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Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition

Esther Sebastián-González,[1,7,9] Marcos Moleón,[2,3] Jean P. Gibert,[4] Francisco Botella,[3] Patricia Mateo-Tomás,[5,8] Pedro P. Olea,[5,6] Paulo R. Guimarães Jr.,[1] and José A. Sánchez-Zapata[3]

[1]*Departamento de Ecologia, Universidade de São Paulo, CEP 05508900, São Paulo, Brazil*
[2]*Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits 2050, Johannesburg, South Africa*
[3]*Departamento de Biología Aplicada, Universidad Miguel Hernández, Avda. de la Universidad, s/n, 03202, Elche, Alicante, Spain*
[4]*School of Biological Sciences, University of Nebraska-Lincoln, 410 Manter Hall, Lincoln, Nebraska 68588-0118, USA*
[5]*Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC-UCLM-JCCM), Ronda de Toledo s/n, 17031 Ciudad Real, Spain*
[6]*Departamento de Ecología, Universidad Autónoma de Madrid, 28046 Madrid, Spain*

Abstract. Disentangling the processes that shape the organization of ecological assemblages and its implications for species coexistence is one of the foremost challenges of ecology. Although insightful advances have recently related community composition and structure with species coexistence in mutualistic and antagonistic networks, little is known regarding other species assemblages, such as those of scavengers exploiting carrion. Here we studied seven assemblages of scavengers feeding on ungulate carcasses in mainland Spain. We used dynamical models to investigate if community composition, species richness and structure (nestedness) affect species coexistence at carcasses. Scavenging networks showed a nested pattern in sites where highly efficient, obligate scavengers (i.e., vultures) were present and a non-nested pattern everywhere else. Griffon Vulture (*Gyps fulvus*) and certain meso-facultative mammalian scavengers (i.e., red fox, *Vulpes vulpes*, and stone marten, *Martes foina*) were the main species contributing to nestedness. Assemblages with vultures were also the richest ones in species. Nested species-rich assemblages with vulture presence were associated with high carcass consumption rates, indicating higher interspecific competition at the local scale. However, the proportion of species stopping the consumption of carrion (as derived from the competitive dynamic model) stabilized at high richness and nestedness levels. This suggests that high species richness and nestedness may characterize scavenging networks that are robust to high levels of interspecific competition for carrion. Some facilitative interactions driven by vultures and major facultative scavengers could be behind these observations. Our findings are relevant for understanding species' coexistence in highly competitive systems.

Key words: *carrion feeding; coexistence; facilitation; interaction network; interspecific competition; nestedness; species richness; Spain; ungulate carcasses; vertebrate scavengers; vultures.*

Introduction

Species sharing resources form ecological assemblages that are hardly ever organized randomly and show well-defined structural patterns (Dunne et al. 2002, Fargione et al. 2003). Disentangling the processes that shape the structure of these assemblages is one of the foremost challenges of contemporary ecology, and it is important to understand the evolution of species interactions (Willis and Whittaker 2002). Recently, growing interest has been shown in those factors favoring species coexistence by either minimizing competition or enhancing facilitation (Davies et al. 2007, Bastolla et al. 2009, Sebastián-González et al. 2010, Allesina and Levine 2011). Such advances are not only central in ecological and evolutionary research, but also can have important consequences for the conservation of biodiversity worldwide (Verdú and Valiente-Banuet 2008).

Dead animals are widely exploited by many vertebrates (Wilson and Wolkovich 2011, Moleón et al. 2014*b*). Carrion is a high-quality food resource that can severely affect scavenger behavior and population dynamics (Cortés-Avizanda et al. 2009, Wilson and Wolkovich 2011, Moleón et al. 2014*b*, Pereira et al. 2014). Scavenging has therefore been claimed as an essential component in food-web models and in empirical approaches that aim to assess how animal communities assemble (DeVault et al. 2003, Wilson and Wolkovich 2011, Moleón et al. 2014*b*). Carrion

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[7] Present address: Department of Biology, University of Hawai'i, Hilo 96720, Hawaii, USA
[8] Present address: Plaza de los Pueblos 9 1°A, 24900 Riaño, León, Spain
[9] E-mail: esebgo@gmail.com

is exploited as an exclusive source of food by obligate scavengers and as an alternative source of food by facultative scavengers (DeVault et al. 2003, Moleón et al. 2014*b*). Among terrestrial vertebrates, vultures are the only obligate scavengers, and they display a vast array of unique adaptations for efficient carrion use, such as low energy-demanding search strategies (Ruxton and Houston 2004, Jackson et al. 2008). Consequently, vultures may outcompete and monopolize carcasses, which may increase competition for carrion within the scavenger guild in which they are present (Sebastián-González et al. 2013, Moleón et al. 2014*b*). In contrast, vulture presence at carcasses may also enhance carrion consumption by facultative scavengers through an array of facilitative interspecific interactions that lead to increasing success in carcass detectability and/or consumption (Moleón et al. 2014*b*). In addition, competitive and facilitative interactions can be reciprocal, and scavenging by facultative scavengers such as large mammalian carnivores, corvids, and birds of prey may both constrain and favor scavenging by vultures, depending on the circumstances (Moleón et al. 2014*b*). Thus, species composition of scavenging assemblages could have implications for scavenger species coexistence.

