Scavenger assemblages in the Neotropics: ecological and behavioral patterns

Comunidades de carroñeros en el Neotrópico: patrones ecológicos y comportamentales

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Programa de Doctorado en Medio Ambiente y Sostenibilidad
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Lara Naves Alegre
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Que Dña. Lara Naves Alegre ha realizado bajo nuestra supervisión el trabajo titulado “Scavenger assemblages in the Neotropics: ecological and behavioral patterns” conforme a los términos y condiciones definidos en su Plan de Investigación y de acuerdo al Código de Buenas Prácticas de la Universidad Miguel Hernández de Elche, cumpliendo los objetivos previstos de forma satisfactoria para su defensa pública como tesis doctoral.

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A mis padres y a mi abuela.

“Val más poco siendo bastante, que muncho siendo poco”

Refrán asturiano

“If my decomposing carcass helps nourish the roots of a juniper tree or the wings of a vulture—that is immortality enough for me. And as much as anyone deserves.”

Edward Abbey. *Desert Solitaire*

"Nothing in life is to be feared; it is only to be understood."

Marie Curie

TABLE OF CONTENTS

LIST OF TABLES **1**

LIST OF FIGURES **3**

SUMMARY **5**

RESUMEN **9**

CHAPTER 1: GENERAL INTRODUCTION **13**

COMMUNITY STRUCTURE AND FUNCTIONING 15
SPECIES INTERACTIONS: COMPETITION AND FACILITATION 17
BEHAVIOR AS A KEY TOOL TO UNDERSTAND ANIMAL INTERACTION NETWORKS 18
STUDY MODEL: THE SCAVENGER GUILD 23
AIMS AND STRUCTURE OF THIS THESIS 29

CHAPTER 2: SUMMARY OF MATERIALS AND METHODS **33**

STUDY AREA 35
STUDY DESIGN 38
METHODS FOR EACH CHAPTER 39

CHAPTER 3. UNCOVERING THE VERTEBRATE SCAVENGER GUILD COMPOSITION AND FUNCTIONING IN THE *CERRADO* BIODIVERSITY HOTSPOT **41**

ABSTRACT 43
INTRODUCTION 44
METHODS 46
  Study area *46*
  Study design and data sampling *47*
  Statistical analyses *49*
RESULTS 50
  Scavenger community *50*
  Carcass consumption patterns *51*
DISCUSSION 56
  The vertebrate scavenger assemblage at the Cerrado biome *57*
  Factors affecting consumption patterns *58*
  Concluding remarks and conservation implications *60*
ACKNOWLEDGEMENTS 60

CHAPTER 4. SCAVENGER ASSEMBLAGES ARE STRUCTURED BY COMPLEX COMPETITION AND FACILITATION PROCESSES AMONG VULTURES **61**

ABSTRACT 63
INTRODUCTION 64
MATERIALS AND METHODS 67
  Study area and scavenger community *67*
  Study design and variables considered *67*
  Activity patterns and time of arrival *68*
  Co-occurrence analyses *69*
  Quantitative analyses *70*
RESULTS 72

Activity patterns and time of arrival *72*
Spatial co-occurrence *73*
Spatio-temporal co-occurrence *74*
DISCUSSION 75
Facilitation processes *76*
Competition processes *78*
CONCLUSIONS 79
ACKNOWLEDGEMENTS 80

CHAPTER 5. SCAVENGING IN THE REALM OF SENSES: SMELL AND VISION DRIVE RECRUITMENT AT CARCASSES IN NEOTROPICAL ECOSYSTEMS 81

ABSTRACT 83
INTRODUCTION 84
METHODS 86
Study area and scavenger community *86*
Study design and variables *86*
Statistical analysis *87*
RESULTS 89
DISCUSSION 93
ACKNOWLEDGEMENTS 96

CHAPTER 6. BEHAVIORAL INTERACTIONS ARE MODULATED BY FACILITATION ALONG A HETEROTROPHIC SUCCESSION 97

ABSTRACT 99
INTRODUCTION 100
MATERIAL AND METHODS 104
Study system *104*
Study design and general variables *104*
Community dynamics metrics *105*
Behavioral data collection *106*
Statistical analyses *106*
RESULTS 110
Community dynamics and species abundances *110*
Behavior throughout carcass consumption *110*
DISCUSSION 113
Vertebrate community composition during heterotrophic succession *113*
The influence of facilitation processes on succession dynamics *114*
Competition intensity over the consumption of an ephemeral resource *115*
Concluding remarks and future perspectives *116*
ACKNOWLEDGEMENTS 116

CHAPTER 7: GENERAL DISCUSSION 117

THE UNIQUENESS OF NEOTROPICAL SCAVENGER COMMUNITIES 119
INTERSPECIFIC INTERACTIONS IN A SCAVENGER COMMUNITY 121
CONTRIBUTION OF THE BEHAVIORAL APPROACH TO THE STUDY OF PROXIMATE CAUSES OF INTERACTIONS 123
CONSERVATION IMPLICATIONS 127
LIMITATIONS AND CAVEATS 129
FUTURE PERSPECTIVES 130

CONCLUSIONS 133

CONCLUSIONES **137**

REFERENCES **141**

APPENDICES **175**

SUPPLEMENTARY MATERIAL TO CHAPTER 3: UNCOVERING THE VERTEBRATE SCAVENGER GUILD COMPOSITION AND FUNCTIONING IN THE *CERRADO* BIODIVERSITY HOTSPOT 177
SUPPLEMENTARY MATERIAL TO CHAPTER 4: SCAVENGER ASSEMBLAGES ARE STRUCTURED BY COMPLEX COMPETITION AND FACILITATION PROCESSES AMONG VULTURES 187
SUPPLEMENTARY MATERIAL TO CHAPTER 5: SCAVENGER ASSEMBLAGES ARE STRUCTURED BY COMPLEX COMPETITION AND FACILITATION PROCESSES AMONG VULTURES 198
SUPPLEMENTARY MATERIAL TO CHAPTER 6: BEHAVIORAL INTERACTIONS ARE MODULATED BY FACILITATION ALONG A HETEROTROPHIC SUCCESSION 209

ACKNOWLEDGMENTS **223**

LIST OF TABLES

Chapter 3: Uncovering the vertebrate scavenger guild composition and functioning in the *Cerrado* biodiversity hotspot **Page**

Table 1 Richness per carcass, abundance, detection and consumption times and consumption rate for each carcass size (large or small). 53

Table 2 Model coefficients for large carcasses by means of one-predictor generalized lineal models (GLMs) showing the relation between scavenging efficiency (abundance, detection and consumption times and consumption rate) and carcass weight, time of carcass placement and vegetation cover. 54

Table 3 Model-averaged coefficients for small carcasses by means of generalized lineal models (GLMs) showing the relation between scavenging efficiency (richness, abundance, detection and consumption times and consumption rate) and carcass weight, time of carcass placement and vegetation cover. 56

Chapter 4: Scavenger assemblages are structured by complex competition and facilitation processes among vultures

Table 4 Facilitation and competition processes that may be occurring in a vertebrate scavenger community related to the co-occurrence patterns and hypotheses established in this work. 66

Chapter 6. Behavioral interactions are modulated by facilitation along a heterotrophic succession

Table 5 Hypotheses explaining potential competition and facilitation processes through behavioral changes in the intensity of aggressiveness of the interactions between species, and variables influencing heterotrophic succession dynamics in a vertebrate scavenger assemblage in the Neotropics. 103

LIST OF FIGURES

Chapter 1: General Introduction **Page**

Figure 1 Network of relationships between the environment, the behavior of individuals, population dynamics of the species and biodiversity. 19
Figure 2 Examples of mixed-species aggregations 21
Figure 3 Classification and adaptations of terrestrial vertebrate scavengers 25
Figure 4 Vultures of the American continent 29
Figure 5 Conceptual framework on the relationships and effects that the behavior and species interactions can have at the level of population, community and ultimate response of the structure and functioning of ecosystems. 31

Chapter 2: Summary of materials and methods

Figure 6 Some of the potential scavenger species that could be recorded in the study area. 36
Figure 7 Map of the study area in the Brazilian *Cerrado*. 37
Figure 8 Difference between an intact and a fully consumed carcass 38
Figure 9 Main external variables, non-related to carrion or scavenger community, that were used in the different chapters of the thesis due to their possible influence on carrion consumption patterns, and on the composition of the scavenger community. 39

Chapter 3: Uncovering the vertebrate scavenger guild composition and functioning in the *Cerrado* biodiversity hotspot

Figure 10 Map of the study area in the Brazilian *Cerrado*, in the state of Piauí (Brazil). We show the locations of 56 monitored carcasses (11 large and 45 small). 47
Figure 11 Images of some of the most frequent scavenger species obtained during this study with camera traps. 51
Figure 12 Percentage of large and small carcasses in which each scavenger species was detected eating. 52
Figure 13 Feeding time (in hours) that each taxonomic group spent eating carrion and percentage of carcasses visited by each group. 55

Chapter 4: Scavenger assemblages are structured by complex competition and facilitation processes among vultures

Figure 14 Daily activity patterns represented as the percentage of activity of scavenging species in the Brazilian *Cerrado*, differentiating between obligate and facultative scavengers. And activity patterns of the four species of vultures found in this scavenger community through the different days of consumption of the two sizes carcasses. 73

Figure 15 Results of the spatial and spatio-temporal co-occurrence analyses between pairs of species, both qualitative co-occurrence and quantitative GLMs (spatial co-occurrence) and GLMMs (spatio-temporal co-occurrence) that relate the abundances of the species. 75

Figure 16 Spatio-temporal co-occurrence for the different days of consumption at large carcasses. 76

Chapter 5. Scavenging in the realm of senses: smell and vision drive recruitment at carcasses in Neotropical ecosystems

Figure 17 The succession of arrival and arrival time since carcass placement of different species to large carcasses and small carcasses. 91

Figure 18 Results of the logistic regression on heterospecific influence on first arrival times, shown separately for large and small carcasses. 92

Chapter 6. Behavioral interactions are modulated by facilitation along a heterotrophic succession

Figure 19 Conditional effects of all the explanatory variables included in the best models (i.e., lower WAIC) obtained for community dynamics analyses: A) richness, B) abundance C) Shannon-Wiener diversity index and D) total turnover. 109

Figure 20 Bayesian mixed model results representing the conditional effects of PC on A) abundance of Cathartes vultures, B) black vulture abundance and C) king vulture abundance. 111

Figure 21 Conceptual illustration of a heterotrophic succession that drives the consumption of large carcasses in a Neotropical scavenger community. 112

SUMMARY

Understanding the processes that allow several species depending on the same resource to coexist are fundamental in the maintenance of biodiversity, ultimately affecting ecosystem functions, and being a key issue in community ecology. The non-random structure of natural communities is driven by multiple biological, ecological, and evolutionary forces, and can be described by habitat utilization, resource availability, and the activity and interactions of the organisms that compose them. These interactions can be antagonistic (e.g., competition) or facilitative (e.g., mutualistic plant-pollinator). However, not all species within a network play the same ecological role or perform it with the same importance, since they will have different ecological traits. Competition between species that coexist within the same guild is particularly interesting because the similarity of their ecological niches increases competition strength. However, positive co-occurrence patterns within guilds may also emerge from facilitation processes, reducing competition and playing an important role in community structure. Carrion is an ephemeral and unpredictable resource in time and space. These characteristics allow a multitude of species to feed on the resource, even forming temporary mixed aggregations with high levels of competitive and facilitative interactions. Such dynamics make scavenger systems an ideal model for studying positive and negative processes across scales using diverse methodological approaches.

This thesis focuses on describing the ecological factors and behavioral patterns that govern a scavenger community in the Neotropics, by the placement and monitoring of two carcass sizes in the field by using camera-trapping. Specifically this thesis aims to assess the following objectives: describe for the first time the scavenger community and identify the factors affecting scavenging efficiency in the Brazilian *Cerrado* (***Chapter 3)***; infer interspecific processes of competition and facilitation through the study of species co-occurrence patterns in this Neotropical guild (***Chapter 4***); analyze possible information transmission cascades within this Neotropical scavenger community (***Chapter 5***); and determine factors driving temporal dynamics of scavenging successions (***Chapter 6***).

In ***Chapter 3***, we describe the vertebrate scavenger community composition of the Brazilian *Cerrado*, a biodiversity hotspot. In addition, we analyzed the effects of vegetation cover, time of carcass placement and carcass weight, on different variables related to community composition and efficiency. We documented a total of 19 vertebrate scavenging species, four species of vultures and 15 facultative scavengers. Carcass size was the most important factor affecting the scavenger assemblage and consumption patterns, while we did

not find an effect of habitat or timing of carrion placement on scavenging patterns. The results show a highly diverse and efficient scavenging vertebrate community in the Brazilian *Cerrado*, and the need to preserve them in the face of the significant habitat transformations suffered by this biodiversity hotspot.

In ***Chapter 4***, we analyzed patterns of spatial and temporal co-occurrence between species, both qualitatively and quantitatively, and determined the activity patterns of the different scavenger species. Our results show complex competitive and facilitative relationships among scavenging species in the Brazilian *Cerrado* that are influenced by carcass size, and change depending on the spatial and temporal scale at which they are analyzed. The scavenger assemblages that consumed large and small carcasses were different, evidencing resource partitioning between obligate and facultative scavengers. Furthermore, as an alternative to reduce competition levels, most species showed differences in their scavenging patterns, in addition to a strong temporal segregation during carcass consumption. Regarding New World vultures, our results suggest a strong interference competition between species with clear differences in their ecological traits (e.g., size, social behavior). However, we also found evidence of facilitation processes between vulture species in the location and access to the interior of the carcasses. Our findings highlight the role of obligate scavengers both in competition and facilitation processes in this vertebrate scavenger community.

To clarify the processes that result in associations between vulture species with different foraging efficiencies, in ***Chapter 5***, we apply a survival-modelling strategy to determine the transmission of social information among different species during carrion location. The use of different senses (smell and sight) within this guild facilitates carcass location through the transmission of social information between species with different carrion foraging efficiencies. Vultures with a highly developed sense of smell play a key role in this process, as they are the first ones to arrive at the carcasses and their presence seems to serve as a visual cue for other species to locate the resource. Our study supports the local enhancement hypothesis within scavengers, whereby individuals locate carcasses by following foraging heterospecifics, also suggesting the importance of the sense of smell in the maintenance of the community structure.

In ***Chapter 6***, we perform the first in-depth analysis of the factors driving temporal dynamics of scavenging successions by using interspecific aggressions as a behavioral proxy of competition intensity. The results show that resource availability shapes behavioral interactions between species. Furthermore, facilitation was related to moments of higher tolerance (i.e., lower aggressiveness), thus reducing competition intensity and affecting community structure and dynamics. Our study highlights the importance of monitoring behaviors that are directly transferable to community function (e.g., those related to foraging and resource consumption), also considering the dynamics of succession over time. This novel framework evidences complex ephemeral successional processes characterized by a fluctuation in facilitation and competition intensity during the consumption of an unpredictable resource linked to key ecosystem processes.

Finally, the general discussion (***Chapter 7***) addresses the implications of the findings obtained in the previous chapters, its contribution to the study of communities from a general perspective, and for scavenger assemblages, including conservation implications. Furthermore, we examine the limitations identified and outline avenues for future research aimed at comprehending the determinants of the balance between positive and negative processes among coexisting species.

RESUMEN

Comprender los procesos que permiten la coexistencia de varias especies que dependen de un mismo recurso es fundamental para el mantenimiento de la biodiversidad, lo que en última instancia afecta a las funciones ecosistémicas, siendo una cuestión clave en la ecología de comunidades. La estructura no aleatoria de las comunidades está impulsada por múltiples fuerzas biológicas, ecológicas y evolutivas, pudiendo describirse mediante la utilización del hábitat, la disponibilidad de recursos y la actividad e interacciones de los organismos que las componen. Estas interacciones pueden ser antagónicas (por ejemplo, competencia) o positivas (por ejemplo, mutualismo planta-polinizador). Sin embargo, no todas las especies de una red desempeñan el mismo papel ecológico, ni lo hacen con la misma importancia, ya que pueden tener rasgos ecológicos diferentes. La competencia entre especies que coexisten dentro del mismo gremio es especialmente interesante porque cuanto más similares son sus nichos ecológicos mayor es la competencia. Sin embargo, los patrones positivos de co-ocurrencia dentro de los gremios también pueden ser debidos a procesos de facilitación, reduciendo la competencia y desempeñando un papel fundamental en la estructura de la comunidad. La carroña es un recurso efímero e impredecible en el tiempo y el espacio. Estas características permiten que multitud de especies se alimenten de este recurso, llegando a formar agregaciones mixtas temporales con altos niveles de interacciones competitivas y de facilitación. Estas dinámicas hacen de los sistemas carroñeros un modelo ideal para estudiar procesos positivos y negativos a distintas escalas, y utilizando diversos enfoques metodológicos.

Esta tesis se centra en describir los factores ecológicos y patrones de comportamiento que gobiernan una comunidad de carroñeros en el Neotrópico, mediante la colocación y seguimiento de carroñas de dos tamaños en el campo mediate fototrampeo. En concreto, esta tesis pretende evaluar los siguientes objetivos: describir por primera vez la comunidad de carroñeros e identificar los factores que afectan a la eficiencia carroñera en el *Cerrado* brasileño (***Capítulo 3***); inferir procesos interespecíficos de competencia y facilitación a través del estudio de los patrones de co-ocurrencia de especies en este gremio neotropical (***Capítulo 4***); analizar posibles cascadas de transmisión de información dentro de esta comunidad de carroñeros (***Capítulo 5***); y determinar los factores que impulsan la dinámica temporal de las sucesiones carroñeras (***Capítulo 6***).

En el ***Capítulo 3*** describimos la composición de la comunidad de vertebrados carroñeros del *Cerrado* brasileño, un punto caliente de biodiversidad. Además, analizamos los

efectos de la cobertura vegetal, el momento de colocación de la carroña y su peso, sobre diferentes variables relacionadas con la composición y eficiencia de la comunidad. Documentamos un total de 19 especies de vertebrados carroñeros, cuatro especies de buitres y 15 carroñeros facultativos. El tamaño de las carroñas fue el factor más importante que afectó a la composición de la comunidad de carroñeros y a los patrones de consumo, mientras que no se observó ningún efecto del hábitat o del momento de la deposición de la carroña. Los resultados muestran una comunidad de vertebrados carroñeros altamente diversa y eficiente en el *Cerrado* brasileño, y la necesidad de preservarlos frente a las significativas transformaciones del hábitat que se están dando en este punto caliente de biodiversidad.

En el ***Capítulo 4***, analizamos los patrones de co-ocurrencia espacial y temporal entre especies, tanto cualitativa como cuantitativamente, y determinamos los patrones de actividad de las diferentes especies carroñeras. Nuestros resultados muestran complejas relaciones competitivas y facilitadoras entre las especies carroñeras en el *Cerrado* brasileño que están influenciadas por el tamaño de la carroña, y cambian dependiendo de la escala espacial y temporal a la que se analicen. Los grupos de carroñeros que consumieron carroñas grandes y pequeñas fueron diferentes, evidenciando la partición de recursos entre carroñeros obligados y facultativos. Además, como alternativa para reducir los niveles de competencia, la mayoría de las especies mostraron diferencias en sus patrones de actividad, además de una fuerte segregación temporal durante el consumo de la carroña. En cuanto a los buitres del Nuevo Mundo, nuestros resultados sugieren una fuerte competencia por interferencia entre especies, con claras diferencias en base a sus rasgos ecológicos (p. ej., tamaño, comportamiento social). Sin embargo, también encontramos evidencias de procesos de facilitación entre especies de buitres en la localización y acceso al interior de las carroñas. Nuestros hallazgos destacan el papel de los carroñeros obligados tanto en los procesos de competencia como de facilitación en esta comunidad de vertebrados carroñeros.

Para entender los procesos que dan lugar a asociaciones entre especies de buitres con distintas eficiencias de búsqueda de alimento, en el ***Capítulo 5*** aplicamos una estrategia de modelado de supervivencia para determinar la transmisión de información social entre distintas especies durante la localización de la carroña. El uso de diferentes sentidos (olfato y vista) dentro de este gremio facilita la localización de las carroñas mediante la transmisión de información social entre especies con diferentes eficiencias de forrajeo. Los buitres con un sentido del olfato muy desarrollado desempeñan un papel clave en este proceso, ya que son los primeros en localizar y llegar a las carroñas y su presencia parece servir de pista visual para que otras especies localicen el recurso. Nuestro estudio apoya la hipótesis de la "mejora local" dentro de los carroñeros, según la cual los individuos localizan las carroñas siguiendo a los heteroespecíficos que buscan alimento, sugiriendo también la importancia del sentido del olfato en el mantenimiento de la estructura de la comunidad.

En el ***Capítulo 6***, realizamos el primer análisis en profundidad de los factores que determinan la dinámica temporal de las sucesiones de carroñeros utilizando las agresiones interespecíficas como indicador conductual de la intensidad de competencia. Los resultados muestran que la disponibilidad de recursos determina las interacciones conductuales entre especies. Además, la facilitación se relacionó con momentos de mayor tolerancia (es decir, menor agresividad), reduciendo así la intensidad de la competencia y afectando a la estructura y dinámica de la comunidad. Nuestro estudio destaca la importancia de monitorizar los comportamientos que son directamente transferibles a la función de la comunidad (por ejemplo, los relacionados con la búsqueda de alimento y el consumo de recursos), considerando también la dinámica de la sucesión a lo largo del tiempo. Este novedoso marco evidencia complejos procesos dinámicos caracterizados por una fluctuación en la facilitación y la intensidad de la competencia durante el consumo de un recurso impredecible vinculado a procesos ecosistémicos clave.

Finalmente, la discusión general (***Capítulo 7***) aborda las implicaciones de los hallazgos obtenidos en los capítulos anteriores, su contribución al estudio de las comunidades desde una perspectiva general, y para el gremio de carroñeros en particular, incluyendo las implicaciones para la conservación. Además, se examinan las limitaciones identificadas y se esbozan vías para futuras investigaciones encaminadas a comprender los determinantes del equilibrio entre procesos positivos y negativos entre especies que coexisten.

CHAPTER 1: GENERAL INTRODUCTION

COMMUNITY STRUCTURE AND FUNCTIONING

Community ecology is the study of patterns of species diversity, abundance and composition , and how organisms interact with each other (Vellend 2010, Levine et al. 2017). Traditional studies of plant and animal communities were merely descriptive, determining species composition and richness (Wallace 1962, Whittaker 1962), followed by an increased interest on how species composition affects ecosystem functioning because of differences in species traits (e.g., Vitousek & Walker 1989, Wedin & Tilman 1993, Power 1995). Moreover, species interactions were studied between pairs of species, however, the need to study the role of species, considering their traits, and the interactions between them simultaneously has lately became evident (Holt 2009, Vellend 2010). Hence, during the last decades, the improvements in complex statistical analyses, and the computational potential, has allowed the development of new fundamental and advanced analytical tools to determine how community structure and composition affect ecosystem functioning and stability (Dunne et al. 2002, Götzenberger et al. 2012, Loreau & de Mazancourt 2013, Sebastián-González et al. 2020a). For example, the structure of food webs, which describe the feeding relationships between species within a community, can provide insights into how energy flows through an ecosystem and how changes in one species can ripple through the entire community (Bascompte and Melián 2005). Additionally, the examination of co-occurrence patterns can reveal how the presence or absence of certain species is influenced by environmental factors, such as habitat type or resource availability and ecological interactions (Gotelli and McCabe 2002, Sebastián-González et al. 2010). Therefore, the focus of community ecology shifted from describing community patterns to understanding the processes underlying these patterns and factors affecting the organization of communities, by using advanced analytical approaches.

The non-random structure of natural communities is driven by multiple biological, ecological, and evolutionary forces, and can be described by habitat utilization, resource availability, and the activity of the organisms that compose them (Schoener 1974, Tilman 1999, Ovaskainen et al. 2017). In this way, the structure of a community can be studied at different scales. On the one hand, an ecological assemblage is defined as species groups within a community found in a specific habitat or location, which can be defined by their spatial and temporal boundaries, without involving interactions between them (Cardinale et al. 2002, Magurran and Henderson 2010). On the other hand, ecological networks are complex systems of interactions between coexisting species within an assemblage and have received enormous interest in recent times (Bascompte 2010, Eklöf et al. 2013, Robinson and

Strauss 2020). These interactions can be antagonistic (e.g., predator-prey relationships, competition) or facilitative (e.g., mutualistic plant-pollinator or frugivory), and other forms of interdependence between species, as parasitism (Delmas et al. 2019), being the key component of biodiversity (Harrison et al. 1991, Thompson 2005, Ullas Karanth et al. 2017, Veit and Harrison 2017, Prugh and Sivy 2020). But not all species within a network play the same ecological role or perform it with the same importance. Thus, identifying which biological characteristics or ecological traits are related to the different roles of the species in the network may be of major importance for understanding the drivers of the networks' functioning (Sebastián-González et al. 2021, Schleuning et al. 2023). Also, the structure and organization of the interactions within a network have been directly related to the stability and their potential resilience to environmental change in some types of interactions, e.g., mutualisms (Bastolla et al. 2009, Sebastián-González 2017). Therefore, ecological networks can be studied at multiple scales, from the interactions between individual organisms to the relationships within entire communities or ecosystems (Tylianakis et al. 2010, Fontaine et al. 2011, Guimarães 2020).

Processes that influence ecological communities and networks, and therefore their species diversity and composition are not static, but rather can change over time and space. Temporal dynamics are essential to gain a mechanistic comprehension of the drivers of community assembly or monitor the effect of disturbances (Ontiveros et al. 2021). Hence, ecological succession is defined as a sequence of changes in an ecological community that are observable in time and space, which provides a conceptual framework for comprehending community and ecosystem dynamics (Connell and Slatyer 1977, Prach and Walker 2011, Begon and Townsend 2020). Most of the research has focused on autotrophic successions (i.e., dominated by autotrophic organisms), during which the starting point is a low biomass point, from which a colonization of species occurs as time goes by, driving an increase in biomass and energy flow (Chang and Turner 2019, Oliveira et al. 2019). In contrasts, heterotrophic successions have received much less attention. This type of succession occurs in the opposite direction, starting from a pulse of biomass (e.g., carrion) that is consumed over time as it is colonized by species, resulting in the disappearance of the resource and the community that has colonized it (Begon and Townsend 2020). In spite of the importance of the temporal dimension in such processes, most of the studies on interaction networks and intra-guild coexistence are based on static approximations over time. This shows the need to include the temporal component at different scales to understand the processes that allow coexistence and sharing of a resource by multiple species (Kronfeld-Schor and Dayan 2003, Seppänen 2007).

SPECIES INTERACTIONS: COMPETITION AND FACILITATION

One of the most studied interactions is competition, i.e., the relationships between organisms that consume the same resources (Schoener 1974, HilleRisLambers et al. 2012). Classically, competition is understood as when an organism consumes a resource that is no longer available to other species, which is then negatively affected (Begon and Townsend 2020). At large scales, co-occurrence of competing species is generally facilitated by their spatial segregation (Kneitel and Chase 2004a). However, ecological guilds are groups of species that share a resource (i.e., they have a similar niche) and co-occur in sympatry, and therefore within which interspecific competition may be especially important among agonistic interactions (May and MacArthur 1972, Simberloff and Dayan 1991, Durant 1998, Holt 2009). Consequently, understanding how communities maintain their diversity despite the coexistence of species belonging to the same guild is an outstanding issue in ecology (Bascompte 2010, Fukami 2010, Levine et al. 2017).

Ecological character displacement principle (i.e., niche differentiation) is one of the fundamental mechanisms to explain coexistence and suggest that coexisting species must differ along their ecological niche, avoiding competitive exclusion by means of resource partitioning and spatial or temporal segregation (MacArthur and Levins 1967, Roughgarden 1976, Davies et al. 2007b, Finke and Snyder 2008, Gravel et al. 2011). In this way, species living in the same place may reduce competition by avoiding each other spatially, occupying or feeding in different areas or moments (Chesson 2000, Amarasekare 2003). As a result, heterogeneous habitats will favor spatial segregation between species (Marrotte et al. 2020). Moreover, species could adapt their circadian activity patterns as well to reduce the temporal overlap of their activity with that of competitors (Ullas Karanth et al. 2017, Zanni et al. 2021). Also, differences in competitive abilities at the interspecific level usually give rise to dominance hierarchies (Galbraith et al. 2017). Therefore, dominant competitors will displace rivals by interference competition, i.e., displacement from the resource by aggression, and thus physically, or by exploitative competition, i.e., they get to the resource first and consume it quickly (Bertelsmeier et al. 2015). In this way, subordinate competitors will avoid the centers of activity or the most densely populated locations of the dominant species (Durant 1998, Schlägel et al. 2020). Summarizing, intra-guild competition might be reduced by differences in morphology, physiology and social behavior, which create differences in species' foraging niches (Davies et al. 2007a, Sogbohossou et al. 2018, Byrne et al. 2019).

Studies on animal communities have classically focused on the negative interactions (i.e., predation and competition), however, within guilds, we can also find positive co-occurrence patterns between species derived from facilitation processes (Kruuk 1967, Veit and Harrison 2017). These positive patterns may also be related to a decrease in the levels of competition, being as important in shaping the structure of communities as negative processes (Stachowicz 2001, Bruno et al. 2003, Wilson and Wolkovich 2011). It has been suggested that facilitative processes may be more evident in some food webs, i.e., scavengers or marine predators (Wilmers et al. 2003, Veit and Harrison 2017). In contrast, other guilds are mainly dominated by competitive relationships, e.g., carnivores, as inter-species competition would be more intense due to their physiological adaptations for predation (Palomares and Caro 1999). But these two ecological networks are linked, so that top-predators can provide carrion to other scavengers, including carnivores that coexist and compete for prey, (Allen et al. 2014, Moleón et al. 2014, Prugh and Sivy 2020). This has been demonstrated in Yellowstone, where wolves have been found to make scavenging pulses more consistent throughout the year (Wilmers et al. 2003). Furthermore, facilitating processes can also result in positive spatio-temporal co-occurrence, i.e., aggregations, between species through the transmission of social information (Sebastián-González et al. 2010, Goyert et al. 2014, Veit and Harrison 2017). In this sense, there is a need to consider all possible interactions, both negative and positive, at the guild level, considering also that these processes can be highly context-dependent.

BEHAVIOR AS A KEY TOOL TO UNDERSTAND ANIMAL INTERACTION NETWORKS

The most rapid responses of organisms to any change are at the behavioral level, prior to possible evolutionary changes (Wong and Candolin 2015). But what do we mean by behavior? Behavior encompasses cognition, learning, social interactions and movement, being related to fitness and studied at different scales (Breed and Moore 2021). Species interactions determine ecological processes, which also influence the biodiversity and stability of ecosystems (Loreau and de Mazancourt 2013). Therefore, in the last decade, behavioral biology has been included in the study of animal networks since the behavior of one species normally influences the behavior of other species through interspecies interactions, leading to cascading effects at the community level (**Figure 1**) (Kurvers et al. 2014, Rahman and Candolin 2022). Thus, the inclusion of behavior in the study of animal guild structure and functioning can provide new insights about the transmission of information between individuals, the importance of certain species in the maintenance of the community structure and the intensity of competition between species, among others (Silk et al. 2018). In this way, monitoring behaviors that are directly transferable to ecosystem functions (e.g., foraging) as opposed to or in addition to those that could have indirect implications (e.g., flight behaviors, which may or may not impact foraging) will be more valuable in anticipating ecosystem impacts (Tuomainen & Candolin 2011, Wilson et al. 2020). Indeed, the need to refine the study of functional relationships between organisms by measuring traits based on behavioral measures has become evident (Schleuning et al. 2023). In this way, behavior can be studied observationally, e.g., by observing animals interacting from observation points (Altmann 1974), or it can be inferred indirectly, e.g., using of GPS collars (Bennison et al. 2018, Wiesel et al. 2019). Thus, most of the published work on behavior is focused on movement ecology, describing spatiotemporal patterns of movement through radio tracking. However, there are certain components of behavior (i.e. hierarchies) that require observational data, either direct or indirect (i.e., remote recordings).

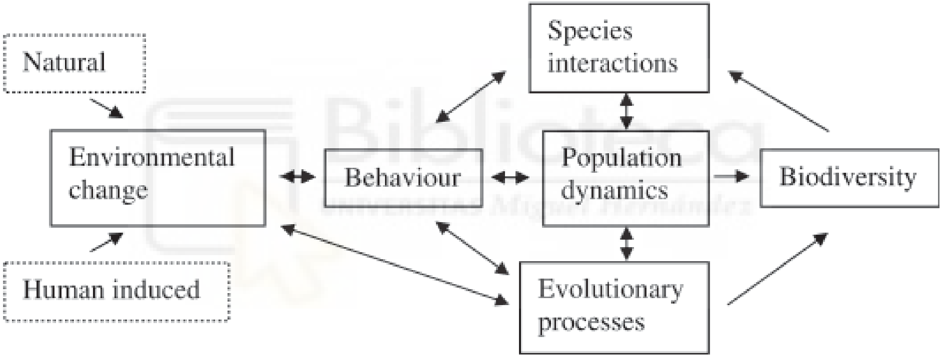


Figure 1. There is a complex network of relationships between the environment, as environmental changes influence the behavior of individuals, and the decisions made by individuals can have direct effects on the population dynamics of the species. Species also interact with each other through behavior, having an indirect effect on biodiversity. Behavior, being directly linked to the fitness of individuals, is directly related to evolutionary processes. Modified from Tuomainen & Candolin 2011.

Decision-making is present in the daily life of animals, e.g., mating, social behavior, foraging, or predator avoidance, driving their behavior and having a deep effect on individual fitness. This process of decision making is complex and, therefore, at the ecological scale, animals have two ways of obtaining information from the environment to make decisions as beneficial as possible (McNamara and Houston 1986). First, through individual learning and, therefore, personal information. Second, through social information, i.e., obtaining information indirectly from the behavior of other individuals or its product (Danchin et al. 2004, Duboscq et al. 2016). Several studies have shown how social information influences animal movement

(Langrock et al. 2014), foraging patterns (Galef and Giraldeau 2001, Valone and Templeton 2002), habitat selection and reproduction (Giraldeau et al. 2002). In this way, social information not only affects an individual's decision making, and therefore its behavior, but also generates correlations between the behaviors of many individuals, potentially having cascading effects at the population and community level (Gil et al. 2018a).

The behavior or the simple presence of an animal produces sensory information that can be picked up and used by other organisms in the environment (Danchin et al. 2004, Dall et al. 2005, Goodale et al. 2010). Information transmission processes have been classically studied between individuals of the same species (Laland 2004), but in recent times, these information transmission processes have also been evidenced between individuals of different species (Seppänen 2007, Jaakkonen et al. 2015). In fact, information provided by selected heterospecific individuals may be equally or more valuable than information provided by conspecifics, because other species differ in ecological traits, behavior, and methods of information gathering (Avarguès-Weber et al. 2013, Goodale et al. 2020). The capacity to use and generate social information must be under strong selection and may have implications at multiple scales in which an individual's behavioral decisions carry over to interspecific interactions and ultimately to the structure of the community (Goodale et al. 2010, Jaakkonen et al. 2015). In addition, information transmission may depend on a multitude of different behavioral interactions (e.g., imitation, recognition of heterospecific alarm calls), so it is essential to take a global view to determine how interactions regulate information transmission and thus ecological networks (Silk et al. 2018). Thus, the use of temporal and spatial data, combined with information on behavioral variations at community level, is fundamental to understand the processes of information transmission and concentration of different species (Goodale et al. 2010).

Box 1. Mixed-species aggregations

Aggregation is defined as a gathering of animals in a place. Mixed-species animal aggregations, also called mixed species colonies, are spatial and temporal groupings of different animals due to heterospecific attraction between them (Goodale et al. 2017). They have been described in birds, mammals, invertebrates and coral fishes (Sinclair 1985, Harrison et al. 1991, Stensland et al. 2003, Heymann and Hsia 2015, Boulay et al. 2019, Goodale et al. 2020). The stationary and dynamic nature of these aggregations is underpinned by the exchange of information between individuals, which drives their interactions (Goodale et al. 2017). In this way, the individual of a species can decide whether to join the group, or not, and when to join or leave it depending on various factors (e.g., identity of the species already present, number of individuals) (Martínez & Gomez 2013, Jones et al. 2017, Johnson et al. 2018). Mixed-species aggregations use to be mediated by the presence of ephemeral (Barton et al. 2013b, Hille et al. 2016) or mobile (Duffy 1989, Thiebault et al. 2016, Veit and Harrison 2017) resources, occurring between species of the same trophic level (**Figure 2**). Thus, this species groups are mediated in many cases by the transmission of information between individuals of different species that consume the same type of resource (Laland and Williams 1997, Rafacz and Templeton 2003, Duboscq et al. 2016, Gil et al. 2019). However, these aggregations can also occur due to the congregation of species for anti-predator functions, e.g., some seabird colonies. These anti-predator advantages are provided by a quicker warning, greater ability to harass the predator, etc. creating a free-predator area (Gameiro et al. 2022). However, it has also been shown that bird colonies or roosts can serve as neuralgic nuclei for the transmission of social information about the location of resources (Galef 2012).

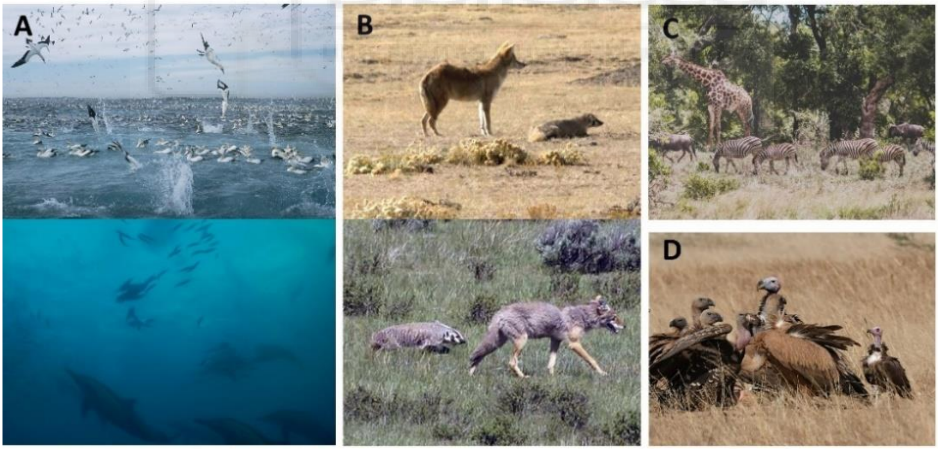


Figure 2. (**A**) Fish schools attract a multitude of species that feed on the resource and compete for it, but it also results in facilitation processes due to an intense exchange of information between a multitude of different predators, e.g., seabirds and dolphins. Photo credit: Galatée Films 2009, see Thiebault et al. 2016. (**B**) Sometimes, animal mixed-aggregations do not include many individuals, as is the case of the mutualism that occurs between coyotes and badgers when hunting (Minta et al. 1992). Photo credit: Kimberly Fraser. (**C**) Aggregations between different herbivores have been shown to reduce the risk of predation. Such as happens in the associations between zebra and wildebeest, where the first uses the second to obtain protection (Sinclair 1985). Photo credit: Taryn Elliott. (**D**) Different species of vultures during carcass consumption in Africa. Photo credit: Eneko Arrondo.

Specifically, foraging behavior is a key aspect in understanding the ecology of a species, as foraging strategies influence the movement of organisms, their behavior and ultimately their fitness (Schoener 1971, Spiegel et al. 2013). Animals may use different strategies and senses to locate food patches. Smell, sight, audition and chemoreception are the main senses used by vertebrate animals during foraging. The use of senses is highly differentiated among taxonomic groups, being their foraging strategy based on the use of one or a combination of several senses depending on the type of resource on which the animal depends (Moulton 1967, Dusenbery 1992, Nevitt 2008, Ruzicka and Conover 2012). However, foraging not only refers to the type and mode of acquiring resources (e.g., food) but also to the acquisition of information about those resources (Clark & Mangel 1984, Harel et al. 2017a). Thus, acquiring information and maintaining information about resources is critical for animals (Jones et al. 2017). The greater the overlap of a resource among species, the greater the competition for the consumption of the resource will be, but there will also be greater benefits from using information about the resource from others (Goodale et al. 2010). This generates a trade-off between competition and the quality of information about the resource that is transmitted between competing conspecifics and heterospecifics (Giraldeau et al. 2002, Gil et al. 2019). Hence, in ecological systems with high intraspecific as well as interspecific competition, such as carnivore or scavenger guilds, behavioral strategies that allow species to gain information to find food and kleptoparasite more efficiently should be expected (Stahler et al. 2002). Particularly, the ability to get information from conspecifics and heterospecifics on the location and quality of resources has mayor implications for species that depend on unpredictable resources both spatially and temporally, e.g., carrion (Stahler et al. 2002, Rafacz and Templeton 2003).

The use of social information can also involve the spatial aggregation of individuals resulting in different benefits, such as reduced predation risk, e.g., due to an increase in the number of individuals of a group that facilitates the detection of a predator (Beauchamp 2013) or an increase in foraging efficiency, e.g., one species makes the resource available to another (see **Box 1**) (Goyert et al. 2014, Thiebault et al. 2016, Martínez et al. 2018). In this way, facilitation processes occur through the transmission and use of social information, such as is "local enhancement", i.e., when an individual detects a resource thanks to the presence or activity of another animal (Arbilly and Laland 2014, Cortés-Avizanda et al. 2014). However, aggregations in resource patches, forming temporary mixed groups of species feeding, will also increase inter- and intraspecific competition (Harrison and Whitehouse 2011, Loukola et al. 2013). Furthermore, the competitive ability of animals to discover and dominate a resource plays an important role in the structure of numerous faunal assemblages, as competitive differences between individuals give rise to dominance hierarchies (Williamson et al. 2016, Galbraith et al. 2017, Kwon and Choi 2020). Likewise, these hierarchies will be important when it comes to whether a species uses a resource that is already being used by other individuals (Binz et al. 2014, Goodale et al. 2017). Consequently, understanding the behavioral processes that allow a multitude of individuals of different species to compete at the same time in the same place for a resource became fundamental.

Species that have different abilities can play key roles in transmitting information (Ward and Zahavi 1973, Jones et al. 2017). For example, social species have a greater ability to communicate, i.e., greater call repertoire and cognitive complexity, which makes it easier for individuals of other species to recognize and use alarm call information against predators (Sewall 2015). However, different abilities of species within a guild (e.g., flight dynamics, foraging behavior) not only imply that some are competitively superior, but also that, competitively inferior species may benefit from the presence of the more competitive ones through the transmission of information (Morinay et al. 2020). In the case of birds, it has been shown that they use visual and olfactory information while foraging, although not all of them have these senses equally developed (Potier et al. 2019, Jackson et al. 2020). Species that use different foraging methods (e.g., use of different senses) will differ in their ability to locate the resource and will provide non-redundant information to the rest of the species. For example, certain species of seagulls are particularly efficient at locating food, and other species follow them, using them as a visual cue to find resource patches (Hoffman et al. 1981).

STUDY MODEL: THE SCAVENGER GUILD

Carrion is a “high-quality form of detritus that is composed entirely of dead animal matter” (Wilson and Wolkovich 2011). The role of scavenger communities (i.e., vertebrate and invertebrate organisms that feed on dead animals) has historically been underestimated in ecology. Nevertheless, with the increase in research focused on this guild in recent decades, the key role of carrion and, therefore, of scavengers in maintaining ecosystem functioning has become evident (Mateo-Tomás et al. 2015, Sebastián-González et al. 2019, 2021). As a result, we now know its importance in decreasing disease transmission (Ogada et al. 2012a), stabilizing food webs (DeVault et al. 2003, Wilson and Wolkovich 2011), and promoting nutrient transmission between environments across the globe, contributing to their recycling (Cederholm et al. 1999, Carter et al. 2007, Beasley et al. 2019). In this way, carrion scavenging has been reported to affect 45% of food-web links worldwide (Wilson and Wolkovich 2011, Schlichting et al. 2019).

