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

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Abstract. Disentangling the processes that shape the organization of ecological assemblages and its implications to species coexistence is one of the foremost challenges of ecology. While 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 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, coexistence, facilitation, interaction network, nestedness, vulture

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). Growing interest has been recently 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 can also 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. 2014a). 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, Pereira et al. 2014, Moleón et al. 2014a). 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. 2014a). Carrion 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. 2014a). 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. 2014a). 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. 2014a). 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. 2014a). 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 Mazancourt 2013). However, we barely know if this generalization can also be applied to assemblages associated to keystone ecological services such as scavenger communities. 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 & 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 directly generalized 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 a more relaxed inter-specific 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 temperate and Mediterranean woods, scrubs and pastures in the north and in the rest of the sites, respectively. All 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 originated from hunting activities. Carcasses were located shortly after animal death (<3 h)

139 either by accompanying the hunters or by following their indications. Carrion consumption was
 140 monitored by camouflaged remote cameras. The cameras were hidden close (4-10 m) to
 141 carcasses immediately after their generation and they operated until carcasses had been
 142 completely consumed, save the skin and skeleton. Carcasses were weighted and then fixed to soil
 143 using picks to avoid animals moving them away from the camera focal point. The cameras were
 144 programmed to record one picture every 1-2 min after activation by movement both at day and
 145 night (using no glow infrared sensors to minimize disturbance). The pictures obtained provided
 146 information on the species that fed on the carcass, and on the time required to consume the
 147 carcass. A species was considered a carcass consumer (i.e., scavenger) when it was clearly
 148 recorded consuming it. Invertebrate presence in our study areas was never large enough to be
 149 considered significant for the consumption rates and was not included in the analyses. When
 150 consumption was suspected but not clearly recorded, we assumed consumption if that species
 151 was already detected consuming at other carcass (see Appendix A for a list of the scavenger
 152 species found in each site, Appendix B for the main characteristics of the hunting remains
 153 techniques, and Blázquez et al. 2009 for a more detailed description of the carcass monitoring
 154 procedure). We then calculated consumption rate of each carcass as the quantity of carrion (kg)
 155 eaten per unit of time (h), from camera activation to total carcass consumption, and we
 156 calculated the consumption rate per site as the average consumption rate of each carcass in that
 157 site. We finally calculated the number of total scavenger species that consumed the monitored
 158 carcasses in each study site (i.e. species richness). As the number of carcasses monitored in each
 159 study site was different, we also used the incidence-based data to build extrapolation curves and
 160 identify if we had sampled the expected total number of scavenger species in each scavenger
 161 community (Chao et al., 2014). All 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 ranged between 0 and 100, being 100 for highly nested networks, while random matrices showed 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), that assumes the probability of the interaction between i and j occurs (i.e., $a_{ij} = 1$) is:

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

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. As the matrices had different sizes, we standardized the results using z-scores of the NODF values (Z-NODF; Ulrich and Gotelli 2007). Z-scores were calculated as:

$$z - score = \frac{Observed_{NODF} - Mean_{NODF \text{ null model}}}{SD_{NODF \text{ null model}}} \quad (b)$$

Z-scores > 0 indicate that nestedness at a given site is greater than the mean nestedness of the randomized matrices, while 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 of each of the scavenger species in each assemblage (CN). In a nested network, when the species i was 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 will have a high and low contribution to nestedness, respectively. 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 re-calculated 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 removing griffon vultures, which are the commonest obligate scavengers in Spain (see above). 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 competitive Lotka-Volterra 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 but obligate scavengers can actually use resources other than carrion, and would thus be 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 comparisons 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 i -th species described by the following expression:

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

In equation (c), N_i (or N_j) is the abundance of the i -th species (or j -th 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 equation (c), 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 to the networks, A , to create a resource utilization overlap matrix (ROM) for each assemblage (Case 1990, Araújo et al. 2008, Baiser et al. 2010), where the elements of the ROM correspond to the interaction terms α_{ij} in (c). The Rom is defined as follows:

$$ROM = [\alpha_{iz}]_{n \times n} \quad (d)$$

where,

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

where α_{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 the diagonal elements (i.e., intra-specific competition or self-regulation) are equal to one, and all non-diagonal elements (i.e., interspecific competition) are smaller or equal to one. Note that equation (e) is in all respects equivalent to MacArthur and Levins (1967) classical approach. Because our matrices are binary, this is, they only have zeros and ones, we do not need to square the denominator. Equation (e) 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 (c).

