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JOEDISON DOS SANTOS ROCHA

Avaliação da importância de vertebrados e invertebrados carniceiros na dinâmica local e global de remoção de carcaças de vertebrados

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JOEDISON DOS SANTOS ROCHA

Avaliação da importância de vertebrados e invertebrados carniceiros na dinâmica local e global de remoção de carcaças de vertebrados

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Ata Nº **119** da sessão de Defesa de Tese de **Joedison dos Santos Rocha** que confere o título de Doutor em **Ecologia e Evolução**, na área de concentração em **Ecologia e Evolução.**

Ao/s **dezesseis dias do mês de agosto do ano de dois mil e vinte e dois (16/08/2022),** a partir das **14h00min**, por videoconferência, seguindo Resolução CONSUNI/UFG Nº 141 de 13 de maio de 2022 e orientações do Ofício Circular no. 34/2022/PRPG/UFG (SEI 23070.030951/2022-07), realizou-se a sessão pública de Defesa de Tese intitulada **"Avaliação da importância de vertebrados e invertebrados carniceiros na dinâmica local e global de remoção de carcaças de vertebrados".** Os trabalhos foram instalados pelo Orientador, **Prof. Dr. Mário Almeida Neto (DECOL/ICB/UFG)**; com a participação dos demais membros da Banca Examinadora: **Prof. Dr. Welinton Ribamar Lopes (DECOL/ICB/UFG)**, membro titular externo; **Prof. Dr. Marcos Bergmann Carlucci (Botânica/UFPR)**, membro titular externo, **Prof. Dr. Luis Mauricio Bini (DECOL/ICB/UFG)**, membro titular interno, **Prof. Dr. João Carlos Nabout (CCET/UEG),** membro titular interno. Durante a argüição os membros da banca **não fizeram** sugestão de alteração do título do **trabalho**. A Banca Examinadora reuniu-se em sessão secreta a fim de concluir o julgamento da Tese tendo sido o candidato **aprovado** pelos seus membros. Proclamados os resultados pelo **Prof. Dr. Mário Almeida Neto**, Presidente da Banca Examinadora, foram encerrados os trabalhos e, para constar, lavrou-se a presente ata que é assinada pelos Membros da Banca Examinadora, ao(s) **dezesseis dias do mês de agosto do ano de dois mil e vinte e dois (16/08/2022)**.

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Projeto Carniceiros do Cerrado

Realização

Apoio

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ÍNDICE

> “Far from being the end, death marks the start of a series of events that together complete the circle of life […], the **process of decay** [of dead organic matter] recycles the dead and resupplies **the building blocks of life**”
>
> Cyrus Martin
>
> *From death comes life* (2016). Current Biology, p. R548.

RESUMO

Carcaças de vertebrados compõem o *pool* de matéria orgânica morta dos ecossistemas, destacando-se como um recurso alimentar para uma gama de organismos vivos, desde micro-organismos até grandes vertebrados. Uma ilha de decomposição se estabelece quando um vertebrado morre, alterando os aportes de nutrientes e a diversidade de micro-organismos no solo, bem como a composição das comunidades vegetais. Animais carniceiros (invertebrados e vertebrados) são os responsáveis pela reciclagem de nutrientes das carcaças, evitando assim que animais mortos acumulem nos ambientes naturais. Com isso, os carniceiros atuam tanto na distribuição dos nutrientes em larga escala quanto na sanitização e saúde dos ecossistemas. Apesar disso, há várias lacunas sobre como esses grupos de carniceiros afetam a dinâmica de remoção de carcaças e seus efeitos no funcionamento dos ecossistemas. Mesmo informações básicas como quais espécies atuam no processo de remoção são escassas na literatura. A presente tese visou elucidar a importância local e global de vertebrados e invertebrados carniceiros para: a) a eficiência de remoção; b) a ciclagem de nutrientes; e c) o controle de doenças em carcaças de vertebrados, bem como d) interações entre ambos os grupos. Inicialmente, um experimento com carcaças enjauladas e não enjauladas (n=16) foi conduzido em uma área conservada de Cerrado para testar o efeito da perda da atuação dos vertebrados sobre o tempo de remoção e aportes de nutrientes para o solo. Após 10 dias, todas as carcaças foram removidas por urubus e invertebrados, sem diferença entre os tratamentos, sugerindo que invertebrados podem compensar a ausência dos vertebrados. Ainda, o experimento demonstrou que aportes de potássio e magnésio aumentam no solo ao redor de carcaças quando os vertebrados estão ausentes. Além das típicas espécies carniceiras (moscas necrófagas e urubus), carcaças foram largamente visitadas por espécies oportunistas ou facultativas (e.g. vespas, borboletas e mamíferos). A partir de duas revisões sistemáticas globais, observamos que a atividade conjunta de vertebrados e invertebrados assegura uma alta eficiência de remoção, em comparação com carcaças removidas experimentalmente na ausência de vertebrados. Adicionalmente, comunidades de vertebrados que são altamente eficientes em remover carcaças são tipicamente compostas por poucas espécies (<10 spp.) e uma maior proporção de aves. Esse resultado evidenciou a contribuição funcionalmente única provida por urubus e corvos ao redor do mundo. Finalmente, com base em um modelo relacionando vertebrados carniceiros com casos de zoonoses, uma maior prevalência de anthrax foi associada com uma alta diversidade de carniceiros facultativos (e.g. águias e mamíferos carnívoros), mas não com a riqueza de urubus/abutres. Assim, o estudo demonstrou que a diversidade de vertebrados representa um importante fator na eficiência de remoção de carcaças. Contudo, invertebrados podem sobrepor a funções dos vertebrados em certos contextos, como observado no Cerrado. A ação de ambos os grupos afeta as taxas de aportes de nutrientes das carcaças para o solo, enquanto parcialmente afetam a propagação de zoonoses ao redor do mundo.

Palavras-chaves: Cerrado, disposição de carcaças, fauna edáfica, fósforo, serrapilheira, serviços ecossistêmicos, urubus, zoonoses.

ABSTRACT

Vertebrate carcasses compose the pool of dead organic matter in the ecosystems, highlighting as a food resource for a plethora of living organisms, from microorganisms to large vertebrates. A decomposition island is established when a vertebrate dies, altering the nutrient inputs and diversity of microorganisms in the soil, as well as the composition of plant communities. Scavenger animals (invertebrates and vertebrates) are responsible for recycling nutrients from carcasses, thus preventing dead animals from accumulating in natural environments. Therefore, scavengers act both in the large-scale distribution of nutrients and in sanitation and ecosystem health. Despite this, there are several gaps regarding how these scavenger groups affect the dynamics of carcass removal and their effects on ecosystem functioning. Even basic information such as which species are involved in the removal process is scarce in the literature. The present thesis aimed to elucidate the local and global importance of vertebrate and invertebrate scavengers for: a) removal efficiency; b) nutrient cycling; and c) disease control in vertebrate carcasses, as well as d) interactions between both groups. First, an experiment using caged and uncaged carcasses (n=16) was conducted in a well-conserved Cerrado area to test the effect of loss of vertebrate actions on removal time and nutrient inputs to the soil. After 10 days, all carcasses were removed by vultures and invertebrates, without difference between treatments, suggesting that invertebrates can compensate for the absence of vertebrates. Also, the experiment showed that potassium and magnesium inputs increase in the soil around carcasses when vertebrates are absent. Besides the typical scavenger species (necrophagous flies and vultures), carcasses were largely visited by opportunistic or facultative species (e.g. wasps, butterflies, and mammals). From two global systematic reviews, we observed that the complementary activity of vertebrates and invertebrates ensures high removal efficiency compared to carcasses removed experimentally in the absence of vertebrates. Furthermore, vertebrate communities that are highly efficient in removing carcasses are typically composed of few species (<10 spp.) and higher proportion of birds. This result highlighted the functionally unique contribution provided by vultures and crows across the world. Finally, based on a model relating scavenger vertebrates to cases of zoonoses, a higher prevalence of anthrax was associated with a high diversity of facultative scavengers (e.g. eagles and mammalian carnivores), but not with the richness of vultures. Thus, the study demonstrated that vertebrate diversity represents an important factor in carcass removal efficiency. However, invertebrates can outperform vertebrate functions in certain contexts, as observed in the Cerrado. The actions of both groups affect the rates of nutrient inputs from carcasses to the soil, while partially affecting the spread of zoonoses around the world.

Keywords: carcass disposal, Cerrado, ecosystem services, litter, phosphorus, soil fauna, vultures, zoonoses.

INTRODUÇÃO GERAL

Matéria orgânica morta é um importante componente para o funcionamento dos ecossistemas, atuando como uma fonte basal de nutrientes e energia nas teias tróficas (Swift et al., 1979; Benbow et al. 2016). Esse componente está direitamente relacionado com a formação dos solos e a produtividade primária vegetal, o que secundariamente afeta a diversidade de herbívoros e outros consumidores (Swift et al. 1979; Swan & Kominoski 2012). A maior parte da matéria orgânica morta que entra nos ecossistemas é de origem vegetal, i.e. serrapilheira (Benbow et al. 2019), de modo que estudos com interações tróficas nesse subsistema tem sido amplamente conduzidos há mais de meio século (veja Kampichler & Bruckner 2009 para uma revisão). No entanto, outro importante subsistema da decomposição tem sido historicamente negligenciado no contexto de teias tróficas, a matéria orgânica morta de origem animal, i.e. carcaças ou "carniça" (Benbow et al. 2016, 2019). Cientistas recentemente vêm reconhecendo a importância de carcaças de animais mortos para a dinâmica, funcionamento e manutenção de biodiversidade nos ecossistemas (sobretudo os terrestres), fato que consolidou o campo "ecologia de carcaças" (tradução livre do inglês *Carrion Ecology*) nos últimos 20 anos (Benbow et al. 2016).

Um os principais focos da ecologia de carcaças é a influência da remoção de animais vertebrados mortos para o *pool* de nutrientes de uma área (Benbow et al. 2016). A deposição de carcaças, diferente da matéria orgânica vegetal, é espacialmente e temporalmente imprevisível, criando "ilhas de decomposição" efêmeras, as quais estabelecem um distúrbio local por alterar o fluxo de energia e nutrientes de uma área (Carter et al. 2007). A ideia de "ilha" proposta por Carter et al. (2007) leva em consideração que o sítio de deposição tanto apresenta entradas de energia e nutrientes, quanto saídas, uma vez que há a dispersão dos necrófagos pela paisagem (Bump et al. 2009). Nesse contexto, organismos necrófagos podem conectar teias tróficas e atuar na ciclagem e distribuição de nutrientes na paisagem (DeVault et al. 2003; Wilson & Wolkovich 2011).

O processo de ciclagem e distribuição dos nutrientes de uma carcaça de vertebrado é mantido por uma rica comunidade que inclui espécies de diferentes reinos da vida (e.g. Eubacteria, Fungi e Animalia), dirigindo assim um processo de colonização com pressões competitivas inter-reinos (DeVault et al. 2003; Forbes & Carter 2016). A ação preliminar dos micro-organismos, sobretudo bactérias do solo e da carcaça, inicia o processo de putrefação que é seguido pela colonização de artrópodes, com destaque para dois importantes grupos: Diptera (e.g. Calliphoridae e Sarcophagidae) e Coleoptera (e.g. Scarabaeidae) (Forbes & Carter 2016). Esses insetos necrófagos desempenham uma importante função de criar condições para a chegada de vertebrados, bem como alterar a disponibilidade da carcaça (DeVault et al. 2003; Pechal et al. 2014). Os vertebrados surgem tardiamente e compreendem um dos grupos mais bem estudados na ecologia de carcaças (DeVault et al. 2003, 2016; Inger et al. 2016; Peisley et al. 2017; Hill et al. 2018).

Os aportes de nutrientes oriundos de uma carcaça de vertebrados para o solo ultrapassam as taxas naturais do sítio de deposição, criando assim *hotspots* biogeoquímicos (Bump et al. 2009). Assim, esses sítios de carcaças podem funcionar como pontos centrais de dispersão (*hubs*) de nitrogênio e fósforo, por exemplo. Essas alterações no solo podem se estender desde poucos dias até vários anos (Barton et al. 2016; Strickland & Wickinkgs 2016), o que contribui para a heterogeneidade da paisagem. Dado que nitrogênio (N) e fósforo (P) são nutrientes cruciais para o crescimento de plantas nos ecossistemas naturais (Kerkhoff et al. 2006; Jiang et al. 2019), é esperado que a deposição de uma carcaça altera não apenas as características locais do solo (i.e., nutrientes e biota), mas também as comunidades locais de plantas e seus consumidores (Bump et al. 2009; Benbow et al. 2016). De fato, alguns estudos têm reportado mudanças no N foliar ou na biomassa em resposta à presença de um animal em decomposição (Bump et al., 2009; veja Barton et al. 2013 para uma breve revisão).

Dentre os grupos que contribuem para a manutenção do processo de remoção de carcaças, as aves de rapina (e.g. urubus, caracarás, gaviões e corujas) destacam-se pela função de quebrar e distribuir os nutrientes contidos nas carcaças para grandes distâncias (Peisley et al. 2017). Dentre essas aves, os urubus e abutres destacam-se como grupos dominantes no processo de remoção de animais mortos nos ecossistemas ao redor do mundo (Ogada et al. 2011; Ogada et al. 2012; Mateo-Tomás et al. 2017). Essas aves são os únicos vertebrados terrestres com adaptações estritas ao hábito necrófago (veja DeVault et al. 2003 para uma revisão), o que as permitem uma maior e mais rápida capacidade de localização e remoção de animais em decomposição (Ogada et al. 2011; Hill et al. 2018). Por isso, urubus e abutres são considerados os únicos carniceiros obrigatórios nos ambientes terrestres. Na ausência dessas aves, outras espécies facultativas podem não compensar o consumo do recurso, o que pode gerar uma redução da distribuição dos nutrientes e um atraso no processo de decomposição (DeVault et al. 2003; Hill et al. 2018). Um estudo no Quênia mostrou que carcaças não removidas pelos abutres demoram três vezes mais tempo para serem decompostas, enquanto aumentam a incidência de carniceiros facultativos, como hienas e chacais (Ogada et al. 2012). Embora os carniceiros facultativos e vertebrados predadores (e.g. águias, raposas e

leões) também tenham relevância para a dinâmica de remoção de carcaças (Mateo-Tomás et al. 2017), eles são apontados como menos eficientes no processo de remoção (Ogada et al. 2011; Hill et al. 2018). Assim, necrófagos obrigatórios, como os urubus, possuem um papel chave no processo de remoção e decomposição de carcaças. Com isso, a perda desses organismos nos ecossistemas pode declinar a ciclagem de nutrientes de matéria orgânica de origem animal em escala local, mas com efeitos que podem se propagar nas teias tróficas desde os microorganismos do solo até predadores de topo (Moleón & Sánchez-Zapata 2015).

