PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2007) **274**, 1101–1108
doi:10.1098/rspb.2006.0232

The nested structure of a scavenger community

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Scavenging is a widespread phenomenon in vertebrate communities which has rarely been accounted for, in spite of playing an essential role in food webs by enhancing nutrient recycling and community stability. Most studies on scavenger assemblages have often presented an oversimplified view of carrion foraging. Here, we applied for the first time the concept of nestedness to the study of a species-rich scavenger community in a forest ecosystem (Białowieża Primeval Forest, Poland) following a network approach. By analysing one of the most complete datasets existing up to now in a pristine environment, we have shown that the community of facultative scavengers is not randomly assembled but highly nested. A nested pattern means that species-poor carcasses support a subset of the scavenger assemblage occurring at progressively species-rich carcasses. This result contradicts the conventional view of facultative scavenging as random and opportunistic and supports recent findings in scavenging ecology. It also suggests that factors other than competition play a major role in determining community structure. Nested patterns in scavenger communities appear to be promoted by the high diversity in carrion resources and consumers, the differential predictability of the ungulate carcass types and stressful environmental conditions.

Keywords: carrion; complex networks; consumer–resource interactions; nestedness; resource predictability; scavenging

1. INTRODUCTION

Understanding the patterns and the processes underlying the structure of communities is one of the main issues in ecology. Vertebrate scavenger communities, together with microbes and arthropods, decomposers of animal matter, play an essential role in terrestrial ecosystems by accelerating the return of nutrients to trophic webs, disseminating such nutrients over a wide area, and diluting potentially infective foci (see review in DeVault *et al.* 2003). However, scavenger assemblages have received comparatively little attention in spite of scavenging being a widespread phenomenon among terrestrial vertebrates. The temporal patchiness of carrion availability might have inhibited evolution towards strict specialization for scavenging in most vertebrates. As a result, obligate scavengers are rare; only vultures show life histories based on the exploitation of carcasses. But facultative scavenging is quite prevalent and, in fact, nearly all predators are scavengers to some extent (DeVault *et al.* 2003).

The use of carrion by vertebrate consumers as an alternative food resource during prey shortages, under stressful environmental conditions or in other critical periods of their lives, may have substantial impacts on population dynamics and, thus, on the structure of animal communities (DeVault *et al.* 2003; Roth 2003; Wilmers *et al.* 2003*a*,*b*; Selva *et al.* 2005). Especially, in cold climate regions, carrion represents an essential trophic resource for the predator community during winter (Jedrzejewska & Jedrzejewski 1998; Selva 2004; Selva *et al.* 2005). These trophic interactions via facultative scavenging may represent 'weak links' in food webs and, as recent evidence suggests, weak links are important for promoting community stability and persistence (McCann *et al.* 1998; Neutel *et al.* 2002).

Since Diamond (1975), who considered competition as the major force shaping community structure, two main research approaches have predominated to understand how species are assembled into communities (Weiher *et al.* 1998). A first path of enquiry comprises the development of models that test for patterns of species co-occurrence which differ from the null hypothesis that species are independent of each other (e.g. Connor & Simberloff 1979). The second approach is ecomorphological and emphasizes patterns considering species traits in the context of competitive exclusion (e.g. Moreno *et al.* 2006). Ecomorphology analyses morphological traits of species to infer their ecological and behavioural characteristics; it often involves the use of guilds. The structure of scavenging guilds has been traditionally studied following a behavioural approach, based on dominance hierarchies observed at carcasses (e.g. Wallace & Temple 1987), or an ecomorphological approach, which relates morphological traits of scavenger species to their feeding ecology (e.g. Hertel 1994), or both (e.g. Kruuk 1967). Guilds composed of obligate scavengers have been considered highly structured by dominance hierarchies and differential patterns of resource use (Kruuk 1967; Wallace & Temple 1987). On the other hand, the scavenging guilds formed mainly by facultative scavengers have been traditionally regarded as opportunistic (Hiraldo *et al.* 1991; Travaini *et al.* 1998). However, most studies on scavenging have some serious limitations to be conclusive in relation to the structure of the guilds: (i) the inclusion in the guild of species of interest to the researcher only (mainly avian scavengers), thus ignoring some potentially relevant members, (ii) the generalized use of artificial exposed carrion or baits instead of 'natural' carcasses, and

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Received 7 November 2006
Accepted 16 January 2007

(iii) the lack of long-term studies covering different seasons and years that are able to record rare scavengers. A recent long-term study on the scavenger community of a natural temperate forest (Białowieża Primeval Forest (BPF), E Poland) overcoming these limitations suggests that the use of carrion resources by facultative scavengers is not random, but a complex process mediated by environmental factors, facilitation processes and behavioural adaptations (Selva *et al.* 2003, 2005; Selva 2004).