We considered 34 different values for β (eq. (c)), ranging from 0.1 to 10 with a step of 0.3. For each β value, we ran the model 1,000 times. During each run, we randomly sampled the per-capita growth rates (r_i) from a uniform distribution between zero and one, 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 (1) the consumption rate (in log-scale) and (2) the proportion of species that stopped consuming the carrion (response variables) with a) species richness, b) presence of obligate scavengers (i.e. vultures; coded as 1/0) and c) nestedness (Z-NODF; explanatory variables). We also tested the relationship between the log-consumption rate and the mean annual precipitation (mm) and mean annual temperature (Celsius degrees) 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 it 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 the analyses were done on R 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; range: 11-17) than in sites lacking them (mean: 6.5; range: 6-7; Table 1). This species increase in sites with vultures was not only due to vultures, given that they were represented by two-three species per site, while the differences in species between areas with and without vultures are of at least 3 species (Appendix A). The extrapolation analysis suggest that observed species richness was not affected by sampling for all but one community: the observed and expected number of species in all the communities were similar with the exception of species-richer community (Toledo), whose estimated species richness was slightly higher than the observed one (Appendix C).

Scavenger assemblages were nested in all the sites with vultures, while 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 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 A 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 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 resulted also 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 spatially autocorrelated nor among sites (Moran's I test = -0.0069, $p = 0.25$) neither 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 D). 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 A), 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 to 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 E 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 D).

DISCUSSION

Using both empirical data and modeling, we explored the relationship 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 while 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 were 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 (Loreau et al. 2001, Hooper et al. 2005). 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 to 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), while others argue that it has destabilizing consequences (Staniczenko et al. 2013, Allesina and Tang 2012). These distinct conclusions are 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 under a nested way can promote coexistence. Theoretical and empirical work are now needed to explore if coexistence is favored via facilitation among the interacting species as theory combining competition and mutualisms predicts to 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 the 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 competition degree among the studied communities.

Selva and Fortuna (2007) also detected high nestedness levels in a scavenger assemblage of an ecosystem lacking vultures (Białowieża forest, Poland). In their study site, top carnivores, such as wolves, are still present. In contrast, large carnivores are mostly absent from all our study sites

nowadays. Given that top carnivore kills have been identified to contribute 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 is 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 the 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 (see above). It is interesting to note that this 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 effect 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, however, scavenging by invertebrates in winter was negligible (Ray et al. 2014). In this study, carcass consumption time ranged from 10 days in summer to 32 in winter. Mean ungulate carcass consumption time in a Polish area during winter was 4-107 days, 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 $3.71 (\pm 5.41 \text{ SD})$ days. In such a short period of time, even if invertebrates could be 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 five days, 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 likely summarizes 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, Pereira et al. 2014, Moleón et al. 2014a, 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. 2014a, 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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SUPPLEMENTAL MATERIAL

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613 Appendices A-E and the Supplement are available online:

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Table 1. Scavenger species richness and nestedness degree in seven scavenging assemblages of Spain. Number of carcasses studied (N), number of scavenger species detected at carcasses, average carrion consumption rate (kg/h), presence/absence of vultures in the study site, nestedness (calculated as the Z-score of the matrix NODF; see main text for complete details), and significance (P -value) of the nested pattern are shown.

Assemblage	N	Species number	Consumption rate (kg/h)	Vultures	Z-NODF	P -value
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
España	30	7	0.02	No	0.17	0.43
Nevada	12	6	0.30	No	-0.37	0.67

Table 2. Generalized Linear Models for both consumption rate and competitive exclusions (i.e. proportion of species that stopped consuming carrion as derived from the competitive dynamic model) 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 the competitive exclusions. We show the coefficients of the models, the *P*-values and the percentage of explained deviance.

	Consumption rate (Kg/h)			Competitive exclusions		
	Coefficient	<i>P</i> -value	% Deviance	Coefficient	<i>P</i> -value	% 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

Figure 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).