Although the extensive but unsolved debate about the species diversity–ecosystem stability hypothesis, there is increasing evidence species diversity exerts a stabilizing effect on natural communities (Hooper et al. 2005, Tilman et al. 2006, Ives and Carpenter 2007, Loreau and de Mazancourt 2013). However, we barely know if this generalization can also be applied to assemblages, such as scavenger communities, associated with keystone ecological services. The only study that addressed the effect of species richness on the functioning of scavenging found a small but positive effect of species richness on carcass consumption rates (Sebastián-González et al. 2013). Nevertheless, this study only focused on small carcasses, which are consumed by a reduced number of vertebrate species, and did not study the implications for species coexistence. Thus, more research is needed to understand the potential stabilizing effect of species richness in a scavenging context.

The nested structure of scavenging networks might also affect the dynamics of the assemblage. Several authors have recently found evidence that scavenging can be organized in a nested way (Selva and Fortuna 2007, Allen et al. 2014), especially as carcass size increases (Moleón et al. 2015). In scavenging networks, a nested pattern emerges when the species feeding on carcasses visited by few consumers are subsets of those species feeding on carcasses visited by more consumers (Selva and Fortuna 2007). Theoretical studies conducted with mutualistic communities suggest that the nested structure may reduce effective competition and, consequently, enhance species coexistence (Bastolla et al. 2009, Suweis et al. 2013, Rohr et al. 2014, but see Allesina and Tang 2012). However, whereas links in mutualistic networks represent interactions between species, links in scavenging networks indicate scavenging species using a specific individual carcass. Thus, these theoretical results cannot be generalized directly to scavenger networks and the implications of nestedness for species coexistence may differ in competitive trophic assemblages, such as those involving scavenging.

Our main goal is to study whether the structural properties arising from trophic interactions within scavenging assemblages facilitate the coexistence of species feeding on carcasses. First, we aim to determine if a nested organization enhances species coexistence in scavenging assemblages, as suggested for mutualistic networks (e.g., Bastolla et al. 2009). Second, as diverse communities have been shown to be more stable than species-poor ones (Tilman 1996, Tilman et al. 2006), we hypothesized that more diverse scavenger communities will also have more relaxed interspecific competition, resulting in higher species coexistence. To test our hypotheses, we first compared nestedness and species richness in seven Spanish scavenging networks with different degrees of competition for food resources (i.e., carcass consumption rates). Then, we evaluated species coexistence using a competitive Lotka-Volterra model parameterized with the structure of the interaction network to quantify the probability that any given species would stop consuming carrion within each assemblage (i.e., competitive exclusions). We finally compared competitive exclusions at different levels of species richness and nestedness. We also evaluated the role of those scavenger species visiting more carcasses (i.e., strong contributors) and of the highly efficient obligate scavengers (i.e., vultures) in determining the competitive dynamics of the scavenger assemblage to identify the main species driving the observed patterns.

Materials and Methods

Study systems

We studied the vertebrate scavenger community that exploits ungulate carcasses in seven sites across mainland Spain (Fig. 1). The sites were located in north (Cordillera Cantábrica, 43°7′ N–6°11′ W, and Valle de Arán, 42°43′ N–0°50′ E), central (Montes de Toledo, 39°23′ N–4°16′ W, and Sierra Morena, 38°30′ N–4°20′ W), and south Spain (Sierra de Cazorla, 38°2′ N–2°51′ W, Sierra Espuña, 37°50′ N 2°27′ W, and Sierra Nevada, 37°5′ N–3°29′ W). Cantábrica and Arán hold important populations of Griffon Vultures (*Gyps fulvus*) and other less abundant vulture species (Mateo-Tomás and Olea 2011). Vultures are also abundant in Toledo, Morena, and Cazorla, but are absent in Espuña and Nevada (Del Moral 2009). Landscapes range from plain sites dominated by Mediterranean savanna-like grasslands ("dehesas") in Toledo and Morena to mountain ridges and valleys covered by

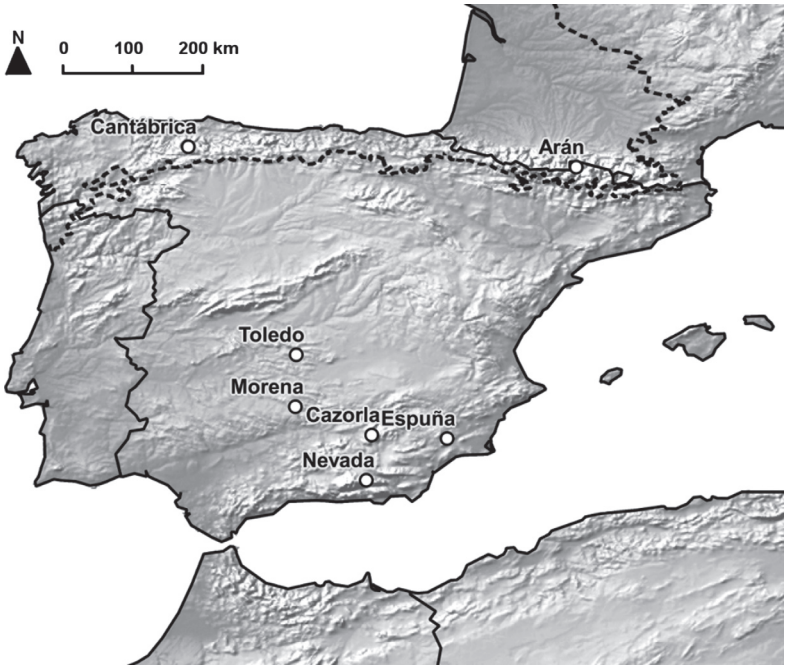


FIG. 1. Map of the Iberian Peninsula including the location of the seven study areas. The dotted line is the limit between the two biogeographic regions in Spain: Mediterranean (South) and Temperate (North).

