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Scavenging in changing environments: woody encroachment shapes rural scavenger assemblages in Europe

Pilar Oliva-Vidal, Esther Sebastián-González and Antoni Margalida

P. Oliva-Vidal (https://orcid.org/0000-0001-6986-9562) ✉ (pilar_olivavidal@hotmail.com) and A. Margalida, Inst. for Game and Wildlife Research, IREC (CSIC-UCLM-JCCM), Ciudad Real, Spain. PO-V also at: Dept of Animal Science, Faculty of Life Sciences and Engineering, Univ. of Lleida, Lleida, Spain. – E. Sebastián-González (https://orcid.org/0000-0001-7229-1845), Dept of Ecology, Univ. of Alicante, Alicante, Spain. AM also at: Pyrenean Inst. of Ecology (CSIC), Jaca, Spain.

Rural abandonment and subsequent vegetation regeneration ('passive rewilding') are expected to increase worldwide, producing cascades of dynamic socioeconomic, landscape and biological changes. Although landscape characteristics strongly influence the structure and functioning of scavengers, little is known about the ecological consequences of passive rewilding due to woody encroachment (i.e. 'landscape closure') on scavenging assemblages. We investigated differences in 'scavenger assemblage composition' (species richness and abundances) and 'scavenging efficiency' (scavenging frequency, detection and consumption times and consumption rates) in a mountain agroecosystem (Pyrenees) undergoing passive rewilding. We monitored 178 carcasses in three landscapes: 'open', 'shrubland' and 'forest', and evaluated the effects of landscape type on 'scavenger assemblage composition' and 'scavenging efficiency' at the community and species levels, while accounting for the influences of carcass size, type and placement time. We also examined whether the locally most abundant and efficient scavenger (i.e. the griffon vulture *Gyps fulvus*) affects scavenging patterns. We found that landscape type was the main factor governing scavenging dynamics. Overall and average scavenger richness were similar in open and shrubland landscapes, while forests contained the lowest number of scavengers, mainly comprising mammals. Unlike mammals, avian scavenging frequency decreased as vegetation cover increased, especially for obligate scavengers (i.e. vultures). Scavenger abundances were highest in open landscapes, and carcasses were detected and consumed more rapidly in these landscapes. Carcass size did not influence detection and consumption times, although it did affect average scavenger richness, abundances and consumption rates. Consumption rates were higher in open landscapes and were strongly associated with the presence of griffon vultures. Interestingly, we found that griffon vultures influenced scavenging dynamics via facilitation processes. However, woody encroachment could reduce the scavenging role of this species, while favoring mammalian facultative scavengers. Finally, our findings highlight the pivotal role of griffon vultures, mediated by landscape characteristics, in reducing carcass persistence.

Keywords: agropastoral landscapes, carrion, farmland abandonment, passive rewilding, Pyrenees, rural abandonment, scavengers, vultures

Introduction

Rural Europe has been shaped by traditional land-use and encompasses a wide diversity of cultural landscapes, especially in mountain regions (Tieskens et al. 2017). European mountain landscapes are the result of several thousand years of interactions between people and agroecosystems and deliver valuable ecosystem services (Bernués et al. 2014), often with exceptional conservation value (Fisher et al. 2012). Over the centuries, agro-livestock practices have promoted biodiversity by preserving high spatial heterogeneity within forest–agricultural mosaic landscapes (Fahrig et al. 2011). However, socioeconomic changes during the 19th and 20th centuries have led to widespread abandonment of rural areas and the loss of landscape heterogeneity, posing major scientific and policy challenges due to the crucial role of traditional farming for biodiversity and ecosystem service maintenance (MacDonald et al. 2000, Plieninger 2006, Cramer et al. 2008, Lasanta et al. 2017, Ustaoglu and Collier 2018). Understanding the ecological consequences of rural abandonment for ecosystem dynamics is key to the design of biodiversity conservation strategies in such areas.

As in most European mountain regions, important landscape changes occurred in the Spanish Pyrenees during the mid-20th century due to rural depopulation and agricultural modernization (Lasanta-Martínez et al. 2005). Traditional livestock farming systems intensified during this period, resulting in a severe decline in sheep numbers and an increase in cattle. Some valleys in this region saw sheep numbers decline by more than 80%, drastically reducing grazing pressure (Lasanta-Martínez et al. 2005) and livestock biomass over large areas (Margalida et al. 2018). This trend is widespread across Europe, where extensive livestock numbers declined by 25% between 1990 and 2010 (Navarro and Pereira 2015). Furthermore, the 'transhumance', a seasonal livestock (mainly sheep) migration – usually across long distances – between winter and summer pastures, is in strong decline (García-Ruiz et al. 2020a). Nowadays, livestock are kept in the valleys during the cold season and moved to adjacent pastures during the summer (i.e. 'transtermitance'). This drastic decline in sheep numbers has caused a significant reduction of livestock pressure, accelerating the processes of vegetation succession, especially in marginal areas (García-Ruiz et al. 2020a). These changes have been characterized by generalized farmland abandonment and subsequent vegetation encroachment, modifying the long-standing forest-agricultural mosaic, reducing the extent of open spaces and increasing the extent of woody landscapes (Poyatos et al. 2003, Lasanta-Martínez et al. 2005, Roura-Pascual et al. 2005, Améztegui et al. 2010). The result is passive landscape restoration, or 'passive rewilding', by natural shrub and tree colonization ('landscape closure'), driving important changes in habitat structure and landscape configuration (Pereira and Navarro 2015, Corlett 2016, Perino et al. 2019).

Although active rewilding has recently been proposed as a conservation strategy to restore the loss of biodiversity and ecosystem functions (Pereira and Navarro 2015), there is ongoing debate regarding the associated impacts on species diversity and community dynamics (Queiroz et al. 2014, Nogués-Bravo et al. 2016, García-Ruiz et al. 2020b). For example, depopulation and agricultural abandonment in rural areas of Japan have posed major conservation challenges owing to changes in species distribution, resulting in increased human–wildlife conflicts (Tsunoda and Enari 2020) and plant encroachment has been associated with losses of mesocarnivore scavenging efficiency in tropical-grassy African savannas (Lima et al. 2021). In Europe, much attention has focused on how natural revegetation leads to an expansion of forest species (Falcucci et al. 2006, Acevedo et al. 2011, Martínez-Abraín et al. 2020), but the effects on species adapted to open-habitats or mountain agro-pastoral landscapes remain poorly understood (Laiolo et al. 2004, Regós et al. 2014). There is therefore a need to identify the ecological impacts of rewilding, and the resulting changes in landscape configuration, on functional assemblages linked to traditional mountain landscapes. Scavengers (i.e. carrion-eating species), form one such important assemblages. Understanding how scavenger assemblages function in different landscape configurations differing in vegetation structure is critical to inform management priorities dealing with passive rewilding.

