeological assemblages in the late Pleistocene-Holocene transition, which are dominated by extant species, such as the guanaco and rheas. The composition of different archeological sites from the late Pleistocene-Holocene transition suggest that the guanacos were the most important prey for human populations, appearing in 92.3% ($N = 24$) of the sites and comprising 65% of the prey remains in most sites (Fig. 1 and Table S2). Moreover, the zooarchaeological record from different regions of South Patagonia suggests that the exploitation of guanaco as prey increased even further during the early-middle Holocene to 80%, or even 94% taken into account the unidentified camelid remains (Fig. 1 and Tables S2-S3). The increase in the guanaco contribution can be observed mainly between 7000–4000 Cal. years ago (Table S4). Two additional indicators of guanaco contribution to human diet, the NISPguanaco/NTAXAcon (number of consumed species) ratio and MNI (minimum number of individuals; Grayson, 1984; Mengoni Goñalons, 1999; Rindel, 2017), display a similar pattern of variation (Table S3 and S4). Other large herbivores such as the horse *Hippidion saldiasi*, the ground sloth *Mylodon* sp. and the camelid *Hemiauchenia paradoxa* can also be found in several late Pleistocene sites (38.46% of the sites have *H. saldiasi* remains, 23.07% *Mylodon* sp. and 7.69% *Hemiauchenia paradoxa*), but are not present in Holocene recent sites (Fig. 1 and Table S2). In the Holocene assemblages there is an increase relative to Pleistocene ones in the occurrence of small herbivores and a considerable increase in the occurrence of rheas (Table S2).

3.3. South Patagonian trophic network

According to our reconstructions, Pleistocene trophic networks in Patagonia would have a modular structure with two main modules. The first consisted of large-bodied predators such as the saber toothed-cat, the patagonian jaguar, and the puma alongside their large-bodied prey which would have included ground sloths, camelids and rheas. Armadillos (*Chaetophractus villosus* and *Zaedyus pichiy*) and the patagonian mara (*Dolichotis patagonum*), a large-sized rodent, would be the species connecting this module to a second module comprising smaller-sized predators such as small felids and canids and their prey, mostly small rodents (Fig. 2). Archeological evidence support humans would have interacted mainly with large-bodied prey (Fig. 1), suggesting humans would have joined the module of large-bodied species (Fig. 2). Human arrival would have caused minor effects on the overall structure of the network with no major changes in modularity, interaction diversity, or average path length (Fig. 3). However, within the module of large-bodied species, the addition of humans increased interaction diversity and reduced the average shortest path length, thus resulting in a more densely connected module (Fig. 3). Although the increase in the expected number of pairwise interactions after human arrival within the module of large-bodied species seems incremental, from 18 to 23, these novel interactions create multiple indirect interactions. The expected number of indirect paths of length $l = 2$ between large-bodied species increased from 86 to 112 (30%) and from 303 to 452 (50%) for paths of length $l = 3$ (Fig. 4). Nearly 25% of these novel indirect paths formed by humans would involve the human-guanaco interaction (Fig. 4). If we model human