Scavengers exploit a resource (carcasses) conventionally considered as ephemeral, rare and unpredictable in terms of its spatio-temporal availability (e.g. Houston 1979; Heinrich 1988). However, recent evidence suggests that carrion resources are relatively predictable and common, and that the main carrion supplies show very different spatial and temporal properties (Wilmers *et al.* 2003*a*,*b*; Selva 2004). This is especially true in the case of ungulates, which constitute the bulk of the carrion supply in many undisturbed terrestrial ecosystems. Ungulate carrion can be very varied in terms of the characteristics of the carcass itself (size, openness, habitat location), predictability, spatial distribution (clumped versus dispersed) and temporal availability (constant versus pulsed). Carrion provided from the kills of large predators is consistent over time, disperse in space and relatively predictable, especially for those scavenger species associating with large predators as a foraging strategy (Stahler *et al.* 2002; Wilmers *et al.* 2003*a*,*b*; Selva 2004; Selva *et al.* 2005). In contrast, natural deaths caused by disease, cold or starvation often appear as a sudden pulse, usually at the end of the winter, thus being highly aggregated in time, relatively randomly distributed and more unpredictable. Weather conditions and food availability play a key role in triggering the biggest pulses of ungulate carrion. Finally, human-caused mortality, namely hunting, might be an important carcass supplier in some areas. In general, carrion from harvested ungulates tends to be more aggregated in space and time and is relatively easy to locate by scavengers (Wilmers *et al.* 2003*a*; Selva *et al.* 2005). In this context of different carrion supplies, this paper investigates the structure of a guild of facultative scavengers in a species-rich vertebrate community in a natural environment.

Structured communities can be described by a departure from randomness, where an assemblage of species is significantly more ordered than would be expected by chance. One of the patterns most commonly observed in local biota is the nested subset structure (e.g. Wright *et al.* 1998). Originally described in island biogeography to illustrate how a pool of animals is redistributed among a set of islands (Atmar & Patterson 1993), nestedness has also been recorded in fragmented forest patches (Fischer & Lindenmayer 2005), mountains (Patterson *et al.* 1996), ponds (Baber *et al.* 2004; McAbendroth *et al.* 2005) and streams (Cook *et al.* 2004). The analysis of nested patterns has been used not only to investigate community structure, but also as a useful tool for conservation management (Worthen 1996; Fischer & Lindenmayer 2005) and for the study of ecological networks (Bascompte *et al.* 2003; Bascompte & Jordano 2006). This study is the first in bringing the concept of nestedness to the study of a scavenger community, where the carcasses are 'islands' and the scavengers are the 'inhabiting species'. A nested pattern occurs when species in poor assemblages are proper subsets of those in progressively more diverse assemblages. In our context, nestedness means that those species feeding on carcasses visited by few species are a subset of the scavenger assemblage occurring at those carcasses visited by many species. Thus, rare scavengers will tend to occur only at the carcasses visited by the common scavengers. Nestedness represents a non-random structural pattern beyond the differential scavenging frequency of the species (i.e. some species feed on carcasses more frequently than others) and it may adequately describe the complex pattern of carcass use by a highly diverse community of scavenger species.

In this paper, we propose the use of nested pattern analysis to investigate the structure of a species-rich scavenger community following a network approach. Our main goal is to elucidate whether the exploitation of carrion resources by facultative scavengers shows this structural pattern or whether it is random. We hypothesized that carrion resources which are more predictable and permanently available would be exploited by a more structured community. We also discuss the contribution to the nestedness of the community of different carrion supplies and scavenger species. Finally, we try to disentangle the factors as well as the ecological and evolutionary processes that may promote nested structure in scavenger communities.

2. MATERIAL AND METHODS

(a) *Study area*

The field data were collected in the Polish part of the BPF (approx. 600 km^2), located in the Polish–Belarussian borderland. It represents the best-preserved woodland of its size, typical for the European lowland temperate forests. Tree stands of BPF are dominated by oak (*Quercus robur*), hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), black alder (*Alnus glutinosa*), Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Open areas (glades and meadows) cover 4% of the study area. BPF is inhabited by a rich animal community. Ungulates are represented by five species: European bison (*Bison bonasus*), moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Forty species of raptors and carnivores, including the wolf (*Canis lupus*) and the lynx (*Lynx lynx*), have been reported. The climate of BPF is transitional between continental and Atlantic types, although continental features prevail. The cold season (1 November–30 March) may cover periods of extreme cold temperatures and deep snow cover. For more detailed information of the study area, please refer to Jedrzejewska & Jedrzejewski (1998) and Selva (2004).

