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RESEARCH PAPER

Unravelling the multi-scale structure of vertebrate scavenger communities: The role of beta-diversity in livestock carcass consumption

María Eugenia Cabrera-García [a,b,*], Patricia Mateo-Tomás [c,*], José Hernán Sarasola [a,b], Juan I. Zanón Martínez [a,d], Beatriz Martínez-Miranzo [a,b,e], Pedro P. Olea [f,g]

[a] *Centro para el Estudio y Conservación de las Aves Rapaces en Argentina (CECARA), Universidad Nacional de La Pampa (UNLPam), La Pampa, Argentina*
[b] *Instituto de Ciencias Ambientales y de la Tierra de La Pampa (INCITAP), Consejo Nacional de Investigaciones científicas y Técnicas (CONICET), Santa Rosa, La Pampa, Argentina*
[c] *Biodiversity Research Institute (CSIC – University of Oviedo – Principality of Asturias), 33600, Mieres, Spain*
[d] *Instituto Multidisciplinario sobre Ecosistemas y Desarrollo Sustentable, Universidad Nacional del Centro de la Provincia de Buenos Aires, Tandil, Buenos Aires, Argentina*
[e] *Department of Biodiversity, Ecology and Evolution, Facultad de CC. Biológicas, Universidad Complutense de Madrid, José Antonio Novais 12, Madrid, 28040, Spain*
[f] *Terrestrial Ecology Group (TEG), Departamento de Ecología, Universidad Autónoma de Madrid, Madrid, Spain*
[g] *Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain*

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ABSTRACT

Understanding the structure of communities across multiple scales is useful for predicting impacts on biodiversity and ecosystem functioning. Scavenging, an important ecological function performed by scavenger assemblages, stands as a significant force shaping ecosystems. Using biodiversity partitioning, we assess the relative contribution of multiple scales (i.e., within and among individual carcasses, species and habitats) to the richness and Shannon diversity of vertebrate scavenger communities consuming anthropogenic food subsidies (i.e. livestock carrion) in central Argentina. We further evaluate the potential effect of carcass and habitat characteristics (including human impact) on the richness, abundance and diversity of vertebrate scavengers. A total of 31 carcasses, 22 of cow and nine of sheep, were monitored using remote cameras in cropland and natural habitats, recording consumption by 10 vertebrate species (four birds and six mammals). 50 % of scavenger species were observed at carcass level ($\alpha_1 = 4.94$ species), a contribution lower than expected by chance. While the turnover of species among carcasses (β_1 diversity) significantly contributed (40 %) to regional richness (γ diversity), turnover of species between carrion types and habitats (β_2 diversity) contributed a smaller fraction (10 %). Partitioning of Shannon diversity showed similar patterns to richness. Scavenger abundance increased during spring and was positively influenced by carcass weight; furthermore, carcasses in croplands supported less abundance that those located in natural habitats. Aligning with the theory of carrion unpredictability in maintaining biodiversity, our results suggest that scavenger species replacement (turnover) at human-mediated carcasses scattered in the field plays a significant role in shaping vertebrate scavenger assemblages.

Introduction

Biodiversity loss is occurring across multiple scales everywhere on the planet (Levin, 2000; Pasari et al., 2013; WWF, 2020). To halt species loss and the consequent degradation of the ecosystem functions and services they support, we need to increase our understanding of the processes that maintain species diversity, from smaller scales up to the regional and global ones (Pasari et al., 2013). Biodiversity is multidimensional and multi-scale, so approaches that integrate different measures of biological diversity (e.g., species richness and diversity) across spatial scales (e.g., Jost, 2010; Paknia & Pfeiffer, 2011) are therefore increasingly recommended for a better understanding of how biodiversity is organized in ecosystems (Socolar et al., 2016). Biodiversity partitioning (Jost, 2007) allows evaluating how communities are structured in space and thus provides useful insights to predict natural and anthropogenic impacts on biodiversity and ecosystem functioning (Mori et al., 2018) and design management conservation planning (Socolar et al., 2016).

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* Corresponding authors.
E-mail addresses: mariaeugenia.cabrera@cecara.com.ar (M.E. Cabrera-García), patricia.mateo@csic.es (P. Mateo-Tomás).

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Decomposition of dead organic matter is a key ecological function supporting biodiversity across ecosystems (Cardinale et al., 2012). A wide diversity of both obligate and facultative scavenging vertebrates and invertebrates feed on dead animal matter, i.e., carrion (Wilson & Wolkovich, 2011; Barton et al., 2013; Mateo-Tomás et al., 2015; Anderson et al. 2009), which creates spatiotemporal biodiversity hotspots (Payne & Moore, 2006; Olea et al. 2019). This scavenging activity contributes to support ecosystem services such as disease regulation, nutrient recycling and biodiversity maintenance (Beasley et al. 2012, 2015; O'Bryan et al. 2018). A deeper understanding of how these scavenger assemblages are structured would therefore contribute to the preservation of biodiversity and the associated ecosystem processes. However, despite increasing interest on scavenging communities (Olea et al. 2019), regardless of their geographical extent (i.e., from local to global), most research to date has focused on describing the structure and function of these species' assemblages from a traditional approach, i.e., focused on species richness and diversity at one single scale (e.g., carcass or study area; Chapman & Sankey 1955; Selva et al. 2003; Wilmers et al. 2003; De Vault et al. 2011; Yeh & Drazen 2011; Killengreen et al. 2012; Anderson & Bell 2014; Sebastián-González et al. 2019; Orihuela-Torres et al. 2021). Contrastingly, although carrion availability in space seems to play a major role in scavenger ecology and evolution (e.g., Ruxton & Houston 2004; Monsarrat et al. 2013; Fluhr et al. 2017), information is lacking on how the composition and structure of scavenger assemblages vary across spatial scales. By linking local (alfa) and regional (gamma) scales, beta-diversity emerges as a useful measure to give further insights on the multiscale dimension of biodiversity (Socolar et al., 2016). In the case of scavenger communities, the beta-component will enhance our understanding of the mechanisms that shape and maintain the scavenger assemblages from individual carcasses to larger scales (e.g., habitats, study areas); this will allow us, for example, to better assess the importance of carcass unpredictability in scavenging ecology and conservation (Socolar et al., 2016). The few studies dealing with the biodiversity of scavenger communities across scales suggest that local processes such as species-sorting through habitat heterogeneity would dominate scavenger community's dynamics together with stochastic forces (i.e., related to carrion unpredictability and scavenging being a widespread strategy among vertebrates; Mateo-Tomás et al. 2019).