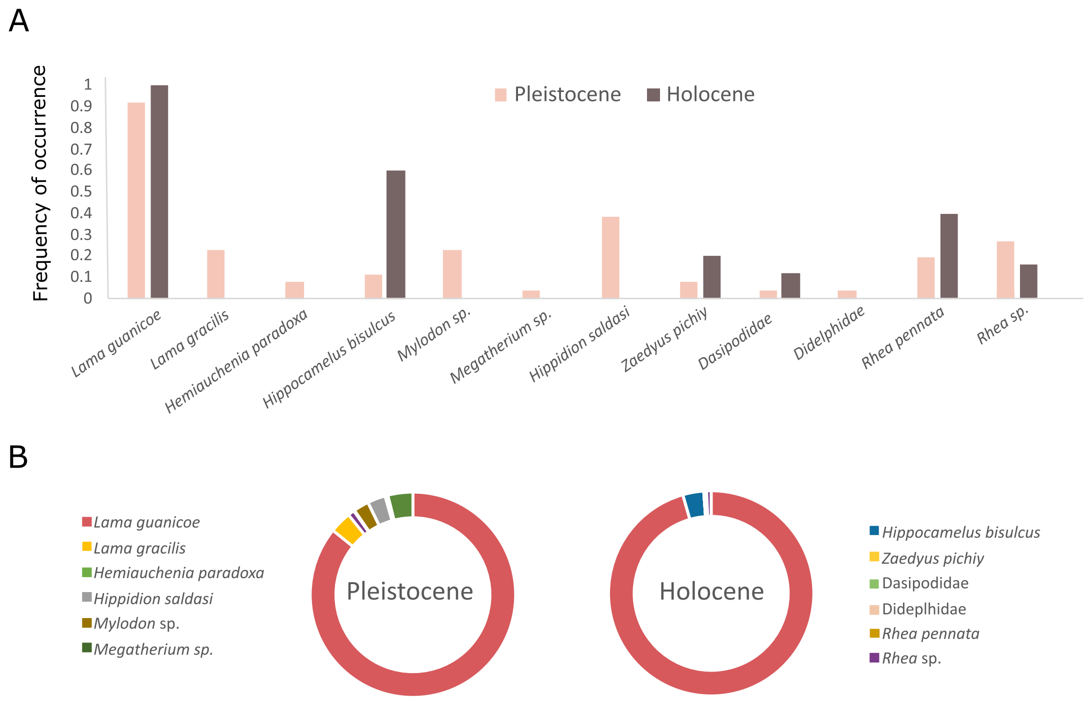

Fig. 1. Zooarcheological record of the Pleistocene-Holocene transition and early-middle Holocene in South Patagonia. A. Frequency of occurrence (proportion of sites/assemblages with records) of each taxon. B. Percentage of records (%NISP) of each taxon.

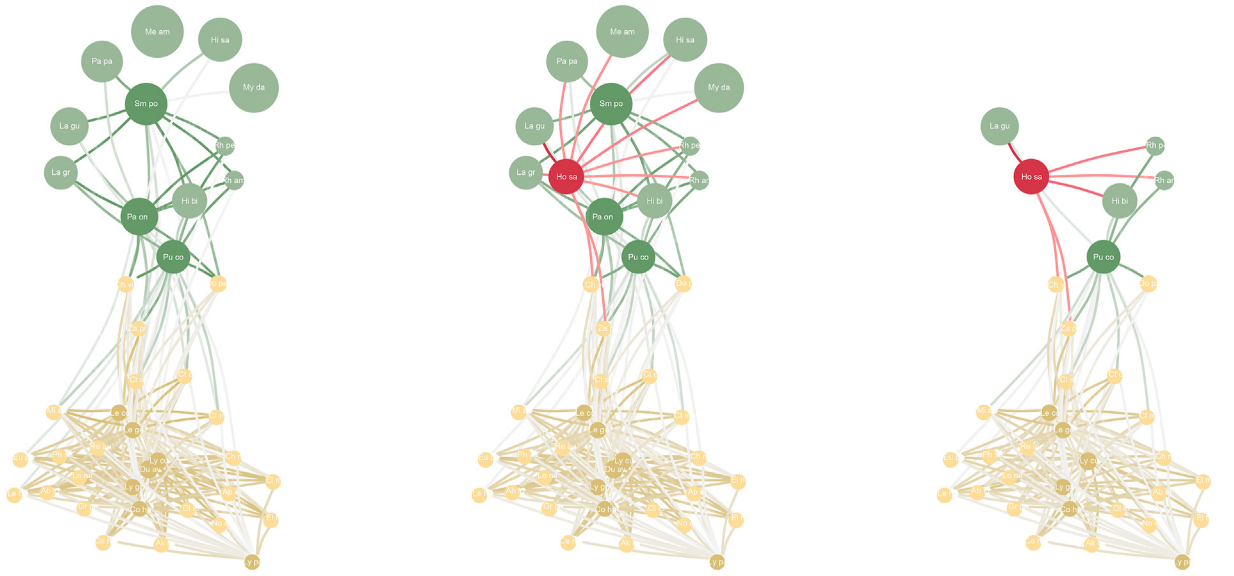

Fig. 2. Trophic networks representing the potential interactions between predators and prey in South Patagonia for three different periods: late Pleistocene, Pleistocene-Holocene transition and early-middle Holocene (from left to right). Circles represent species and the links the possible interactions between them. The tone of links is darker for interactions with higher probability. The two main colors represent the two main network modules. Darker circles represent predators and lighter circles the prey. Humans and their potential interactions are highlighted in a different color. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

interactions as a function of body size, results of structural analyses are the same (Figs. S3 and S4), and the increase in the number of indirect paths exceeds 60% (Table S6).