Despite the essential role of scavengers in providing regulatory services by efficiently removing carrion from ecosystems (Moleón et al. 2014, DeVault et al. 2016), the effects of rewilding or other changes in habitat configuration on scavenging dynamics have not been extensively investigated (but see Cortés-Avizanda et al. 2015, García-Barón et al. 2018, van Klink et al. 2020). For example, Arrondo et al. (2019) found that in mountainous areas of south-east Spain, sheep carcasses in open pasturelands were detected and consumed faster than wild ungulate carcasses in more heterogeneous areas. Thus, partially abandoned mountain agroecosystems inhabited by both facultative scavengers (species that scavenge opportunistically, e.g. mammalian carnivores, raptors and corvids) and obligate scavengers (species that depend totally on carrion, i.e. vultures) present an ideal opportunity to improve our understanding of how vegetation encroachment affects scavenging dynamics.

Carrion occurs unpredictably in time and space, and provides an ephemeral, valuable food resource. It has high nutritional value and is generally rapidly consumed following the multiple complex interactions that structure scavenger communities and stabilize food webs (Wilson and Wolkovich 2011, Moreno-Opo et al. 2016, Sebastián-González et al. 2020). However, vegetation cover and structure may influence the ability of scavengers to locate and access carcasses, affecting consumption patterns and efficiency (Selva et al. 2005, Moleón et al. 2019, Pardo-Barquín et al. 2019). An increase in shrub and forest cover may favor carcass detection by scavengers that mainly use odor cues to locate food, such as mammals (DeVault and Rhodes 2002, Enari and Enari 2021), to the detriment of avian scavengers that mainly rely on visual cues, such as Old World vultures (Ruxton and Houston 2004).

To better understand these dynamics, we monitored a large number of carcasses (> 170) of several types and sizes, representing the widest carrion diversity appearing in a mountain agroecosystem in which the four European vulture species coexist with important facultative scavenger populations. Our main goal was to describe the 'scavenger assemblage composition' (species richness and abundances) and 'scavenging efficiency' (scavenging frequency, detection and consumption times and consumption rates) at both the community and species levels in three landscape types ('open'; semi-closed or 'shrubland'; and closed or 'forest') where passive rewilding processes occur. We also evaluated whether carcass size, type (herbivore/carnivore) and placement time (morning/afternoon) influenced carcass consumption patterns.

Our general hypothesis was that landscape type, carcass size and type, and placement time influence both scavenger assemblage composition and scavenging efficiency. We predicted: 1) that carcasses placed in open areas would be detected and exploited more rapidly, mainly by avian scavengers (i.e. species relying on sight for carcass detection), than those placed in shrublands and forests, which would mainly be consumed by mammals (i.e. species relying on scent for carcass detection); 2) that herbivore carcasses would show higher scavenger species richness, abundance and consumption rates, as carnivore carcasses are known to be avoided by carnivores (Moleón et al. 2017); 3) that carcasses deployed in the morning would be exploited faster, since the more efficient vultures are inactive at night; 4) that larger carcasses would be consumed at a faster rate and by a richer and more abundant scavenger assemblage than small ones, as found by Moleón et al. (2015) in African assemblages; and 5) that consumption by griffon vultures would influence the composition and efficiency of the scavenger assemblage, as this species is known to have higher consumption rates and to facilitate carrion location (Cortés-Avizanda et al. 2014). Our research provides a novel approach to the study of the effects of passive rewilding and 'landscape closure' on scavenging dynamics in mountain landscapes.

Material and methods

Study area

The Pyrenees is a mountain range extending over more than 50 000 km² in the north-east of the Iberian Peninsula. The study area is on the southern slope and covers around 170 000 ha. This area is characterized by a wide range of altitudes (from ~500 to > 3000 m a.s.l.) and shows significant climatic variation, which offers contrasting landscapes and great vegetational diversity. In the cultivated lands of the lower valleys (< 700 m a.s.l.), Mediterranean shrubland and mixed woodlands of oak *Quercus ilex*, *Q. faginea* and Scots pine *Pinus sylvestris* predominate. Montane forest zones occur at the middle altitudes (700–1600 m a.s.l.), mainly dominated by Scots pine, European beech *Fagus sylvatica* and a wide variety of scrublands, open grasslands and pasturelands. In the upper mountain areas (1600–1800 m a.s.l. upwards), mountain pines *Pinus uncinata* are abundant, and above the treeline (2300 m a.s.l.), a mosaic of different types of alpine pastures dominate (Ninot et al. 2007). Historically, these landscapes have been shaped by human activity (e.g. long-term use for crops, livestock and forestry created an increase in open areas at the expense of forest, Roura et al. 2005) but more recent rural abandonment and shepherding decline have led to an increase in natural vegetation cover in previously open areas .

Extensive and semi-extensively reared livestock (cattle, sheep and horses) provide most of the biomass for the scavenger guild (Colomer et al. 2011). Extensive livestock are kept outdoors from April to October, depending on the weather conditions, and some transhumant herds migrate to high summer pastures. Important populations of wild herbivorous ungulates, mainly red deer *Cervus elaphus*, roe deer *Capreolus capreolus*, Pyrenean chamois *Rupicapra pyrenaica* and fallow deer *Dama dama* are present. Of the obligate scavengers within a 30 km radius of the central study area, almost 900 pairs of griffon, 16 pairs of cinereous *Aegypius monachus*, 21 pairs of bearded *Gypaetus barbatus* and 50 pairs of Egyptian vultures *Neophron percnopterus* breed in the area. Regarding facultative scavengers, the study area holds a rich community of avian (e.g. corvids and raptors) and mammal species, while shepherd and free-ranging hunting dogs are also frequent (Supporting information).