Here, we considered three classical measures of biological diversity (i.e., species richness, abundance, and true Shannon diversity) across scales in vertebrate scavenger communities heavily subsidized by anthropogenic food (i.e., livestock carcasses) in La Pampa, Argentina. To the best of our knowledge, this is the first time that a biodiversity partitioning approach is used to assess both the changes in the structure of vertebrate scavenger communities from individual carcass to regional scales and the main factors shaping them. To illustrate the potential of this approach, we assessed the influence of carcass type (cow and sheep) and habitat (forest and natural pastures vs. crops), two major factors known to shape scavenger communities elsewhere (Turner et al. 2017; Pardo-Barquín et al. 2019), on the spatial variation of diversity (i.e., α-, β-, and γ-diversities). We also evaluated the potential effect of carcass and habitat characteristics, including human impact, on the richness, abundance and diversity of the vertebrate scavenger communities consuming livestock carcasses. Based on previous studies highlighting the importance of habitat heterogeneity and carcass unpredictability for scavengers (e.g., Monsarrat et al. 2013; Fluhr et al. 2017; Mateo-Tomás et al. 2019), we hypothesized a significant role of the beta-component, both between carcasses and habitats, in determining the structure of the vertebrate scavenger communities, contributing more than expected to increase their richness and diversity.

Materials and methods

Study area

The study area overlaps with two ecoregions: the Espinal in the mid-west and the Pampas in the east of La Pampa province (Cabrera 1976; Brown et al. 2006), comprising ∼ 94.635 km^2 in central Argentina (Fig. 1). The Espinal is a xerophilic forest ecosystem characterized by the dominant tree known as *caldén* (*Neltuma caldenia*) with grassland and bush covers. Plateaus, valleys, hills, and plains (ranging from ∼50 to ∼200 m.a.s.l.; Cano et al. 1980) characterize the topography. Climate is temperate-arid with very high temperatures in summer (up to 45 °C) when most of the scarce rainfall falls (300–550 mm/year; Fernández & Busso 1997). The Pampas region was highly modified, and it is currently covered by a matrix of crops and pastures with small patches of *caldén*. Climate is temperate-humid, with precipitation ranging from ∼700 to ∼1200 mm/year, decreasing from Northeast to Southwest. Annual average temperatures vary between 14 and 20 °C and decrease towards the South (Matteucci et al. 2012).

Most of the land in the region is privately owned and managed for livestock, mainly cattle, hunting, and cultivation, which are the main economic activities in La Pampa province (Viglizzo et al. 2001); and only <1 % of land is a protected local reserve (González-Roglich et al. 2012). In the Espinal, cattle raising is characterized by a classical extensive production system and includes around 6 % of the national herd and beef livestock production in Argentina (i.e., ∼3,100,000 animals in 2020; SENASA (2021a)); sheep farming is scarcer, with a census of 272,528 animals in 2020 (SENASA 2021b). Agriculture involves crop rotation and cultivated pastures to feed livestock (Cano et al. 2004). Although both ecoregions have been significantly altered by human activities, the Espinal retains vast areas of wild woodlands and grasslands, which are deemed to constitute a more natural environment compared to the Pampas.

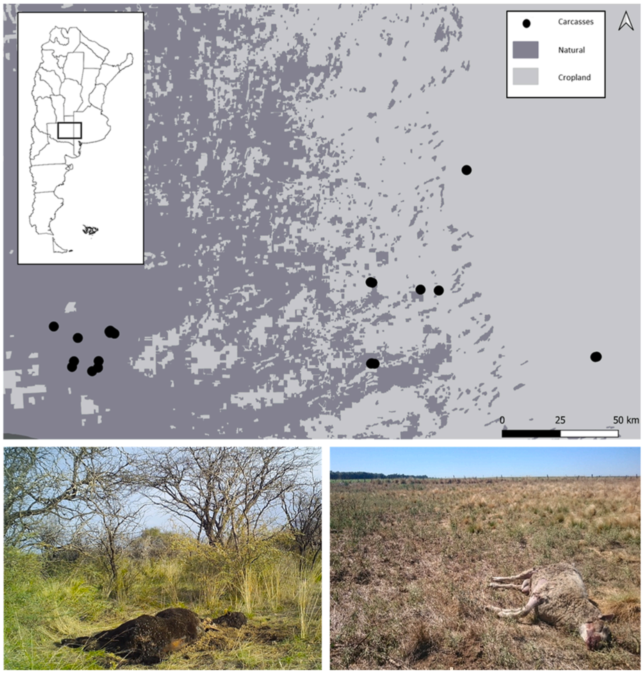

Fig. 1. Spatial distribution of carcasses (black dots) in the study area (La Pampa province in the centre of Argentina) according to the main habitat types. Black dots do not coincide with the total number of monitored carcasses (N = 31) because in some cases they overlap. The two photographs below show different types of carcasses (cow on the left and sheep on the right) in different habitats (natural and cropland, respectively). Photo credits: Mª Eugenia Cabrera-García.