(b) *Dataset*

Information on ungulate carcasses was obtained from various sources. A parallel radiotracking study on wolves and snowtracking of wolves and lynx provided most kills of large predators. Information on (potential) carcass locations was also obtained from foresters, hunters, rangers, local people and scientific personnel working in BPF. Some carcasses of harvested animals were obtained from hunters and then exposed by us. When a carcass was located, we recorded the species, cause of death, time elapsed since death or exposition (days) and habitat type (forest versus open areas). The initial biomass of the carcasses was estimated by weighing, additional visual estimations and reference body masses of ungulates (Jedrzejewska & Jedrzejewski 1998; Selva *et al.* 2003; Selva 2004).

A total of 137 ungulate carcasses were freshly recovered from December 1997 to January 2002, mainly during the cold season ($n=112$). The utilization of carcasses by scavengers was monitored in systematic inspections ($n=1334$). In each inspection, we recorded the species of vertebrates, mainly birds and mammals, which had visited the carcass, based on direct observations, tracks in the snow and other signs (feathers, scats, pellets and calls). The species present at carcasses were considered to have been scavenging on them. During each inspection, we collected all droppings of scavengers and brushed up the snow surface or sand placed around the carcass to clean up the tracks. We tried to keep the time spent at carcasses short to minimize possible disturbance. The monitoring was finished when all edible biomass had been consumed and only bones, completely clean of flesh, remained.

The sample of monitored carcasses included 62 wolf kills, 10 lynx kills, 24 naturally dead ungulates and 41 harvested animals. Wolf and lynx kills referred to fresh kills of both predators and they usually consisted of remains. Wolf prey are large animals, mostly red deer. Their remnants are easily visible in the snow, as they are spread around and the ground is often covered in blood. By contrast, lynx feed on a kill (mainly roe deer or young red deer) for few days and they often guard and camouflage their prey against scavengers. Dead ungulates included intact carcasses of animals (mainly wild boar) that had died from disease, starvation or cold, usually at concealed locations. Harvested animals included the whole bodies of culled and hunted ungulates, which were subsequently abandoned or deliberately exposed. Most often they were not intact carcasses, as they had been opened or some body parts (e.g. skull) removed by hunters. In BPF, hunting takes places all year round, but more intensively during winter and autumn. Additional details of the field methods are given by Selva (2004) and Selva *et al.* (2003, 2005).

(c) *Nestedness analysis*

While traditional food webs are represented as unipartite graphs (e.g. Pimm 1982), that is, relations depicting who-eats-whom through several trophic levels, the carcass utilization by facultative scavengers can be described by means of bipartite graphs (as mutualistic networks, see Jordano *et al.* 2003). In this context, bipartite graphs depict the relationships between (but not within) two distinct sets: ungulate carcasses (resources) and scavenger species (consumers; figure 1). Carcass use by scavengers can be represented as a matrix, with carcasses as rows and scavenger species as columns (figure 2). Each element of the matrix is 1 if that particular species feeds on that particular carcass and 0 otherwise. In this presence/absence matrix, if carcasses are arranged in the order of decreasing number of scavenger species visiting them, and scavenger species are ranked in the order of decreasing number of occurrences on carcasses, the upper left of the matrix will be filled in a roughly triangular shape.

We estimated an index of matrix nestedness (N) using ANINHADO software (Guimaraes & Guimaraes 2006), a modified version of the NESTEDNESS CALCULATOR software, originally developed by W. Atmar & B. D. Patterson in 1995 (AICS Research, University Park, NM) to characterize how species are distributed among a set of islands (Atmar & Patterson 1993). ANINHADO, as its predecessor NESTEDNESS CALCULATOR, first reorganizes the matrix by arranging rows (carcasses) and columns (scavenger species) from the ones with more presences to the ones with more absences in a way that maximizes nestedness (Atmar & Patterson 1993; Guimaraes & Guimaraes 2006). Given 137 carcasses, 26 scavenger species and 759 presences, an isocline of perfect nestedness is calculated for the real data matrix (figure 2). Absences to the left of the isocline and presences to the right of the isocline are recorded as unexpected. For each unexpected presence or absence, a normalized measure of global distance to the isocline is calculated and these values are averaged. Using an analogy with physical disorder, this measure is called temperature (T) with values ranging from 0 to 100 (Atmar & Patterson 1993; Guimaraes & Guimaraes 2006). In this paper, since we emphasize nestedness or order instead of disorder, we define the level of nestedness (N) as $N=(100-T)/100$, with values ranging from 0 to 1 (maximum nestedness, see Bascompte *et al.* 2003). Using ANINHADO software, we have also calculated the contribution of each line (carcass) and column (scavenger species) to T, called idiosyncratic temperature (IT), and transform these values as above for N (nestedness contribution, $NC=(100-IT)/100$). The IT of each scavenger species (or carcass) quantifies how much its pattern of scavenging (or of being scavenged) departs from the expected pattern under a perfectly nested community. The average value of IT for all species (or all carcasses) is the temperature of the matrix.

