ORIGINAL PAPER

Comparing scavenging in marine and terrestrial ecosystems: a case study with fish and gull carcasses in a small Mediterranean island

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Abstract

Carrion consumption by scavengers is a key component of both terrestrial and aquatic food webs. However, there are few direct comparisons of the structure and functioning of scavenging communities in different ecosystems. Here, we monitored the consumption of 23 fish (seabream *Sparus aurata*) and 34 bird (yellow-legged gull *Larus michahellis*) carcasses on a small Mediterranean island (Isla Grosa, southeastern Spain) and surrounding waters in summer to compare the structure of the scavenger assemblages and their carrion consumption efficiencies in terrestrial and shallow water habitats. Scavenging was highly efficient both in marine and terrestrial environments, especially in the presence of a highly abundant vertebrate scavenger species, the yellow-legged gull. The vertebrate scavenger community was richer in the marine environment, whereas the invertebrate community was richer on land. The scavenger network was usually well-structured (i.e., nested), with the exception of the community associated with fish terrestrial carcasses, which were almost monopolized by yellow-legged gulls. In contrast, gulls left conspecific carcasses untouched, thus allowing longer persistence of gull carcasses on land and their exploitation by a diverse insect community. Our study shows important differences in the scavenging process associated with environment and carcass type. Promising avenues for further eco-evolutionary and applied research arise from the comparison of scavenging processes in terrestrial and marine ecosystems, from small islands to continents.

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Introduction

Structural and functional comparisons among ecosystems have led to major advances towards ecological synthesis. Owing to the distinct physical-chemical properties of air and water, aquatic and terrestrial food webs differ in architecture and complexity, as well as in the rapidity and magnitude of nutrient and energy flow through the different trophic pathways (Chase, 2000; Cebrian & Lartigue, 2004; Shurin et al., 2006; Nowlin et al., 2008). For instance, detritus or dead organic matter, is often recycled at faster rates in water (Cebrian & Lartigue, 2004; Shurin et al., 2006; Nowlin et al., 2008). However, empirical comparisons on how high-quality detritus such as carrion (i.e. dead animal tissues) are partitioned among consumers in terrestrial and aquatic systems are largely lacking (see Quaggiotto et al. (2016) for an exception). Given the prominent role of carrion in ecosystem dynamics (DeVault, Rhodes & Shivik, 2003; Wilson & Wolkovich, 2011; Barton et al., 2013; Moleón et al., 2014; Moleón & Sánchez-Zapata, 2015), this knowledge gap undermines our understanding of the ecological contrasts and similarities between aquatic and terrestrial trophic networks.

Some general patterns are observed in scavenging studies in both marine and terrestrial environments: firstly, scavenging is a widespread behaviour in carnivorous species; secondly, scavenger assemblages are usually structured (as opposed to randomly organized; Selva & Fortuna, 2007); thirdly, there are key scavenging species that may dominate carcasses in different communities and ecological conditions; fourthly, carcasses of different types are often associated with distinct scavenger communities (see reviews in Britton & Morton, 1994, DeVault, Rhodes & Shivik, 2003, Wilson & Wolkovich, 2011, Beasley, Olson & DeVault, 2012, Barton et al., 2013, Moleón et al., 2014, Pereira, Owen-Smith & Moleón, 2014, Sebastián-González et al., 2019, Moleón, Selva & Sánchez-Zapata, 2020, Sebastián-González et al., 2020). At the same time, some differences between marine and terrestrial systems become apparent. Marine carcasses undergo greater horizontal and vertical mobility and are preserved for longer due to salinity, thermal stability and limited bacterial growth (Beasley, Olson & DeVault, 2012), which may have favoured the evolution of a wider community of marine invertebrates and vertebrates that rely strongly on scavenging, especially in the deep sea (Isaacs & Schwartzlose, 1975; Smith & Baco, 2003). Also, the diffusion of carrion cues should differ through water and air, as chemical substances are more frequent in the former and visual cues in the latter (Behringer, Karvonen & Bojko, 2018). This may differentially affect carcass detection and consumption patterns in marine and terrestrial ecosystems (Beasley, Olson & DeVault, 2012; Quaggiotto et al., 2016). Thus, simultaneous investigation of carcass consumption patterns in marine and terrestrial environments is strongly desirable (Quaggiotto et al., 2016). This would help to not only directly assess and compare differences in nutrient cycling between-ecosystems, but also better understand carrion-related processes in the understudied marine environment (Beasley, Olson & DeVault, 2012; Moleón & Sánchez-Zapata, 2015, 2021).

Small islands are particularly suitable scenarios to carry out comparative scavenging studies between terrestrial and marine systems because of their well-defined geographical extent and low environmental heterogeneity. This is especially evident on land, where trophic networks are much simpler than on the mainland (Whittaker & Fernández-Palacios, 2007), and are often dominated by one or few superabundant seabird species (Simeone et al., 2003; Duhem et al., 2008). Thus, vertebrate scavenger species richness is generally lower in these simplified terrestrial ecosystems compared to the surrounding waters, which could also diminish the chances of finding species that may functionally replace other scavengers on land. This may have consequences also for the invertebrate community of scavengers, as recent studies have found that intraspecific scavenging is infrequent in vertebrates (Selva et al., 2005; Olson et al., 2016; Moleón et al., 2017; Gonzálvez et al., 2021). Thus, in small islands, carcasses of the dominant scavenger species, which may be an important fraction of the total carrion biomass, are likely mostly available to other, less abundant and/or efficient scavenging animals (Muñoz-Lozano et al., 2019) and this is expected to influence the rate at which carrion is recycled (Olson et al., 2016; Moleón et al., 2017). However, the fragile and peculiar natural communities and ecological processes of small islands are seriously jeopardized by severe human impacts in many regions of the world (Medail & Quezel, 1997), such as the Mediterranean basin (Halpern et al., 2008; Poher et al., 2017). Therefore, understanding the structure and functioning of terrestrial and aquatic scavenging communities in small islands is an urgent need.