Figure 2. Nestedness and consumption rates of seven scavenging assemblages in mainland Spain. A) Z-score of the nestedness value measured with the NODF metrics (Z-NODF) is shown. The Z-score was re-calculated 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 or red fox; triangles). The open symbols represent non-significant nested patterns. The dotted 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 (kg/h) for each assemblage. We re-calculated 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.

Figure 3. Relationship between the average consumption rate (kg/h) in the seven studied scavenging assemblages and A) Z-score of the nestedness value (Z-NODF). B) Species richness (S). Each point represents one study site. The consumption rate is presented in a logarithmic scale.

Figure 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) Z-score of the nestedness value (Z-NODF). Regression curve: $R^2 = 0.843$, $P = 0.003$. 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

656 calculated through a competitive Lotka-Volterra model parameterized with the structure of the
657 interaction network (see main text for complete details).

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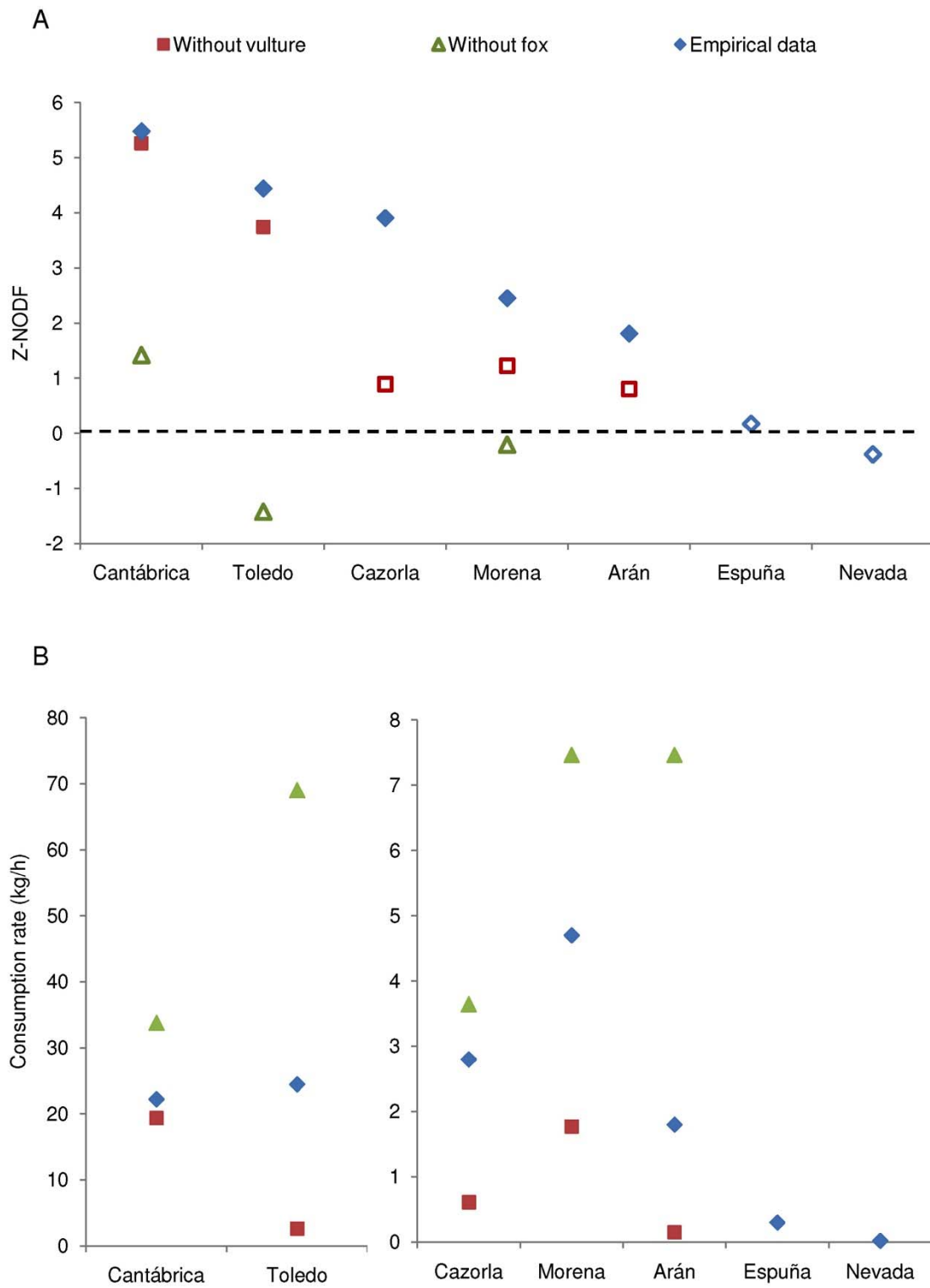
659 Fig. 1