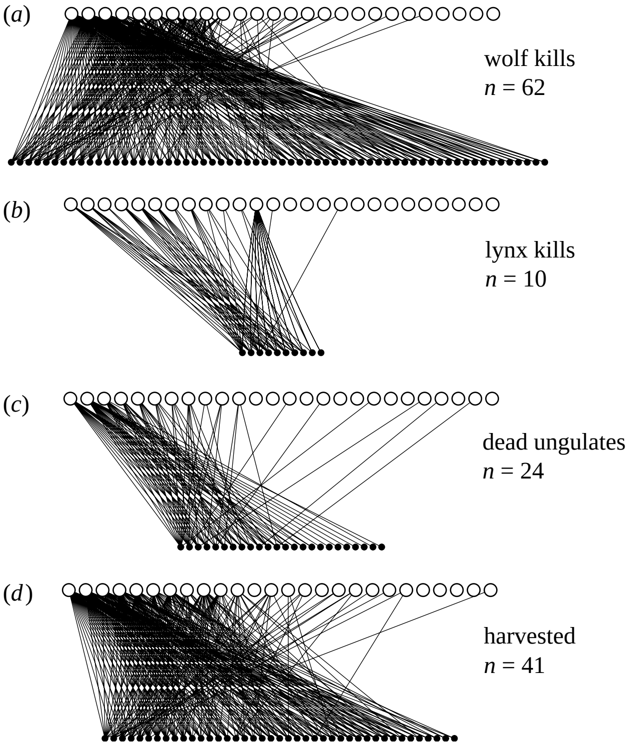
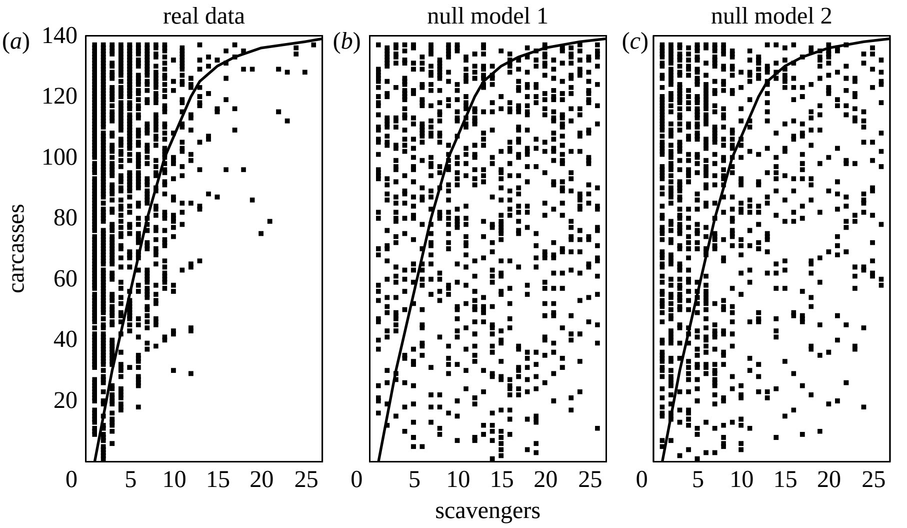


Figure 1. Bipartite graphs depicting scavenging relations (interactions) between the species of facultative scavengers (open circles) and ungulate carcasses (filled circles) of different origin: (*a*, *b*) predation, (*c*) natural causes other than predation and (*d*) human harvesting. Each line linking a scavenger species and a carcass indicates that that particular scavenger fed on that particular carcass. Carcasses are arranged from left to right in the order of decreasing number of scavenger species visiting them. All scavenger species are represented and also arranged from left to right in the order of decreasing number of occurrences on all carcasses.



1 raven (*Corvus orax*)
2 fox (*Vulpes vulpes*)
3 wolf (*Canis lupus*)
4 raccoon dog (*Nyctereutes procyonoides*)
5 jay (*Garrulus glandarius*)
6 wild board (*Sus scrofa*)
7 buzzard (*Buteo buteo*)
8 pine marten (*Martes martes*)
9 white-tailed eagle (*Haliaeetus albicilla*)
10 great tit (*Parus major*)
11 free-ranging dog
12 lynx (*Lynx lynx*)
13 micromammals (Rodentia, Soricidae)
14 badger (*Meles meles*)
15 goshawk (*Accipiter gentilis*)
16 magpie (*Pica pica*)
17 polecat (*Mustela putorius*)
18 golden eagle (*Aquila chrysaetos*)
19 squirrel (*Sciurus vulgaris*)
20 blue tit (*Parus caeruleus*)
21 hooded crow (*Corvus corone cornix*)
22 weasel (*Mustela nivalis*)
23 crested tit (*Parus cristatus*)
24 stoat (*Mustela erminea*)
25 lesser-spotted eagle (*Aquila pomarina*)
26 great-spotted wood pecker (*Dendrocopos major*)

Figure 2. Binary matrices representing (*a*) the real scavenger community and (*b*, *c*) two randomized communities (one replicate for each null model). A filled square indicates an observed presence of species *j* on carcass *i*. Numbers label carcasses (rows) and scavenger species (columns). Carcasses are arranged in the order of decreasing number of scavenger species visiting them, and scavenger species are ranked in the order of decreasing number of occurrences on carcasses, in a way that both minimizes unexpectedness. The line represents the isocline of perfect nestedness. The scavenger species and their corresponding rank number in the nested matrix (real data) are listed below.