By simultaneously studying different carcass types (i.e., bird vs. fish) in shallow water and on land in a small Mediterranean island, we aim to explicitly compare the scavenging process between marine and terrestrial environments. In particular, we focus on a) the scavenger community

structure and b) scavenging efficiency. Our general hypothesis is that the structure and composition of the scavenger community will differ between environments and carcass types, leading to subsequent differences in carrion consumption efficiency.

Materials and methods

Study area

Isla Grosa is a small, protected Mediterranean island (area: 16 ha; max. altitude: 98 m a.s.l.) located 2.5 km from the coast of Murcia region (southeastern Spain; Fig. 1; Jiménez, 2018). Around 65% of the island is covered by shrub vegetation, mainly *Lycium intricatum, Withania frutescens* and *Salsola* spp. (Esteve-Raventós & Chueca, 1986). The coastline is mostly rocky, with some sandy beaches. Near the coast, the seabed is dominated by an extensive seagrass meadow of *Posidonia oceanica* (Marín-Guirao et al., 2018).

The scavenging vertebrate fauna on land mainly consists of seabirds, especially yellow-legged gull (*Larus michahellis*; no. of breeding pairs: c. 1959; Martínez-Sánchez et al., 2017). This species is also the main contributor to carrion

Fig. 1. Location of gull and fish carcasses on Isla Grosa (southeastern Spain, Mediterranean Sea).

biomass on the island, especially during the breeding season due to nestling natural mortality (pers. observ.). Other, less abundant seabirds include the European shag (*Phalacrocorax aristotelis*; no. of breeding pairs: c. 12; CEUEMA, 2017); European storm-petrels (*Hydrobates pelagicus*) and Audouin's gulls (*L. audouinii*) are occasional visitors. Birds of prey are absent during non-migration periods, with the exception of a resident, breeding pair of peregrine falcons (*Falco peregrinus*; García-Morell, 2004). Other potential vertebrate scavengers on the island are Montpellier snakes (*Malpolon monspessulanus*). The terrestrial scavenging invertebrate community is dominated by Coleoptera (beetles), Diptera (flies) and Hymenoptera (ants).

The underwater vertebrate community of scavengers is mainly composed of fish species, such as *Sparus* spp., *Diplodus* spp., *Oblada* spp. and several species of Mugilidae and Blenniidae (Hofrichter, 2004; Aguado-Giménez et al., 2018). Marine invertebrates, such as octopuses (mainly, *Octopus vulgaris*), gastropods (Gastropoda) and crabs (Brachyura) are also abundant.

Field data collection

We monitored the consumption of fish (gilt-head seabream *Sparus aurata;* $n = 23$; mean weight: 453.2 ± 43.2 g) and gull (subadult and adult yellow-legged gulls; $n = 34$; mean weight: 769.2 ± 174.5 g) carcasses in the terrestrial and marine environments of Isla Grosa. Thus, we studied four conditions that can naturally occur in the study area, according to the environment and carcass type: terrestrial gull carcasses (hereafter, "TG"), terrestrial fish carcasses ("TF"), marine gull carcasses ("MG"), and marine fish carcasses ("MF"). The fieldwork was done in summer (July and August 2018), i.e., when the natural availability of gull carcasses in the island is maximum (see above). Carcasses were deployed in three rounds (11, 14 and 10 carcasses per round on land and 5, 8 and 9 underwater), with approximately one week between consecutive rounds. They were placed at daytime (at different hours) and randomly, ensuring a minimum distance between simultaneous, neighbouring carcasses of 27 m on land and 7 m underwater (Fig. 1). We recorded carcass deployment date and time, and coordinates, which were used to calculate the distance to the shoreline and the distance to the nearest carcass at time of deployment.

Carcasses were monitored until their complete consumption (i.e., only bones and feathers/scales left) or for seven days if carcasses were not completely consumed. For each visit (marine environment) and image (terrestrial environment), we recorded the scavenger species visiting the carcass (to calculate carcass detection times) and feeding on it (to estimate other metrics; see below). Gull carcasses came from two nearby wildlife rescue centres and fishes were obtained from the nearest fish market. Carcasses did not show macroscopic lesions or other evidence of disease and
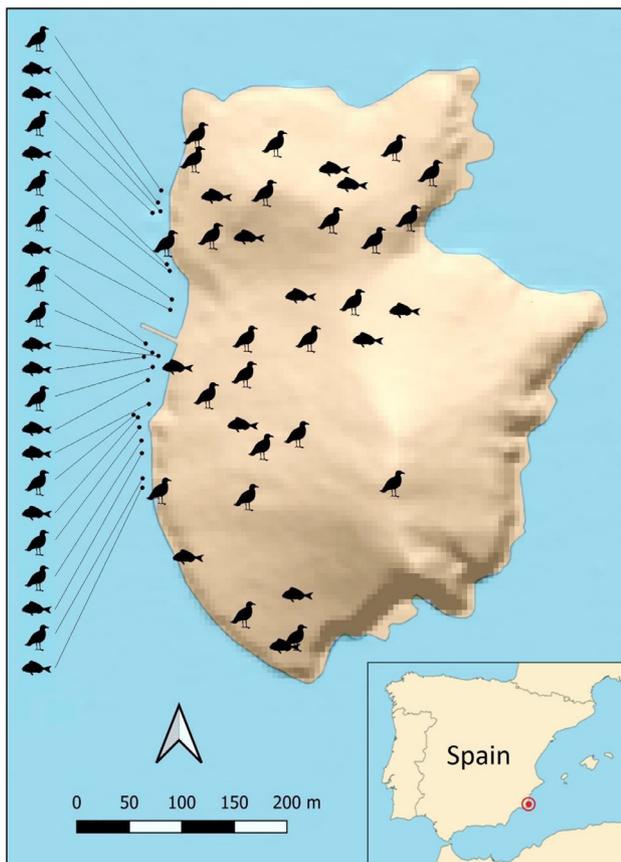
were frozen at −20 °C until the day before their deployment, when they were defrosted at room temperature.