Carrion is a resource that has several characteristics that make it unique. It is an isolated patch of high nutritive and ephemeral resource (Beasley et al. 2019) being its availability in ecosystems influenced by the structure of the vertebrate and invertebrate communities (Houston 1985, DeVault et al. 2003). In addition, carrion is generally unpredictable in both space and time. The fact that carrion is not a ubiquitous resource allows an enormous diversity of scavengers with different capabilities (e.g., different competitive and foraging abilities) to consume it, which otherwise could not sustain such a high scavenger richness due to the principle of competitive exclusion (i.e., two species that have identical ecological niches cannot coexist in the same habitat as one species will outcompete the other, leading to the exclusion of the latter) (Beasley et al. 2019). In this, way, within terrestrial vertebrate scavengers, we can distinguish species with diverse ecological, behavioral and life history traits, resulting in two main functional groups: obligate scavengers and facultative scavengers (**Figure 3**) (DeVault et al. 2003). Obligate scavengers include only vultures (Accipitridae and Cathartidae families), as they are the only vertebrates that depend exclusively on carrion as a resource, being the most efficient vertebrate scavengers because of their adaptations to this form of feeding and their ability to monopolize the resource (Benbow, M. Eric, Jeffery K. Tomberlin 2016). In contrast, facultative scavengers include those organisms that consume carrion when it is available, but do not depend exclusively on it (**Figure 3**). Thus, within the facultative scavengers, we find a wide range of scavenging behaviors, from animals that hardly scavenge at all to others that do it frequently, including large mammals, meso-carnivores, birds and reptiles (**Figure 3**) (DeVault and Krochmal 2002, DeVault et al. 2003, Sebastián-González et al. 2021). Although the abundance of invertebrate scavengers and microbial carrion decomposers far exceeds that of vertebrate scavengers, the role of vertebrate scavengers has also been proven to be essential in this ecological function (DeVault et al. 2003, Gutiérrez-Cánovas et al. 2020). On the one hand, some vertebrate scavengers are often also predators, and therefore play a fundamental role by providing carrion to the ecosystem through their kills (Hunter et al. 2007, Allen et al. 2014). On the other hand, vertebrate scavengers also consume the largest quantity of vertebrate carrion biomass (e.g., 88.0 ± 8.3 % of carrion placed by Moleón *et al.* 2015 in African savannas was consumed by vertebrates) (DeVault et al. 2003, Beasley et al. 2019, Sebastián-González et al. 2019, Gutiérrez-Cánovas et al. 2020).

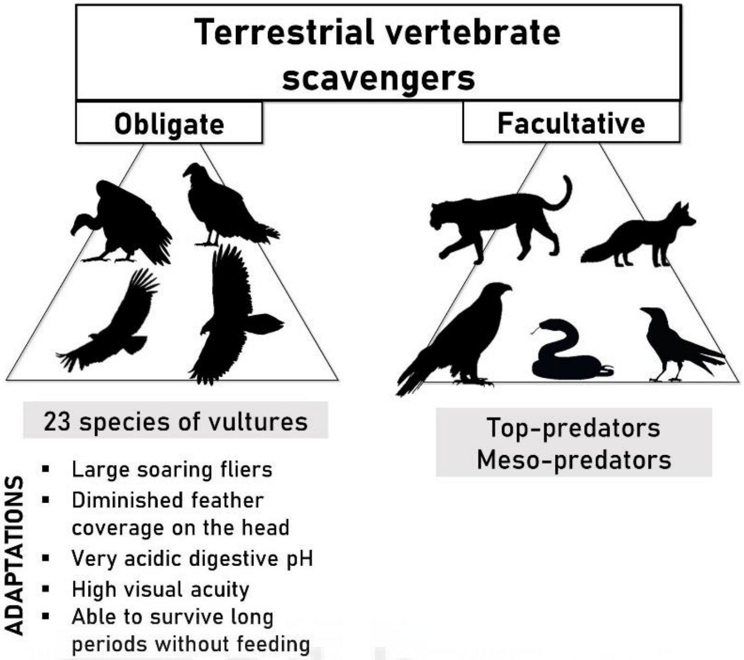


Figure 3. Terrestrial vertebrate scavengers can be classified into two groups. On the one hand, obligate scavengers (left side), which include only vultures, and which feed almost exclusively on already dead animal remains. On the other hand, we find the group of facultative scavengers (right side), which use other sources of resources, but also feed on carrion, finding organisms which scavenge occasionally, to others that use this resource very prominently in their diet.

Carcasses may create ephemeral hotspots of biological activity through the interactions of a multitude of species that feed on it. This implies a high richness of potential scavenger species resulting in high levels of interspecific competition, especially in rich communities (Ruxton & Houston 2004, Barton et al. 2013, Allen et al. 2014). To reduce competition, coexisting scavengers may use different strategies, such as establishing hierarchical patterns in the use of the resource, with the hierarchy directly related to certain ecological traits, such as body size or age (Kruuk 1967, Wallace and Temple 1987, Houston 1988, Kendall 2013, Moreno-Opo et al. 2020). Species with low competitive capacities (e.g., small body size) may reduce competition in carcasses through other strategies, such as by avoiding direct confrontations by segregating spatially and temporally in the use of carrion (Kruuk 1967, Blázquez et al. 2009, Kendall 2013, Olea et al. 2022) or by grouping with individuals of the same species (Blázquez et al. 2009, Kendall 2014). Specifically, vultures are the most specialized species in the consumption of carrion, sharing many physiological and morphological adaptations that make them very efficient when exploiting this resource

(**Figure 3**) (DeVault et al. 2003). They have also developed some strategies to decrease competition, for example, having different morphologies in the beak, that allow them to feed on different parts of the carcass (Kruuk 1967, Kendall 2014) or segregating in space and time (Olea et al. 2022).

Carrion consumption by vertebrate scavengers is influenced by several factors. Some are intrinsic to the carcass, some are related to the composition of the scavenger community in the area, while others depend on external factors related to the availability of resources in the system (i.e., both carrion and other complementary resources) and habitat. First, it has been observed the influence of the species to which the carcass belongs, the size of the carcass and its origin on scavenging patterns. Thereby, as the carcass size increases, the more scavengers will be able to consume it, and this in turn will affect consumption rates (Sebastián-González et al. 2013, Moleón et al. 2015a, Olson et al. 2016). Moreover, carcass type (i.e., species to which it belongs) influences carrion consumption patterns in several ways. Domestic ungulate carcasses tend to be detected and consumed more quickly than carcasses from wild ungulates, being also consumed by different assemblages of scavengers (Arrondo et al. 2019). In addition, mammalian carnivores avoid consuming carnivore carcasses to prevent disease transmission risk (Moleón et al. 2017, Muñoz-Lozano et al. 2019). Lastly, it has also been found that in certain systems, carcasses from the remains of predator kills are more attractive than carcasses from intact dead ungulates (Selva et al. 2005).

Second, the presence of certain key scavenger species influences scavenging processes (Gutiérrez-Cánovas et al. 2020). This is because not all scavengers play the same role within this guild, since depending on their functional traits, they will have different scavenging efficiencies (Gutiérrez-Cánovas et al. 2020). Vultures, being the only obligate scavengers, present a series of adaptations to this way of life, such as their large size, their ability to glide long distances with low energy expenditure, high information transmission capacity (e.g., high socialization), and their adaptation to the toxins and pathogens present in carrion (e.g., a very acidic digestive pH) (Houston 1979, Ruxton and Houston 2004, Shivik 2006, Jackson et al. 2008, Beasley et al. 2019). These adaptations make them able to consume larger quantities of carrion and at a higher rate than facultative scavengers. Thus, adaptations such as soaring flights or high visual acuity mean that communities where vultures are present have higher foraging rates and efficiency than those without obligate scavengers (Morales-Reyes et al. 2017, Hill et al. 2018). It has also been shown that scavenging birds are more efficient than mammals in locating carrion (Houston 1979, Ruxton and Houston 2004, Selva et al. 2005). However, large carnivores can also play a key role in scavenger assemblages, by limiting access to the carrion to other scavengers due to their dominance, by providing carrion by killing their prey, or also by opening the carcasses, facilitating access to the interior for scavengers who do not have the capacity (Selva et al. 2005, Hunter et al. 2007, Allen et al. 2014). Vultures, when present, will monopolize carrion because of their greater competitive ability due to their adaptations (Ruxton and Houston 2004). However, it has also been found that vulture presence on carcasses also increases carrion consumption by facultative scavengers through certain facilitation interactions related to carrion detection and consumption (Moleón et al. 2014). But these facilitation interactions can also occur in the opposite direction, from facultative scavengers to vultures (Moleón et al. 2014, Gutiérrez-Cánovas et al. 2020). This unequal role between species involves that scavenger communities are not randomly organized (Sebastián-González et al. 2016, 2020a). Thus, the diversity of the scavenger community affects its structure, while the community structure affects the dynamics of the scavenger community. Specifically, some studies have shown that a high species richness, together with a nested organization, means a higher tolerance of interspecific competition (Selva and Fortuna 2007, Sebastián-González et al. 2016).

Third, external factors such as alternative resource availability, seasonality in carrion supply, or habitat structure have also been found to influence scavenger patterns (Ruzicka and Conover 2012, Inagaki et al. 2020). However, the role of vegetation cover in carcass consumption patterns has been little studied (but see Pardo-Barquín et al. 2019, Stiegler et al. 2020). Dense vegetation cover may influence those scavengers who rely exclusively on visual cues to find carrion, like most avian scavengers (e.g., Old World vultures), making them unable to locate and access carcasses (Bamford et al., 2009, Ogada, Torchin, et al., 2012). Conversely, non-avian scavengers might be able to find carcasses even in areas with high vegetation cover because they can rely on both visual and olfactory cues (Arrondo et al., 2019, Moleón et al., 2019).

There are 23 species of vultures (i.e., obligate scavengers) worldwide, that have been classically divided into New World and Old World species. These two groups of obligate scavengers are phylogenetically unrelated, but share characteristics directly derived from their feeding ecology, e.g., lack of feathers on the head or soaring flight, being a clear example of evolutionary convergence (Houston 1985, Ruxton and Houston 2004). Most scientific literature have focused on the 16 vulture’s species which inhabit Asia, Europe and Africa (i.e., Old World), while New World Vultures have received much less attention, which results in poor information on some ecological and biological aspects of these species (**Figure 4**) (Santangeli et al. 2022).

The 7 species of New World vultures are distributed in an extensive area from North to South America. But the distribution of each species varies according to habitat preferences and availability (Thiollay et al. 1994). Unlike Old World vultures, none of which are found in forested environments, 5 of the New World vulture species inhabit tropical rainforests: King Vulture (*Sarcorhamphus papa*), Black Vulture (*Coragyps atratus*), Greater Yellow-headed vulture (*Cathartes melambrotus*), Lesser Yellow-headed vulture (*Cathartes burrovianus*) and Turkey Vulture (*Cathartes aura*) (Houston 1985). These habitat differences between the two groups of obligate scavengers have derived in a very different foraging behavior of these two assemblages. On the one hand, flight techniques, specifically flight heights, are different between species, e.g., Cathartid species (genus *Cathartes*) fly at lower altitudes than griffon vultures (genus *Gyps*) (Houston 1985, Duriez et al. 2014). On the other hand, Old World vultures only use vision to locate carrion, while some New World vulture species have a highly developed sense of smell. New World vulture species of the genus *Cathartes* show highly developed olfactory bulbs with a high number of mitral cells (Grigg et al. 2017, Potier 2019, Potier et al. 2019, Campbell 2021). This developed sense of smell, combined with the ability to fly long distances with minimum energy expenditure (Duriez et al. 2014), means that some New World vultures are very effective at locating carrion even in dense habitats. As a result, they may be the primary scavengers in some Neotropical habitats (Houston 1985, 1986, 1988, Mallon et al. 2013). In addition, it has been described how species of the genus Cathartes consume a greater proportion of small carcasses, which they find thanks to their sense of smell, thus avoiding higher levels of competition in larger carcasses (Houston 1988). Moreover, it has also been established that there is a clear hierarchy among the New World species, where those of larger body size, such as the King vulture, dominate over the smaller ones, such as the turkey vulture (Houston 1988). In addition, the importance of sociality for the success of these species has also been demonstrated (Wallace and Temple 1987, Mallon et al. 2013). This social hierarchy, together with the differences in foraging behaviors and capacities among coexisting species in the Americas, implies a temporal variation in the use of carrion, resulting in a succession in the consumption of this resource (Mallon et al. 2013).

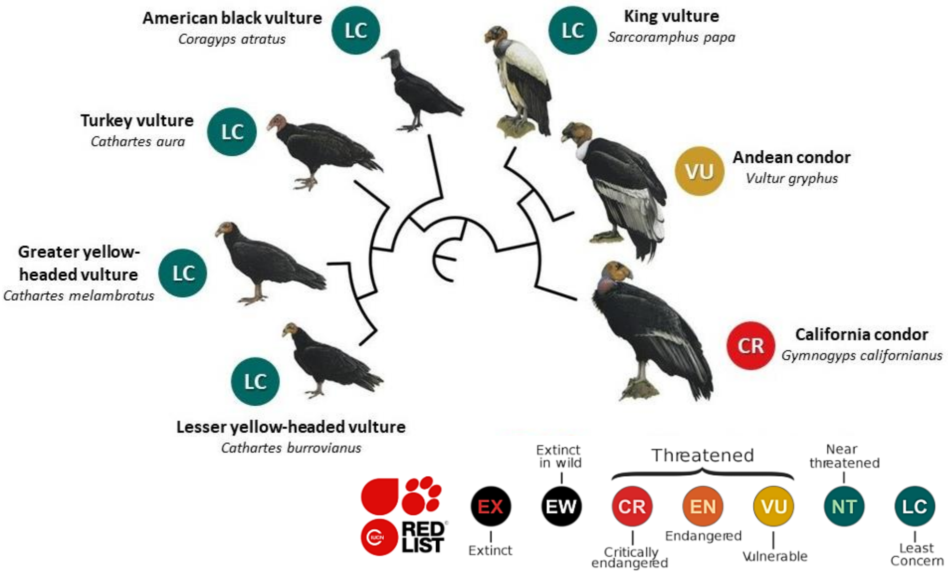


Figure 4. On the American continent we find 7 species of vultures (i.e., obligate scavengers), 5 of which are not listed as endangered. However, this classification is based on very limited information, which could cast doubt on the reality of their population trends. Modified from Johnson *et al.* 2016.

AIMS AND STRUCTURE OF THIS THESIS

The general aim of this thesis is to contribute to understanding the structure, functioning and processes of facilitation and competition undergoing carrion consumption in a Neotropical scavenger community from the Brazilian *Cerrado* (**Figure 5**). To achieve this objective, the current thesis is divided into 4 chapters in which the following specific objectives are proposed:

1. To describe and characterize the vertebrate scavenger community and scavenging patterns at carrion resources in the Brazilian *Cerrado*, as well as to determine the main factors influencing them.
2. To determine competitive and facilitation processes between species that belong to the same guild and are therefore exposed to highly competitive environments, by analyzing spatio-temporal cooccurrence patterns of the vertebrate scavenger species at carcasses in this Neotropical system.
3. To identify and rank the Neotropical scavenger species with different ecological traits (e.g., behavioral attributes) that influence the processes of information transmission during carcass location and recruitment at carcasses.

4. To understand the underlying dynamics of heterotrophic successions that occurs during the consumption of an ephemeral resource (i.e., carrion) through the study of scavengers' behavioral patterns and community metrics.

In this way, this thesis describes, at different scales, a scavenger guild very little known until now. For this purpose, different methodological approaches were used to achieve each objective, starting by analyzing the more general patterns of the structure and functioning of this guild (**Chapter 3**), passing through spatio-temporal patterns of consumption of different types of carrion (**Chapter 4**), the order of arrival of the species to the resource and the possible exchange of information between them (**Chapter 5**), to finally evaluate through a behavioral approach the community dynamics and changes in competition and facilitation patterns from the time the first scavenger locates a carcass until it is completely consumed **(Chapter 6**). Each of the chapters is presented as an individual scientific article, consisting of its own abstract, keywords, introduction, methodology, results and discussion.

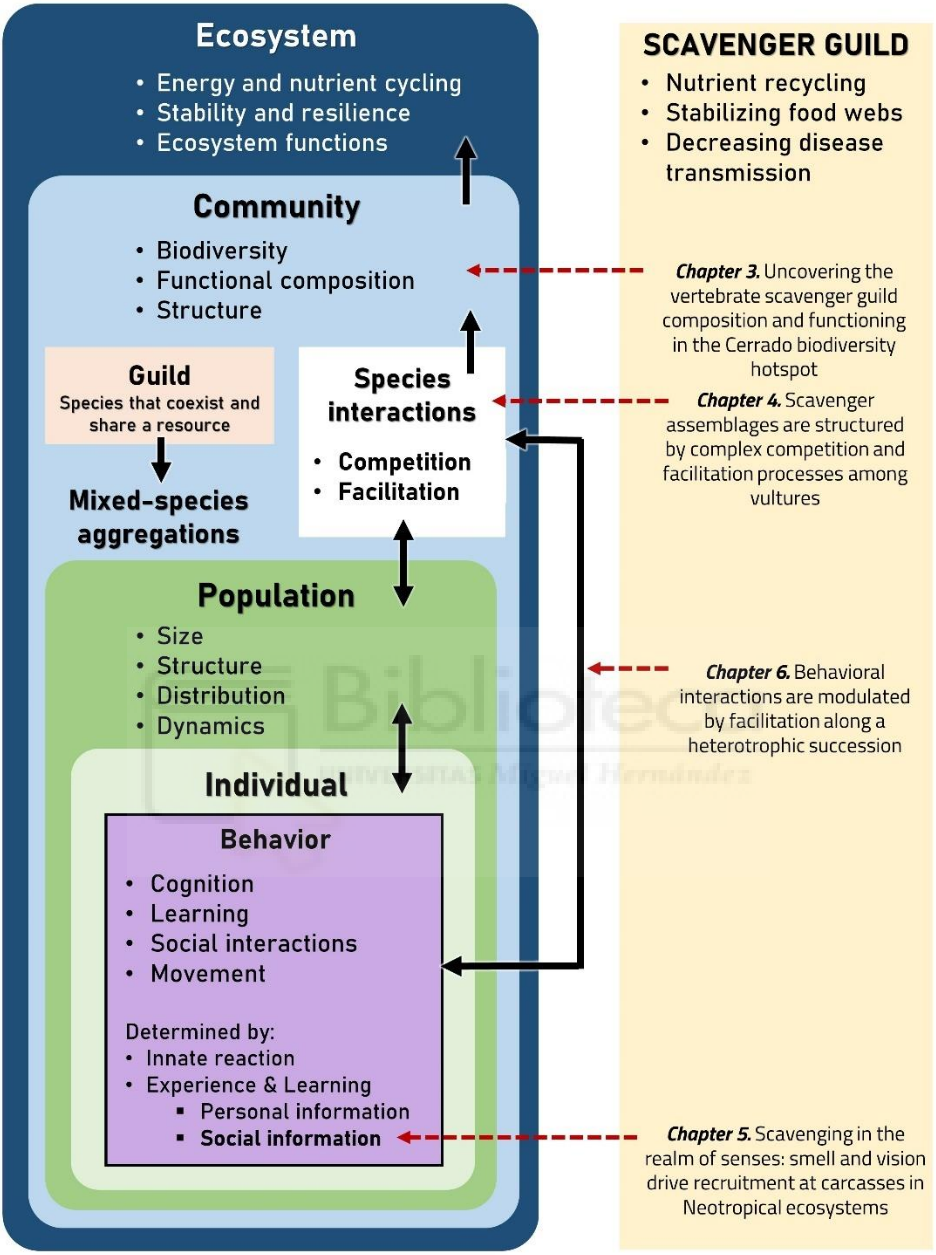


Figure 5. Conceptual framework on the relationships and effects (represented by black arrows, the tips of which indicate the possible directions of effects) that the behavior and species interactions can have at the level of population, community and ultimate response of the structure and functioning of ecosystems. On the right side (yellow box) the different chapters of the thesis are framed, focusing on a scavenger community, relating each chapter to the different ecological levels (represented by red dashed arrows), ultimately affecting the ecological processes influenced by scavenging. Adapted from Rahman & Candolin 2022.

CHAPTER 2: SUMMARY OF MATERIALS AND METHODS

The present thesis was carried out based on data collected during a single field season in the surroundings of the *Nascentes do Rio Parnaíba* National Park in Brazil. Therefore, the study area and sampling design, common for all chapters, will be described in two general sections. Furthermore, different analytical methods associated with ecology, ethology, and community dynamics were used for the development of the thesis, which will be explained separately for each chapter.

STUDY AREA

The study was conducted in the surroundings of the *Nascentes do Rio Parnaíba* National Park, located in the state of Piauí (Brazil), in the north-eastern Brazilian *Cerrado* (**Figure 7**). The *Cerrado* biome, also called Brazilian savanna, is one of the largest biodiversity hotspots on the planet (Myers et al. 2000). It is the largest savanna in South America and is the second largest biome in Brazil, covering 1.8 million km^2 (21% of Brazil's land area), following the Amazon (Silva et al. 2006). The climate is characterized by two very distinct and predictable seasons, with a wet season from October to March and a dry season from April to September, with annual rainfall ranging between 1300 and 2300 mm, while the average annual temperature is 23°C. Its complex geology and topography give rise to a heterogeneous landscape composed of woodlands, savannas, grasslands, and gallery and dry forests (Klink and Machado 2005, Sano et al. 2019). Also, it is known as the world's most diverse savanna, with over 7000 species of vascular plants, roughly 200 species of mammals, and over 800 species of birds, among which we find a large proportion of endemic species (Myers et al. 2000, Tubelis and Cavalcanti 2001, Klink and Machado 2005). The study area hosts a complex and diverse vegetation, with up to 5 different vegetation configurations: *Cerrado sensu stricto*, floodplains, *cerradão*, gallery forest, and *carrasco* (Ribeiro and Walter 1998). There is a great plant diversity in the area, from herbaceous species to fruiting tree species like buritī (*Mauritia flexuosa*) or puçá (*Mouriri pusa*).

Box 2. Potential scavenger species in the *Cerrado* biome

Despite the enormous biodiversity hosted in the Brazilian *Cerrado* and the impact it is suffering, there are still some very unknown groups of organisms, such as scavengers. According to the species distributions established by IUCN, in the *Cerrado* there are five of the seven species of the New World vultures (Cathartidae): turkey (*Cathartes aura*), greater yellow-headed (*C. melambrotus*), lesser yellow-headed (*C. burrovianus*), American black (*Coragyps atratus*), and king (*Sarcoramphus papa*) vultures (**Figure 6**) (IUCN 2022). The three species of vultures belonging to the genus *Cathartes* would be particularly efficient in locating carrion due to their developed sense of smell (Potier 2019). Moreover, we also find large carnivores, as jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Vynne et al. 2011). These two top-predators will supply the other scavengers with carrion from the deaths of their prey, but they can also feed on carrion, as occurs in other systems (Bauer et al. 2005). Furthermore, the *Cerrado* also has many potential scavengers such as medium-sized mammals (e.g., ocelots, *Leopardus pardalis* or jaguarundis, *Herpailurus yaguarondi* or hoary foxes, *Lycalopex vetulus*) and many raptor species (e.g., southern caracaras, *Caracara plancus*, and roadside hawks, *Rupornis magnirostris*) (**Figure 6**) (Trolle et al. 2007, Lima 2009, Dénes et al. 2017).

Figure 6. Some of the potential scavenger species that could be recorded in the study area. (**A**) American black vulture. Photo credit: own photo. (**B**) Turkey vulture. (**C**) King vulture. Photo credit: Christian Sanchez. (**D**) Lesser yellow-headed vulture. (**E**) Greater yellow-headed vulture. Photo credit: Bradley Hacker. (**F**) Jaguar. (**G**) Puma. (**H**) Southern caracara. (**I**) Roadside hawks. (**J**) Maned wolf (*Chrysocyon brachyurus*). Photo credit: own photo. (**K**) Jaguarundi. Photo credit: Gabriel Arroyo. (**L**) Yellow-headed caracara (*Milvago chimachima*). Photo credit: own photo. (**M**) Hoary fox (*Lycalopezx vetulus*). Photo credit: Carlos Henrique Luz Nunes de Almeida. The rest of the images were obtained from the free image bank Pixabay.

In the last 40 years, the *Cerrado* has undergone severe transformations with more than half of the area found in this ecoregion been converted to pastures, agricultural areas and livestock ranching (Silva et al. 2006, Strassburg et al. 2017, Trabaquini et al. 2017). If the rates of deforestation and habitat destruction are maintained, it has been calculated that this biome will be completely modified by 2030 (Klink and Machado 2005). Specifically, native vegetation cover in the park and surrounding areas has decreased due to increased anthropogenic activities— largely as a result of family farming and land conversion to monoculture and pasture. Fires (both anthropogenic and natural) are also an increasing threat to the native vegetation (Klink and Machado 2005) (**Figure 7**).

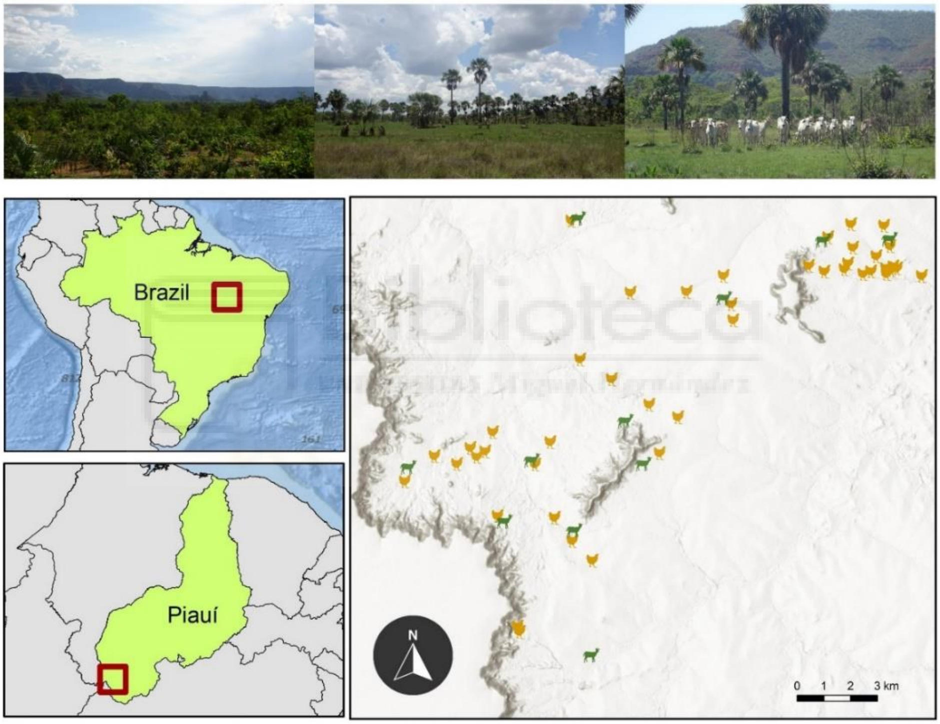


Figure 7. Map of the study area in the Brazilian *Cerrado*. This area is characterized by a wide mosaic of habitats, ranging from grasslands to woodlands (photos above). We show the locations of 56 monitored carcasses, 11 large and 45 small. In our study area, the main activity is extensive livestock farming (mainly cattle and goats; photo on the upper right).

STUDY DESIGN

Fieldwork was conducted during November 2018. We placed two types of fresh carcasses differing categorically in size: (1) large, goat (*Capra hircus*) carcasses weighing between 20 and 40 kg (n = 11) and (2) small, entire chickens (*Gallus gallus*) or chicken parts weighting between 0.075 and 2 kg (n = 45) (**Figure 7**). Carcasses were placed randomly and fixed to the ground or to trees or shrubs to prevent the scavengers from displacing them.

Figure 8. (**A**) The carcasses were weighed and placed intact (without being opened). (**B**) A carcass was judged totally consumed when only the skin and skeleton were left.

Carcasses were monitored using automatic cameras (Browning Strike Force pro HD) activated by movement. Each carcass was monitored until its total consumption (**Figure 8**) by two cameras, one programmed to take photos and the other to record videos. We obtained a total of 2501 videos and 27,448 images. We checked all the archives (i.e., photos and videos) to identify all the consumers, the scavenger species, in each of the carcasses. A species was considered a scavenger when it was clearly detected eating carrion in at least one camera. Thus, for each archive we determined (1) the carcass to which it belongs, (2) the date and time when the archive was taken, (3) the species present in the archive, and (4) its abundance. In addition, we considered different covariates (**Figure 9**). Moreover, we used a different set of files (both in number of files and type) depending on the objectives of each chapter.

Figure 9. Main external variables, non-related to carrion or scavenger community, that were used in the different chapters of the thesis due to their possible influence on carrion consumption patterns, and on the composition of the scavenger community.

METHODS FOR EACH CHAPTER

In **Chapter 3**, to calculate scavenging efficiency, we estimated "detection time" (defined as, time elapsed since carcass was placed until the first consumer was registered); "consumption time", "consumption rate" (carrion biomass consumed divided by consumption time), "percentage of visited carcasses" and "feeding time" for each scavenger species. Then, we used univariate generalized linear models to analyze if there were differences on scavenger richness, abundance, detection time, consumption time and consumption rate between large and small carcasses. Because differences in consumption patterns were found between them, we also used GLMs, using as explanatory variables: "carcass weight", "time of carcass placement" and "vegetation cover", and our response variable were scavenger richness, abundance, detection time, consumption time and consumption rate.

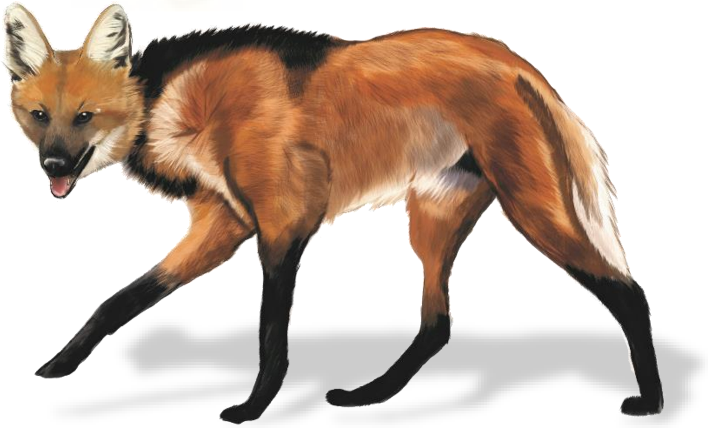
In **Chapter 4**, we used permutational multivariate analysis of variance (PERMANOVA), to determine if there were differences in the species composition of the scavenger communities of the two carcasses sizes. Then, we used co-occurrence analyses to identify possible associations between species. We analyzed spatial co-occurrence considering the presence at a carcass of the species, and spatio-temporal co-occurrence (i.e., same time on the same carrion) considering presence in the same image. In both cases, we performed the analyses for large and small carcasses separately. In addition, we also analyzed spatio-temporal co-occurrence (presence/absence data) in large carcasses for each day of consumption, to see if there were changes in species relationships over time. Finally, we analyzed associations between species pairs also quantitatively using GLMs. Thus, we used as response variable the abundance per carrion/image (i.e., spatially and spatio-temporal) of each species, and as explanatory variables, the abundances per carcass/imagen of the rest of the species together with the covariate "vegetation cover", and "day of consumption".

In **Chapter 5**, to determine how the first arrival time of each focal species depends on the previous presence of heterospecifics we followed a survival-modelling strategy. We converted the irregular camera-trap data into regular interval data. We used the first occurrence (i.e., first arrival) of each species in each of the carcasses as response variable, considering the presence of other species in earlier times as explanatory variables. However, to account for possible confounding effects (not related to species interactions) that could influence species arrival, we also included a linear predictor which summarized all confounding effects that could also be influencing the arrival of the species. In this way, by using GLMs, we tested different combinations of influencer species, its presence or abundance, and several previous times that could affect the arrival of another species (i.e., response variable).

Finally, in **Chapter 6**, to study the succession process of carrion consumption, we used only the data from large carcasses. First, we calculated the variable percentage of total carcass consumption for each archive, to temporarily locate it at the corresponding point of consumption. Second, to analyze the possible facilitation process during the carrion opening process, we defined a binomial variable, called carcass opening status (i.e., closed and open status). Then, to examine changes in competition intensity, we recorded all behavioral interactions by observing the videos. In this way, we focused on aggressive interactions, as a proxy of levels of interspecies competition. Thus, by using Bayesian mixed models we analyzed changes in richness, abundance, species turnover, diversity, total interactions and proportion of aggressive interactions throughout the process of carcass consumption. In addition, the number of individuals of each of the species present, together with the carcass opening status were included as covariates.

CHAPTER 3. UNCOVERING THE VERTEBRATE SCAVENGER GUILD COMPOSITION AND FUNCTIONING IN THE *CERRADO* BIODIVERSITY HOTSPOT

Naves-Alegre, L., Z. Morales-Reyes, J. A. Sánchez-Zapata, C. J. Durá-Alemañ, L. Gonçalves Lima, L. Machado Lima, and E. Sebastián-González. 2021. Uncovering the vertebrate scavenger guild composition and functioning in the Cerrado biodiversity hotspot. Biotropica 53:1582–1593.



ABSTRACT

Scavenging is widespread among vertebrates, being very important for maintaining certain ecosystem functions. Despite this, the scavenger communities remain poorly known in some biomes, especially in the Neotropics. Our main objective was to describe for the first time the scavenger community and identify the factors affecting scavenging efficiency in the Brazilian *Cerrado*. We analyzed the effects of vegetation cover, time of carcass placement and carcass weight, on scavenger species richness, individual abundances, carcass detection and consumption times, and carcass consumption rate. We monitored 11 large and 45 small carcasses using automatic cameras. We documented a total of 19 vertebrate scavenging species, four species of vultures and 15 facultative scavengers. We found that carcass size was the most important factor affecting the scavenger assemblage and consumption patterns. Large carcasses were dominated by vultures, whereas small carcasses were consumed mainly by facultative scavengers. We also found differences between large and small carcasses in all carcass consumption variables except for detection time. However, we did not find an effect of vegetation cover or time of carcass placement on scavenging patterns. The negligible role of mammals and non-raptor birds in large carcasses is also noteworthy, probably due to the consumption and foraging efficiency of the vultures, and the more frugivorous habits of the mesocarnivores. Our results show a highly diverse and efficient scavenging vertebrate community in the Brazilian *Cerrado*, and the need to preserve them in the face of the significant habitat transformations suffered by this biodiversity hotspot.

INTRODUCTION

The role of scavenger communities (i.e., carrion-eaters) has been underestimated until recently in ecological studies, even though they regulate important ecological processes and ecosystem functions (e.g., accelerating nutrient cycle, structuring food webs) (Ogada et al. 2012a, Sebastián-González et al. 2016) and therefore provide important ecosystem services (e.g., decreasing disease transmission and infection rates) (Ogada et al. 2012a, DeVault et al. 2016, Donázar et al. 2016). Among terrestrial vertebrate scavengers, we can differentiate two major functional groups: obligate scavengers (i.e., vultures) and facultative scavengers. Vultures are totally dependent on carrion, while facultative scavengers include other resources besides carrion in their diet, having a gradient in the propensity to scavenge, with species that scavenge very frequently to others that only scavenge occasionally (Ruxton and Houston 2004, Allen et al. 2014). Thus, not all scavengers have the same role within the scavenger guild. Vultures and large mammalian carnivores have a great influence on the structure of scavenger communities through competition and facilitation processes (Allen et al. 2015, Sebastián-González et al. 2016). Consequently, scavenger communities are organized on a non-random basis (Selva and Fortuna 2007), being governed by complex factors, such as the presence of key species, the differential predictability of the carcass, and environmental conditions (Moleón et al. 2015b, Sebastián-González et al. 2016, 2020a).

Carrion consumption by vertebrate scavengers is influenced by several factors. Some are intrinsic to the carcass, such as carcass origin (cause of death) or the species to which it belongs (Selva et al. 2005, Arrondo et al. 2019). Also, large carcasses allow for a greater richness of scavengers, in addition to influencing carcass consumption rate (Sebastián-González et al. 2013, Moleón et al. 2015b, Olson et al. 2016). Other factors that influence scavenging patterns are directly related to the presence of specific scavenger species (Gutiérrez-Cánovas et al. 2020). Scavenging birds have some adaptations that often make them more efficient than mammals at locating carrion (Houston 1979, Ruxton and Houston 2004, Selva et al. 2005). In addition, within avian scavengers, vultures consume larger amounts of carrion biomass and at higher rates than facultative scavengers due to their adaptations for a scavenging lifestyle (e.g., soaring flights and high visual acuity), so communities in which vultures are present have a high scavenging efficiency (Morales-Reyes et al. 2017, Hill et al. 2018). It is also important to highlight the role of large carnivores since they can limit the access and availability of carrion to other scavengers by playing the role of dominant scavengers in the community, eating large amounts of carrion at very high rates.

However, large predators can also provide carrion by killing prey and leaving remains available to other scavengers and by facilitating access to the interior of the carcass by opening it (Selva et al. 2005, Hunter et al. 2007, Allen et al. 2014).

There are also external factors that affect the use of carcasses by scavengers, such as alternative resource availability, seasonality in carrion supply, or habitat structure (Ruzicka and Conover 2012, Moleón et al. 2015b, Inagaki et al. 2020). However, the role of vegetation cover in carcass consumption patterns has been little studied (but see Pardo-Barquín et al. 2019, Stiegler et al. 2020). Dense vegetation cover may influence those scavengers who rely exclusively on visual cues to find carrion, like most avian scavengers, making them unable to locate and access carcasses (Bamford et al. 2009, Ogada et al. 2012b). Conversely, non-avian scavengers might be able to find carcasses even in areas with high vegetation cover because they can rely on both visual and olfactory cues (Arrondo et al. 2019, Moleón et al. 2019).

The *Cerrado* biome, also called Brazilian savanna, is one of the largest biodiversity hotspots on the planet (Myers et al. 2000). It is the largest extension of savanna in South America, being the second largest biome in Brazil after the Amazon and the world's richest savanna, with more than 7000 species of vascular plants, around 200 species of mammals and more than 800 species of birds (Myers et al. 2000, Klink and Machado 2005). In recent decades, it has undergone severe transformations and many of the habitats found in this ecoregion have been converted to pastures and agricultural areas (Strassburg et al. 2017).

Despite the enormous biodiversity hosted in the Brazilian *Cerrado* and the great impact it is currently suffering due to habitat destruction, the role of certain guilds in this area, such as scavengers, is still unknown. In the *Cerrado*, there are five of the seven species of the New World vultures (Cathartidae): turkey (*Cathartes aura*), lesser yellow-headed (*C. burrovianus*), greater yellow-headed (*C. melambrotus*), American black (*Coragyps atratus*), and king (*Sarcoramphus papa*) vultures. A characteristic feature of some of these vulture species is their developed sense of smell, as they have highly developed olfactory bulbs, which is not found in any of the Old World vulture species (Potier et al. 2019). This ability, together with the potential to fly great distances with little energy expenditure (Duriez et al. 2014), means that New World vultures are especially efficient at locating carrion even when vegetation is dense. Thus, they may be the main scavengers in some areas of the Neotropics, although this has yet to be investigated (Houston 1985, 1988, Mallon et al. 2013). In addition to vultures, this biome holds many potential facultative scavengers such as jaguars (*Panthera onca*) and pumas (*Puma concolor*), which might also supply the scavenger community with carrion by killing their prey. Furthermore, the *Cerrado* also has many potential scavengers such as medium-sized mammals (e.g., ocelots, *Leopardus pardalis*, and hoary foxes, *Lycalopex vetulus*) and many raptor species (e.g., southern caracaras, *Caracara plancus*, and roadside hawks, Rupornis magnirostris) (Lima 2009, Dénes et al. 2017).

The main goal of this study is to characterize the vertebrate scavenger community and scavenging patterns at carrion resources in the Brazilian *Cerrado*, as well as to determine the main factors influencing them. Our general hypothesis is that resource size and its spatiotemporal distribution influences the structure of the scavenger guild and the consumption patterns. First, we predict that community composition will vary among carcasses with different sizes, resulting in richer communities in larger carcasses and we expect higher consumption rate and lower detection time for larger carcasses (DeVault et al. 2004, Moleón et al. 2015b, Olson et al. 2016). Second, we test whether vegetation cover influences scavenging patterns, predicting that carcass detection time will be longer in areas with greater vegetation cover. Third, we assess the effect of time of day (morning vs afternoon) of carcass placement. We predict that carcasses deployed during the daytime will be detected and consumed faster because avian scavengers are diurnal and have high scavenging efficiency (Butler and du Toit 2002, Selva et al. 2005, Olson et al. 2016). We discuss the importance of this scavenger community in the context of conservation, focusing on the transformation that this biome is undergoing and the potential threats to its scavenger species.

METHODS

Study area

The study was conducted in the surroundings of the Nascentes do Rio Parnaíba National Park, located in the state of Piauí (Brazil), in the north-eastern Brazilian *Cerrado* (**Figure 10**). The *Cerrado* biome is composed of woodlands, savannas, grasslands, and gallery and dry forests (Klink and Machado 2005). The study area hosts a complex and diverse vegetation, with up to 5 different vegetation configurations: *Cerrado* sensu stricto, floodplains, cerradão, gallery forest, and carrasco (Ribeiro and Walter 1998). There is a great plant diversity in the area, from herbaceous species to fruiting tree species like buritī (*Mauritia flexuosa*) or puçá (*Mouriri pusa*). In the last two decades, native vegetation cover in the park and surrounding areas has decreased due to increased anthropogenic activities— largely as a result of family farming and land conversion to monoculture and pasture. Fires (both anthropogenic and natural) are also an increasing threat to the native vegetation (Klink and

Machado 2005). In our study area, the main activity is extensive livestock farming (mainly cattle and goats). There are no paved roads in this area and within the park, only a few dirt roads generally with private access.

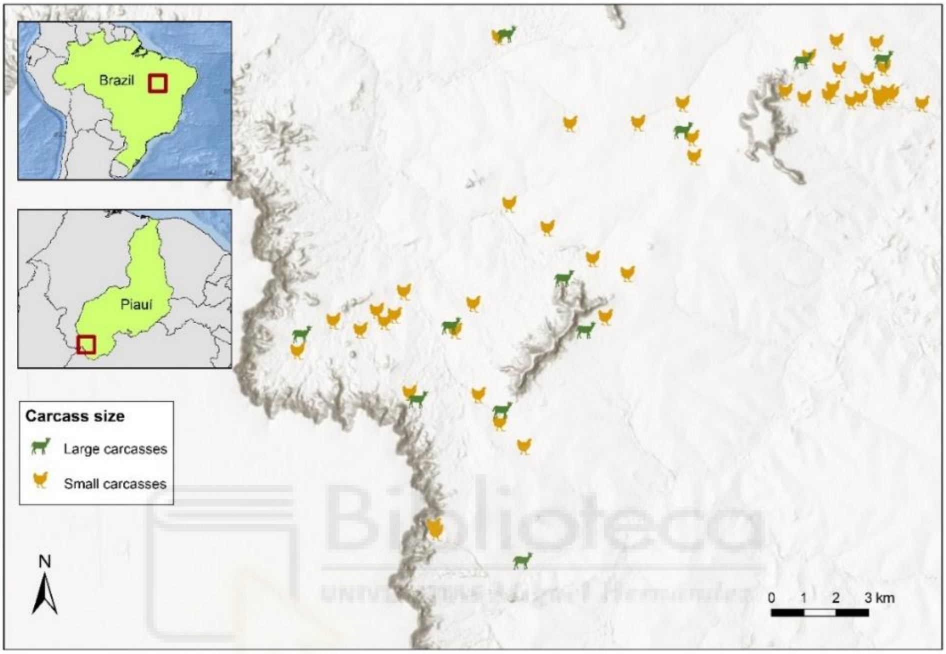


Figure 10. Map of the study area in the Brazilian *Cerrado*, in the state of Piauí (Brazil). We show the locations of 56 monitored carcasses (11 large and 45 small).