temperate and Mediterranean woods, scrubs and pastures in the north and in the rest of the sites, respectively. All of the sites are totally or partially protected as regional (Cantábrica, Morena, Cazorla, Espuña) or national parks (the other three). See Mateo-Tomás et al. (2015) for a more detailed description of the study sites.

Carcass monitoring

To evaluate the scavenging patterns, we used 216 (range 12–48 per site) wild ungulate remains originating from hunting activities. Carcasses were located shortly after animal death (<3 h), either by accompanying the hunters or by following their indications. Carrion consumption was monitored by camouflaged remote cameras. The cameras were hidden close (4–10 m) to carcasses immediately after their generation and they operated until carcasses had been completely consumed, save the skin and skeleton. Carcasses were weighted and then fixed to soil using picks to avoid animals moving them away from the camera focal point. The cameras were programmed to record one picture every 1–2 min after activation by movement both day and night (using no-glow infrared sensors to minimize disturbance). The pictures obtained provided information on the species that fed on the carcass, and on the time required to consume the carcass. A species was considered a carcass consumer (i.e., scavenger) when it was clearly recorded consuming it. Invertebrate presence in our study areas was never large enough to be considered significant for the consumption rates and was not included in the analyses. When consumption was suspected but not clearly recorded, we assumed consumption if that species was already detected consuming at other carcass (see Appendix S1 for a list of the scavenger species found in each site, Appendix S2 for the main characteristics of the hunting remains techniques, and Blázquez et al. (2009), for a more detailed description of the carcass monitoring procedure). We then calculated consumption rate of each carcass as the quantity of carrion (kg) eaten per unit of time (h), from camera activation to total carcass consumption, and we calculated the consumption rate per site as the average consumption rate of each carcass in that site. We finally calculated the number of total scavenger species that consumed the monitored carcasses in each study site (i.e., species richness). Because the number of carcasses monitored in each study site was different, we also used the incidence-based data to build extrapolation curves and identify whether we had sampled the expected total number of scavenger species in each scavenger community (Chao et al. 2014). All of the experiments were performed in autumn and winter between 2005 and 2013. All the fieldwork met national and international legal requirements.

Nestedness analysis

For each assemblage, we constructed a matrix, **A**, where each row represented scavenger species *i* and each column represented carcass *j*. Matrix cell a_{ij} was 1 when species *i* consumed carcass *j,* and 0 otherwise (Selva and

Fortuna 2007). Network nestedness was measured as NODF (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al. 2008). The metric ranges between 0 and 100, being 100 for highly nested networks, while random matrices show intermediate NODF values. As some degree of nestedness can arise even when species scavenged randomly, we compared NODF values with a null distribution of NODF values to identify if the network was more nested than expected by a theoretical benchmark. We used the null model II (Bascompte et al. 2003), which assumes that the probability of the interaction between i and j occurs (i.e., $a_{ij} = 1$) is

$$P_{ij} = \left(\frac{P_i}{C} + \frac{P_j}{R} \right) \Big/ 2 \quad (1)$$

where P_i is the number of carcasses used by species i, P_j is the number of species visiting the carcass j, C is the number of carcasses recorded, and R is the number of species recorded. Thus, this null model controls for the effects of species richness, number of sampled carcasses, number of species records, and heterogeneity in the use of distinct resources. Because the matrices had different sizes, we standardized the results using z scores of the NODF values (Z-NODF; Ulrich and Gotelli 2007), calculated as

$$z\,\text{score} = \frac{\text{Observed}_{\text{NODF}} - \text{Mean}_{\text{NODF null model}}}{\text{SD}_{\text{NODF null model}}}. \quad (2)$$

Any z scores >0 indicate that nestedness at a given site is greater than the mean nestedness of the randomized matrices, whereas z scores <0 suggest that nestedness was lower than the mean nestedness of the randomized matrices. All analyses were performed using ANINHADO (Guimarães and Guimarães 2006).

We also calculated the contribution to the nested pattern (CN) of each of the scavenger species in each assemblage. In a nested network, when the species i is recorded in a smaller number of carcasses than species k, the carcasses consumed by a species i form a subset of the carcasses consumed by a species k. Species following this pattern and deviating from it, respectively, will have a high and low contribution to nestedness. To evaluate the role of key species in the network structure and in the consumption patterns, we removed the species that contributed the most to nestedness and we recalculated Z-NODF and consumption rate for the sites where the nestedness was significant. To evaluate the role of obligate scavengers, we performed a similar set of analyses, but removed Griffon Vultures, which are the commonest obligate scavengers in Spain. To do so, we removed the column showing the consumption pattern of this species in the matrix (i.e., whose carcasses were consumed by this species).