Carcaças de vertebrados apresentam um alto teor de água e nutrientes, dos quais podem ser imediatamente transferidos para o solo e os organismos que as consomem (Carter et al. 2007; Barton et al. 2016). Plantas que crescem nos locais onde carcaças foram removidas podem apresentar uma maior quantidade de N foliar, favorecendo assim o crescimento de espécies tolerantes aos distúrbios causados no solo (Carter et al. 2007; Bump et al. 2009). Isso pode reduzir a riqueza de plantas enquanto aumenta, em longo prazo, a abundância de espécies tolerantes, afetando assim a produção de biomassa vegetal de uma área. Com isso, um impacto nos vertebrados necrófagos, por serem os principais carniceiros, pode causar uma maior concentração de nutrientes *in loco,* aumentando assim o enriquecimento nutricional local e restringindo a distribuição dos nutrientes para distâncias maiores do que o sítio de deposição. Finalmente, essa retenção de nutrientes de carcaças no solo e o efeito sobre a biomassa vegetal pode também afetar a ciclagem de nutrientes da matéria orgânica vegetal por reduzir a atividade dos microorganismos do solo (Li et al. 2015).

Embora as carcaças de vertebrados sejam de fato uma rica fonte de nutrientes e energia com benefícios para os consumidores e para a integridade dos ecossistemas, essas ilhas de decomposição podem também funcionar como focos de doenças (Borchering et al. 2017; Escobar et al. 2020). Dessa forma, outro importante serviço ecossistêmico provido por animais carniceiros (invertebrados e vertebrados) é a contribuição no controle de doenças que possuem animais como vetores, reservatórios ou hospedeiros, i.e. zoonoses (Ogada et al. 2011; O'Bryan et al. 2018). No entanto, assim como o processo de ciclagem de nutrientes, essa relação ainda é complexa, controversa e pouco compreendida, de modo que há tanto evidências positivas em favor da importância dos carniceiros, quanto negativas. Por exemplo, um experimento em lagos utilizando girinos de salamandra como carcaça experimental mostrou que a comunidade de insetos necrófagos reduziu em mais de 44% a prevalência de infecções do *Ranavirus* (Sage et al. 2019). Estudos semelhantes com foco em vertebrados necrófagos são escassos. Por exemplo, um experimento de exclusão de carniceiros em carcaças de zebras na Namíbia não observou influência da ação dos necrófagos vertebrados sobre a prevalência de anthrax nos sítios de decomposição (Bellan et al. 2013). Por outro lado, o declínio de espécies de urubus na Índia é correlacionado com um aumento nos casos de peste bubônica e raiva devido à maior permanência de carcaças em campo, atraindo assim ratos e cães ferais (Prakash et al. 2003; Markandya et al. 2008). Ainda, há um consenso que organismos mais especializados no consumo de carcaças, tal como os urubus, são fortemente resistentes a doenças devido, principalmente, ao baixo

pH estomacal e ao sistema imunológico adaptado (Blumstein et al. 2017). Dado que urubus são dominantes no processo de remoção e assim conseguem excluir ou reduzir competivamente a presença de carniceiros facultativos (Ogada et al. 2011; Mateo-Tomás et al. 2017), isso pode contribuir com o controle de doenças que surgem em animais silvestres ou domésticos e que potencialmente podem vir a infectar seres humanos. Por exemplo, um estudo nos EUA detectou a presença de cães, gatos e vacas em carcaças de cervídeos, o que pode potencialmente expor humanos a encefalopatia espongiforme ("doença da vaca louca"; Jennelle et al. 2009). Dessa forma, com a conservação da comunidade de necrófagos e decompositores, a contribuição no controle de zoonoses pode emergir como um efeito secundário da manutenção da ciclagem de nutrientes das carcaças, sobretudo em áreas mais pobres e rurais, onde potencialmente há menos investimentos em infraestrutra sanitária (Gangoso et al. 2013).

Os serviços ecossistêmicos providos pelos grandes carniceiros são mantidos tanto por espécies comuns quanto raras e ameaçadas de extinção (Mateo-Tomás et al. 2017). Os abutres do velho mundo, por exemplo, são fortemente impactados por intoxicação com drogas veterinárias e/ou chumbo em carcaças (Ogada et al. 2011). Nas Américas, embora a maioria das espécies de urubus não está em categorias de ameaças, a alta especialização e eficiência nos processos de remoção em áreas agrícolas, estradas, ambientes urbanos e naturais justificam sua conservação. A manutenção da estrutura das comunidades de necrófagos obrigatórios pode reduzir a incidência de doenças em seres humanos e contribuir para tornar os ambientes naturais e urbanos mais limpos. De fato, os urubus americanos prestam um valoroso serviço para nós seres humanos ao remover toneladas de matéria orgânica por ano. Um estudo pioneiro com o urubu-de-cabeça-vermelha (*Cathartes aura*) estimou que apenas essa espécie consegue remover 1000 toneladas de matéria orgânica por ano, um serviço que custaria mais de 500 mil dólares se fosse feito por humanos (Grilli et al. 2019).

A compreensão do papel de organismos necrófagos na manutenção de funções ecossistêmicas é necessária para gerar informações a favor da sua conservação e manejo, dado que elas não possuem apelo para conservação devido à natural aversão das pessoas por algo relacionado à decomposição (DeVault et al. 2003). Com isso, potenciais ameaças às comunidades de carniceiros são pouco conhecidas, sobretudo nas Américas. De fato, manter espécies comuns, como os urubus americanos, a salvo de ameaças de extinção é mais vantajoso e barato do que tentar recuperá-las de uma extinção eminente (Redford et al. 2013). Com isso, a presente tese visou analisar e medir os papeis desempenhados por carniceiros vertebrados e invertebrados em diferentes facetas do processo de remoção de carcaças de vertebrados, desde o padrão de colonização de carcaças em áreas de Cerrado, abarcando interações entre grupos de carniceiros e uma modelagem focada no controle de zoonoses em escala global.

LITERATURA CITADA

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B. & Manning, A.D. (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia*, **171**, 761–772.

Barton, P.S., McIntyre, S., Evans, M.J., Bump, J.K., Cunningham, S.A. & Manning, A.D. (2016) Substantial long-Term effects of carcass addition on soil and plants in a grassy eucalypt woodland. *Ecosphere*, **7**, 1–11.

Bellan, S.E., Turnbull, P.C.B., Beyer, W. & Getz, W.M. (2013) Effects of Experimental Exclusion of Scavengers from Carcasses of Anthrax-Infected Herbivores on Bacillus anthracis Sporulation, Survival, and Distribution. *Applied and Environmental Microbiology*, **79**, 3756–3761.

Benbow, M.E., Barton, P.S., Ulyshen, M.D., Beasley, J.C., DeVault, T.L., Strickland, M.S., Tomberlin, J.K., Jordan, H.R. & Pechal, J.L. (2019) Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, **89**, e01331.

Benbow, M.E., Tomberlin, J.K. & Tarone, A.M. (2016) Introduction to Carrion Ecology, Evolution, and Their Applications. In: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M (eds). *Carrion Ecology, Evolution, and their Applications*. CRC Press, Taylor & Francis Group, Boca Raton, USA, p.13-30.

Blumstein, D.T., Rangchi, T.N., Briggs, T., De Andrade, F.S. & Natterson-Horowitz, B. (2017) A Systematic Review of Carrion Eaters' Adaptations to Avoid Sickness. *Journal of Wildlife Diseases*, **53**, 577–581.

Borchering, R.K., Bellan, S.E., Flynn, J.M., Pulliam, J.R.C. & McKinley, S.A. (2017) Resource-driven encounters among consumers and implications for the spread of infectious disease. *J. R. Soc. Interface*, **14**, 20170555.

Bump, J.K., Webster, C.R., Vucetich, J.A., Peterson, R.O., Shields, J.M. & Powers, M.D. (2009) Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. *Ecosystems*, **12**, 996–1007.

Carter, D.O., Yellowlees, D. & Tibbett, M. (2007) Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften*, **94**, 12–24.

DeVault, T.L., Beasley, J.C., Olson, Z.H., Moleón, M., Carrete, M., Margalida, A. & Sánchez-zapata, J.A. (2016) Ecosystem Services Provided by Avian Scavengers. *Why Birds Matter: Avian Ecological Function and Ecosystem Services* (eds C.H. Şekercioğlu, D.G. Wenny, & C.. Whelan), pp. 235–270. Chicago, USA.

DeVault, T.L., Rhodes Jr, O.E., Shivik, J.A., Rhodes, O.E., Shivik DeVault, J.A., DeVault, T.L. & Rhodes, O.E.

(2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos*, **102**, 225–234.

Escobar, L.E., Pritzkow, S., Winter, S.N., Grear, D.A., Kirchgessner, M.S., Dominguez-Villegas, E., Machado, G., Peterson, A.T. & Soto, C. 2020. The ecology of chronic wasting disease in wildlife. *Biological Reviews*, 95, 393-408.

Forbes, S.L. & Carter, D.O. (2016) Processes and Mechanisms of Death and Decomposition of Vertebrate Carrion. *In*: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M (eds). *Carrion Ecology, Evolution, and their Applications*. CRC Press, Taylor & Francis Group, Boca Raton, USA, p.13-30.

Gangoso, L., Agudo, R., Anadón, J.D., Riva, M. de la, Suleyman, A.S., Porter, R. & Donázar, J.A. (2013) Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. *Conservation Letters*, **6**, 172–179

Grilli, M. G., Bildstein, K.L., Lambertucci, S.A. (2019) Nature's clean-up crew: Quantifying ecosystem services offered by a migratory avian scavenger on a continental scale. *Ecosystem Services*, **39**, 100990.

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E. & Belant, J.L. (2018) Effects of vulture exclusion on carrion consumption by facultative scavengers. *Ecology and Evolution*, **8**, 2518–2526.

Inger, R., Per, E., Cox, D.T.C. & Gaston, K.J. (2016) Key role in ecosystem functioning of scavengers reliant on a single common species. *Scientific Reports*, **6**, 2–6.

Jennelle, C.S., Samuel, M.D., Nolden, C.A. & Berkley, E.A. (2009) Deer Carcass Decomposition and Potential Scavenger Exposure to Chronic Wasting Disease. *Journal of Wildlife Management*, **73**, 655–662.

Jiang, J., Wang, Y-P., Yang, Y., Yu, M., Wang, C. & Yan, J. (2019) Interactive effects of nitrogen and phosphorus additions on plant growth vary with ecosystem type. *Plant Soil*, **440**, 523–537.

Kampichler, C. & Bruckner, A. (2009) The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews*, **84**, 375–389.

Kerkhoff, A.J., Fagan, W.F., Elser, J.J. & Enquist, B.J. (2006) Phylogenetic and Growth Form Variation in the Scaling of Nitrogen and Phosphorus in the Seed Plants. *The American Naturalist*, **168**, E103–E122.

Li, H-C., Hu, Y-L., Mao, R., Zhao, Q. & Zeng, D-H. (2015) Effects of Nitrogen Addition on Litter Decomposition and CO2 Release: Considering Changes in Litter Quantity. *PloS One*, **10**, e0144665.

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S. & Dhavala, K. (2008) Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. *Ecological Economics*, **67**, 194–204.

Mateo-Tomás, P., Olea, P.P., Moleón, M., Selva, N. & Sánchez-Zapata, J.A. (2017) Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography*, **26**, 1459–1470.

Moleón, M. & Sánchez-Zapata, J.A. (2015). The living dead: time to integrate scavenging into ecological teaching. *BioScience*, **65**, 1003–1010.

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M. & McDonald-Madden, E. (2018) The contribution of predators and scavengers to human well-being. *Nature Ecology and Evolution*, **2**, 229–236.

Ogada, D.L., Keesing, F. & Virani, M.Z. (2012) Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences*, **1249**, 57–71.

Ogada, D.L., Torchin, M.E., Kinnaird, M.F. & Ezenwa, V.O. (2011) Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. *Conserv. Biol.*, **26**, 453–460.

Pechal, J.L., Benbow, M.E., Crippen, T.L., Tarone, A.M. & Tomberlin, J.K. (2014) Delayed insect access alters carrion decomposition and necrophagous insect community assembly. *Ecosphere*, **5**, 1–21.

Peisley, R.K., Saunders, M.E., Robinson, W.A. & Luck, G.W. (2017) The role of avian scavengers in the breakdown of carcasses in pastoral landscapes. *Emu*, **117**, 68–77.

Prakash, V., Pain, D.J., Cunningham, A.A., Donald, P.F., Prakash, N., Verma, A., Gargi, R., Sivakumar, S. & Rahmani, A.R. (2003) Catastrophic collapse of Indian White-backed *Gyps bengalensis* and Long-billed *Gyps indicus* vulture populations. *Biological Conservation*, **109**, 381–390.

Redford, K.H., Berger, J. & Zack, S. (2013) Abundance as a conservation value. *Oryx*, **47**, 157–158.

Sage, M.J.L., Towey, B.D. & Brunner, J.L. (2019) Do scavengers prevent or promote disease transmission? The effect of invertebrate scavenging on Ranavirus transmission. *Functional Ecology*, **33**, 1342-1350.

Strickland, M.S. & Wickings, K. 2016. Carrion Effects on Belowground Communities and Consequences for Soil

Processes. *In*: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M (eds). *Carrion Ecology, Evolution, and their Applications*. CRC Press, Taylor & Francis Group, Boca Raton, USA, p.93-105.

Swan, C.M. & Kominoski, J.S. (2012) Biodiversity and Ecosystem Function of Decomposition. eLS, John Wiley & Sons, Ltd: Chichester.