Study design and data sampling

We studied carcass consumption patterns by the community of vertebrate scavengers during November 2018. We placed two types of fresh carcasses differing categorically in size: (1) large, goat carcasses weighing between 20 and 40 kg (n = 11) and (2) small, entire chickens or chicken parts weighting between 0.075 and 2 kg (n = 45). All carcasses were weighted prior to placement, and carcass weight was also included as a continuous variable in all analyses (more details below and in the statistical analysis section). Carcasses were placed randomly within our study area. Large carcasses were placed at least 1.5 km apart to maximize independence between samples (Morales-Reyes et al. 2017). The minimum distance between small carcasses was 150 m; thus, we analyzed whether there was spatial autocorrelation among samples for all response variables subsequently used in the analyses: richness, abundance, consumption time, consumption rate, and detection time, and for the residuals of the models, using the *Moran.I* function in the *ape* package (Paradis et al. 2015), and we confirmed their spatial independence (for more details, see **Table S1**). Also, we constructed the species accumulation curves for large and small carcasses using *accumresult* function in the *BiodiversityR* package (Kindt and Kindt 2019), which showed us that the sampling effort had been sufficient to identify all vertebrate scavenger species (**Figure S1**). Carcasses were fixed to the ground by placing pickets or by tying them with ropes to trees or shrubs to prevent the scavengers from displacing them from the camera focus. Carcasses were monitored using automatic cameras (Browning Strike Force pro HD) activated by movement. We placed cameras 5–10 meters from carcasses. Two cameras were placed in front of each carcass. One camera was programmed to take two pictures every 30 seconds and the other to record a video of one-minute length every two minutes in case there was movement. Cameras were programmed to work 24 hr a day and were maintained until carcasses were completely consumed. A carcass was judged totally consumed when only the skin and skeleton were left (Blázquez et al. 2009, Moleón et al. 2015b, Sebastián-González et al. 2016). Only one of the small carcasses was not completely consumed (80% consumed), while one of the large carcasses was not monitored until the end of its consumption due to camera failure. Because of this, these two carcasses were excluded from the consumption time and consumption rate analyses. A species was considered a scavenger when they were clearly detected eating carrion in at least one camera. First, we checked the photographs to identify all the consumers in each of the carcasses. Second, we visualized the videos to avoid possible failures in species detection or identification. All vulture species were considered obligate scavengers. Facultative scavengers were classified into four categories: other raptors, other birds, mammals, and reptiles (see **Table S2**). The amount of biomass consumed by invertebrate scavengers and decomposers was insignificant as no activity was observed even in carcasses that took longer to be consumed, probably due to the high temperatures that dried carrion, so it was not considered in the analyses.

We first calculated two variables to describe the scavenging patterns by species and taxonomic groups: “percentage of visited carcasses” (i.e., proportion of carcasses that were consumed by each species) and “feeding time” (i.e., time that each scavenger species spent eating carrion at each monitored carcass). To determine the “feeding time” by species, we calculated the time elapsed between one image in which the species appeared and the next in which it was also present. If the time between these images was less than two minutes, it was assumed that the species had been feeding all that time between photographs, so duration of different feeding occasions was summed. If the time between pictures was more than two minutes, it was assumed that the species had stopped feeding and feeding time was not added as we considered that they were separate feeding events. Then, we calculated five more variables describing the scavenger community and the scavenging efficiency that were used as response variables in our models. We used two response variables related to the scavenger community: (i) "richness" (i.e., number of scavenger species detected consuming carrion in each carcass) and (ii) "abundance" (i.e., maximum number of unequivocally different individuals of all scavenger species, by identifying the highest number of individuals appearing simultaneously on an image). We also measured three more response variables related to scavenging efficiency: (iii) "detection time" (i.e., time elapsed since carcass was placed until the first consumer was recorded);(iv) "consumption time" (i.e., time elapsed since carcass was available until it was fully consumed);and (v) "consumption rate" (i.e., kilograms of carrion consumed per hour by dividing the carrion biomass divided by consumption time). We considered predictor variables concerned with carcasses that could influence consumption patterns: (i) "carcass weight," measured weight in kg of the carcass placed (i.e., 0.075– 40 kg); (ii) "time of carcass placement," classified in "morning" (from sunrise to 12:00 hr) and "afternoon" (from 12:00 hr until sunset); and (iii) "vegetation cover," determined by the approximate percentage of surface area covered by trees and shrubs within a 5 m radius around the site where the carcass was placed, indicating how visible the carcass was from the sky (i.e., for avian scavengers). We also considered one more explanatory variable related to the scavengers: (iv) "detector group," which refers to the olfactory ability of the species that detected the carcass. Due to the difficulty of comparing the sense of smell of the different taxa, we established the following groups: birds with high olfactory capacity, birds with low olfactory capacity, mammals, and reptiles (see **Table S2** for details at species level) (Moulton 1967, Halpern 1992, Gilbert and Chansocheat 2006).

Statistical analyses

We tested whether there were differences in variables related to the scavenger community and scavenging efficiency between large and small carcasses. To do so, we used univariate generalized linear models (GLMs) to analyze the influence of carcass type on (1) scavenger richness, with a Poisson distribution (log link function), and (2) abundance, (3) detection time, (4) consumption time, and (5) consumption rate, the four of them rounded to achieve a better fit of the residues and fitted to a negative binomial distribution (log link function). Because the consumption patterns differed between the two carcass types (see Results), we performed one-predictor GLMs for large carcasses and multivariate GLMs for small carcasses separately to address our last two hypotheses on the influence of "vegetation cover" and "time of carcass placement" on consumption patterns. Thus, we used as response variables: (1) “richness,” (2) “abundance,” (3) “detection time,” (4) “consumption time,” and (5) “consumption rate” using the same distributions and link functions as in the initial univariate GLMs. For these models, we used as explanatory variables: “carcass weight,” “time of carcass placement,” and “vegetation cover.” Furthermore, because the olfactory capacity of the species is important for detecting the carcass for the first time, when our response variable was “detection time,” we also included the “detector group” as an explanatory variable. No interactions were included in any model. For GLMs, we used the *glm* function in the *lme4* package (Bates et al. 2007). The selection of models was based on Akaike's information criteria for small sample sizes (AICc). We explored all alternative models using the function *dredge* in the *MuMIn* package (Bartoń 2019). Only models with an ΔAICc <2 (i.e., top-ranking models) were considered (Burnham & Anderson 2002). We calculate the deviance explained (D^2) by the top-ranking models with an ΔAICc <2 using the formula D^2 = (null deviance – residual deviance)/null deviance × 100 (Burnham & Anderson 2002). For multivariate GLMs (i.e., small carcasses models), when we got more than one candidate model, we calculated model-averaged coefficients using the *model.avg* function in the MuMIn package (Bartoń 2019). We considered that a predictor variable had statistical support in a model when its confidence interval did not contain the value 0. All analyses were run in R 3.3.3 (R Core Team 2022).

RESULTS

Scavenger community

Overall, we detected 19 vertebrate scavenger species (**Figures 11 and 12; Table S2**). We identified four species of obligate scavengers (turkey, lesser yellow-headed, American black, and king vultures) and 15 facultative species, including five species of other raptors, five species of mammals, three species of reptiles, and two species of other birds. All species within the vertebrate scavenger guild are listed as Least Concern except the maned wolf (*Chrysocyon brachyurus*), listed as Near Threatened. We also detected some species whose current population trend is decreasing at the global scale, including vultures, other raptors, and mammals (**Table S2**).

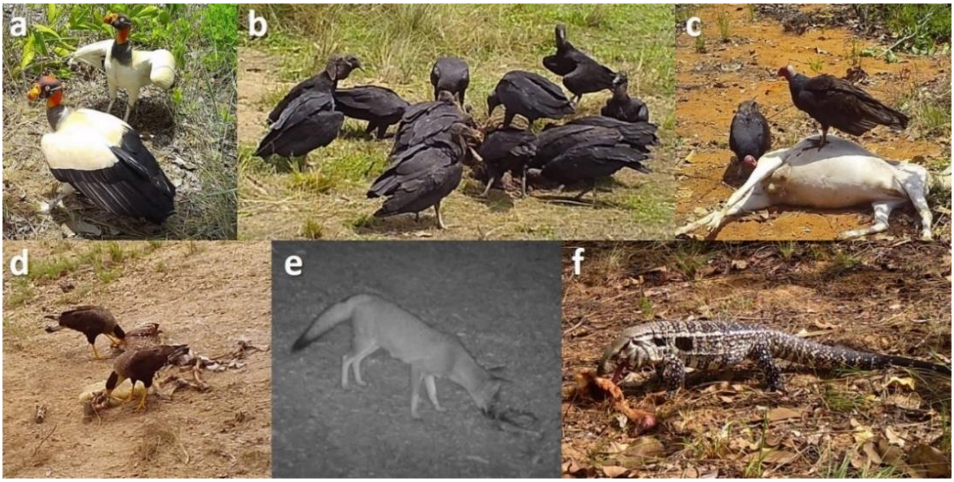


Figure 11. Images of some of the most frequent scavenger species obtained during this study with camera traps. (**a**) King vultures (*Sarcoramphus papa*), (**b**) American black vultures (*Coragyps atratus*), (**c**) turkey vultures (*Cathartes aura*), (**d**) southern caracaras (*Caracara plancus*), (**e**) hoary fox (*Lycalopex vetulus*), and (**f**) black-and-white tegu (*Salvator merianae*).

Carcass consumption patterns

Most of the carcasses (98.2%) were totally consumed by vertebrates. Considering all carcasses together, the most frequent scavenger species were turkey vultures (48.2% of visited carcasses), followed by the southern caracara (46.4%) and the king vulture (33.9%; **Figure 12**). Vultures were the first detectors in 41% of carcasses, followed by other raptors (19.6%). Turkey vultures were the most common first detector species (30.4% of carcasses), followed by the southern caracara (10.7%) (**Figure S2**).

Large carcasses (i.e., goats) were consumed by six species, all of them raptors. We recorded at least three of the four vulture species at all the large carcasses, as well as other raptors at 90% of them. Small carcasses (i.e., chickens) were consumed by the entire scavenger community. Raptors (excluding vultures) were recorded at 51.1% of small carcasses, followed by obligate scavengers (35.6%), mammals (28.9%), reptiles (22.2%), and other birds (6.7%; **Figure 13**). We recorded a total feeding time on carcasses of 235.8 hr, of which 222.2 hr corresponded to the consumption of large carcasses and 13.6 hr to the consumption of small carcasses. Vultures were the species that spent more time scavenging at all carcasses considered together (208.1 hr in total, 88.26% of the total time), followed by other raptors (26.7 hr, 11.31%) (**Figure 13**).

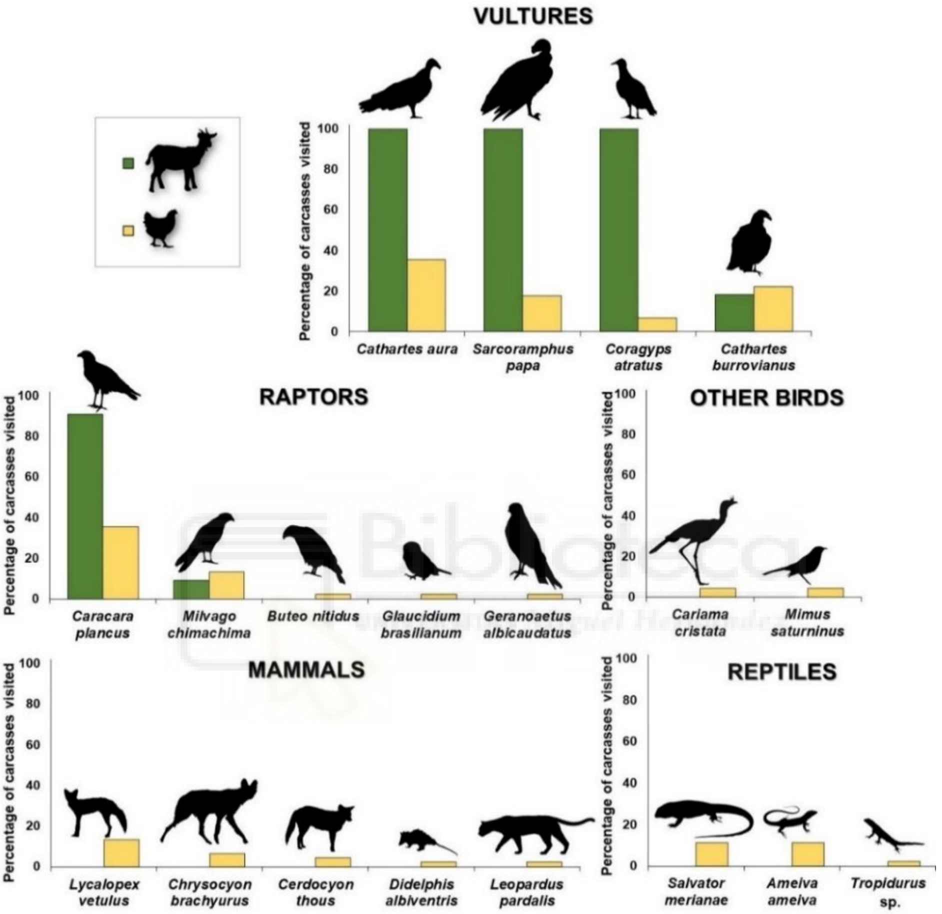


Figure 12. Percentage of large and small carcasses in which each scavenger species was detected eating. Small carcasses were consumed by 19 scavenger species, while large carcasses fed exclusively four vultures and two other raptor species.

Table 1. Richness per carcass, abundance, detection and consumption times and consumption rate for each carcass size (large or small). Values represent mean ± standard deviation (SD), range and sample size (n). The differences between large and small carcasses are shown by the value of the coefficient referring in all cases to small carcasses. The estimate of the parameters and the 95% confidence interval (CI) are shown.

	Large carcasses			**Small carcasses**			**Comparison**	
	Mean ± SD	**Range**	**n**	**Mean ± SD**	**Range**	**n**	**Coefficient (small carcasses)**	***CI***
Richness	4.18 ± 0.60	3-5	11	2 ± 1.17	1-6	45	-0.738	-1.087 – -0.375
Abundance	28.72 ± 8.22	19-43	11	3.42 ± 3.39	1-18	45	-2.128	-2.509 – -1.762
Detection time (h)	18.83 ± 9.22	1.5-27.33	11	21.45 ± 22.62	0.08-125.82	45	0.125	-0.601 – 0.771
Consumption time (h)	48.41 ± 14.41	46.55-98.97	10	13.55 ± 19.56	0.4-114.77	44	-0.712	-1.276 – -0 .204
Consumption rate (kg/h)	0.46 ± 0.19	0.228-0.83	10	0.12 ± 0.34	0.002-1.54	44	-1.387	-2.563 – -0.440

Table 2. Model coefficients for large carcasses by means of one-predictor generalized lineal models (GLMs) showing the relation between scavenging efficiency (abundance, detection and consumption times and consumption rate) and carcass weight, time of carcass placement and vegetation cover. Time of carcass placement was not retained in any model. The estimate of the parameters and the 95% confidence interval (CI) are shown. Coefficients are not presented for the model whose response variable is scavenger richness because the only top-ranking model was the null model.

Response variable	Model	Estimate	CI
Abundance	(Intercept)	2.478	1.880 – 3.080
	weight	0.031	0.010 – 0.051
Detection time	(Intercept)	5.406	3.542 – 7.339
	weight	-0.091	-0.160 – -0.023
Consumption time	(Intercept)	3.973	3.779 – 4.167
	vegetation cover	0.007	0.002 – 0.012
Consumption rate	(Intercept)	4.617	3.823 – 5.407
	weight	0.052	0.025 – 0.080

Of all the species registered, the king vulture spent the highest number of hours feeding on carcasses (77.9 hr, 33.06%), followed by the American black vulture (77.1 hr, 32.70%) and the turkey vulture (49.2 hr, 20.90%). The American black vulture spent 76.9 hr (34.6% of total time) foraging in large carcasses, followed by the king vulture (76.7 hr, 34.52%). In small carcasses, the turkey vulture (5.7 hr, 41.83%) and the southern caracara (2.6 hr, 18.99%; **Figure S3**) spent more time than the other species. Carcass size was an important factor affecting the scavenger community. GLM analyses showed that both scavenger richness and abundance were greater in large carcasses than in the small ones (**Table 1**). The size of the carcass also affected the carcass consumption patterns, as consumption time and consumption rate were nearly four times higher in large carcasses (**Table 1**). We found no difference in detection time between large and small carcasses. When analyzing chicken and goat carcasses separately, we found that carcass weight, time of carcass placement, and vegetation cover had different effects depending on carcass size (**Tables 2** and **3**). For large carcasses, richness was not influenced by any factor, as the null model was the only top-ranking model obtained (**Table S3**). We also found that the null model was one of the top-ranking models for detection time and consumption time for large carcasses. For small carcasses, null model was a top-ranking model for scavenger richness and consumption time. Carcass weight influenced the scavenger community (**Tables 2** and **3**, **Tables S3** and **S4**). In large carcasses, weight increased the scavenger abundance. Carcass weight strongly affected consumption patterns, since it was also included in the top-ranking models as a predictor of detection time and consumption rate (**Table 2**). In small carcasses, weight also influenced the scavenger community and consumption patterns, having a positive effect on richness, abundance, and consumption rate. Detection time was negatively affected by weight, although in this model the weight had no statistical support (**Table 3**). Vegetation cover had a positive effect on the consumption time for large carcasses (**Table 2**). In contrast, vegetation cover had no effect on any of the variables for small carcasses, although it was included in some of the top-ranking models (**Table 3**, **Table S4**). Time of carcass placement did not affect the scavenger community and consumption patterns. This variable did not appear in any of the top-ranking models for large carcasses (i.e., goat carcasses), although it was included in some of the top-ranking models for small carcasses (i.e., chicken carcasses), but with no effect (**Tables 2** and **3**, **Tables S3** and **S4**). The detector group (i.e., olfactive capacity) did not influence detection times neither in large nor in small carcasses, since this variable was not included in any of the top-ranking models (**Tables S3** and **S4**).

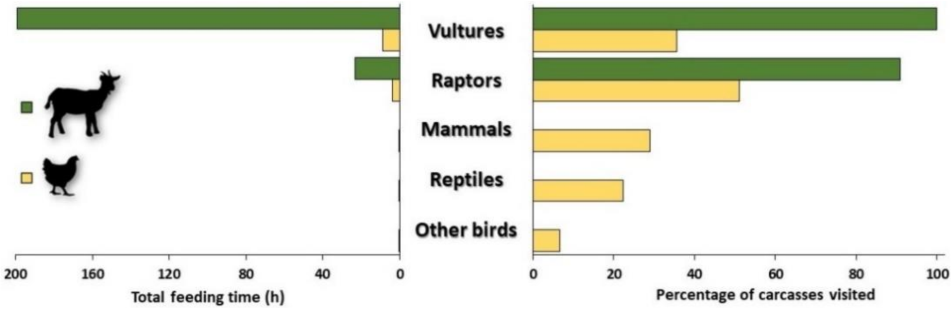


Figure 13. Feeding time (in hours) that each taxonomic group spent eating carrion (left panel) and percentage of carcasses visited by each group (right panel). The results are represented separately for small (yellow) and large (green) carcasses.

Table 3. Model-averaged coefficients for small carcasses by means of generalized lineal models (GLMs) showing the relation between scavenging efficiency (richness, abundance, detection and consumption times and consumption rate) and carcass weight, time of carcass placement and vegetation cover. The estimate of the parameters and the 95% confidence interval (CI) are shown.

Response variable	Model	Estimate	CI
Richness	(Intercept)	0.456	0.023 – 0.888
	weight	0.273	0.002 – 0.68
	time: afternoon	0.094	-0.15 – 0.703
Abundance	(Intercept)	0.591	0.15 – 1.032
	time: afternoon	0.255	-0.023 – 0.852
	weight	0.671	0.312 – 1.029
Detection time	(Intercept)	3.018	2.216 – 3.82
	vegetation cover	0.006	-0.003 – 0.023
	weight	-0.587	-1.212 – -0.089
	time: afternoon	0.237	-0.118 – 1.139
Consumption time	(Intercept)	3.444	2.99 – 3.896
	vegetation cover	0.002	-0.005 – 0.017
	weight	-0.042	-0.64 – 0.27
Consumption rate	(Intercept)	2.899	1.99 – 3.806
	weight	2.071	1.261 – 2.881
	vegetation cover	0.004	-0.008 – 0.031

DISCUSSION

Despite the increasing number of studies on vertebrate scavenging, little is known about the scavenger communities in the Neotropics. In fact, as far as we know, this paper is the first to describe the highly diverse and efficient scavenging vertebrate community in the Brazilian *Cerrado* biome. Carcass size was the main factor affecting consumption patterns, with different assemblages of consumers depending on whether the carcass was large or small (goat vs. chicken carcasses), as evidenced in previous studies (DeVault et al. 2004, Moleón et al. 2015b, Olson et al. 2016). However, we were unable to detect an effect of vegetation cover or time of carcass placement in the consumption patterns of both carcass sizes, maybe due to the high scavenging efficiency of the species in this community.

The vertebrate scavenger assemblage at the *Cerrado* biome

The community of vertebrate scavengers in the north-eastern Brazilian *Cerrado* includes at least 19 vertebrate species. In fact, nearly 100% of carcasses were consumed by vertebrates, whereas invertebrates played a negligible role. We detected four species of New World vultures, as well as 15 facultative scavengers including raptors (5 species), other birds (2), mammals (5), and reptiles (3), showing that scavenging by vertebrates is widespread in this biome. This community is among the most diverse scavenger communities described worldwide, with 15 of the 19 of the species detected here being exclusive to the Neotropics (Sebastián-González et al. 2019, IUCN 2020). We find few scavenging communities with higher species richness in the literature, like the Polish temperate forests, with up to 36 species (Selva et al. 2005), or the Californian forests, with 29 species (Allen et al. 2014). Despite the large number of potential scavenger species in this community (Lima 2009, Dénes et al. 2017), our results highlight scavenging efficiency of vultures, over other taxonomic groups. In agreement with previous studies (Ogada et al. 2012b, Morales-Reyes et al. 2017, Hill et al. 2018, Arrondo et al. 2019), vultures were the most efficient scavengers, being the main consumers in terms of both occurrence frequency and consumption time in all types of carcasses. Top predators such as pumas and jaguars that were detected in the area (through signs and camera traps) did not consume carrion, which contrasts with the important scavenging role of top predators in other ecosystems, such as African savannas (Moleón et al. 2015b) or temperate forests (Selva et al. 2005). In our study area, other raptors also played an important role in terms of percentage of visited carcasses and feeding time, contrasting with other systems where carnivores are the main scavengers (Moleón et al. 2015b, Cunningham et al. 2018, Inagaki et al. 2020). This may be related to the diet of the canid species that coexist in the Brazilian *Cerrado*, as they consume a great variety and quantity of fruits and insects (Juarez and Marinho-Filho 2002) compared to other areas where mesocarnivores like red foxes (*Vulpes vulpes*) consume a greater proportion of animal prey (Padial et al. 2002). However, our results are only based on the wet season, when there is a greater availability of fruits than the dry season, so more studies would be necessary to determine whether the dependence of these species on carrion could be greater when there are fewer fruits available. These differences between communities could also be due to mesocarnivores being more abundant in those areas where there are no apex predators and also because of a weaker competition for the resource and a lower risk of predation at carcasses (Allen et al. 2015, Cunningham et al. 2018, O'Bryan et al. 2019, Moleón and Sánchez-Zapata 2021).

Factors affecting consumption patterns

In agreement with our first prediction, assemblages of scavenging species consuming large and small carcass were different. Vultures were the most efficient consumers of large carcasses, almost monopolizing them (Ruxton and Houston 2004). In contrast, smaller carcasses were consumed mainly by facultative scavengers (i.e., medium-sized mammals, reptiles, and other raptors). In agreement with recent studies, the average richness of scavenger species per carcass was higher in large carcasses than in the small ones (Moleón et al. 2015b, Turner et al. 2017, Sebastián-González et al. 2019). However, total species richness was higher in small carcasses. This may be because large carcasses were consumed mainly by obligate and dominant scavenger species (i.e., vultures and other raptors), whereas small carcasses might be quickly removed by other opportunistic facultative scavengers. Frequency of mesopredator occurrence (i.e., mammals and reptiles) and other birds was higher in small carcasses, a common pattern in other areas (DeVault et al. 2004, Moleón et al. 2015b, Olson et al. 2016, Turner et al. 2017). The behavior of smaller carnivores (i.e., medium and small mammals and reptiles) at large carcasses might be influenced by the "landscape of fear" induced by predation risk (Cortés-Avizanda et al. 2009, Willems and Hill 2009, Moleón and Sánchez-Zapata 2021). In contrast, the number of individuals consuming a carcass diminished with decreasing carcass size. This is because small carcasses were often totally consumed by a single individual, while large carcasses usually persist longer in the environment, allowing more individuals to consume it (Sebastián-González et al. 2013, Turner et al. 2017). Supporting our expectations, our results show differences between large and small carcasses in all consumption variables except for detection time. Carcass size did not affect detection time, which may be due to the high foraging efficiency of the vulture species in the community (Houston 1985, Mallon et al. 2013, Moleón et al. 2015b), as is the case on the African savanna (Moleón et al. 2015b). The species that first detected more carcasses was the turkey vulture, followed by the southern caracara. These two species are not only guided by the sense of sight and hearing, like most raptors, but also have a developed sense of smell (Houston 1985, Potier et al. 2019). It has been hypothesized that these evolutionary differences between New and Old world vulture guilds (e.g., olfactory capacities of some species) are due to the type of habitat in which they have evolved; Old World vultures are distributed in areas of open habitat, while most New World species (except the two condor species) are mainly distributed in Neotropical forests (Houston 1985). This clearly differentiates the New World from the Old world bird guild, giving American vultures a clear advantage when locating carrion regardless of vegetation cover (Houston 1988, Mallon et al. 2013). By contrast, consumption time and consumption rate were significantly higher in large carcasses, coinciding with the results obtained in other scavenger communities (Moleón et al. 2015b). If we compare our results with five other studies conducted using chickens or similar carcasses, we observe that all of them obtained lower consumption rates than ours (reviewed in Sebastián-González et al. 2020). In contrast, for large carcasses, compared to six other studies in which they also used goat or sheep carcasses, our observed consumption rate was average (reviewed in Sebastián-González et al. 2020). This suggests that the rich vertebrate scavenger guild in the *Cerrado* is very efficient in removing carcasses, especially those of small sizes. Contrary to our prediction that vegetation cover influences scavenging patterns, we did not find a significant influence of vegetation cover on the ability of scavengers to locate the carcasses. However, detection and consumption times were generally higher in areas of dense vegetation in all carcasses. Previous studies showed that dense vegetation may prevent carrion localization by vertebrates, promoting carrion consumption by invertebrates (Ruzicka and Conover 2012), because high vegetation densities may leave insufficient space for the vultures to take off (Bamford et al. 2009), and carcasses in open habitats are detected and consumed faster (Arrondo et al. 2019). However, this factor does not seem to be relevant in our system, probably because of the olfactory capacity of the main scavenger species. Likewise, our prediction that time of carcass placement influences consumption patterns was not supported by the analyses. Existing research has shown that mammals are more active than raptors during the afternoon and are thus the first to find carrion when it is located in the late afternoon. This increases detection times, because mammals are less efficient at finding carrion than vultures and other raptors (Butler and du Toit 2002, Ruxton and Houston 2004). However, this does not occur in the *Cerrado* system because other species (i.e., mammals and other raptors) could be functionally replacing vultures for carcass detection during the afternoon. This study has certain methodological limitations that are important to consider. Data collection was carried out in one month and exclusively during the wet season (that lasts from November to April). Although previous research has shown changes in carrion consumption patterns among seasons, these have been carried out in temperate zones with a strong seasonality and have highlighted that the factor that most influences carrion acquisition is temperature (DeVault et al. 2004, Selva et al. 2005). However, even though the Brazilian *Cerrado* has two distinct seasons (i.e., wet and dry), the average temperatures in this area are 18 and 28°C during the dry and wet seasons, respectively. This variation is unlikely to affect the scavenger patterns (Dias 1992). It would be interesting to carry out the same field experiment in the dry season, to see whether there are any changes in the scavenging patterns. The sample size of large carcasses is not very large (n = 11). However, as shown by the species accumulation curves, we identified the same scavenger community in almost all large carcasses, so we can conclude that there is little variability in the species that use this type of carcass.

Concluding remarks and conservation implications

This is the first time the *Cerrado* scavenging community is described, and our findings emphasize the importance of the functions and ecosystem services provided by the scavenger guild in this Neotropical region. Several factors have been shown to influence the composition of scavenger communities, such as habitat, topography, and climate (Mateo-Tomás et al. 2017, Turner et al. 2017, Sebastián-González et al. 2019, 2020a). Nevertheless, it has been concluded that human disturbance is the factor that most affects the richness of scavengers (Sebastián-González et al. 2019) and also influences the way scavenger assemblages are structured and their efficiency at the global scale (Sebastián-González et al. 2020a). In the last decades, habitat loss rate in the Brazilian *Cerrado* has been very high due to the transformation of the territory for human use (Klink and Machado 2005, Strassburg et al. 2017). This may be negatively affecting populations of species restricted to this biome and their ecological functions, although the population sizes of many species are not well known (e.g., king vultures) (IUCN, 2020). Research on wildlife is scarce in this region and has focused mainly on protected areas and key species, but more studies at the functional group level are needed to understand the functioning and dynamics of communities and thus the importance of conserving them (Klink and Machado 2005, Strassburg et al. 2017). Our results highlight the diversity and functionality of the vertebrate scavenger community at the *Cerrado*, which adds to the need to conserve this global biodiversity hotspot.

ACKNOWLEDGEMENTS

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CHAPTER 4. SCAVENGER ASSEMBLAGES ARE STRUCTURED BY COMPLEX COMPETITION AND FACILITATION PROCESSES AMONG VULTURES

Naves-Alegre, L., Z. Morales-Reyes, J. A. Sánchez-Zapata, and E. Sebastián-González. 2022. Scavenger assemblages are structured by complex competition and facilitation processes among vultures. Journal of Zoology 318:260–271.

ABSTRACT

Understanding the factors that allow multiple species to coexist and share resources is an outstanding question in community ecology. Animals that share resources tend to use different strategies to decrease potential competition, through morphological adaptations, establishment of hierarchies, behavioral adaptations or spatial or temporal segregation. The main objective of this study was to infer interspecific processes of competition and facilitation through the study of species co-occurrence patterns in a vertebrate scavenger guild in de Brazilian *Cerrado*. We analyzed patterns of spatial and temporal co-occurrence between species pairs, both qualitatively and quantitatively, and determined the activity patterns of the different scavenger species. For this purpose, we placed and monitored 11 large (i.e. goat) and 45 small (i.e. chicken) carcasses by camera-trapping, obtaining a total of 27 448 images. Our results show complex competitive and facilitative relationships among scavenging species in the Brazilian *Cerrado* that are influenced by carcass size and change depending on the spatial and temporal scale at which they are analyzed. The scavenger assemblages that consumed large and small carcasses were different, evidencing resource partitioning between obligate and facultative scavengers. Furthermore, as an alternative to reduce competition levels, most species showed differences in their scavenging patterns, in addition to a strong temporal segregation during carcass consumption. Regarding New World vultures, our results suggest a strong interference competition between species with clear differences in their ecological traits (e.g. size, social behavior). However, we also found evidence of facilitation processes between vulture species in the location and access to the interior of the carcasses. Our findings highlight the role of obligate scavengers both in competition and facilitation processes in this vertebrate scavenger community. Future research should focus on investigating which species play the most important role in the structure and dynamics of this community, also considering intraspecific and behavioral patterns.

INTRODUCTION

Understanding the factors that allow multiple species to coexist and share resources is an outstanding question in community ecology (Kneitel and Chase 2004b, Bascompte 2010). Several studies have found that the coexistence of interacting species may be driven by both agonistic (e.g. prey-predator dynamics, competition for resources) and facilitative (e.g. mutualistic interactions) processes (Harrison and Whitehouse 2011, Ullas Karanth et al. 2017, Veit and Harrison 2017, Prugh and Sivy 2020). Among agonistic interactions, interspecific competition may be especially important in situations of strong competition because organisms must develop diverse strategies to prevent it (Jonathan Davies et al. 2007). One of the most important strategies adopted is niche differentiation, where two organisms living in the same environment use different ecological niches to coexist, differing in what, where or when they eat (Roughgarden 1976, Finke and Snyder 2008).

Competition between coexisting species that belong to the same guild is especially interesting, because the more similar the ecological niche of two species is, the larger the competition among them (May and MacArthur 1972). Animals that share resources tend to use different foraging strategies to decrease this potential competition, through morphological adaptations, establishment of hierarchies, behavioral adaptations or spatial or temporal segregation (Carrete et al. 2010, Sogbohossou et al. 2018). In this sense, the scavenger guild is an interesting assemblage because carrion offers highly nutritive biomass concentrated in space and time, which tends to be unpredictable and ephemeral (DeVault et al. 2003, Moleón et al. 2019). All these characteristics result in many individuals of different species being able to consume carrion and thus potentially sharing the same resource (Cortés-Avizanda et al. 2012, Kane et al. 2014).

Within the scavenger guild, we can find obligate (i.e. vultures) and facultative scavengers (i.e. generalist species such as other raptors, corvids, mammals or reptiles). This implies a high richness of potential coexisting scavenger species resulting in high levels of interspecific competition (Ruxton and Houston 2004, Allen et al. 2014). To reduce competition, coexisting scavengers may use different strategies, such as establishing hierarchy patterns in the use of the resource, with the hierarchical order of the species depending on their ecological traits (Kruuk 1967, Houston 1988, Kendall et al. 2012). For example, body size may facilitate dominance during aggressive interactions, so larger species will lead consumption at carcasses (Allen et al. 2014, Moreno-Opo et al. 2020). Species with low competitive capacities (e.g. small body size) may reduce competition in carcasses through other strategies, such as by conspecific aggregations in the resource or by avoiding direct confrontations by changing their spatial or temporal foraging patterns (Blázquez et al. 2009, Kendall 2014). Specifically, vultures are most specialized species in the consumption of carrion, sharing many physiological and morphological adaptations that make them very efficient when exploiting this resource (DeVault et al. 2003). They have also developed some strategies to decrease competition, for example having different morphologies in the beak, that allow them to feed on different parts of the carcass (Kruuk 1967, Kendall 2014) or segregating in space and time.

Spatial and temporal segregation has been described both within Old and New World vultures (Kruuk 1967, Cortés-Avizanda et al. 2012, Kendall et al. 2012, Moreno-Opo et al. 2016). Also, some works have shown how some facultative species reduce costs related to interactions by spending less time in the carcass and increasing the speed at which they consume it, thus avoiding obligate scavengers which stay longer in the vicinity of the carcass (Moreno-Opo et al. 2016). In addition, in areas where obligate scavengers are absent, differences in scavenger consumption patterns both in time and space have been described among facultative bird scavengers with different competitive capacities (Blázquez et al. 2009).

One way to understand these patterns of facilitation or exclusion that occur between species that coexist in the same habitat and that consume the same resource, is through co-occurrence patterns. These patterns can indicate the presence of direct and indirect interactions between species (Gotelli and McCabe 2002). It has been described that a negative co-occurrence between two species may reflect a competitive exclusion among these species, while a positive co-occurrence could indicate a process of facilitation (Sfenthourakis et al. 2006, Sebastián-González et al. 2010). Despite the abundance of research on competitive interactions among scavengers, studies at community level, including all vertebrate scavenger species, are not available. Such community-level studies are needed to understand the patterns of competition and facilitation that influence vertebrate community structure and functioning (Sebastián-González et al. 2016). The main objective of this study is to determine competitive and facilitation processes between species, by analyzing spatio-temporal co-occurrence patterns of the vertebrate scavenger species at carcasses in the Brazilian *Cerrado*. In this way, we want to answer the following questions: Are facilitation processes occurring between species with different carcass opening skills, and/or between species with different foraging strategies? How do species with different competitive capacities manage competition at different scales? We establish specific hypotheses related to these questions (see **Table 4** for hypotheses and further details). As a specific objective, we describe the daily activity patterns and the mean time of arrival to the carcasses of the

Table 4. Facilitation and competition processes that may be occurring in a vertebrate scavenger community related to the co-occurrence patterns and hypotheses established in this work.

Process	Description of the process	Co-occurrence	Hypothesis	References
Facilitation	Some species can access and open hard skin carcasses (i.e., goat carcasses) by passing through the skin, allowing the access to other species.	Positive co-occurrence patterns	**1.** There will be facilitation processes and thus species with a larger body size or stronger beaks (i.e., king vultures) and species with less ability to open carrion (e.g., *Cathartes* species, American black vultures) will positively associate in the same carrion, even at the same time.	(Kruuk, 1967; Selva *et al.*, 2003)
Facilitation	Species with higher search efficiency, due to differences in flight ability or sensory ability (e.g., olfactory capacity), will serve as a visual cue of the presence of carrion for other species.	Positive co-occurrence patterns	**2.** The presence in a carcass of species with olfactory capacity (i.e., turkey, lesser yellow-headed vultures and southern caracara) and with lower flying height (i.e., *Cathartes* species) will serve as a signal for other species of the community to locate the carrion, giving rise to positive co-occurrence of these species.	(Kruuk, 1967; Houston, 1988; Cortés-Avizanda *et al.*, 2012; Kane *et al.*, 2014; Veit & Harrison, 2017)
Competition	Exploitative competition or resource competition, i.e., when organisms consume and therefore compete for the same resource.	Negative spatial co-occurrence patterns	**3.** Exploitative competition will result in spatial segregation between species. Thus, species with greater consumption capacity (e.g., larger body size, specialists) may consume some carcasses completely or monopolize its consumption, precluding the use of the resource by other species.	(Gotelli *et al.*, 2010; Moreno-Opo *et al.*, 2016; Palomares *et al.*, 2016)
Competition	Interference competition, i.e., one species reduces the ability of other species to exploit a shared resource by direct interactions (e.g., aggressive interactions).	Negative spatio-temporal co-occurrence patterns	**4.** There is a hierarchy whereby some species are competitively superior (e.g., larger species), and therefore competitively inferior species will avoid co-occurring on the same carcass at the same time (i.e., temporal segregation) to avoid direct confrontations.	(Kronfeld-Schor & Dayan, 2003; Blázquez *et al.*, 2009; Moreno-Opo *et al.*, 2020)

different scavenger species in the community. These results will allow us to know the role of each species in the competition and facilitation processes that may occur during carrion consumption and, therefore, in the structure of this vertebrate assemblage.

MATERIALS AND METHODS

Study area and scavenger community

The study was carried out in the *Cerrado* grasslands of North-eastern Brazil (Piauí state). Our study area contains a mosaic of vegetation ranging from woodlands to dry and gallery forests to savannas and grasslands (Ribeiro and Walter 1998). There is a rainy season from December to March and a dry season from April to November. Annual rainfall ranges from 1200 to 1300 mm and the average annual temperature is 23°C. In our study area, we find four species of New World vultures (Cathartidae), turkey (Cathartes aura), lesser yellow-headed (*C. burrovianus*), American black (*Coragyps atratus*) and king (*Sarcoramphus papa*) vultures. We also find at least 14 species of facultative scavengers, from medium-sized mammals (e.g. hoary foxes *Lycalopex vetulus*), several raptor species (e.g. southern caracara *Caracara plancus*) and some reptiles (see Naves-Alegre *et al.*, 2021 for details on the study area and the scavenger assemblage).

Study design and variables considered

We studied the co-occurrence patterns between scavenger species through the placement of carcasses monitored by automatic cameras (Browning Strike Force pro HD). All cameras were placed approximate 1.5 m from the carcass, tied to a tree and configured to take 2 photographs per trigger with a delay of 30 seconds, as long as there was movement in front of the lens. Since carrion size is one of the factors that most affects the structure and functioning of scavenger assemblages (Moleón et al. 2015c, Naves-Alegre et al. 2021), we placed 56 fresh carcasses during November 2018, distinguishing two sizes: (1) large, that is domestic goats (*Capra hircus*) weighing 20–40 kg (n = 11), and (2) small, that is entire chickens or chicken fragments (*Gallus gallus*) weighing between 0.075 and 2kg (n = 45), (see study area map in the Appendix S1, **Figure S1**). All carcasses were placed randomly, large ones at a minimum distance of 1.5 km among them (Morales-Reyes et al. 2017). Small carcasses were placed at a minimum distance of 150 m and in higher numbers to more realistically simulate the dynamics of a natural system, where smaller organisms are found at higher densities and have higher mortality rates due to their shorter life span (White et al. 2007, Rossberg et al. 2008). The independence of the samples was confirmed by analyzing the spatial autocorrelation between them and confirmed their spatial independence (see Naves-Alegre *et al.*, 2021 for further details).

We obtained 27 448 images (24 980 images for large carcasses and 2468 images for small carcasses). All the images were visualized, and we extracted several variables. First, we identified the *presence per carcass* and *presence per image* of all detected species, that is presence (1) or absence (0) of a scavenger at a carcass or image level (see the list of species in the Appendix S1, **Table S1**). For quantitative analyses, we established the *abundance per carcass* for each detected species, which was defined as the maximum number of unequivocally different individuals from a species that appeared simultaneously in the same image or that could be individualized during the consumption of the carcass because of age/sex differences, color patterns or distinct marks (e.g. injuries). We also calculated the *abundance per image* for each species, defining it as the total number of individuals of a species observed in an image.

For the quantitative analyses, we also considered two other covariables that are known to affect the relations between species (Naves-Alegre et al. 2021): (i) *vegetation cover*, defined as the percentage cover of trees and shrubs within a 5-m radius of the carcass location, the (ii) *time of carcass placement*, differentiating between carcasses placed during the *morning* (i.e. from sunrise to 12:00 h) and the *afternoon* (i.e. from 12:00 h until sunset). Because the main scavengers in this community are diurnal (i.e. vultures and facultative raptors), being preferentially active during the hottest hours of the day, the time of carcass placement could affect consumption patterns. Finally, we also used (iii) *the day of consumption* (i.e. whole days from the date the first scavenger species appears until carcass total consumption), because competition levels may vary during the consumption of the resource.

Activity patterns and time of arrival

We represented the activity patterns of scavenger species throughout the day, measured as the percentage of photographs in which a species appears throughout the hourly periods that compose the 24 hours of the day (i.e. we divided the 24 hours into 1 hour periods) out of the total number of photographs in which that species appears. To simplify these results, we grouped the scavenger species into (a) vultures, (b) facultative birds (i.e. all birds except vultures), (c) mammals and (d) reptiles. In addition, we represented the activity of each vulture species (i.e. turkey, American black, lesser yellow-headed and king vultures) according to the *day of consumption* of the carcass. Finally, we calculated the mean *time of* *arrival* of each species at the carcasses in which they were recorded, that is minutes from the time the carcass was placed until the first individual of each species appears in a carcass.