Dynamic model

We used a Lotka-Volterra competition model parameterized with the structure of the interaction network compiled for all of our seven scavenger communities to quantify the mean probability that any given species would be excluded from the system. Competitive exclusions in our model must be interpreted as species that stopped consuming carrion, rather than species that died out. This stems from the fact that most species except obligate scavengers can actually use resources other than carrion, and thus are unlikely to become extinct in nature just because they are excluded from the scavenger community. Because we are not modeling those external resources here, the competitive exclusions yielded by our model need to be regarded as species that were driven to stop consuming carrion due to high competition levels. Communities undergoing fiercer competition should yield a higher proportion of species that may stop consuming carrion than those undergoing weaker competition. We assumed that a population was competitively excluded from the system if its size went below 1 individual. We used a Lotka-Volterra competitive model because its dynamics are fully characterized and it has well-known mathematical properties, which in turn makes our results easy to interpret and provides a simple baseline for comparison with future studies (Byers and Noonberg 2003).

Our model tracks the abundances of n competing species over time, with the rate of change of the ith species described by the following expression:

$$\frac{dN_i}{dT} = \frac{r_i N_i}{K_i} \left(K_i - \beta \sum_{j=1}^{n} \alpha_{ij} N_j \right). \quad (3)$$

In Eq. 3, N_i (or N_j) is the abundance of the ith species (or jth species), r_i is its per capita growth rate under exponential growth, K_i is its carrying capacity in the absence of competitors, α_{ij} is the competitive effect of species j upon species i (α_{ii} represents intraspecific competition), and β is a scaling parameter that allows us to enhance or diminish the effect of the competitive interactions (or interaction strength) in the model. When $\beta = 0$, competitive interactions do not affect the population dynamics and all the populations undergo exponential growth. When $\beta > 0$, competitive interactions drive the population dynamics and its effect increases with β.

To parameterize Eq. 3, we estimated interaction parameters α_{iz} based on the structure of the interaction network for each scavenger community (i.e., the overlap between population niches). In particular, we used the matrices associated with the networks, **A**, to create a resource utilization overlap matrix (**ROM**) with $n \times n$ elements for each assemblage (Case 1990, Araújo et al. 2008, Baiser et al. 2010), where the elements (α_{ij}) of the **ROM** correspond to the interaction terms of species i and j in Eq. 3. The matrix is defined as follows:

$$\mathbf{ROM} = \left| \alpha_{iz} \right|_{n \times n} \quad (4)$$

where

$$\alpha_{iz} = \frac{\sum_j a_{ij} a_{zj}}{\sum_j a_{ij}} \quad (5)$$

where a_{ij} is an element of matrix **A** and is 1 if species i consumes carcass j, and 0 otherwise. Thus, the **ROM** has nonzero elements wherever two species share at least one resource item (i.e., a carcass). All of the diagonal elements (i.e., intraspecific competition or self-regulation) are equal to 1, and all non-diagonal elements (i.e., interspecific competition) are ≤1. Note that Eq. 5 is in all respects equivalent to the classical approach of MacArthur and Levins (1967). Because our matrices are binary, this is, they only have zeros and ones, we do not need to square the denominator. Eq. 5 can be understood as the total number of shared carcasses between species i and z divided by the number of resources consumed by species i. We used the **ROM** to parameterize Eq. 3.

We considered 34 different values for β (Eq. 3), ranging from 0.1 to 10 with a step of 0.3. For each β value, we ran the model 1000 times. During each run, we randomly sampled the per capita growth rates (r_i) from a uniform distribution between 0 and 1, and the carrying capacities (K_i) from a uniform distribution between 200 and 500 individuals. By doing so, we controlled the effect of the growth rate and carrying capacity on the competitive dynamics. We also sampled the initial conditions for each species from a uniform distribution between 25 and 100 individuals, which allowed us to control the effect of initial species abundance on the competitive dynamics. For all the considered parameter combinations, population sizes generally reached equilibrium before 50 time steps. To ensure that all the populations were at equilibrium, we allowed the model to run for 250 time steps during each simulation before measuring the proportion of species that stopped consuming carrion yielded by the model.

Statistical analyses

We first determined if the carcass consumption rates were spatially autocorrelated both within and among study sites using the Moran's I test. Second, we used univariate (i.e., one predictor variable) generalized linear models (GLMs) to study the relationship between the consumption rate (in log scale) and the proportion of species that stopped consuming the carrion (response variables) with (1) species richness, (2) presence of obligate scavengers (i.e., vultures; coded as 1/0), and (3) nestedness (Z-NODF; explanatory variables). We also tested the relationship between the log-transformed consumption rate and the mean annual precipitation (mm) and mean annual temperature (degrees Celsius) during autumn and winter months to identify possible biases in consumption rates due to climatic conditions. We calculated the climatic variables taking into account the data available from September 2005 to September 2011 (SIA 2015). We used Gaussian error distributions for modeling the response variables. For the models describing the competitive exclusions, we also tested the effect of nestedness and species richness as quadratic response variables because this describes the behavior of the relationship more accurately. We repeated the analyses using the estimated number of species for a proportion of sampling of the community equal for all the sites resulting from the rarefaction/extrapolation analyses. All of the analyses were done in R version 2.15.1 (R Development Core Team 2012). The spatial autocorrelation analysis was done using the *ape* package (Paradis et al. 2004).

