

# Community Structure of South American Carnivores in the Past and Present

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Understanding the causes that structure natural communities has long been an important goal for biologists. The question of what regulates the distribution and abundance of species in communities is central because it connects widespread processes (e.g., competition, predation), historical effects, and the interactions of these competing mechanisms with the mixture dependent on the habitats and organisms involved. Carnivores (mammals with a carnivorous diet), particularly, play a crucial role in maintaining the structure and stability of communities through predation, competition, or by altering prey behavior and prey habitat selection. For this reason, they have been used as a model to understand the effects of competition or top-down control in community structure. Although carnivores are naturally rare, due to their position at the top of the food web, their removal can have a variety of cascading effects within the community (Ripple et al. 2013).

Current diversity of South American terrestrial carnivorans (mammals of the Order Carnivora) is relatively high, with 40 out of 245 species (ca. 16%) of the order occurring in this subcontinent (Hunter 2011). But the geological record shows that a rich diversity of meat-eaters also inhabited South America in the past (Prevosti and Soibelzon 2012). During the lower-middle Miocene, carnivores from this part of the world were mainly represented by some groups of didelphimorphian marsupials and the extinct metatherian

clade Sparassodonta, and carnivorans only migrated to South America starting in the late Miocene (Marshall 1978; Prevosti and Soibelzon 2012; Prevosti et al. 2013). Although interesting advances regarding community structure of modern South American carnivores have been made during the last decades (see below), knowledge about the structure of historical assemblages is still poor. Determining the structure and dynamics of present and past food webs will be useful to gain insight into the forces that model carnivoran communities.

In November 2012, aimed at updating the state of knowledge about this topic, we organized the symposium “Community structure of South American carnivores in the past and present” in Buenos Aires, Argentina, at the *II Congreso Latinoamericano de Mastozoología y XXV Jornadas Argentinas de Mastozoología*. Our main idea was to discuss predator–prey relationships and carnivore community structure in different mammalian assemblages and ages, using diverse study approaches to improve the understanding of the ecology, paleoecology, and evolution of South American carnivores. This was evident in the selection of topics covered by the contributions presented (see below), ranging from paleoecology, morphology, and cranial morphometrics to trophic segregation, intraguild predation, and functional diversity of species assemblages. To contextualize this event (and this volume), we further offer a brief background highlighting the principal advances and approaches used to study structure of carnivore communities that inhabit or inhabited South America during the last 19 million years (from the late early Miocene to the present).

The structure of the carnivore communities (i.e., the degree of overlap and pattern of distribution of predator species based on body size, diet, and locomotory habits, and the inferred intraguild interactions and prey/predator relationships) of fossil assemblages of South America is scantily studied. Most paleoecological studies are limited to paleoautecological

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inferences (e.g., dietary habits), first based on the general description of bones and teeth (e.g., Lund 1839; Muñiz 1845; Marshall 1977a, 1978; Berta 1989; Cartelle and Langguth 1999) and only recently on statistical techniques (e.g., Van Valkenburgh 1991, 1999; Prevosti and Palmqvist 2001; Prevosti 2006; Soibelzon and Tartarini 2009; Figueirido and Soibelzon 2009). Similarly, paleosinecological studies, or the analysis of the structure of the carnivore communities in the past, are also very limited. Van Valkenburgh (1991; see also Van Valkenburgh 1999), using body size and craniodental indexes, generated a morphospace of the Pleistocene carnivores and suggested that the presence of several large hypercarnivore canids was related to the scarcity of other large hypercarnivores (e.g., felids). Using species frequencies in an early Pleistocene level of the Buenos Aires province (Argentina), Berman (1994) considered that the notoungulate *Mesotherium*, the ground sloth *Scelidotherium*, and the glyptodont *Neosclerocalyptus* were important prey of *Smilodon*. Later, Fariña (1996) estimated the number of species and the biomass of predators and prey in the late Pleistocene of Buenos Aires, and suggested that the community was “out of balance” because few carnivores were present in comparison to the number and biomass of large mammals and mega-mammals. The hypothesis of Fariña (1996) was further revised by Prevosti and Vizcaíno (2006), who found several biases and problems in his approach, and proposed an alternative hypothesis suggesting a more balanced scenario between carnivores and prey. They also discussed prey–predator relationships and potential intraguild interactions based on dietary habits and body size inferences for predators and potential prey species. Fariña’s (1996) method was then reused by Vizcaíno et al. (2010) to propose that some of the Santa Cruz Formation (late early Miocene) mammal assemblages were out of balance, with proportionally few Sparassodonta. In the same way, Fariña et al. (2014) went further and included new Pleistocene mammal assemblages in their analysis, finding new evidence to support the scenario described in Fariña (1996). However, since Vizcaíno et al. (2010) and Fariña et al. (2014) did not correct the methodological biases and errors pointed out by Prevosti and Vizcaíno (2006), their conclusions about the faunal unbalance may not be reliable.