Carcass monitoring

From October 2017 to August 2019, we monitored 178 carcasses (herbivores, n = 154; carnivores, n = 24) of different species ranging in size from 1 to 100 kg, placed across three landscape types (open, n = 70; shrubland, n = 71; and forest, n = 37). Herbivore carcasses consisted of sheep/goat *Ovis aries*/*Capra hircus* (n = 60, mean ± SD = 47.65 ± 12.53 kg, including lambs/kids: n = 31, 9.34 ± 6.33 kg); wild boar *Sus scrofa* (n = 40, 53.20 ± 22.47 kg); roe deer (n = 8, 22.04 ± 3.60 kg); and European rabbit *Oryctolagus cuniculus* (n = 15, 1.48 ± 0.29 kg). Carnivore carcasses (mean weight ± SD = 5.71 ± 3.14 kg) consisted of red fox *Vulpes vulpes* (n = 6), European badger *Meles meles* (n = 9), stone marten *Martes foina* (n = 2) and domestic cat *Felis catus* (n = 7). Carcasses were placed between 600 and 1750 m a.s.l. (i.e. the mountain sectors where passive rewilding is widespread, García-Ruiz and Lasanta 1990), and were randomly distributed among the three landscape types over all altitudes. We selected each landscape type according to the vegetation cover within a 25 m radius from the center of the carcass (Supporting information). For open landscapes, we chose large open areas (e.g. grasslands) without shrub/tree cover (i.e. shrub and tree cover < 5%) (Fig. 1A–D). For shrublands, we selected sites with abundant vegetation cover (i.e. shrub and tree cover ranging 50–70%), mainly large (e.g. *Buxus sempervirens* and *Juniperus* sp.) and medium-size shrub species (e.g. *Genista scorpius* and *Rosa* sp.), or dispersed trees (mainly oak species) (Fig. 1E–G). Regarding forest landscapes, we placed carcasses in mature pine and beech forests with moderate canopy closure (i.e.
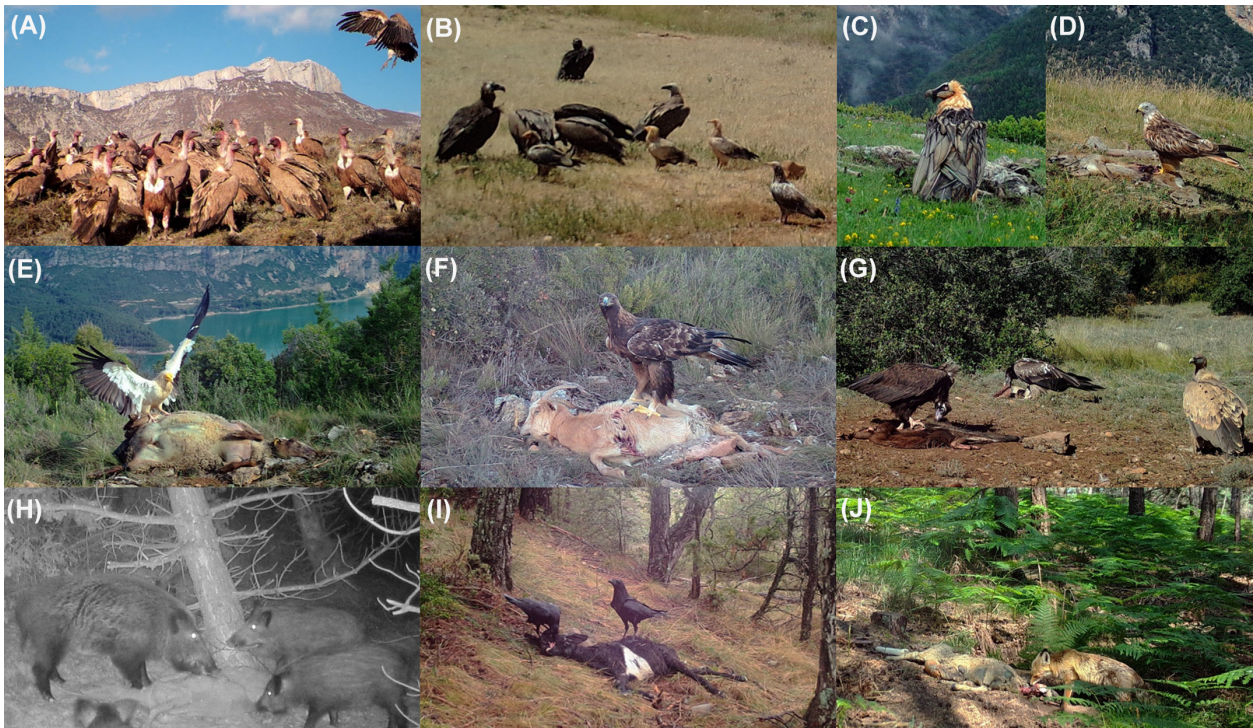
Figure 1. Images of some of the most frequent scavengers recorded in the three landscape types studied: 'open' (A–D), 'shrubland' (E–G) and 'forest' (H–J). (A) Griffon vultures *Gyps fulvus*, (B) cinereous *Aegypius monachus*, Egyptian *Neophron percnopterus* and griffon vultures, (C) bearded vulture *Gypaetus barbatus*, (D) red kite *Milvus milvus*, (E) Egyptian vulture, (F) golden eagle *Aquila chrysaetos*, (G) cinereous, bearded and griffon vultures, (H) wild boars *Sus scrofa*, (I) common ravens *Corvus corax* and (J) red fox *Vulpes vulpes*.

tree cover > 90%), allowing some visibility of the forest floor (Fig. 1H–J). Most carcasses in shrublands and forests were placed in areas where there was historical evidence of rewilding, e.g. from open landscapes to shrublands, or from shrublands to forests. Scavenging activity was recorded at all carcasses except for one stone marten placed in a shrubland. Carcasses were obtained from legal farms and slaughterhouses or collected as road kills.

Carcasses were monitored using Moultrie motion-triggered remote cameras (M-990i 10MP, M-999i 20MP and S-50i 20MP). Cameras were attached to a tree close to the carcasses (5–10 m away) and were programmed to take three consecutive photos when movement was detected, with a one-second delay between photos, and a delay of 15 s before the next set of photos. Carcasses were weighed and fixed to the ground using inconspicuous iron stakes to prevent scavengers moving them away from the camera focus. Carcasses were placed at random between dawn and dusk and separated by at least 1 km to maximize independence (Morales-Reyes et al. 2017). Once a carcass was consumed, we waited at least one month before placing another carcass closer than 1 km from the previous placement. A species was considered a 'consumer' when it was clearly recorded feeding on a carcass. When consumption was suspected, but not clearly recorded, we assumed consumption if that species had already been detected consuming another carcass (Sebastián-González et al. 2019). Carcasses were monitored continuously (24 h day^{-1}) until scavenging ended (i.e. only

bones and/or skin remained) or the carcass was removed by a scavenger.

Scavenging measures

For each landscape type, we calculated the following variables relating to scavenger assemblage composition: 1) 'total richness' (number of vertebrate scavenger species recorded at all carcasses) and 2) 'richness' (number of vertebrate scavenger species per carcass). Richness was calculated individually for each species and also for birds and mammals separately. For some analyses we grouped scavengers by 'taxon' (avian or mammalian) and as 'obligate' or 'facultative', or at the species level. We also recorded 3) the 'abundance' (maximum number of unequivocally different individuals of each species per carcass). This was calculated by counting the highest number of individuals appearing simultaneously in a picture, and by differentiating individuals of different age, sex or individual features (Sebastián-González et al. 2019). Regarding scavenging efficiency (i.e. carcass location and consumption ability), we first calculated the scavenging frequency (i.e. percentage of consumed carcasses) for each species in each landscape type. Then, for each carcass and landscape type we estimated: 1) 'detection time' (time elapsed in hours between carcass placement and the arrival of the first scavenger), and separately for birds and mammals; 2) 'total consumption time' (time elapsed in hours between carcass placement and its complete consumption); 3) 'active consumption time'

(time elapsed in hours between start of carcass consumption and its complete consumption); and 4) 'consumption rate' (kilograms of carrion biomass consumed divided by carcass consumption time). To calculate consumption rates, we excluded the carcass stomach contents and the unconsumed parts from the carcass weight, so that the consumed biomass was calculated as: (initial weight of the carcass) − (weight of unconsumed remains) − (weight of stomach contents). Unconsumed remains were weighed at the end of each trial (Moleón et al. 2015) and stomach contents were estimated as 10% of the animal weight (Selva et al. 2004).