Results

Richness and nestedness

The number of scavenger species detected at carcasses ranged from 6 in Nevada (3 avian and 3 mammalian facultative scavengers) to 17 in Toledo (2 obligate scavengers, 10 avian, and 5 mammalian facultative scavengers). Species richness was higher in sites with vultures (mean 14 species; range 11–17 species) than in sites

Table 1. Scavenger species richness and nestedness degree in seven scavenging assemblages of Spain, with number of carcasses studied (N), number of scavenger species detected at carcasses, average carrion consumption rate, presence/absence of vultures in the study site, nestedness, and significance of the nested pattern.

Assemblage	N	No. species	Consumption rate (kg/h)	Vultures present	Z-NODF	P
Toledo	35	17	24.50	Yes	4.44	<0.001
Cantábrica	48	15	22.20	Yes	5.15	<0.001
Morena	42	15	4.70	Yes	2.45	0.01
Arán	22	12	1.79	Yes	1.81	0.03
Cazorla	27	11	2.86	Yes	3.91	<0.001
Espuña	30	7	0.02	No	0.17	0.43
Nevada	12	6	0.30	No	−0.37	0.67

Notes: Nestedness was calculated as the z score of the matrix NODF. See *Methods: Dynamic model* for complete details.

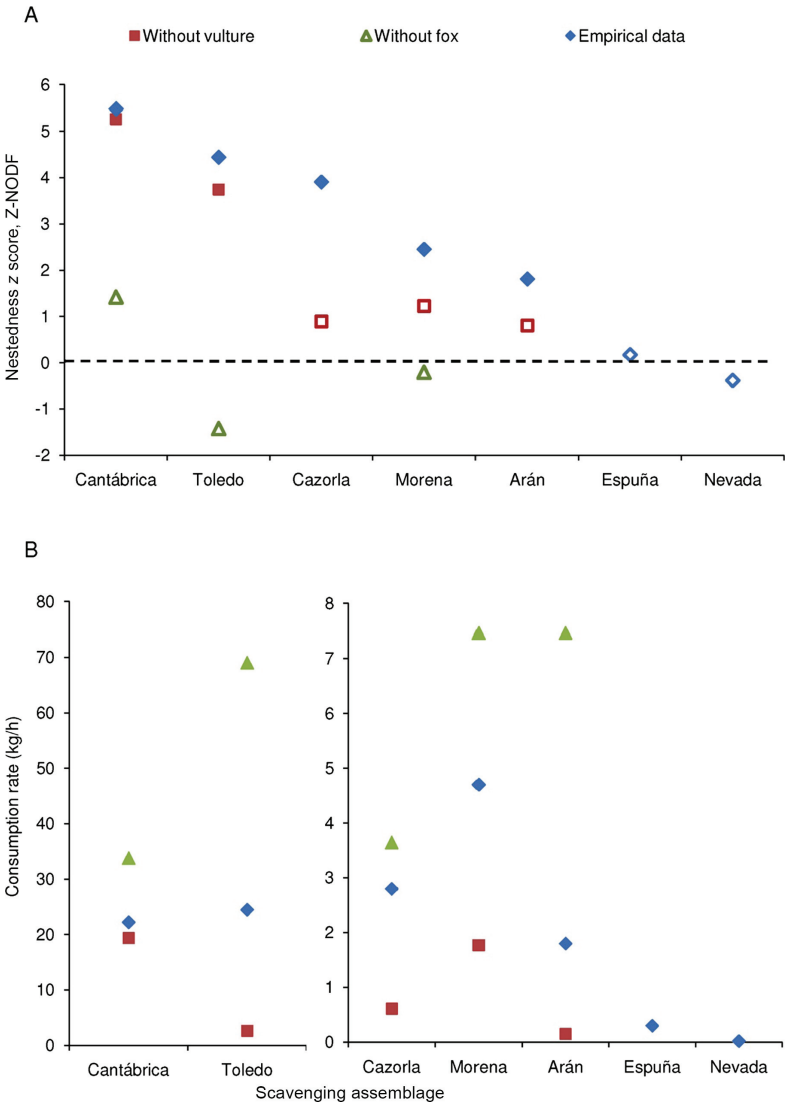


FIG. 2. Nestedness and consumption rates of seven scavenging assemblages in mainland Spain. Empirical data (diamonds) are for all scavenger species in each assemblage, including vultures and foxes. (A) The *z* score of the nestedness value measured with the NODF metrics (Z-NODF) is shown. The *z* score was recalculated for the nested communities after excluding scavenging by Griffon Vultures (squares) and the species that contributed the most to the nested pattern, i.e., Griffon Vulture (squares) or red fox (triangles). The open symbols represent nonsignificant nested patterns. The dashed line represents the limit between those assemblages where nestedness at a given site is greater (positive values) or lower (negative values) than the mean nestedness of the randomized matrices. (B) Average carcass consumption rate for each assemblage. We recalculated the rates using only those carcasses that were not visited by Griffon Vultures (squares) and red foxes (triangles) to assess the relative role of each species in carrion consumption efficiency.

lacking them (mean 6.5 species; range 6–7 species; Table 1). This species increase in sites with vultures was not due only to vultures, given that they were represented by 2–3 species per site, whereas the differences in species between areas with and without vultures are of at least three species (Appendix S1). The extrapolation analysis suggests that observed species richness was not affected by sampling, except for one community: the observed and expected number of species in all the communities were similar with the exception of a species-rich community (Toledo), with estimated species richness slightly higher than the observed one (Appendix S3).