Predator–prey relationships for the large hypercarnivore canids of the Pleistocene (e.g., *Procyon*, *Theriodictis*) were inferred using stable isotopes (Prevosti and Schubert 2013) or the estimated body mass of the canids and their potential prey, and the known prey/predator relationships in living carnivorans (Prevosti and Palmqvist 2001; Prevosti et al. 2009). Figueirido and Soibelzon (2009; see also Soibelzon and Schubert 2011) interpreted that the presence of several small-sized bear species with less carnivorous diet in the late Pleistocene of South America, in comparison to the only species recorded in the early-middle Pleistocene, is related to

the presence of more large carnivorous species in the late Pleistocene. But available data do not support this interpretation, because early-middle Pleistocene assemblages have similar numbers of carnivorans (or large carnivorans) as the late Pleistocene (see Prevosti and Soibelzon 2012; Prevosti et al. 2013). Martin (2008, 2013) studied the taphonomy of late Pleistocene caves of southern Patagonia and interpreted some of them as dens of an extinct form of jaguar (*Panthera onca mesembrina*), which consumed camelids, horses, and ground sloths (*Mylodon*). Using dental indices, body size, stable isotopes, and taphonomy, Prevosti and Martin (2013) reconstructed the carnivore guild of southern Patagonia in the latest Pleistocene, and discussed potential prey/predator relationships. Soibelzon (2011), based on dental anatomy, suggested that the procyonids of the late Miocene-Pliocene (*Cyonasua* and *Chapalmalania*) had a more predatory habit than living ones, and that they became extinct because the immigration of other carnivorans to South America, as was discussed about the extinction of *Chapalmalania* and the immigration of bears by Kraglievich and de Olazabal (1959). But the dentition of these extinct procyonids lack functional carnassials and the development of large shearing crests typical of more predaceous carnivorans. Recently, a fused caudal vertebra of a glyptodont with bite marks was interpreted as produced by the giant procyonid *Chapalmalania* (de los Reyes et al. 2013). Finally, Cione et al. (2009) discussed that the extinction of large carnivores in the late Pleistocene could produce a “top-down” effect that could contribute to the extinction of large mammals and mega-mammals in South America, but the available information do not allow a test of this idea.

About older faunas, punctual evidence of one specimen of a medium-sized sparassodont (*Lycopsis longirostris*) of the middle Miocene of Colombia should be mentioned, because it contains remains of a rodent (*Scleromys colombianus*) (Marshall 1977b). Croft (2001, 2006; see also Wroe et al. 2004; Vizcaíno et al. 2010) using xenograms, prey-predators richness relationships, and abundance of predators of the Cenozoic ages of South America, concluded that pre-Pleistocene faunas have low numbers of predators. Prevosti et al. (2012), based on new collections, published information, and in that moment ongoing paleoecological works on sparassodonts (Argot 2004; Ercoli and Prevosti 2011; Ercoli et al. 2012), revised the diversity and structure of mammalian predators of the Santa Cruz Formation (late early Miocene). They found a high diversity of predators (11 species of sparassodonts) that fall in the range of modern communities, and a good separation of sparassodont taxa based on the combination of body size, diet, and locomotory habits, but they did not use statistical methods to evaluate this segregation. Finally, the hypothesis of a competitive replacement of sparassodonts by carnivorans was evaluated by Prevosti et al. (2013) using richness curves of these groups along time, diet, and body size inferences to evaluate the

existence of temporal and ecological overlap between them. They found some temporal but no ecological overlap, and interpreted that environmental changes could be the cause of the extinction of Sparassodonta. Recently, Engelman and Croft (2014) discussed the possibility that the rise of large carnivorous didelphoid marsupials during the late Miocene-Pliocene and the first record of a large procyonid in the “middle” Pliocene could be related to the extinction of small carnivorous and large omnivorous sparassodonts, respectively (see also Goin and Pardiñas 1996; Prevosti et al. 2013; Zimic this volume).