Co-occurrence analyses

We used co-occurrence analyses to identify possible associations between species. We used the 'coocur' package in R (Griffith et al. 2016), which uses the probabilistic model of species co-occurrence by Veech (2013). This approach utilizes presence/absence data, and it calculates an expected probability that two species coincide, determining whether the co-occurrence of the different pairs of species is therefore higher (positive co-occurrence) or lower (negative co-occurrence) than expected, or if it is random. Using this method, we studied the co-occurrence between species pairs both spatially (i.e. species occurring at the same carcass) and spatio-temporally (i.e. species occurring in the same image: same time at the same carcass) for large and small carcasses separately.

a) Spatial co-occurrence

Initially, to determine whether to perform the cooccurrence analyses for large and small carcasses separately or together, we used permutational multivariate analysis of variance (PERMANOVA), to determine whether there was a segregation between species in the consumption of the two carcasses sizes. On the one hand, we used the Jaccard dissimilarity that only considers the presence or absence of the species, that is *presence per carcass*, and on the other hand, the Bray–Curtis dissimilarity, which contemplates the abundance of each of the species, that is *abundance per carcass*. For both PERMANOVAs, we used the 'adonis' function of the 'vegan' package (Oksanen et al. 2007).

Subsequently, we analyzed the co-occurrence of species by the variable *presence per carcass* of those species that appeared in more than 7 carcasses for both large and small carcasses (see **Table S2** for further details).

b) Spatio-temporal co-occurrence

For all spatial–temporal co-occurrence analyses, we used the variable *presence per image* of those species that appeared in more than 100 images (see **Table S2B**). First, due to the long consumption times of large carcasses, we analyzed the spatio-temporal co-occurrence patterns for each different *day of consumption* separately (i.e. first, second, third or fourth). We divided all the images according to the *day of consumption* to which they belonged. Because we had a very different number of images for each *day of consumption*, we selected a subsample of pictures from each day by using 'sample' function in R. We determined the minimum number of photographs required to carry out the analyses, by repeating the co-occurrence analyses for different numbers of photographs from each *day of consumption* (i.e. 200, 400, 800, 1000, 1500), obtaining that the minimum number of images required for consistent results is 1000. In this way, we decided to use the maximum number of images above 1000, so we randomly selected 1500 photos from the first, second and third day of consumption, and 1184 images from the fourth day (maximum number of images obtained). Images from day 5 and 6 were not considered because they were not enough to run reliable analyses (52 and 2, respectively).

Second, we analyzed the spatio-temporal co-occurrence for large carcasses throughout all their consumption period. Since we previously found differences in co-occurrence patterns between consumption days, we used the 'sample' function to obtain a sub-sample of images for each of the days of consumption, in the same way as the analysis described above (i.e., 1500 images for days 1, 2 and 3, and 1184 for day 4). In this way, we considered the same approximate proportion of images during the entire period of carcass consumption. We ran the co-occurrence analysis for large carcasses using all the selected images together (5,684 in total). Finally, we also analyzed the spatio-temporal co-occurrence patterns for the small carcasses, for which we used all the images obtained (*n* = 2,468).

Quantitative analyses

As co-occurrence analyses only use presence and absence data, we quantitatively analyzed associations between pairs of species by using generalized linear models (GLMs) for the spatial scale and generalized linear mixed models (GLMMs) for the spatio-temporal scale, to study the possible effect that the number of individuals of a species has on the presence and abundance of another species. These analyses were carried out for large and small carcasses separately (see **Table S2** for further details).

a) Spatial analyses

For the spatial analyses, we ran a GLM for each species that appeared in more than seven carcasses using as response variable its *abundance per carcass*. We made this selection because to fit the models we need each species to have enough positive occurrences in the total of carcasses. We used as explanatory variables the *abundance per carcass* of all the other species that also appeared in more than seven carcasses, together with two covariables: *vegetation cover* and time of *carcass placement*.

For the spatial models referring to large carcasses, because we only had a sample of eleven carcasses, we performed one-predictor GLMs with each of the explanatory variables. For the large carcass models, we used as response variable the *abundance per carcass* of the following species: (1) turkey vulture, (2) king vulture, (3) American black vulture and (4) southern caracara. For turkey, king and American black vultures' models we used a negative binomial distribution (log link function), and for Southern caracara models we used a Poisson distribution (log link function). In contrast, several-predictor models were performed for the spatial models of the chicken carcasses (*n* = 45). For these carcasses, we used as response variables: (1) turkey vulture, (2) lesser yellow-header vulture, (3) king vulture and (4) southern caracara. All models were fitted to a Poisson distribution (log link function).

b) Spatio-temporal analyses

For the spatio-temporal analyses, we ran a GLMM for each species that appeared in more than 100 images using as response variable its *abundance per image*. We used as explanatory variables the abundance per image of the other species that also appear in more than 100 imagens of each carcass size, together with two covariables: vegetation cover and day of consumption, and the carcass identity as random factor.

For large carcasses, we ran multivariate mixed models using as response variable the abundance per image of the following species: (1) turkey vulture, (2) lesser yellow-header vulture, (3) king vulture, (4) American black vulture and (5) southern caracara. We used a Poisson distribution (log link function) for all species' models.

For small carcasses, we used all the images obtained. We ran several-predictor GLMMs using as response variable the *abundance per image* of the following species: (1) turkey vulture, (2) lesser yellow-header vulture, (3) king vulture, (4) southern caracara and (5) yellow-headed caracara. We used Poisson distribution (log link function) for all the species.

We used the *glm* and *glmer* functions in 'lme4' package for spatial GLMs and spatial–temporal GLMMS analyses, respectively (Bates et al., 2015). For several-predictor GLMs (i.e. small carcasses analyses), we selected the best models based on Akaike's information criteria for small samples (AICc) from all potential models. We only selected the models with an AICc value <2. In cases where we obtained more than one model, we calculated the model-average coefficients using the *model.avg* function in the *MuMIn* package (Bartoń 2019).

RESULTS

We detected 18 scavenger species in the carcasses (see **Table S1** for complete list of species). Four of these were New World vultures (i.e. obligate scavengers; family Cathartidae), that is turkey (*Cathartes aura*), lesser yellow-headed (*C. burrovianus*), American black (*Coragyps atratus*) and king (*Sarcoramphus papa*) vultures. We also found 14 species of facultative scavengers, seven facultative birds (e.g. southern caracaras *Caracara plancus*), five medium-sized mammals (e.g. hoary foxes *Lycalopex vetulus*) and two reptiles (e.g. black-and-white tegu *Salvator merianae*).

Activity patterns and time of arrival

Vultures showed a mainly diurnal activity (**Fig. 14**). The lesser yellow-headed vulture was exclusively detected during the day, with two peaks of activity between 10 a.m. and 12 p.m. and between 3 p.m. and 5 p.m. The turkey vulture maintained its activity throughout the day, being around 81% of its detections between 8 a.m. and 5 p.m. The American black vulture had a very similar activity to turkey vulture, being active mainly during the day, between 6 a.m. and 7 p.m. However, American black vulture showed some nocturnal activity during the consumption of one of the carcasses. Finally, the king vulture was detected between 6 a.m. and 6 p.m., with a peak of activity during the early morning hours (i.e. 40% of its activity recorded between 6 a.m. and 9 a.m.) (**Fig. 14a**). Facultative birds were mainly diurnal, being more active in the morning, between 8:00 a.m. and 1:00 p.m. (59% of the detections). Mammals showed a mainly nocturnal activity pattern (83%). Reptiles were diurnal, focusing 100% of their activity between 8 a.m. and 3 p.m. (**Fig. 14b**).

In large carcasses, not all vulture species appeared at the same carcass consumption timeline. The lesser yellow-headed vulture focused its activity during the first day of carcass consumption, while the turkey vulture was mainly active on the first and second days. American black and king vultures had a longer lasting activity, being more active on the second day than on the first. For all vulture species, from the third day onwards, the activity dropped (**Fig. 14c**). Species' mean arrival times at carcasses were highly variable (**Table S3**). We detected the shortest arrival times for the species of the genus Cathartes, that is Turkey vulture and Lesser yellow-headed vulture, with mean arrival times at carrion of 77 and 82 minutes, respectively. While the longest detection times were those of two facultative species, that is ocelot and red-legged seriema, with 6105 and 10 620 minutes, respectively.

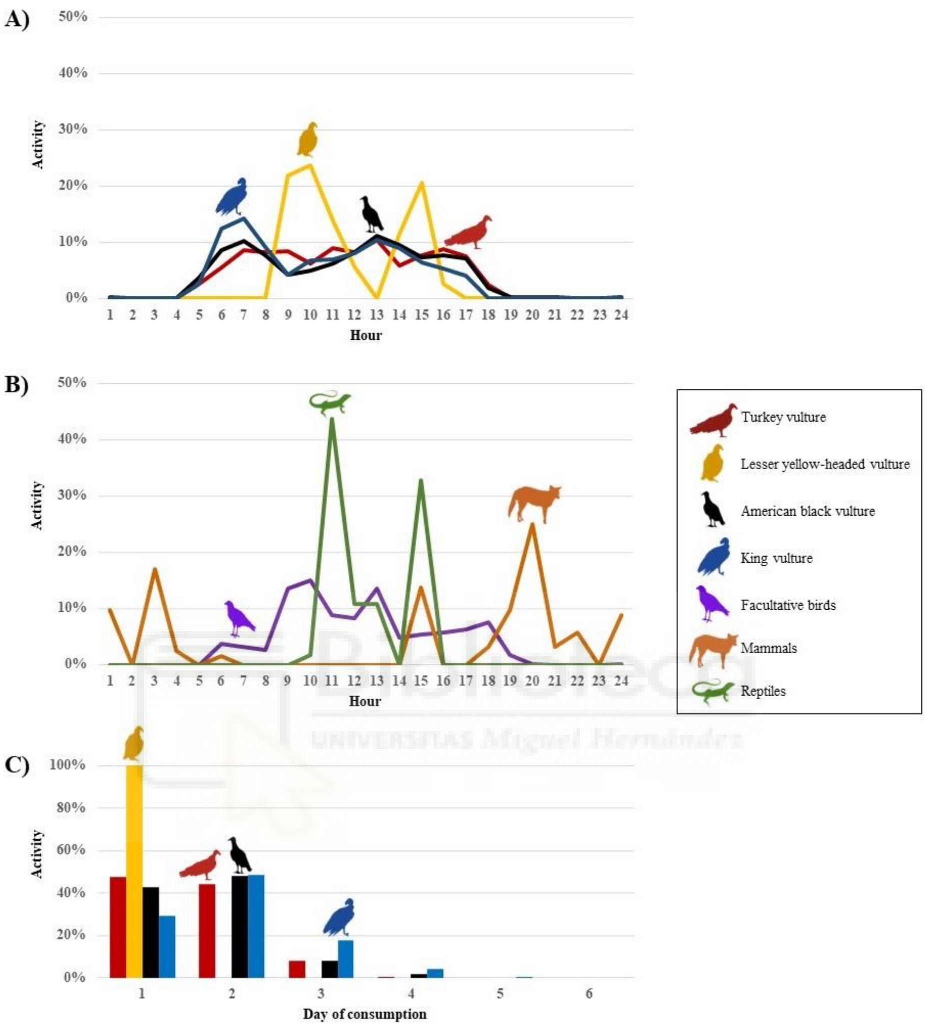

Figure 14. Daily activity patterns represented as the percentage of activity of scavenging species in the Brazilian *Cerrado*, differentiating between (**a**) obligate and (**b**) facultative scavengers. (**c**) Activity patterns of the four species of vultures found in this scavenger community through the different days of consumption of the two sizes carcasses.

Spatial co-occurrence

PERMANOVA results showed that there was a segregation between species that consume large and small carcasses (**Table S4**). For large carcasses, we did not find positive or negative associations, meaning that the 6 species pairs co-occurred randomly (**Fig. 15**). In contrast, GLMs (quantitative analyses) for large carcasses showed a positive relationship between the abundance per carcass of turkey and king vultures, and a negative relationship between the abundance of the king vulture and the southern caracara (**Fig. 15**, **Table S5**). For small-sized carcasses, we only obtained one positive association between turkey and king vultures out of 6 species pairs (**Fig. 15**). Quantitative analyses also showed a positive relationship between these two species. We also found a positive association between the abundance per carcass of king and lesser yellow-headed vultures (see **Fig. 15**, **Table S6**). None of the covariates had a significant effect on either large or small carcasses (see **Tables S5** and **S6**).

Spatio-temporal co-occurrence

We obtained diverse patterns of spatio-temporal co-occurrence in small and large carcasses. For large carcasses, we recorded 1 positive and 8 negative associations out of 10 species pairs. Quantitative GLMMs showed predominantly negative relationships between species' abundance per image except for the positive relationship between king and American black vultures. On the contrary, the variable day of consumption had significant effects for most of the species, while the vegetation cover did not seem to have any effect (**Fig. 15**, **Table S7**).

We also obtained variations in the co-occurrence patterns among the 10 pairs of species obtained as a function of the day of consumption for large carcasses (**Fig. 16**). During the first day of consumption, we obtained mainly negative patterns (8 negative associations), as opposed to two positive relationships. On the second day, the number of negative relationships between pairs of species was lower (4), and the positive relationships were maintained between the same species. On the third day, negative co-occurrence relationships continued to predominate (4), as opposed to positive ones (1). Finally, during the fourth day, the negative relationships decreased (3), and there were two positive relationships (Fig. 3).

For the small carcasses, we could test associations between 10 species-pairs. Eight showed negative associations while only 1 was positive (**Fig. 15**). The results of the quantitative GLMMs support positive relationships between king and turkey vultures. The remaining quantitative relationships between species were negative and concordant with the qualitative co-occurrence results (**Fig. 15**, **Table S8**). The variables day of consumption and vegetation cover significantly affected the abundance per image of some species (for more details, see **Fig. 15**).

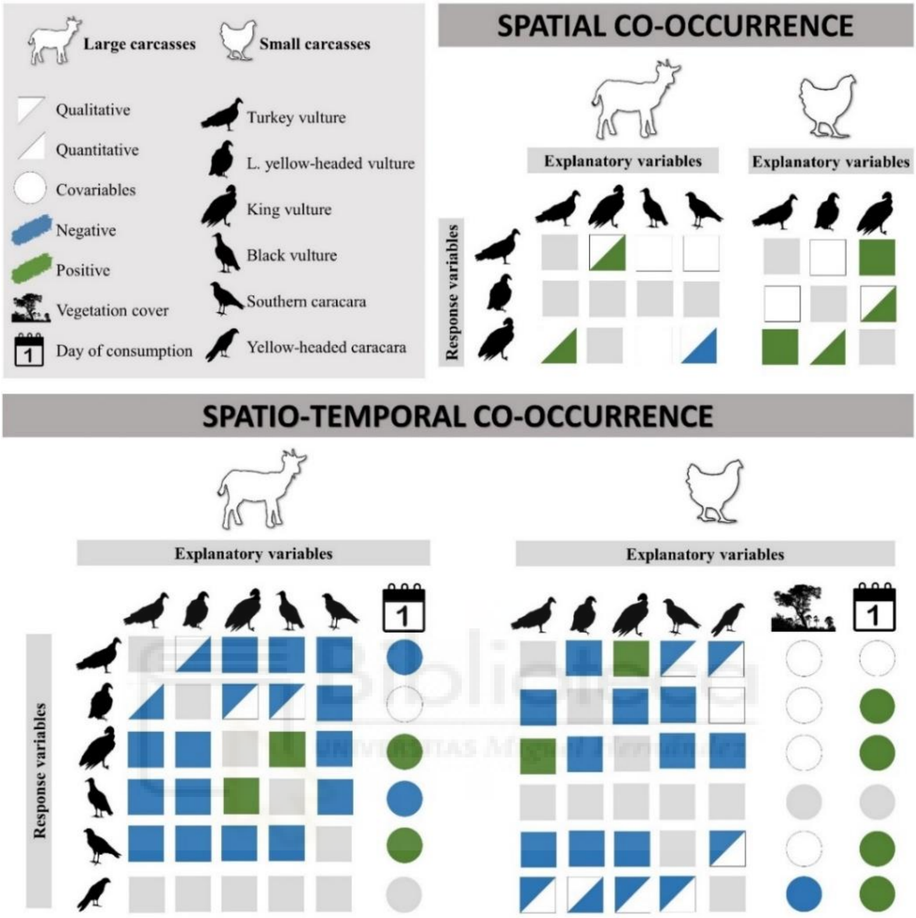

Figure 15. Results of the spatial and spatio-temporal co-occurrence analyses between pairs of species, both qualitative co-occurrence and quantitative GLMs (spatial co-occurrence) and GLMMs (spatio-temporal co-occurrence) that relate the abundances of the species. Negative associations are shown in blue and positive associations in green. Only the species associations (squares) and covariates (circles) incorporated in the GLMs and GLMMs that were significant for any of the species were represented. For more details, see Appendix S1 (**Tables S5–S8**).

DISCUSSION

Competition and facilitation relationships between species belonging to the same guild are fundamental because they determine community's functioning and ultimately shape its structure (Bascompte 2010). By examining fine-scale spatio-temporal co-occurrence patterns among scavenging species in the Brazilian *Cerrado*, our results show complex patterns of competition and facilitation that were mainly affected by carcass size. Most scavengers in this community showed differences in their activity patterns in addition to a strong spatio-temporal segregation between them during carcass consumption. Vultures co-occur at all large carcasses although both temporal association and segregation might modulate facilitation and intraguild competition for this resource.

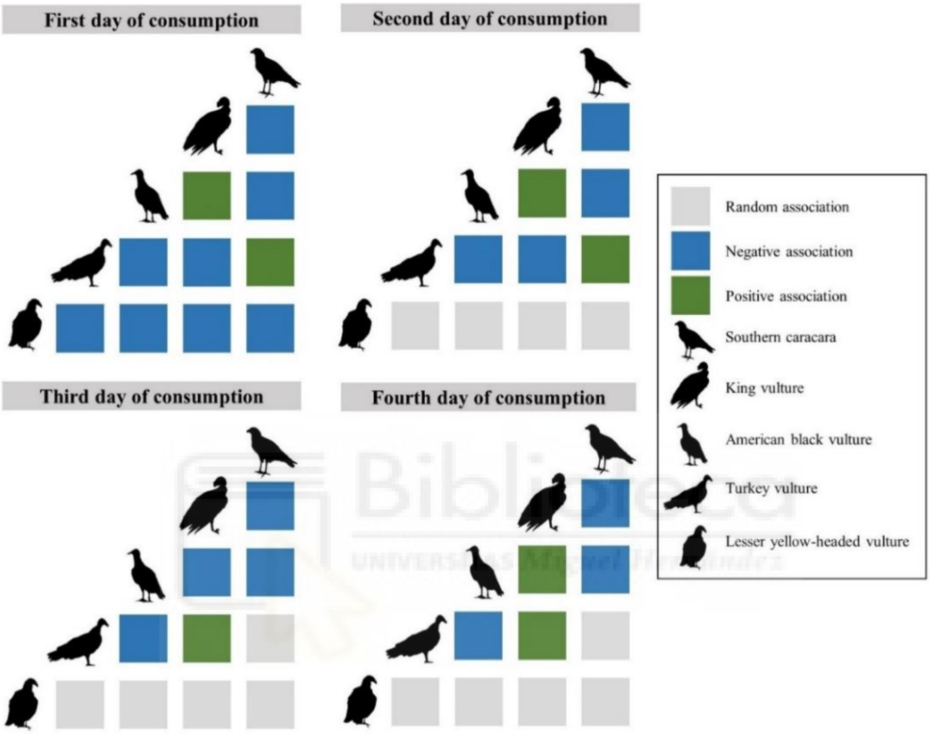

Figure 16. Spatio-temporal co-occurrence for the different days of consumption at large carcasses. Yellow-headed caracara is not included because it only appeared in one of the photographs used for this co-occurrence analysis.

Facilitation processes

Our results evidence that two different facilitation processes may be taking place between vulture species and that their relative importance changes with the size of the carcass. First, the spatial and spatio-temporal association in large carcasses among species with different abilities to open hard skin carcasses seems to evidence a facilitation process in the access to the carcass interior, supporting our first hypothesis (see **Table 4**). In this way, species that that cannot open carcasses (i.e. turkey vulture or American black vulture) would benefit from the presence of larger species or species with stronger beaks (i.e. king vulture), as has already been described in other communities (Stahler et al. 2002, Selva et al. 2003, Kane et al. 2014). Secondly, although we also found positive associations (both spatially and temporally) among vultures in small carcasses, it is unlikely that the same facilitation process is occurring given that the skin of this carcass type is easily penetrable by all species and given the differences in the average consumption times of both types of carcasses (large carcasses: 48.41 hours, vs. small carcasses: 13.55 hours) (Naves-Alegre et al. 2021). Indeed, these associations include vultures with developed olfactory capacity (e.g. turkey vulture) and vultures that only rely on sight. This would support our second hypothesis (see **Table 4**), suggesting a facilitation process in carrion location in which species with keen searching abilities would signal the presence of small carcasses to other species (Houston 1985, 1988, Wallace and Temple 1987, Gomez et al. 1994). Such positive spatial associations have already been described in other systems, such as in Africa, being explained by facilitation processes when finding carcasses, or due to a preference for the consumption of certain parts of the carcass (Kendall et al. 2012). It is important to mention that this facilitation effect could also be playing a role in the localization of large carcasses, but more studies are needed to confirm these processes.

Common associations of species eating the same carrion at the same time (i.e. positive spatio-temporal co-occurrence) may not always suggest a facilitation process between the species involved. These results could have two alternative explanations: (a) species are competitively equal in direct confrontation, for example when the difference in size between them is compensated by the social nature of one of them or its higher aggressive behavior; (b) the species are specialized in the consumption of different parts of the carcass (e.g. king vultures feed mainly on skin and tendons while American black vultures remove soft tissues) (Houston 1988, del Hoyo et al. 1994), as found for other scavenger species (Kendall et al. 2012, Kendall 2014, Moreno-Opo et al. 2020). Therefore, behavioral studies are necessary to be able to discern exactly what type of processes are taking place at any given moment, given that the process of facilitating the carcass localization will be important in the early stages of the carcass, moving on to a situation of competition between species as it is being consumed. Vegetation structure has been described as a fundamental factor that shapes vertebrate scavenger communities at different scales (Pardo-Barquín et al. 2019). Our results support a previous study showing that this factor has no effect on interspecific interactions due to the high efficiency of the *Cerrado* scavenger community (Naves-Alegre et al. 2021). However, we found a mainly negative effect of vegetation structure on the recruitment capacity of the species, that is on quantitative co-occurrences at the spatio-temporal level. Thus, a denser vegetation cover means a lower abundance of some species in a carcass at a given time. This may be due to interference in the transmission of intraspecific visual information, or as described above, dense vegetation cover may complicate access to carrion and thus limit the facilitation processes between species (Ruzicka and Conover 2012, Pardo-Barquín et al. 2019).

Competition processes

Many papers have described processes of exploitative competition between species sharing the same resources, which in many cases give rise to different scales of spatial segregation (Gotelli et al. 2010, Palomares et al. 2016, Tsunoda et al. 2017). Contrary to these previous studies and to our own third hypothesis (see **Table 4**), our findings showed no evidence of spatial segregation between species, although the small sample of large carcasses may be masking some process. However, PERMANOVA analyses showed a strong differentiation between the scavenger communities that consumed the two carcass types. Vultures monopolized large carcasses, while small carcasses were consumed by multiple species (Moleón et al. 2015b, Naves-Alegre et al. 2021). This is an evidence of resource partitioning, which allows facultative species with a lower competitive capacity to consume small carcasses where the risk of interaction with other species is lower (Tsunoda et al. 2017). Resource partitioning among vertebrate scavenger species has previously been described in diverse ecosystems, such as the Mediterranean (Blázquez et al. 2009) or in temperate forests of Europe and North America (van Dijk et al. 2008, Moreno-Opo et al. 2016).

Contrary to what has been observed for spatial co-occurrence patterns, our results highlight temporal segregation patterns between multiple species, a process described in other systems (Kronfeld-Schor and Dayan 2003, Moreno-Opo et al. 2020). According to our fourth hypothesis (see **Table 4**) this process would be a result of the interference competition derived from the hierarchy among species, segregating the competitively inferior ones (e.g. facultative scavengers or turkey vulture) to avoid direct confrontations with larger species (i.e. king vulture) and with social vultures that appear in large groups (i.e. American black vultures) (Kronfeld-Schor and Dayan 2003, Moreno-Opo et al. 2020). In large carcasses, because of their long consumption times, these spatio-temporal relationships between pairs of species change during the consumption timeline, indicating that competition levels do not remain the same throughout the consumption of the resource (Moreno-Opo et al. 2015, Moleón et al. 2019). On the contrary, many negative spatio-temporal relationships detected in small carcasses could be driven by these being mainly consumed by a single species, so that, in general, different species do not coincide at the same time on the same carcass.

Time partitioning is described as an important mechanism for reducing competition between coexisting species (Frey et al. 2017) and has been evidenced in previous studies on scavengers (Butler and du Toit 2002, Ruxton and Houston 2004). Thus, we did not find many spatio-temporal patterns among facultative species (e.g. mammals or reptiles), highlighting the differences in activity patterns between mammals, reptiles and birds. We found that mammals were mainly nocturnal, while reptiles and all bird species, both facultative and obligate scavengers were active mainly during the day. Moreover, the co-occurrence in carcasses of certain facultative species may be low because they are competitively displaced by the obligate scavengers (Ulrich et al. 2014), reducing the number of interactions between obligate scavengers and most of the facultative species (Sebastián-González et al. 2013, Moreno-Opo et al. 2016). By contrast, in other systems, facultative or smaller species have been found associated with some carnivores that open carrion (e.g. Stahler et al. 2002, Selva et al. 2003).

CONCLUSIONS

This work highlights how the *Cerrado* scavenger community structure is governed by complex processes of facilitation and competition. These interactions between species seem to be very influenced by carcass size (Moleón et al. 2015b, Naves-Alegre et al. 2021) and also change depending on the spatial and temporal scale at which they are analyzed, as previous research has shown (Kneitel and Chase 2004b, Ullas Karanth et al. 2017). However, it is noteworthy that most species showed a strong temporal segregation during carcass consumption, as an alternative to reduce competition levels (Kronfeld-Schor and Dayan 2003). The fundamental role of obligate scavengers in these processes is also emphasized, as these species were involved in most of the species-pair associations, especially in facilitation processes (i.e. location and access to the carcasses). In addition, these inter-species relationships do not always appear to be bidirectional, but rather one of the species is the trigger for the attraction or repulsion of another, that is the facilitation or competition process. Further work is needed to determine which species play the most important role in the structure and dynamics of this community, for example by considering the order of access to carcasses (Alvarez et al. 1976, Hunter et al. 2007). It is also necessary to study the interactions of vertebrate and invertebrate scavengers, especially in those systems where there are no obligate or large scavengers, as in these systems carcasses remain available for longer time periods, facilitating their use by invertebrates. Also, in the future it will be important to determine not only the interspecific patterns but also the intraspecific ones, because they may also affect the functioning of this guild.

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CHAPTER 5. SCAVENGING IN THE REALM OF SENSES: SMELL AND VISION DRIVE RECRUITMENT AT CARCASSES IN NEOTROPICAL ECOSYSTEMS

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ABSTRACT

Social information, acquired through the observation of other individuals, is especially relevant among species belonging to the same guild. The unpredictable and ephemeral nature of carrion implies that social mechanisms may be selected among scavenger species to facilitate carcass location and consumption. Here, we apply a survival-modelling strategy to data obtained through the placement and monitoring of carcasses in the field to analyse possible information transmission cascades within a Neotropical scavenger community. Our study highlights how the use of different senses (smell and sight) within this guild facilitates carcass location through the transmission of social information between species with different carrion foraging efficiencies. Vultures with a highly developed sense of smell play a key role in this process, as they are the first to arrive at the carcasses and their presence seems to serve as a visual cue for other species to locate the resource. Our study supports the local enhancement hypothesis within scavengers, whereby individuals locate carcasses by following foraging heterospecifics, also suggesting the importance of the sense of smell in the maintenance of the community structure.

INTRODUCTION

Social information refers to the acquisition of cues by monitoring how other individuals interact with the environment (Danchin et al. 2004). The use of this kind of information is increasingly recognized as a widespread phenomenon in biology (Martínez et al. 2018, Goodale et al. 2020). Social information transmission is known to influence animal movement (Langrock et al. 2014), foraging patterns(Galef and Giraldeau 2001), habitat selection and reproduction (Giraldeau et al. 2002). Traditionally, social information was understood to occur between individuals belonging to the same species (i.e. conspecifics) since they share their ecological needs (Laland 2004). Later on, information transmission processes have also become evident between individuals of different species (i.e. heterospecifics) that share and compete for a resource (Seppänen 2007, Jaakkonen et al. 2015). While most studies have focused on information exchanges among conspecifics, fewer have analysed social facilitation between species from the same guild, where a strong influence in guild structure is expected because this information transmission may reduce competition costs (Seppänen 2007, Goodale et al. 2010, Jaakkonen et al. 2015, Orr et al. 2019).

Carrion is an unpredictable and ephemeral resource that can be exploited by many species, even at the same time (DeVault et al. 2003). Thus, social mechanisms to facilitate carrion location and consumption may be selected among scavenger species since individual foraging would be very costly (Ruxton and Houston 2004, Jackson et al. 2008). Social information can pass through individuals unintentionally as cues, e.g. vultures flying in circles and descending to the ground attract other vultures and carnivores (Kruuk 1967, Veen 1977, Kane & Kendall 2017); or intentionally as signals to obtain something in return, e.g. corvids attract raptors or mammalian carnivores to carcasses to tear the skin and access the meat, as they do not have the capacity to do so (Heinrich 1988, Danchin et al. 2004).

Many studies have mentioned the facilitation between scavenger species in locating carrion, but very few have described and analysed this process in detail (Kane et al. 2014, Kane and Kendall 2017, Jackson et al. 2020). For obligate scavengers (i.e. vultures), it is not exactly known how social transmission occurs when vultures locate carcasses, but there are two hypotheses about it. On the one hand, the 'local enhancement' hypothesis, whereby individuals locate carcasses by seeing conspecifics feeding at a point (Cortés-Avizanda et al. 2014, Kane et al. 2014). On the other hand, the 'vulture chains' hypothesis states that vultures establish visual chains while they are flying to the carcass, that are used for carrion signalling (Jackson et al. 2008). In either case, there is a positive influence of the number of vultures arriving at a carcass and a decrease in the time needed for the arrival of new individuals (Jackson et al. 2008, Cortés-Avizanda et al. 2014). So far, these two assumptions have been established and tested intraspecifically for a single vulture species, even if different vulture species can feed together at a carcass at the same time (Houston 1988, Kendall et al. 2012, Moreno-Opo et al. 2020).

As described for other guilds, there may be interspecific differences in the scavenger information transmission cascades (Goodale et al. 2020). Some species may 'initiate' or 'lead' the information transmission process, being important for the maintenance of these cascades and thus for the carrion consumption process (Hoffman et al. 1981, Harrison and Whitehouse 2011). In particular, it has been suggested that information transmission mechanisms (i.e. capacity to generate and use information provided by others) may be more deeply rooted in specialist (e.g. vultures) than in generalist species (e.g. facultative species) (Martínez et al. 2018, Jackson et al. 2020). Also, the generation and use of social information can depend on species competitive ability (e.g. due to differences in size) and foraging efficiency (e.g. use of different senses) (Buckley 1997, Goodale et al. 2020). Thus, the likelihood of individuals to join, follow or stay feeding at a carcass can depend on the presence of other species with particular traits (e.g. largest beak, ability to smell), translating into characteristic patterns of arrival of the species to the carcass (Kane and Kendall 2017). The analysis of temporal data on species occurrence combined with species traits may indicate what benefits may be sought by some species following others (Sridhar and Shanker 2013, Goodale et al. 2020).

Experimental work is still critically needed to determine what social information is used and how it is used in different natural scenarios. Therefore, in this study, we aim to combine data obtained through the monitoring of carcasses in the field and the realization of models in which we analyse possible information transmission cascades within a Neotropical scavenger community. This guild has been less studied, even though some vulture species have a developed sense of smell. Therefore, we identify and rank the scavenger species that influence the process of locating and recruitment at carcasses according to different species traits (e.g. morphological or behavioural attributes) that define their roles within the assemblage (Goodale et al. 2010, Orr et al. 2019). We tested: (1) if scavengers use social information to find carcasses, in particular, if species with higher foraging efficiency (i.e. developed sense of smell) arrive first, discovering carcasses and serving as cues for others, (2) if the information transmission occurs immediately through local enhancement or if the timescale at which the transmission takes place is longer, (3) how the presence and abundance of species with different competitive capacities influence the information transmission within the assemblage, and thus the order of arrival of species to a carcass and (4) which species traits are most influential in the generation of information and its social transmission.

METHODS

Study area and scavenger community

The fieldwork was carried out in the *Cerrado* savannah, Piauí state, Northeastern Brazil. This biome has a tropical climate with two seasons, the dry season (i.e. from April to September) and the wet season (i.e. from October to March). The vegetation is very diverse, ranging from grasslands to closed forest canopy (Ratter et al. 1997, Ribeiro and Walter 1998). This area holds four species of American vultures (Cathartidae): turkey (*Cathartes aura*), lesser yellow-headed (*Cathartes burrovianus*), American black (*Coragyps atratus*) and king (*Sarcoramphus papa*) vultures. Also, facultative scavengers are present, including five species of other raptors, such as southern caracaras (*Caracara plancus*) and yellow-headed caracaras (*Milvago chimachima*), as well as mammals (5 species), reptiles (3) and other facultative birds (2) (further details in electronic supplementary material, **table S1**) (Naves-Alegre et al. 2021).

Study design and variables

During November 2018, we placed 55 carcasses differentiated into two sizes: large carcasses (*n* = 10), between 20 and 40 kg, corresponding to goat carcasses; and small carcasses (*n* = 45), in which we grouped chicken pieces and whole chickens, between 0.075 and 2 kg. We monitored each carcass until its complete consumption (48.41 ± 14.41 h for large carcasses and 13.55 ± 19.56 h for small carcasses) (Naves-Alegre et al. 2021) using two automatic cameras (Browning Strike Force pro HD), one set up to take images and the other to take videos (see Naves-Alegre *et al.* 2021 for more details). The camera was automatically activated by the animal when it was detected. We placed carcasses separating orr 2019the larger ones by a minimum of 1.5 km and the smaller ones by a minimum of 150 m, considering them as independent replicates (see Naves-Alegre *et al.* 2021 for more details of the location of the carcasses). Carcasses were placed during the day, both in the morning (before 12.00, *n* = 31) and in the afternoon (up to sunset, *n* = 24). We worked mainly with the images, but we used the videos (henceforth both called ‘archives’) when we did not have any image due to camera failure. We obtained a total of 27 092 archives (i.e. 24 624 for goat carcasses and 2468 for chicken carcasses). For each one, we determined: (1) the carcass to which it belongs (i.e. carcass ID), (2) the date and time when the archive was taken, (3) the time between carcass placement and the archive (time since carcass placement), (4) the species present in the archive (presence) and (5) their abundances, i.e. the numbers of individuals of each species (abundance). We further quantified, for each carcass, the percentage of shrub and tree cover in a 5 m radius around the point where we placed the carcass (vegetation cover). Vegetation cover could affect information transmission so that a higher cover would make it more difficult for a species to receive visual cues (Orr et al. 2019, Pardo-Barquín et al. 2019).

Statistical analysis

Because differences in community structure and consumption patterns were found between the two carcass sizes (Naves-Alegre et al. 2021), we analysed the data for large and small carcasses separately. The use of camera-trap data to model multi-species time-series dynamics is complicated because the images are not taken at regular intervals, but only when a species is present. Thus, the absence of a species is indicated by the absence of images from it, but this should be considered as data (on species absence), not as missing data. To resolve this, we converted the irregular camera-trap data into regular interval data. We denoted the time interval by Δt, and used $\Delta t = 10$ min in our main analyses (see Supporting information for sensitivity analyses where we use either Δt =1 minute or $\Delta t = 1$ hour instead). We denoted by y_{ijt} the maximum count of individuals of species j in carcass i from any image taken during time interval t. We indexed time so that $t = 1$ corresponds to the interval starting when the carcass was placed into the field.

Our main focus was to ask how the first arrival time of each focal species depends on the previous presence of heterospecifics. We included as 'focal species' those species that had appeared in at least 5 carcasses and used the first occurrence (i.e., first arrival) in each of the carcasses as the response variable (see Table S1). To account for possible confounding effects (not related to species interactions) that we thought could be influencing species arrival, we first established a baseline model in which we modelled 'focal species' abundance y_{ijt} with a Poisson regression, where we used as predictors (i) 'vegetation cover', (ii) 'time of the day', and (iii) 'time since carcass placement'. We included 'vegetation cover' as a continuous covariate ranging from 0 to 1. We included 'time of the day' through linear combination of the periodic functions $\sin(2\pi h/24)$ and $\cos(2\pi h/24)$, where $h \in [0,24]$ is the hour of the day when the image or video was taken. We included both first and second order effects of 'time since carcass placement' to account for the species abundances peaking at intermediate times since carcass placement. We note that the influence of 'time since carcass placement' can be either due to confounding factors (e.g., the stage of decay of the carcass) or due to species interactions (e.g., the late arrival of the species being explained by the focal species using other species as a cue). As these two cannot be conclusively separated from observational data, we performed a sensitivity analysis where 'time since carcass placement' was either included or excluded in the baseline model (see Supporting information). We denoted the linear predictor of the fitted baseline model by L_{ijt}. We note that this linear predictor summarizes the effects of all confounding effects into a single variable.

To ask how the first arrival times of the species depend on the presence of heterospecifics, we followed a survival-modelling strategy. We denoted by p_{ijt} the presence ($p_{ijt} = 1$ corresponding to $y_{ijt} > 0$) or absence ($p_{ijt} = 0$ corresponding to $y_{ijt} = 0$) of species j in carcass i from any image taken during time interval t. We considered, for each carcass and each 'focal species', the data only until the first arrival of each of the species, so that the sequence of the data p_{ijt} (i.e., response variable) over time intervals t is of the form of a series of zeros (absences) followed by one (presence). We modelled these data with logistic regression, where the predictors (i.e., explanatory variables) were the linear predictor L_{ijt} from the baseline model (to account for confounding effects and avoid overloading the model with covariates due to our small sample size), and the presence of other species in earlier times h_{ijt}. To consider the possibility of a species arriving at the carcass regardless of whether another species has been there previously, we consider the model that only includes the linear predictor L_{ijt} (i.e., without including the previous presence of another species) as a null model. In particular, the first and second order effects of 'time since carcass placement' model the baseline probability of when the focal species typically appears to the carcass. If the prior presence of some other species turns out to have e.g., a positive effect, it means that, the focal species is likely to appear earlier than predicted by the null model if prior presence of other species was recorded in the carcass, whereas it is likely to appear later than predicted by the null model if prior presence of other species was not recorded in the carcass.

We considered several alternatives to define the presence of other species in earlier times (h_{ijt}) to evaluate different hypotheses for the transmission of information between species. We varied the following axes: (A) who the influencer is (i.e., the species or set of species that arrive in the carcass prior to the focal species and that may be influencing its appearance); (B) at what time-scale the influence takes place (i.e., how long does the visual cue of the presence of other species last); (C) is it the presence or abundance of the influencer that matters? Concerning (A), we either considered (A1) all the species other than the focal species irrespective of their identity; (A2) those avian species that can smell, i.e., *Cathartes* species, with an olfactory bulb up to four times larger than other sympatric vultures (e.g., black vultures) (Grigg et al. 2017, Potier 2019, Potier et al. 2019); (A3) each individual species, however restricting the analyses to only those species detected occurring before the focal species at least five times. Concerning (B), we considered the data for the influencer either (B1) during the previous 10 minutes; (B2) during the previous 30 minutes; (B3) during the previous hour, following the methodology established by Orr *et al.* (2019); or (B4) during the previous 4 hours; to detect whether information cascades were occurring on a larger time scale, as would occur in the vulture chain hypothesis. Concerning (C), we considered (C1) the presence-absence of the influencer, (C2) the proportion of time-intervals during which the influencer was present; or (C3) the maximum abundance of the influencer during the focal time period (i.e., values determined in the alternatives of hypothesis B). Some of these predictors are correlated, and thus they are not independent alternatives, but comparison about their relative fits to the data may, however, yield valuable suggestions on the likely drivers of the heterospecific interactions.

All analyses were conducted in the R programming environment (Andy Bunn 2017) using generalized linear models (GLMs) with a Poisson distribution (log link function) or a Bernoulli distribution (logit link function). For GLMs we used the *glm* function in the *lme4* package (Bates et al. 2007). We selected the best models based on Akaike's information criteria for small samples (AICc) from all potential models (including null model) using the *AICc* function in the *MuMIn* package (Bartoń 2019), and we choose only those with an ΔAICc <2 (i.e., top-ranking models) (Burnham & Anderson 2002). Finally, we calculated the goodness of fit for the top-ranking models through the percentage of deviance explained (D^2) (Burnham & Anderson 2002):

$$D^2 = \frac{null\ deviance - residual\ deviance}{null\ deviance}\ x\ 100$$

RESULTS

Some species in the community were recorded commonly as the first to reach the carcass (e.g. *Cathartes* species, with a first arrival time of 25.61 ± 17.82 h), while we never observed some other species to arrive as the first ones (**figure 17**). The arrival of the species to large carcasses was more predictable than their arrival to small carcasses, as for small carcasses there was greater variability in the times it took for species to reach the carcass (**figure 17**, see electronic supplementary material, **table S2** for further details). We observed several cases where species influenced each other's arrival positively, but not any case of a negative influence (**figure 18**). In particular, the king vulture and the southern caracara were positively influenced by the previous occurrences of the other species. This result was highly robust, as we observed such a positive influence almost independently on how we constructed the biotic predictor, i.e. whether we considered as the influencer all species or only some of them, whether we considered the *presence* or *abundance* of the influencer, or whether we considered the *presence* of the influencer over short or long time-intervals (the predominance of green squares in **figure 18** for these species). Furthermore, these results held whether we discretized the data to Δt = 1 min, Δt = 10 min or Δt = 1 h intervals, and whether we included or excluded the *time since carcass placement* in the baseline model (see electronic supplementary material). Interestingly, for both the king vulture and the southern caracara, at large carcasses we observed the strongest influence of the *abundances* of *all other species*, whereas at small carcasses the presence of influencers *with olfaction* (especially the turkey vulture; with a first arrival time to small carcasses of 29.14 ± 17.00 h, electronic supplementary material, **table S2**) had the highest effect, being included in the top-ranking models (green squares marked with thick borders in **figure 18**). Also at small carcasses, the lesser yellow-headed vulture (19.60 ± 18.43 h, electronic supplementary material, **table S2**) was influenced by the previous *presence* of *all other species*, especially by the proportion of time that the other species were present shortly before the focal time (i.e. alternatives of B; **figure 18**).