Scavenger assemblages were nested in all of the sites with vultures, whereas the assemblages in Espuña and Nevada (sites without vultures) were not significantly nested (Table 1). The red fox (*Vulpes vulpes*) was the species that contributed the most to nestedness (CN value) in Cantábrica, Toledo, Nevada, and Morena (CN > 62.81); the stone marten (*Martes*

foina) in Espuña (CN = 66.67); and the Griffon Vulture in Cazorla and Arán (CN > 65.02; see Appendix S1 for the contribution to nestedness of each species). When we excluded the species that contributed the most to nestedness from the observed scavenging matrix, all of the assemblages became non-nested (Fig. 2A), but the elimination of the Griffon Vulture showed different patterns. In the scavenger communities where the Griffon Vulture presented the highest (Cazorla and Arán) or the second highest (Morena) contribution to nestedness, the elimination of this species also resulted in a loss of the nestedness. However, both Cantábrica and Toledo assemblages, where the Griffon Vulture had a moderate contribution to nestedness, conserved the nested pattern after removal of this species.

Carrion consumption rates

The average consumption rate was highly variable in the different systems, ranging from >22.20 kg/h in Toledo and Cantábrica to <0.30 kg/h in Nevada and Espuña (Table 1). Carcass consumption rates were not autocorrelated spatially or among sites (Moran's I test = −0.0069, P = 0.25), or within sites (Moran's I test, all $P > 0.28$), and were not related to climatic conditions (precipitation and temperature, univariate GLMs, all $P > 0.47$). The GLMs relating average consumption rate with nestedness degree, presence of obligate scavengers, and species richness were all significant (Table 2, Fig. 3). Species-rich, nested assemblages with presence of vultures had the highest carrion consumption rates. The results were similar when using the species richness estimated for an equal sampling (Appendix S4). The models testing the effect of nestedness and species richness showed the highest percentage of explained deviance. However, when we recalculated consumption rates excluding those carcasses visited by the species that contributed the most to nestedness (Griffon Vulture and red fox; Appendix S1), mean consumption rates for each assemblage showed contrasting patterns. Even if all assemblages became non-nested after excluding the species that contributed the most to nestedness (independently of this species being the fox or the vulture), consumption rates were lower when foxes were present than when Griffon Vultures were present (Fig. 2B). This suggests that species richness and, to a lower extent, vulture presence and not nestedness, are the variables increasing carcass consumption rates. These results also show that, as expected, consumption rates are lower when foxes are present than when Griffon Vultures are present.

Competitive exclusions

The proportion of species that stopped consuming carrion, as derived from the competitive dynamic model, was lower in sites without vultures (i.e., Nevada and Espuña) than in richer sites with vultures (Fig. 4). However, this proportion was similar for all the nested communities (Fig. 4). These results were robust to variations in the interaction strength (β), indicating a consistent pattern for the different degrees of interaction effect (see Appendix S5 for the proportion of species that stopped consuming the carrion at different levels of β).

Univariate GLMs indicated that the proportion of species that stopped consuming carrion was also related to species richness, the presence of vultures, and nestedness. Both richness and nestedness relationships fitted better under a quadratic model with a concave-down shape (Table 2, Fig. 4), suggesting that the negative effects of high levels of competition for the resources found in some assemblages are partially compensated by their high species richness and a nested organization of their interactions. The results were similar when using the species richness estimated for an equal sampling (Appendix S4).

TABLE 2. Generalized linear models for consumption rate and competitive exclusions in relation to species richness, nestedness (Z-NODF), and presence of vultures; species richness and nestedness were also tested as quadratic terms in the model testing their relationship with competitive exclusions.

Model	Consumption rate (kg/h)			Competitive exclusions		
	Coefficient	P	Deviance (%)	Coefficient	P	Deviance (%)
Richness	0.563	0.002	88.13	0.0013	0.015	72.49
Richness +				0.136	0.0048	
(Richness)^2				−0.069	0.047	90.91
Nestedness	1.092	0.003	85.23	0.027	0.013	74.15
Nestedness +				0.138	0.008	
(Nestedness)^2				−0.058	0.110	87.36
Vulture	4.451	0.012	75.07	0.121	0.005	81.50

Notes: Competitive exclusions are the proportion of species that stopped consuming carrion as derived from the competitive dynamic model. Model coefficients, P values, and the percentage of explained deviance are shown.