Terrestrial experiment

We placed 23 gull and 12 fish carcasses within the topographically accessible area of the island (Fig. 1). To record vertebrate scavengers, we placed one infrared motion-triggered camera (Bushnell Trophy Cam and Bushnell Aggressor) at 3−5 m from each carcass, programmed to record one photograph and one 10- to 15-second-long video every minute when detecting movement (Moleón et al., 2015).

To record necrophagous (i.e., carrion-eating) and necrophilous (i.e., associated with carrion) insects, we sampled each carcass at noon at days 3 and 7 from carcass deployment. These visits enabled documentation of the insect fauna associated with the first two main stages of carcass decomposition (fresh/bloated and active decomposition) while minimizing potential disturbances to vertebrate scavenger activity (Muñoz-Lozano et al., 2019). We visually inspected the carcasses on each visit at a distance of >2 m to record the morphospecies of the most mobile insects visiting the carcass. Then, we approached the carcass to identify the morphospecies of the insects (adults and larvae) present on, under and around the carcass within a 1 m radius. Finally, we collected at least one individual of each morphospecies per carcass for later identification, at least at genus level (except for Formicidae, which were identified to family level). Fly maggot samples were stored in a portable fridge, before being killed in hot water (100 °C for 30 s) and fixed in ethanol (Adams & Hall, 2003). Adult insects and Coleopteran larvae were placed in ethanol immediately after collection (Amendt et al., 2006).

Marine experiment

We fixed 11 gull and 11 seabream carcasses to the seabed at c. 2 m depth (average distance to the shoreline: 13.6 ± 5.9 m; Fig. 1). We snorkelled to visit each carcass five times per day, at these time intervals: 8:00−11:00, 11:00−14:00, 14:00−17:00, 17:00−20:00, and 20:00−23:00 (UTC+2). Carcasses were approached in two steps to record vertebrate and invertebrate scavengers: firstly, we observed the carcass from >5 m to record the most mobile and elusive scavengers; secondly, we made a one-minute inspection close to the carcass to record other scavengers. We recorded one video during each visit using an underwater camera to double-check data collected and help in species identification.

Data analyses

To evaluate the scavenger community structure, firstly, for each carcass, we calculated the scavenger species richness as the minimum number of different species feeding on each carcass during the entire consumption process, in total ("richness") and separately for vertebrates ("vertebrate richness") and invertebrates ("invertebrate richness"). For each environment (terrestrial or marine) and carcass type (gull and fish), we used a richness accumulation curve with random permutations of samples (Gotelli & Colwell, 2001) to test whether sample size (number of carcasses) was large enough to detect all the scavenger species in the community, i.e. if the curve reached an asymptote. Secondly, for each environment and carcass type, we analysed species co-occurrence and nestedness of the scavenging network. Co-occurrence analyses were used to detect the species appearing in the same carcass more (positive co-occurrence) or less frequently (negative co-occurrence) than expected by chance, which could indicate positive and negative interspecific associations, respectively (Gotelli & McCabe, 2002). To do so, we used the cooccur() function from the *cooccur* package in R (Griffith, Veech & Marsh, 2016). We analysed the nestedness of the different scavenging assemblages using the nested() function from the *bipartite* package in R (Dormann et al., 2009). A scavenging network is considered nested when the species feeding on carcasses consumed by few scavengers are a subset of those species feeding on carcasses consumed by larger numbers of scavengers (Selva & Fortuna, 2007; Sebastián-González et al., 2016). We computed the NODF metric (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al., 2008), ranging from 0 (not nested) to 100 (perfectly nested). We then tested the significance of the nestedness by comparing the NODF value with that obtained by randomizing the value using a null model that controlled for the effects of species richness and sample size and maintains the heterogeneity in the number of interactions across species and carcasses (Sebastián-González et al., 2015).

To assess scavenging efficiency, we first estimated the "detection time", i.e., time between carcass deployment and the arrival of the first scavenger (in h; Moleón et al., 2015). We also recorded the arrival of the first vertebrate and invertebrate scavenger to calculate "detection time by vertebrate scavengers" and "detection time by invertebrate scavengers", respectively.

Secondly, we calculated whether each carcass was completely consumed (i.e., only bones and feathers/scales left) or not after seven days since carcass deployment ("consumption after seven days").

Generalized linear models (GLMs) were carried out to explain the changes in "richness", "vertebrate richness", "invertebrate richness", "detection time", "detection time by vertebrate scavengers", "detection time by invertebrate scavengers" and "consumption after seven days" (response variables) according to environment (marine and terrestrial), carcass type (fish and gull), deployment hour, distance to the shoreline (in m), and distance to the nearest carcass (in m) as explanatory variables. We used Gaussian error and identity link function for detection time variables, Poisson

error and log link function for species richness variables, and binomial error and logit link function for "consumption after seven days". We fitted all possible GLMs with one or more explanatory variables, always guaranteeing a minimum of 10 observations per parameter included in the model (Hardy & Bryman, 2004). We also fitted a null model (without explanatory variables) for each response variable and included the interaction between environment and carcass type. We calculated the Akaike's Information Criterion for small sample sizes (AICc; using the function AICc() of the package *AICcmodavg*; Mazerolle, 2019) to identify the most parsimonious model (i.e. lowest AICc). To compare the goodness of fit of the selected models (ΔAICc<2), we computed the proportion of explained deviance (D^2 = (null deviance-residual deviance)/null deviance*100; Burnham & Anderson, 2002). All analyses were conducted in R 3.6.2 (R Core Team, 2018).