On-ground carcass monitoring

A total of 31 carcasses of cows and sheep killed by accident or disease were monitored during 2017–2020 (Appendix A). Eleven cows and 5 sheep carcasses corresponded to the Espinal ecoregion (hereafter natural habitat) and 11 cows and 4 sheep to the Pampas (hereafter cropland). These carcasses consisted of whole bodies obtained through collaboration with farm owners and workers, who contacted us after locating a dead animal in their farms (Fig. 1). Carcasses remained in the same place where the animal died. Only those carcasses that were exposed for <48 h and mostly unconsumed (i.e., only eyes and <10 % of the body lacking) were monitored. Carcasses were monitored from their location in the field until their total consumption (or until only bones and skin remain) using motion-triggered remote cameras (Mateo-Tomás et al. 2015, 2017). We used camouflaged Browning ® BTC-5HDP cameras equipped with soundproofing and infrared systems to reduce possible disturbances to fauna. Cameras were installed at 3–6 m from the carcasses in order to be able to photograph all animals that accessed the carrion in an area of ~100 m^2. Before placing the cameras, carcasses and their immediate surroundings (~25–50 m radius) were inspected for signs (i.e., feathers, faeces, tracks) of scavenging species (Selva 2004). Carcass weight was estimated by taking reference measurements of the animal size in the field and using available references (Inchausti & Tagle 1982) together with the expertise of the livestock owners. Carcasses monitored simultaneously were separated at least 1 km (Fig. 1), except for three cows at cropland, which the farm owner moved together to a single site. As the same results were obtained with and without these three carcasses in the analyses (see Results), they were finally included to maintain a similar sample size among habitats.

A species was considered as consuming a carcass when an individual was seen either pecking, biting or tearing any part of the carrion in at least one photograph. When this action was not clearly visible, we were guided by the position of the body (e.g., if it was pushing with its paws or claws or if its head was inside of some part of the carrion). Finally, the abundance of each scavenging species per carcass was estimated as the largest number of individuals of that species simultaneously recorded in one photograph (Mateo-Tomás et al. 2015, 2017; Pardo-Barquín et al. 2019). Although this approach only yields a minimum abundance per species, it prevents overestimating species' abundances by counting the same individual several times at the same carcass; this method has been extensively used to study the community ecology of vertebrate scavengers elsewhere (e.g., Ogada et al. 2012; Moleón et al. 2015; Mateo-Tomás et al. 2015, 2017; Pardo-Barquín et al. 2019). To further improve the identification of unique individuals, we also looked for individual marks (e.g., fur patterns, scars, metal rings, tailless) to identify different individuals in different pictures at the same carcass.

At each monitored carcass, we recorded ten variables that could influence the presence of scavenging species through carcass and habitat characteristics (Table 1). Following Pardo-Barquín et al. (2019), these variables accounted for land use/land cover within 1 km radius around the carrion. We further considered human impact by recording the distance from the carcass to the closest inhabited place, electric infrastructure and roadway. Carcass species (i.e., cow and sheep) and weight, and the season when mostly monitored (i.e., autumn, winter, spring and summer) were also retrieved.

Table 1
Response and explanatory variables considered to explain the influence of habitat on the richness, abundance and diversity of vertebrate scavenger communities at livestock carcasses in La Pampa province, Argentina.

Variable	Description
Response variables	
Richness	Number of vertebrate species recorded scavenging at a carcass
Diversity	Shannon diversity $e^{H'}$, where $H' = -\sum_{i=1}^{s} p_i \log_2 p_i$ p_i is the proportion of individuals of species i from the total number of individuals of all species recorded scavenging at a carcass
Abundance	Minimum abundance of unique individuals recorded per species and carcass. Estimated as the maximum number of individuals per species that were recorder in the same photo at a carcass. Individuals were unique marks (e.g., fur patterns, scars, tailless, metal rings in birds) were looked for in other pictures for inclusion in the final count
Explanatory variables	
Pastures	Surface covered by pastures within 1-km radius around the carcass (range: 0–3.1 km^2)
Forest	Surface covered by forests within 1-km radius around the carcass (range: 0–3.1 km^2)
Crops	Surface covered by crops within 1-km radius around the carcass (range: 0–3.1 km^2)
Electric infrastructures	Shortest linear distance to the closest electric infrastructure (range: 0.08–15.31 km)
Inhabited places	Shortest linear distance to the closest inhabited place (range: 2.59–94.18 km)
Roadways	Shortest linear distance to the closest road (range: 0.99–13.53 km)
Carcass species	Carcass species, i.e. cow and sheep
Carcass weight	Carcass weight (range: 20–450 kg)
Season	Season, i.e. autumn, winter, spring and summer, when a carcass was monitored