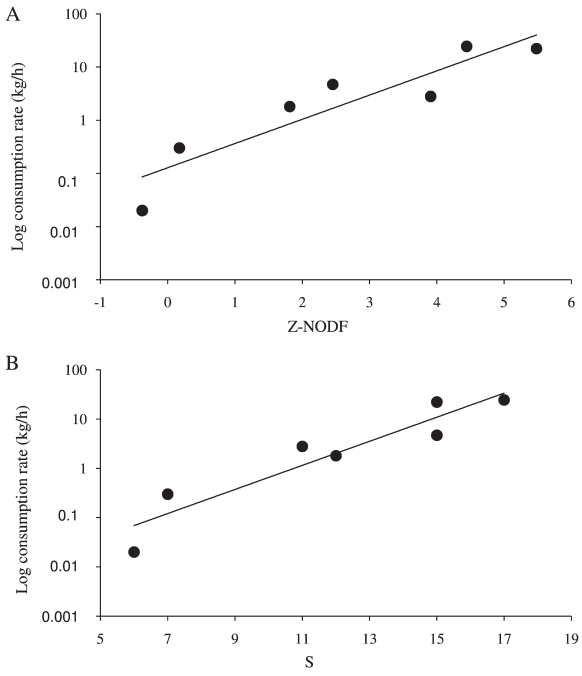


FIG. 3. Relationship between the average consumption rate (shown on a log scale) in the seven studied scavenging assemblages and (A) the *z* score of the nestedness value (Z-NODF) and (B) species richness, *S*. Each point represents one study site. The consumption rate is presented on a logarithmic scale.

DISCUSSION

Using both empirical data and modeling, we explored the relationships among structure, competition, and species coexistence in trophic networks of terrestrial vertebrate scavengers.

The scavenging network of highly competitive communities, i.e., those with higher carcass consumption rates, was nested, species-rich, and included obligate scavengers whereas those where the consumption rates were low, presented a non-nested structure, lower number of species, and absence of vultures. The modeled dynamics of the studied systems indicated that the probability of showing competitive exclusions (i.e., species stopping carrion consumption) was higher in highly competitive assemblages (i.e., where consumption rates where high). Strikingly, however, competitive exclusions partially stabilized at high richness and nestedness values, so that further competition increases did not result in parallel increases of competitive exclusions. This suggests that high species richness and nestedness may characterize scavenging networks that are robust to high levels of interspecific competition for carrion.

Different mechanisms could explain the contribution of species richness to coexistence. More species can make a complementary use of the available resources through niche differentiation as well as through facilitation processes, decreasing the competition between the species (Hooper et al. 2005, Loreau and de Mazancourt 2013). In the scavenger community, different eco-morphological characters and interspecific dominance hierarchies can lead to an ordered resource partitioning (e.g., Hertel 1994, Hertel and Lehman 1998). Also, communities with more species may also have a higher chance of having key species with ecological roles not found in species-poor communities (Orians 1969, MacArthur 1972). For example, vultures can facilitate carcass location by other species (e.g., scavengers watching alighting vultures; Schaller 1972) and improve consumption efficiency (e.g., by providing access to the interior of thick-skinned carcasses; Álvarez et al. 1976).

In the last few years, there has been a fruitful debate about the implications of nestedness in ecological networks for species coexistence and community persistence. In mutualistic assemblages, some authors have suggested that nestedness enhances coexistence (Okuyama and Holland 2008, Bastolla et al. 2009, Suweis et al. 2013, Rohr et al. 2014), whereas others argue that it has destabilizing consequences (Allesina and Tang 2012, Staniczenko et al. 2013). These distinct conclusions are

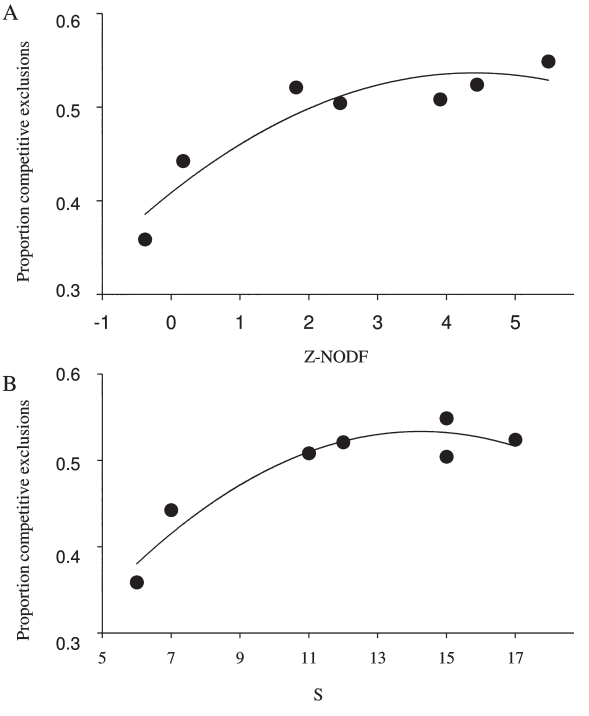


FIG. 4. Relationship between the proportion of competitive exclusions (i.e., proportion of species that stopped consuming carrion as derived from the competitive dynamic model) in the seven modeled scavenging assemblages and (A) the *z* score of the nestedness value, Z-NODF, (regression curve: $R^2 = 0.843$, $P = 0.003$), and (B) species richness, S (regression curve: $R^2 = 0.909$, $P = 0.007$). Each point represents one study site. The proportion of competitive exclusions was calculated through a competitive Lotka-Volterra model parameterized with the structure of the interaction network (see *Methods: Dynamic model* for complete details).

based on different assumptions and on different definitions of stability for ecological networks. In trophic assemblages and using numerical simulations, Thébault and Fontaine (2010) indicated that nestedness is comparatively less important than compartmentalization (i.e., the existence of groups of cohesively related species) as a driver of species persistence. Our study is the first one analyzing how nestedness affects consumption patterns in a community of scavengers competing for food resources. Our results reinforce the idea that the organization of the consumption patterns in a nested way can promote coexistence. Theoretical and empirical work is now needed to explore whether coexistence is favored via facilitation among the interacting species, as theory combining competition and mutualisms predicts for mutualistic assemblages (Bastolla et al. 2009). In our system, we show evidence that the effect of nestedness on coexistence is especially important in communities where the competition for resources is high. We suggest that in addition to the differences in approaches and stability definitions, some contrasting results in previous studies may be influenced, at least partially, by the differences in the degree of competition among the studied communities.