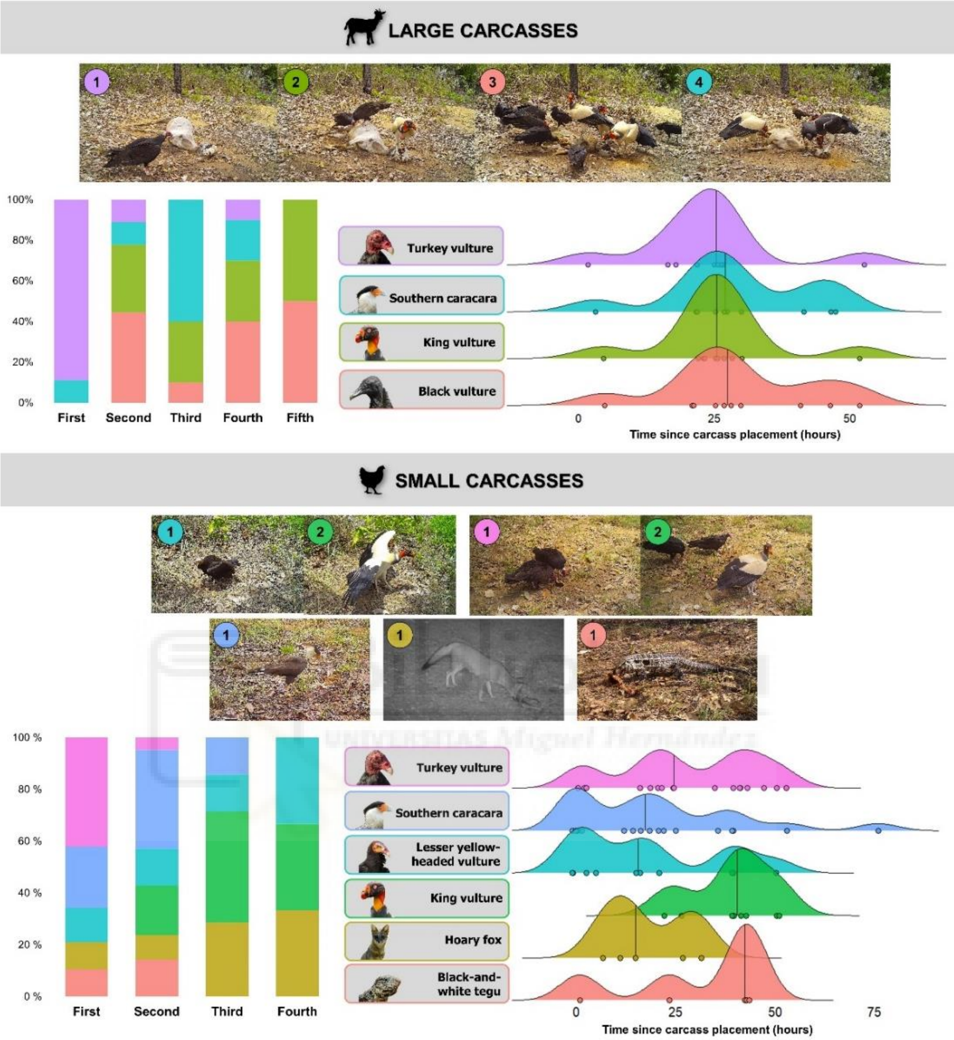

Figure 17. The succession of arrival (bar plots) and arrival time since carcass placement (smoothed plot) of different species to large carcasses and small carcasses. The photographs exemplify consumption patterns, numbers in each image refer to the chronological arrival of a new species and the colour of the number refers to the species. Bar plots represent the percentage of times that each of the focal species (i.e., different colours) reached the carcasses in the different positions (i.e., x-axis; from the first position to the fifth one). The smoothed plots show, for each of the focal species (i.e., y-axis), their frequency with which they arrived at different times since carcass placement (i.e., x-axis in hours). The vertical line in the frequency curves represents the median value of the arrival time for each species. See **Table S2** for further details.

Our results were not conclusive on whether the American black vulture was or was not influenced by the previous *presence* of heterospecifics, as in some of the model variants we did record a significant effect while in other model variants we did not do so (see electronic supplementary material, Information). We did not obtain any influence of heterospecifics on their arrival for turkey vultures, hoary foxes (19.13 ± 10.46 h) and the black-and-white tegu (31.45 ± 18.51 h), either because there were not enough previous occurrences of other species to fit the models, or because their influences were not significant (**figure 18**). As expected, the linear baseline predictor L_{ijt} had a positive effect for all species, even if the effect was not significant for some cases (**figure 18**).

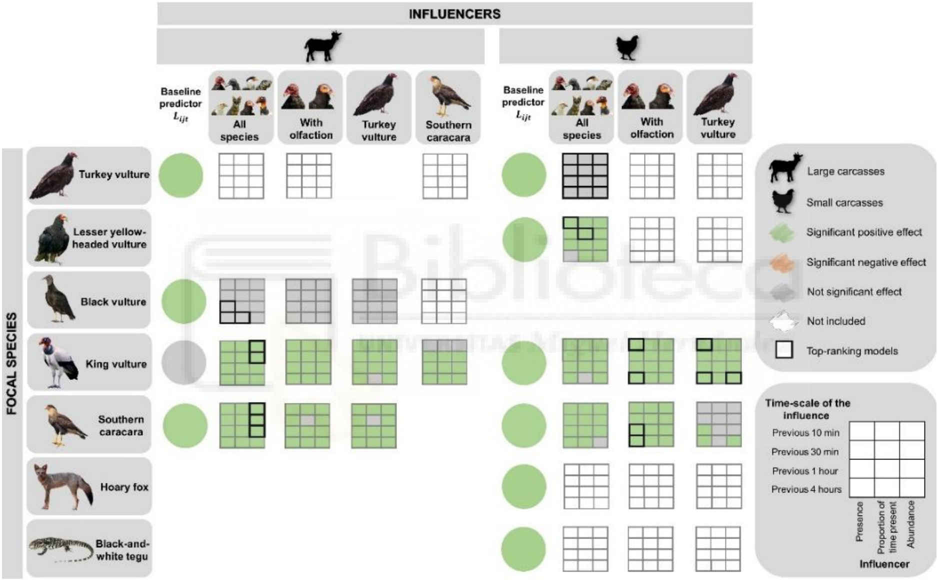

Figure 18. Results of the logistic regression on heterospecific influence on first arrival times, shown separately for large and small carcasses. Circles refer to the influence of the baseline predictor L_{ijt}, and the squares to the heterospecific influence. Positive and significant ($p<0.05$) influence on the occurrence (i.e., first appearance) of each focal species is indicated in green; non-significant effects are indicated in grey and model combinations not considered are shown in white. The absence of squares indicates that there is no model for that focal species. The different combinations for B1-B4 (i.e., importance of the presence or abundance of the influencer) and C1-C3 (i.e., previous time considered) assumptions are represented in the mini-squares. See Tables S3 and S4 for further details. The results are shown here for the data discretized to time resolution of Δt=10 min, and for the case where the time since carcass placement was included in the baseline model. See Supporting Information for corresponding results for data discretized to time resolution of Δt=1 min or Δt=1 hour, and the case where the time since carcass placement was excluded in the baseline model.

DISCUSSION

Disentangling the use of social information between species that share a resource and exhibit different foraging capabilities is fundamental to understand the interspecific interactions and how a guild is structured (Forsman et al. 2002). Our results show how the use of different senses (smell and vision) to find carrion allows for facilitation processes through the transmission of information between scavengers in a Brazilian *Cerrado* community. American vulture species with high olfactory ability are the first to arrive at the carcasses and initiate visual information cascades that will indicate species with a lower foraging efficiency (e.g. limited olfactory ability) the presence of the carcasses. In general, signal reception and subsequent response seem to take place in short times, which supports the 'local enhancement' hypothesis, so that when any individual sees a heterospecific feeding at a location, it may approach and locate the carcass (Jackson et al. 2008, Arbilly and Laland 2014). Furthermore, these patterns of information transmission appear to be strongly influenced by the size of the resource, being fundamental in the location of small carcasses.

Our findings support that scavenger species in this Neotropical guild rely on olfactory (e.g. *Cathartes* vultures, mammals) and visual cues (e.g. most avian scavengers) to locate carcasses. This result contrasts with the foraging behaviour of scavenger guilds in Eurasia and Africa, in which only mammals have a highly developed sense of smell, whereas vultures rely only on visual cues to locate carrion (Houston 1985, Potier et al. 2019). In our system, vulture species with a developed sense of smell seem to have a clear advantage over those lacking this ability, since they are the first ones that arrive to most carcasses (Houston 1986, 1988). This dominance of vultures at large and small carcasses in Neotropical ecosystems contrasts with the dominant role of meso-carnivores and raptors at small carcasses in other biomes (Moleón et al. 2015b).

We highlight the role of the turkey vulture, as it is consistently the first one locating large carcasses and it does not depend on any species to locate the smaller ones (Wallace and Temple 1987, Houston 1988, Potier et al. 2019). On the contrary, our models show that the first occurrence of the lesser yellow-headed vulture depends on the previous presence of other species, despite they had short arrival times and a highly developed sense of smell (Houston 1985, Grigg et al. 2017, Campbell 2021). Therefore, our findings could be due to differences in these species' relative abundance in the study area (L Naves-Alegre, JA Sánchez-Zapata, E Sebastián-González 2018, unpublished data). Foraging behaviour refers to both the acquisition of resources and the way in which information about those resources is acquired (i.e. personal experience and social information) (Clark and Mangel 1984). Although our data are correlational, our results show the existence of temporal associations between species, suggesting a facilitation process locating carrion (i.e. increase in foraging efficiency), since the presence of heterospecifics at the carcasses positively influences the appearance of new species (Heyes and Galef Jr. 1996, Galef and Giraldeau 2001). This agrees with social information taking a fundamental role when resources are unpredictable, as happens with carrion (Deygout et al. 2010). Previous research has shown that species using different foraging behaviour (e.g. different senses) act as initiators of mixed-species feeding aggregations in multiple systems (Duffy 1989, Harrison et al. 1991). Our results show that vulture species with developed sense of smell generate this information since their presence serves as a visual cue for other species to locate the carcasses. Our findings also show that, once a species with olfactory capacity arrives at the carcass, the rest of the species may join independently of the identity of the species, creating information cascades but without following a specific order of arrival. Through the reception of social information, individuals with lower foraging capacity may visually follow the ones with higher capacity (e.g. developed olfaction) that have previously arrived to the carrion following olfactory cues (Heinrich 1988). However, the decision to join a group of individuals from other species must involve a balance between the potential benefits (e.g. access to the resource) and costs (e.g. aggressive interactions) (Martínez et al. 2018). Similarly, the individual who generates the initial cue (e.g. turkey vultures) will benefit from arriving in first place but is not expected to profit from the arrival of other species, since there is a possibility of being displaced by new individuals who arrive at the carcass (e.g. larger species like king vultures). This has been seen for turkey vultures, which used to be displaced after the arrival of other species (Wallace and Temple 1987, Houston 1988, Buckley 1997).

Furthermore, facilitation processes through social information cascades seem to be influenced by carcass size and the temporal scale. On the one hand, our results show how the presence of species with a developed olfactory capacity (i.e. turkey and yellow-headed vultures) especially influences the arrival of other species at small carcasses. This may be because small carcasses are more difficult to locate, i.e. the intensity of the visual cue is stronger at large carcasses due to their larger size. Although it is also possible that the olfactory cue may be stronger at large carcasses (i.e. more rotting biomass). Therefore, having a developed sense of smell may be a fundamental advantage for reaching small carcasses first, since the difficulty of finding them is higher. In addition, at small carcasses the mere presence of an individual from another species would serve as a visual signal, while at large carcasses the maximum abundance is more important. This could be because the number of individuals consuming a carcass is larger at the large ones, generating a stronger visual signal (Naves-Alegre et al. 2021). On the other hand, cues were perceived on a different timescale by the different species, since some of them arrived at the carcass immediately upon perception of the cue (e.g. 10 min) and others required longer periods of time (e.g. up to 4 h). This could be because not all species respond to the presence of other species equally, probably due to differences in foraging efficiency, abundance and competitive abilities among them (Kendall 2013, Reichert et al. 2021). We found that most species responded quickly to the previous presence of heterospecifics, which supports the 'local enhancement' hypothesis against the hypothesis of a wider chain of information (e.g. 'vulture chains' hypothesis) (Arbilly and Laland 2014).

Interestingly, mammals and reptiles do not seem to be influenced by the previous presence of other species. This contradicts what happens in other systems where birds influence the arrival (i.e. recruitment) of carnivores, or vice versa (Kruuk 1967, Kane and Kendall 2017). Both mammals and reptiles have a developed sense of smell and chemoreception, respectively, which would allow them to locate carrion without depending on vulture species. This lack of use of social information may also be due to the quick consumption of small carcasses (i.e. the only ones that are consumed by most facultative scavengers), as the first individual to locate the carcass is the one consuming it completely in most cases (Naves-Alegre et al. 2021).

Our study highlights how the use of different senses (i.e. smell and sight) within a Neotropical scavenger guild gives rise to facilitation processes in locating carcasses using heterospecific social information. Species with a higher efficiency in finding carcasses (e.g. highly developed smell) play a key role in this process, as they seem to serve as a visual cue for the rest of the species. The use and transmission of social information is subject to strong selection pressures and can influence the individuals from the same or different species to the community structure (Seppänen et al. 2007, Goodale et al. 2010). This makes essential to continue investigating how senses influence the processes of social information transmission and its relative importance depending on different factors, considering both heterospecific and conspecific information, and including all the species of the scavenging community.

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CHAPTER 6. BEHAVIORAL INTERACTIONS ARE MODULATED BY FACILITATION ALONG A HETEROTROPHIC SUCCESSION

Naves-Alegre L, Sebastián-González E, Sánchez-Zapata JA. Behavioral interactions are modulated by facilitation along a heterotrophic succession (*submitted to Ecology*).

ABSTRACT

Competition and facilitation drive ecological successions. The inclusion of behavioral data in the study of ecological communities is still scarce. However, may be a key tool to analyze interaction networks, providing us insights into temporal trends in non-static facilitation and competition processes within animal heterotrophic successions. In this way, we perform the first in-depth analysis of the temporal dynamics driving a scavenging succession, and factors affecting them, by using interspecific aggression as a behavioral proxy of competition intensity. Our results show that resource availability shapes behavioral and facilitation interactions between species. Furthermore, facilitation was related to moments of higher tolerance (i.e., lower aggressiveness), thus reducing the intensity of competition, and affecting community structure and dynamics. This novel framework evidences a complex ephemeral successional process characterized by a fluctuation in the facilitation and competition intensity during the consumption of an unpredictable resource whose consumption is linked to key ecosystem processes.

INTRODUCTION

Ecological succession is one of the most studied processes in community ecology, being defined as a sequence of changes in an ecological community that are observable in time and space (Connell and Slatyer 1977, Begon and Townsend 2020). Two different types of successions have been described. On the one hand, autotrophic succession starts with an ecosystem with low biomass due to a disturbance, that increases over time as species colonization occurs, also increasing the flow of energy in the ecosystem. On the other hand, heterotrophic successions begin from an ephemeral resource (e.g., dung, carrion, fruit) and thus a peak in resource availability that disintegrates as succession progresses, resulting in the disappearance of the community (Begon and Townsend 2020).

Successions provide a conceptual framework for comprehending community and ecosystem dynamics (Prach and Walker 2011). Thus, understanding how successions occur is still essential in modern ecology because disturbance regimes are being altered, putting biodiversity at risk and thus modifying ecosystem services (Pulsford et al. 2016, Chang and Turner 2019). Several theoretical backgrounds have been proposed to describe the colonization of species along the succession (Connell and Slatyer 1977, Pulsford et al. 2016, Koffel et al. 2018). In this sense, Facilitation and Inhibition Models, developed by Coonnell & Slatyer (1997), should be highlighted. The Facilitation Model established that succession process begins with the colonization of the early species (i.e., pioneer species), which modify the environment, making it less suitable for the establishment of other pioneering species, but enhancing the establishment of late species. Contrary, the Inhibition or Competition Model establishes that the modifications made by pioneer species favor them and prevent the establishment of late species. Nevertheless, most of these classical models of community ecology have been tested using time static measurements (e.g., different succession stages). However, with the development of new techniques and analytical tools, the importance of understanding the dynamics of communities over time and successions as a continuous process has become evident (Collins et al. 2008).

In classical ecology, two species sharing the same requirements will develop different strategies to avoid high levels of competition, e.g., niche differentiation. Alternatively, it has also been assumed that the intensity of competition has an inverse relationship to phylogenetic relatedness between species that coexist (Rangel et al. 2018). However, one of the limitations in studies on community dynamics (i.e., succession) is the difficulty of measuring variations in the intensity of competition between species that coexist and have the same ecological requirements (Pulsford et al. 2016). This problem could be addressed in animal communities through behavioral studies, since the most immediate response of animals to any change is at the behavioral level (Bro-Jørgensen et al. 2019). In the last decade, behavioral biology has been included in the study of animal networks since the behavior of a single species influences the behavior of other species through interspecies interactions, leading to cascading effects at the community level, and determining ecological processes (Kurvers et al. 2014, Rahman and Candolin 2022). Indeed, the need to refine the study of functional relationships between organisms by measuring traits based on behavioral measures has become evident (Schleuning et al. 2023). Specifically, aggressive behaviors have been associated in the literature to competition for a limited resource. Because some aggressive interactions can be harmful or fatal, animals will often reserve them for situations where the perceived risk is high (Mohamad et al. 2010, Kilgour et al. 2020). Thus, by studying behavioral patterns, and, specifically, trends over time in aggressive interactions among organisms that coexist, share a resource, and are phylogenetically related (e.g., obligate scavengers), we might understand changes in the intensity of competition between species through resource consumption (Kilgour et al. 2020, Wilson et al. 2020). Nevertheless, this requires observational studies in natural situations, since other indirect methods (e.g., radiotracking) cannot provide information at the scale needed to discern patterns of interactions between species.

The decomposition of organic matter is fundamental in all ecosystems, as it is a key element in the cycle of matter and energy (Moore et al. 2004, Benbow et al. 2019). Specifically, carrion is a unique resource due to its high nutritional content and its ephemeral and unpredictable nature, both temporally and spatially (Barton et al., 2013, 2019). Nevertheless, most of the scientific work has focused on autotrophic successions (Chang and Turner 2019, Rezende et al. 2021). Furthermore, the study of successions that occur during the consumption and decomposition of the bodies of dead organisms has focused on invertebrate species and microorganisms (Moura et al. 2005, Pechal et al. 2013, Sladecek et al. 2021, Dawson et al. 2022). But, although the role of these organisms is very important in certain systems, vertebrate scavengers consume the greatest amount of vertebrate carrion biomass, playing a key role in carrion recycling (DeVault et al. 2003, Gutiérrez-Cánovas et al. 2020). Carrion of a certain size allows the consumption of multiple individuals of different species at the same time (Moleón et al. 2015), which implies very high levels of competition, occurring among both conspecific and heterospecific individuals (Moreno-Opo et al. 2020, Naves-Alegre et al. 2022a). Furthermore, different facilitation processes have also been described in scavenger communities, in the provision of carrion by carnivores (Allen et al. 2014), in the location of the carcass (Sebastián-González et al. 2016, Naves-Alegre et al. 2022b) and for carcass opening (Selva et al. 2003, Naves-Alegre et al. 2022a). The process of carcass opening refers to tearing apart the hard ungulate skin, which can only be done by a few scavenger species (e.g., those with the largest body size, or with powerful beaks), and thus giving access to the inside of the carcass for all scavengers. But this event has only been studied with time-static measurements, relating it to the total time of carrion consumption (Selva et al. 2003), association patterns between species with different skin-opening abilities (Kendall 2013, Naves-Alegre et al. 2022a) or the relationship between the number of skin apertures and the frequency of feeding of a given species (Alvarez et al. 1976). Hence, carrion is an ideal system to study temporal changes in the competition and facilitation processes that occur within vertebrate organisms during a heterotrophic succession, since the community changes rapidly over time and carcasses could be easily monitored.

In this study, we investigate the underlying dynamics of heterotrophic succession in a Neotropical vertebrate scavenger community, comparing it with classical theoretical background (Connell and Slatyer 1977, Pulsford et al. 2016). First, we analyze changes over time in the scavenger assemblage to understand the temporal dynamics of this ephemeral succession (Collins et al. 2008, Rezende et al. 2021). Second, we identify temporal patterns in behavioral processes to assess the competitive and facilitative interactions that drive the dynamics of carrion consumption. In this way, we assume a direct relationship between levels of aggressiveness and competition, while moments of reduced aggressiveness may reflect higher tolerance and/or facilitation processes (Mohamad et al. 2010, Kilgour et al. 2020). We establish specific hypotheses related to these objectives (see **Table 5** for hypotheses and further details).

Table 5. Hypotheses explaining potential competition and facilitation processes through behavioral changes in the intensity of aggressiveness of the interactions between species, and variables influencing heterotrophic succession dynamics in a vertebrate scavenger assemblage in the Neotropics.

Theoretical background	Hypothesis	Expected pattern	References
Heterotrophic successions (e.g., animal successions) start from an ephemeral resource that becomes available to the community. The resource begins to be colonized and consumed by different species. It is the community itself that ends up with the resource, collapsing the succession.	**1)** Community assembly and dynamics will vary as the heterotrophic succession progresses, until the complete disappearance of the resource, which will lead to the disappearance of the community.	Scavenger richness, abundance and diversity will show a bimodal trend along the carcass consumption process. There will be an increase in these variables at the beginning of the succession, as the recruitment of individuals of different species occurs. This trend will reach a maximum when the carcass community reaches its carrying capacity. Then, the biomass of the resource will begin to decrease until the disappearance of the community. Species turnover will be large at first, as more species are recruited. At the end of the succession, when the carrion is practically consumed, the turnover will increase again because the composition of the community will be less stable, with a higher species loss.	Briers 2006; Collins *et al.* 2008; Magurran and Henderson 2010; Rezende *et al.* 2021
Facilitation Model: pioneer species alter the conditions making the environment less favorable for them, but more suitable for later successional species. This succession model occurs most often in primary successions and animal successions.	**2)** The dynamics of the heterotrophic succession that occurs during the consumption of a medium/large sized carcass will be driven by a facilitation process produced by the opening of the carcass skin. This aperture can only be carried out by some of the species of the community, which will make the entire resource biomass available to the rest.	Pioneer species will be present during the first part of the succession, and will not inhibit the establishment of later species. Scavenger richness, abundance and diversity will be higher when the carcass is opened, since this is the time when all species in the community will be able to consume the resource. Turnover will be higher when the carcass is opened and the resource is fully available, allowing more species to come and consume it. Aggressiveness levels will be higher before carcass opening, since the availability of the resource will be limited. Once the carcass is opened, competition levels will decrease, since more resource will be available.	Álvarez *et al.* 1976; Connell and Slatyer 1997; Selva *et al.* 2003; Kendall 2013; Naves-Alegre *et al.* 2022a
Inhibition Model: pioneer species modify the environment in such a way that it becomes less suitable for the colonization of other, later species. This model establishes that succession will therefore be driven by the dominant species.	**3)** Competition levels will remain high throughout the carrion consumption process, so that when the dominant species reaches the carcass, general levels of aggressiveness will increase among the individuals of other species that will not be able to access the resource.	Pioneer species will be present during the first part of the succession and will inhibit the establishment of later species. As succession progresses and the resource becomes colonized, we expect that competition among individuals for the resource will increase, leading to a corresponding increase in aggression levels. However, once a certain point of the succession is reached, aggression levels will decrease as individuals become satiated or because there is not enough resource available.	Brown 1964; Connell and Slatyer 1997; Mohamad *et al.* 2010; Georgiev *et al.* 2013; Allen *et al.* 2014; Briffa *et al.* 2015; Kilgour *et al.* 2020; Moreno-Opo *et al.* 2020
	4) Aggressiveness will be driven by the dominant species.	King vulture will drive aggressions, as it has been described as the dominant species in the Neotropical scavenger hierarchy due to its larger size.	

MATERIAL AND METHODS

Study system

The study was carried out in the neotropical savanna called *Cerrado*, in the north-eastern of Brazil (state of Piauí). The Brazilian *Cerrado* is one of the largest biodiversity hotspots on the planet, with an extension of over 2 million km² (Klink and Machado 2005). We focused on the species of avian scavenger that had been recorded consuming large carcasses in this community (Naves-Alegre et al. 2021). Thus, we considered four vulture species (i.e., obligate scavengers): turkey (*Cathartes aura*), lesser yellow-headed (*Cathartes burrovianus*), black (*Coragyps atratus*) and king (*Sarcoramphus papa*) vultures; and two species of facultative avian scavengers: Southern caracara (*Caracara plancus*) and Yellow-headed caracara (*Milvago chimachima*).

Study design and general variables

During November 2018, we placed 11 goat carcasses ranging from 20 to 40 kg in weight and at least 1.5 km apart, to maximize spatial independence. Each carcass was monitored by two automatic cameras (Browning Strike Force pro HD model), one configurated to take photos and the other to record video (see Naves-Alegre *et al.* 2021 for more details on the fieldwork design). In this way, we obtained a total of 2501 videos and 27,448 images (jointly referred to as "archives" from here onwards).

We assigned an ID to each archive, and we registered the following variables: 1) the *carcass* to which it belongs, 2) date and time, 3) *richness* (i.e., number of species present), 4) the *abundance* of each species present (i.e., maximum number of unequivocally different individuals of a species registered in the video) and 5) the number of individuals *actively feeding* of each species, defined as those individuals that were observed feeding for at least one third of the duration of the video (i.e., over 20 seconds). Furthermore, to estimate the moment of consumption of the carcass, we calculated the variable 6) *percentage of total carcass consumption* for each archive. To this end, we considered the *time since carcass detection* (i.e., time elapsed between the detection of the carrion and the time the file was taken) and the *time of complete carcass consumption* (i.e., time elapsed between the detection of the carrion and the complete consumption of the carcass) (Wenting et al. 2022). Thus, we calculated:

$$PC_{ik} = \frac{T_{ik} - CD_k}{CC_k - CD_k} \times 100$$

where PC_{ik} is the *percentage of total carcass consumption* of an archive *i* from a carcass *k*. T_{ik} is the data and time of the archive *i* in carcass *k*. CD_k is the *time of carcass detection* and CC_k is the *time of complete carcass consumption* (see Table S1 for details on the variables).

We used 20,656 archives for general community analyses, with records of all scavenger species present and their abundance. Maximum time of the consumption process of each carcass was recorded (i.e., from $PC = 0$ to $PC = 100$), eliminating files after the complete consumption of the carcass. For behavioral analysis, we used only the videos, which were one minute long and set to be taken every 3 minutes. We discarded one carcass, because the videos were poorly focused. From the resulting videos, we first selected those videos in which more than one individual appeared, as our main objective was to focus on interactions. Second, we took a sample of videos from each carcass by selecting them in an alternating pattern (e.g., viewing 1 out of 3 videos) so that they covered the entire process of carcass consumption (n = 573 videos; see Table S2 for further details). Moreover, to determine if there was a change in the pattern of interactions before and after the carcass opening, we established the *time of carcass opening* for each carcass, at which the ventral part of the carcass had an aperture large enough to consider that all species (regardless of their capacity, i.e., body size, size of the carcass) could dispose of the total biomass of the carcass. The opening of carcasses was located on average at 25% of the *PC* (Table S3). Consequently, we defined a binomial variable we called *carcass opening status*, whereby videos with date and time before the time of carcass opening where classified into *closed* (n = 149); and videos after the opening date and time were classified as *open* (n = 424).

Community dynamics metrics

To understand how the scavenger community changes throughout the succession process and the effect of the possible facilitation process due to carcass opening (hypotheses 1 and 2), we initially calculated 1) the richness and 2) total abundance of species present in the different points of the carcass consumption (i.e., *PC*). Then, we conducted community dynamics analyses by using *codyn* R package (Hallett et al. 2016), using as time variable the *PC* and as replicate variable the *carcass*. In this way, we calculated 3) dynamic changes in species richness throughout the process of carcass consumption considering both species losses and gains, i.e., total turnover (*turnover* function). Additionally, we calculated 4) the Shannon-Wiener diversity index along the carcass consumption process using the *community_diversity* function (see Appendix S1 in Supporting Information).

Behavioral data collection

For the extraction of behavioral data, we only considered vulture species because they monopolized the consumption of large carcasses (Table S4), interactions of the rest of the species were scarce, in addition to the fact that they play a major role in the processes of facilitation and competition in this community (Naves-Alegre et al. 2022a). We defined *interaction* as any action between two vultures that involved one responding to the presence or activity of the other, whether by intentional (e.g., direct attack) or unintentional (e.g., displacement) behavior of the initiator individual (Table S5) (Moreno-Opo et al. 2020). We did not distinguish between individuals, given the difficulty of tracking them throughout the playback of a video, as individuals move in and out of the camera's field of view, and because most of these species lack patterns that would allow us to identify individuals easily. For this reason, we quantified the total number of interactions between all the individuals observed in a video (regardless of their identity), i.e., focal-animal sampling (Altmann 1974). Furthermore, we sampled several kinds of interactions indicating different levels of aggressiveness and hierarchy between individuals, differentiating interactions initiated by the different vulture species (i.e., turkey, lesser yellow-headed, black and king vultures; Table S5). Given the very small sample of interactions obtained for vultures of the genus Cathartes, i.e., turkey and lesser yellow-headed vultures, we considered these two species together (hereafter designated Cathartes vultures) because of the similarity in their behavioral traits and scavenging efficiency (Houston 1988). Behavioral data extraction from the videos was carried out by a single person, to increase consistency in the interpretation of the behaviors.

Statistical analyses

We used Bayesian mixed models to analyze changes in some of the community dynamics metrics and fluctuations in the competition levels throughout the carcass consumption process. On the one hand, to determine whether changes in community richness and abundance occurred during carcass consumption and the effect of carcass opening (hypotheses 1 and 2), we modeled 1) species richness (*poisson* distribution, link = "log"), 2) total turnover (*gaussian* distribution, link = “identity”), 3) total species abundance (*poisson* distribution, link = "log"). Moreover, to determine changes in community diversity s, we also modeled 6) the Shannon index (*gaussian* distribution, link = “identity”). We initially included in all models the explanatory variables: i) *PC* and ii) *carcass opening status*. Moreover, to determine the variation in the abundance of each species along the carcass consumption, we used univariate models, using as response variables 1) the abundance of Cathartes vultures, 2) the abundance of black vultures and 3) the abundance of King vultures; and as explanatory variable i) *PC* (all fitted with a *poisson* distribution, link = "log").

On the other hand, to analyze possible changes in the intensity of competition (hypotheses 2 and 3), we considered attack and theft interactions together (henceforth referred to as "*aggressive interactions*") as those are the two types of interactions that involved the highest level of aggressiveness and intentionality, and are therefore a good proxy to measure the level of competition. Thus, we assumed that the remaining interactions, i.e., affiliative and retreat interactions (henceforth referred to as "*non-aggressive interactions*"), will represent less competitive situations, masking facilitation processes and/or moments of higher tolerance between individuals, as these kind of interactions represent non-aggressive relationships, avoiding direct confrontations, and thus reflecting a certain degree of tolerance and the existence of pre-established hierarchies among individuals (Mohamad et al. 2010, Grossel et al. 2022). We analyzed 4) the total number of interactions, regardless of the kind of interaction, to determine general changes in interactions numbers between individuals through the carcass consumption process. In this case, in addition to the previously mentioned predictors (i.e., *PC* and *carcass opening status*), we also added iii) total abundance, iv) Cathartes vultures' abundance, v) black vultures' abundance, and vi) king vultures' abundance as explanatory variables. We fitted these models to a poisson distribution (link = "log"). We did not include the number of individuals of each species *actively feeding* in any of the models since these variables were highly correlated (Pearson's |r| > 0.70) with each species' abundance (see Fig. S1).

Second, we evaluated the changes in aggressiveness intensity (i.e., competition intensity) along the whole process of carcass consumption. We used mixed aggregated *binomial* regression models (link = "logit"), where the response variable was modelled as: $y_{interaction_i} \sim Binomial(y_{total_i}, p_i)$, where $y_{interaction}$ was the number of an interaction type in a *i* video recorded, y_{total} was the total number of interactions recorded in this *i* video, and p_i was the probability that all recorded interactions were of the type of interaction we model, i.e., $p_i \sim uniform(0,1)$. In this way, we analyzed: 1) the proportion of *aggressive interactions*, 2) the proportion of *non-aggressive interactions*, 3) the proportion of *interspecific aggressive interactions*, and 4) the proportion of *interspecific non-aggressive interactions.* We included as explanatory variables: i) *PC*, ii) the *carcass opening status*, iii) the total *abundance* of all species considered together, iv) Cathartes vultures abundance, v) black vultures abundance, and vi) king vultures abundance. We built a full model for each previous response variable following the form:

$$logit(p_i) = \alpha_{0i} + \beta_1\mathrm{PC} + \beta_2\mathrm{PC}^2 + \beta_3\mathrm{PC}^3 + \beta_4\mathrm{CarcassStatus}_i + \beta_5\mathrm{CathartesVultures}_i + \beta_6\mathrm{BlackVulture}_i + \beta_7\mathrm{KingVulture}_i + \epsilon$$

where p_i is the probability that a type of interaction is recorded in video *i*. *PC* was included in all full models as a degree 3 polynomial to determine if its effect was not linear (hypothesis 3). α_{0i} refers to the intercept, y β are the parameters of the different covariates considered.

We included *carcass* as random intercept in all models to consider the differences in the consumption of each carcass and the differences in their initial size (i.e., initial biomass). We built all possible models for each response variable by testing all combinations of variables, selecting the best model (i.e., top-ranking model) by comparing its fit using the widely applicable information criterion WAIC (Gelman et al. 2014), selecting the model with the lower WAIC value. We fitted all mixed models within a Bayesian approach using the *brm* function from the *brms* package (Bürkner 2017), using non-explicative default Student t priors (df = 3, mean = 0, scaling factor = 10). All Bayesian models consisted of four chains, each with a minimum of 2000 iterations and 1000 burn-in samples. We confirmed the convergence of the models by inspecting the mixed of the Markov chains and making sure that in all cases the maximum Gelman-Rubin statistic (i.e., Rhat value) was 1.0 (Hilbe et al. 2009). We determined a strong statistical effect of model parameter when the 95% Bayesian Credible Interval (CI) did not overlap zero. All models were fitted in R (R Core Team 2022).

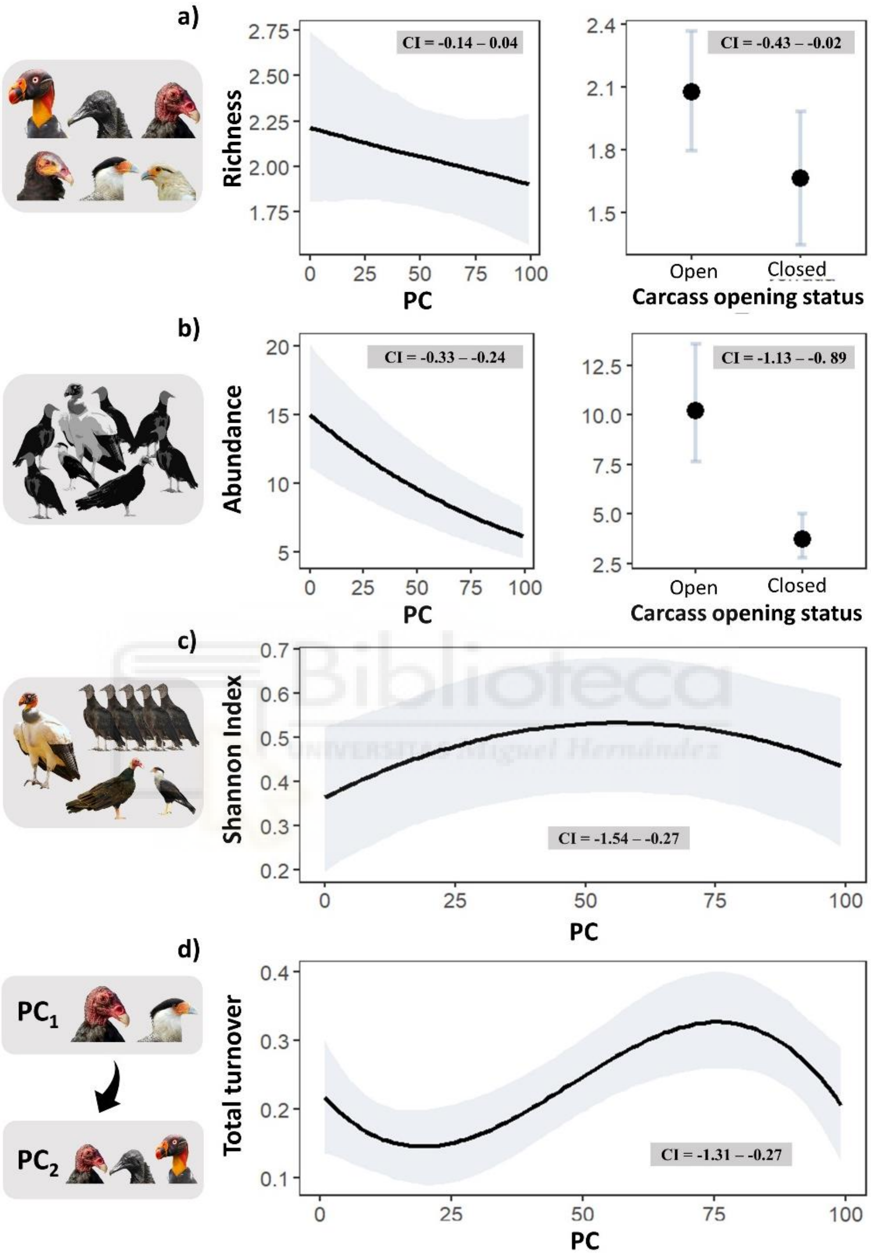


Figure 19. Conditional effects of all the explanatory variables included in the best models (i.e., lower WAIC) obtained for community dynamics analyses: **A**) richness, **B**) abundance **C**) Shannon-Wiener diversity index and **D**) total turnover. Black lines represent predicted posterior means, and shadowbands and grey boxes show 95% confidence intervals (i.e., CI). For more details, see Appendix S2 (**Table S6**).

RESULTS

Community dynamics and species abundances

On average, we registered 2.02 ± 0.84 species per archive (i.e., video or image), with a total abundance of 6.82 ± 6.57 individuals per archive. The results of the models did not show statistical support for the influence of *PC* on richness, although this variable was included in the best model (i.e., lower WAIC, **Table S6**). However, when the carcass was closed, the richness was statistically lower than when the carcass was open (**Fig. 19**). Furthermore, the overall abundance of species was statistically affected by *PC*, so that as carcasses were consumed, abundance decreased (see **Fig. S2** for details). Similarly, the opening status also had a strong statistical effect. We found that abundance was higher when the carcass was already open than when it was closed (**Fig. 19**). Specifically, the models analyzing separately the abundances of the species showed a strong influence of *PC* on all of them (**Fig. 20**, **Table S7**). Finally, we found that the Shannon-Wiener diversity index and total turnover varied along the *PC*, having a strong nonlinear effect on both (**Fig. 19**).

Behavior throughout carcass consumption

In the remaining 409 videos, we recorded 2048 aggressive interactions, 356 retreats, and four affiliative interactions (see **Table S8** for further details). Bayesian mixed models performed for the whole carcass consumption process showed that *PC* had a strong statistical support in most of the variables. Thus, we found a cubic effect of this variable in the number of total interactions recorded, the proportion of interspecific displacements, the proportion of aggressive interactions and the proportion of interspecific aggressive interactions. On the other hand, our results showed that the proportion of interspecific non-aggressive interactions was not influenced by this variable (**Fig. 21**). Furthermore, we found a notable effect of the *carcass opening status*, with a higher number of total interactions and a higher proportion of aggressive interactions when the carcass was *open*. In contrast, we found an opposite effect when we analyzed the proportion of non-aggressive interactions, which was higher when the carcass was closed (see Supplementary Material, **Table S9**).

The American black vulture initiated most of the aggressive interactions (68.4%), followed by the King vulture (28.9%) and finally, the Cathartes vultures, initiating only 2.7% of the aggressive interactions recorded (see Supplementary Material, **Table S8**). In this way, top-ranking models did not include the total abundance of the species, but the models did show an effect of the abundance of each species separately (see **Fig. 21**). In fact, each species had

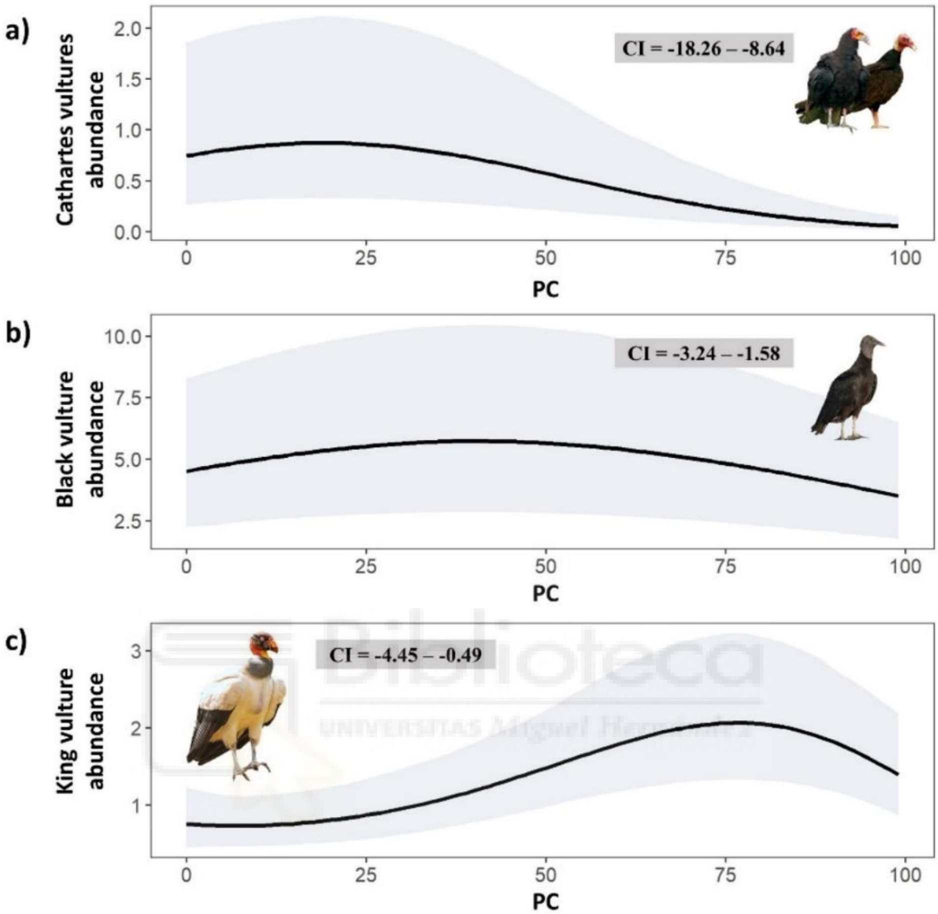
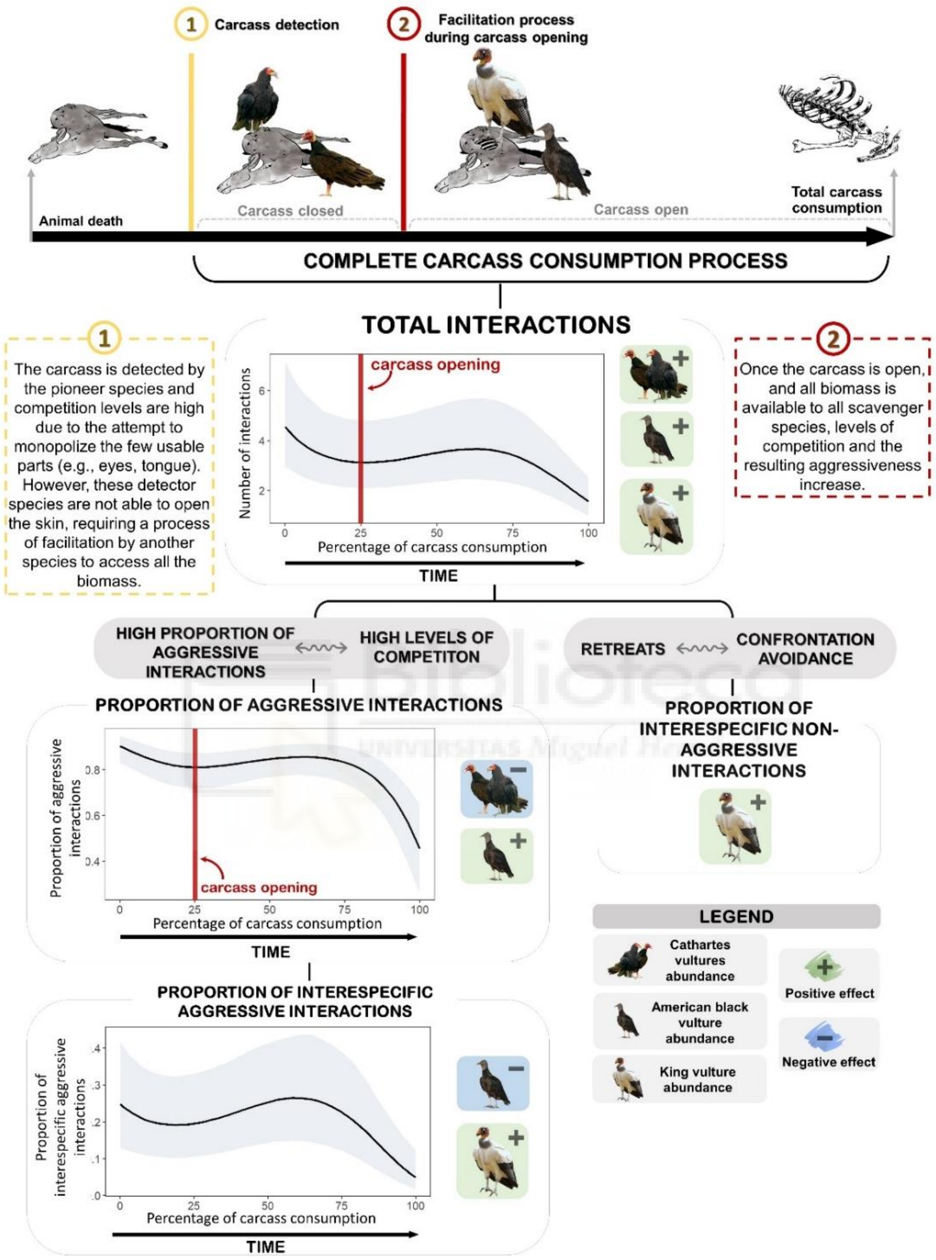


Figure 20. Bayesian mixed model results representing the conditional effects of PC on **A**) abundance of Cathartes vultures, **B**) black vulture abundance and **C**) king vulture abundance. Black lines represent predicted posterior means, and shadowbands and grey boxes show 95% confidence intervals (i.e., CI). For more details, see Appendix S2 (**Table S7**).

a different influence on the behavioral dynamics throughout carcass consumption. Black vultures had a positive effect on the proportion of aggressive interactions recorded, whereas Cathartes had a strong negative effect. Finally, there was a positive influence of the presence of the king vulture on the proportion of interspecific interactions, both in the case of non-aggressive and aggressive interactions (**Fig. 21**, **Table S9**).