Late Pleistocene extinctions extirpated most large predators and herbivores, dismantling the module of large-bodied species thus reducing network modularity (Fig. 2). This resulted in a more connected network where species are linked through shorter paths (Fig. 3). Again, these effects are more pronounced among the survivors of the module of large-bodied species, where all surviving species would have become connected, reducing average path length (Fig. 3). Such structural changes also impacted species roles within the network. The puma which was the smallest among the

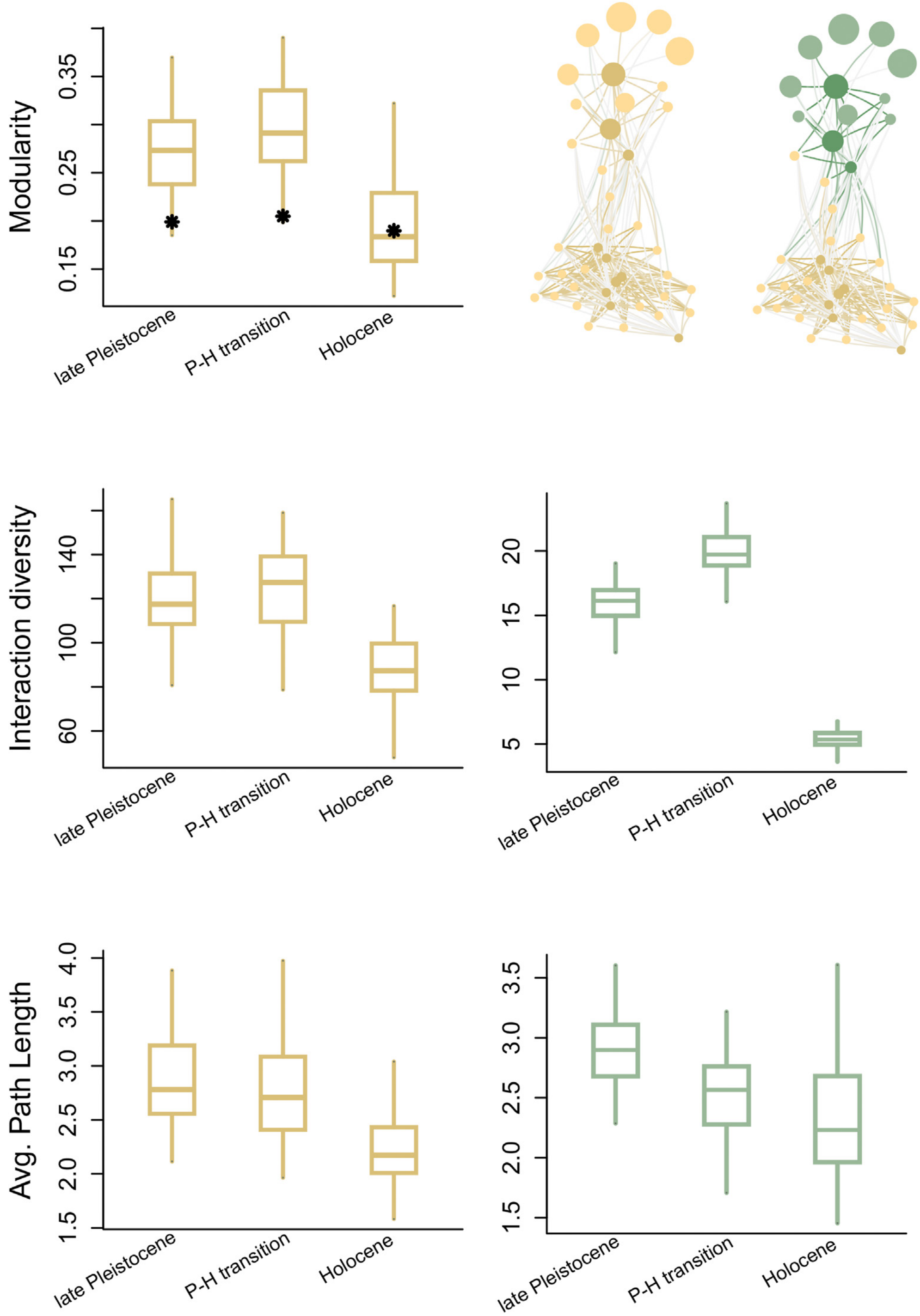

Fig. 3. Structure of trophic networks representing of South Patagonia for three different periods: late Pleistocene, Pleistocene-Holocene transition, and early-middle Holocene. Boxplots represent the distribution of each network metric for 1000 reconstructed networks representing each period. The panels to the left display values for metrics computed for the entire network while the right panel show the metrics computed only for the module of large-bodied species. The asterisks in the modularity graphic depicts the expected modularity for random networks of the same size and number of interactions.