Selva and Fortuna (2007) also detected high nestedness levels in a scavenger assemblage of an ecosystem lacking vultures (Bialowieza forest, Poland). In their study site, top carnivores, such as wolves, are still present. In contrast, large carnivores are mostly absent from all of our study sites nowadays. Given that top-carnivore kills have been identified as contributing substantially to nestedness (Selva and Fortuna 2007), top-carnivore absence could explain the lack of nestedness in our vulture-lacking assemblages. Moreover, Selva and Fortuna (2007) found that nestedness was higher in winter than in warmer seasons (in winter, competition for food was greater), a pattern that is consistent with our findings. This emphasizes the idea that nestedness in scavenging assemblages may emerge in environments where the competition for food resources is high, and is consistent with the results of Allen et al. (2014) and Moleón et al. (2015) obtained in sites that retain a full community of vertebrate scavengers, including vultures and large mammalian carnivores.

Our analyses indicate that not all scavenger species contribute equally to nestedness, with vultures and some major facultative scavengers (mostly the red fox) being the strongest contributors. This highlights the key role that facultative scavengers play in scavenging communities even where obligate scavengers are present (Moleón et al. 2015). Given the relationship found between nestedness and species coexistence, this result suggests that vultures and major scavengers might favor the coexistence of species in the scavenging guild more than other species. Although vultures are correlated with high interspecific competition, they may also have a positive impact on other scavenger species, through different forms of facilitation. It is interesting to note that these facilitative effects share similarities with processes observed in mutualistic networks (Saavedra et al. 2011, Stouffer et al. 2012), where strong contributors supply a large number of connected species with food or pollination services (Bascompte and Jordano 2007), being the most important species for the whole network to persist. However, we cannot rule out other possible explanations, especially taking into account that species richness also favored species coexistence, irrespective of the species involved. Unfortunately, the low number of study assemblages and the high correlation between the variables did not allow for an effective separation of the effects of nestedness and species richness on the proportion of competitive exclusions. Thus, more research is needed to identify the relative importance of each factor.

Invertebrates and microorganisms may influence scavenging patterns by vertebrates, especially in vertebrate-poor sites where scavenging rates are low and carrion is available for long periods of time (DeVault et al. 2003, Ray et al. 2014). Moreover, carrion consumption by invertebrates and microorganisms is more important in relatively warm and humid areas and seasons (DeVault et al. 2004). For instance, invertebrates at ungulate carcasses in a German area consumed 85% of carrion biomass in summer, but scavenging by invertebrates in winter was negligible (Ray et al. 2014). In this study, carcass consumption time ranged from 10 d in summer to 32 d in winter. Mean ungulate carcass consumption time in a Polish area during winter was 4–107 d, depending on the carcass type, and vertebrate scavengers consumed most of carrion (Selva 2004). In our study areas, carrion consumption rates by the diverse local community of vertebrate scavengers were very high, leaving a smaller chance for invertebrates and microorganisms to benefit from the carcasses. Mean carcass consumption time in our study areas and monitoring period (the coolest seasons, i.e., autumn and winter) was 3.71 ± 5.41 d (mean ± SD). In such a short period of time, even if invertebrates were present in the carrion (Tomberlin et al. 2011), the amount of the resource they consumed in the studied carcasses was relatively small in comparison to the consumption by vertebrates. A visual inspection of the pictures from five carcasses with detection rates higher than 5 d, showed not significant changes in the carrion volume between day 1 and just before the first vertebrate scavenger entered. Thus, the patterns of community structure and competition of the vertebrate scavenger guild probably summarize the process of carrion consumption in our study system.

Our findings have implications not only for community persistence, but also for biodiversity conservation. Extinctions of certain scavengers such as vultures could trigger detrimental cascading effects for populations of other scavengers for which carrion supply is also an important food resource (Sánchez-Zapata et al. 2010, Moleón et al. 2014*b*, Pereira et al. 2014, Mateo-Tomás et al. 2015). Thus, our results advocate

for the strict protection of these species, which are declining and endangered almost everywhere (Ogada et al. 2012, Moleón et al. 2014*a*,b). Fortunately, our results also show that some facultative scavengers could buffer to some extent the effect of vulture loss on the scavenging network structure. Nevertheless, scavenging rate was much lower in the absence of vultures, and reduced carcass consumption rate may have important consequences for the functioning of the ecosystems. For example, in India, a dramatic reduction in the population of vultures incurred in high human health costs derived from increases in dogs and rabies (Green et al. 2004, Markandya et al. 2008).

To summarize, our results indicate that scavenging networks showing high consumption rates are species rich and structured in a nested way, which may favor the coexistence of more interacting species.

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