1

The carcass is detected by the pioneer species and competition levels are high due to the attempt to monopolize the few usable parts (e.g., eyes, tongue). However, these detector species are not able to open the skin, requiring a process of facilitation by another species to access all the biomass.

2

Once the carcass is open, and all biomass is available to all scavenger species, levels of competition and the resulting aggressiveness increase.

Figure 21. Conceptual illustration of a heterotrophic succession that drives the consumption of large carcasses in a Neotropical scavenger community. We consider the beginning of the succession when the carcass is found by the first individual (i.e., pioneer species; yellow) until it is completely consumed (i.e., only the bones and skin remain). This community dynamics are mainly driven by a facilitation process due to the opening of the carcass skin (red). Through the study of interactions, we can discern variations in the

intensity of competition, so high proportion of aggressive interactions reflect high levels of competition, while non-aggressive interactions (i.e., those that avoid confrontation) reflect higher levels of tolerance. Thus, effects of PC (i.e., percentage of carcass consumption) on the total number of interactions, the proportion of aggressive interactions and the proportion of interspecific aggressive and non-aggressive interactions are represented. Black lines symbolize predicted means, while the grey bands indicate the 95% credible intervals. The positive (green) and negative (blue) effects of the abundances of the different scavenger species on the interactions recorded in this succession are displayed. Only those variables that had strong statistical support, i.e., whose confidence intervals did not overlap 0, are showed. For more details, see Appendix S2 (**Table S9**).

DISCUSSION

The relationship between competitive and facilitative interactions within species in a succession determines its dynamics, so it is essential to use temporal approximations to study these processes and understand what factors influence them. In this study, we provide the first in-depth analysis of the community dynamics of a vertebrate heterotrophic succession. We determine changes in the intensity of competition, which remains a challenge in autotrophic successions (Pulsford et al. 2016), and the existence of a key facilitation event along the process of carrion consumption and resource availability, by combining temporal and behavioral analysis. Our results show high overall competition levels (i.e., high aggressiveness) that varied throughout the succession process, being influenced by the facilitation process resulting from carcass opening, as well as by the community composition at the carcass at a given time.

Vertebrate community composition during heterotrophic succession

Supporting our first hypothesis, we found that species abundance, diversity, and turnover changed as the process of carcass consumption progressed, showing very different patterns. First, we detected a linear decrease in the abundance of individuals as the resource was being consumed, contrary to what has been described for autotrophic successions, where abundance initially tends to increase when carrion colonization begins (Begon and Townsend 2020). We did not find an initial increase in abundance, perhaps because scavenger recruitment at carcasses in our study system is very fast (i.e., 10 to 30 minutes) (Naves-Alegre et al. 2022b). Second, species diversity also varied over time, with a concave-dawn trend, so the scavenger community reached its higher diversity at the midpoint of the succession. Third, we also found that species turnover changed following a complex pattern (i.e., cubic form), contrasting with the patterns found in autotrophic successions, in which the highest turnover rates are recorded at the early stages (Kaarlejärvi et al. 2021). Species turnover has been related to productivity in plant communities, so it would therefore be necessary to analyze whether higher levels of turnover indicate higher rates of carrion consumption (Chalcraft et al. 2004). Moreover, we found no support for our prediction that species richness changes along the carcass consumption process, contrary to what has been found in studies on insect successions (Moura et al. 2005). This may be because we only registered six scavenger species present in the carcass, two of which (i.e., king and black vultures) dominated the carcass during practically the entire succession. Future research in more diverse scavenger assemblages may elucidate whether there are changes in richness trends over resource consumption.

The influence of facilitation processes on succession dynamics

Carcass opening has already been established as a facilitative process in vertebrate scavenger communities in other ecosystems, although it has only been described with time-static measurements (Alvarez et al. 1976, Selva et al. 2003, Naves-Alegre et al. 2022a). As expected if the Facilitation Model is the main process that drives this succession (hypothesis 2), pioneer species did not prevent the arrival of the later ones. Thus, species with greater competitive ability (either because of their social character or their larger size, i.e., American black and king vultures, respectively, Wallace & Temple 1987) dominated the middle and final stages of the succession (Menéndez and Gutiérrez 1999, Dawson et al. 2022). This pattern may also be partly related to local enhancement (i.e., a facilitation process in which pioneer species signal the presence of carrion to other species) previously demonstrated in this community, and not, or not only, by the carcass opening process (Naves-Alegre et al. 2022b). Moreover, as expected, there was also an effect of the carcass opening on species richness and abundance. These two variables were statistically larger once the carcass was opened, which may be due to the resource being available for the entire assemblage from that moment on, in agreement with what has been previously stablished (Selva et al. 2003). In contrast, neither species diversity nor species turnover through succession were influenced by this process.

Furthermore, this facilitation process not only influenced the structure of the community, but also affected behavioral patterns. Consequently, the total number of interactions recorded, and the proportion of aggressive ones were also influenced by carcass opening, being both larger when the body was open than when it was closed. This indicates that when the carcass is closed, tolerance levels between species are higher, perhaps because of their inability to access the resource (Kilgour et al. 2020). Once the carcass is opened by the species with the largest body size (i.e., King vulture), the levels of aggressiveness increase again, since the entire resource becomes available for all species (Kendall 2013). These findings suggest that this process has generally led to a reduction of competition within this scavenger guild by increasing tolerance among individuals at earlies stages of scavenger consumption. Nevertheless, once the carcass is opened, the Inhibition Model is a better descriptor of this succession, as the levels of competition increase. Thus, these results support previous assumptions that ephemeral successions are initially driven by the Facilitation Model (Connell and Slatyer 1977, Menéndez and Gutiérrez 1999). However, this also contrasts with previous research on successions of dung and carrion-insect communities, where it is evident that facilitation is not the main successional mechanism in these ephemeral communities (Michaud and Moreau 2017, Sladecek et al. 2021).

Competition intensity over the consumption of an ephemeral resource

Complex patterns of competitive mechanisms have been established in plant communities depending on the availability of limiting resources (Koffel et al. 2018). Our results show how the competence between scavengers, both conspecifics and heterospecifics, vary during the consumption process of this ephemeral resource. Aggressiveness starts from very high levels at the beginning of carcass colonization, probably because pioneer individuals defend the resource when they find it. This is consistent with what has been demonstrated in other studies, which establishes that in non-dominated resources, i.e., without an "owner", more aggressive individuals have a greater competitive capacity, and therefore a greater probability of dominating and exploiting the resource (Brown 1964, Kilgour et al. 2020). However, after this initial stage of highly competitive intensity, we observed a decrease in this aggressiveness as species present were not able to fully exploit the carcass. This is consistent with our results, which showed how the closed state of the carcass supported lower levels of competition in general.

In autotrophic communities it has been established that the identity of the species forming the assemblages does not influence the general dynamics of the succession (Maggi et al. 2011). In contrast, our results show a specific effect of the different species on behavioral and competition dynamics, showing the existence of a hierarchy between species (Wallace and Temple 1987, Houston 1988). On the one hand, the abundance of larger and competitively superior species (i.e., king vulture) did not influence the general levels of aggressiveness recorded, although it was the only species that positively affected the proportion of interspecific aggression. On the other hand, the role of the black vulture in the general levels of aggressiveness is highlighted, since this species led practically all intraspecific aggressions, the most frequent interaction type in this succession, because of its social behavior. Therefore, these two species lead the levels of competition, evidencing the importance of certain functional traits (i.e., body size and sociality) in the species hierarchy and, therefore, the competitive dynamics of this succession, supporting the Competition Model (Connell and Slatyer 1977).

Concluding remarks and future perspectives

Our study highlights the importance of monitoring behaviors that are directly transferable to community function (e.g., those related to foraging and resource consumption) (Wilson et al. 2020), also considering the dynamics of succession over time, rather than just comparing time-static measurements at different stages of the succession. In particular, we provide valuable insights into the factors that influence the dynamics of carrion consumption, a key process in the structure and functioning of ecosystems (Benbow et al. 2019). First, we demonstrate that competition intensity does not remain constant throughout the succession, being influenced by both resource availability and the facilitation process of carcass opening. Second, facilitation processes influence the community from its structure to the behavioral level, thus showing the possible importance that facilitation may be having in other systems (e.g., with presence of large carnivores or where tougher-skinned ungulate carrion is available) (Selva et al. 2003, Kendall 2013, Allen et al. 2014, Moleón et al. 2015). Future research could benefit from a more comprehensive and integrated approach that considers the complex and dynamic behavioral interactions between scavenger species, together with factors related to species traits, the resource (e.g., carcass size) and environmental factors (e.g., habitat characteristics). Globally, it would be necessary to integrate behavioral approaches in the study of the functioning and structure of ecological communities. Understanding the mechanisms underlying these successional processes at different scales is fundamental because of their implications for ecosystem health and functioning (Rezende et al. 2021, Wenting et al. 2022), allowing us to assess the deterioration of functioning in highly human-impacted systems (Loreau and de Mazancourt 2013).

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CHAPTER 7: GENERAL DISCUSSION

Research in ecology attempts to address the fundamental question of how organisms coexist, interacting with their environment and with other organisms. Identifying the processes that influence these interactions is a key step in advancing towards a more mechanistic understanding of the functioning of the ecosystems (Blaum et al. 2011, Hart et al. 2016). Community-wide approaches, considering both positive and negative interactions, together with new tools and data (e.g., behavior information and statistical methods) may help us analyze these processes and their changes at different scales and in a dynamic way (Levine et al. 2017). These methods are especially interesting in communities where spatiotemporal co-occurrence is high, i.e., in those guilds where heterospecific aggregations occur, since interactions between organisms will be intense and complex (Hancock and Milner-Gulland 2006, Seppänen et al. 2007). The ephemeral and unpredictable nature of resources such as carrion promote simultaneous presence and/or feeding of heterospecifics (Beasley et al. 2019). These aggregations around a resource are optimal systems for analyzing the ecology and dynamics of interactions between species belonging to the same guild, and the key role of social information transmission (Goodale et al. 2010, Gu et al. 2017). Therefore, the scavenger guild is an ideal study system, where a multitude of individuals of different species interact while feeding on carrion (Wilson and Wolkovich 2011, Kendall 2013, Barton and Bump 2019, Moleón et al. 2019). This generates high levels of competition, but also information transmission processes that facilitate the location and consumption of the resource (Jackson et al. 2008, Deygout et al. 2010, Cortés-Avizanda et al. 2014). In this way, this thesis evidences that the composition and functioning of a Neotropical scavenger guild is influenced by resource characteristics (i.e., carcass size) and external factors (i.e., habitat structure), and by complex dynamic processes of facilitation and competition involving several species, which vary in the spatial and temporal scales.

THE UNIQUENESS OF NEOTROPICAL SCAVENGER COMMUNITIES

The efficiency of scavenger communities is influenced by factors such as scavenger richness and abundance (Mateo-Tomás et al. 2017), habitat characteristics (Pardo-Barquín et al. 2019), temperature (Krofel et al. 2012, Turner et al. 2017), human impact (Sebastián-González et al. 2019) and carcass features (Selva et al. 2005, Moleón et al. 2015b). As can be seen throughout this thesis, during the last two decades, the study of scavenger communities and the processes that affect carrion consumption have increased enormously. However, scavengers in the Neotropics have been neglected. In this way, this thesis shows clear differences in the functioning and factors influencing Neotropical and non-Neotropical scavenger systems, as we describe for the first time the diverse and efficient scavenger community of the Brazilian *Cerrado* biome (***Chapter 3***, Naves-Alegre et al. 2021).

Scavenger foraging abilities, i.e., the use of the senses of sight and smell, their ability to tear the skin and access the interior of the carcass, and their scavenging behavior (e.g., activity patterns) determine the availability and use of carrion in a system (Houston 1979, Selva et al. 2005, Gutiérrez-Cánovas et al. 2020). Vultures (i.e., the only obligate scavengers) are the most efficient organisms at finding and consuming carrion worldwide (i.e., consuming greater amounts of carrion and at higher rates than facultative scavengers) (***Chapter 3***, Hill et al. 2018, Morales-Reyes et al. 2017, Naves-Alegre et al. 2021). Accordingly, our results show the high efficiency of the four species of vultures in the *Cerrado* community, being the main consumers (***Chapter 3***, Naves-Alegre et al. 2021), as well as playing a fundamental role in the competition and facilitation processes during scavenging (***Chapter 4***, Naves-Alegre et al. 2022a).

American vultures of the genus *Cathartes* have a highly developed sense of smell, related to their evolution in more forested environments (Houston 1979, 1985, 1988, Potier et al. 2019). This ecological trait is the main difference with Eurasian and African vultures (Bang 1964, Gomez et al. 1994, Potier et al. 2019) and implies that factors that have been shown to affect carrion consumption in other scavenger assemblages are not as important in this system as they are in Old World environments. In this way, results from this thesis show that vegetation cover had little influence on scavenger assemblages, scavenging patterns (***Chapter 3***, Naves-Alegre et al. 2021, Houston, 1988, Mallon et al., 2013) or patterns of co-occurrence among species (***Chapter 4***, Naves-Alegre et al. 2022a). By contrast, in Old World scavenger systems only mammals possess a highly developed sense of smell, which confers them an advantage when searching for carrion in densely vegetated areas (DeVault et al. 2004, Moleón et al. 2019). Consequently, Old World vultures have been relegated to open habitats (Houston 1985), while facultative scavengers, particularly mammalian carnivores, dominate forested regions in Europe, Africa, and Asia (Selva et al. 2003, 2005, Inagaki et al. 2020, Stiegler et al. 2020). Thus, habitat characteristics strongly influence the functioning (e.g., longer consumption and detection times in closed habitats) and structure (e.g., negative effect of forested areas on scavenger richness) of scavenger guilds in Eurasia and Africa (Arrondo et al. 2019, Pardo-Barquín et al. 2019, Stiegler et al. 2020). However, in contrast to our results, studies conducted in North American scavenger systems, where some of these vulture species with olfactory capabilities are also present (i.e., Turkey vulture), have found that habitat type influences carcass detection (DeVault et al. 2004, Smith et al. 2017, Turner et al. 2017). This may be because the Neotropical scavenger community studied in this thesis has a greater diversity of vultures than the one in North America (with only one or two species of vultures), so the processes of facilitation and information transmission between them would be more effective (Duboscq et al. 2016, Jones et al. 2017). Therefore, social information transmission may be reducing the influence of vegetation structure in the *Cerrado* scavenger community (***Chapter 5***, Naves-Alegre et al. 2022b).

Furthermore, carcass size is a very important factor in the consumption of carrion in all systems, influencing the composition of scavengers consuming the resource, the abundance of scavengers, consumption rates and underlying processes (Ogada et al. 2012b, Moleón et al. 2015b, Turner et al. 2017, Naves-Alegre et al. 2021, 2022a, b). Larger carcasses were consumed by more individuals and more species on average per carcass, having also larger consumption times and consumption rates (***Chapter 3***, Naves-Alegre et al. 2021), in concordance with what has been found in other scavenger systems (Moleón et al. 2015b, Turner et al. 2017, Sebastián-González et al. 2019). However, contrary to previous studies (reviewed in Sebastián-González et al., 2020), detection time in the *Cerrado* was not affected by the size of the resource, as Neotropical vultures were also very efficient in locating and consuming small carcasses due to its developed sense of smell and social information transmission, (***Chapter 3***, Naves-Alegre et al. 2021).

INTERSPECIFIC INTERACTIONS IN A SCAVENGER COMMUNITY

Ecological interactions affect different aspects of biodiversity, connecting populations of different species, structuring them (Elton 1946, Bailey et al. 2006, Persson et al. 2018, Guimarães 2020, Sandal et al. 2022). In a broad sense, competition has traditionally been acknowledged as the primary mechanism through which communities of plants and animals are structured (Schoener 1983, Menge and Sutherland 1987). Therefore, the study of interactions in animal communities has focused on those of a negative nature, being competition and predator-prey processes extensively studied (Sommer 1999, O'Brien et al. 2003, Watts and Holekamp 2008, Beauchamp 2013, de Satgé et al. 2017, Caravaggi et al. 2018, Damas-Moreira et al. 2020, Allen et al. 2021, Pal et al. 2022). However, positive patterns have been shown to be equally important in the structuring and dynamics of communities, but scientific literature on animal species has mainly focused on seed-dispersal and pollination mutualistic interactions (Fleming et al. 1987, Higashi 1993, Jordano et al. 2007, Corlett 2009, Bascompte and Jordano 2013, Valiente-Banuet et al. 2015).

Facilitation processes stand out among the positive interactions because they occur between organisms that also compete for resources (Bruno et al. 2003). Their implications in community diversity have been well documented in plant communities (reviewed by Brooker *et al.* 2008) or sessile organisms (Duggins 1981, Kawai and Tokeshi 2007), but have been far less studied in mobile communities (Arsenault and Owen-Smith 2002, Odadi et al. 2011a, Filazzola et al. 2017, Zhong et al. 2021). These differences in knowledge between organisms are mainly due to the methodological complexity involved in demonstrating the existence of facilitation processes (e.g., the difficulty of conducting experimental studies with wildlife).

Although the literature on interactions has always focused on an intraspecific perspective, or in species pairwise interactions, the results of ***Chapter 4*** and ***Chapter 6*** highlight the complexity of the competition and facilitation processes that occur within a guild, evidencing the importance of studying interactive processes in multi-species contexts (Blaum et al. 2011, Seibold et al. 2018, Pal et al. 2022). Conspecific and heterospecific interactions generate similar selective pressures on the sensory and cognitive mechanisms that regulate social behavior (Binz et al. 2014, Oliveira and Bshary 2021). Studying the communities or guilds at a global level, and how the species that form them interact is fundamental to understanding the evolutionary processes and evolutionary forces that have made them develop, e.g., different traits.

Different facilitation processes have been associated with scavenger communities (Selva et al. 2003, Allen et al. 2014, Kane et al. 2014, Kane and Kendall 2017, Jackson et al. 2020), however, most of them have not been studied in detail. This thesis brings an important contribution by analyzing, at different scales, the facilitation processes related to carcass location and opening, and the factors that influence them in a vertebrate scavenger community (***Chapter 4***, ***Chapter 5***, ***Chapter 6,*** Naves-Alegre et al. 2022b, 2022a). ***Chapter 5*** further shows how the facilitation process between species during carcass location is due to the use of different senses (i.e., smell and sight) (Naves-Alegre et al. 2022b). This result supports that the transmission of information is more useful between species with different traits (e.g., different foraging skills), promoting intra-guild coexistence (Duboscq et al. 2016, Jones et al. 2017, Veit and Harrison 2017). The incorporation of social interactions with other organisms may improve animals' foraging strategies, being these mechanisms fundamental in the context of unpredictable and ephemeral resource availability (e.g., carrion) or heterogeneous environments (Hancock and Milner-Gulland 2006). Our findings are consistent with previous results found on a global spatial scale that have shown that species with high olfactory acuity and social foraging behavior are the most efficient scavengers, foraging at more carcasses (Sebastián-González et al. 2021).

Animal studies considering the combination of competitive and facilitative processes are still very scarce (Forsman et al. 2002, Barrio et al. 2013). Overall, the results obtained in this thesis show the importance of integrating positive and negative interactions (Prugh and Sivy 2020), as it would not be possible to interpret the co-occurrence patterns observed between species without them (***Chapter 4***, Naves-Alegre et al. 2022a). Additionally, ***Chapter 6*** shows how these two processes are connected to each other, with facilitation affecting competition intensity. Regarding scavengers, factors affecting the magnitude and the direction of the facilitation and competition between vultures and large carnivores are multiple (Moleón et al. 2014). Moreover, when talking about competition and facilitation in the scientific literature, reference is usually made to static processes, which can be affected by different factors. In general, these processes are studied over broad time scales (e.g., between seasons) (Odadi et al. 2011a). Research conducted on plants has revealed that the interplay between competition and facilitation is contingent upon environmental gradients. In highly stressful environments, facilitation interactions tend to prevail (Maestre et al. 2009, Koffel et al. 2018). Nevertheless, when stress is induced by resource scarcity, competition tends to supplant facilitation (Holmgren et al. 1997). Conversely, animal studies suggest that in less productive or harsher (i.e., more stressful) environments, competitive interactions tend to dominate (Odadi et al. 2011b). Our results obtained in ***Chapter 6*** evidence that facilitation and competition between species should not be treated as static, but that they can vary on very short-time scales (i.e., the duration of the consumption of a carcass), being influenced by resource availability.

CONTRIBUTION OF THE BEHAVIORAL APPROACH TO THE STUDY OF PROXIMATE CAUSES OF INTERACTIONS

One of the main challenges in the study of interactions between individuals is to measure their intensity, the strength with which they occur. The limitations associated with quantifying the degree of competition and the selection of adequate proxies have been clearly demonstrated in the study of plant communities (Wilson and Lee 2000, Pulsford et al. 2016). Behavior can influence interactions in a direct way, being able to impact the direction and intensity of these interactions (Jonathan Davies et al. 2007, Yackulic et al. 2014, Gross et al. 2017). The behavior of a species in this respect has evolved as a function of the species with which it coexists, especially those species with which it interacts in some way (Wong & Candolin 2015). Therefore, working with animal communities has an advantage over plant communities, since animals carry out their activities in an observable and measurable way through behavior. Thus, behavioral studies allow us to understand the animal's decision making, and therefore their cognition, way of learning, social interactions, and movement (Breed & Moore 2021). Behavioral approaches have been classically used for the study of some interactions, such as predator-prey relationships (Burton et al. 2022, Ortiz-Jimenez et al. 2022). In addition, it has also been used to evaluate the impacts of exotic species, and the influence they have on the behavior of the native ones (Harrington et al. 2009, Price-Rees et al. 2013, Kwon & Choi 2020). In this way, several methodologies have been developed that allow us to study and monitor species behavior (e.g., GPS telemetry, accelerometers) (Wiesel et al. 2019, Yu et al. 2022). However, these methodologies do not provide information on what is happening around the organism at a given time that directly affects its behavior, i.e., the external stimuli that generate a response. In general, the lack of studies based on animal communities that have tested the combination of different types of interactions (i.e., positive and negative), variations in these as a function of temporal and environmental gradients, and multispecies approaches, is mainly due to the difficulty of studying the underlying processes (Barrio et al. 2013). In this way, the observational study of behavior allows us to obtain data on the immediate (i.e., short time scale) response of individuals to signals from other individuals or other stimuli which can also be measured observationally. Barrio et al. (2013) in their meta-analysis about animal interactions, report that 72% of the papers they used for the study were based on observational data, establishing that observational studies are fundamental to understanding the mechanisms underlying animal interactions (Darmon et al. 2012).

Obtaining direct wildlife data through field-based observations has several limitations, such as the influence of the observer's presence, the need to make great efforts to obtain a sufficient sample, as well as other logistical problems (Bridges and Noss 2011). However, the recent development and price reduction of devices that allow the remote acquisition of data has meant that indirect methodologies, e.g., the use of automatic cameras, have become fundamental in ecological research (O'Connell et al. 2011). Camera-trapping has been widely used to describe vertebrate communities (***Chapter 3***, Srbek-Araujo and Chiarello 2005, Naves-Alegre et al. 2021), estimate species abundances and densities (Karanth 1995, Gerber et al. 2012, Efford and Mowat 2014, Steenweg et al. 2016, Gilbert et al. 2021), and study animals' activity and movement patterns (***Chapter 4***, ***Chapter 5***, Marnewick et al. 2006, Frey et al. 2017, Naves-Alegre et al. 2022a, 2022b). One of the main advantages of this technique is that is considered a non-invasive methodology, although some authors have found a response from some species to the presence of cameras (Meek et al. 2014, 2016). Overall, the results of this thesis show how the use of this methodology allows the collection of a multitude of data automatically and simultaneously at different spatially independent points (i.e., depending on the number of cameras placed). Besides, although this methodology has been widely used for image acquisition, video recording by camera-trapping opens a world of possibilities for studying wild animals' behavior (***Chapter 6***, Caravaggi et al. 2020). Thus, data obtained from image and video inspection combined with novel analytical approaches can allow the study of fundamental processes in behavioral ecology (***Chapter 5***, ***Chapter 6***, Caravaggi et al. 2017, Naves-Alegre et al. 2022b).

Over the last two decades, there has been a significant surge in the study of horizontal information transmission (named "social information") and its use among individuals of the same species but also among heterospecific individuals (Laland & Williams 1997, Giraldeau et al. 2002, Farine et al. 2015, Gil et al. 2018b, 2019). The use of social information is an enormous evolutionary advantage, taking place in various contexts, including foraging and predator avoidance. Through these information exchange processes, the presence of a resource can led to the attraction of individuals of different species to a site (i.e., "local enhancement" or "heterospecific attraction") (Mönkkönen et al. 1996) resulting in positive co-occurrence patterns and the formation of temporary multi-specific aggregations (***Chapter 4***, ***Chapter 5***, Boulay et al. 2019, Goodale et al. 2020, Naves-Alegre et al. 2022a, 2022b). Therefore, the transmission of information between organisms that use the same resource has been studied among different organisms, such as seabirds (Veit and Harrison 2017), fish schools (Ioannou et al. 2011), migrations (Couzin 2018), vultures (Cortés-Avizanda et al. 2014, Harel et al. 2017b). The rise of the study of information transmission between different species has evidenced the existence and importance of a multitude of facilitation processes in the animal kingdom. In this way, even though classical species aggregations related to the consumption of a resource have been believed to be driven primarily by competitive processes, our results evidence the existence of a key facilitation process during carcass location driven by the transmission of social information (***Chapter 5**,* Naves-Alegre *et al.* 2022b), in line with what has been suggested by previous studies (Goodale et al. 2017, Gu et al. 2017).

Traditionally, the social behavior of gregarious species, which live or perform certain fundamental activities together with conspecifics, has been studied. However, socialization can also be understood between individuals of different species, and the performance of any behavior generates sensory information that can be used by others. A clear example of this is collective behavior, which has been studied in animal groups (e.g., fish schools, birds flocks), and is a consequence of interactions between individuals (Couzin 2018, Jolles et al. 2020). Thus, collective behavior has fundamental biological functions, such as foraging. Within this collective behavior, the ability of an animal to optimize its social behavior according to the available social information is called social competence, and can bring benefits to the individual, e.g., by promoting tolerance with other individuals (Taborsky 2021). Vultures are characterized by high social competence since multiple species have a social lifestyle, their habitat generalism results in the co-occurrence of different species, and their tendency to interact not only with conspecifics but also with other species during communal feeding at carcasses (van Overveld et al. 2022). Our methodological approach allows us to know the high tolerance between New World vulture species, which is reflected in the positive spatio-temporal patterns between them, showing that these species feed at the same time (Naves-Alegre et al. 2022a). In addition, the results of ***Chapter 6*** show the existence of different roles among vulture species interacting during carrion consumption, which evidences the existence of established hierarchies. These hierarchies are due to social competition, consequently, as individuals acquire more experience in social confrontations and the information received by the audience (i.e., social information) increases, social hierarchies become more established (Williamson et al. 2016, Taborsky 2021).

Changes in biotic and abiotic factors influencing behavior can affect evolutionary processes by promoting individual behavioral responses (Sih et al. 2011). In fact, the inclusion of behavior in ecology has been mainly driven by the need to understand decision making and flexibility in the face of environment (Holway, David, and Suarez 1999, Berger-Tal et al. 2011, Gordon 2011, Cooke et al. 2014, Wong & Candolin 2015). Behavioral flexibility will determine in the future how global changes will affect different species, so behavioral studies are needed to understand how each species can respond to different contexts and its variations, and the effects that these changes will have on the role that behavior plays in the ecosystem (Wong & Candolin 2015). Findings from this thesis highlight the importance of monitoring behaviors that are directly transferable to community functions (e.g., those related to foraging and resource consumption) (Wilson et al. 2020). Such behaviors can also have effects on species demographic parameters, thus influencing population dynamics (Breed & Moore 2021). Hence, ethological tools (i.e., related to animal behavior) can be a fundamental in the study of certain ecological processes, providing a new perspective to understand proximate causes of different ecological processes that cannot be studied indirectly, especially in the identification of stimuli that trigger behavioral responses directly linked to key functions in the ecosystem (Bateson & Laland 2013).

CONSERVATION IMPLICATIONS

Biodiversity reaches its highest levels in tropical zones, which host 80% of species (Muenchow et al. 2018). Many research and conservation efforts in the Neotropics have been focused on tropical forests, such as the Amazon. However, arid and semi-arid environments have been neglected (e.g., *Cerrado* biome) (Shennan-Farpón et al. 2021). Approximately one-third of the world's birds are found in the Neotropics, but they have been much less studied than the rest (Buechley et al. 2019, Soares et al. 2022). In fact, 80% of the scavenger species documented in this thesis are exclusive to the Neotropics (Sebastián-González et al. 2019, IUCN 2022). These findings evidence the great diversity of the Brazilian *Cerrado*, characterized by its high proportion of endemic species (Strassburg et al. 2017). Nevertheless, the Brazilian *Cerrado* has experienced a high rate of habitat loss due to human activities, which may have detrimental effects on species populations and their ecological functions (Klink and Machado 2005, Strassburg et al. 2017). Furthermore, previous studies have also predicted how climate change may affect certain taxa in this biome, expecting a loss of mammal richness, generating changes in species composition at large spatial and temporal levels (Hidasi-Neto et al. 2019).

This thesis emphasizes the importance of the functions and ecosystem services provided by the scavenger guild in this Neotropical region. Biodiversity loss reduces the efficiency with which ecological communities influence ecosystem functioning, so understanding the processes that underlie community patterns is critical (Cardinale et al. 2012). In this regard, human disturbances have been identified as the primary factor that affects scavenger richness (Sebastián-González et al., 2019), shaping the structure of scavenger assemblages and their efficiency on a global scale (Sebastián-González et al., 2020). Thus, changes in the composition and diversity of scavenger communities may significantly impact the ecosystem functions that these scavengers provide (Mateo-Tomás et al. 2017). Our results highlight the need to conserve the behaviors and traits that govern the facilitation processes, which would be linked to an increase in population densities and consequently an increase in diversity in certain areas (Bruno et al. 2003, Smale et al. 2022). In this way, *Chapter 3* and *Chapter 4* show the importance of diversity and complementarity of traits in facilitation processes that are taking place in this Neotropical scavenger community, calling for a trait- and behavior-based conservation approach (Nevitt 2008). The identification of these fundamental ecological traits throughout the thesis has allowed us to identify vultures as key species in the processes of competition and facilitation in this guild (Chapter 4, Naves-Alegre et al. 2022b). Therefore, conservation efforts should be focused on these species, to maintain facilitation cascades and community structures (Sebastián-González et al. 2021, Naves-Alegre et al. 2022b, Smale et al. 2022). However, population sizes of most of these essential scavenger species, including king vultures, remain poorly known (IUCN 2022).

Competitively dominant species, considered keystone species, can reduce the diversity of a community by displacing competitively inferior species (Bruno et al. 2003). Therefore, regions where vulture populations have been severely diminished, so that they no longer fulfill their ecological function (i.e., functionally extinct), have led to an increase in populations of facultative scavengers that have replaced the vultures' role (Pain et al. 2003, Ogada et al. 2012b, Moleón et al. 2014, Morales-Reyes et al. 2017). In particular, the most diverse communities of vertebrate scavengers have been described in systems with no obligate scavengers or with only one of their species present (Selva et al. 2005, Allen et al. 2014, 2015). Accordingly, our results show that Neotropical facultative scavengers only consumed small-sized carcasses, and within non-obligate scavengers, facultative raptors were dominant, both in percentage of carcasses visited and time spent in them (***Chapter 3***, Naves-Alegre et al. 2021). In contrast, in other systems, carnivores such as canids (e.g., foxes) have been described as competitive facultative scavengers (Morales-Reyes et al. 2017, Arrondo et al. 2019). However, in tropical environments, these taxa may be more dependent on other types of highly available resources (e.g., insects and fruit) (Juarez and Marinho-Filho 2002).

Large carnivores compete with vultures in certain ecosystems, e.g., in the African savanna, even being competitively superior once they are at carcasses (Kendall et al. 2012, Kendall 2013, Moleón et al. 2014, 2015b). Top predators such as pumas and jaguars inhabit the Brazilian *Cerrado* (Sebastián-González et al. 2020b), however they did not consume carrion, which contrasts with the important scavenging role of top predators in other ecosystems (Selva et al. 2005, Moleón et al. 2015b, Inagaki et al. 2020). Previous work establishes that the transformation and destruction of the *Cerrado* have been occurring in recent decades (Colli et al. 2020). This implies that we could already be facing a transformed study system, where the abundance of some organisms, e.g., large carnivores, would be significantly lower than what is typically observed in a natural system, and therefore their role as scavengers would be null due to their low densities in the area. Also, some authors have shown that large carnivores in the *Cerrado*, such as jaguars, are especially sensitive to human disturbance, and are therefore found mainly in the larger areas of well-preserved forests, which may be also influencing our results (Vynne et al. 2011). In addition, the persecution of large carnivores in these areas may also have played a fundamental role (Palmeira et al. 2008, Balbuena-Serrano et al. 2021), and they may have selected shy-personality carnivores, which avoid areas of human presence (e.g., noises, smells) or manipulated elements (e.g., such as experimental carcass placed in the field). However, the potential presence of large carnivores on bigger carcasses (which would naturally be the remains of their prey kills) would influence the avoidance by smaller carnivores of this type of resource, i.e., "landscape of fear", where the risk of encounters with potential competitors or predators would be greater (Willems and Hill 2009, Moleón and Sánchez-Zapata 2021).

With increasing threats to diversity worldwide, but especially in the Neotropics, and the lack of knowledge that has become evident for most New World vulture species, evidence of a potential crisis in Latin American vultures has become clear (Santangeli et al. 2022). This could lead to a decrease in the populations of neotropical vultures in the *Cerrado*, or even the disappearance of some of them, and this would lead to a degradation of the ecosystem function of the scavenger guild in the area (e.g., increased disease transmission) (Ogada et al. 2016). Vulture decline would also involve a positive impact on the populations of facultative scavengers (Ogada et al. 2012b, Hill et al. 2018). Specifically, the increase in carnivore populations could also increase perceived conflicts between humans and wildlife (de Souza et al. 2018, Schulz et al. 2021).

LIMITATIONS AND CAVEATS

In this thesis, we have identified some limitations and caveats that should be taken into account in future research. First, data collection was carried out in one month and exclusively during the wet season. Previous research has shown changes in carrion consumption patterns among seasons, these have been carried out in temperate zones with a strong seasonality and have highlighted that the factor that most influences carrion acquisition is temperature (DeVault and Rhodes 2002, DeVault et al. 2004, Selva et al. 2005, Sebastián-González et al. 2016). Even though the Brazilian *Cerrado* has two distinct seasons, the average temperatures in this area are 18 and 28°C during the dry and wet seasons, respectively, so this variation is unlikely to affect the scavenger patterns (Dias, 1992). However, differences in precipitation could play a fundamental role in the scavenging patterns of this community. On the one hand, it is during the wet season in the *Cerrado* that the availability of other resources, e.g., fruits, is greater, so this could be affecting the scavenging patterns of facultative species. On the other hand, it has also been found that precipitation can affect the olfactory capabilities of the species, which would influence carrion detection times and potentially affecting facilitation processes related to carcass location (Savage 1977, Ruzicka and Conover 2012).

Second, another methodological limitation is the low sample size of large carcasses. A larger sample size would allow to perform multivariate models in ***Chapter 3*** to test the influence of different factors at the same time (i.e., multiple-predictor models) on consumption patterns in large carcasses. In ***Chapter 5***, we employed a linear predictor to summarize the collective influence of variables that are not directly associated with the target species. The limited sample size of the large carcasses precluded individual modeling of such variables. The findings revealed a significant impact of this predictor on the arrival of most of the species to carcasses, highlighting the need to identify the specific components, e.g., the effect of vegetation cover, that contribute to the transmission of social information. In ***Chapter 5*** it would also be required to increase the sample of large carcasses, in order to record whether there are patterns of repulsion between species, as have been found in other mixed species aggregations (Martínez et al. 2018).

Third, in ***Chapter 6*** we did not consider the possible divergence in the preferences of each species in the consumption of different parts of the carcass (e.g., American black vulture is specialized in feeding on soft tissues, while the king vulture is capable of tearing off tendons and patches of skin) (Houston 1988), as has been found in other Old World vulture communities (Kendall et al. 2012, Kendall 2014, Moreno-Opo et al. 2020). Although this could be a process of niche segregation that promotes coexistence between species and influences aggressive interactions between them (Moreno-Opo et al. 2020). In addition, also in Chapter 4, we did not analyze small-sized carcasses consumption patterns. Knowing the behavioral dynamics that occur in this type of resource, where the facilitation process in the opening of the carcass skin does not exist (i.e., all species can tear it), this would allow us to understand in greater detail the role of food availability in the intensity of competition.

FUTURE PERSPECTIVES

The inclusion and integration of positive and negative interactions in the study of communities has been shown to be a key step in understanding their dynamics, structure and functioning (Stachowicz 2001, Bruno et al. 2003, Wilson and Wolkovich 2011, Prugh and Sivy 2020). But it is also necessary to understand how these processes are affected by variations in the composition of the community itself or by external factors, such as environmental characteristics, to anticipate possible disruptions due to the current global change that is taking place (Tylianakis et al. 2008, Bellard et al. 2014, Hidasi-Neto et al. 2019). Thus, based on the results obtained in this thesis, new research opportunities have arisen.

First, it is necessary to understand the characteristics of individuals (e.g., sex, age, personality) and ecological traits that influence interspecific and intraspecific interactions, particularly in the context of the transmission of information and facilitation processes (Monterroso et al. 2020, Morinay et al. 2020, Sebastián-González et al. 2021, Schleuning et al. 2023). Therefore, further research is needed to fully identify the mechanisms underlying coexistence and the role of different traits in promoting it.

Second, external factors can influence the transmission of information between species. For instance, habitat structure can affect visual cues detection, while environmental factors such as temperature can influence odor perception (Houston 1979, DeVault and Rhodes 2002). In addition, in anticipation to changes in certain environmental conditions (e.g., temperature, humidity), it is necessary to know how sensory environments may be affected and whether this would affect the information transmission process (Ålund et al. 2022).

Third, the importance of integrating demographic variables of the species that interact in the processes of competition and facilitation becomes evident, to see what influence they have on the functions of the species themselves. In this way, it will be possible to establish whether low densities of a key species can have repercussions on the cascades of interactions, affecting the functionality of the community, or it may also affect the direction of interactions due to its influence on the perception of stress (Odadi et al. 2011a, Barrio et al. 2013).

Fourth, to infer how facilitation processes ultimately affect ecosystem functioning, it would be necessary to compare the efficiency of the community studied in this thesis with the efficiency of similar Neotropical communities that lacked some of the key species in the facilitation processes. The composition of temporal aggregations of species varies in relation to environmental gradients (O'Donnell 2017), so these changes in the assemblages will affect the interaction networks and hierarchies, and therefore the behavioral patterns of aggressiveness and tolerance between species (Kwon and Choi 2020). Information transmission processes may also be affected in systems where key species are not present (Martínez et al. 2018).

And fifth, future ecological research could benefit from the integration of ethological methodologies to understand the potential mechanisms underlying species interactions within communities. These tools will allow us to integrate the intensity and behavioral dynamics of interactions between species, together with factors related to species traits, the resource (e.g., carcass size) and environmental factors (e.g., habitat characteristics). Specifically, vultures are particularly interesting as a system for studying behavioral evolution and cognition, given that they exhibit a great variety of foraging innovations and are found in a complex social environment, both intra- and interspecific (van Overveld et al. 2022). In addition, behavioral tools may allow us to determine the ontogeny of the behaviors in this system, helping us to understand variations in the reproductive success of the species in the community, including the success of the community as a whole (Bateson and Laland 2013). However, I also emphasize the need to carry out facilitation-focused studies using behavioral approaches in guilds that have been classically established as dominated by competitive processes, like carnivores (Palomares and Caro 1999).

CONCLUSIONS

1. New World vultures stand out for their role as key species in carrion consumption in the Neotropics, also being involved in most of the competition and facilitation processes in the community. However, the diversity of facultative species was large, with several taxa involved, although they only participated in the consumption of small-sized carcasses.

2. The ephemeral and unpredictable nature of carrion promotes temporary aggregations of individuals from different species, highlighting the importance of identifying mechanisms enabling coexistence and high levels of tolerance. Therefore, understanding these processes and their implications requires community-wide approaches.