Therefore, if $NC \geq N$, the species used carcasses as expected from the actual level of nestedness of the entire community. If $NC < N$, carcass use by the species did not match the expected pattern according to the nestedness shown by the real community, and we say then that the species is idiosyncratic in its scavenging pattern.

(d) *Null models*

To assess the significance of nestedness, we built two null models to contrast the observed value with the distribution of nestedness values from the 1000 resulting randomized matrices. Especially null model 2 is supposed to control for passive sampling (Jonsson 2001).

(i) *Null model 1 (lacks heterogeneity and nestedness)*

This model probabilistically maintains the observed number of presences, but these are completely reshuffled among all scavenger species–carcass pairs. In other words, each scavenger–carcass pair has the same probability to interact. This probability is estimated as the number of presences in the original matrix divided by the number of possible presences (number of carcasses × number of scavenger species, i.e. equivalent to the network connectance). This model neither maintains the number of scavenger species visiting each carcass (degree of carcasses hereafter) nor the number of carcasses visited by each scavenger (degree of scavengers hereafter) and also lacks nestedness. A replicate of this null model for the community under study is shown in figure 2.

(ii) *Null model 2 (lacks nestedness)*

This model also probabilistically maintains the observed total number of presences. It approximately maintains the degree of carcasses and the scavengers, but does not maintain nestedness. Now, the probability of drawing a presence of the scavenger *j* on the carcass *i* is the arithmetic mean of the presence probability of carcass i (i.e. fraction of ones in row i) and scavenger j (i.e. fraction of ones in column j). Thus, the probability of drawing a presence is proportional to the degree of both carcasses and scavengers. Figure 2 shows a replicate of this null model for the study community. For additional details on null models 1 and 2, see Bascompte *et al.* (2003).

3. RESULTS

The nestedness value for the real scavenger community ($N=0.91$) was significantly larger than the mean values of the randomized communities generated by the null models (mean + s.d.: $N=0.353 \pm 0.022$ for null model 1; $N=0.612 \pm 0.025$ for null model 2, $p<0.001$). Even when accounting for random sampling and heterogeneity of both scavengers and carcasses, the scavenger assemblage was significantly more nested than expected by chance.