Swift,. M.J., Heal, O.W. & Anderson, J.M. (1979) Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Wilson, E.E. & Wolkovich, E.M. (2011) Scavenging: How carnivores and carrion structure communities. *Trends in Ecology and Evolution*, **26**, 129–135.

OBJETIVOS

Geral

- Determinar os efeitos de diferentes grupos de animais carniceiros sobre a manutenção de suas principais funções ecossistêmicas no Cerrado e em escala global: remoção de carcaças, ciclagem de nutrientes de carcaças, decomposição de serrapilheira e controle de zoonoses.

Específicos

- Descrever a composição temporal da comunidade de vertebrados necrófagos visitantes das carcaças (Capítulo I);
- Verificar o efeito da ausência dos vertebrados sobre o tempo de remoção das carcaças (Capítulo I);
- Comparar os efeitos da ausência e presença de vertebrados sobre as concentrações locais de nutrientes no solo sob as carcaças de vertebrados, bem como ao redor delas (Capítulo I);
- Avaliar os efeitos da decomposição das carcaças sobre a decomposição de serrapilheira no Cerrado (Capítulo I);
- Descrever os principais grupos de insetos e seus diferentes usos de carcaças de vertebrados no Cerrado (Capítulo II);
- Testar como as interações entre invertebrados e vertebrados carniceiros afetam o processo de remoção de carcaças globalmente (Capítulo III);
- Descrever a composição de comunidades de vertebrados carniceiros ao redor do mundo (Capítulo IV);
- Testar se vertebrados necrófagos estão associados com casos de zoonoses globais (Capítulo V);

ORGANIZAÇÃO DA TESE

A presente tese está organizada em cinco capítulos, sendo que **capítulo I** trata dos achados gerais de um experimento conduzido no Parque Nacional das Emas no estado de Goiás em fevereiro de 2020, incluindo uma análise do tempo de remoção das carcaças, aporte de nutrientes para o solo e decomposição de serrapilhera, comparando carcaças removidas com e sem a participação de vertebrados necrófagos. O **capítulo II** consiste de uma nota curta (*short communication*) sob re os padrões de visitação de grupos de insetos nas carcaças do mesmo experimento. O **capítulo III** traz uma revisão sistemática em escala global focada em avaliar o efeito da interação entre invertebrados e vertebrados no processo de remoção de carcaças. O **capítulo IV** descreve uma lista global de vertebrados necrófagos, bem como padrões de riqueza desses animais ao redor do mundo. Por fim, o **capítulo V** consiste de uma modelagem em escala global para inferir sobre a importância de carniceiros no controle de zoonoses, utilizando a doença de anthrax como modelo.

CAPÍTULO I

Consequences of the loss of large scavengers for carrion removal, soil nutrients and litter decomposition in Brazilian savannas

> "Besides the '*green world*' composed of living organisms, another outstanding '*brown world*' exists which consists of dead organic matter"
>
> P.P. Olea et al. (2019) - Carrion Ecology and Management, p. 1.

ABSTRACT

Vertebrate carcasses create an important pool of nutrients that directly provides resources for both necrophagous and decomposer organisms, including insects (mainly flies and beetles) and large vertebrates (mainly vultures). The latter plays an important role in the carrion removal process, given that they can find carcasses quickly and speed up their removal. The ongoing decline of scavenger populations may delay the carcass removal process, potentially affecting soil nutrient inputs. Here, we tested whether the absence of large vertebrate scavengers can increase: i) the carrion removal time, ii) nutrient inputs in the soil, and iii) whether these changes in the soil decrease litter decomposition in a Cerrado grassland, Brazil. We used caged carcasses to simulate the absence of vertebrate scavengers on carcasses, compared to uncaged controls. After the full removal process, we collected soil samples and placed tea bags (litter model) in the soil. All carcasses were removed after 10 days. We recorded only two vulture species, which fed on 50% of the control carcasses. The absence of vertebrates did not increase the carcass removal time on average. However, we observed higher potassium and magnesium contents in the exclusion treatment compared to the control and areas around all carcasses (>40 cm). Litter decomposition was also not affected by treatments, including in areas around the carcasses. Taken together, these findings suggest that, in well-preserved communities in the Brazilian Cerrado, the ecological function of carcass removal by vertebrates can be, at least partially, compensated by invertebrate scavengers.

Keywords: carrion ecology, Cerrado, ecosystem function, necrophagous, soil nutrient, tea bag, vulture.

INTRODUCTION

Vertebrate carcasses are an unpredictable resource of high nutritional quality, but poorly understood in trophic networks (Wilson & Wolkovich 2011). Scientists have recognized the value of dead animals (mainly vertebrates) for the dynamics, functioning, and maintenance of biodiversity in ecosystems (Benbow et al. 2016). A key aim of this novel field is to evaluate the influence of dead vertebrate animals on the nutrient pool of an area (Benbow et al. 2016). The deposition of these carcasses in the ecosystems creates a concentrated pool of nutrients that support a complex and diverse community of consumers and decomposers, i.e. soil microorganisms, arthropods, and

vertebrates (Carter et al. 2007). High nutrient input and the interactions among different taxa in carcass sites create a local disturbance, which changes soil communities, fauna, plant diversity, and the flow of energy and nutrients that contribute to landscape heterogeneity (Carter et al. 2007; Bump et al. 2009a, b; Barton et al. 2016).

Carcasses create local biogeochemical hotspots by inputting nutrients at rates higher than observed at the deposition site (Bump et al. 2009b). Thus, carcass sites can act as hubs of carbon and other nutrients (such as nitrogen), so impacts can propagate across the landscape through the movement of necrophagous organisms with greater mobility (e.g. vultures and beetles; Carter et al. 2007). Decomposing microbes (i.e. bacteria and fungi) and insects with low mobility act primarily on local inputs, while scavenger vertebrates (mainly vultures and other raptors) play a complementary role in breaking down and distributing the nutrients contained in the carcasses over long distances (Peisley et al. 2017; Barton et al. 2019). Among these birds, vultures are considered a dominant group (Ogada et al. 2012; Mateo-Tomás et al. 2017). These birds are the only terrestrial vertebrates with strict adaptations to the scavenger habit (DeVault et al. 2003), which allows a greater and faster localization and removal of the carcasses (Ogada et al. 2012; Hill et al. 2018). In the absence of these large scavengers, other facultative species may not compensate for the resource consumption, which may lead to reduced nutrient distribution and a delay in the decomposition process (DeVault et al. 2003; Hill et al. 2018). For instance, carcasses not consumed by vultures can take almost three times more to be removed (Ogada et al. 2011). Other facultative species also have relevant contributions to the dynamics of carcass removal, such as foxes and lions (Mateo-Tomás et al. 2017), even though they are less efficient. Despite these findings in African savannas, the scavenger community in Brazilian savannas (Cerrado) is poorly known (but see Demo et al. 2013), as well as their function in the carrion decomposition process. Indeed, the decline of scavengers may disrupt trophic interactions and ecosystem functions such as nutrient cycling at different spatial scales.

Vultures and other facultative large-bodied scavengers are often pointed out as the main carrion-eaters, which can consume most of the available carcass biomass (Olson et al. 2012; Mateo-Tomás et al. 2017; Benbow et al. 2019). Thus, scavenging by large vertebrates can likely control the local nutrient discharges by avoiding a massive input at the carcass site, which may reduce nutrient inputs to the soil. This may be beneficial to the

belowground community, which acts in litter decomposition. For instance, increases of N in the soil are often associated with reduced rates of litter decomposition (Hawlena et al. 2012; van Diepen et al. 2015; Chen et al. 2019). High influxes of carcass-derived organic matter into the soil, such as proteins, may decrease the activity of the belowground community on litter (Hawlena et al. 2012). However, the relationship between nutrient inputs from vertebrate carcasses and litter is poorly known, therefore, an open avenue in ecological research (Strickland & Wickinkgs 2016).

Many studies worldwide have shown that vertebrate scavenger populations are declining, such as in Africa and Europe (Ogada et al. 2012; Ogada et al. 2015). Habitat degradation, hunting, use of veterinary drugs (e.g. diclofenac), power lines, and policies of mechanized carcass removal are the main threats to vertebrate scavengers (Ogada et al. 2015; Arrondo et al. 2018). However, threats to the American scavengers are poorly known, which may underestimate the true state and importance of the conservation of these species in Brazil. Carrion-eaters do not have much conservation appeal from the general audience in comparison to other birds and mammals. However, these species may provide unique functional contributions that affect not only other scavengers, but also plants, soil fauna, insectivorous birds, and parasitoid insects (Barton et al. 2013; Moreno-Opo & Margalida 2013).

Here, we aimed to evaluate the effects of large scavenger losses on the vertebrate carcass removal process, including their consequences for the soil nutrient contents and litter decomposition. Specifically, we addressed the following questions: (i) does the absence of vertebrate scavengers on carcasses increase removal time? (ii) Can this absence of vertebrate scavengers lead to higher concentrations of soil nutrients (e.g. N, P, and K)? (iii) Given that vertebrate scavengers can scatter some carcass parts around the initial deposition site (e.g. > 1 m from the perimeter of large carcasses, i.e. >50 kg; Melis et al. 2007; Bump et al. 2009b), can these scattering events increase the inputs of nutrient in the soil beyond the carcass? (iv) Can the absence of vertebrate scavengers on carcasses promote a delay in litter decomposition in the soil due to a likely overconcentration of nutrients? Given that vertebrate scavengers can breakdown the carcasses and feed on most of the available biomass (DeVault et al. 2003; Peisley et al. 2017), we expected that local overconcentration of nutrients would be avoided in the control while contributing to a better distribution of them across the landscape and a faster removal time.

METHODS

Study area

The study was carried out in a native grassland area in the Emas National Park (17°56'40.0"S 52°59'17.4"W), Goiás state, Brazil. The study area is located in southwestern Goiás and harbors 132,787 ha of different types of grasslands and woodlands in the Cerrado biome (Figure 1). The annual mean temperature reaches 24º C between June and August (dry season) and ranges between 17 and 18º C during the rainy season (January to March). The mean annual rainfall ranges from 10 (June) to 453 mm (February) throughout the year (MMA-IBAMA & CEBRAC 2004). The park shows several types of soil (e.g. latosols, podzolic, litholic, and sandy ones), but the whole experiment was conducted in an area of red latosol, the most common soil type of the park (IBGE 2021). Our study was carried out in February-March 2020, during the rainy season of the Cerrado. During our study, the daily temperature ranged from 21º to 32º C, while relative humidity ranged from 54 to 93% (Figure 2).

Figure 1 – Study area in Emas National Park, Goiás, Brazil. The third photo (from left to right) shows a cage used in the experiment. Photos: Joedison Rocha.

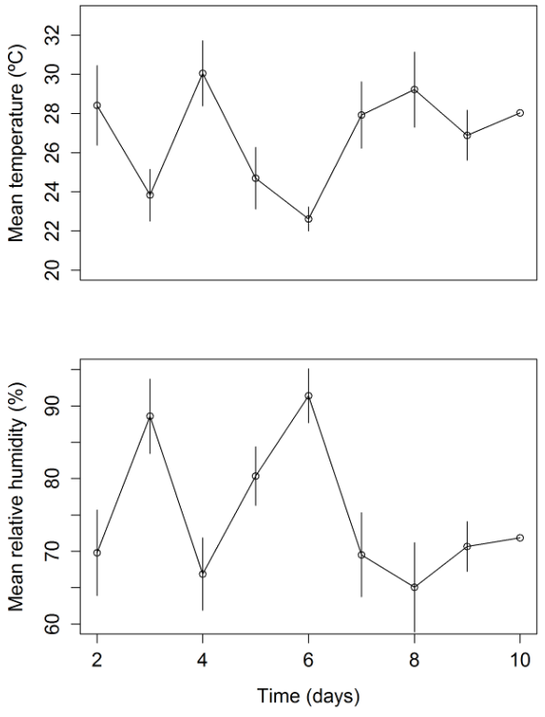

Figure 2 – Daily mean temperature and relative humidity (±SD) measured during fieldwork.

Experimental carcasses and design

We used 16 carcasses of two common species of the Cerrado (Giant anteater, *Myrmecophaga tridactyla*, n=10, and Southern Tamandua, *Tamandua tetradactyla*, n=6, ranging from 0.90 to 24.5 kg) acquired by authorized donations of an animal rehabilitation center and scientific collections of the Federal University of Goiás, as well as an individual collected in a road. All carcasses were frozen from the collection date to the start of the experiment.

The experimental design consisted of eight experimental blocks separated by a minimum of 300 m. We used blocks to control any bias from soil and vegetation heterogeneity. Each block received two carcasses (10 m apart) of the same anteater species with biomasses as close as possible. We placed a metal cage assembled by a chicken wire mesh (2 m long, 1.5 m wide, and 1 m tall) over one of the carcasses in each block to avoid carcass consumption by large vertebrate scavengers (exclusion treatment; Figure 3). The control consisted of another paired carcass of the block without a cage. In this case, we fixed the control carcass to the ground using stakes and wire to prevent that large animal from removing it from the sampling site.

Large scavenger community and carcass removal monitoring

At each control carcass, we placed a motion-trigged infrared camera (Bushnell Trophy HD Cam Essential E3) to a stake ~2 m from carcasses and about one meter high throughout the day and night for 10 days. We set up the cameras to record 20-s videos when activated with a time lag of one minute between activations. Furthermore, we visited each experimental block once a day (after 16 h, n=9 days, and after 7 h, n=1) to monitor the removal

process. We visited the blocks mainly in the late afternoon to avoid interfering with the avian scavenger behaviors, given that raptors are most active between late morning and early afternoon. Thus, we recorded the decomposition phase of carcasses (fresh, bloated, active decay, advanced decay, and dry; Payne 1965; Carter et al. 2007), presence of insect taxa, removal pattern (e.g. disarticulation, tissue scattering, and consumed parts), temperature, and relative humidity. When a carcass reached the dry phase, i.e., only bones, skin, cartilage, and some other hard tissues remain; we considered the carcass as removed. Four carcasses were fully buried by dung beetles, making it difficult to assess the decomposition stage. Thus, we considered that these carcasses were removed on the second day after burial, given that we dug two buried carcasses after three days and found only a few bones.