Statistical analyses

To characterize the vertebrate scavenger community at livestock carcasses in the study area we calculated species richness and Shannon diversity following the framework of Jost (2006, 2007) of 'true' diversities (Tuomisto 2011) for an assemblage. True diversities (^{q}D) were estimated using the following equation:

$$^{q}D = \left(\sum_{i=1}^{S} p_i^{q} \right)^{1/(1-q)}$$

where S is the number of species within a site, p_i is the relative abundance of the i^{th} species and q is the "order" of the diversity (i.e., the parameter that indicates its sensitivity to common and rare species; Jost 2006). Here, we used $q = 0$ and $q = 1$ to calculate ^{0}D (equivalent to species richness) and ^{1}D (equivalent to the exponential of Shannon entropy), respectively. These measures were then converted to effective number of species (Ricotta, 2008; Jost et al., 2010). Calculations were made at four different scales: i) individual carcass, ii) carcass species (cow or sheep), iii) habitat (natural or cropland), and iv) the whole area. To allow further comparisons among scales, we estimated the vertebrate scavenger community also for an equal sample completeness (or coverage) using the incidence-based approach (i.e., a sampled fraction of the total species recorded at each scale equal for all the scales to compare; Table 2; see Chao et al. 2014). In addition, we calculated the minimum abundance of scavenging bird and mammal species for the same scales (see above; Table 2).

Species richness and diversity were partitioned into different spatial components following the multiplicative partitioning approach (i.e., $\gamma = \alpha$ x β; Whittaker, 1972; Jost, 2006, 2007). Therefore, our hierarchical partitioning approach included richness and diversity values as effective number of species: i) within (α_1) and between (β_1) individual carcasses, ii) within (α_2) and between (β_2) carcass species and/or habitats and iii) in the entire study area ($\gamma_{\text{whole-area}}$).

To compare multiplicative beta across different assemblages with different sample sizes, we standardized beta by using the formula (Jost 2007):

Table 2

Main characteristics of the vertebrate scavenger communities recorded at livestock carcasses of cow and sheep in cropland and natural habitats in the centre of Argentina. Species richness, abundance and diversity of scavengers are shown considering different spatial scales.

	Total scavengers	Carcass species		Habitat		Habitat			
						Natural		Cropland	
		Cow ($N = 22$)	Sheep ($N = 9$)	Natural ($N = 16$)	Cropland ($N = 15$)	Cow ($N = 11$)	Sheep ($N = 5$)	Cow ($N = 11$)	Sheep ($N = 4$)
Observed richness (Sobs)	10	9	9	9	9	8	9	8	6
Estimated richness	10	9	9	9	9	8	9	8	6
[S 0.99 (IC 95 %)]	(9.4–10.6)	(8.7–9.2)	(8.2–9.8)	(8.1–10)	(8.1–9.9)	(7.3–8.7)	(7.9–10.1)	(7.5–8.5)	(5–7)
Observed Shannon diversity	6.3	5.9	6.5	5.5	5.7	4.9	5.9	5.7	4.5
Estimated Shannon diversity	6.3	5.9	6.6	5.5	5.7	5.0	5.9	5.7	4.5
[S 0.99 (IC 95 %)]	(6.3–6.8)	(5.9–6.3)	(6.6–7.5)	(5.5–6)	(5.7–6.3)	(5.0–5.4)	(5.9–7.0)	(5.7–6.5)	(4.3–5.0)
Observed sample coverage	1	1	1	1	1	1	1	1	1
Number of scavenger birds' species	4	4	4	4	3	4	4	3	2
(%)	(40 %)	(44.4 %)	(44.4 %)	(44.4 %)	(33.3 %)	(50 %)	(44.4 %)	(37.5 %)	(33.3 %)
Number of scavenger mammal' species	6	5	5	5	6	4	5	5	4
(%)	(60 %)	(55.6 %)	(55.6 %)	(55.6 %)	(66.7 %)	(50 %)	(55.6 %)	(62.5 %)	(66.7 %)
Minimum abundance of scavenging birds	394	296	98	292	102	214	78	82	20
(%)	(61.9 %)	(61.5 %)	(62.8 %)	(67.1 %)	(50.5 %)	(64.1 %)	(77.2 %)	(55.8 %)	(36.4 %)
Minimum abundance of scavenging mammals	243	185	58	143	100	120	23	65	35
(%)	(38.1 %)	(38.5 %)	(37.18 %)	(32.9 %)	(49.5 %)	(35.9 %)	(22.8 %)	(44.2 %)	(63.6 %)

$$\left({}^{q}D_{\beta} - 1\right)/(N - 1)$$

where ${}^{q}D_{\beta}$ is the β diversity of order q (see above) and N is the number of samples evaluated. It measures the proportion of differentiation (or turnover rate) between assemblages, ranging from 0 (no differentiation between assemblages) to 1 (complete differentiation).

To further identify key factors influencing the structure of these vertebrate scavenging communities, we ran Generalized Linear Models (GLMs) with species richness, diversity or abundance per carcass as response variables and carcass characteristics and environmental variables as explanatory variables (Table 1). The variables with Spearman correlation coefficient $r_s > |0.5|$) were separately included in the models to reduce multicollinearity. Interactions between all these variables were also checked. A Poisson error distribution was used for richness and abundance and a Gaussian error distribution for diversity. The analyses were performed using the package *Stats* in R software (R Development Core Team 2020). We used multimodel inference to select the best models and explanatory variables (Burnham & Anderson 2002). Models were ranked using the corrected Akaike`s Information Criterion (AICc). We built a 95 % confidence set of models by starting with the highest Akaike weight (ω_m) and adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95. Multimodel inference was used by undertaking a model averaging approach where the coefficients of each variable were estimated from all models within the 95 % probability, weighted by ω_m (i.e., $\Sigma\omega_m = 0.95$) to get unconditional coefficients. Before inference, we removed the more complex models with ΔAIC-value higher than that of simpler models within which they were nested (Richards 2008). Weights were rescaled to sum to one after filtering. To know the relative contribution of each variable we calculated their Akaike weights (ω_i) by summing, from the set of models within the 95 % probability, the weights of those containing the variable. Variables with the highest weight ($\Sigma\omega_m$) were the more important. Although it would be expected that our selection approach would minimize multicollinearity among explanatory variables in each model - that avoiding recent issues about the reliability of model averaging approaches (Cade 2015) - we also calculated Z and *P* values for each model predictor. We obtained these values by running one single model considering all the explanatory variables included in the set of best models (MacNally et al. 2018).