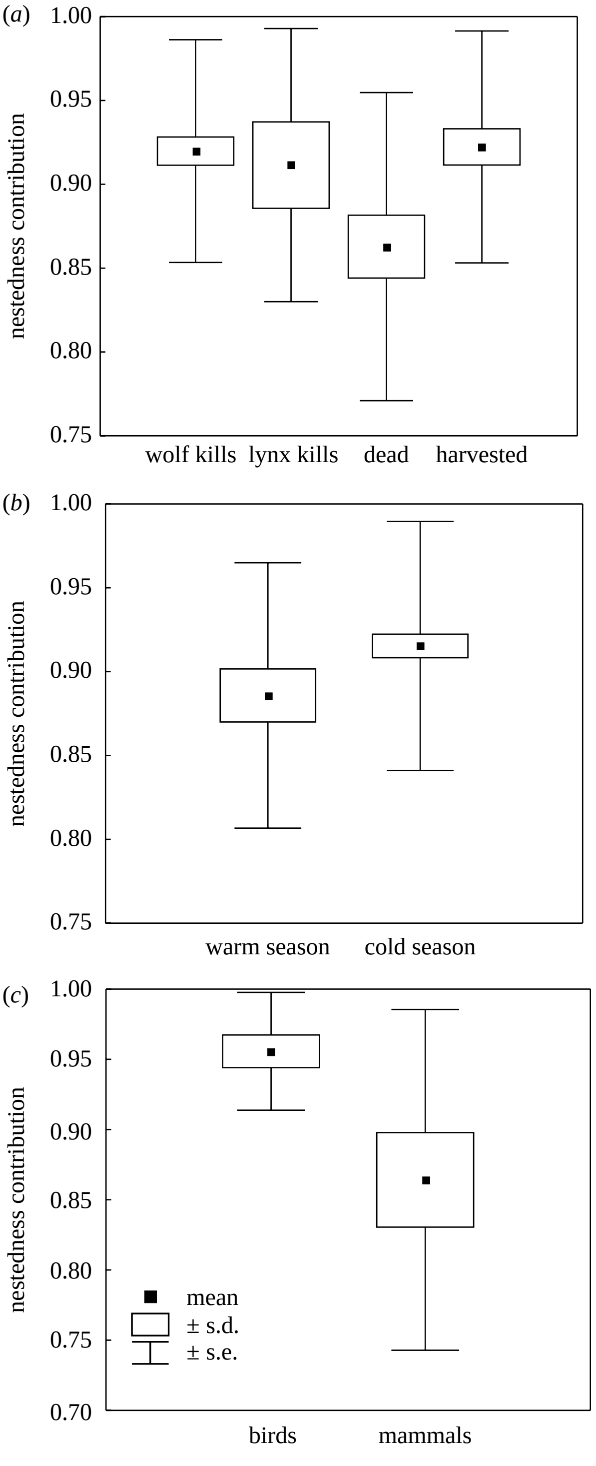


Figure 3. Contribution to the nestedness of the scavenger community (mean ± s.e., s.d.) of (*a*) different carcass types; (*b*) carcasses available in the cold versus warm season and (*c*) avian and mammalian scavengers.

There was a core set of species (main scavengers) feeding on the majority of the most visited carcasses, to which the less frequent scavengers (which tended to feed on the most visited carcasses) were attached. Carcasses receiving a low number of visits were scavenged by those species which visited most of the carcasses (figures 1 and 2).

Owing to the high level of nestedness of the real community, the idiosyncratic values (contribution to nestedness) of scavenger species and carcasses were also very high. The nestedness contribution varied among carcasses of different origin (Kruskal–Wallis one-way ANOVA, $H = 9.297$, $p < 0.05$; figure 3*a*). Kills of large predators and harvested ungulates contributed more to the nestedness of the community than dead ungulates. The dead ungulates were also the carcasses with the lowest number of species visiting them, thus occupying lower ranks in the nested matrix. Winter carcasses contributed more to the nested structure than those carcasses available in the warm season (figure 3*b*; Mann–Whitney *U*-test, $n_1 = 112$, $n_2 = 25$, $U = 1759$, $p < 0.05$). Carcasses available during the cold season also had a higher degree. The nestedness contribution of the carcasses was neither related to their biomass nor duration ($n = 137$, Spearman rank correlation $r_s = 0.13$, $p = 0.12$ and $r_s = 0.02$, $p = 0.85$, respectively). Carcass biomass and duration were correlated ($n = 137$, $r_s = 0.57$, $p < 0.0001$). The carcasses with higher rank order (top positions, lower row number) in the nested matrix (figure 2), and thus utilized by more species, were those with larger biomass ($n = 137$, $r_s = -0.34$, $p < 0.0001$) and available for longer periods ($n = 137$, $r_s = -0.23$, $p < 0.01$). The habitat where a carcass was located (forest versus open areas) did not influence its contribution to nestedness (Mann–Whitney *U*-test, $n_1 = 100$, $n_2 = 37$, $U = 1998.5$, $p = 0.47$).

Avian scavengers contributed significantly more to community nestedness than mammals (figure 3*c*, Mann–Whitney *U*-test, $n_1 = 13$, $n_2 = 13$, $U = 124$, $p < 0.05$). Additionally, the relationship between the nestedness contribution and the degree of scavengers showed a different pattern for birds and mammals. For avian scavengers, their high contribution was not significantly related to their degree (figure 4, $n = 13$, $r_s = -0.31$, $p = 0.31$). Thus, all birds contributed much to community nestedness independent of their scavenging frequency (figure 4). However, the nestedness contribution of mammals clearly decreased with higher degree of scavengers ($n = 13$, $r_s = -0.86$, $p < 0.001$, figure 4). In general, rare scavengers tended to be nested; however, idiosyncrasies were common among the main mammalian scavengers (figure 4). The frequency of carcass use by facultative scavengers did not reflect their relative abundance. The clearest example was the white-tailed eagle (*Haliaeetus albicilla*), which scavenged twice as much as the great tit (*Parus major*), a fourfold more common species (see Jedrzejewska & Jedrzejewski 1998 for density data).