Soil sampling and analysis

We firstly determined and marked the limits of the direct core area covered by each carcass (ACC), i.e. an elliptical area immediately below the carcass, which varies according to the dimensions of each experimental carcass deposited on the ground on its side (see Figure 4). The area under the paws and tail was not considered in the ACC determination. Based on the ACC, where it is expected that there will be a greater disturbance to the soil via carcass inputs, we also selected another two radial areas around each carcass (i.e. 40 and 120 cm from the ACC) to evaluate a likely scattering of carcass nutrients due to the activity of large scavengers. The ACC was also considered as the "*radius 0*". After the total removal of all deployed carcasses, we took 2-3 small soil cores (~5 cm in diameter to a depth of 10 cm) using an auger in each radius area (Figure 4). All core samples were pooled on site. Finally, our samples were air-dried for at least a week before analysis in a laboratory specialized in soil fertility. In addition to the control and exclusion treatments, we initially considered a "no carcass" treatment, i.e., a natural area without the presence of carcasses paired 10 m away from each carcass in each block, to control natural soil conditions in the absence of any carcass. However, we did not consider this treatment because our observations during fieldwork showed that the scattering of carcass parts barely reached >40 cm from the carcasses (ACC). The radial distance of 120 cm used in both treatments acts as a "no carcass" area, especially for most of our small carcasses (i.e. <10 kg).

Figure 3 – Cage used to exclude large scavengers on our experimental carcasses in Emas National Park., Goiás, Brazil. On the bottom face, there is no mesh, which allows the carcass to be in full contact with the ground. Red circles highlight the position of bars to hold the cage to the ground (~13 cm). On the right we show a scheme of our experimental design, highlighting the random position of treatments in the blocks. Blocks were at a distance of 100 m from the transect and control had carcasses without cages.

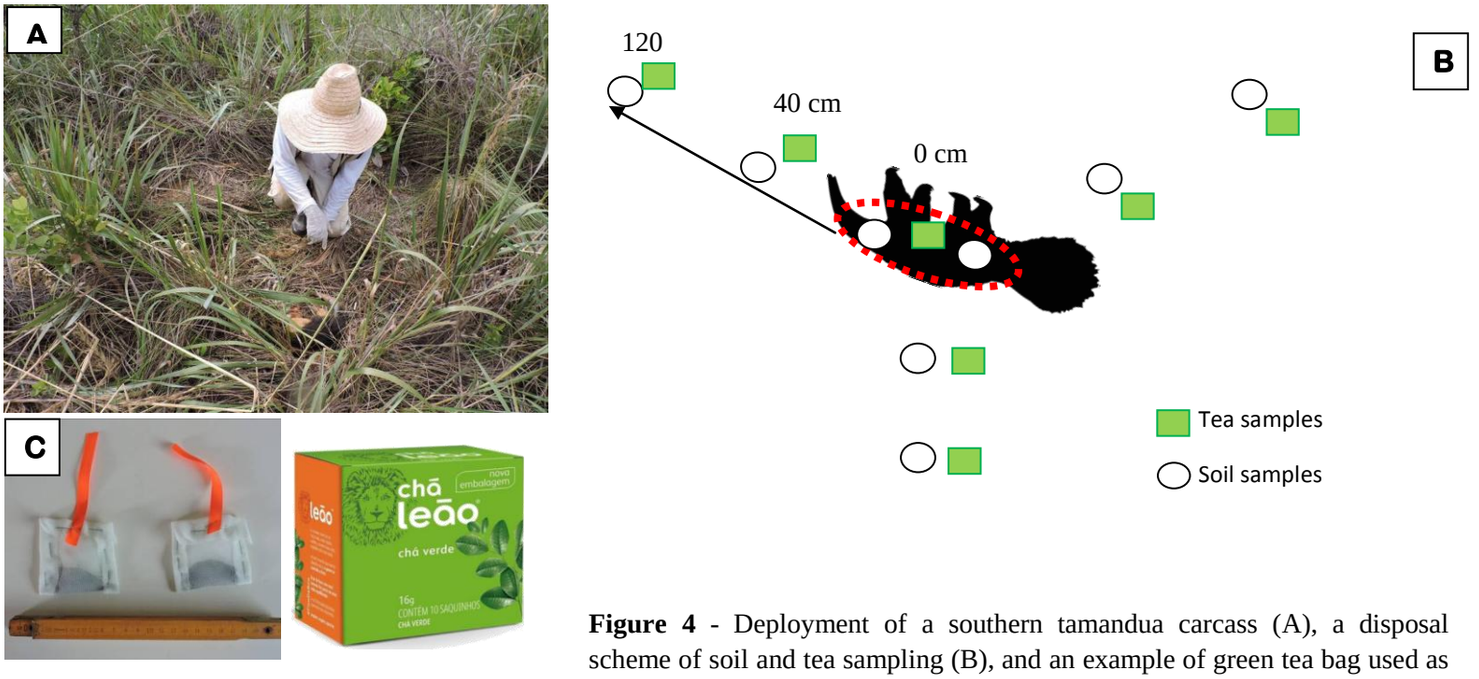

Figure 4 - Deployment of a southern tamandua carcass (A), a disposal scheme of soil and tea sampling (B), and an example of green tea bag used as litter model (C).

Methods used to measure all soil variables for each radius followed the "Manual of Soil Methods of Soil Analysis" published by the Brazilian Agricultural Research Corporation (EMBRAPA; Teixeira et al. 2017). Thus, total nitrogen (N%) was determined based on the Kjeldahl digestion method, which consists of mineralization of the N present in the organic matter of the soil until the formation of ammonium (NH_4^+) by oxidation using sulfuric acid at high temperature. The determination of available phosphorus (P, in mg/dm³) and exchangeable potassium (K^+, mg/dm^3) used an extraction method by Mehlich-1 solution (HCl 0.05 mol/L and H_2SO_4 0.0125 mol/L) and spectrophotometry, while organic matter content (in g/kg) consisted in the difference between the dried mass of the sample and its respective residual mass after incineration in a muffle furnace. Exchangeable magnesium (Mg^{2+}, $cmol_c/dm^3$) and calcium (Ca^{2+}, $cmol_c/dm^3$) were extracted using a solution of KCl 1 mol/L and determined by complexometric titrations.

Litter decomposition

To measure the impact of carcasses and large scavenger losses on litter decomposition, we used dried green tea as a model for plant-derived organic matter. All tea samples were from the same brand (Leão® 16 g, pack of 10 bags) and acquired in a local market. Due to the fragility of the original tea bags, we replaced them with bags made from polyester fabric and staples (~8x8 cm; Figure 4), which allows interactions with bacteria, fungi, and some microfauna species without decomposing the bag. Also, we tied a visible strap in each bag to facilitate the location and collection of the bag after the experiment. To measure the initial biomass, we previously dried 20 tea bags (~15% of the total) in a drying oven at 70º C for 48 h. Thus, we considered the initial tea biomass as 1.654 g (± 0.151 SD).

We placed two tea bags within three radial distances from the area covered by carcasses (n=96) in both treatments: 0 (i.e. ACC), 40, and 120 cm. After soil collections, tea bags were superficially deployed in the ground (~5 cm deep) to be collected seven days later. Recovered samples were preliminarily air-dried for at least four sunny days and then in an oven at 70º C for 48 h after removing the soil outside the bag. Finally, the mean loss between bags in each radius was obtained by subtracting from the initial estimated biomass.

Data analyses

We tested the effect of the removal of large scavengers on the mean removal time using a linear mixed effect model fitted by restricted log-likelihood with experimental blocks as a random effect (i.e. only intercepts) and treatments (control and exclusion) plus carcass biomasses as explanatory variables. The normality and homogeneity of residuals were checked by graphical inspection. We used a simple Kaplan-Meier survival analysis to describe the observed removal time by days (R package survival; Therneau & Lumey 2019). Given that carcass burial by dung beetles generated a new and unexpected source of variance in our experiment (two carcasses in both treatments), we explored this beetle effect by comparing carcasses removed by them, insects in general, and vultures, as *a posteriori* analysis. Also, we used a linear mixed effect model as described above, i.e. the type of removal plus carcass biomass as explanatory variables.

To compare mean soil nutrient contents (N, P, K, organic matter content, Mg, and Ca) between treatments at the ACC (*radius 0*) and across the other radii, we also used linear mixed effect models fitted by restricted log-likelihood (LME) with experimental block as a random effect for each selected soil response variable (random intercepts). To test the direct effect of large scavenger exclusion on carcasses, we firstly fitted a set of models using the treatments as predictors for each response variable (nutrient contents) considered only the ACC. After this, another set of models for each soil variable was fitted to test a likely effect of nutrient scattering around the carcasses between carcass treatments, i.e. treatments (control and exclusion) and the radii (categorical variable with three levels: 0, 40, and 120 cm from the ACC) were used as an interaction term in the models. We also added the carcass biomass in all soil models to control its likely effect on nutrient inputs. A similar set of models was used to compare the mean tea biomass loss between treatments and radii for carcass treatments, i.e. a model based only on the ACC and another one to test the effect of nutrient scattering on tea biomass loss. To improve the normality and homogeneity of residuals, which were checked by graphical inspection, some response variables were log-transformed in all soil and tea models (arcsine square root transformation was used for N). All models

and figures were obtained using the package nlme (version 3.1-140; Pinheiro et al. 2019) and ggplot2 (version 3.3.5; Wickham 2016) in the R environment (R Core Team 2015).

RESULTS

Carcass removal time

All carcasses were removed after 10 days (Figure 5). Control samples were removed in nine days, totaling a mean removal time of 170.26 h (±33.71 SD), while exclusion ones took 194.26 h (±45.58) in 10 days. We did not observe difference of carcass removal time between treatments ($t_{df=6}$ =1.073, SE= 17.653, p=0.324). Also, carcass biomasses had no significant effect on the removal time ($t_{df=6}$=2.308, SE=9.591, p=0.060; Figure 6).

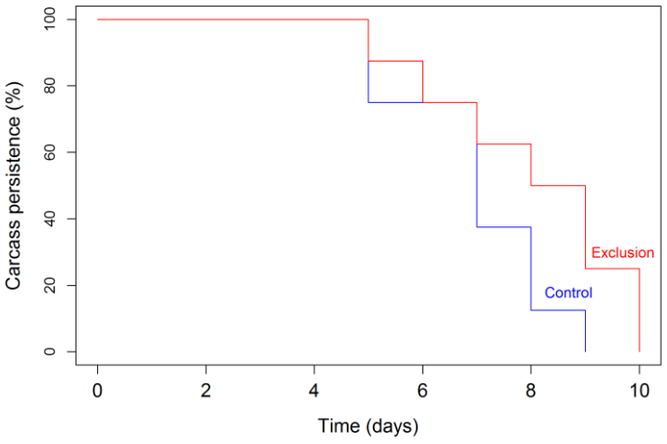

Figure 5 – Simple Kaplan-Meier survival analysis describing the carcass persistence (% of carcasses not completely removed, before the dry phase) throughout the experiment in Emas National Park, Brazil (2020). The lines represent the raw data of this experiment.

We recorded two large scavenger species feeding on 50% of available carcasses (control), Turkey Vulture (*Cathartes aura*) and Lesser Yellow-headed Vulture (*Cathartes burrovianus*). Also, two mammal species visited the carcass sites, a Maned Wolf (*Chrysocyon brachyurus*) and a Six-banded Armadillo (*Euphractus sexcinctus*), but they did not feed on the carcasses (Figure 7). Vulture visits varied from one to two individuals per record. However, we observed only an individual feeding at a time on carcasses. An antagonist encounter was observed between *C. aura* and *C. burrovianus*, in which the first species excluded the other one from feeding on the carcass.

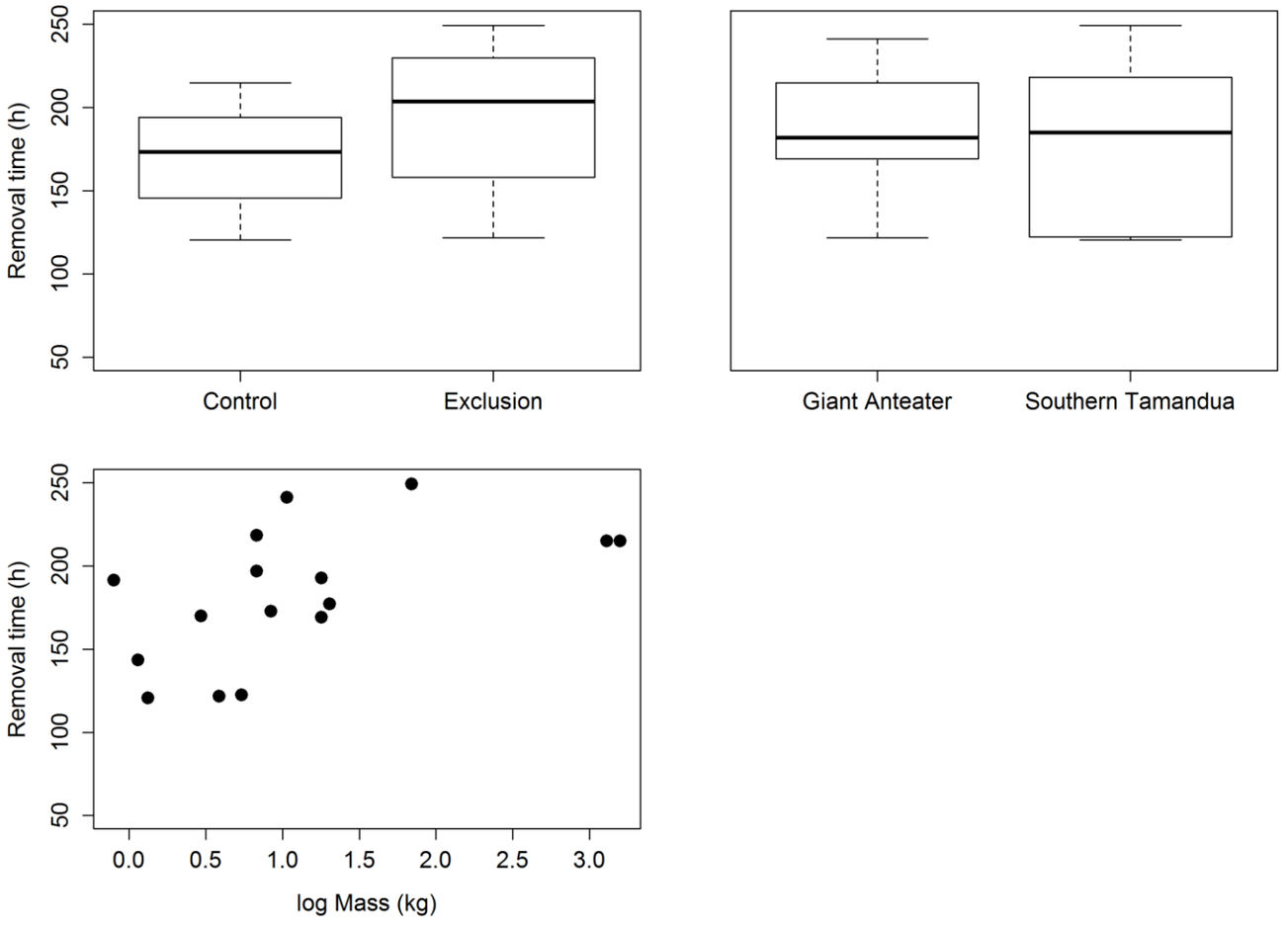

Figure 6 – Comparisons of the mean removal time of our experimental carcasses between treatments, carcass species (*Myrmecophaga tridactyla* and *Tamandua tetradactyla*, respectively), and the relationship with the carcass biomasses. Exclusion treatment only allows removal by invertebrates, while control allows both invertebrates and vertebrate scavengers.