Results

Scavenger community

According to the species richness accumulation curve, our sample size was enough to detect most scavenger species, especially those feeding on MG (see Appendix A: Fig. S1). In general, scavenger species richness was higher in TG (Table 1, Fig. 2, see Appendix A: Fig. S1). Vertebrate richness was higher in the marine (10 species; especially, in gull carcasses) than in the terrestrial environment, where only yellow-legged gulls were recorded, feeding exclusively on fish carcasses. Invertebrate richness was similar between MG and MF, whereas it was higher in TG. On land, a minimum of 18 insect species were detected on TG, while eight of them were recorded on the only TF from which insects' samples could be taken (the other TF were consumed by gulls before the first insect sampling). Richness, vertebrate richness and invertebrate richness were best explained by the model including the interaction between environment and carcass type (Table 2, see Appendix A: Fig. S1).

Regarding species co-occurrence at gull carcasses, we found four co-occurrences on land (two positives and two negatives; all between insects) and two positive co-occurrences underwater (between *Diplodus* spp. fishes and between them and *Octopus vulgaris*). We did not find any species co-occurring more or less frequently than expected by chance in fish carcasses (see Appendix A: Table S2). The scavenging network was nested for TG and MG (NODF = 55.25 in terrestrial and 67.55 in marine environments, P<0.001 in both cases) and MF (NODF = 49.28, P<0.001). TF were almost monopolized by yellow-legged gulls, thus preventing nestedness (NODF = 19.44, P = 0.548; Fig. 3).

Scavenging efficiency

According to the models (Table 2, see Appendix A: S1), detection time (by both vertebrates and invertebrates) and detection time by invertebrate scavengers was shorter in the terrestrial environment and for fish carcasses, mostly due to the presence of insects (usually flies) in all terrestrial carcasses a few seconds after their deployment (see Appendix A: Fig. S2). Regarding detection time by vertebrates, the null model was included within the set of selected models, indicating that none of the studied variables was relevant to explain this response variable (Table 2, see Appendix A: Table S1). The proportion of carcasses completely consumed after seven days was higher in the marine environment (61.9% vs. 31.4% in the terrestrial environment) and for fish carcasses (95.4% vs. 8.3% for gull carcasses; Table 1, see Appendix A: Fig. S2), as confirmed by the selected model (Table 2, see Appendix A: Table S1).

Discussion

How organic matter is recycled through food webs has concerned ecologists for decades (Odum, 1968; Moore et al., 2004). However, the need to add scavenging to food web models of different ecosystems has only recently

Table 1. Variables related to scavenger community (richness, vertebrate richness, and invertebrate richness) and scavenging efficiency (detection time, detection time by vertebrate scavengers, detection time by invertebrate scavengers and consumption after seven days, expressed as percentage), for each environment and carcass type. Mean ± standard deviation (and n) is shown.