Changing the focus toward modern carnivores, the number of publications regarding aspects of community structure has increased notably in the past two decades. First, several articles have analyzed the degree to which the niches of sympatric species overlap, considering the dietary habits (e.g., Johnson and Franklin 1994a; Farrell et al. 2000; Walker et al. 2007; Zapata et al. 2007; Bianchi et al. 2013), microhabitat use (e.g., Sollmann et al. 2012), or activity patterns (e.g., Di Bitetti et al. 2009; Lucherini et al. 2009; Romero-Muñoz et al. 2010). Other authors performed studies considering two or three niche dimensions simultaneously (i.e., diet, space, and time), addressing complete assemblages or particular dyads in canids (e.g., Johnson and Franklin 1994b; Jiménez et al. 1996; Juárez and Marinho-Filho 2002; Jácomo et al. 2004; Vieira and Port 2007) and felids (e.g., Scognamillo et al. 2003; Di Bitetti et al. 2010). Further, since the ecological overlap among species can differ under anthropogenic or natural disturbances, the effects of different human activities (e.g., introduced species [Polisar et al. 2003; Novaro et al. 2000; Palacios et al. 2012; Valenzuela et al. 2013], habitat modification [Lyra-Jorge et al. 2010; Andrade-Núñez and Aide 2010; Lantschner et al. 2012]) or natural phenomena (e.g., “El Niño Southern Oscillation” [Jaksic et al. 1997], increased flooding [Canepuccia et al. 2008]) on the community structure has been revised. Local differences in abundances or density of sympatric carnivores were also evaluated (e.g., Pereira et al. 2011; Kasper et al. 2012).

Behavioral interactions among carnivores were also studied in South American carnivore communities. Donadio and Buskirk (2006) explored the influence of body size, diet, predatory habits, and taxonomic relatedness on interspecific killing, employing data that included several species from this subcontinent. Hunter and Caro (2008) also assessed the potential for interspecific competition and predation within the assemblage of mammalian carnivores in the Americas, and their continental-scale approach captured the diversity of potential killing interactions within a large set of carnivores, including 77 species with different degrees of phylogenetic relatedness and variation in range overlap. Other publications have focused on particular groups; for example, Di Bitetti et al. (2010) studied niche partitioning and species coexistence in a felid assemblage, generating hypotheses

about behavioral differences that may facilitate species coexistence, whereas Oliveira et al. (2010) proposed the “Ocelot effect” (i.e., the ocelot *Leopardus pardalis* restricts the success of other minor felid populations) as a mechanism of determining the dynamics of the mesopredator community in Neotropical forests.

Morphology of South American modern carnivores was also the center of attention, assuming that niche relationships of species in a community are reflected in their morphological adaptations. Zapata et al. (2008) used an ecomorphological approach to examine trophic diversity in the terrestrial carnivore assemblage from the Argentinean Patagonia, by selecting measures related with the shape and size of carnivore mandibles and teeth. They found that species grouped in the morphospace in four morphoguilds, following a carnivory-omnivory-insectivory/herbivory gradient. While carnivores with a specialized dental pattern for consumption of meat (i.e., felids and mustelids) cluster in one of the extremes of the morphospace and species with specialized dental patterns for grinding invertebrates and vegetal materials (i.e., mustelids) score in the opposite side, the species with generalized dental patterns (i.e., canids) scatter in the center. On the other hand, Morales and Giannini (2010) studied the Neotropical felid assemblage on the basis of craniodental variables reflecting morphofunctional variation, adding to their analysis factors such as phylogenetic covariation, geographical distribution, habitat use, and activity patterns. They found that the species tend to segregate in morphospace plus one or more factors (e.g., habits) that make interspecific overlap in niche space minimal. They also reconstructed the historical assembly of the Neotropical felid guild on the basis of dated phylogenies, biogeographic history, and the fossil record, finding a pattern of successive invasions and speciation in which new lineages occupied previously vacant areas of morphospace, or new species occupied overlapping areas but with contrasting habits.