Considering the three observed removal patterns, i.e. rapid decay caused by fly and beetle larvae activity (mainly in exclusion carcasses, n=8), part scattering by vultures (n=4), and removal after total or partial burial by dung beetles (Scarabaeidae, n=4), buried carcasses were removed faster than those removed by vultures or insects in general ($t_{df=5}$ =-3.310, SE= 16.305, p=0.021; Figure 10). We did not observe a difference between the removal time by vultures and other insects (mainly flies and beetles; $t_{df=5}$ =1.503, SE= 16.568, p=0.193). Finally, carcass biomass did not show a significant effect in this model ($t_{df=5}$ =0.393, SE= 8.226, p=0.710).

Figure 7 – Large vertebrate scavengers and visitors of our experimental carcasses. Photos were generated from 20-s videos recorded by motion-trigged cameras. From left to right, scavengers (top): Turkey Vulture (*Cathartes aura*) and Lesser Yellow-headed Vulture (*Cathartes burrovianus*). Other visitors: Six-banded Armadillo (*Euphractus sexcinctus*) and Maned Wolf (*Chrysocyon brachyurus*).

Soil nutrient content

We observed a difference between treatments at the ACC only for K content, which was higher in the exclusion treatment ("radius 0"; Figure 8, Appendix S1). For all ACC models, we did not detect a significant effect of the experimental carcass biomasses (Appendix S1). We were not able to fit models for Mg and Ca due to their small values at radius 0. Considering the other radii around the carcasses, we observe a significant effect of the interaction between the radial distance from the ACC and the treatments for K and Mg (Figure 8). Thus, these nutrient contents were greater at radius 0 of the exclusion treatment compared to other radii and the control, while no significant difference was observed across radii of the control and between radii 40 and 120 cm of the exclusion (Appendix S1). In general, a greater concentration of K was observed in the exclusion treatment compared to the control. P and Mg also showed higher contents on average in the exclusion treatment, but this

pattern was similar to that observed in the control. Also, carcass biomass did not affect these soil models across radii and the Ca model was not fit due to the small values of the variable.

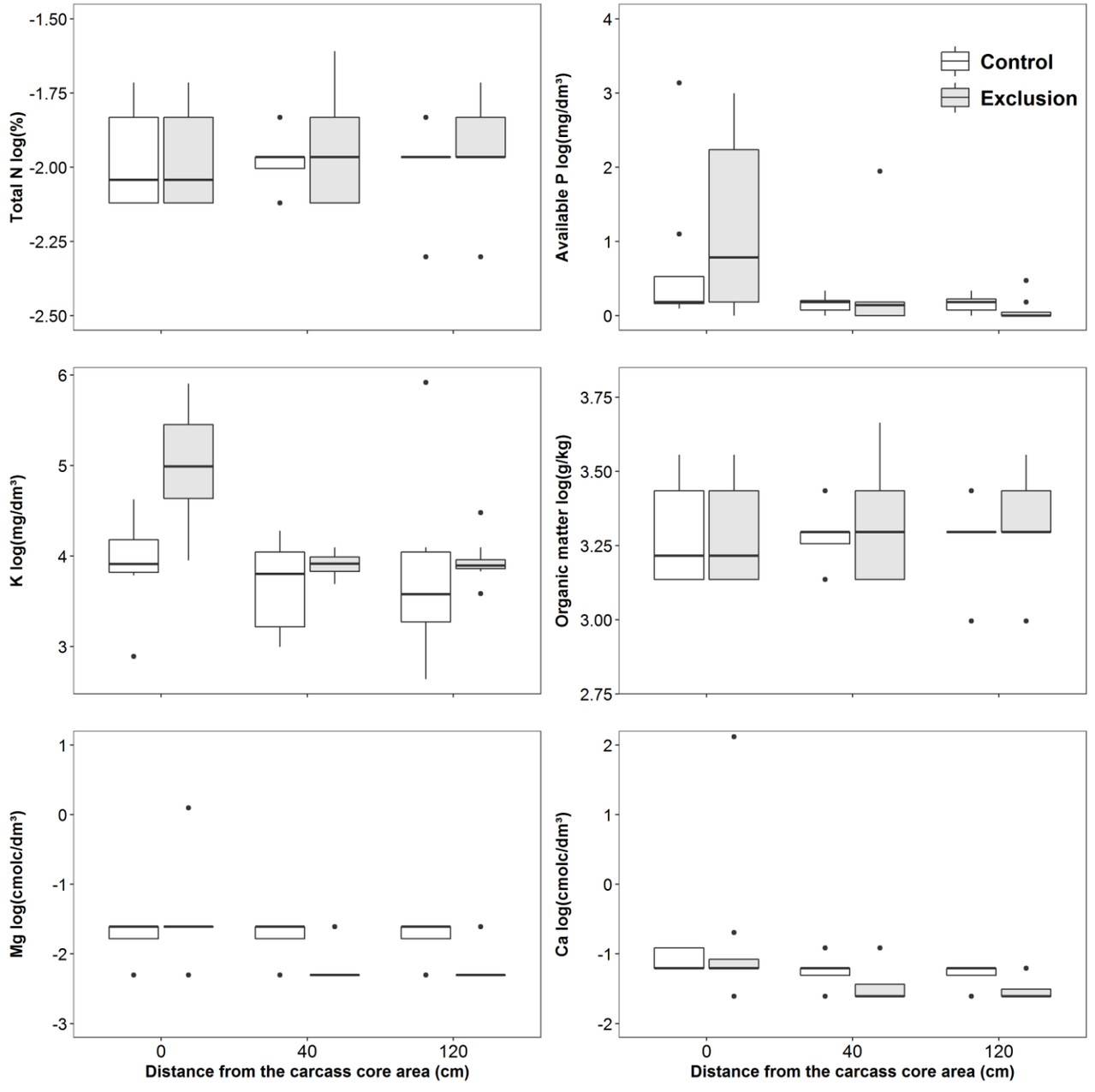

Figure 8 – Comparisons of mean values of soil nutrient contents between treatments (control and exclusion). The x-axis shows the radial distance around the area covered by the carcasses (ACC, or radius 0), where samples of soil were collected. We only observe a significant difference in the comparison between control and exclusion at the radius 0 for K content. Also, we detected that the soil content of K and Mg was higher at radius 0 of the exclusion compared to other radii and the control (see statistical details in Appendix S1).

Litter decomposition

Tea biomass loss did not differ between treatments (Figure 9). Despite the mean loss being lower at the radius 0 of both treatments, the interaction between distance from the ACC and treatments did not show a significant effect either (Appendix S1).

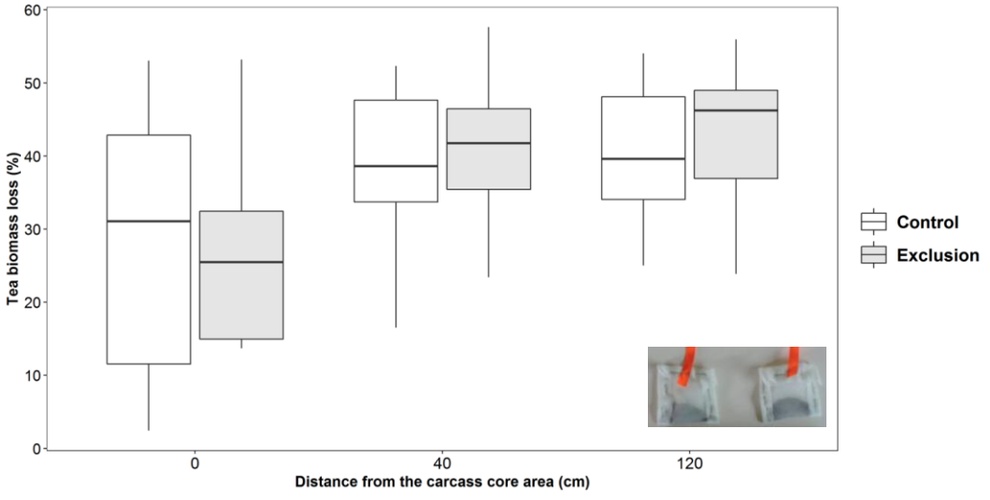

Figure 9 – Comparisons of green tea biomass losses (model for litter decomposition) among treatments (control and exclusion). The x-axis shows also the radial distance from the area covered by the carcasses (radius 0). No significant difference was observed between treatments and radii.

DISCUSSION

Our study showed that under the warm, well-preserved, and rainy conditions of our study area, the scavenger community composed of insects (mainly flies and dung beetles) and vertebrates (vultures) sustains the carcass removal function. As expected, vultures were the main necrophagous vertebrates, given the almost absence of facultative scavenger mammals. Contrary to our expectations, losses of large scavengers (vultures) did not prolong the removal time of carcasses, suggesting that insects can compensate for these losses to some degree or play a redundant function alongside the vultures. However, it is important to note that the rainy season in Cerrado may provide some advantages for insect scavengers, given that high temperatures (> 27º C) and high relative humidity (> 90%) can strongly increase necrophagous insect activity and therefore, the carrion removal (Wang et al. 2008;

Sebastião & Castro 2019). Our study suggests some degree of redundancy between invertebrates and vertebrates, given that the removal time of carcasses scavenged by insects in general and vultures did not show a difference.

Rainy periods not only increase the activity of invertebrates on carcasses, but can also reduce the feeding activity of vultures and other raptors. In our study, we recorded heavy rainfall throughout the experiment, which may have prevented the presence of vultures on carcasses. Indeed, our cameras showed that vultures avoid rains, including short rainy periods on sunny days, i.e. abandoning the carcass immediately after the start of any rain event. Other extreme climate events, such as heavy snowfall, can also prevent avian scavengers from detecting carcasses while favoring the arrival of other facultative mammalian scavengers (Enari & Enari 2021). A similar relation may have occurred in our experiment, i.e. extreme climate events (rainfall) preventing the arrival of vultures and favoring necrophagous insects on carcasses.

Necrophagous insects, such as burying beetles, can monopolize the carcasses by burying them before the arrival of other scavengers (Carter et al. 2007; Sugiura & Hayashi 2018). Thus, high carrion removal rates by invertebrates are possible even in the presence of vertebrates, especially in small carcasses (e.g. mice; Sugiura & Hayashi 2018; Muñoz-Lozano et al. 2019; Romero 2020). In our experiment, dung beetles removed some carcasses quickly by burying them in less than three days, which prevented the arrival of vertebrates and even necrophagous flies. However, we believe these beetles did not replace the vertebrate scavengers, given that from all available carcasses for these insects in our study, they were able to remove 25%, while vultures were able to remove 50% of the available carcasses for them. Thus, both invertebrates and vertebrates support the carrion removal function in the Cerrado.

Our soil analyses are also consistent with the observed pattern of carcass removal. Contents of P, organic matter, and N were not affected by vertebrate scavengers, which may suggest that the ability of caged carcasses in inputting nutrients into the soil does not depend on the type of removing agent. This was an unexpected result, given that we expected higher nutrient contents in the soil beneath exclusion carcasses. Fly maggots in the absence of vertebrates can capture most of the available nutrients in the carcasses, especially carbon, N, and P (Barton et al.

2019). Vertebrate carcasses show a higher concentration of carbon and N, compared to our other selected nutrients, in their internal organs, muscles, and skin, which are parts strongly consumed by invertebrates (Barton et al. 2019). Given that water-soluble salts, such as K, are associated with carcass fluids, this nutrient can be rapidly lost from carcasses as soon as the removal process starts (Parmenter & MacMahon 2009). Here, the carcass openness promoted by the vultures may have enhanced these inputs at the control sites, which could explain the observed higher concentration of K in the control. Finally, skeletal-based nutrients such as P, Ca, and Mg can be lost very slowly from carcasses at the early decomposition stages, given that bones and other associated tissues are not consumed by scavengers in the dry stage of the removal process (Parmenter & MacMahon 2009). Indeed, it is expected that nutrients such as Ca and P increase in the soil beneath the carcasses after several months or years after the animal death (Melis et al. 2007). In general, the high activity of invertebrates on carrion mediated by the rainy conditions of the Cerrado may have compensated for the nutrient inputs generated by the vertebrate breakdowns.