Statistical analyses

We investigated factors affecting scavenger assemblage composition and scavenging efficiency by fitting generalized linear models (GLMs), where 'richness', 'avian/mammalian richness', 'abundance', 'detection time', 'total and active consumption time' and 'consumption rate' were the response variables; and 'landscape type' ('open', 'shrubland', 'forest'), 'carcass type' (herbivore or carnivore), 'placement time' (morning, from dawn to midday; afternoon, from midday to dusk) and 'carcass weight' (kg) were predictors. We also used the 'taxon' (avian or mammalian) of the first detector as a categorical predictor to test for differences in carcass detection time using univariate (i.e. single-predictor variable) GLMs, where 'detection time' (hours) was the response variable. We used Poisson error distributions and log link functions to model 'richness'; negative binomial error distributions and log link functions for 'abundance'; and Gaussian error distributions and identity link functions for 'detection time', 'total and active consumption times' and 'consumption rate', in all analyses. 'Detection time', 'consumption times' and 'consumption rate' were log-transformed to improve normality assumptions. We compared the unconsumed remains (i.e. skin and skeletal remains, in kg) of medium-size ungulates among landscape types using the Kruskal–Wallis test.

We also performed GLMs at the species level to investigate factors influencing scavenging frequency according to the same predictors: 'landscape type', 'carcass type', 'placement time' and 'carcass weight', using a binomial error distribution. For each species, we only used the presence/absence matrix of those landscapes in which the consumption of at least one carcass was detected. We fitted models with all possible combinations and subsets of the predictor variables. We selected the model with the lowest AICc, but when there was more than one model with a ΔAICc < 2 relative to the best model, we used a model-averaging function in the 'MuMIn' package (Barton 2013). This function averages parameter estimates across all considered models for each dependent variable where the respective parameter appeared, weighted by the relative importance of each model. We also calculated the percentage of deviance explained (i.e. the amount of variability explained) of each model. Finally, because one of our goals was to evaluate whether the presence of griffon vultures at carcasses could affect scavenging dynamics, we evaluated the relationship between all the composition and efficiency variables and the presence of griffon vultures using single-predictor GLMs with a binomial error distribution. We checked the model assumptions using statistical tests for normality and homogeneity of variance, and the fit of all models was visually inspected using residual versus fitted values and Q–Q plots. All analyses were performed using R ver. 3.6.1 (<www.r-project.org>).

Results

Differences in scavenger assemblage composition

We analyzed 286 572 photos and detected 19 vertebrate scavenger species (Supporting information). Total species richness in open and shrubland landscapes was similar (18 and 17 species, respectively), including the four European vultures, while forests showed the lowest scavenger richness (nine species) (Table 1). Mean scavenger richness was dependent on landscape type (open > shrubland > forest, Table 1) although GLM analyses revealed that it was only significantly lower in forests and that it increased with carcass size (Table 2, Supporting information). Mean avian species richness was slightly higher in open landscapes compared with shrublands, and up to eight times higher compared with forests, and also increased with carcass size. In contrast, mean mammalian richness only increased with carcass size (Table 1, 2, Supporting information). Placement time and carcass type did not influence scavenger richness (Table 2).

Table 1. Measures of scavenger assemblage composition recorded in each landscape type: total scavenger richness, scavenger richness, avian and mammalian scavenger richness and scavenger abundance per carcass. Values represent the mean ± standard deviation and range. The number of obligate and facultative avian and mammalian species and the number of carcasses monitored are shown.

	Open	Shrubland	Forest	Total
Total richness	18	17	9	19
Richness	4.70 ± 1.75 [1–9]	3.97 ± 1.88 [0–8]	2.65 ± 1.25 [1–7]	
Avian richness	2.77 ± 1.36 [0–5]	1.90 ± 1.47 [0–6]	0.35 ± 0.67 [0–3]	
Mammal richness	1.93 ± 1.04 [0–5]	2.07 ± 0.85 [0–4]	2.30 ± 0.94 [1–4]	
Scavenger abundance	51.5 ± 37.7 [2–124]	28.2 ± 24.8 [0–89]	4.3 ± 2.7 [1–12]	
Avian species	12	11	4	13
Mammal species	6	6	5	6
Obligate scavengers	4	4	1	4
Facultative scavengers	14	13	8	15
Number of carcasses	70	71	37	178

Table 2. Models (GLMs) used to assess the effect of landscape type ('open', 'shrubland' and 'forest'), carcass weight (kg), carcass type (herbivore and carnivore) and placement time (morning and afternoon) on the composition of scavenger assemblages (scavenger richness, avian and mammalian species richness, scavenger abundance) and scavenging efficiency (carcass detection time, consumption times and consumption rate). We present the model-averaged coefficients and standard error (SE) for models with AICc < 2. Significant p-values (< 0.05) are highlighted in bold. The percentage of explained deviance of the model (i.e. percentage of the variability explained by each model 'D²') is shown.

Response variable	Model	Coefficient	SE	p-value	D²
Scavenger richness	Open	0.133	0.082	0.105	**40%**
	Forest	−0.311	0.118	**0.009**	
	Carcass weight	0.224	0.039	**< 0.001**	
	Carcass type (herbivore)	−0.109	0.133	0.417	
	Placement (afternoon)	0.128	0.098	0.195	
Avian richness	Open	0.325	0.113	**0.003**	**43.1%**
	Forest	−1.562	0.291	**< 0.001**	
	Carcass weight	0.308	0.054	**< 0.001**	
	Carcass type (herbivore)	−0.076	0.202	0.707	
Mammalian richness	Open	−0.105	0.120	0.383	**13.1%**
	Forest	0.159	0.138	0.251	
	Carcass weight	0.121	0.053	**0.024**	
	Placement (afternoon)	0.220	0.137	0.110	
Scavenger abundance	Open	0.489	0.115	**< 0.001**	**65.1%**
	Forest	−1.461	0.158	**< 0.001**	
	Carcass weight	0.636	0.060	**< 0.001**	
	Carcass type (herbivore)	0.259	0.179	0.150	
	Placement (afternoon)	0.184	0.131	0.162	
Detection time	Open	−0.852	0.297	**0.004**	**15.4%**
	Forest	0.725	0.358	**0.04**	
	Carcass weight	−0.183	0.136	0.182	
	Carcass type (herbivore)	−0.356	0.407	0.385	
	Placement (afternoon)	0.989	0.321	**0.002**	
Total consumption time	Open	−1.306	0.281	**< 0.001**	**31.3%**
	Forest	1.221	0.338	**< 0.001**	
	Carcass type (herbivore)	−1.190	0.366	**0.001**	
	Placement (afternoon)	1.176	0.300	**< 0.001**	
Active consumption time	Open	−1.761	0.396	**< 0.001**	**31.7%**
	Forest	1.772	0.479	**< 0.001**	
	Carcass weight	0.206	0.202	0.311	
	Carcass type (herbivore)	−2.023	0.552	**< 0.001**	
	Placement (afternoon)	1.570	0.427	**< 0.001**	
Consumption rate	Open	1.270	0.299	**< 0.001**	**49.7%**
	Forest	−1.178	0.363	**0.001**	
	Carcass weight	1.112	0.152	**< 0.001**	
	Carcass type (herbivore)	1.350	0.433	**0.002**	
	Placement (afternoon)	−1.020	0.330	**0.002**	

Mean scavenger abundance was almost double in open compared with shrubland landscapes, and up to 12 times higher compared with forests (Table 1). It increased with carcass size but was not affected by placement time or carcass type (Table 2, Supporting information). The most abundant avian scavengers were griffon vultures, followed by *Corvus* spp. and Egyptian vultures. Wild boars, domestic dogs and red foxes were the most abundant mammals (Supporting information).