3. Neotropical scavenger communities are structured by complex and integrated competition and facilitation processes that vary at temporal and spatial scales.

4. The presence of different behavioral or morphological traits within a guild promotes coexistence through the transmission of information between species, generating heterospecific facilitation processes. In this way, the use of different senses (i.e., smell and sight) within a Neotropical scavenger guild facilitates carrion location by using social information. In addition, the ability of some species to open the skin of the carcass (e.g., due to larger body size) allows competitively inferior species to access the resource.

5. Monitoring behaviors that are directly transferable to community functions and considering the dynamics of succession over time allows to detect variations in the intensity of competition throughout the consumption of an ephemeral resource. Interactions should not be treated as static processes, as they are highly dynamic on small timescales and influenced by species hierarchies.

6. Biodiversity loss due to human impact in hotspots such as the Brazilian *Cerrado* is of major concern. Therefore, understanding the distinctive characteristics of Neotropical guilds and their role for ecosystem functioning is crucial to developing effective conservation efforts. Specifically, the absence of large carnivores as scavengers and the limited role of meso-carnivores in this scavenger assemblage highlight the need for further research.

CONCLUSIONES

1. Los buitres del Nuevo Mundo destacan por su papel como especies clave en el consumo de carroña en el Neotrópico, estando además involucrados en la mayoría de los procesos de competencia y facilitación que se dan en la comunidad. Sin embargo, la diversidad de especies facultativas fue alta, con varios taxones implicados, aunque sólo participaron en el consumo de carroñas de pequeño tamaño.

2. La naturaleza efímera e impredecible de la carroña promueve agregaciones temporales de individuos de diferentes especies, evidenciando la importancia de identificar los mecanismos que permiten la coexistencia y los altos niveles de tolerancia. Por lo tanto, entender estos procesos y sus implicaciones requiere enfoques a nivel de comunidad.

3. Las comunidades de carroñeros neotropicales están estructuradas por procesos complejos e integrados de competencia y facilitación que varían a escalas temporales y espaciales.

4. La presencia de diferentes rasgos comportamentales o morfológicos dentro de un gremio promueve la coexistencia a través de la transmisión de información entre especies, generando procesos de facilitación heteroespecíficos. De esta manera, el uso de diferentes sentidos (es decir, olfato y vista) dentro de un gremio de carroñeros neotropicales facilita la localización de carroña mediante el uso de información social. Además, la capacidad de algunas especies para abrir la piel la carroña (por ejemplo, debido a un mayor tamaño corporal) permite que especies competitivamente inferiores accedan al recurso.

5. El monitoreo de comportamientos directamente transferibles a las funciones de la comunidad y la consideración de las dinámicas de sucesión a lo largo del tiempo permiten detectar variaciones en la intensidad de la competencia durante el consumo de un recurso efímero. Las interacciones no deben tratarse como procesos estáticos, ya que son altamente dinámicas en escalas temporales pequeñas y están influidas por las jerarquías entre las especies.

6. La pérdida de biodiversidad debida al impacto humano en puntos calientes como el *Cerrado* brasileño es motivo de gran preocupación. Por lo tanto, comprender las características distintivas de los gremios neotropicales y su papel en el funcionamiento del ecosistema es crucial para desarrollar esfuerzos de conservación eficaces. En concreto, la ausencia de grandes carnívoros como carroñeros y el papel limitado de los meso-carnívoros en este gremio ponen de manifiesto la necesidad de seguir investigando.

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APPENDICES

SUPPLEMENTARY MATERIAL TO CHAPTER 3: Uncovering the vertebrate scavenger guild composition and functioning in the *Cerrado* biodiversity hotspot

APPENDIX I. Methods

We analyzed spatial autocorrelation for small carcasses (i.e. chickens), because some were located within 200 m of each other. For this we used the *Moran.I* function in the *ape* package, which determines the degree of spatial autocorrelation between the data set, for a given variable (Fotheringham et al. 2000, Paradis et al. 2015). We tested whether there was any spatial relationship for all response variables subsequently used in the analyses: richness, abundance, consumption time, consumption rate and detection time. We also tested whether there was any spatial relationship for top-ranking models' residuals.

Table S1. Results for spatial correlation for all response variables (A) and for models' residuals (B). We obtain the value computed by the *Moran.I* function (observed), the expected value under the null hypothesis (expected), the standard deviation (SD) and the p-value.

A)

Response variables	**Observed**	**Expected**	**SD**	***p-value***
richness	-0.048	-0.023	0.03	0.401
abundance	-0.0038	-0.023	0.031	0.526
detection time	-0.036	-0.023	0.0311	0.691
consumption time	-0.043	-0.023	0.0311	0.524
consumption rate	-0.04	-0.023	0.0311	0.568

B)

Model residuals	**Observed**	**Expected**	**SD**	***p-value***
richness model	-0.011	-0.023	0.043	0.791
abundance model	-0.01	-0.023	0.043	0.768
detection time model	0	-0.023	0.044	0.599
consumption time model	-0.009	-0.023	0.045	0.745
consumption rate model	0.051	-0.023	0.038	0.052

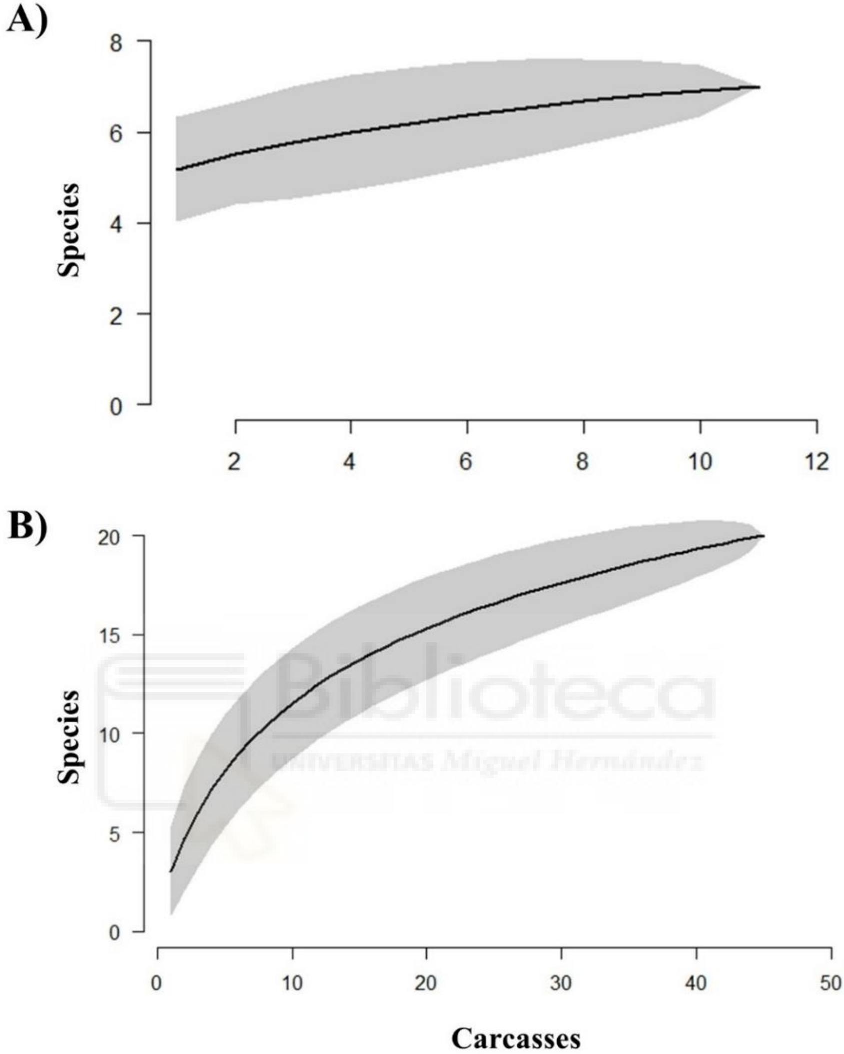

Figure S1. Species accumulation curves and standard error (grey shadow) to measure the sampling effort in order to estimate the vertebrate scavenger species richness in the Brazilian *Cerrado*. A) Number of large carcasses monitored and B) number of small carcasses monitored.

APPENDIX II. Results

Table S2. Set of the 19 species that were recorded consuming carrion. For each of them we specified the common name, the scientific name, the taxonomic group (vulture, other raptor, other bird, mammal or reptile), the functional group (obligate or facultative scavenger), the detector group (birds with high olfactory capacity, birds with low olfactory capacity, mammals and reptiles) and the conservation status (according to IUCN Red List categories) and population trend at the global scale (IUCN 2020). Conservation status: NT: Near Threatened; LC: Least concerned. Population trend: increasing (+); decreasing (–); stable (0); unknown (?).

Common name	Scientific name	Taxonomic group	Functional group	Detector group	Conservation status	Population trend
American black vulture	*Coragyps atratus*	Vulture	Obligate	Bird with low olfactory capacity	LC	+
King vulture	*Sarcoramphus papa*	Vulture	Obligate	Bird with low olfactory capacity	LC	–
Lesser yellow-headed vulture	*Cathartes burrovianus*	Vulture	Obligate	Bird with high olfactory capacity	LC	0
Turkey vulture	*Cathartes aura*	Vulture	Obligate	Bird with high olfactory capacity	LC	0
Ferruginous pygmy-owl	*Glaucidium brasilianum*	Other raptor	Facultative	Bird with low olfactory capacity	LC	–
Grey-lined hawk	*Buteo nitidus*	Other raptor	Facultative	Bird with low olfactory capacity	LC	–
Southern caracara	*Caracara plancus*	Other raptor	Facultative	Bird with high olfactory capacity	LC	+
White-tailed hawk	*Geranoaetus albicaudatus*	Other raptor	Facultative	Bird with low olfactory capacity	LC	+
Yellow-headed caracara	*Milvago chimachima*	Other raptor	Facultative	Bird with low olfactory capacity	LC	+
Chalk-browed mockingbird	*Mimus saturninus*	Other bird	Facultative	Bird with low olfactory capacity	LC	0
Red-legged seriema	*Cariama cristata*	Other bird	Facultative	Bird with low olfactory capacity	LC	0
Crab-eating fox	*Cerdocyon thous*	Mammal	Facultative	Mammal	LC	0
Hoary fox	*Lycalopex vetulus*	Mammal	Facultative	Mammal	LC	?
Maned wolf	*Chrysocyon brachyurus*	Mammal	Facultative	Mammal	NT	?
Ocelot	*Leopardus pardalis*	Mammal	Facultative	Mammal	LC	–
White-eared opossum	*Didelphis albiventris*	Mammal	Facultative	Mammal	LC	0
Black-and-white tegu	*Salvator merianae*	Reptile	Facultative	Reptile	LC	0
Calango	*Tropidurus sp.*	Reptile	Facultative	Reptile	LC	?
Giant ameiva	*Ameiva ameiva*	Reptile	Facultative	Reptile	LC	0

Table S3. AICc-based model selection for large carcasses to assess the effect of carcass weight (kg), time of placement (morning or afternoon), shrub and vegetation cover (in %), and the detector group (used exclusively for the detection time models) on scavenger richness per carcass (number of species), scavenger abundance (number of unequivocally different individuals) and scavenging efficiency (detection time, consumption time and consumption rate). Number of estimated parameters (k), AIC_c values, AIC_c differences (ΔAIC_c), Akaike weights (AIC_{cw}) and deviance explained (D^2) by selected models (i.e., those with an ΔAICc < 2, also called top-ranking models) are shown. Selected models are in bold.

Response variable	**Model**	**k**	**AICc**	**ΔAIC_c**	**AICcw**	**D^2**
Scavenger richness	**null**	**1**	**39.6**	**0**	**0.568**	**0**
	weight	2	42.6	3	0.127	
	hour	2	42.6	3.02	0.125	
	cover	2	42.7	3.04	0.124	
Scavenger abundance	**weight**	**2**	**76.7**	**0**	**0.423**	**37.08**
	null	1	82.1	5.4	0.028	
	hour	2	83.6	6.95	0.013	
	cover	2	83.8	7.13	0.012	
Detection time	**weight**	**3**	**87**	**0**	**0.521**	**35.55**
	null	**2**	**88.5**	**1.48**	**0.249**	**0**
	cover	3	91.3	4.3	0.061	
	hour	3	92.4	5.4	0.035	
	det	4	95.2	8.15	0.009	
Consumption time	**cover**	**3**	**89.2**	**0**	**0.538**	**44.8**
	null	**2**	**90.8**	**1.65**	**0.236**	**0**
	weight	3	93	3.79	0.081	
	hour	3	95.1	5.93	0.028	
Consumption rate	**weight**	**3**	**131.1**	**0**	**0.547**	**59.53**
	null	2	136	4.87	0.048	
	cover	3	136.6	5.51	0.035	

Table S4. AICc-based model selection of small carcasses to assess the effect of carcass weight (kg), time of placement of carcass placement (morning or afternoon), shrub and tree cover (in %), and the detector group (used exclusively for the detection time models) on scavenger richness per carcass (number of species), scavenger abundance (number of unequivocally different individuals) and scavenging efficiency (detection time, consumption time and consumption rate). Number of estimated parameters (k), AIC_c values, AIC_c differences (ΔAIC_c), Akaike weights (AIC_{cw}) and deviance explained (D^2) by selected models (i.e., models with an ΔAICc < 2, also called top-ranking models) are shown. Selected models are in bold.

Response variable	**Model**	**k**	**AIC_c**	**ΔAIC_c**	**AIC_{cw}**	**D^2**
Scavenger richness	**weight**	**2**	**139**	**0**	**0.299**	**14.68**
	weight + time of placement	**3**	**139.5**	**0.58**	**0.223**	**21.24**
	null	**1**	**140.6**	**1.65**	**0.131**	**0**
	vegetation cover + weight	3	141.1	2.13	0.103	
	time of placement	2	141.2	2.24	0.097	
	vegetation cover + time of placement + weight	4	141.8	2.83	0.072	
	vegetation cover	2	142.8	3.84	0.044	
	vegetation cover + time of placement	3	143.5	4.54	0.031	
Scavenger abundance	**time of placement + weight**	**4**	**197.4**	**0**	**0.462**	**32.26**
	weight	**3**	**198.3**	**0.95**	**0.288**	**26.15**
	vegetation cover + time of placement + weight	5	199.7	2.35	0.142	
	vegetation cover + weight	4	200.5	3.09	0.098	
	time of placement + weight	3	206.8	9.42	0.004	
	vegetation cover + time of placement	4	207.8	10.44	0.003	
	null	2	208.3	10.89	0.002	
	vegetation cover	3	208.6	11.25	0.002	
Detection time	**vegetation cover + weight**	**4**	**369**	**0**	**0.208**	**12.73**
	time of placement + weight	**4**	**369.2**	**0.13**	**0.196**	**12.52**
	vegetation cover + time of placement + weight	**5**	**369.4**	**0.4**	**0.17**	**16.29**
	weight	**3**	**369.9**	**0.82**	**0.139**	**7.11**
	vegetation cover	**3**	**371**	**2**	**0.077**	**4.98**
	null	2	371.4	2.37	0.064	
	time of placement + weight	3	371.5	2.42	0.062	

	vegetation cover + time of placement	4	372	2.97	0.047	
	detector group + weight	6	375.8	6.71	0.007	
	detector group + time of placement + weight	7	375.9	6.81	0.007	
	vegetation cover + detector group + weight	7	376.1	7.09	0.006	
	detector group	5	376.5	7.47	0.005	
	vegetation cover + detector group + time of placement + weight	8	376.8	7.78	0.004	
	vegetation cover + detector group	6	377.2	8.2	0.003	
	detector group + time of placement + weight	6	377.6	8.57	0.003	
	vegetation cover + detector group + time of placement	7	378.8	9.75	0.002	
Consumption time	**null**	**2**	**398.2**	**0**	**0.353**	**0**
	vegetation cover	**3**	**399.5**	**1.26**	**0.188**	**2.07**
	weight	**3**	**399.8**	**1.63**	**0.157**	**1.35**
	time of placement	3	400.5	2.3	0.112	
	vegetation cover + weight	4	401.5	3.33	0.067	
	vegetation cover + time of placement	4	401.9	3.65	0.057	
	time of placement + weight	4	402.2	4.03	0.047	
	vegetation cover + time of placement + weight	5	404	5.83	0.019	
Consumption rate	**weight**	**3**	**456.5**	**0**	**0.611**	**21.01**
	vegetation cover + weight	**4**	**457.4**	**0.93**	**0.384**	**23.13**
	null	2	467.5	10.97	0.003	
	vegetation cover	3	468	11.54	0.002	

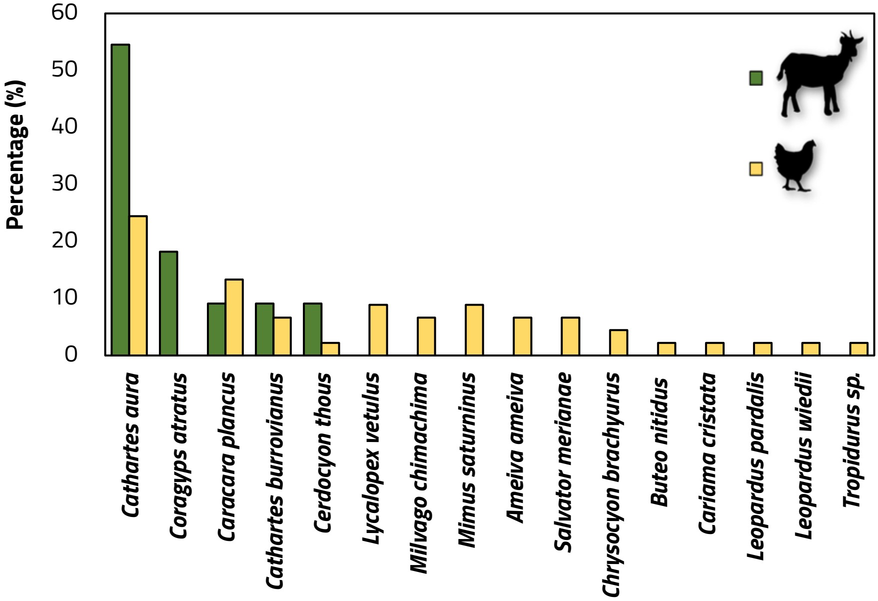

Figure S2. Proportion of carcasses that were detected first by each species (i.e., where the species was the first detector). The first to arrive were mainly vultures, some raptors and foxes.

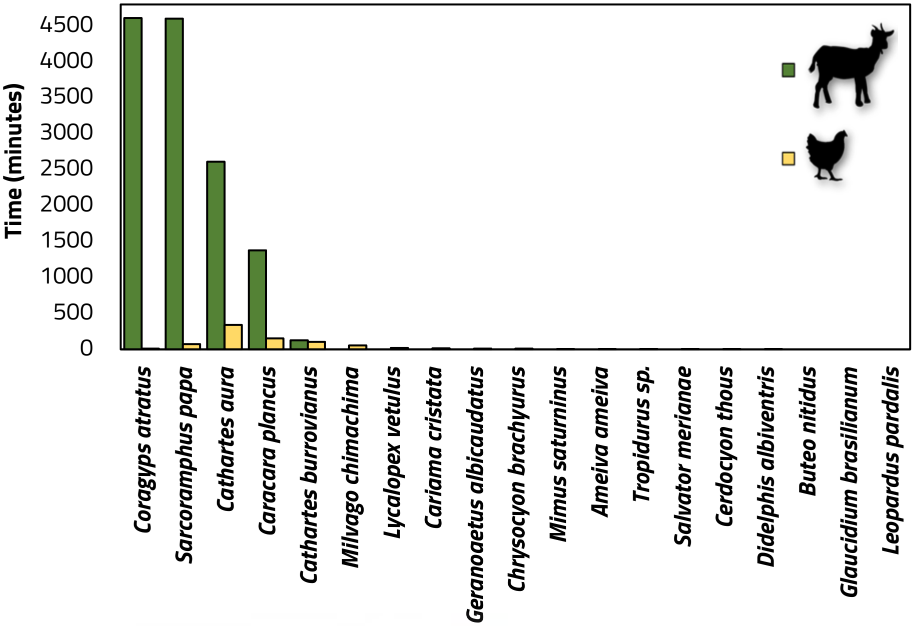

Figure S3. Total consumption time (minutes) of each scavenger species. Vulture species spent the most time feeding.

SUPPLEMENTARY REFERENCES

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SUPPLEMENTARY MATERIAL TO CHAPTER 4: Scavenger assemblages are structured by complex competition and facilitation processes among vultures

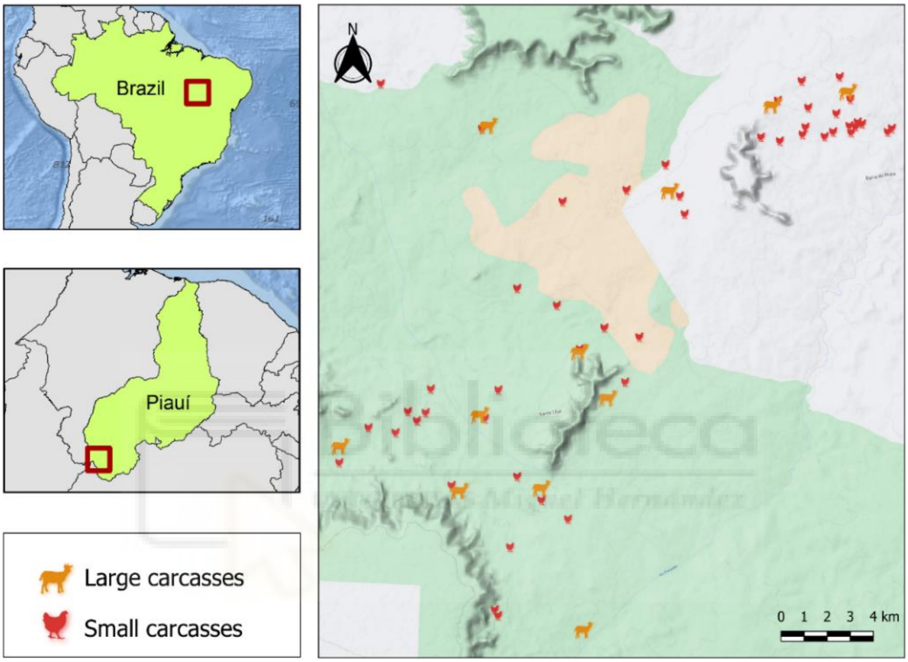


Figure S1. Map of the study area in Piauí, Brazil. We show the locations of all carcasses placed in the field, differentiating between large carcasses (orange, n = 11) and small carcasses (red, n = 45).

Table S1. Species recorded consuming carrion in this study. For each of them, we specified the common name, the scientific name, the taxonomic group (vulture, other bird, mammal or reptile) and the functional group (obligate or facultative scavenger).

Common name	Scientific name	Taxonomic group	Functional group
American black vulture	*Coragyps atratus*	Vulture	Obligate
King vulture	*Sarcoramphus papa*	Vulture	Obligate
Lesser yellow-headed vulture	*Cathartes burrovianus*	Vulture	Obligate
Turkey vulture	*Cathartes aura*	Vulture	Obligate
Grey-lined hawk	*Buteo nitidus*	Other bird	Facultative
Southern caracara	*Caracara plancus*	Other bird	Facultative
White-tailed hawk	*Geranoaetus albicaudatus*	Other bird	Facultative
Yellow-headed caracara	*Milvago chimachima*	Other bird	Facultative
Chalk-browed mockingbird	*Mimus saturninus*	Other bird	Facultative
Red-legged seriema	*Cariama cristata*	Other bird	Facultative
Crab-eating fox	*Cerdocyon thous*	Mammal	Facultative
Hoary fox	*Lycalopex vetulus*	Mammal	Facultative
Maned wolf	*Chrysocyon brachyurus*	Mammal	Facultative
Ocelot	*Leopardus pardalis*	Mammal	Facultative
White-eared opossum	*Didelphis albiventris*	Mammal	Facultative
Black-and-white tegu	*Salvator merianae*	Reptile	Facultative
Calango	*Tropidurus sp.*	Reptile	Facultative
Giant ameiva	*Ameiva ameiva*	Reptile	Facultative

Table S2. Summary of the analyses used and the species included in each analysis. **A)** Analyses performed at different scales, for which the R package and function used, the type of data, the unit of analysis, and the sample size for large and small carcasses are specified. **B)** For each of the vertebrate scavenger species detected in the community we determined: the spatial and temporal co-occurrence models for large and small carcasses in which they were included; and for the spatial and spatio-temporal quantitative models (also for large and small carcasses), those species included as response variables. Included species are represented with an X, missing species were not included in these analyses because of their low sample size.

A)

Analysis	**Measures**	**R package**	**function**	**data type**	**unit**	**Large carcasses (N)**	**Small carcasses (N)**
PERMANOVA	Jaccard dissimilarity	vegan	adonis	presence/ absence (0/1)	carcass	11	45
	Bray-Curtis dissimilarity	vegan	adonis	abundance	carcass	11	45
Co-occurrence analyses	Spatial co-occurrence	coocur	cooccur	presence/ absence (0/1)	carcass	11	45
	Spatio-temporal co-occurrence	coocur	cooccur	presence/ absence (0/1)	image	5684	2468
	Spatio-temporal co-occurrence throughout large carcasses consumption period	coocur	cooccur	presence/ absence (0/1)	images	5684	0
Quantitative analyses	Spatial analyses	lme4	glm	abundance	carcass	11	45
	Temporal analyses	lme4	glmm	abundance	image	5684	2468

B)

	Spatial co-occurrence and quantitative analysis		**Spatio-temporal co-occurrence and quantitative analysis**	
Species	**Large carcasses**	**Small carcasses**	**Large carcasses**	**Small carcasses**
American black vulture	X		X	
King vulture	X	X	X	X
Lesser yellow-headed vulture		X	X	X
Turkey vulture	X	X	X	X
Southern caracara	X	X	X	X
Yellow-headed caracara				X

Table S3. Mean *times of arrival* at the carcasses of all detected species (i.e., 18 scavenger species) represented in minutes and ordered from smallest to largest.

Species	**Mean arrival time (minutes)**
Cathartes aura	77.00
Cathartes burrovianus	81.53
Lycalopex vetulus	89.68
Tropidurus sp.	90.00
Salvator merianae	96.21
Milvago chimachima	99.65
Caracara plancus	102.76
Chrysocyon brachyurus	115.08
Sarcoramphus papa	115.83
Coragyps atratus	180.29
Geranoaetus albicaudatus	970.00
Ameiva ameiva	1238.75
Buteo nitidus	1790.00
Mimus saturninus	1950.00
Didelphis albiventris	2050.00
Cerdocyon thous	2820.00
Leopardus pardalis	6105.00
Cariama cristata	10620.00

Table S4. Results of the PERMANOVA analyses testing dissimilarity in the vertebrate scavenger community depending on carcass size (large vs. small). All *p*-values were calculated based on 9999 permutations. The degrees of freedom (D.f.), sum of squares (*SS*), pseudo R^2, pseudo *F*-statistic and the *p*-value. Significant *p*-values are in bold.

Method	Source	D.f.	*SS*	R^2	*F*	*p*
Jaccard	Carcass size	1	2.8826	0.13055	8.1086	**< 0.001**
	Residual	54	19.1973	0.86945		
	Total	55	22.0799	1		
Bray-Curtis	Carcass size	1	2.5612	0.12651	7.8209	**< 0.001**
	Residual	54	17.6838	0.87349		
	Total	55	20.245	1		

Table S5. Model coefficients for large carcasses by means of generalized lineal models (GLMs) showing the relation between the *abundance per carcass* of turkey, king and American black vultures and southern caracara and the other species abundance, *time of carcass placement* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and signification (*p*-value) are shown. Significant *p*-values are in bold.

Response variable	Models	Estimate	SE	*p*
Cathartes aura	(Intercept)	1.83	0.35	0.00
	Coragyps atratus	-0.03	0.02	0.14
	(Intercept)	0.52	0.41	0.20
	Sarcoramphus papa	0.13	0.05	**0.02**
	(Intercept)	1.36	0.48	0.00
	Caracara plancus	0.00	0.22	1.00
	(Intercept)	1.76	0.29	0.00
	vegetation cover	-0.02	0.01	0.11
	(Intercept)	1.29	0.22	0.00
	time of carcass placement: afternoon	0.25	0.41	0.53
Coragyps atratus	(Intercept)	3.12	0.36	0.00
	Sarcoramphus papa	-0.06	0.05	0.30
	(Intercept)	3.09	0.31	0.00
	Cathartes aura	-0.08	0.07	0.24
	(Intercept)	2.47	0.45	0.00
	Caracara plancus	0.16	0.21	0.44
	(Intercept)	2.60	0.29	0.00
	vegetation cover	0.01	0.01	0.41
	(Intercept)	2.75	0.21	0.00
		0.18	0.40	0.65
Sarcoramphus papa	(Intercept)	2.14	0.33	0.00
	Coragyps atratus	-0.02	0.02	0.24
	(Intercept)	1.29	0.27	0.00

	Cathartes aura	0.12	0.05	**0.02**
	(Intercept)	2.34	0.29	0.00
	Caracara plancus	-0.29	0.14	**0.04**
	(Intercept)	1.75	0.28	0.00
	vegetation cover	0.00	0.01	0.86
	(Intercept)	1.75	0.20	0.00
	time of carcass placement: afternoon	0.15	0.37	0.69
Caracara plancus	(Intercept)	0.46	0.49	0.35
	Coragyps atratus	0.01	0.03	0.58
	(Intercept)	1.11	0.42	0.01
	Sarcoramphus papa	-0.07	0.07	0.28
	(Intercept)	0.69	0.40	0.08
	Cathartes aura	0.00	0.09	1.00
	(Intercept)	0.88	0.36	0.01
	vegetation cover	-0.01	0.01	0.53
	(Intercept)	0.69	0.25	0.01
	time of carcass placement: afternoon	0.00	0.48	1.00

Table S6. Model-averaged coefficients for small carcasses by means of generalized lineal models (GLMs) showing the relation between the *abundance per carcass* of turkey, king and lesser yellow-headed vultures and southern caracara and the other species abundance, *time of carcass placement* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and signification (*p*-value) are shown. Significant *p*-values are in bold.

Response variable	Model	Estimate	SE	*p*
Cathartes aura	(Intercept)	-0.62	0.43	0.16
	vegetation cover	-0.01	0.01	0.42
	Sarcoramphus papa	1.15	0.24	**< 0.001**
	Caracara plancus	0.10	0.18	0.57
	Cathartes burrovianus	-0.09	0.17	0.61
	time of carcass placement: afternoon	0.02	0.13	0.87
Sarcoramphus papa	(Intercept)	-3.63	1.32	0.01
	Cathartes aura	0.75	0.24	**< 0.001**
	Cathartes burrovianus	0.73	0.27	**0.01**
	vegetation cover	0.01	0.02	0.53
Cathartes burrovianus	(Intercept)	-1.47	0.45	0.00
	Sarcoramphus papa	1.07	0.32	**< 0.001**
	Cathartes aura	-0.07	0.15	0.67
	time of carcass placement: afternoon	-0.10	0.31	0.74
	vegetation cover	0.00	0.01	0.75
Caracara plancus	(Intercept)	-0.45	0.25	0.08
	Cathartes aura	0.03	0.09	0.72
	Sarcoramphus papa	0.03	0.15	0.84
	vegetation cover	0.00	0.00	0.85

Table S7. Model coefficients for large carcasses by means of generalized mixed models (GLMMs) showing the relation between the *abundance per image* of turkey vulture, lesser yellow-headed vulture, king vulture, black vulture, southern caracara and the other species abundances, *day of consumption* and *vegetation cover*. The estimate of the parameters, the standard error (SE) and signification (*p*-value) are shown. Significant *p*-values are in bold.

Response variable	Model	Estimate	SE	*p*
Cathartes aura	(Intercept)	0.68	0.57	0.23
	Coragyps atratus	-0.19	0.01	**< 0.001**
	Sarcoramphus papa	-0.31	0.01	**< 0.001**
	Cathartes burrovianus	-1.10	0.06	**< 0.001**
	Caracara plancus	-0.10	0.02	**< 0.001**
	vegetation cover	0.00	0.02	0.85
	day of consumption	-0.46	0.01	**< 0.001**
Cathartes burrovianus	(Intercept)	16.70	28.47	0.56
	Cathartes aura	-0.63	0.07	**< 0.001**
	Coragyps atratus	-20.15	22.56	0.37
	Sarcoramphus papa	-20.27	24.49	0.41
	Caracara plancus	-1.95	0.17	**< 0.001**
	day of consumption	-28.53	28.47	0.32
	vegetation cover	0.00	0.10	1.00
Sarcoramphus papa	(Intercept)	-1.27	0.24	0.00
	Coragyps atratus	0.29	0.01	**< 0.001**
	Cathartes burrovianus	-4.61	1.25	**< 0.001**
	Cathartes aura	-0.42	0.01	**< 0.001**
	Caracara plancus	-0.34	0.01	**< 0.001**
	day of consumption	0.41	0.01	**< 0.001**
	vegetation cover	-0.01	0.00	0.20
Coragyps atratus	(Intercept)	1.25	0.27	0.00
	Sarcoramphus papa	0.26	0.00	**< 0.001**
	Cathartes burrovianus	-4.88	0.98	**< 0.001**
	Cathartes aura	-1.11	0.01	**< 0.001**
	Caracara plancus	-0.17	0.01	**< 0.001**
	day of consumption	-0.72	0.01	**< 0.001**
	vegetation cover	0.01	0.01	0.30
Caracara plancus	(Intercept)	-2.19	0.91	0.02
	Sarcoramphus papa	-0.41	0.02	**< 0.001**
	Cathartes burrovianus	-1.32	0.15	**< 0.001**
	Cathartes aura	-0.04	0.01	**0.00**
	Coragyps atratus	-0.10	0.01	**< 0.001**
	day of consumption	0.39	0.02	**< 0.001**
	vegetation cover	-0.02	0.02	0.42

Table S8. Model coefficients for small carcasses by means of generalized mixed models (GLMMs) showing the relation between the *abundance per image* of turkey vulture, lesser yellow-header vulture, king vulture, southern caracara and yellow-headed caracara, *day of consumption and vegetation cover*. The estimate of the parameters, the standard error (SE) and signification (*p*-value) are shown. Significant *p*-values are in bold.

Response variable	Model	Estimate	SE	*p*
Cathartes aura	(Intercept)	-6.23	3.77	0.10
	Milvago chimachima	-6.52	12.36	0.60
	Sarcoramphus papa	0.09	0.02	**< 0.001**
	Cathartes burrovianus	-0.26	0.05	**< 0.001**
	Caracara plancus	-0.14	0.08	0.07
	vegetation cover	0.00	0.03	0.98
	day of consumption	-0.17	0.11	0.13
Cathartes burrovianus	(Intercept)	-11.98	2.52	0.00
	Cathartes aura	-0.33	0.08	**< 0.001**
	Milvago chimachima	-0.16	0.13	0.22
	Sarcoramphus papa	-0.57	0.17	**< 0.001**
	Caracara plancus	-0.21	0.07	**< 0.001**
	day of consumption	0.78	0.28	**0.01**
	vegetation cover	0.03	0.04	0.52
Sarcoramphus papa	(Intercept)	-16.62	4.05	0.00
	Cathartes burrovianus	-0.87	0.25	**< 0.001**
	Cathartes aura	0.20	0.05	**< 0.001**
	Caracara plancus	-0.50	0.19	**0.01**
	Milvago chimachima	-612.12	96.76	**< 0.001**
	day of consumption	3.83	1.02	**< 0.001**
	vegetation cover	0.04	0.05	0.38
Caracara plancus	(Intercept)	-6.65	1.29	0.00
	Sarcoramphus papa	-0.45	0.13	**< 0.001**
	Cathartes burrovianus	-0.35	0.08	**< 0.001**
	Cathartes aura	-0.26	0.13	**0.05**
	Milvago chimachima	-26.54	472072.33	1.00
	day of consumption	1.04	0.22	**< 0.001**
	vegetation cover	0.02	0.03	0.49
*Milvago chimachima**	(Intercept)	-1.37	0.23	0.00
	Cathartes aura	-21.92	1130.16	0.98
	Cathartes burrovianus	-0.57	0.17	**< 0.001**
	Caracara plancus	-20.81	1846.10	0.99
	Sarcoramphus papa	-19.36	2794.84	0.99
	day of consumption	1.12	0.13	**< 0.001**
	vegetation cover	-0.04	0.01	**< 0.001**

* a GLM was performed since the GLMM did not converge for this species

SUPPLEMENTARY MATERIAL TO CHAPTER 5: Scavenger assemblages are structured by complex competition and facilitation processes among vultures

Table S1. Scavenger species registered in the community. For each of them, we specified the common name, the scientific name and the taxonomic group (i.e., vulture, other bird, mammal or reptile).

Common name	**Scientific name**	**Taxonomic group**
American black vulture*	*Coragyps atratus*	Vulture
King vulture*	*Sarcoramphus papa*	Vulture
Lesser yellow-headed vulture*	*Cathartes burrovianus*	Vulture
Turkey vulture*	*Cathartes aura*	Vulture
Grey-lined hawk	*Buteo nitidus*	Other bird
Southern caracara*	*Caracara plancus*	Other bird
White-tailed hawk	*Geranoaetus albicaudatus*	Other bird
Yellow-headed caracara	*Milvago chimachima*	Other bird
Chalk-browed mockingbird	*Mimus saturninus*	Other bird
Red-legged seriema	*Cariama cristata*	Other bird
Crab-eating fox	*Cerdocyon thous*	Mammal
Hoary fox*	*Lycalopex vetulus*	Mammal
Maned wolf	*Chrysocyon brachyurus*	Mammal
Ocelot	*Leopardus pardalis*	Mammal
White-eared opossum	*Didelphis albiventris*	Mammal
Black-and-white tegu*	*Salvator merianae*	Reptile
Calango	*Tropidurus sp.*	Reptile
Giant ameiva	*Ameiva ameiva*	Reptile

* Species considered as focal species in the analyses

Table S2. Times of first arrival of each species from carcass placement and maximum abundance (i.e., average number of individuals present in each carcass size) of each species separately for large and small carcasses, both represented as the mean and standard deviation, i.e., $\overline{X}$ ± SD.

	Species	Arrival time ($\overline{X}$ ± SD; hours)	Abundance ($\overline{X}$ ± SD)
Large carcasses	Turkey vulture	23.93 ± 12.64	4.40 ± 2.88
	American black vulture	29.56 ± 13.74	18.90 ± 9.81
	King vulture	26.06 ± 11.48	4.90 ± 1.97
	Southern caracara	29.10 ± 13.34	3.40 ± 4.84
Small carcasses	Turkey vulture	29.14 ± 17.00	0.69 ± 1.14
	Lesser yellow-headed vulture	19.60 ± 18.43	0.33 ± 0.67
	King vulture	39.91 ± 10.19	0.20 ± 0.46
	Southern caracara	21.55 ± 21.24	0.67 ± 0.88
	Hoary fox	19.13 ± 10.46	0.11 ± 0.32
	Black-and-white tegu	31.45 ± 18.51	0.11 ± 0.32

Table S3. Model coefficients for large carcasses by means generalized lineal models (GLMs) showing the influence of the linear predictor (L_{ijt}) and the biotic predictor (h_{ijt}: influence of heterospectifics) on each of the scavenging species. The biotic predictor considered the presence-absence (*presence*), the proportion of time present (*time*) or the maximum abundance (*abundance*) during the previous focal time (*t*) of all species together (all), only birds with olfactory capacity (can smell) or each species separately (common name of the species). Model for turkey vulture only shows the abiotic factor, as other species did not appear previously in the same carcasses enough times. Only top-ranking models are represented (i.e., ΔAICc <2). Estimate and its p-value (*p*) for abiotic and biotic predictors, and deviance explained (D^2) by top-ranking models are showed. Significant p-values for biotic predictor are in bold.

Focal species	**Influencer**	**Presence, abundance or time**	***t***	L_{ijt} **(estimate)**	**biotic predictor (estimate)**	L_{ijt} **(p)**	**biotic predictor (p)**	**ΔAICc**	**D^2**
Turkey vulture				1.66		0.00			19.25
King vulture	All	Abundance	30mins	-0.01	1.04	0.98	**0.00**	0.00	34.49
	All	Abundance	10mins	0.11	1.04	0.73	**0.00**	0.30	34.24
American black vulture	All	Presence	1h	1.10	2.10	0.04	0.07	0.00	25.53
	All	Presence	4h	1.22	1.91	0.02	0.09	0.70	24.97
	All	Time	4h	1.44	1.54	0.01	0.08	1.99	23.92
Southern caracara	All	Abundance	10mins	4.04	0.59	0.00	**0.00**	0.00	39.39
	All	Abundance	30mins	4.10	0.51	0.00	**0.00**	1.61	38.09
	All	Abundance	1h	4.33	0.51	0.00	**0.00**	1.78	37.94

Table S4. Model coefficients for small carcasses by means generalized lineal models (GLMs) showing the influence of the linear predictor (L_{ijt}) and the biotic predictor (h_{ijt}: influence of heterospecifics) on each of the scavenging species. The biotic predictor considered the presence-absence, the proportion of time present or the maximum abundance during the previous focal time (*t*) of all species together (all), only birds with olfactory capacity (can smell) or each species separately (common name of the species). Models for hoary fox and black-and-white tegu in small carcasses only show the abiotic factor because we only obtained the abiotic model, as other species did not appear previously in the same carcasses enough times. Only top-ranking models are represented (i.e., ΔAICc <2). Estimate and its p-value (*p*) for abiotic and biotic predictors, and deviance explained (D^2) by top-ranking models are showed. Significant p-values for biotic predictor are in bold.

Focal species	**Species**	**Presence, abundance or time**	***t***	**L_{ijt} (estimate)**	**biotic predictor (estimate)**	**L_{ijt} (p)**	**biotic predictor (p)**	**ΔAICc**	**D^2**
Turkey vulture	All	Time	4h	0.80	-8.73	0.00	0.42	0.00	13.26
	All	Presence	10mins	0.78	0.87	0.00	0.40	0.88	12.90
	All	Abundance	4h	0.80	-0.37	0.00	0.56	1.01	12.85
	All	Time	1h	0.79	-2.07	0.00	0.62	1.08	12.82
	All	Presence	4h	0.79	-0.26	0.00	0.73	1.31	12.73
	All	Abundance	1h	0.79	-0.25	0.00	0.77	1.33	12.72
	All	Presence	30mins	0.78	0.30	0.00	0.78	1.36	12.71
	All	Abundance	10mins	0.79	0.08	0.00	0.86	1.41	12.69
	All	Presence	1h	0.79	-0.15	0.00	0.89	1.42	12.68
	All	Time	30mins	0.79	-0.30	0.00	0.89	1.42	12.68
	All	Abundance	30mins	0.79	-0.03	0.00	0.97	1.44	12.68
Lesser yellow-headed vulture	All	Presence	10mins	0.87	2.53	0.00	**0.00**	0.00	16.01
	All	Time	30mins	0.88	3.10	0.00	**0.00**	0.36	16.01
King vulture	Cathartes aura	Presence	10mins	0.48	4.64	0.01	**0.00**	0.00	45.99
	With olfaction	Presence	10mins	0.50	4.60	0.01	**0.00**	0.13	45.88
	Cathartes aura	Presence	4h	0.64	4.10	0.00	**0.00**	0.83	45.35
	With olfaction	Presence	4h	0.65	4.09	0.00	**0.00**	0.88	45.31
	Cathartes aura	Abundance	4h	0.85	2.31	0.00	**0.00**	1.83	44.57
Southern caracara	With olfaction	Presence	4h	1.12	2.33	0.00	**0.00**	0.00	15.84
	With olfaction	Presence	1h	1.06	2.44	0.00	**0.00**	1.62	15.22
Hoary fox				0.81		0.01		0.00	12.10
Black-and-white tegu				0.95		0.06		0.00	19.88

FIGURE CAPTIONS

Figure S1. Results of the logistic regression on heterospecific influence on first arrival times, shown separately for large and small carcasses. Circles refer to the influence of the baseline predictor L_{ijt}, and the squares to the heterospecific influence. Positive and significant ($p<0.05$) influence on the occurrence of each focal species is indicated in green; non-significant effects are indicated in gray and model combinations not considered are shown in white. The absence of squares indicates that there is no model for that focal species. The different combinations for B1-B4 (i.e., importance of the presence or abundance of the influencer) and C1-C3 (i.e., previous time considered) assumptions are represented in the mini-squares. In Fig. 2 of the main text, we show results for data discretized to time resolution of Δt=10 min, and the case where the time since carcass placement was included in the baseline model. Here we show results also for other choices of these parameters: A) Δt=1 min with time since carcass placement excluded, B) Δt=1 min with time since carcass placement included, C) Δt=10 min with time since carcass placement included, D) Δt=10 min with time since carcass placement included, E) Δt=1 hour with time since carcass placement excluded, and F) Δt=1 hour with time since carcass placement included.