large predators of the Pleistocene became the largest predator alongside humans, thus increasing in species strength (Fig. 5). Conversely, the strength of extant large prey first increases with the arrival of humans and then drops as most of their interactions are lost with their predators (Fig. 5).

4. Discussion

Although most recent studies acknowledge anthropogenic impacts contributed to late Quaternary Extinctions, the nature and relative role of such impacts is still vigorously debated (Cione et al., 2003; Grayson and Meltzer, 2003; Koch and Barnosky, 2006; Surovell and Waguespack, 2008; Prescott et al., 2012; Sandom et al.,

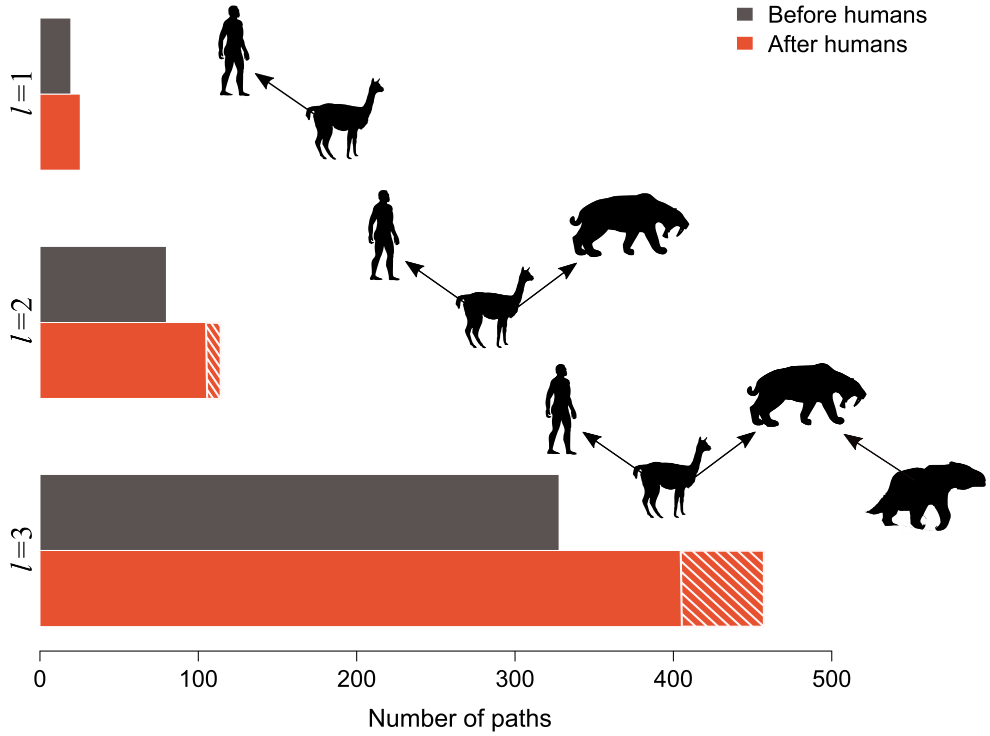

Fig. 4. Number of paths of length $l = 1$, $l = 2$, and $l = 3$ before and after the insertion of humans in predator-prey trophic networks of South Patagonia. The dashed area represents the paths including the human-guanaco interaction. The diagrams show examples of paths of each length that could include humans.