Differences in scavenger efficiency

Avian and mammalian scavenging frequency showed clear differences according to landscape type and carcass size (Fig. 2). Birds scavenged at 91.4, 73.1 and 27% whereas mammals scavenged at 90, 97.2 and 100% of the carcasses in open, shrubland and forest landscapes, respectively. Obligate scavengers, except for the Egyptian vulture, consumed carrion significantly more frequently in open landscapes than in shrublands (Fig. 2, Supporting information). Griffon vultures were the most frequent scavenger, followed by bearded, Egyptian and cinereous vultures (Fig. 2). Facultative avian scavenging frequency did not differ between open and shrubland landscapes, except for the red kite *Milvus milvus* (Supporting information). Ravens *Corvus corax* and golden eagles *Aquila chrysaetos* were the most frequent facultative avian scavengers (Fig. 2). Only ravens, Eurasian jays *Garrulus glandarius*, golden eagles and griffon vultures consumed carcasses within forests (Fig. 2). Mammals scavenged carcasses in all landscapes to a similar extent, except for the wild boar and *Martes* spp. (Fig. 2, Supporting information). Foxes and wild boars were the most frequent mammalian scavengers. GLMs confirmed that, except for the Egyptian vulture, kites
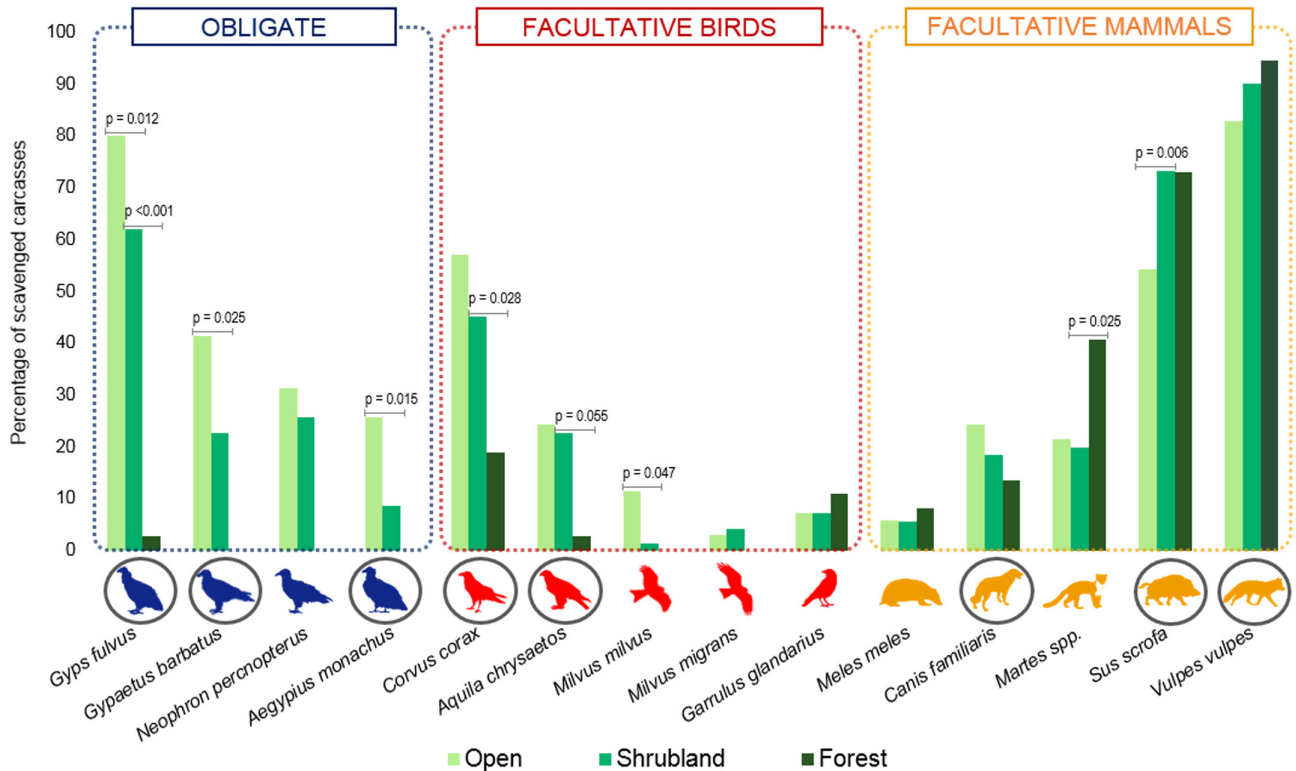
Figure 2. Scavenging frequency (percentage of consumed carcasses) of the main vertebrate scavengers recorded in each landscape type. Significant p-values among landscape types and significant effect (circles) of carcass size (i.e. preference for large carcasses, Supporting information) are shown for each species. Obligate (blue square), avian facultative (red square) and mammalian facultative (orange square) scavengers are shown.

Milvus spp., badger and *Martes* spp., species visited carcasses more frequently as carcass size increased (Fig. 2, Supporting information).

Landscape type influenced both the main carcass detector species (Fig. 3) and detection time (open < shrubland < forest, Table 2, 3). Carcasses were detected faster in open landscapes, while detection times increased significantly in shrublands and forests. Carcasses placed in the morning were detected more rapidly, while carcass size and type did not influence detection time (Table 2). In all landscapes, birds detected carcasses significantly faster than mammals (Fig. 4, Supporting information), although birds discovered only four carcasses within forests. Mean total consumption time was 2.5 times faster in open than shrubland landscapes, and up to five times faster than in forests (Table 3). Regarding carcass type, herbivore carcasses were consumed more rapidly than carnivore carcasses (Table 2). In addition, carcasses placed during the morning were exploited faster, while carcass size did not influence consumption times (Table 2). Active consumption time showed a similar pattern to that of total consumption time (Table 2 and 3). Consumption rate was three times higher in open than in shrubland landscapes, and up to 12 times higher than in forests (Table 3). It increased with carcass size and was higher for herbivore than for carnivore carcasses, decreasing when carcasses were placed in the afternoon (Table 2, Supporting information). The percentage

of unconsumed parts of medium-sized ungulates (n = 82, mean ± SD = 51.03 ± 17.8 kg) was less in open (8.1%) than shrubland (10.6%) and forest (14.6%) landscapes (Kruskal–Wallis test, $\chi^2_2 = 10.9$, p < 0.05).

The influence of griffon vultures on scavenging dynamics

GLMs revealed that griffon vultures influenced the scavenger assemblage composition and scavenging efficiency (Fig. 5, Supporting information). Scavenger richness, avian richness and abundance per carcass were higher when griffon vultures consumed them, although this did not influence mammalian richness. Both birds and mammals arrived faster at carcasses when griffon vultures exploited them. Consumption times decreased when griffon vultures were among the consumers of a carcass (80 versus 362 h with and without the participation of griffon vultures, respectively) and consumption rates were notably higher (7.6 versus 0.06 kg h^{-1} with and without the participation of griffon vultures, respectively).