|	Marine environment		Terrestrial environment	
Response variable	Fish	Gull	Fish	Gull
Richness	3.30 ± 1.70 (10)	4.27 ± 2.15 (11)	1.50 ± 1.73 (12)	6.78 ± 1.48 (23)
Vertebrate richness	1.90 ± 1.60 (10)	3.00 ± 1.73 (11)	1.00 ± 0.00 (12)	0.00 ± 0.00 (23)
Invertebrate richness	1.40 ± 1.07 (10)	1.27 ± 0.65 (11)	0.50 ± 1.73 (12)	6.78 ± 1.48 (23)
Detection time (h)	0.85 ± 1.89 (10)	3.09 ± 4.34 (11)	0.00 ± 0.00 (12)	0.00 ± 0.00 (23)
Detection time by vertebrate scavengers (h)	13.85 ± 12.19 (10)	20.16 ± 25.13 (11)	9,08 ± 15.72 (12)	12.67 ± 17.08 (19)
Detection time by invertebrate scavengers (h)	7.55 ± 13.04 (10)	10.09 ± 13.39(11)	0.00 ± 0.00 (12)	0.00 ± 0.00 (23)
% of carcasses consumed after 7 days	100% (10)	27.27% (11)	91.67% (12)	0% (23)
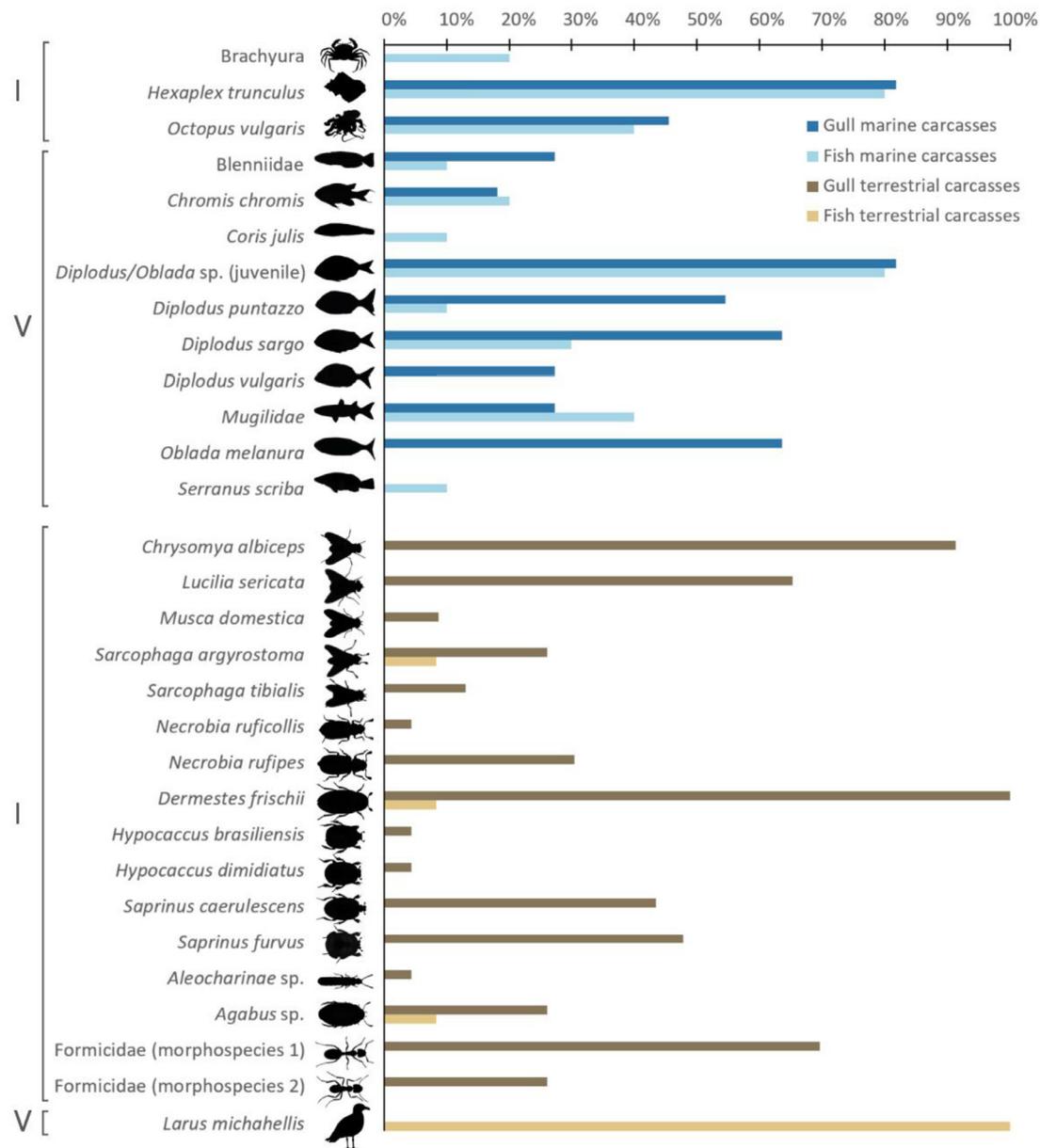
Fig. 2. Percentage of occurrence (number of carcasses of a given type and environment visited by a given species or group, divided by the total number of carcasses of that type in that environment, multiplied by 100) of each scavenger species or group at each carcass type and environment. Vertebrate and invertebrate scavengers are identified by a V (vertebrates) or an I (invertebrates). Juveniles of *Diplodus/Oblada* sp. were taken into account to quantify species richness only when adults of any of these genera were not detected.

been emphasized (Beasley, Olson & DeVault, 2012; Moleón & Sánchez-Zapata, 2015, 2021, Quaggiotto et al., 2016). Here, we unravelled the scavenging assemblage associated with two carcass types and quantified carrion consumption efficiency in an insular system, explicitly comparing shallow water and terrestrial environments. Overall, we found differences in both the structure and functioning of the scavenging networks between ecosystems (see Fig. 4 for a synthesis of the main results). The most remarkable difference was in the relative contributions of vertebrates and invertebrates to the scavenger community: the vertebrate richness was higher underwater than on land, while the opposite was true for

invertebrates (Fig. 2). This agrees with the fact that islands, especially small islands, normally support a reduced diversity of terrestrial vertebrates (Whittaker & Fernández-Palacios, 2007). Also, terrestrial necrophagous and necrophilous insects are usually much smaller than marine invertebrate scavengers, which may allow more insect species to gather around a given carcass. In turn, increased invertebrate scavenger richness on terrestrial carcasses was likely leading to more opportunities for inter-specific interactions between carrion invertebrates on land (see Appendix A: Table S2). For instance, we observed negative co-occurrences probably linked to resource competition between ants and histerid

Table 2. Selected generalized linear models (ΔAICc<2) showing the relation between environment (marine or terrestrial), carcass type (fish or gull), deployment hour, distance to the shoreline, and distance to the nearest carcass on the response variables related to scavenger community (richness, vertebrate richness and invertebrate richness) and scavenging efficiency (detection time, detection time by invertebrate scavengers and consumption after seven days). The estimate of the parameters, the standard error of the parameters (SE) and the degrees of freedom of the models (DF) are shown.