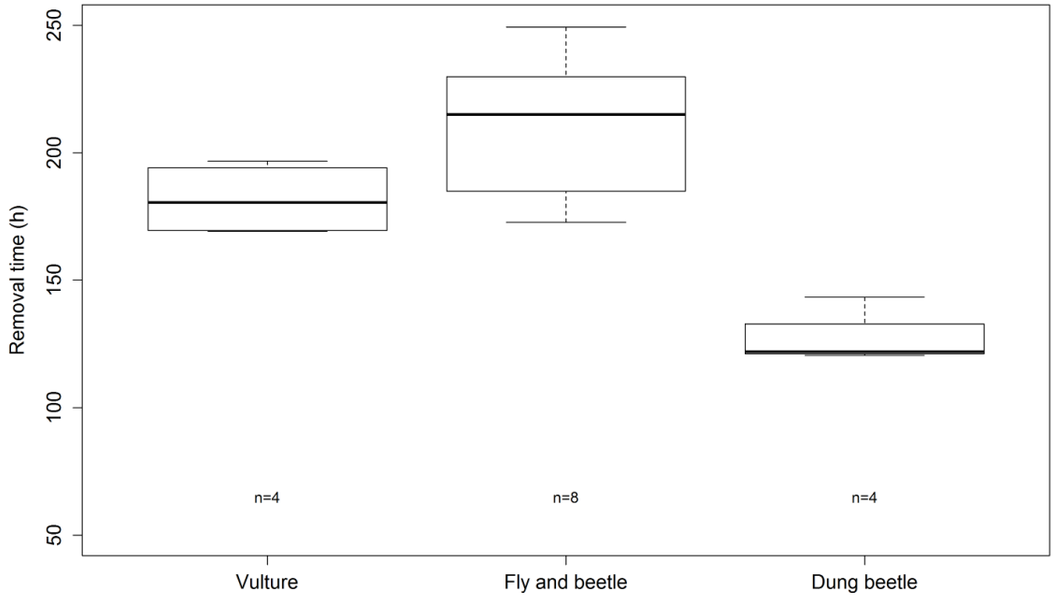

Figure 10 – *A posteriori* comparisons of removal time among carcass removing agents, i.e. those removed mainly by "Vulture", "Fly and beetle", and "dung beetle" (burying) in our experiment in Emas National Park, Brazil. The difference of the "Dung beetle" compared to the other removing agents was significant ($p<0.030$).

The early local disturbance in the soil seems not to affect litter decomposition. The higher content of K in the control also seems not to affect the process. We expected that a likely high nutrient input from carcasses would cause some inhibition of the microbial communities. This change would trigger a cascade effect on soil fauna, given that soil microorganisms can digest and soften plant-derived organic matter, thus improving the access and quality of these food resources for invertebrates (Benbow et al. 2019). However, the litter decomposition showed a pattern similar to natural conditions (areas without carcasses) due to a likely time-lagged response to the initial carcass disturbance.

Our experiment observed that both vertebrate and invertebrate scavengers sustain the function of carrion removal in the Cerrado, in which vultures are the main vertebrate scavengers. The absence of vultures on carcasses did not affect their removal times, but changed the inputs of some carcass fluid-associated nutrients (K and Mg) into the soil. Thus, well-conserved grassland areas support high stability of key ecosystem functions, such as carrion removal. Given the seasonal effect of rainfall, we also encourage long-term studies to elucidate the scavenging efficiency in drier periods of the year.

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REFERENCES

Arrondo, E., Maleón, M., Cortés-Avizanda, A., Jiménez, J., Beja, P., Sánchez-Zapata, J.A. & Donázar, J.A. (2018) Invisible barriers: Differential sanitary regulations constrain vulture movements across country borders. *Biological Conservation* 219, 46–52.

Barton, P.S. & Evans, M.J. (2017) Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. *Ecological Entomology* 42, 364–374.

Barton, P.S., Cunningham, S.A., Lindenmayer, D.B. & Manning, A.D. (2013) The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems. *Oecologia* 171, 761–772.

Barton, P.S., McIntyre, S., Evans, M.J., Bump, J.K., Cunningham, S.A. & Manning, A.D. (2016) Substantial long-Term effects of carcass addition on soil and plants in a grassy eucalypt woodland. *Ecosphere*, 7, 1–11.

Barton, P.S., Strong, C., Evans, M.J., Higgins, A. & Quaggiotto, M-M. (2019) Nutrient and moisture transfer to insect consumers and soil during vertebrate decomposition. *Food Webs* 18, e00110.

Benbow, M.E., Barton, P.S., Ulyshen, M.D., Beasley, J.C., DeVault, T.L., Strickland, M.S., Tomberlin, J.K., Jordan, H.R. & Pechal, J.L. (2019) Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. *Ecological Monographs*, 89, e01331.

Benbow, M.E., Tomberlin, J.K. & Tarone, A.M. (2016) Introduction to Carrion Ecology, Evolution, and Their Applications. In: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M (eds). *Carrion Ecology, Evolution, and their Applications*. CRC Press, Taylor & Francis Group, Boca Raton, USA, p.13-30.

Bump, J.K., Peterson, R.O. & Vucetich, J.A. (2009a) Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. *Ecology* 90, 3159–3167.

Bump, J.K., Webster, C.R., Vucetich, J.A., Peterson, R.O., Shields, J.M. & Powers, M.D. (2009b) Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees

a competitive advantage. *Ecosystems* 12, 996–1007.

Carter, D.O., Yellowlees, D. & Tibbett, M. (2007) Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften* 94, 12–24.

Chen, F-S., Wang, G.G., Fang, X-M., Wan, S-Z., Zhang, Y. & Liang, C. (2019) Nitrogen deposition effect on forest litter decomposition is interactively regulated by endogenous litter quality and exogenous resource supply. *Plant Soil* 437, 413–426.

Demo, C., Cansi, E.R., Kosmann, C. & Pujol-Luz, J. R. (2013) Vultures and others scavenger vertebrates associated with man-sized pig carcasses: a perspective in Forensic Taphonomy. *Zoologia* 30, 574–576.

DeVault, T.L., Rhodes Jr, O.E., Shivik, J.A., Rhodes, O.E., Shivik DeVault, J.A., DeVault, T.L. & Rhodes, O.E. (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102, 225–234.

Enari, H. & Enari, H.E. (2021) Not avian but mammalian scavengers efficiently consume carcasses under heavy snowfall conditions: a case from northern Japan. *Mammalian Biology* 101, 419–428.

Guo, J., Fu, X., Liao, H., et al. (2016) Potential use of bacterial community succession for estimating post-mortem interval as revealed by high-throughput sequencing. *Scientific Reports* 6, 1–11.

Hawlena, D., Strickland, M.S., Bradford, M.A. & Schmitz, O.J. (2012) Fear of Predation Slows Plant-Litter Decomposition. *Science*, **336**, 1434.

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E. & Belant, J.L. (2018) Effects of vulture exclusion on carrion consumption by facultative scavengers. *Ecology and Evolution* 8, 2518–2526.

IBGE – Instituto Brasileiro de Geografia e Estatística. (2021) BDiA: Banco de Dados de Informações Ambientais-Pedologia. Versão 2.15.0. Available in https://bdiaweb.ibge.gov.br/#/consulta/pedologia [accessed 09 Fev. 2022].

Mateo-Tomás, P., Olea, P.P., Moleón, M., Selva, N. & Sánchez-Zapata, J.A. (2017) Both rare and common species support ecosystem services in scavenger communities. *Global Ecology and Biogeography* 26, 1459–1470.

Melis, C., Selva, N., Teurlings, I., Skarpe, C., Linnell, J. D. & Andersen, R. (2007) Soil and vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland. *Ecological Research* 22, 807-813.

MMA-IBAMA, Ministério do Meio Ambiente – Instituto Brasileiro do Meio Ambiente e dos Recursos Renovaveis & CEBRAC - Fundação Centro Brasileiro de Referência e Apoio Cultural. (2004) *Plano de Manejo do Parque Nacional das Emas* (Coordenação Geral: Fernando Paiva Scardua). MMA-IBAMA, Brasília. Disponível em http://www.icmbio.gov.br/portal/images/stories/imgs-unidades coservacao/parna_emas.pdf. Acesso em agosto de 2018.

Moreno-Opo, R. & Margalida, A. (2013) Carcasses provide resources not exclusively to scavengers: Patterns of carrion exploitation by passerine birds. *Ecosphere* 4, 105.

Muñoz-Lozano, C., Martín-Veja, D., Martínez-Carrasco, C., Sánchez-Zapata, J.A., Morales-Reyes, Z., Gonzálvez M. & Moleón, M. (2019) Avoidance of carnivore carcasses by vertebrate scavengers enables colonization by a diverse community of carrion insects. *PLoS ONE* 14, e0221890.

Ogada, D., Shaw, P., Beyers, R.L., Buij, R., Murn, C., Thiollay, J.M., Beale, C.M., Holdo, R.M., Pomeroy, D., Baker, N., Krüger, S.C., Botha, A., Virani, M.Z., Monadjenm, A. & Sinclair, A.R.E. (2015) Another Continental Vulture Crisis: Africa's Vultures Collapsing toward Extinction. *Conservation Letters* 9, 1-9.

Ogada, D.L., Keesing, F. & Virani, M.Z. (2012) Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249, 57–71.

Ogada, D.L., Torchin, M.E., Kinnaird, M.F. & Ezenwa, V.O. (2011) Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. *Conservation Biology* 26, 453–460.

Olson, Z.H., Beasley, J.C., DeVault, T.L. & Rhodes Jr, O.E. (2012) Scavenger community response to the removal of a dominant scavenger. *Oikos* 121, 77–84.

Parmenter, R.R. & MacMahon, J. A. (2009) Carrion decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. *Ecological Monographs* 79, 637–661.

Payne, J.A. (1965) A summer carrion study of the baby pig *Sus scrofa* Linnaeus. *Ecology* 46, 592–602

Peisley, R.K., Saunders, M.E., Robinson, W.A. & Luck, G.W. (2017) The role of avian scavengers in the breakdown of carcasses in pastoral landscapes. *Emu* 117, 68–77.

Pereira, E.K.C., Andrade-Silva, J., Silva, O., Santos, C.L.C., Moraes, L.S., Bandeira, M.C.A., Silva, C.R.R. & Rebêlo, J.M.M. (2017) *Solenopsis saevissima* (Smith) (Hymenoptera: Formicidae) Activity Delays Vertebrate Carcass Decomposition. *Sociobiology* 64, 369–372.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S. & Willigen, B.V. (2019) Package nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140.

R Core Team. (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Romero, A. (2020) The fate of small-mammal carrion is affected by carcass size and visual conspicuousness in a Neotropical rainforest. *Therya* 11, 423–431.

Sebastião, M. & Castro, C.P.E. (2019) A Preliminary Study of Carrion Insects and Their Succession in Luanda, Angola. *Journal of Medical Entomology* 56, 378–383.

Strickland, M.S. & Wickings, K. (2016) Carrion Effects on Belowground Communities and Consequences for Soil Processes. In: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M (eds). Carrion Ecology, Evolution, and their Applications. CRC Press, Taylor & Francis Group, Boca Raton, USA, p.93-105.

Sugiura, S. & Hayashi, M. (2018) Functional compensation by insular scavengers: the relative contributions of vertebrates and invertebrates vary among islands. *Ecography* 41, 1173–1183.

Teixeira, P.C., Donagemma, G.K., Fontana, A. & Teixeira, W.G (eds.). (2017) Manual de Métodos de Análise de

Solo. 3ª ed. Embrapa, Brasília, Brasil.

Therneau, T.M. & Lumley, T. (2019) Package survival: Survival analysis, R package version 2.44-1.1.

Van Diepen, L., Frey, S.D., Sthultz. C.M., Morrison, E.W., Mimocha, R. & Pringle, A. (2015) Changes in litter quality caused by simulated nitrogen deposition reinforce the N-induced suppression of litter decay. *Ecosphere* 6, 205.

Wang, J., Li, Z., Chen, Y., Chen, Q. & Yin, X. (2008) The succession and development of insects on pig carcasses and their significances in estimating PMI in south China. *Forensic Science International* 179, 11–18.

Wickham H. (2016) ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. Available in https://ggplot2.tidyverse.org.

Wilson, E.E. & Wolkovich, E.M. (2011) Scavenging: How carnivores and carrion structure communities. *Trends in Ecology and Evolution* 26, 129–135.

SUPPLEMENTARY MATERIALS

Appendix S1 – Linear mixed-effect models for each soil variable and tea biomass loss comparing treatments (control and exclusion) at the area immediately below the carcasses (R0) and at a distance of 40 and 120 cm from the R0.

Table S1 – Legend for the model's variables and parameters

Variable	Meaning
R0 (radius 0)	Direct area covered by each experimental carcass
Estimate	Effect estimates fitted by linear mixed-effect models using restricted log-likelihood - R package nlme (cran.r-project.org/web/packages/nlme/nlme.pdf)
treatE	Exclusion treatment compared to control (i.e. carcass without cages)
biomass	Carcass biomass
treatE:radiusR3	Interaction term showing the relation between the exclusion treatment (treatE) and the radius of 40 cm from ACC (radiusR3), in comparison to the control
treatE:radiusR5	Interaction term showing the relation between the exclusion treatment (treatE) and the radius of 120 cm from ACC (radiusR5), in comparison to the control
asin(sqrt) N (%)	Arcsine square root transformation for nitrogen content (%) or log-transformed for "Soil_radii"
P (mg/dm3)	Phosphorus content in mg/dm³ or log-transformed in Soil_radii
K (mg/dm3)	Potassium content in mg/dm³ or log-transformed in Soil_radii
Organic matter (g/kg)	Organic matter content in g/kg or log-transformed in Soil_radii
log Mg (cmolc/dm3)	Magnesium content in cmolc/dm³ or log-transformed in Soil_radii
log Ca (cmolc/dm3)	Calcium content in cmolc/dm³ or log-transformed in Soil_radii. However, given the small values of this variable, the model was not fitted

Table S2 - Fitted models for R0 (Soil nutrient contents)

Response	Variable	Estimate	Std. Error	DF	t-value	P
asin(sqrt) N (%)	(Intercept: treatC)	0.381	0.015	7	26.100	0.000
	treatE	0.000	0.014	6	-0.008	0.994
	biomass	0.000	0.001	6	0.203	0.846
P (mg/dm3)	(Intercept)	3.069	2.997	7	1.024	0.340
	treatE	2.217	3.796	6	0.584	0.581
	biomass	0.218	0.269	6	0.810	0.449
K (mg/dm3)	(Intercept)	37.452	28.900	7	1.296	0.236
	treatE	118.511	36.150	6	3.278	**0.017**
	biomass	3.887	2.614	6	1.487	0.188
Organic matter (g/kg)	(Intercept)	26.798	2.051	7	13.067	0.000
	treatE	-0.016	2.002	6	-0.008	0.994
	biomass	0.041	0.207	6	0.197	0.850
log Mg (cmolc/dm3)	NA	NA	NA	NA	NA	NA
	Not fitted					
log Ca (cmolc/dm3)	NA	NA	NA	NA	NA	NA
	Not fitted					

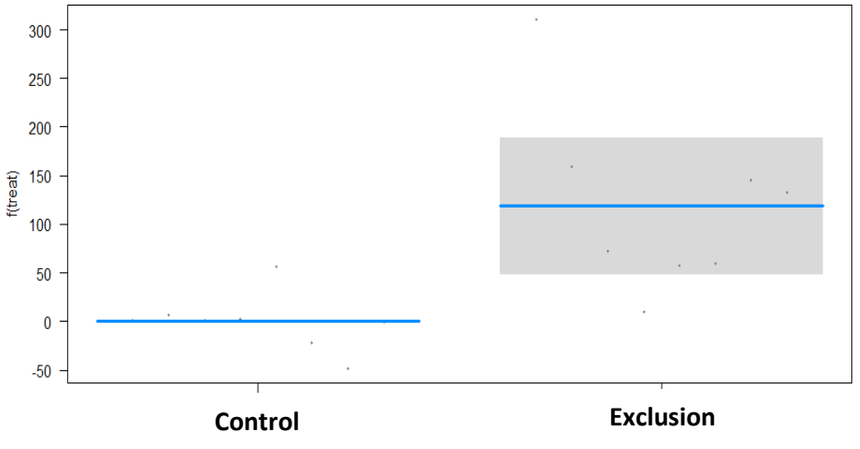

Figure S3 – Visualization of partial residuals for the K model, showing the difference between treatments, generated by the R package visreg (cran.r-project.org/web/packages/visreg/visreg.pdf).