Discussion

Allowing passive rewilding has been recognized as a novel conservation strategy in abandoned European agricultural
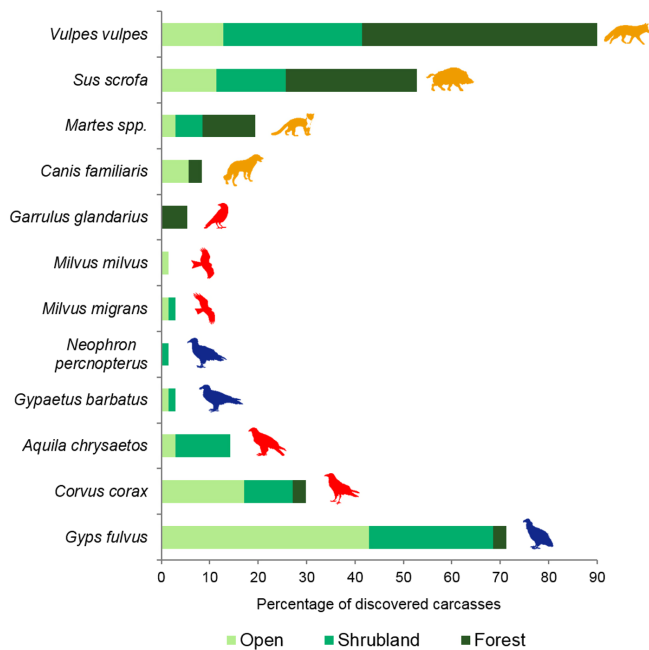
Figure 3. Main carcass detector species (%) in each landscape type. Avian scavengers were the main detectors in open landscapes (44.3% by obligate and 22.9% by facultative species). Both birds (51.4%) and mammals (48.6%) discovered carcasses in shrublands to a similar extent, while mammals were the main detectors (89.2%) in forest landscapes. Griffon vultures *Gyps fulvus* and red foxes *Vulpes vulpes* were the main detectors in open and forest landscapes, respectively. The percentages were calculated on the basis of carcasses monitored in each landscape type.

landscapes, where it is estimated that between 2000 and 2030, up to 20 million ha may have been released from agricultural use (Pereira and Navarro 2015). Rewilding processes may increase carrion availability due to the expansion and increased abundance of wild ungulates (Acevedo et al. 2011), but little is known about the effects of passive rewilding on vertebrate scavenging communities (Mateo-Tomás et al. 2015). Previous studies have highlighted habitat type as an important factor influencing carcass utilization (Arrondo et al. 2019, Pardo-Barquín et al. 2019, Stiegler et al. 2020). However, this study is the first to assess the effects of woody encroachment or 'landscape closure' due to farmland abandonment and undergrazing on the functioning of scavenging guilds in mountain agroecosystems.

Our findings indicate that landscape type is a major factor influencing scavenger assemblage composition and scavenging efficiency. However, carcass size and the presence of griffon vultures also modulated the functioning of scavenging assemblages. Carcasses were more frequently visited by avian scavengers in open landscapes, while in shrub and forest landscapes mammals dominated at carcasses. In addition, open landscapes were associated with higher scavenger abundances, faster carcass detection and consumption times and higher consumption rates, and favored rapid carcass location and more efficient consumption by griffon vultures. We found that carcass size influenced the composition of scavenger assemblages (i.e. higher scavenger richness and abundance at larger carcasses). However, regarding scavenging efficiency, carcass size only affected carcass consumption rates (i.e. carcasses with larger biomass were consumed more rapidly), suggesting that landscape type is the main factor determining carrion discovery and consumption times in agroecosystems inhabited by both obligate and facultative scavengers .

Contrary to our expectations, we detected a similar number of obligate and facultative scavenger species in open and shrubland landscapes. Furthermore, the mean number of species per carcass was similar in both. These results differ from those of Arrondo et al. (2019), who found that sheep carcasses in open areas were visited by fewer species but showed higher mean scavenger richness than wild ungulates placed in more heterogeneous sites. This discrepancy could be related to the wide diversity of carcass types we monitored. The provision of more carcass sizes/types may result in greater carrion exploitation by scavenger assemblages. For example, we detected higher scavenger species in both open and shrubland landscapes compared with those recorded in previous studies (Arrondo et al. 2019). We also found higher average avian richness in open landscapes, which could be related to the high scavenging frequency of griffon vultures and ravens at these carcasses, since these species could indicate the location of food to other scavenging birds (Cortés-Avizanda et al. 2012, Orr et al. 2019). On the contrary, our results demonstrate that carcasses within forests were consumed by fewer species, mainly mammals as has been reported in other temperate forests (Inagaki et al. 2019, Pardo-Barquín et al. 2019, Tobajas et al. 2022).

The adaptive abilities of scavengers to locate and exploit carrion (i.e. visual/olfactory abilities, capacity to break into carcasses and foraging behavior), determine carcass detection and utilization (Selva et al. 2005). Our findings revealed that birds found carcasses faster than mammals across all landscape types studied. This is probably because birds are generally better adapted to locating food because they can fly and

Table 3. Scavenging efficiency measures recorded in each landscape type: overall detection time (h), avian and mammalian detection time (h), total and active consumption time (h) and consumption rate (kg h^{-1}) per carcass. Values represent the mean $\pm$ standard deviation and range.

| Landscape	Detect. time	Avian detect. time	Mammalian detect. time	Total consum. time	Active consum. time	Consum. rate
Open	21.90 $\pm$ 29.54 (0.02–182.13)	15.4 $\pm$ 19.17 (0.02–70.80)	34.91 $\pm$ 40.99 (0.16–182.13)	80.91 $\pm$ 152.55 (0.22–945.56)	59.0 $\pm$ 143.94 (0.10–945.27)	7.89 $\pm$ 16.27 (0.004–82.12)
Shrubland	43.20 $\pm$ 63.25 (0.10–394.46)	24.56 $\pm$ 37.34 (0.1–189.18)	53.93 $\pm$ 52.70 (1.87–241.67)	207.12 $\pm$ 274.40 (0.90–1234.16)	163.93 $\pm$ 244.0 (0.13–1044.98)	2.70 $\pm$ 7.82 (0.0005–48.11)
Forest	65.32 $\pm$ 67.03 (0.32–297.05)	22.65 $\pm$ 33.93 (0.32–72.0)	70.50 $\pm$ 68.50 (5.50–297.05)	411.12 $\pm$ 336.91 (1.25–1261.98)	345.79 $\pm$ 51.30 (0.03–1008.82)	0.66 $\pm$ 3.66 (0.002–22.32)
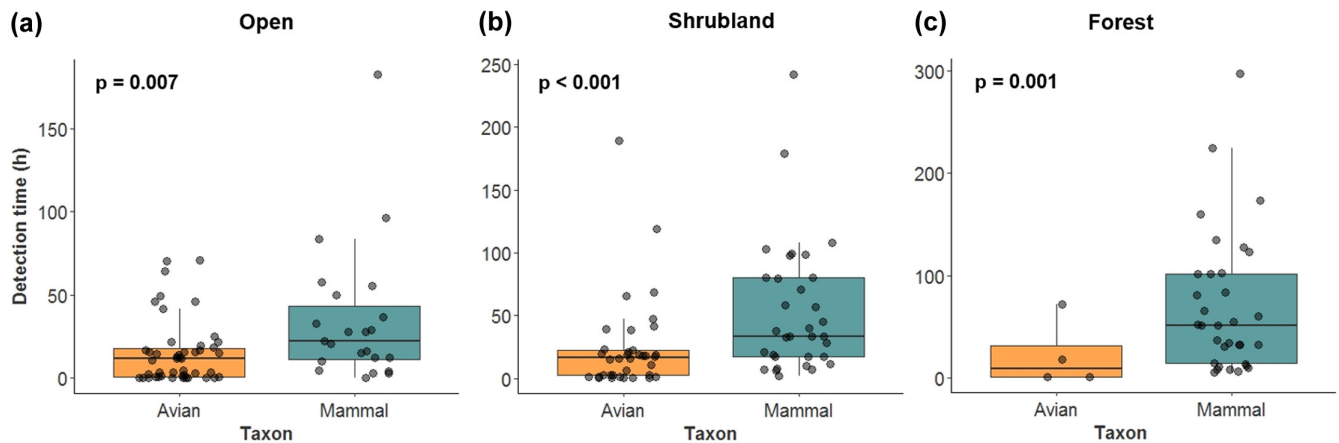
Figure 4. Boxplots and carcass detection times values (hours) at each carcass for birds and mammals in the three landscape types studied. Significant values of the univariate generalized linear models (Supporting information) are shown.