Finally, robust data on the ecology and life-history traits (e.g., reproductive lifespan, number and size of offspring) are still needed for most Neotropical carnivores. Since communities usually include a mix of species having different evolutionary relationships, life-history traits and strategies can differ dramatically among sympatric taxa. As a result of this data gap, our knowledge about South American carnivores is largely partial, and important hypotheses about community structure remain virtually untested.

In this context, the aim of our symposia was to act as a catalyst for researchers interested in structure of carnivore communities. The seven contributions compiled in this volume cover a wide range of approaches, taxonomic groups (Carnivora, Sparassodonta, Didelphimorphia), and ages. These papers are complementary to previous contributions or go beyond, bringing interesting synthesis or unexplored new research lines.

First, Ercoli, Prevosti, and Forasiepi studied the community structure of carnivores of the Santa Cruz Formation (late early Miocene). Based on body size, diet (derived from a dental index), and locomotion (from a morphogeometric study of limb bones), these authors evaluated through statistical techniques the existence of segregation between sparassodont species, testing if they have a random, systematic, or aggregated pattern. They found that the distribution of species in the morphospace delimited by the mentioned variables is systematic, indicating the presence of good separation among predators and minimizing competition. They also evaluated potential predator–prey links using body mass information of sparassodonts, and potential and the known predator–prey body mass relationships. They also discussed the existence of competence between Sparassodonta and the “terror birds” (Phorusrhacidae).

Zimicz studied the change in diversity, body size, and diet of carnivorous Didelphimorphian in the late Miocene-Pliocene, and its correlation with small-sized sparassodonts (Hathliacyniidae) diversity, to explore the existence of a competitive replacement of small sparassodonts by didelphimorphians. She found some overlap in size, but not in dental index (and in the multivariate space) between them, and concluded that they use different ecological “space” and that the extinction of the Hathliacyniidae was probably related to environmental changes.

Morales and Giannini’s work is a bridge between paleontological and neontological studies, because it explores changes in the Neotropical felid assemblage since the late Pleistocene extinction. They used cranial and skeletal measurements, multivariate techniques, and phylogenetic comparative methods to analyze a possible segregation of felids in the present and in the Pleistocene, trying to identify if phylogeny, size, or functional aspects explain the distribution of felids in the morphospace. They stated that size was the principal factor that structured the ensemble, but that the phylogeny has also affected the pattern of distribution in the assemblage. On the other hand, Schiaffini and Prevosti present a similar work focused on the living small carnivores of southern South America, using geometric morphometrics instead of “traditional” methods. Phylogenetic relationships explained a large part of the structure of this guild, but size, diet, and habitats also contributed to separate species.

Zapata, Delibes, Travaini, and Procopio performed an interesting study that also is a bridge, but in this case between morphological and ecological approaches. They studied the diet and morphometric indexes of some carnivores of Patagonia and found a good correspondence in one season (spring–summer) but not in the other (fall–winter). This work showed that at fine scales (e.g., annual variation) morphology could not correctly reconstruct prey–predator relationships, but at a larger scale there is a good correlation between

morphology and diet as was reported by other authors (e.g., Van Valkenburgh 1988, 1989; Palmqvist et al. 1999; Friscia et al. 2007).

Oliveira and Pereira evaluated the role of intraguild predation and interspecific killing as structuring forces of carnivore communities in South America. They found that the hypercarnivorous jaguars, pumas, and ocelots are the species most likely to have significant impact on the guild, and suggested that intraguild predation and interspecific killing are not random and reflect widespread interactions that influence carnivore community structure.

Finally, Fariás and Svensson assessed the vulnerability of the functional richness of South American carnivore assemblages, both at continental and regional levels. They assessed through simulations the form of the association between functional richness and species richness, finding low functional redundancy and high sensitivity to global extinctions. The authors suggested the existence of non-compensatory responses to environmental stressors by functionally redundant species and, thus, sensitivity of carnivore functional richness to ongoing trends in land conversion and habitat degradation. On the other hand, they observed that functional richness at regional scale paralleled latitudinal gradients in species richness, but vulnerability did not entirely match these variables in space, nor did it risk estimates that accounted for regions’ conservation status.

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