Finally, to further explore the factors explaining variation in the abundance of the scavenger species at carcasses, we performed Redundancy Analysis (RDA) considering the same explanatory variables as in the GLM (Table 1). We ran RDA to select the best model as that with the lowest Akaike Information Criteria (AIC) value from 200 permutations with the "step" function in the package *vegan* (Oksanen et al. 2019) in R (R Development Core Team 2020).

Results

Structure and composition of the vertebrate scavenger community in LA PAMPA

A minimum total of 637 individuals of 10 different species (4 birds and 6 mammals) of scavengers were recorded scavenging cow and sheep carcasses ($N = 31$) in the whole study area (Table 2Fig. 2). Two species were obligate scavengers (turkey *Cathartes aura* and black *Coragyps atratus* vultures) and the remaining eight species were facultative ones (Appendix B). Birds outnumbered mammals (61.9 % vs. 38.1 %). The most abundant species was the Southern caracara (*Caracara plancus*; 38.5 % of the minimum total of scavenger individuals recorded), followed by the Pampas fox (*Lycalopex gymnocercus;* 14.8 %; Appendix B). The total number of scavenger species recorded was the same in natural habitats and croplands and at cow and sheep carcasses (9 species). However, the minimum abundance of scavengers was higher in natural habitats (68 %) than in croplands (32 %) and in cattle (77 %) than in sheep (23 %) (Table 2). A mean of 5 species (±SE: 1, range = 6–9) and 20 individuals (±SE: 15, range = 7–75) were recorded per carcass. The inspection of the carcasses before placing the cameras did not reveal the presence (i.e., feathers, faeces, tracks) of other species not recorded in the cameras.

The multiscale biodiversity partitioning showed that scavenger diversity at carcasses was non-randomly distributed across scales. From the 10 species observed in the whole area, 50 % of them were found at carcass level ($\alpha_1 = 4.94$ species), a contribution lower than expected under a random allocation (Table 3; Fig. 4). Species' change among carcasses (β_1) significantly contributed, more than expected, to increased scavenger richness (up to 90 % of the total richness in the area, $\alpha_2 = 9.00$). Beta diversity between carcass species was not significantly different from random but showed a difference of 11 % ($\beta_2 = 1.11$) between the scavenger assemblages found at cows and sheep; indeed, a species turnover was observed, with the white-eared opossum (*Didelphis albiventris*) only appearing at cow carcasses (i.e., 13.6 %, 3 out of 22), while Molina's hog-nosed skunk (*Conepatus chinga*) did so at sheep carcasses (i.e., 33.3 %, 3 out of 9). The same difference in β_2 (i.e., 11 %) was obtained when comparing scavenger assemblages between habitats. This was due to the turnover of black vultures, which only appeared in natural habitats, and white-eared opossums, only recorded in croplands. When controlling for carcass species, beta diversity between habitats

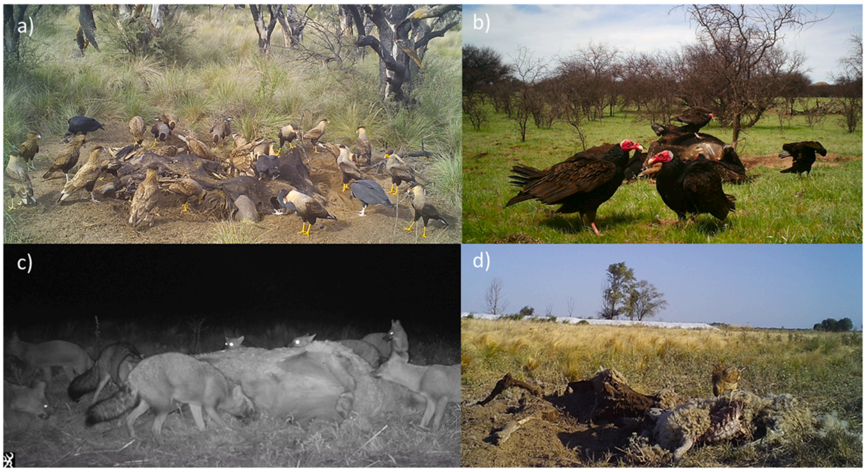

Fig. 2. Some of the most frequent scavengers recorded in the two habitats studied included: a) the Southern caracaras *Caracara plancus,* black vultures *Coragyps atratus* and large hairy armadillo *Chaetophractus villosus*, and b) turkey *Cathartes aura* and black vultures, in both pictures were consuming a cow carcass in a natural habitat; c) Pampas foxes *Lycalopex gymnocercus* and d) chimango caracara *Phalcoboenus chimango* were here recorded feeding on a sheep carcass in cropland habitat. Photo credits: Mª Eugenia Cabrera García.

(β_2) was significantly higher than expected for both cows and sheep (see Appendixes C, D and E).