Table S4 – Linear mixed-effect models to compare soil nutrient contents among radii (0, 40, and 120 cm from the R0)

Response	Variable	Estimate	Std. Error	DF	t-value	P
log N (%)	(Intercept)	-1.992	0.061	34	-32.810	0.000
	treatE	-0.001	0.069	34	-0.015	0.988
	radiusR3	-0.010	0.069	34	-0.139	0.890
	radiusR5	-0.013	0.069	34	-0.190	0.851
	biomass	0.003	0.005	34	0.579	0.567
	treatE:radiusR3	0.042	0.097	34	0.431	0.669
	treatE:radiusR5	0.048	0.097	34	0.494	0.625
log P (mg/dm3)	(Intercept)	0.579	0.266	34	2.180	0.036
	treatE	0.545	0.361	34	1.508	0.141
	radiusR3	-0.508	0.361	34	-1.408	0.168
	radiusR5	-0.499	0.361	34	-1.382	0.176
	biomass	0.017	0.015	34	1.151	0.258
	treatE:radiusR3	-0.383	0.511	34	-0.749	0.459
	treatE:radiusR5	-0.634	0.511	34	-1.241	0.223
log K (mg/dm3)	(Intercept)	3.930	0.213	34	18.428	0.000
	treatE	1.076	0.290	34	3.711	**0.001**
	radiusR3	-0.267	0.290	34	-0.920	0.364
	radiusR5	-0.153	0.290	34	-0.526	0.602
	biomass	0.001	0.012	34	0.082	0.935
	treatE:radiusR3	-0.830	0.410	34	-2.025	**0.050**
	treatE:radiusR5	-0.914	0.410	34	-2.230	**0.032**
log Organic matter (g/kg)	(Intercept)	3.269	0.061	34	53.522	0.000
	treatE	-0.001	0.069	34	-0.015	0.988
	radiusR3	-0.010	0.069	34	-0.139	0.890
	radiusR5	-0.007	0.069	34	-0.102	0.919
	biomass	0.003	0.005	34	0.567	0.574
	treatE:radiusR3	0.043	0.098	34	0.441	0.662
	treatE:radiusR5	0.050	0.098	34	0.508	0.615
log Mg (cmolc/dm3)	(Intercept)	-1.763	0.143	34	-12.302	0.000
	treatE	0.301	0.195	34	1.546	0.131
	radiusR3	0.000	0.195	34	0.000	1.000
	radiusR5	0.000	0.195	34	0.000	1.000
	biomass	-0.004	0.008	34	-0.493	0.625
	treatE:radiusR3	-0.733	0.276	34	-2.660	**0.012**
	treatE:radiusR5	-0.733	0.276	34	-2.660	**0.012**
log Ca (cmolc/dm3)	NA	NA	NA	NA	NA	NA
	Not fitted					

Table S5 – Linear mixed-effect models for % Tea biomass loss in comparison between treatments

R0 only

Variable	Estimate	Std. Error	DF	t-value	P
(Intercept)	33.776	6.245	7	5.409	0.001
treatE	0.416	7.490	6	0.056	0.958
biomass	-1.129	0.577	6	-1.956	0.098

Among radii

Variable	Estimate	Std. Error	DF	t-value	P
(Intercept)	31.098	4.849	34	6.413	0.000
treatE	0.228	6.122	34	0.037	0.971
radiusR3	10.443	6.121	34	1.706	0.097
radiusR5	11.814	6.121	34	1.930	0.062
biomass	-0.599	0.324	34	-1.850	0.072
treatE:radiusR3	2.485	8.656	34	0.287	0.775
treatE:radiusR5	3.494	8.656	34	0.403	0.689

CAPÍTULO II

(SHORT COMMUNICATION)

Vertebrate carcasses can provide food resources for both scavenger and non-scavenger insects in the Brazilian Cerrado

"Flies buzzing on the putrid belly,

Black battalions of maggots

[…]

Like wind and running water,

or the rhythmic whisper and hiss

of rice rinsed in a sieve".

Charles Baudelaire (1857) - *Une Charogne*.

Translated by Eleanor Brown

ABSTRACT

Vertebrate carcasses are a widespread food source for vertebrate and insect scavengers across ecosystems. However, several non-scavenger arthropods can also interact with carrion for feeding or breeding. Here, we documented patterns of insects visiting vertebrate carcasses in an experimental study in the Brazilian Cerrado. In addition to the typical scavenger groups (flies, beetles, and ants), we observed Hemiptera, Hymenoptera (bees and wasps), Orthoptera, and Lepidoptera species visiting the carcasses. These insect groups used carcasses as a direct food source (carcass tissues) or to drink liquids (e.g. condensed moisture and blood), breed, and ambush prey. We also observed events of total carcass burial by beetles. Thus, our study shows that vertebrate carcasses can create occasional feeding and breeding sites for both scavenger and non-scavenger invertebrates in a Neotropical savanna.

Keywords: carrion ecology, carcass burial, carcass removal, decomposition, necrophagous, scavenging.

Flies and beetles comprise the most studied and known scavenger groups around the world (Pechal et al. 2014; Anderson et al. 2019). Together, these insect groups can remove entire carcasses both in the absence and presence of vertebrates, being also the first animals to arrive on carcasses (Olson et al. 2012; Sugiura & Hayashi 2018; Olea et al. 2019). Thus, the early colonization of necrophagous insects in carcasses is a crucial event to trigger the decomposition process, given that the openness of carcasses by maggots (mainly flies) modulates the arrival of other invertebrate and vertebrate scavengers, as well as the growth of aerobic microorganisms (Carter et al. 2007; Anderson et al. 2019). Studies have also pointed out that the absence or a low abundance of these scavenger insects on carcasses can strongly prolong their removal times (Pechal et al. 2014; Barton & Evans 2017). Decaying carcasses also attract many other invertebrate groups, which can contribute to the removal dynamics due to the consumption of carcass tissues and the predation of scavenging maggots, such as ants and parasitoid wasps (Anderson et al. 2019; Eubanks et al. 2019). Despite the recognized importance of flies, beetles, and even ants (see Eubanks et al. 2019 for a review) in removing carrion, the nutritional and ecological value of vertebrate carcasses for non-scavenger invertebrates remains unclear and poorly documented.

In February 2020, we assembled an experiment using 16 anteater carcasses (10 *Myrmecophaga tridactyla*, and six *Tamandua tetradactyla*, 0.90-24.5 kg) in a grassland area of the Emas National Park, Goiás state, Brazil (17°56'40.0"S, 52°59'17.4"W). The main aim of the experiment was to evaluate the effects of excluding the activity of vertebrate scavengers on the carrion removal process, without changing the activity of invertebrates and microbes on carcasses. Therefore, we used eight caged carcasses (exclusion treatment) paired with other carcasses available to the entire scavenger community (control). We also recorded the activity of invertebrates while monitoring the carcasses once a day (mainly after 16 h) until their full removal. Thus, we observed several insect groups visiting the carcasses during the experiment time, as well as undocumented records of key interactions between invertebrates and carcasses in the Brazilian Cerrado. To not disturb the experiment that was in progress, we did not collect invertebrates from the carcasses, but only recorded the presence of main groups by visual inspections for about five minutes in each carcass per day. Control carcasses took nine days to be fully removed, while the exclusion ones took 10 days.

In both treatments, we observed eight insect groups: flies, beetles, Hemiptera, ants, bees, wasps, Orthoptera, and, Lepidoptera (Figures 1 and 2). Insect visits on carcasses were evenly distributed over the 10-day experiment, only some groups were not recorded on the first days and the last days (Figure 2). Also, the composition of insect groups did not vary between treatments ($ANOSIM_{(Jaccard)}$ r=-0.030, p=0.572; Figure 2). Flies, beetles, and ants were observed mainly removing carcass tissues (adults and/or larvae) and nestling (Figure 1 A1-3, B2, D3). Intriguingly, we observed beetles burying entire carcasses (two samples in both treatments), which were fully removed in only two days without intervention from most invertebrate and vertebrate scavengers (Figure 3). Indeed, the total burial prevented the arrival of other scavengers, given that even adult flies were poorly recorded around the burial sites. Other dung beetles also caused partial burial in almost all available carcasses, as well as we observed some individuals dragging carcass parts into tunnels (Figure 3). Although we were not able to accurately identify the burying beetle species, we observed a greenish small dung beetle associated with the buried tunnels carcasses and Silphidae individuals (probably *Oxelytrum* sp.) around or in the partial and total burial sites (Figure 3). Silphidae beetles were also observed preying on carcass larvae (Figure 3).

Figure 1 – Scavenger and non-scavenger insects attending anteater carcasses in the Brazilian Cerrado: A1 - flies (mainly Calliphoridae, Sarcophagidae, and Fanniidae - highlighted in the red circle); A2-3 - dung beetles, highlighting the tunnels (red circles); B1-3 – Hemiptera and ants; C1-3 – bees; D1-E3 – Orthoptera and Lepidoptera, and F1-3 – wasps or wasp-liked flies.

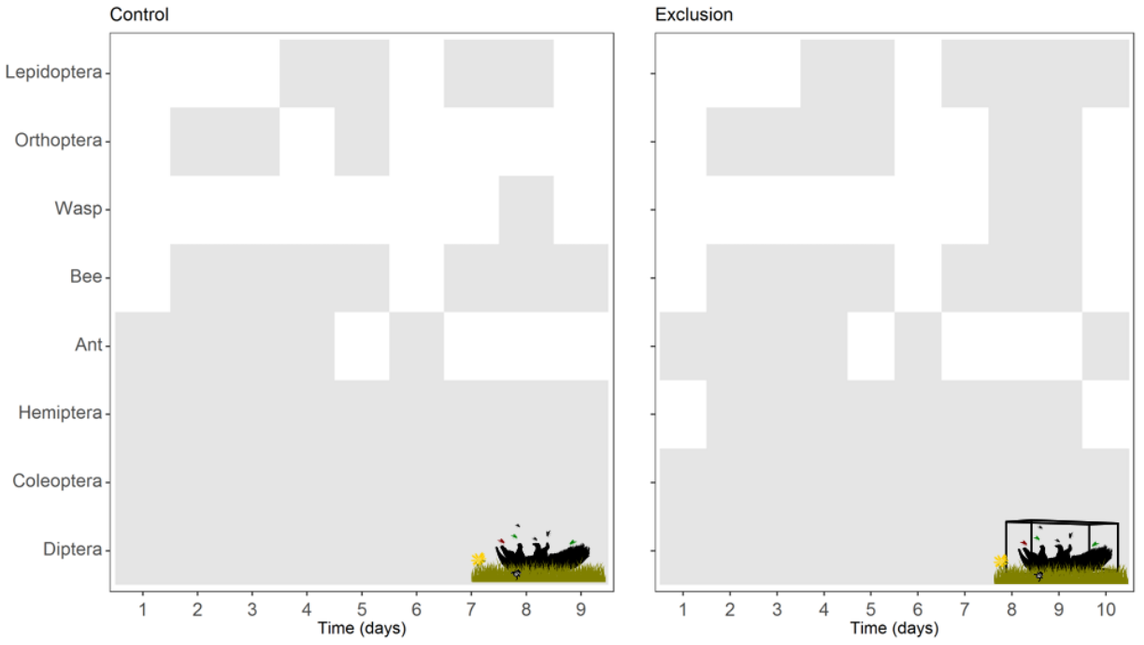

Figure 2 – Pattern of insect visiting (presence only) during our 10-day experiment in Emas National Park, February 2020. The exclusion treatment refers to caged carcasses, which avoid consumption by large vertebrate scavengers.

To date, carcass burial behavior is poorly documented in the Cerrado, compared to the well-known ecology of *Nicrophorus* spp. ("burying beetles", Silphidae) in the northern hemisphere (Scott 1998, Sugiura & Hayashi 2018). However, we believe that the observed burial events were not caused by Silphidae species, given that these beetles in the Cerrado are recorded mostly at the advanced decomposition stage and they depend on carcass larvae, especially the adult form (Lira et al. 2018). Our findings are similar to the predatory behavior observed in a dung beetle of Argentina (*Canthon chalybaeus*, Scarabaeidae), which after killing a snail, buried the carcass by creating a soil pile digging underneath and around the carcass (Martín et al. 2021). Other *Canthon* spp. have also been observed burying dung in forested habitats (Carvalho et al. 2018). Perhaps, dung beetles in the well-conserved grasslands of Emas National Park play a similar role in removing carrion.