Figure S1. A)

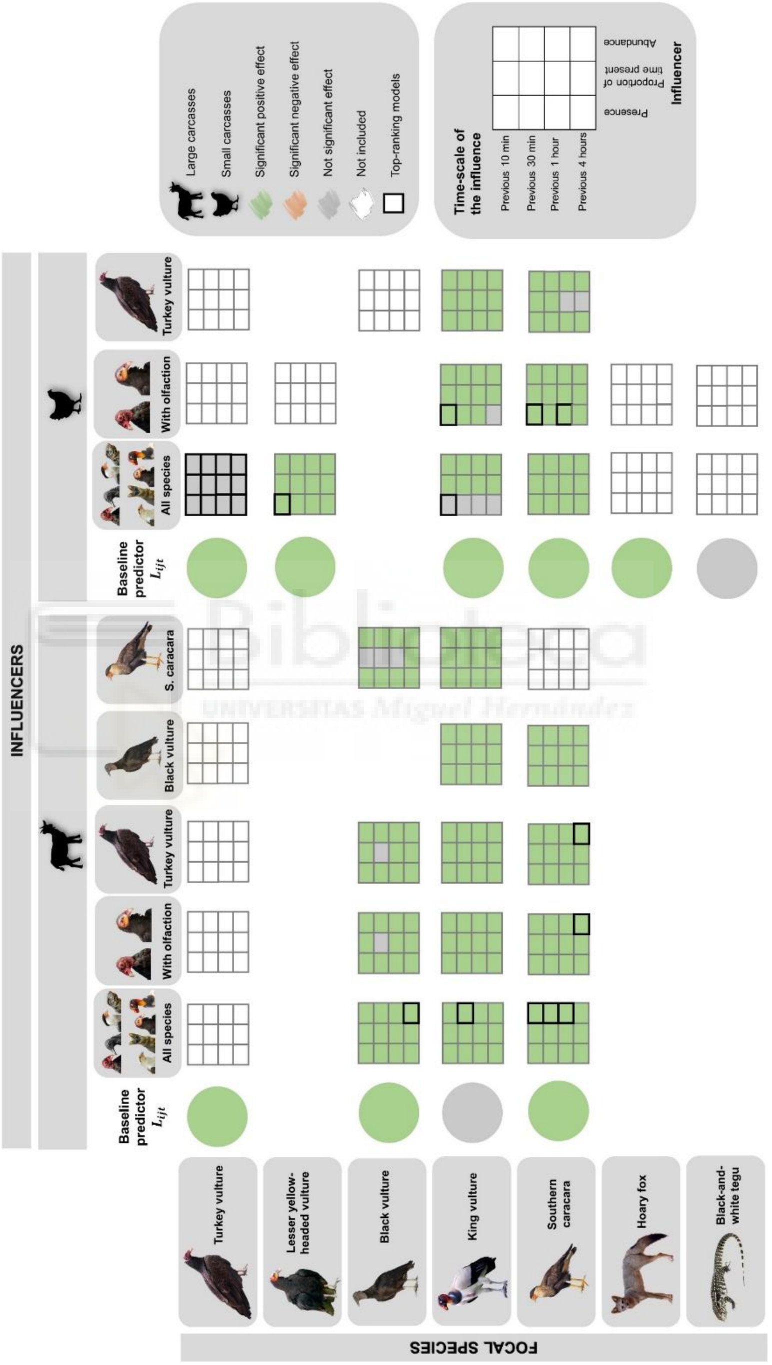

INFLUENCERS
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Black vulture
S. caracara
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Large carcasses
Small carcasses
Significant positive effect
Significant negative effect
Not significant effect
Not included
Top-ranking models
Time-scale of the influence
Previous 10 min
Previous 30 min
Previous 1 hour
Previous 4 hours
Presence
Proportion of time present
Abundance
Influencer
Turkey vulture
Lesser yellow-headed vulture
Black vulture
King vulture
Southern caracara
Hoary fox
Black-and-white tegu
FOCAL SPECIES

Figure S1. B)

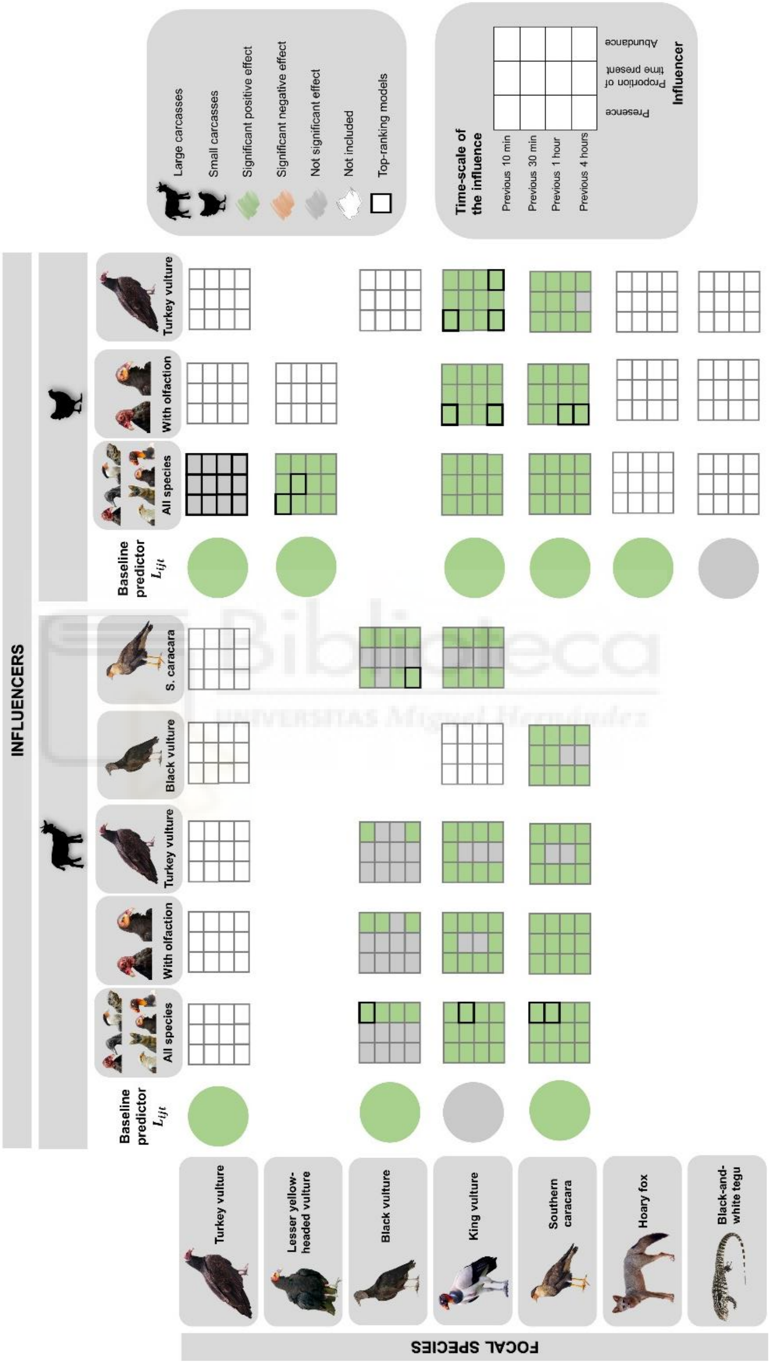

Large carcasses
Small carcasses
Significant positive effect
Significant negative effect
Not significant effect
Not included
Top-ranking models
Time-scale of the influence
Previous 10 min
Previous 30 min
Previous 1 hour
Previous 4 hours
Presence
Proportion of time present
Abundance
Influencer
INFLUENCERS
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Black vulture
S. caracara
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Turkey vulture
Lesser yellow-headed vulture
Black vulture
King vulture
Southern caracara
Hoary fox
Black-and-white tegu
FOCAL SPECIES

Figure S1. C)

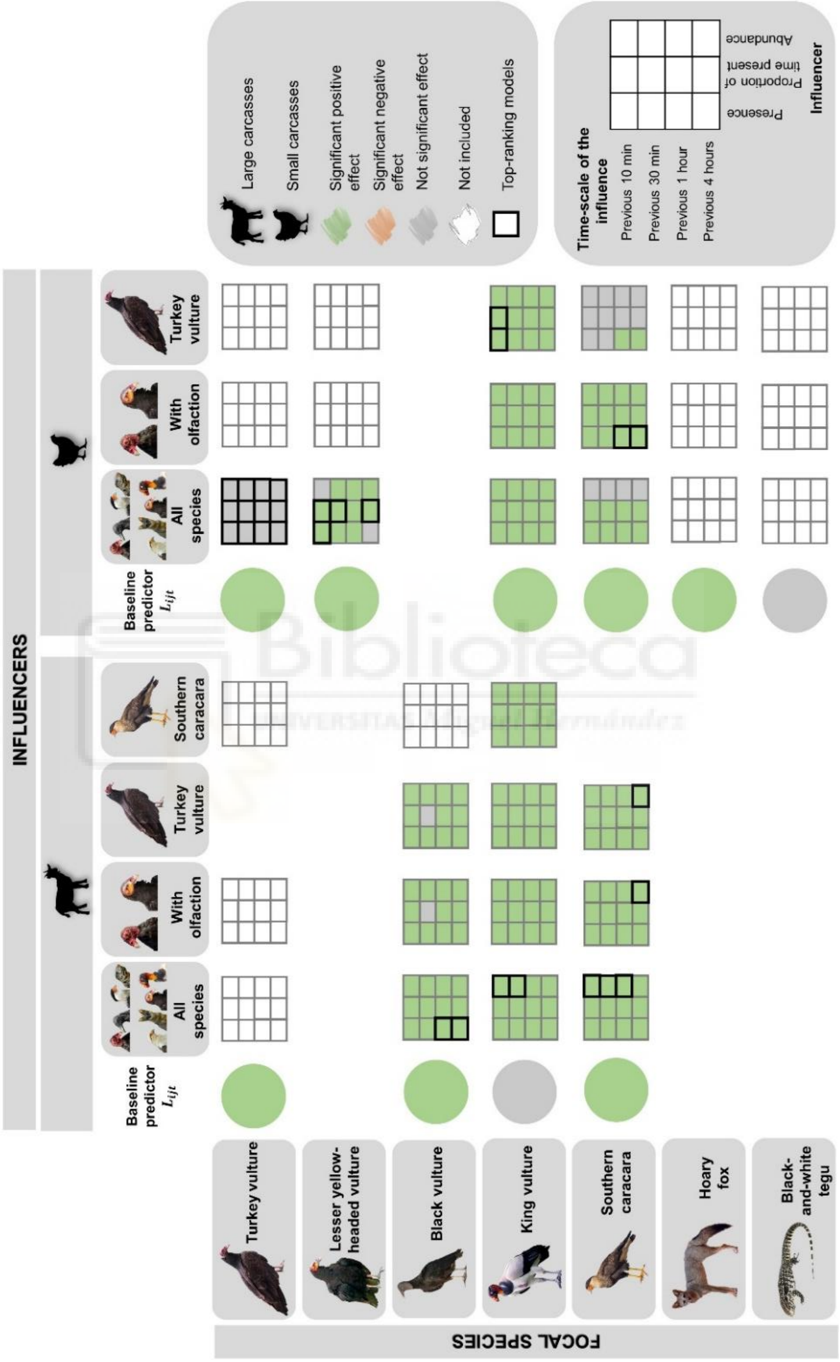

INFLUENCERS
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Southern caracara
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Large carcasses
Small carcasses
Significant positive effect
Significant negative effect
Not significant effect
Not included
Top-ranking models
Time-scale of the influence
Previous 10 min
Previous 30 min
Previous 1 hour
Previous 4 hours
Presence
Proportion of time present
Abundance
Influencer
Turkey vulture
Lesser yellow-headed vulture
Black vulture
King vulture
Southern caracara
Hoary fox
Black-and-white tegu
FOCAL SPECIES

Figure S1. D)

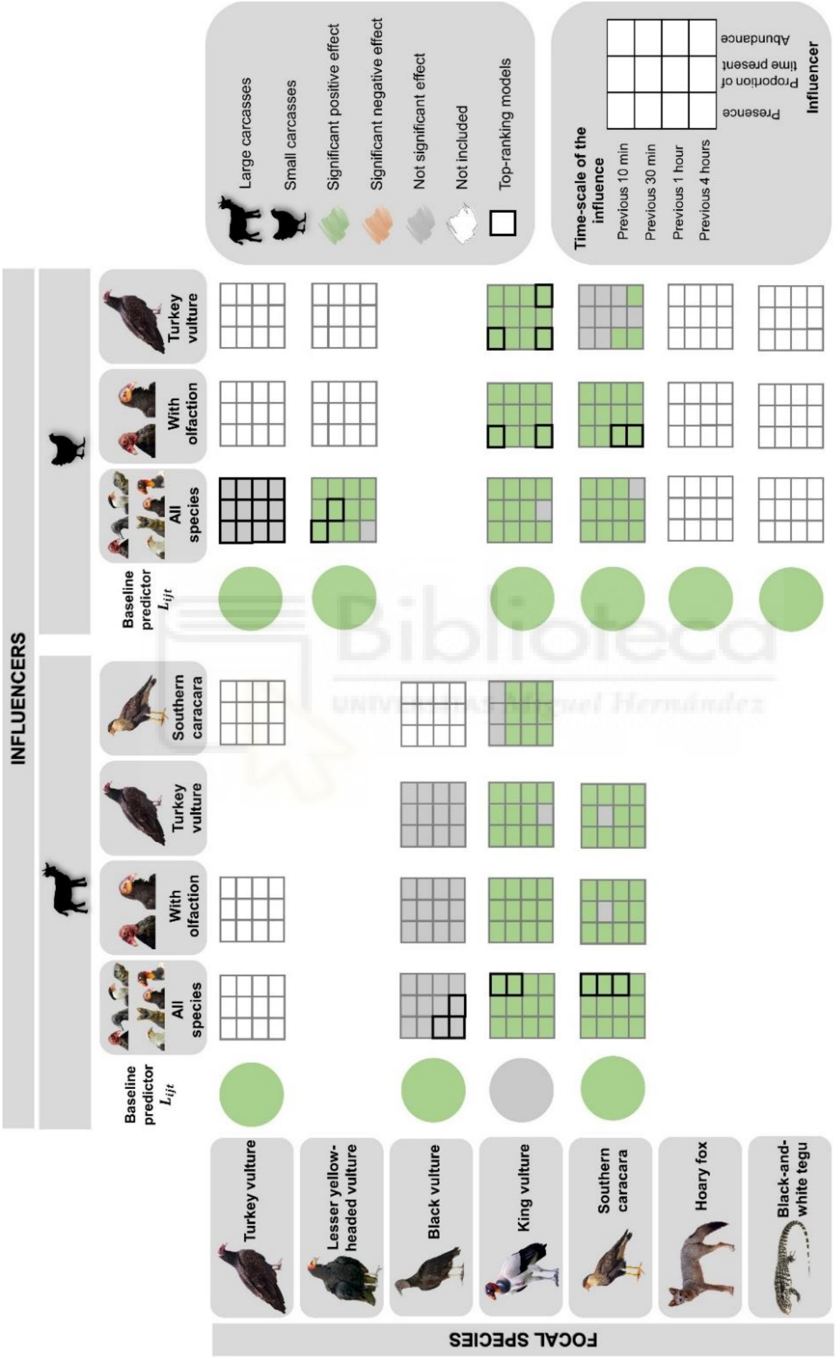

INFLUENCERS
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Southern caracara
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
Large carcasses
Small carcasses
Significant positive effect
Significant negative effect
Not significant effect
Not included
Top-ranking models
Time-scale of the influence
Previous 10 min
Previous 30 min
Previous 1 hour
Previous 4 hours
Presence
Proportion of time present
Abundance
Influencer
FOCAL SPECIES
Turkey vulture
Lesser yellow-headed vulture
Black vulture
King vulture
Southern caracara
Hoary fox
Black-and-white tegu

Figure S1. E)

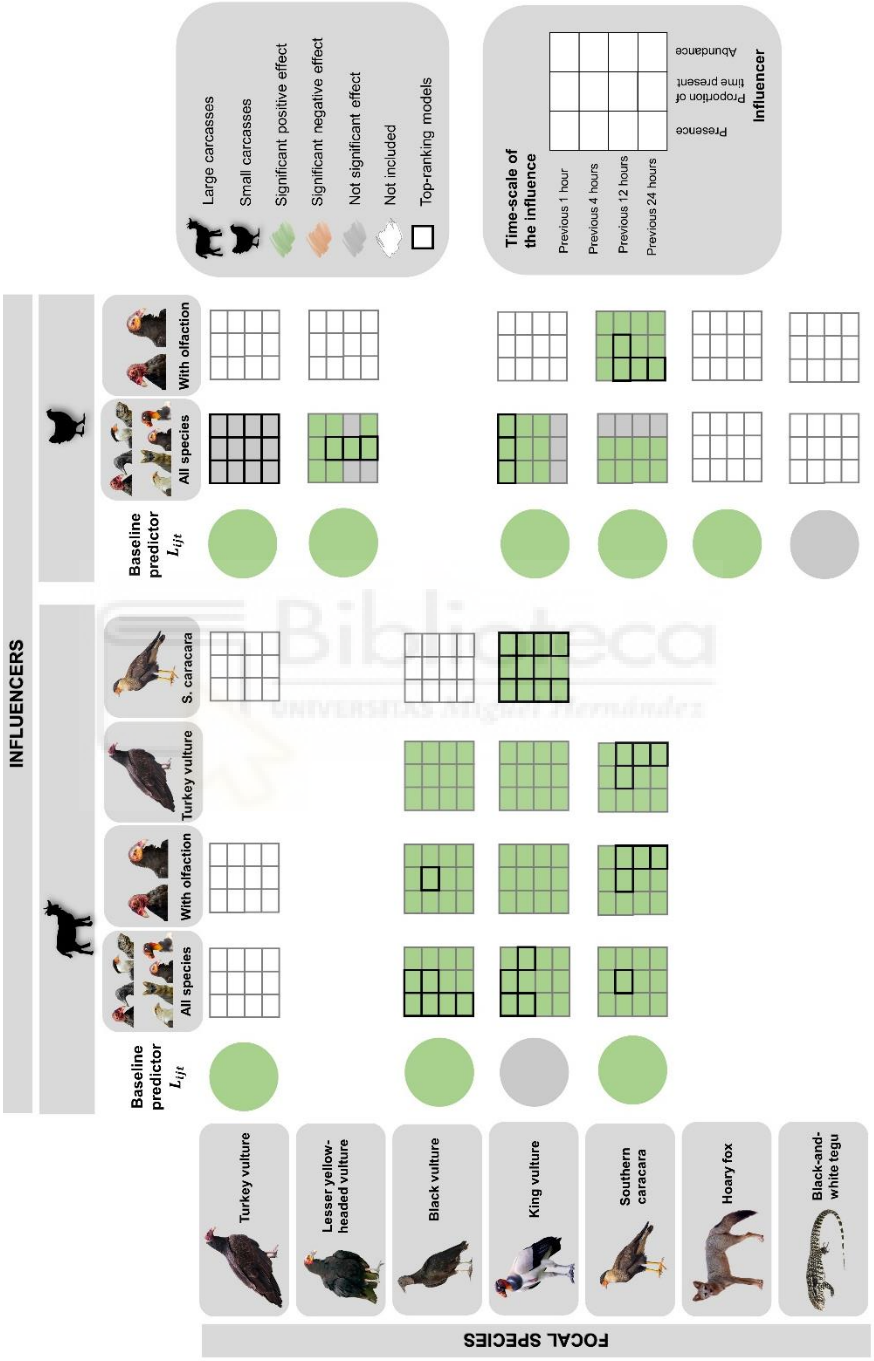
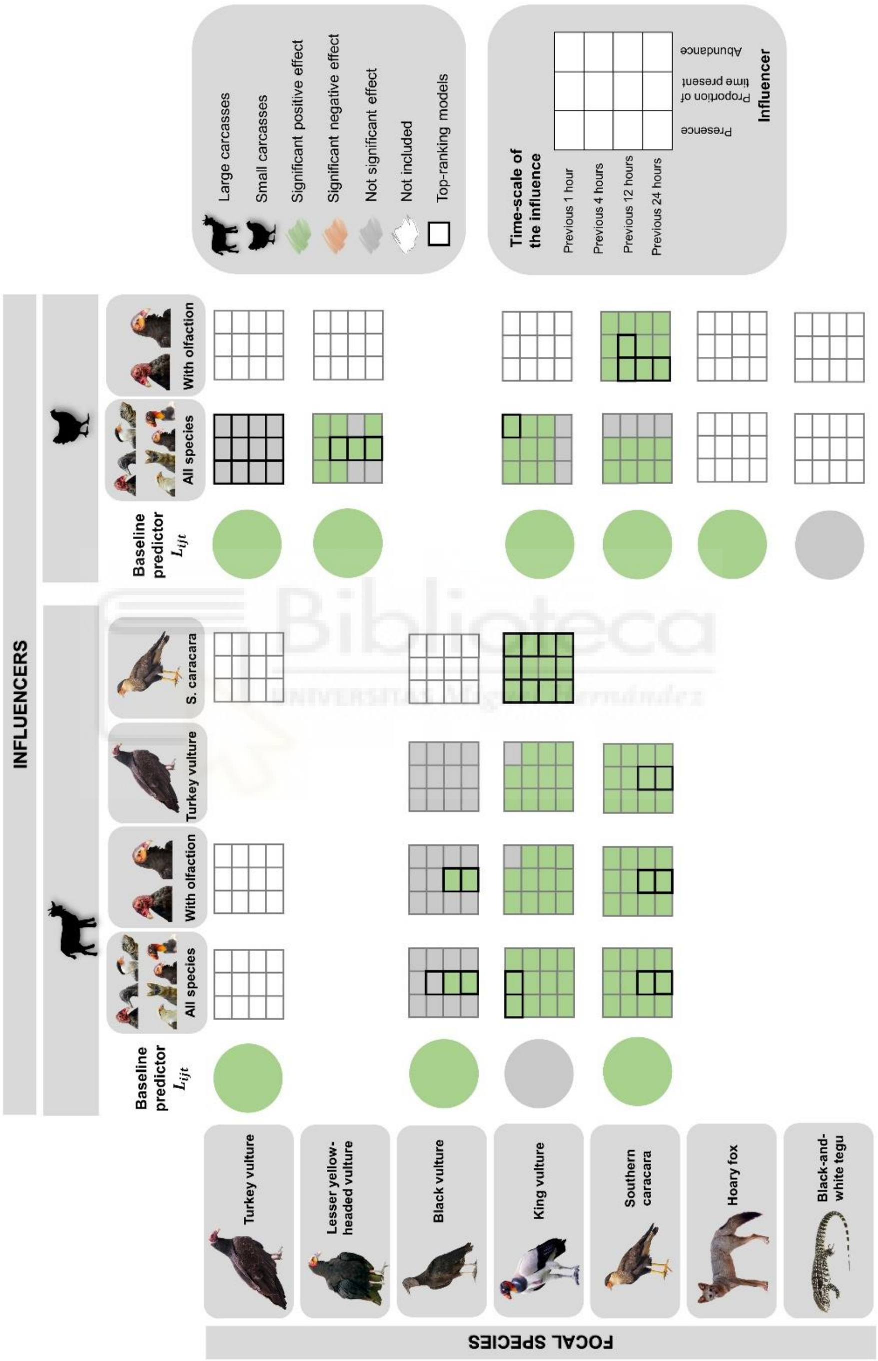

INFLUENCERS
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
S. caracara
Baseline predictor L_{ijt}
All species
With olfaction
Large carcasses
Small carcasses
Significant positive effect
Significant negative effect
Not significant effect
Not included
Top-ranking models
Time-scale of the influence
Previous 1 hour
Previous 4 hours
Previous 12 hours
Previous 24 hours
Presence
Proportion of time present
Abundance
Influencer
Turkey vulture
Lesser yellow-headed vulture
Black vulture
King vulture
Southern caracara
Hoary fox
Black-and-white tegu
FOCAL SPECIES

Figure S1. F)


Large carcasses
Small carcasses
Significant positive effect
Significant negative effect
Not significant effect
Not included
Top-ranking models
Time-scale of the influence
Previous 1 hour
Previous 4 hours
Previous 12 hours
Previous 24 hours
Presence
Proportion of time present
Abundance
Influencer
INFLUENCERS
Baseline predictor L_{ijt}
All species
With olfaction
Turkey vulture
S. caracara
FOCAL SPECIES
Turkey vulture
Lesser yellow-headed vulture
Black vulture
King vulture
Southern caracara
Hoary fox
Black-and-white tegu

SUPPLEMENTARY MATERIAL TO CHAPTER 6: Behavioral interactions are modulated by facilitation along a heterotrophic succession

APPENDIX S1: Community metrics equations

To understand how the scavenger community changes throughout the succession process we first calculated total species turnover (Collins et al. 2008):

$$turnover_{total} = \frac{S_g + S_l}{S_{total}}$$

where S_g and S_l are the number of species gained and lost, respectively, between two time-points. S_{total} is the total number of species observed in both time-points.

Then, we also calculated Shannon-Wiener diversity index (*H*) along the carcass consumption process (Shannon and Weaver 1949, Mouillot and Leprêtre 1999), using:

$$H = -\sum \left(\frac{n_i}{N}\ x\ \ln\frac{n_i}{N}\right)$$

where n_i is the number of individuals of each species *i* and *N* is the total number of individuals at the carcass.

APPENDIX S2: Supplementary tables

Table S1. Detailed description of the non-behavioral variables associated with each video used in the study.

Variable	Description
ID	Unique identifier code for each archive (video or photo)
carcass	Identifier for each of the monitored carcasses
date and time	Day and time when the archive was recorded
abundance	Maximum number of unequivocally different individuals of a species registered in the archive
individuals actively eating	Individuals that were observed feeding for at least one third of the duration of the video
percentage of carcass consumption	Percentage of consumption of the carcass at the moment each archive was recorded
time of carcass detection	Moment when the carcass was detected by the first scavenger
time since carcass detection	Time since the carcass was detected by the first scavenger, i.e., since the first consumer appears
time of complete carcass consumption	Time elapsed from the time the first consumer arrives until the carcass is completely consumed
time of carcass opening	Moment during the consumption of the carcass at which its ventral part has an aperture large enough to consider that all species (regardless of their capacity, i.e., body size, size of the carcass) can access the interior
carcass opening state	Binomial variable: 1) closed, and 2) open, i.e., videos recorded after the carcass opening.

Table S2. Number of videos selected for each of the carcasses (i.e., total selected videos). We also differentiate between videos belonging to the different stages of the carcass (i.e., closed and open states).

Carcass	Total videos	Total videos from the close state	Total videos from the open state	Total selected videos	Selected videos from the close state	Selected videos from the open state
CA1	202	100	102	42	16	26
CA2	160	89	71	58	17	41
CA3	311	147	164	72	29	43
CA4	164	44	120	51	11	40
CA5	83	9	74	39	4	35
CA7	303	48	255	54	6	48
CA8	331	57	274	64	10	54
CA9	304	133	171	62	22	40
CA10	315	180	135	66	33	33
VA1	328	2	326	65	1	64
total	**2501**	**809**	**1692**	**573**	**149**	**424**

Table S3. Percentage of consumption (i.e., PC) which coincides with the *time of carcass opening* of each carcass.

Carcass	PC of carcass opening
CA1	9.90
CA2	21.48
CA3	67.18
CA4	3.71
CA5	31.89
CA7	3.13
CA8	7.75
CA9	60.15
CA10	43.74
VA1	0.54

Table S4. Number of individuals present and actively eating per video. We plot the mean, standard deviation and maximum number of individuals recorded per video. Only the videos from which behavioral data were extracted were used to calculate *individuals eating per video* variable.

Species	Individuals per archive ($\bar{X}$ ± SD)	Maximum individuals per archive	Individuals eating per video ($\bar{X}$ ± SD)	Maximum individuals eating per video
Turkey vulture	0.99 ± 1.66	10	0.28 ± 0.69	3
Lesser yellow-headed vulture	0.03 ± 0.21	2	0.01 ± 0.14	2
Cathartes vultures	1.02 ± 1.66	10	0.29 ± 0.71	3
American black vulture	6.03 ± 7.30	42	2.59 ± 2.53	20
King vulture	1.30 ± 1.56	7	0.93 ± 1.10	5
Southern caracara	0.45 ± 0.53	3	0.12 ± 0.39	2
Yellow-headed caracara	0.00 ± 0.05	2	0	0

Table S5. Overview of the different variables and interactions registered between New World vultures during the observation of the videos recorded by the camera traps.

Behavioral term	Definition
1. Agonistic interactions	
Attack	Aggression or attempted aggression by using the beak, claws, or open wings, with the intention of displacing the target individual from its position or to avoid being displaced.
Theft	Remove or attempt to remove food from the beak or claws of another individual that is feeding at that moment.
Retreat	One of the individuals moves away (victim) in the presence of the other (initiator), without any aggressive gesture or conflict, by giving up his position.
2. Non-agonistic interactions	
Affiliative	Non-aggressive intent, may involve feather preening, or food sharing (the latter commonly between individuals of the same species of different ages).
3. Role in the interaction	
Initiator	Individual who intentionally or unintentionally initiates interaction on another individual.
Victim	Individual who receives the interaction.
4. Classification according to the participants	
Intraespecific interaction	The initiator and the victim of the interaction belong to the same species.
Interespecific interaction	The initiator and the victim of the interaction belong to different species.

Table S6. Estimated coefficients for the best models evaluating the probability of the different interactions during complete carcass consumption process according to the time of consumption and the abundance of the different species present.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Richness							
Intercept	0.73	0.07	0.6	0.87	1.00	887	964
PC	-0.05	0.05	-0.14	0.04	1.00	1511	1558
Carcass opening status: closed	-0.22	0.11	-0.43	-0.02	1.00	1512	1556
Abundance							
Intercept	2.3	0.13	2.04	2.57	1.00	311	272
PC	-0.29	0.02	-0.33	-0.24	1.00	1143	1399
Carcass opening status: closed	-1.01	0.06	-1.13	-0.89	1.00	1107	1084
Shannon Index							
Intercept	0.48	0.07	0.32	0.62	1.00	275	435
PC	0.49	0.35	-0.21	1.18	1.00	2193	1405
PC^2	-0.89	0.33	-1.54	-0.27	1.00	2274	1460
Total turnover							
Intercept	0.22	0.02	0.18	0.27	1.00	1640	1168
PC	0.78	0.27	0.23	1.31	1.00	4628	2068
PC^2	-0.23	0.27	-0.75	0.31	1.00	4067	2108
PC^3	-0.79	0.27	-1.31	-0.27	1.00	3189	2271

Table S7. Estimated coefficients for the best models (i.e., lower WAIC) analyzing trends in the abundance of the different species during the entire carcass consumption process.

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Number of Cathartes vultures							
Intercept	-0.82	0.41	-1.63	0.05	1.00	700	602
PC	-16.34	1.9	-20.28	-12.71	1.00	1437	1655
PC^2	-7.42	1.43	-10.39	-4.66	1.00	1440	1765
Number of black vultures							
Intercept	1.61	0.32	0.97	2.21	1.00	603	828
PC	-1.45	0.44	-2.3	-0.6	1.00	2034	1777
PC^2	-2.42	0.43	-3.24	-1.58	1.00	1849	1561
Number of king vultures							
Intercept	0.14	0.21	-0.29	0.58	1.00	626	939
PC	6.65	0.99	4.74	8.64	1.00	2126	2118
PC^2	-2.31	0.92	-4.05	-0.55	1.00	2060	2054
PC^3	-2.47	1.01	-4.45	-0.49	1.00	2180	2176

Table S8. Number of interactions of each type (i.e., attacks, thefts, retreats and affiliative interactions) specifying the species that initiates the interaction (i.e., initiator) and the species that receives it (i.e., victim). We differentiate between the interactions occurring during the open stage and the closed stage of the carcass.

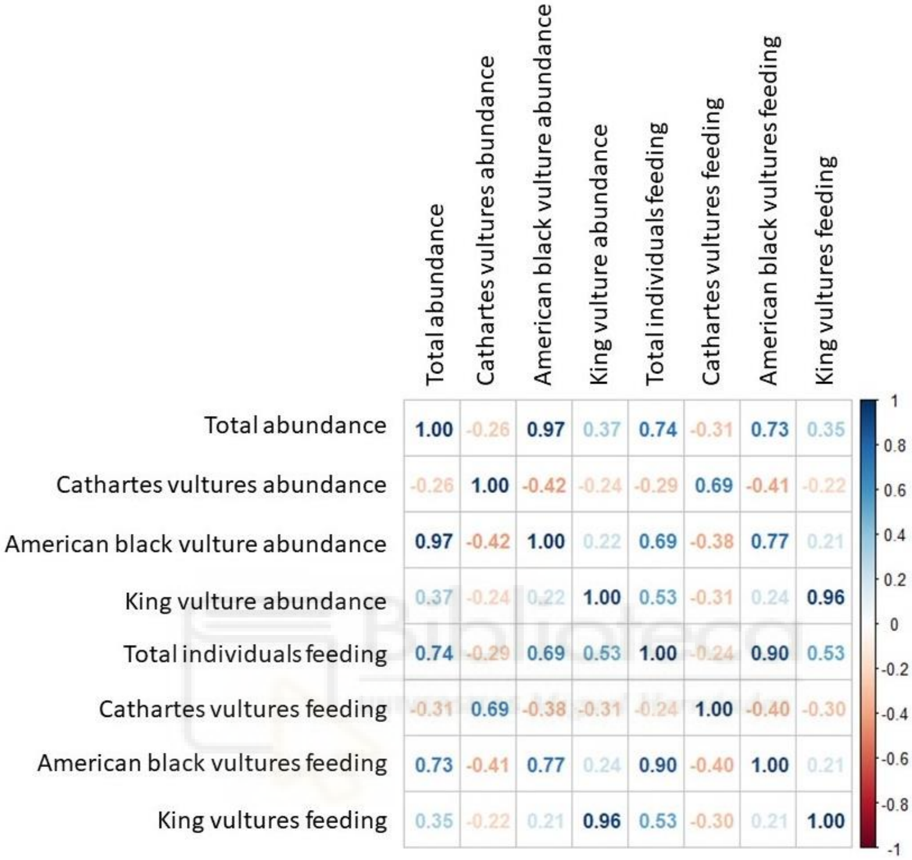
Interaction	Initiator	Victim	Closed stage	Open stage	Total
Attack	**Cathartes vultures**	Cathartes vultures	22	28	50
		Black vulture	1	3	4
		King vulture	0	0	0
	Black vulture	Cathartes vultures	9	6	15
		Black vulture	137	1225	1362
		King vulture	0	6	6
	King vulture	Cathartes vultures	1	10	11
		Black vulture	37	450	487
		King vulture	0	91	91
Theft	**Cathartes vultures**	Cathartes vultures	0	1	1
		Black vulture	0	1	1
		King vulture	0	0	0
	Black vulture	Cathartes vultures	0	1	1
		Black vulture	1	12	13
		King vulture	1	3	4
	King vulture	Cathartes vultures	0	0	0
		Black vulture	0	0	0
		King vulture	0	2	2
Retreat	**Cathartes vultures**	Cathartes vultures	30	17	47
		Black vulture	1	1	2
		King vulture	0	0	0
	Black vulture	Cathartes vultures	1	0	1
		Black vulture	26	163	189
		King vulture	0	2	2
	King vulture	Cathartes vultures	0	9	9
		Black vulture	5	76	81
		King vulture	0	25	25
Afiliative	**Black vulture**	Black vulture	0	3	3
	King vulture	King vulture	0	1	1

Table S9. Estimated coefficients for the best models evaluating the probability of the different interactions during complete carcass consumption process according to the time of consumption and the abundance of the different species present.

	Estimate	Est. Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Total interactions							
Intercept	1.20	0.20	0.81	1.62	1.00	423	734
PC	-3.33	0.92	-5.14	-1.49	1.00	1477	1525
PC^2	-1.34	0.63	-2.62	-0.09	1.00	1727	1250
PC^3	-3.13	0.66	-4.51	-1.85	1.00	2359	1390
Carcass opening status: closed	-0.54	0.08	-0.70	-0.39	1.00	1633	1183
King vulture abundance	0.21	0.02	0.16	0.26	1.00	1844	1247
American black vulture abundance	0.51	0.03	0.46	0.57	1.00	1648	1522
Proportion of non-aggressive interactions							
Intercept	-1.57	0.23	-2.02	-1.12	1.00	1106	1316
PC	7.48	2.43	2.65	12.22	1.00	1870	2056
PC^2	3.64	1.83	0.00	7.17	1.00	2600	2323
PC^3	6.97	1.80	3.40	10.42	1.00	2520	2064
Carcass opening status: closed	0.47	0.21	0.06	0.88	1.00	2547	2291
King vulture abundance	0.12	0.07	-0.02	0.27	1.00	2127	1838
American black vulture abundance	-0.24	0.09	-0.43	-0.06	1.00	2114	2136
Cathartes vultures abundance	0.34	0.08	0.19	0.50	1.00	2407	2298
Proportion of interespecific non-aggressive interactions							
Intercept	-1.42	0.33	-2.05	-0.76	1.00	700	476
King vulture abundance	0.78	0.14	0.51	1.08	1.00	1877	1331
Proportion of aggressive interactions							
PC	-7.69	2.45	-12.39	-2.87	1.00	2140	2155
PC^2	-3.51	1.84	-7.12	0.00	1.00	2579	2234
PC^3	-6.87	1.83	-10.44	-3.38	1.00	3061	2444
Carcass opening status: closed	-0.47	0.21	-0.89	-0.05	1.00	2484	2164
King vulture abundance	-0.11	0.07	-0.26	0.03	1.00	2417	2089
American black vulture abundance	0.24	0.10	0.05	0.42	1.00	2394	2174
Cathartes vultures abundance	-0.33	0.08	-0.48	-0.18	1.00	2412	2274

Proportion of interespecific aggresive interactions							
Intercept	-1.40	0.37	-2.13	-0.65	1.01	632	963
PC	-4.55	2.22	-8.94	-0.35	1.00	2367	1865
PC^2	-5.85	1.79	-9.44	-2.47	1.00	2232	2020
PC^3	-5.57	1.76	-9.10	-2.16	1.00	2693	2284
American black vulture abundance	-0.28	0.08	-0.43	-0.12	1.00	2580	2044
King vulture abundance	0.71	0.07	0.56	0.86	1.00	2370	1887

APPENDIX S3: Supplementary figures



	Total abundance	Cathartes vultures abundance	American black vulture abundance	King vulture abundance	Total individuals feeding	Cathartes vultures feeding	American black vultures feeding	King vultures feeding
Total abundance	1.00	-0.26	0.97	0.37	0.74	-0.31	0.73	0.35
Cathartes vultures abundance	-0.26	1.00	-0.42	-0.24	-0.29	0.69	-0.41	-0.22
American black vulture abundance	0.97	-0.42	1.00	0.22	0.69	-0.38	0.77	0.21
King vulture abundance	0.37	-0.24	0.22	1.00	0.53	-0.31	0.24	0.96
Total individuals feeding	0.74	-0.29	0.69	0.53	1.00	-0.24	0.90	0.53
Cathartes vultures feeding	-0.31	0.69	-0.38	-0.31	-0.24	1.00	-0.40	-0.30
American black vultures feeding	0.73	-0.41	0.77	0.24	0.90	-0.40	1.00	0.21
King vultures feeding	0.35	-0.22	0.21	0.96	0.53	-0.30	0.21	1.00

Figure S1. Correlation graph showing the value of Pearson's correlation coefficient between the different variables. A high correlation is shown between the abundance of each species present in the carcass and the number of individuals feeding.

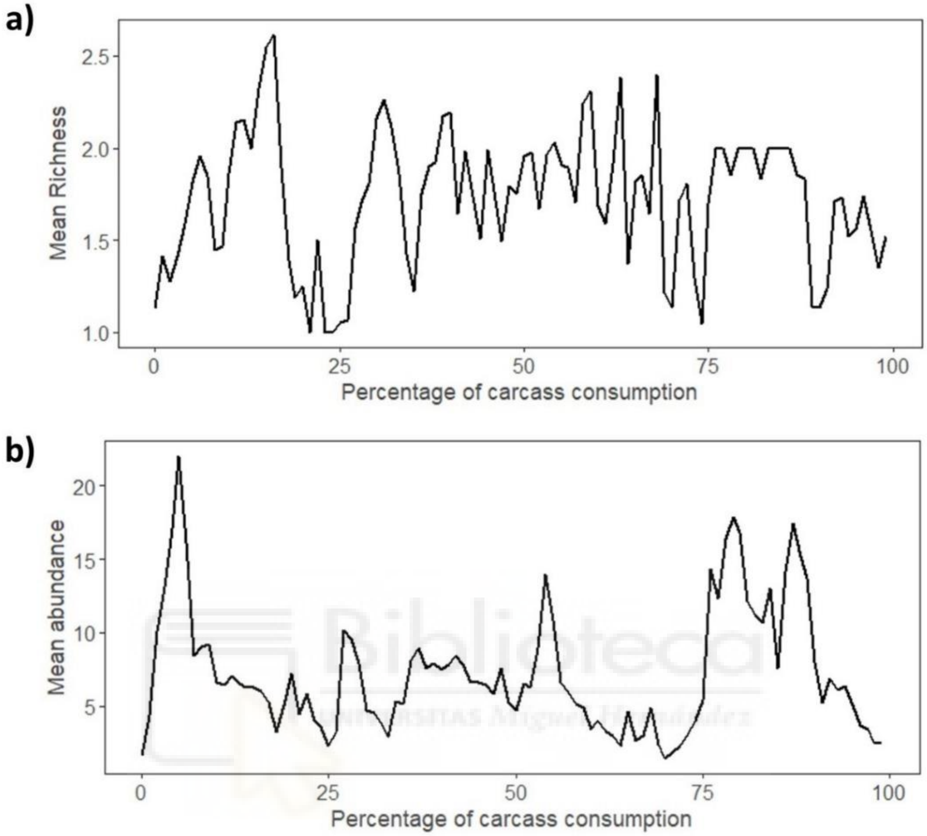


Figure S2. a) Mean richness and b) mean abundance for all carcasses throughout the carcass consumption process (i.e., percentage of carcass consumption).

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