Shannon diversity at individual carcasses (α_1) was also significantly lower than expected, with a contribution of beta diversity (β_1) larger than random (Table 3). When grouping carcasses by species, neither α_2 nor β_2 differed from expected; yet controlling for carcass species, beta diversity between habitats was higher than expected in sheep (see Appendixes C, D and E). Shannon diversity at habitat scale ($\alpha_2 = 5.58$) was significantly lower than expected by random, while beta diversity ($\beta_2 = 1.13$) contributed more than expected to increase scavenger diversity in the whole study area ($\gamma = 6.33$) (Table 3).

Factors explaining the structure and composition of vertebrate scavenger communities

Neither mean species richness nor mean diversity of vertebrate scavengers per carcass varied significantly with carcass characteristics, habitat type, human impact or season. Contrastingly, the minimum number of individuals recorded at a carcass significantly increased in spring, compared to summer and winter (Table 4). The best final model also showed that the abundance of vertebrate scavengers increased with carcass weight and decreased at carcasses located in cropland. These three variables were the most important (i.e., Akaike weight $\omega_i = 1.0$).

Table 4
Results of the single final model for abundance; all the variables were combined within the set of best models ($\Sigma\omega_m = 0.95$; i.e., AICc ranging between 257.15 and 259.53).

Abundance best model	Z value	*P*	AICc
(Intercept)	37.824	<0.001	257.15 – 259.53
Distance to roads	1.363	*0.173*	
Summer	−4.832	***<0.001***	
Autumn	−2.320	***0.020***	
Winter	−5.775	***<0.001***	
Carcass weight	3.843	***<0.001***	
Cropland	−5.175	***<0.001***	
Carcass weight: Cropland	−1.138	*0.255*	
Null Model			*411.39*

The best model resulting from the RDA analysis was significant ($F = 3.43$, $P = 0.005$) and accounted for 40.6 % of the total variation in the scavenger community (Fig. 3). Most of this variation (33.9 %) was explained by the first axis, which clearly grouped the carcasses found in croplands, where scavenger species such as chimango caracara (*Phalcoboenus chimango*) and large hairy armadillo (*Chaetophractus villosus*) were more abundant. In contrast, vultures seemed to avoid this type of habitat for foraging. Southern caracaras were more abundant at larger

Table 3
Multiplicative partitioning of scavenger richness and diversity (as effective number of species) at 31 carcasses of sheep and cow, in natural and cropland habitats in central Argentina. The *P* values were obtained from 10,000 permutations to form a null distribution of each diversity component at each spatial scale. γ-diversity (i.e., $\gamma_{\text{whole-region}}$) is decomposed into i) within (α_1) and between (β_1) carcass, ii) within (α_2) and between (β_2) carcass species and/or habitats in terms of effective number of species.

	Carcass species				***Habitat***			
Species richness	Obs.value	Exp. value	Z value	p	Obs. value	Exp. value	Z value	p
α_1	4.94	6.20	−9.04	**<0.001**	4.94	6.20	−9.03	**<0.001**
α_2	9.00	9.55	−1.57	0.404	9.00	9.65	−1.93	0.245
β_1	1.79	1.53	4.05	**<0.001**	1.83	1.56	4.22	**<0.001**
β_2	1.11	1.05	1.61	0.404	1.11	1.04	1.99	0.112
$\gamma_{\text{whole-area}}$	10.00	10.00	0.00	1.00	10.00	10.00	0.00	1.00

	Carcass species				***Habitat***			
Shannon diversity	Obs.value	Exp. value	Z value	p	Obs. value	Exp. value	Z value	p
α_1	3.76	4.91	−10.53	**<0.001**	3.76	4.91	−10.65	**<0.001**
α_2	6.24	6.25	−0.13	0.885	5.58	6.27	−8.19	**<0.001**
β_1	1.67	1.27	11.16	**<0.001**	1.49	1.28	7.44	**<0.001**
β_2	1.01	1.01	0.11	0.885	1.13	1.01	9.17	**<0.001**
$\gamma_{\text{whole-area}}$	6.33	6.33	0.00	1.00	6.33	6.33	0.00	1.00

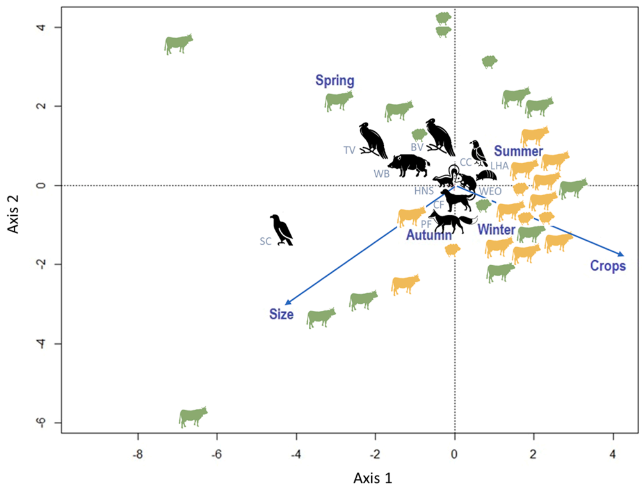

Fig. 3. Results of the redundancy analysis (RDA) performed for the scavenger community consuming livestock carcasses. Colours represent different habitats: natural in green and cropland in orange; different forms represent the type of carcasses: cow and sheep. Explanatory variables are shown in blue. Abbreviations refer to the name of the scavenging species, being Southern caracara (SC), turkey vulture (TV), wild boar (WB), black vulture (BV), hog-nosed skunk (HNS), dog *Canis familiaris* (CF), Pampas fox (PF), chimango caracara (CC), large hairy armadillo (LHA), white-eared opossum (WEO). Silhouettes from iconsdb. See Appendix F for icon credits.

carcasses. The second axis explained the 4.5 % of the variation observed and was associated with seasonality. The Turkey vulture, a migrant species present in the study area from spring to early autumn, was more abundant at carcasses during spring. Contrastingly, sedentary species such as the Pampas fox showed higher abundances at carcasses during autumn. Similar results were obteined without three cows simultaneously monitores in cropland (Fig. E.1).