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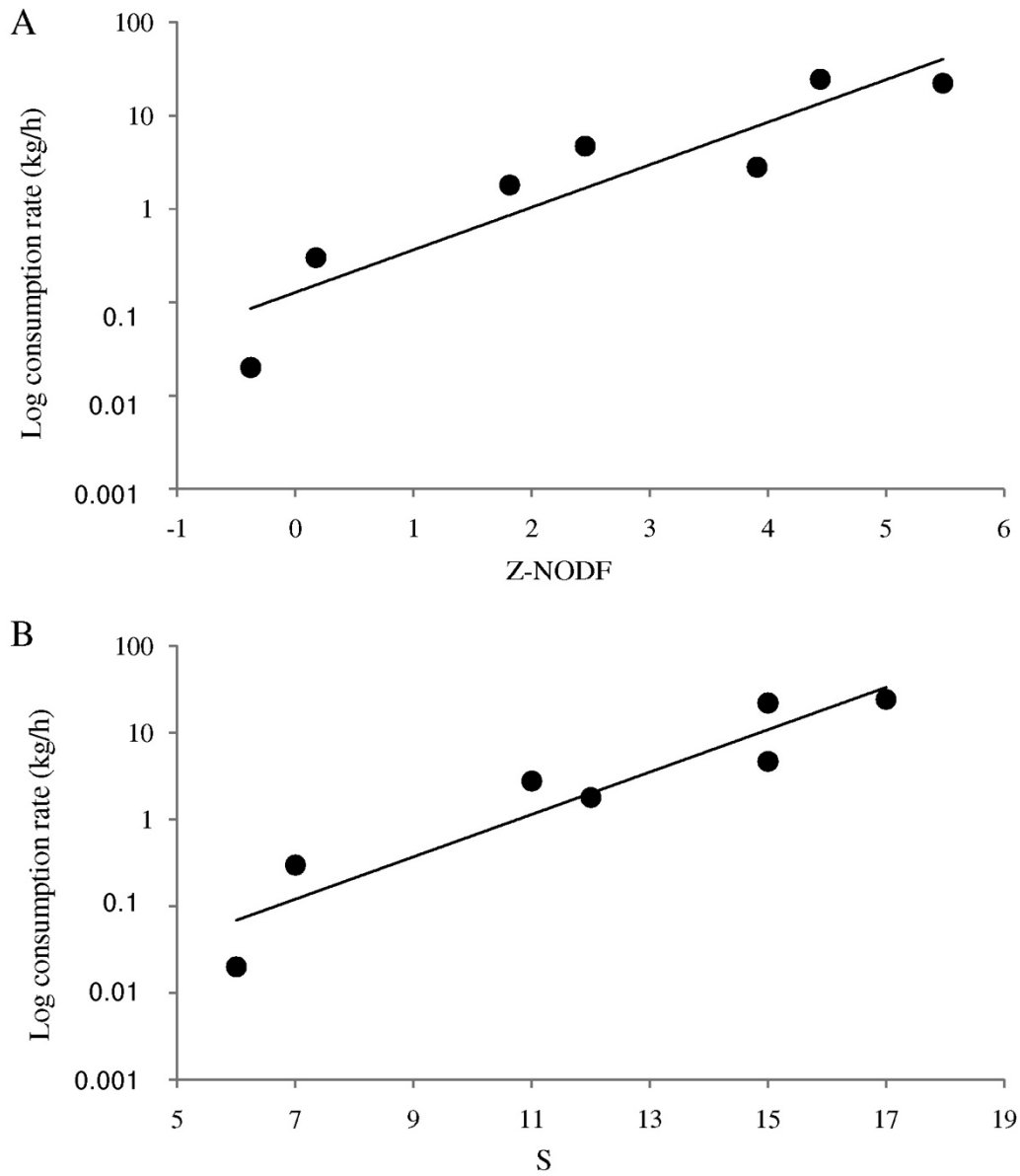
662 Fig. 2