4. DISCUSSION

The present study is the first attempt to characterize the architecture of carrion consumer–resource interactions using the concept of nestedness and represents an important step in disentangling the pattern of organization in a scavenger community. By analysing one of the most complete and current datasets existing in a pristine environment, we have unambiguously shown that the community of facultative scavengers in BPF is not randomly assembled but highly nested. The degree to which a community departs from a null model represents a quantitative measure of community structure. Therefore, our result reveals a highly structured pattern of resource use by carrion consumers and contradicts the conventional view of facultative scavenging as a random and opportunistic phenomenon (see review in DeVault *et al.* 2003). Species scavenging patterns and the factors that govern them are complex (Selva *et al.* 2003, 2005), but

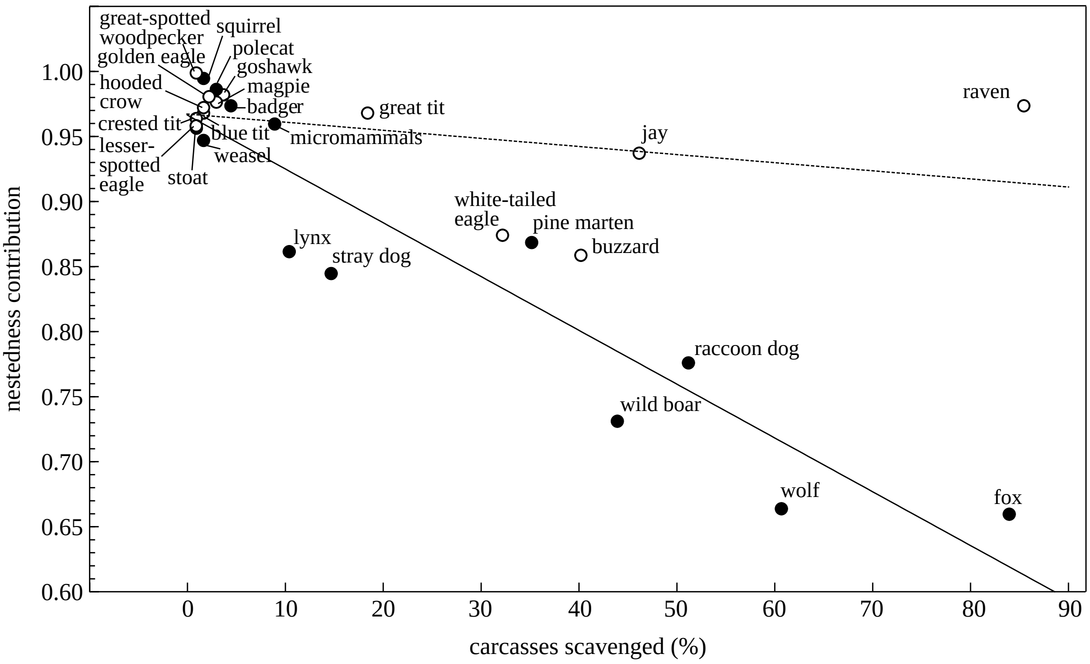


Figure 4. Relationship between the contribution to community nestedness of each scavenger species and its degree, shown as percentage of carcasses scavenged upon. The continuous line represents the correlation for mammals (filled circles) and the broken line for birds (open circles).

this complexity does not necessarily equal randomness or absence of pattern. Nestedness values significantly lower than those expected for a random matrix may suggest compartmentalization, a pattern indicative of antagonistic interactions and competition as the process structuring communities. The extremely high degree of nestedness of our dataset suggests that factors other than competition play a major role in determining community structure. Thus, it also questions the classical and long-debated idea of competition as the governing force structuring communities (e.g. Diamond 1975; Pianka 1980; Feeley 2003) and scavenger assemblages in particular (Kruuk 1967; Wallace & Temple 1987).

Following the network approach, nested communities have been described as highly cohesive and asymmetric (Bascompte *et al.* 2003; Bascompte & Jordano 2006; Guimaraes *et al.* 2006). Nestedness implies that there is a core of taxa with a high density of interactions. In plant–animal mutualistic networks, generalist species form a dense core, to which specialists are attached. Parallel, in the assemblage of facultative scavengers carrion-specialist species contained most interactions, i.e. exploited efficiently most carcasses, independently of the season or carcass type and, thus, built the network cohesively around them. Species well adapted to scavenge, like common ravens (*Corvus corax*) or red foxes (*Vulpes vulpes*), should be in fact ubiquitous, whereas those species more limited in their scavenging capacities, should occur in a subset of carcasses. Rare or sporadical scavengers tended to associate with the main scavenger species and to be missing from species-poor carcasses. Thus, non-specialist scavengers did not scavenge randomly, but on those carcasses where carrion specialists were present. Therefore, this nested structure was not related to passive sampling, species abundance or the high heterogeneity in the scavenger degree.