Discussion

Our diversity partitioning approach points towards a key role of species' shifts among carcasses (i.e., beta component) in determining the richness and diversity of the vertebrate scavenger community (i.e., gamma component). While both species richness and Shannon diversity at individual carcasses were lower than expected by random, the beta component was significantly higher than expected, contributing to increase both the species richness and diversity of the scavenger assemblages. The fact that similar patterns were observed regarding the significant role of the beta component both in richness and diversity partitioning, would not only reinforce the importance of this beta component in shaping scavenger assemblages, but would also suggest absence of major biases due to our minimum abundance estimations in the case of diversity. Furthermore, since Shannon diversity accounts for both species' abundance and richness, this would also prevent potential biases associated to our abundance estimations. The similarity in species composition across our assemblages would also minimize possible under- or overestimations of abundances associated with, for example, more or less gregarious species. In addition to agree with scavenging being a widespread feeding strategy among vertebrates (Wilson & Wolkovich 2011), our results are also in line with previous works suggesting that carcass spatiotemporal unpredictability would enhance the richness and diversity of vertebrate scavengers, in clear contrast to food supplies concentrated at supplementary feeding points, where scavenger assemblages often show lower richness and diversity (Monsarrat et al. 2013; Cortés-Avizanda et al. 2016; Fluhr et al. 2017). Additionally, in agreement with previous works (Pardo-Barquín et al. 2019), the hierarchical partitioning approach allowed us to identify the habitat as a key driver of the structure and composition of the scavenger communities. Regardless of the carcass species (i.e., cow or sheep), both beta richness and beta diversity were significantly higher than expected among habitats, contributing to increase both parameters (between 10 and 27 %) at the larger scale of the whole study area (Appendix C). This result supports the habitat-heterogeneity hypothesis, which proposes that an increase in number of different habitats can lead to an increase in species diversity (MacArthur & MacArthur 1961; but see also Allouche et al. 2012). However, the carcass species contributed less than the habitat to increase the diversity of the scavenger assemblages, with only the beta diversity being significantly higher than expected (11 %) in the cropland habitat (Appendix C).

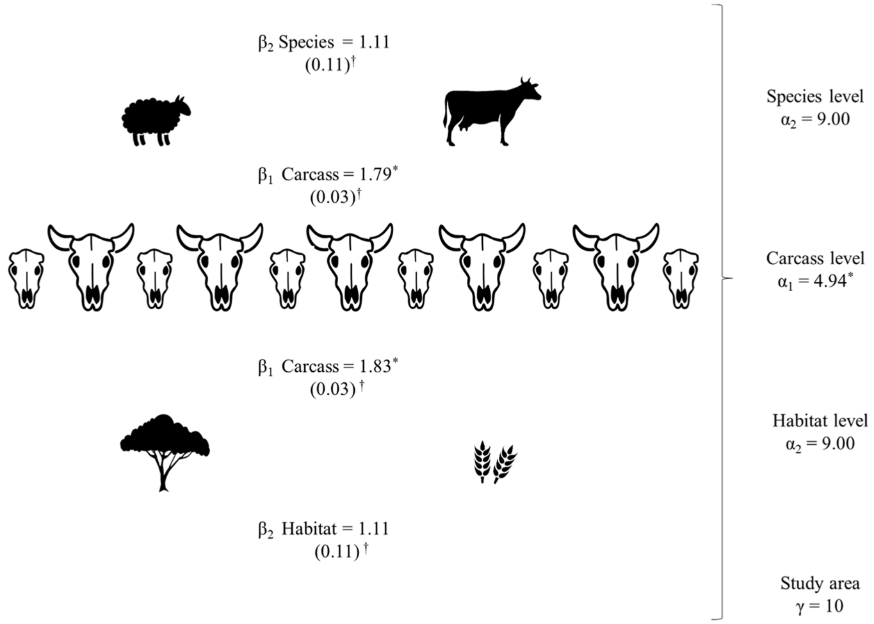

Fig. 4. Conceptual model explaining the multiplicative partitioning of scavenger richness (as effective number of species): within (α_1) and between (β_1) carcasses, ii) within (α_2) and between (β_2) carcass species and/or habitats and iii) in the entire study area ($\gamma_{\text{whole-area}}$), at 31 carcasses of sheep and cow monitored in cropland and natural habitats in central Argentina. See Appendix F for icon credits. *p-valor $<$ 0.05; † Standardized beta by using the formula Jost 2007 (see above).

As the first study describing the vertebrate scavenger community consuming large carcasses (i.e., livestock) in central Argentina, our results show that birds and mammals dominated carcass consumption in the study area, agreeing with that described in different scavenger communities across the world (Mateo-Tomás et al. 2015, Sebastián-González et al. 2019, Gomo et al. 2020, Orihuela-Torres et al. 2021). However, although avian scavengers (61,9 %) were more abundant than mammals (38.1 %) at the livestock carcasses monitored in La Pampa region, the richness of mammals (six species) was greater than that of birds (four species), contrasting with the general pattern of more avian than mammalian species observed for vertebrate scavenger communities worldwide (Mateo- Tomás et al. 2015). In fact, the avian scavenger richness recorded in our study was lower than that described at small carcasses of lagomorphs in the Patagonian steppe ecoregion in western Argentina (Travaini et al. 1998; Brown et al. 2006), which could correspond to lagomorphs being key prey of many raptors (Travaini et al. 1998). Our results contribute thus to enlarge the information available on vertebrate communities relying on anthropogenic food subsidies in the form of carrion. In the face of global change, this information would help to improve our understanding of the scavenger communities increasingly consuming human-mediated carrion such as hunting remains or livestock carcasses (Oro et al. 2013; Mateo-Tomás et al. 2015).