have acute eyesight (Ruxton and Houston 2004, Potier et al. 2016). However, vegetation cover affects the rate and speed at which carrion is discovered by a species (Ogada et al. 2012). We found that avian scavengers were the main detectors in open landscapes whereas both birds and mammals discovered carcasses in shrublands equally easily. Conversely, mammals detected almost 90% of the carcasses within forests. On the other hand, our results showed that increased vegetation cover led to higher detection times, since scavengers found carcasses in open landscapes up to three times faster than in forests. For example, birds found carcasses more rapidly in open landscapes (~15 h) than shrublands and forests (~25 h). Also, similar to the findings of Lima et al. (2021), mammals discovered carrion more rapidly in open landscapes than forests (~35 h versus ~70 h).

Unlike mammals, avian scavenging frequency decreased as vegetation cover increased. Overall, obligate scavengers consumed carrion more frequently in open landscapes, while this preference was not observed for the most frequent but less efficient biomass consumers (i.e. facultative avian and mammalian scavengers, Morales-Reyes et al. 2017, Arrondo et al. 2019). Birds, which rely mainly on visual cues to detect food, found carcasses easily in open landscapes and rarely detected them underneath dense forest cover (Moleón et al. 2019). Conversely, the well-developed olfactory sense of mammals plays a larger role in food discovery, making them better adapted to foraging in closed landscapes (Enari and Enari 2021). Despite this, some birds, such as corvids and eagles, are extremely efficient in locating carcasses, which could explain our observed scavenging frequency of these species within forests (Selva et al. 2005).

In accordance with our predictions, we found that carcass size is an important factor driving scavenging patterns in terms of scavenger assemblage composition (Moleón et al. 2015, Moreno-Opo et al. 2015, Turner et al. 2017, Stiegler et al. 2020). The greater biomass provided by large carcasses (above ~25 kg) helped explain the higher scavenger richness and abundances we observed at these carcasses (Moleón et al. 2015, Turner et al. 2017). However, contrary to our expectations,

neither detection time nor total and active consumption times were related to carcass size (Moleón et al. 2015, Turner et al. 2017), suggesting that, in rewilding situations, landscape type is the major factor influencing carcass detection and the time until complete consumption. Despite this, larger carcasses showed higher consumption rates, which could be attributed to exploitation by highly efficient griffon vultures (Sebastián-González et al. 2016). Indeed, our results suggest that griffon vultures play a similar role in terms of consumption rates as that observed for large facultative scavengers in African scavenging assemblages (Moleón et al. 2015), since consumption rates were ~125 times higher when carcasses were consumed by this species.

As expected, carrion removal was faster in open landscapes than within forests, because of the absence of vultures and dominance of mammals in forested areas (Morales-Reyes et al. 2017). In fact, our findings showed that griffon vultures play a crucial role in reducing carcass persistence. Carcasses that were consumed by griffon vultures persisted much less (~3 days) than those that were not consumed by this species (~15 days), highlighting their crucial regulatory service in maintaining healthy ecosystems. Both total and active consumption times increased when carcasses were deployed during the afternoon, since scavenging birds are generally inactive at night. Otherwise, our results support the view that vegetation encroachment leads to longer carcass persistence times. Increased carcass persistence in a landscape has been shown to increase carcass decomposition rates and the likelihood of disease transmission (Markandya et al. 2008, Ogada et al. 2012, Buechley and Şekercioğlu 2016), while both obligate and facultative scavengers can recycle carrion more efficiently than decomposers (DeVault et al. 2003, Ray et al. 2014).