Response variable	Model	Parameter	Estimate	SE	DF
Richness	environment * carcass type	Intercept	1.45	0.15	52
		carcass type (fish)	−0.26	0.23	
		environment (terrestrial)	0.46	0.17	
		CT (f):E (t)	−1.25	0.34	
Vertebrate richness	environment * carcass type	Intercept	2.98	0.30	52
		carcass type (fish)	−1.07	0.44	
		environment (terrestrial)	−2.98	0.37	
		CT (f):E (t)	2.06	0.57	
Invertebrate richness	environment * carcass type	Intercept	0.24	0.27	52
		carcass type (fish)	0.10	0.38	
		environment (terrestrial)	1.67	0.28	
		CT (f):E (t)	−2.70	0.56	
Detection time	environment + carcass type + hour	Intercept	1.36	1.35	51
		carcass type (fish)	−0.96	0.60	
		environment (terrestrial)	−2.27	0.62	
		hour	1.66	1.88	
	environment * carcass type	Intercept	3.09	0.62	52
		carcass type (fish)	−2.24	0.90	
		environment (terrestrial)	−3.09	0.75	
		CT (f):E (t)	2.24	1.16	
	environment + hour	Intercept	1.12	1.36	52
		environment (terrestrial)	−2.13	0.62	
		hour	1.34	1.89	
	environment + carcass type	Intercept	2.45	0.54	53
		carcass type (fish)	−0.89	0.58	
		environment (terrestrial)	−2.14	0.59	
Detection time by invertebrate scavengers	environment + hour	Intercept	−3.84	4.68	52
		environment (terrestrial)	−10.32	2.13	
		hour	18.88	6.51	
	environment + carcass type + hour	Intercept	−3.42	4.72	51
		carcass type (fish)	−1.68	2.09	
		environment (terrestrial)	−10.57	2.16	
		hour	19.45	6.57	
Consumption after seven days	environment + carcass type	Intercept	−1.11	0.67	53
		carcass type (fish)	5.91	1.37	
		environment (terrestrial)	−2.59	1.23	
	environment + carcass type + distance to nearest carcass	Intercept	−0.87	0.77	52
		carcass type (fish)	6.07	1.44	
		environment (terrestrial)	−2.35	1.27	
		distance to nearest carcass	−0.01	0.01	

beetles, as both predate on necrophagous fly larvae (Nuorteva, 1970; Bonacci et al., 2011).

With the exception of TF, all scavenger communities were highly nested (i.e. structured; Selva & Fortuna, 2007; Fig. 3). Given the direct relationship between nestedness and consumption efficiency in scavenging networks (Sebastián-González et al., 2020), this result indicates that the studied nested scavenger assemblages are highly efficient in recycling carrion. However, contrary to the general pattern observed in other studies on land and at sea (Beasley, Olson & DeVault, 2012; Moleón et al., 2015), we found that the non-nested and low-diversity community scavenging on TF was one of the most efficient (Table 1, Appendix A: Fig. S2). This was clearly associated with the presence of an abundant vertebrate scavenger, the yellow-legged gull, which quickly monopolized and consumed the fish carcasses before the invertebrate community could exploit them (see a similar example in Henderson et al.,
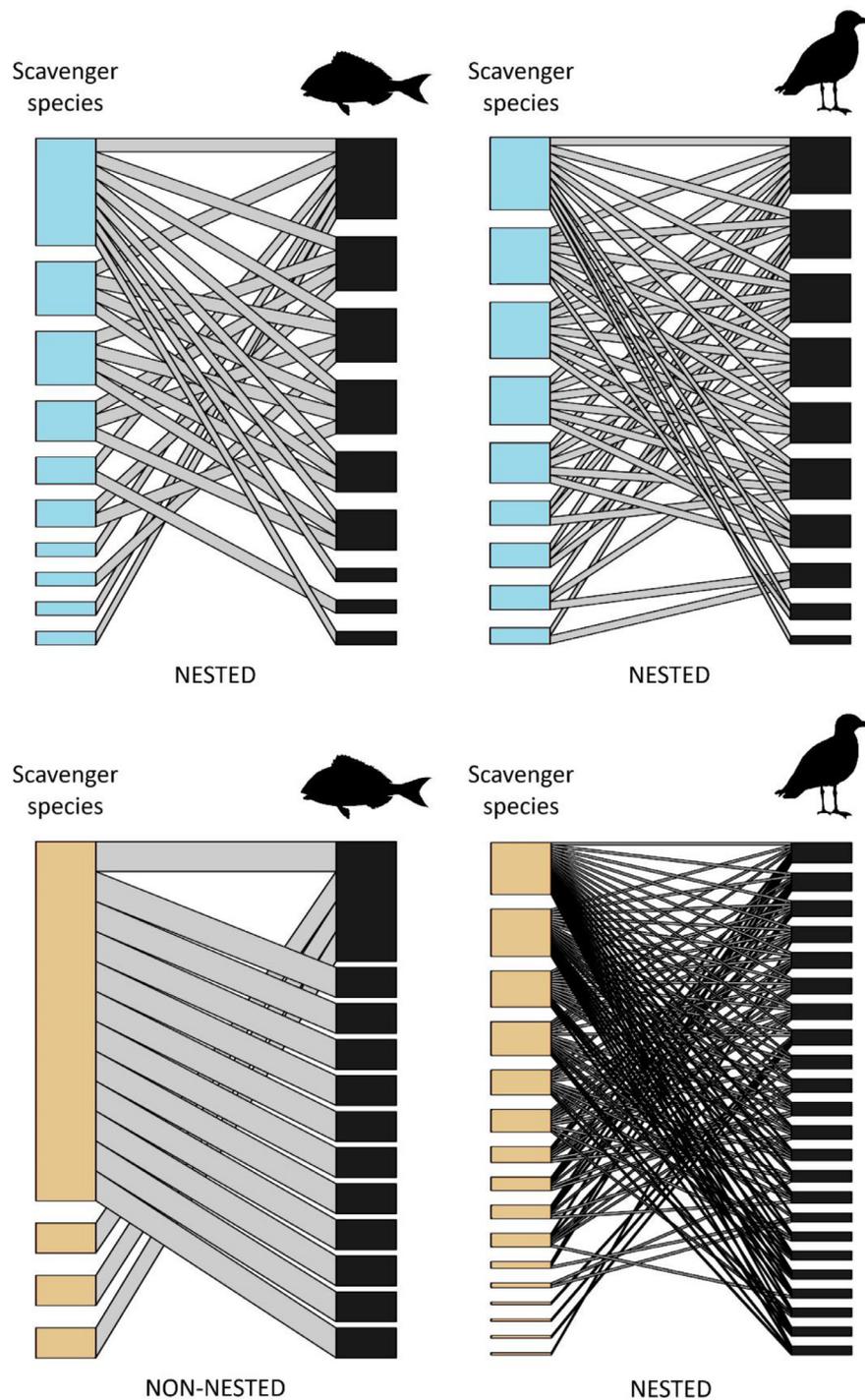
Fig. 3. Nestedness of the scavenger community for each environment and carcass type. Scavenger species are represented by blue (marine species) and brown (terrestrial species) squares, and carcasses are represented by black squares. Carcass type is identified by the silhouette of a fish or a gull. Lines link the consumed carcass with the consumer scavenger species.