In our study, compositional differences among habitats (i.e., beta diversity) seemed to be mainly due to replacement of one species, i.e., the black vulture appeared in natural habitats and the white-eared opossum did so in croplands. While obligate scavengers such as turkey and black vultures were practically absent in croplands, the white-eared opossum was exclusively registered at carcasses located in this habitat. In fact, opossums are considered to prefer fragmented forest areas, close to buildings and with a less complex vegetation structure (Cruz et al. 2019). Contrastingly, low breeding habitat suitability for vultures could explain their absence in croplands (Travaini et al. 1995). Although fewer Southern caracaras were also recorded at carcasses monitored in cropland (Fig. 3), as an abundant opportunistic species (Travaini et al. 1995; López 2020), this raptor was the most abundant vertebrate scavenger at livestock carcasses in the whole study area (i.e., with a minimum total abundance of 245 individuals whose presence was recorded in all the monitored carcasses by one; Appendix B), outnumbering turkey and black vultures (i.e., a minimum total of 50 and 61 individuals, respectively, registered in both cases in the 32.3 % of the carcasses), so interspecific competition with vultures could occur (e.g., Travaini 1998; Baladrón et al. 2017). A similar pattern to that of caracaras was observed for the Pampas fox, the most abundance mammalian scavenger in our sample (i.e., with a minimum total abundance of 94 individuals recorded in all the monitored carcasses; Appendix B), and whose presence increased in autumn. Carrion could become a key resource for the species during this season due to the dispersion of juveniles but also because of the limited availability of alternative food sources (Read & Wilson, 2004). The higher abundance of wild boars (*Sus scrofa*) at carcasses located in natural habitats (i.e., the 88.1 % of the minimum total abundance) is consistent with this habitat having been optimal for the species since it was first introduced to the La Pampa province in 1904–1906 (Pescador et al. 2009). Contrastingly, another opportunistic mammalian species, i.e., the large hairy armadillo, appeared in greater abundance at cow carcasses monitored in croplands (i.e., the 57.4 % of the minimum total abundance), and especially in summer. The large hairy armadillo has been described as eating carrion (i.e., guanaco, sheep; Arriagada et al. 2017), but its greater abundance at large carcasses in summer could be explained by the large accumulation of larvae, which it also consumes (Lashley et al. 2018).

The abundance of vertebrate scavengers at carcasses was higher in spring, reaching lowest values in summer and winter. Although these results would contrast with carrion becoming a key food resource under extreme weather conditions (e.g., cooler seasons; Selva et al. 2003), several studies have demonstrated that vertebrate scavenging decreases in warm weather, likely due to increased activity of decomposers at higher temperatures (De Vault et al. 2004; Sawyer et al. 2022). Vertebrate scavengers' abundance increased also at larger carcasses, i.e., cow carcasses in our study area, agreeing with the general pattern of carcass size previously reported in other vertebrate scavenger communities worldwide (Selva et al. 2005; Moleón et al. 2015; Turner et al. 2017; Sebastián-González et al. 2019).

In conclusion, our hierarchical partitioning analysis shows a relevant role of species replacement among carcasses in determining the species richness and diversity of vertebrate scavenger assemblages, something observed also at the larger metacommunity scale (Mateo-Tomás et al. 2019). While previous works highlight the key role of carrion unpredictability for preserving scavenging species and communities (Ruxton & Houston 2004; Monsarrat et al. 2013; Cortés-Avizanda et al. 2016; Fluhr et al. 2017), our results provide additional insights on the mechanisms underlying it by exploring how the scavenger community is organized across spatial scales. Furthermore, a significant decrease in scavengers' abundance was observed at individual carcasses within croplands compared to those located in less modified and altered natural habitats. Since the monitored carcasses took longer to be consumed in croplands than in more natural habitats (mean ± SE: 25.0 ± 5.5 *vs.* 11.3 ± 1.8 days, respectively), further attention should be paid to what extent habitat transformation would affect carcass consumption as a key ecological function supported by scavengers. This would be especially interesting in systems like the study area, without large obligate scavengers such as Andean condors (*Vultur gryphus*) and large carnivores like pumas, which have been identified as functionally dominant scavengers rapidly consuming carrion in other ecosystems (Mateo-Tomás et al. 2017; Méndez et al., 2024).

CRediT authorship contribution statement

María Eugenia Cabrera-García: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Patricia Mateo-Tomás:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **José Hernán Sarasola:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Funding acquisition. **Juan I. Zanón Martínez:** Writing – review & editing, Methodology, Investigation, Funding acquisition. **Beatriz Martínez-Miranzo:** Writing – review & editing, Resources, Methodology, Investigation. **Pedro P. Olea:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2025.01.008.

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Further reading

Olea, P. P., Iglesias, N., & Mateo-Tomás, P. (2022). Temporal resource partitioning mediates vertebrate coexistence at carcasses: The role of competitive and facilitative interactions. *Basic and Applied Ecology, 60*, 63–75.