Birds, which are better adapted than mammals to a scavenger way of life, contributed more to the nested structure of the community. In fact, only birds have evolved into obligate scavengers in the recent past, and all scavenger assemblages regarded as structured in previous studies were formed by bird species (Kruuk 1967; Wallace & Temple 1987). Avian scavengers show morphological and behavioural adaptations for efficiently locating and exploiting carcasses, such as soaring flights, visual acuity, social foraging, recruitment to carcasses, information sharing or association with large predators (Houston 1979; Heinrich 1988; Heinrich *et al.* 1993; Stahler *et al.* 2002; Wilmers *et al.* 2003*a*; Wright *et al.* 2003; Ruxton & Houston 2004). Avian scavengers can travel fast, search very large areas while foraging and, thus, they can cope better with variations in the spatial and temporal distribution of carrion resources (Houston 1979; Wilmers *et al.* 2003*a*; Ruxton & Houston 2004; Selva *et al.* 2005). Conversely, mammals are more territorial and show an energetically more expensive locomotion. This limitation in their movements could prevent mammals from locating some carcasses, thus increasing the number of unexpected absences. That may be the case with some of the main mammalian scavengers in BPF, such as wolves or red foxes, which were idiosyncratic in their pattern of occurrence at carcasses. Competitive and facilitative interactions (Kruuk 1967; Houston 1979; Wallace & Temple 1987; Stahler *et al.* 2002; Selva *et al.* 2003, 2005; Wilmers *et al.* 2003*a*) may also be related to the differential pattern of nestedness contribution in birds and mammals.

The split into nested and idiosyncratic taxa in our study appears to relate to the differences not only in life-history strategies and adaptations for scavenging, but also in the relative importance of different carrion resources for each species. Rare scavengers showed, in general, a very high contribution to community nestedness, whereas some of the most frequent carrion consumers did not. Non-specialist scavengers tended to occur in species-rich carcasses, which corresponded to those of larger biomass and longer duration. Small or more ephemeral carcasses may be more difficult to be discovered by species that scavenge sporadically. These scavengers use ungulate carrion only in very critical moments of their lives, when forced by detrimental environmental conditions (e.g. lack of food, low temperatures). Common scavengers, which rely on carcasses for longer periods, are more efficient in exploiting most carcasses, even those of small size or available for very short periods. Thus, the heterogeneity of carcasses in their biomass and duration can be important in promoting nestedness. Carrion-specialist species have also developed preferences for some carcass types and avoidance for others (Selva *et al.* 2003; Wilmers *et al.* 2003*a*; Selva *et al.* 2005), a fact that could be related to the lower nestedness contribution of some main scavengers.

The carrion resources with the highest contributions to the nestedness of the community were those that were more predictable and consistent over time. Carcasses that were constantly supplied (ungulates killed by predators or men) contained most interactions and rare scavengers tended to occur at them. Constant resources may facilitate the appearance of adaptations for an efficient exploitation and may be used by many species, contributing to create structure in the community. However, species richness was lower at dead ungulates. They were visited by few scavengers, mainly by carrion specialists, better adapted to track this pulsed resource (Wilmers *et al.* 2003*a*; Selva *et al.* 2005). Habitat heterogeneity can prevent or promote the formation of nested subsets (Wright *et al.* 1998; Feeley 2003; Fischer & Lindenmayer 2005). In BPF, ungulate carcasses were randomly distributed; only harvested ungulates showed a slight spatial aggregation (Selva 2004). Although some scavengers were selective towards the habitat where the carcass was located (Selva *et al.* 2005), habitat heterogeneity did not seem to be related to nestedness.

The carrion supply is more abundant and predictable in the cold season (Selva 2004), and winter carcasses contributed significantly more to the nested structure of the scavenger community. Nestedness has been shown to be higher under stressful environmental conditions (Worthen *et al.* 1998; Baber *et al.* 2004; Cook *et al.* 2004). In the highly seasonal northern climates, winter is a period of food scarcity and harsh weather conditions, when carcasses represent a crucial food resource for the predator–scavenger community (Jedrzejewska & Jedrzejewski 1998; Selva *et al.* 2003, 2005). The assemblage of facultative scavengers in BPF was more structured in wintertime.

To sum up, the factors structuring nested subsets in scavenger communities can be viewed as filters that restrict the occurrence at carcasses of some species via characteristics of both the species and the carcasses (Wright *et al.* 1998; Cook *et al.* 2004; McAbendroth *et al.* 2004). The wide spectrum of carrion resource types, especially in relation to their temporal availability, and the gradient in carcass use by scavengers, determined by the differential adaptations and trophic needs of the species, may generate nestedness. This study may also shed light on the importance of trophic interactions via facultative scavenging.

We thank Jordi Bascompte, Pedro Jordano, Paulo Guimaraes, Christopher Wilmers and two anonymous referees for their excellent suggestions that greatly improved the clarity and accuracy of the paper. We also thank the Mammal Research Institute PAS staff and the Polish–Spanish Cooperation Programme for the support provided to N.S. during fieldwork. Declan O'Mahony kindly revised the English language. N.S. is greatly indebted to Emily Nicholson for literature-searching facilities. During this work, M.A.F. was funded by the Spanish Ministry of Education and Science (fellowship BES-2004-6682).

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