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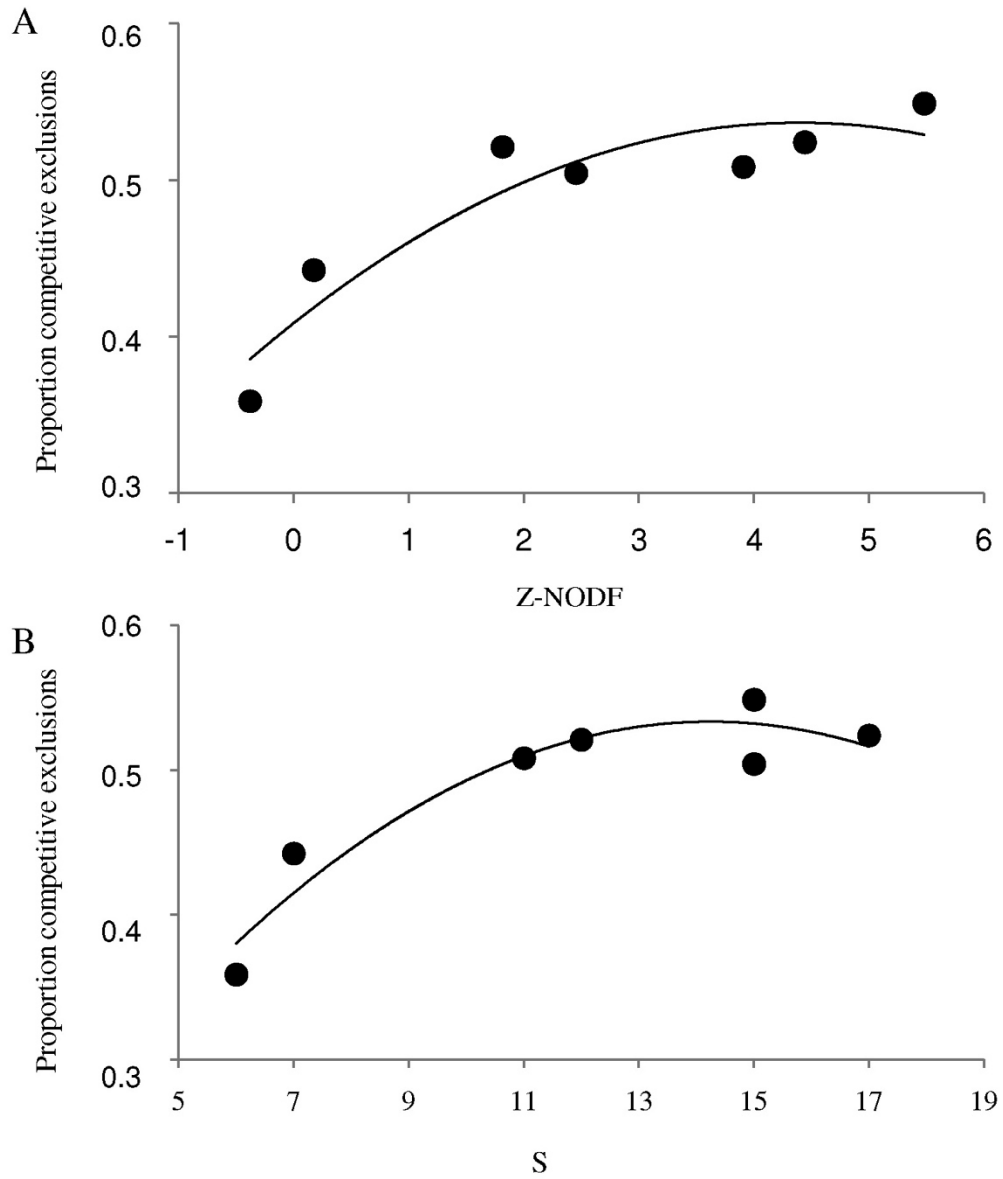
665 Fig. 3



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668 Fig. 4



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