2020). In accordance with the functional equivalence hypothesis (Hubbell, 2005), this indicates that local abundance of a vertebrate facultative scavenger can govern scavenging efficiency over other functional attributes of the scavenger community, such as niche complementarity and key traits (e.g. large home ranges; Gutiérrez-Cánovas et al., 2020). Large colonies of seabirds, many of which are

facultative scavengers, are a common feature of small islands in the Mediterranean Sea (Duhem et al., 2008) and elsewhere (Simeone et al., 2003), which suggests that our findings may be extrapolated to other small insular systems (Quaggiotto et al., 2016).

Our findings support the recent recognition that not all carcass types are equivalent (Moleón et al., 2017;
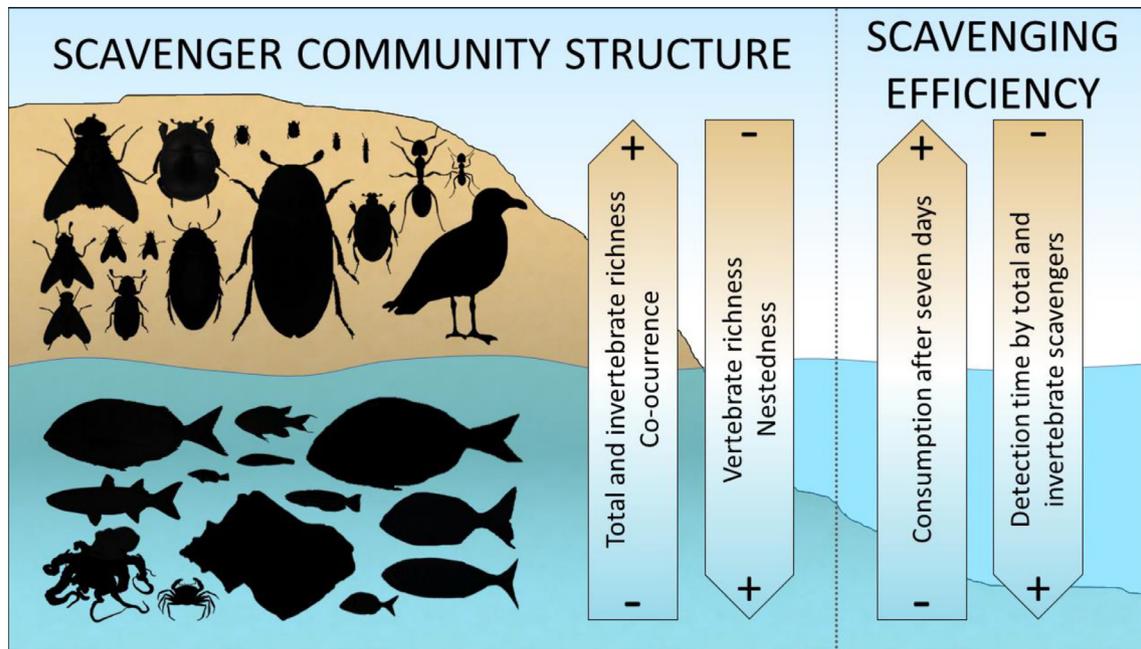
Fig. 4. Summary of the main differences in the structure and functioning of the scavenging community between the terrestrial and marine environments, as inferred from our results. Each silhouette represents one scavenger species, and its size is proportional to the percentage of carcasses visited in each environment. For silhouettes, see Fig. 2.

Mashaly et al., 2019). In our study of carcasses of different species but similar size (seabream and gull), the main differences were due to the avoidance of conspecific carcasses by gulls (seabreams were not recorded at any carcass type). Cannibalistic scavenging seems to be a rare behaviour in vertebrates (Selva et al., 2005; Olson, Beasley & Rhodes, 2016; Moleón et al., 2017; Gonzálvez et al., 2021; Moleón & Sánchez-Zapata, 2021), likely to reduce exposure to parasites (Moleón et al., 2017; Gonzálvez et al., 2021). In other islands with a richer community of avian scavenger species, it is expected that scavenging of bird carcasses would be more efficient than in our study, as carcasses may be consumed by different species. This could enhance carrion recycling rates and diminish scavenging opportunities to necrophagous insects (Muñoz-Lozano et al., 2019), which could negatively affect island carrion insect diversity. Moreover, the longer persistence of gull carcasses due to the absence of heterospecific vertebrate consumers in our study area could have enabled not only a richer, but also a more structured invertebrate scavenger community (Muñoz-Lozano et al., 2019; see Fig. 3). The trade-offs between the benefits obtained from carrion supplied by different seabird species (Sánchez-Piñero & Polis, 2000) and the limitations imposed by increased competition for carrion from scavenging seabirds (due to heterospecific consumption) on necrophagous insects deserve to be investigated in future empirical studies. These studies should be framed into island biogeography (MacArthur & Wilson, 1967) and take into consideration not only seabird species richness and abundance, but also the use that such birds make of the island (e.g., nesting and/or roosting; Sánchez-Piñero &

Polis, 2000). Also, the role of predictable anthropogenic food subsidies, such as fisheries discards, fish farms and dumps, on the abundance and composition of the seabird communities in small islands (Oro et al., 2013) might be a largely understudied topic in carrion ecology with important applied implications. In our study island, the large colony of yellow-legged gulls is greatly maintained by the food provided by nearby fish farms (Aguado-Giménez et al., 2016). In addition, it is worth highlighting that different carcass types may be associated also with different searching and handling times. In our case, the likely lower handling time of fishes may have also contributed to the observed higher consumption efficiency of fish compared to gull carcasses in the marine environment. The simultaneous occurrence of these very different carcass types could be a feature of small islands, where fish and bird carcasses may be found both on land and underwater. However, the chances of finding carrion inputs from the sea on land, and vice versa, would decrease as the distance from the shoreline increases, which in turn could affect the scavenging patterns.