We found that carnivore carcasses persisted longer and showed lower consumption rates than herbivore carcasses (Oliva-Vidal et al. 2021, Peers et al. 2021). However, contrary to our predictions, we detected no differences in species richness, abundance and detection time between herbivore and carnivore carcasses. Indeed, some avian scavengers such
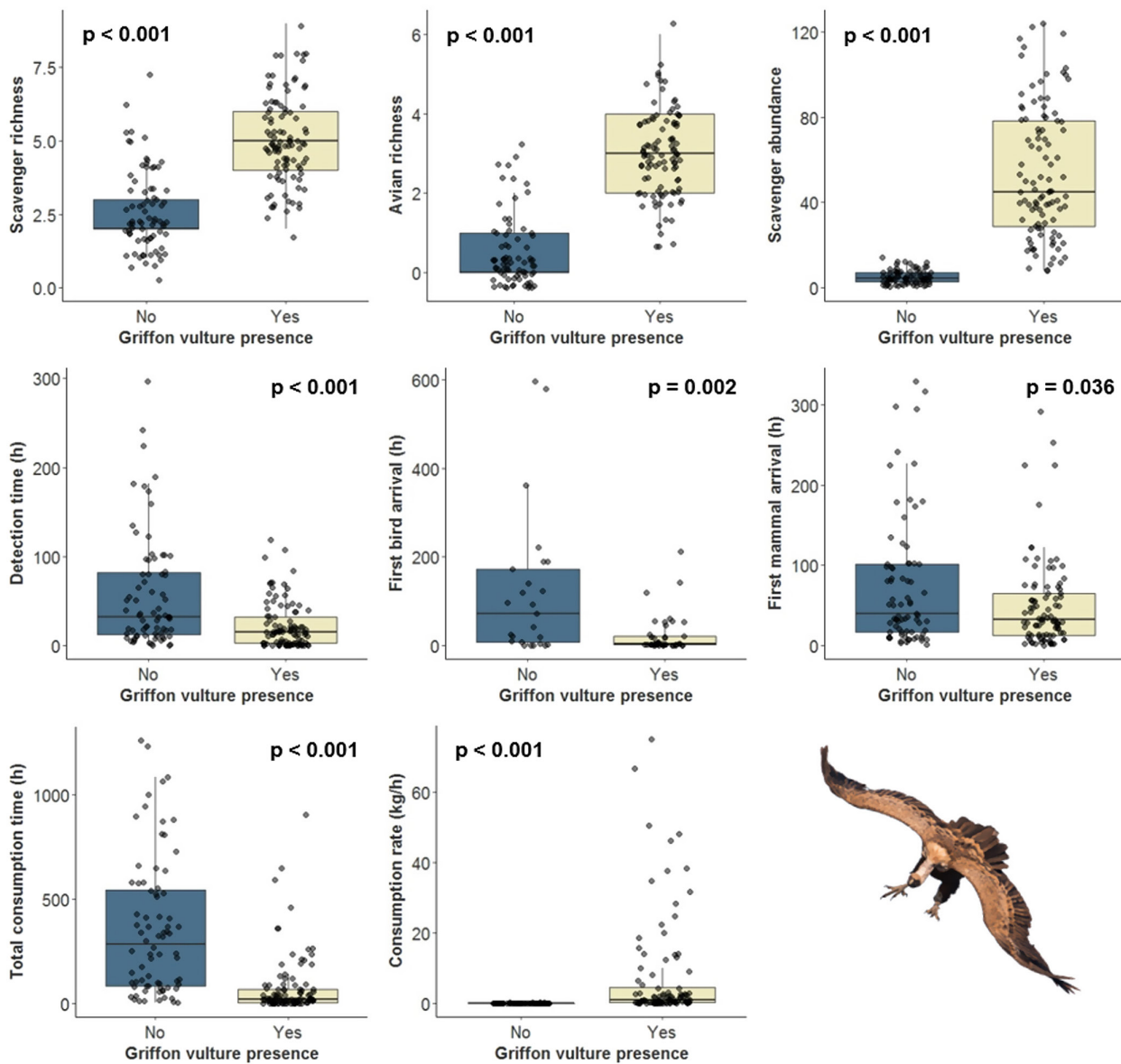
Figure 5. Boxplots showing the significant univariate relationships between the presence of griffon vultures at carcasses and the scavenger assemblage composition, scavenging efficiency and arrival time (h) of the first bird and mammal after griffon vulture appearance (Supporting information). Dots represent real data.

as golden eagles and red kites were more frequent at carnivore carrion. This could be attributed to the smaller size of carnivore carcasses, which may make them harder for griffon vultures to detect. Further, we recorded conspecific necrophagy at all red fox and at 57.5% of wild boar carcasses, where wild boars consumed mainly bone remains from conspecifics. The conspecific necrophagy we observed in red foxes contrasts with the findings of Moleón et al. (2017). They evidenced avoidance of carnivore and conspecific consumption by other carnivores, and attributed this behavior to a strategy to reduce the probability of disease transmission. However, our observations suggest that conspecific carcasses can provide an alternative resource for red foxes and other scavengers in certain areas or circumstances (Oliva-Vidal et al. 2021).

Overall, griffon vultures consumed 80% of the carcasses in open landscapes and 62% in shrublands. These findings support the idea that their functional traits (e.g. effective foraging strategies and conspecific visual information transfer, Cortés-Avizanda et al. 2014, Gutiérrrez-Canovas et al. 2020) make griffon vultures the most frequent, abundant and efficient scavengers in our study area. However, our results also show that landscape rewilding may jeopardize their high scavenging efficiency because increasing shrub and, especially, tree cover, hinder their ability to locate carrion and reduce both their scavenging frequency and, ultimately, their abundance in more closed landscapes (Ogada et al. 2012, Martin-Díaz et al. 2020). The higher griffon vulture abundances in open areas could also relate to landscape characteristics in

other ways, since high vegetation cover may leave insufficient clear space for them to take-off easily (Bamford et al. 2009).

We found strong evidence for the dominant role of griffon vultures in shaping scavenging through conspecific and heterospecific trophic facilitatory processes (Sebastián-González et al. 2016, 2021). First, more avian scavenger species consumed carcasses when griffon vultures exploited them. Mammalian richness was not influenced, perhaps because of the low number of diurnal mammal species in our study area. Second, because of their effective use of social information from conspecifics in their foraging strategy, a greater number of griffon vultures will gather to feed on a carcass (e.g. more than a hundred individuals can be attracted to a carcass once it is discovered). Third, both birds and mammals (mainly foxes, which can forage at the same time as griffon vultures) arrived faster at carcasses discovered by griffon vultures. These findings are consistent with Kane et al. (2017), who found that mammals might find carrion twice as fast when following vultures. Although griffon vultures consumed almost all of the meat biomass, we observed that bone remains provide an essential resource for some species (e.g. bearded vultures) and are valuable resources for mammals (especially red fox and wild boar), because bones are as energetically rich as meat over the long term (Blasco et al. 2019). Thus, in our study area griffon vultures may provide three major trophic facilitatory functions: 1) signaling carcass location; 2) facilitating access to the interior of carcasses offering feeding opportunities to less powerful species (i.e. access to small meat pieces, tendons, skin and skeletal remains); and 3) providing resources to more specialist species such as bearded or cinereous vultures (Moreno-Opo et al. 2015).

Concluding remarks

Scavengers are subject to large-scale habitat changes, such as farmland abandonment, which is projected to increase worldwide (Pereira and Navarro 2015, Tsunoda and Enari 2020, Lima et al. 2021). The abandonment of rural grazing and farmland practices often results in drastic landscape changes through general processes of vegetation encroachment (passive rewilding) and consequent 'landscape closure' (García-Ruiz et al. 2020b). The effects of habitat type on the functioning of scavenging assemblages have been previously recognized, and understanding the ecological consequences of passive rewilding is necessary to harmonize the coexistence of humans and scavengers. Our findings show that, in rewilding agroecosystems, landscape type is the main factor governing scavenging dynamics through its influence on the composition of scavenger assemblages and their scavenging efficiency. We demonstrate that progressive vegetation encroachment could jeopardize a hugely important functional group (i.e. vultures, which provide crucial ecosystem and scavenging services), reducing the scavenging efficiency of the assemblage (Morales-Reyes et al. 2017). While open landscapes promote carcass removal by the most efficient avian scavengers, in more forested landscapes mammals dominated at carcasses. Moreover, woody encroachment increases carcass persistence, which is known to result in negative ecological, economic and human health consequences (Markandya et al. 2008). We highlight the high consumption rates of griffon vultures as well as their role in driving trophic facilitatory processes, especially to endangered avian scavengers. Our results suggest that future studies should explore the necessity of maintaining open areas (e.g. by supporting traditional pastoral practices) to mitigate the ecological impact of rural abandonment on the functioning of scavenger assemblages.

Author contributions

Pilar Oliva-Vidal: Conceptualization (equal); Investigation (lead); Formal analysis (equal); Methodology (equal); Resources (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Esther Sebastián-González**: Conceptualization (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Antoni Margalida**: Conceptualization (equal); Project administration (lead); Funding acquisition (supporting); Resources (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.9zw3r22hn> (Oliva-Vidal et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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