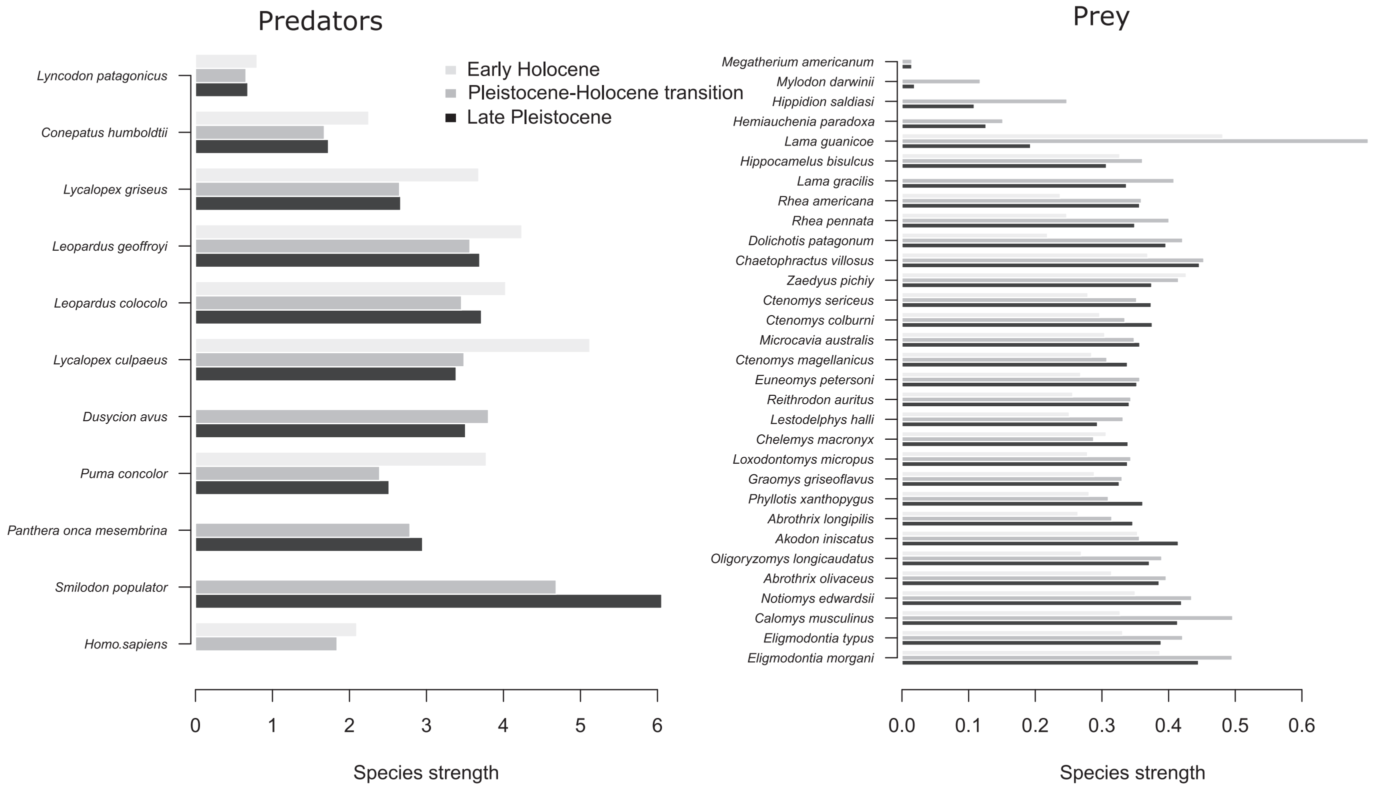

Fig. 5. Species strength of each species within trophic networks representing the potential interactions between predators and prey in South Patagonia for three different periods: late Pleistocene, Pleistocene-Holocene transition and early-middle Holocene. Bars depict mean values computed for 1000 reconstructed networks representing each period.

2014; Broughton and Weitzel, 2018). In South Patagonia, the fossil record indicates that at the time of the establishment of human populations, late Pleistocene assemblages contained a rich set of megafaunal species (Miotti, 2012; Martínez et al., 2016; Villavicencio et al., 2016; Miotti et al., 2018). We show that as humans became part of South Patagonian assemblages, interacting mainly with large species, the addition of a few novel interactions to trophic networks was sufficient to create several novel paths for indirect interactions between large terrestrial vertebrates. The extinctions that followed led to assemblages that are largely depauperate in large-bodied species and trophic networks that lost part of their structural complexity.