Potential biases and lessons for future research

Given the different characteristics of scavengers (e.g., large vs. small-sized species) and environments, we used different observation methods: camera-trapping for vertebrate scavengers in terrestrial carcasses and direct observation otherwise, with collection of specimens in the case of terrestrial invertebrates. This led also to different sampling frequency, with nocturnal surveys being scarce underwater.

However, in total we obtained 11,819 pictures and videos, conducted 150 insect samplings (for insects, we sampled the period of maximum activity; Muñoz-Lozano et al., 2019), collected over 1550 insect individuals, and carried out 685 visits to marine carcasses. This intensive sampling effort led to the detection of most of the species of the insular scavenger community, though, according to our species richness accumulation curve, the richness of the scavenger community at fish, marine carcasses and gull, terrestrial carcasses was probably somewhat underestimated (see Fig. S1). However, further sampling effort would have likely allowed us to detect more invertebrate species in both the marine and terrestrial environments, so no important changes in between-ecosystem differences in total and invertebrate species richness are expected. With regard to vertebrate species richness, our results are conservative: in the case that additional sampling would result in increased richness of scavenging fish species (see Fig. S1), the difference between marine and terrestrial vertebrate richness would be even higher, as the studied terrestrial community of scavengers was completely or, at least, largely limited to gulls. Further samples would slightly increase the opportunities for finding associations (either positive or negative) between species at carcasses, as well as the nestedness of the networks (except for fish carcasses on land, which are clearly almost monopolized by gulls). Undetected marine scavengers are probably mostly nocturnal, though we were able to detect typically nocturnal species (e.g., *Octopus vulgaris*) during the first and the last visits of the day. Moreover, some species with reduced mobility (e.g., *Hexaplex trunculus*) were near or on the carcasses (i.e., detectable) during all day. The cliffs that surround most of the island only allowed us to sample its west coast, but we do not expect important differences in the rest of the coast because of its small size.

In relation to taxonomic identification, most scavengers were identified at the species level in both the terrestrial and marine environments. Only three vertebrate and five invertebrate scavengers were identified at the family or genus level (see Fig. 2). Given that these taxonomic inaccuracies were equally distributed between environments, the potential effect of this bias in our results is probably little. In addition, we always considered morphospecies or monospecific groups, which guarantees adequate calculation (and replication) of the metrics used: species richness, co-occurrence of species and nestedness of the community.

Our study was conducted during one season, i.e., summer. In the studied island, there is relatively little seasonality in environmental conditions, as indicated by moderate temperature oscillations between summer (June-August mean air and water surface temperature: 24.8 °C and 24.6 °C, respectively) and winter (December-February mean air and water surface temperature: 12.3 °C and 15.2 °C, respectively; www.ncdc.noaa.gov). Moreover, all the scavengers recorded in this study were resident species. Thus, no important seasonal changes in the composition of the scavenger community are expected. However, how seasonality in species abundance and the availability of carrion, which is heavily dependent on gull reproduction (due to juvenile mortality; pers. observ.), could affect the structure of the scavenging community and the efficiency of carrion consumption in each season both on land and underwater remains unknown. Thus, further research exploring the effects of seasonality in a gradient of environmental conditions and scavenger communities could help to better understand the ecological similitudes and differences between ecosystems.

Finally, we must recognize that natural carcasses in marine environments may move by currents, and internal decomposition may make them buoyant. This could give access to other scavengers to the carrion, including terrestrial species (Beasley et al., 2012; Moleón et al., 2019). However, not all marine carcasses move or float. Exploring the scavenging patterns of mobile carcasses is a methodologically complex challenge that would need specific investigation. In this line, the ongoing development of more efficient and cheaper devices for biomonitoring marine processes will likely offer exciting opportunities in scavenging research. This includes the refinement of species richness estimates, the consideration of important additional parameters such as scavenger abundance (Mateo-Tomás et al., 2017) and daily activity (Amorós et al., 2020), and the exploration of deeper waters, which eventually would lead to finer between-ecosystem comparisons.

Conclusions

Through exploring scavenging processes in different ecosystems simultaneously, this study helps to bring together marine and terrestrial ecologists. In addition, our findings lead to a better knowledge of carrion cycling in islands and shallow waters, which have received little attention from carrion ecologists (Beasley, Olson & DeVault, 2012, Henderson et al., 2020). In general, we found that scavenging was highly efficient in both marine and terrestrial environments, especially in the presence of an abundant vertebrate scavenger species. However, we found some distinctions between ecosystems, mainly related to the structure of the scavenging assemblages (Fig. 4). Our results also indicate that similarities and differences between ecosystems are strongly dependent on carcass type. Establishing universal patterns in carrion recycling will require further simultaneous aquatic-terrestrial comparisons in other insular systems of different characteristics (e.g. size and distance to mainland) in different regions, as well as in continental coastal areas and freshwater environments.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2022.01.006.

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