There is evidence of nearly all extinct megafauna in the zooarchaeological record of South Patagonia, supporting the interaction between humans and large-bodied prey (either by hunting live animals or scavenging of carcasses). However, the most frequent species recorded both in terms of the frequency of sites and in frequency of records within sites is an extant species, the guanaco (Miotti and Salemme, 1999; Miotti et al., 2018). Therefore, the archeological evidence does not endorse an Overkill model for South Patagonia. We are aware that this is not enough to totally discard this hypothesis for two main reasons. First, the archeological and paleontological records are always incomplete and subjected to sampling bias (Surovell and Waguespack, 2008). Secondly, as the Overkill hypothesis predicts an absence of killing sites due to the supposed high rate of extinction, it is almost impossible to totally refute it (Martin, 1973, 1984; Grayson and Meltzer, 2003). Nevertheless, the high usage of an extant species —the guanaco— relative to extinct ones, certainly does not support the Overkill model for South Patagonia, either in its original “blitzkrieg” form or in a smoother and slower variant (Cione et al., 2009; Villavicencio et al., 2016; Metcalf et al., 2016; Moscardi et al., 2020). Some recent studies have suggested that the Pleistocene guanaco populations of South Patagonia are not closely related with the Holocene ones (Metcalf et al., 2016; Moscardi et al., 2020), thus indicating a local extinction of the guanaco in South Patagonia during the Pleistocene. If so, considering the high consumption of guanaco shown by the zooarchaeological data during the Pleistocene-Holocene transition (65—81%), an argument in favor of the overhunting of this species, on regional scale, could be sustained. Still, this would not be enough to support overkill for the other species that actually died out. Therefore, we suggest that the direct effect of human hunting is unlikely to have been an important driver of late Quaternary Extinctions in South Patagonia.

Analyzing reconstructed Pleistocene trophic networks, we show that the presence of humans as a new element in these ecological communities could have impacts beyond the direct effect of hunting. The arrival of a new predator considerably increases the number of possible paths connecting species indirectly. Indirect paths of length two connect predators via their shared prey, allowing indirect effects of humans on the abundance of other large carnivores. Thus, the increase in these indirect paths implies an increase in the potential effects of competition (Wootton, 1994; Simmons et al., 2019). Increased competition among carnivores in response to humans has been proposed as a potential mechanism contributing to extinctions of predators (Ripple and Van Valkenburgh, 2010; Villavicencio et al., 2016). Scavenging of leftovers or stealing of carcasses by humans could also have reduced resource availability for other predators impacting them indirectly (Ripple and Van Valkenburgh, 2010). Competition could also have induced prey switching by other predators, raising predation pressure on herbivores that were less consumed prior to human arrival (Ripple and Van Valkenburgh, 2010) and fueling apparent competition dynamics (Holt and Bonsall, 2017). Such an indirect effect of humans on the abundance of herbivores is represented by indirect paths of length three in the network, which we show to increase even further when humans are added to the network. The fact that many of these novel indirect paths would involve the human-guanaco interaction increases the potential impact of such indirect effects. Paleontological data indicate guanacos would have been abundant in South Patagonia during the Pleistocene (Miotti and Salemme, 1999; Villavicencio et al., 2016; Metcalf et al., 2016; Moscardi et al., 2020), while according to the zooarcheological record, the consumption rate of guanacos by humans would have been high compared to other species (Miotti et al., 2018). With large populations and high reproductive rate, guanacos may have subsidized population growth of humans increasing their direct and indirect impact over other species. Thus, the human-guanaco interaction would have been a strong link in these past trophic networks and strong interactions are known to amplify the effects of abundance changes making interaction networks less stable (Rooney and McCann, 2012).

By establishing a denser web of interrelations, novel indirect pathways facilitate the propagation of the effects of perturbations (McCann 2011), which may have increased the vulnerability of late Pleistocene communities to external factors, including climate change (Brook et al., 2008; Pires et al., 2015). Late Pleistocene climatic oscillations and corresponding vegetation shifts certainly had demographic impacts over South American Pleistocene species (Cione et al., 2003). The latest Pleistocene climate warming, ca. 12,500 Cal. years BP, resulted in the reduction of open areas and the proliferation of the *Nothofagus* forest (McCulloch et al., 2000; Cione et al., 2009; Kilian and Lamy, 2012), possibly reducing the populations of large mammals living in open environments by the time humans arrived (the “Broken Zig-Zag hypothesis”; Cione et al., 2003, 2009, 2015). Any effects of such temperature and landscape changes would have spread more efficiently through a more connected network. The modular structure of the Patagonia trophic network would have limited the direct and indirect impacts of human arrival to the module of large-sized animals. Large-bodied mammals are more susceptible to demographic fluctuations than smaller-sized ones due to lower reproductive rates (Damuth, 1981; Johnson, 2002; Cardillo et al., 2005). The combination between these intrinsic life-history attributes and the topologically restricted effects of humans may help us to better understand the apparent conflicting evidence on the impact of climate, hunting and prolonged coexistence of humans and megafauna in South Patagonia (Villavicencio et al., 2016; Metcalf et al., 2016), partially explaining late Quaternary extinction patterns. Thus, we can think of these indirect effects as a potential mechanism to explain the impact of humans over large-body species without strong evidence of overkilling. These results reinforce that humans needed not to be particularly efficient predators or show strong preferences for the largest prey to impose significant changes in the system dynamics (Alroy, 2001; Zuo et al., 2013; Pires et al., 2015).

In this context, it is important to remark that humans are qualitatively different from other predators, establishing complex interactions with the ecological environment (Darimont et al., 2015) and other unique behaviors such as mass or communal hunting (Carlson and Bement, 2018), predation on predators (Darimont et al., 2015), hunting of animals in prime age and optimal physical condition (unlike other carnivores, which often prey on juvenile or senile individuals; Stiner, 1990) and feeding at multiple trophic levels (Stiner, 2001). All these factors, which were not accounted for here, would have caused humans to have even further direct and indirect impacts over other species, besides creating perturbations that exceed the direct effects of hunting.

Both the distribution of radiocarbon dates of archeological sites and molecular studies suggest that human populations displayed relatively low densities during the Pleistocene-Holocene transition

(Borrero, 1994; Borrero and Franco, 1997; Barberena et al., 2015; Zubimendi et al., 2015; Perez et al., 2016, 2017; Prates et al., 2020). After the late Quaternary Extinctions, humans experienced a small population decline in South Patagonia (Perez et al., 2017; Prates et al., 2020), likely related to the impoverishment of the prey assemblage, which could even have led to processes of local extinction or abandonment of certain areas (Borrero, 1994; Paunero, 2009; Borrero and Martin, 2017). However, coalescence analysis using mitochondrial DNA for all Patagonia suggests that both human and guanaco populations increased abruptly around 7500 years ago (Miotti and Salemme, 1999; Perez et al., 2016, 2017; Miotti et al., 2018; Moscardi et al., 2020). The demographic expansion of guanacos or recolonization of the south by northern populations during the early Holocene (Metcalf et al., 2016; Moscardi et al., 2020) may have been favored by the extinction of other large-bodied herbivores. The zooarchaeological evidence shows that human populations display an increase in the consumption of guanaco around the same time (Miotti, 2012; Miotti and Salemme, 1999; Perez et al., 2016, 2017; Moscardi et al., 2020), together with the increase in the consumption of armadillos, one of the species connecting the two modules in the Pleistocene-Holocene transition trophic network. With the demise of the other large vertebrates, humans would have behaviorally switched to a diet consisting almost exclusively of guanacos (Miotti and Salemme, 1999; Miotti, 2012; Miotti et al., 2018; Moscardi et al., 2020). This “specialization” in an abundant resource with high turnover, together with the shift towards smaller prey (Perez et al., 2016; Miotti et al., 2018; Moscardi et al., 2020) may have allowed human populations to thrive despite the loss of most large potential prey.

5. Conclusion

By combining network modeling tools with the impressive archeological and paleontological record of South Patagonia we show that human arrival increased the trophic connectivity between megafaunal species by creating multiple novel indirect paths linking them. In this sense, our results show that even without high levels of extinct megafauna hunting, human presence as a new predator may have changed the dynamics of late Pleistocene communities, thus increasing the chance of extinction of more vulnerable species. In addition to indirect effects of human arrival, such as increased competition among carnivores, indirect paths may have increased the vulnerability of the community to habitat alteration caused by the climate warming at the end of the late Pleistocene (Cione et al., 2009; Kilian and Lamy, 2012). Current communities are not only downsized, but structurally simpler versions of the late Pleistocene ones and the lower level of modularity and much denser organization make them vulnerable to current threats.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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