The third most common insect group on carcasses was Hemiptera, which was recorded on almost all days. These insects were mainly recorded on the skin, fur, wounds, and natural cavities of carcasses (e.g. mouth and nose), which may suggest the consumption of liquids such as blood and condensed moisture or salts (Figure 1 B1-3, E3). The presence of this group on carcasses and dung has been documented in some studies around the world,

including feeding on carcass tissues and scavenging insects (Constant 2007). Here, we also documented the predatory behavior of a Hemiptera individual on a Fanniidae fly or a wasp (see Figure 3). Similarly, bees, Orthoptera, and Lepidoptera individuals were also recorded in wounds, fur, and natural cavities, maybe taking liquids and salts too (Figure 1 C1-3, D1-3, E1-3). Finally, we recorded wasps at the end of the experiment (Figure 2), which suggests a search for potential prey or host (Figure 1 F1-3). Parasitoid wasps have been observed on carcasses, despite only a few studies being available (e.g. Frederickx et al. 2012). Predatory insects (likely parasitoids too) play a function in reducing the density of maggots, which can also prolong the carcass availability time in the ecosystems (Eubanks et al. 2019). Despite this, limiting the activity of fly maggots can be beneficial for other scavengers, such as vertebrates. For instance, carrion insects can remove carcasses weighing up to 10 kg within three days in African forests, but the higher diversity of predatory ants in Neotropical forests can increase the removal time by more than two weeks (Houston 1985). Thus, we highlight that vertebrate carcasses can create an ephemeral hotspot of species diversity and ecosystem functions in a Brazilian savanna.

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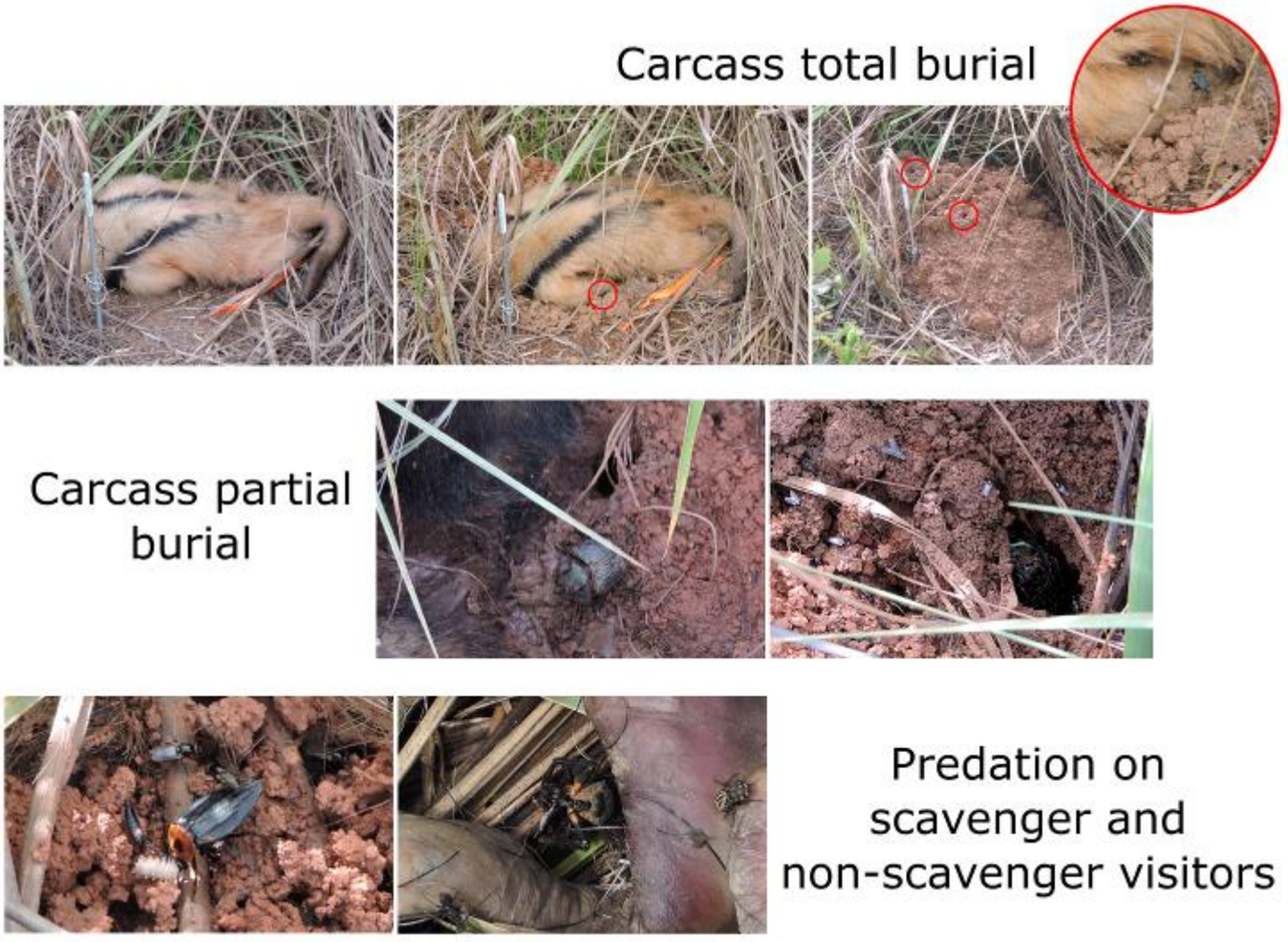


Figure 3 – Key insect behaviors observed on carcasses: burial by dung beetles (highlighting the insect likely responsible for the burial and the tunnels entrances, red circles) and predation on larvae by Silphidae beetles and on adult flies (or a wasp) by a predatory Hemiptera.

REFERENCES

Anderson GS, Barton PS, Archer M, Wallace JR. 2019. Invertebrate Scavenging Communities. In: Olea PP, Mateo-Tomás P, Sánchez-Zapata JA (eds). *Carrion Ecology and Management*. Springer Nature, Switzerland, pp. 45–69.

Barton PS, Evans MJ. 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecological Entomology **42**:364–374.

Carter DO, Yellowlees D, Tibbett M. 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften **94**:12–24.

Carvalho RL, Frazão F, Ferreira-Châline RS, Louzada J, Cordeiro L, França F. 2018. Dung burial by roller dung beetles (Coleoptera: Scarabaeinae): An individual and specific-level study. International Journal of Tropical Insect Science **38**, 373–380.

Constant J. 2007. Note on coprophily and necrophily in the Hemiptera Heteroptera. Entomologie **77**, 107–112.

Eubanks MD, Lin C, Tarone AM. 2019. The role of ants in vertebrate carrion decomposition. Food Webs **18**:e00109.

Frederickx C, Verheggen F, Haubruge E. 2013. The community of Hymenoptera parasitizing necrophagous Diptera in an urban biotope. Journal of Insect Science **13**:1–14.

Houston DC. 1985. Evolutionary Ecology of Afrotropical and Neotropical Vultures in Forests. Ornithological Monographs **36**:856–864.

Lira LA, Macedo MP, Pujol-Luz JR, Vasconcelos SD. 2018. Diel Activity and Effect of Carcass Decomposition on the Attractiveness to the Forensically Important Species *Oxelytrum discicolle* (Coleoptera: Silphidae). Journal of Forensic Sciences **64**, 799–804.

Martín CM, Guanuco AdV, Cortez V, Verdú JR. 2021. First observation on the predation of a nonarthropod species by a dung beetle species: The case of *Canthon chalybaeus* and the snail *Bulimulus apodemetes*. PLOS ONE **16**, e0258396.

Olea PP, Mateo-Tomás P, Barton PS. 2019. Invertebrate scavengers matter. Science **363**:1161–1162.

Olson ZH, Beasley JC, DeVault TL, Rhodes Jr OE. 2012. Scavenger community response to the removal of a dominant scavenger. Oikos **121**:77–84.

Pechal JL, Benbow ME, Crippen TL, Tarone AM, Tomberlin JK. 2014. Delayed insect access alters carrion decomposition and necrophagous insect community assembly. Ecosphere **5**:1–21.

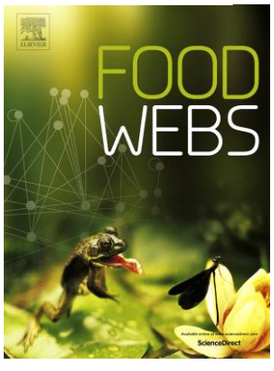
Scott MP. 1998. The Ecology and Behavior of Burying Beetles. Annual Review of Entomology **43**, 595–618.

Sugiura S, Hayashi M. 2018. Functional compensation by insular scavengers: the relative contributions of vertebrates and invertebrates vary among islands. Ecography **41**:1173–1183.

CAPÍTULO III

Evaluating the effect of interactions between invertebrates and vertebrates on scavenging efficiency: a global modeling and systematic review

Submetido à



Be kind to me, a mess

I represent persistence – in the dirty thing

Things larger than me

I do not fear

[…]

Pushing up the hill rolling around

I feel myself at work.

Doreen Gildroy (2002). *Dung beetle*. The Little Field of Self.

Evaluating the effect of interactions between invertebrates and vertebrates on scavenging efficiency: a global modeling and systematic review

Joedison Rocha[a*], Luisa G. Carvalheiro[a,b], Mário Almeida-Neto[a,b]

[a]Programa de Pós-graduação em Ecologia e Evolução, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia 74.001-970, Brasil.

[b]Departamento de Ecologia, Instituto de Ciências Biológicas, Universidade Federal de Goiás, Goiânia 74.001-970, Brasil.

*****Corresponding author at: santos.joedison@gmail.com

Abstract

Carrion removal is an important ecosystem function provided by specialist and opportunistic scavengers, including invertebrate and vertebrate species. Despite advances in carrion ecology in the last decades, the roles and interactions between scavenging groups on carrion remain poorly understood. Here, we reviewed 91 studies to evaluate the diversity and ecological functions provided by invertebrates on 7475 vertebrate carcass inputs across the globe, as well as their scavenging efficiency in the presence and absence of large vertebrates. We found records of more than 1500 invertebrate species (mostly beetles and flies) on carcasses, of which >70% were documented as carrion-eaters. Together with microorganisms, these species can fully remove large inputs of carcasses in the absence of vertebrate scavengers. However, such absence of vertebrates delays the removal process, taking 30% more days to be fully removed, while also increasing daily carcass consumption rates by invertebrates. Thus, invertebrates consume more carrion in the absence of vertebrates, but they do not fully compensate for the functions provided by vertebrates. Overall, this review highlights the complementary function of invertebrates and vertebrates in removing carrion, given that the scavenging efficiency is higher when both groups are acting on carcasses. Finally, we encourage studies addressing interactions and drivers of diversity among invertebrate groups (scavengers vs. predators), microbes, and their effects on vertebrates.

Keywords: blowflies, carcass removal, Carrion Ecology, decomposition, functional compensation, trophic interactions.

1. Introduction

The deposition of vertebrate carcasses creates a concentrated and ephemeral pool of nutrients in the ecosystems, serving as a food resource for complex and diverse communities of invertebrates, vertebrates, and microorganisms (Carter et al., 2007). The interactions of these scavenger groups on vertebrate carrion maintain important ecosystem functions, such as nutrient cycling and distribution throughout the landscape, which, in turn, affect soil nutrient content and the local diversity of plants (Barton et al., 2016; Bump et al., 2009; Carter et al., 2007).

Vertebrate scavengers are often considered the main agents of carrion removal, as highlighted by an increasing body of evidence focused on them (DeVault et al., 2003; Hill et al., 2018; Peisley et al., 2017). In contrast, the role of invertebrates in the carrion removal process has received less attention in the ecological literature, despite the historical interest in forensic research (Benbow et al., 2019; Olea et al., 2019; Payne, 1965). Across global ecosystems, invertebrates play several functions in the carrion removal process. Firstly, they can remove large inputs of carcasses in about two weeks, without the intervention of vertebrate scavengers (Ekanem and Dike, 2010; Joy et al., 2006). Also, some beetle species can monopolize entire carcasses by burying them (Hoback et al., 2020; Sugiura and Hayashi, 2018). Other invertebrate groups such as predatory ants and parasitoid wasps that prey on maggots can influence the carrion removal time by reducing their densities (Eubanks et al., 2019; Houston, 1985). These distinct roles of invertebrates on carcasses affect their temporal availability for other invertebrates and vertebrate scavengers, which can facilitate, prevent or delay their arrival on carcasses (Houston, 1985; Pereira et al., 2017; Sugiura and Hayashi, 2018; Turner et al., 2021). Therefore, the presence of invertebrates may structure key competitive and/or facilitative interactions with other scavengers (invertebrates and vertebrates) and microbial decomposers (DeVault et al., 2004; Shukla et al., 2018), thus affecting the entire process of carrion removal across global ecosystems.

Experimental studies have shown that when the activity of vertebrate scavengers is prevented or reduced, carcasses take a longer time to be fully removed (Hill et al., 2018; Ogada et al., 2011; Olson et al., 2012; Peisley et

al., 2017). Therefore, could we assume that invertebrate scavengers do not fully compensate for the functions played by vertebrates on carrion? This is an intriguing question, given that there is also evidence that invertebrate scavengers can increase their carrion consumption rate if the local diversity of vertebrates is reduced, suggesting some functional compensation (Sugiura and Hayashi, 2018). Also, invertebrates can outcompete vertebrates by removing the majority of carcasses, even those available to them (Abernethy et al., 2016; Ray et al., 2014; Trumbo, 1990). Given this conflicting evidence, ecological studies (often focused on vertebrates) together with the vast number of forensic ones (often focused on invertebrates) provide an avenue to better understand the roles of both scavenger groups on carcasses across the globe.

Here, we assembled a large database after a global systematic review to evaluate the following questions: A) what are the species and taxonomic groups of invertebrates that visit or feed on vertebrate carcasses? B) What are the functions provided by invertebrate species in the carcass removal process? C) Does the overall scavenging efficiency decrease in the absence of vertebrate scavengers? Given that vertebrates are often considered the main agents of carrion removal in the ecosystems (Benbow et al., 2019; DeVault et al., 2003), we expect that the removal time of carcasses across habitats is greater in the absence of these scavengers.

2. Methods

2.1. Data search

We searched for studies reporting invertebrates on vertebrate carcasses (articles and notes) published between 1971 and 2021 using Web of Science and Scopus databases. We searched for studies with combinations of the following terms in their titles, abstracts, and keywords: (invertebrate* OR insect*) AND ("carrion removal" OR "carcass removal" OR "carrion decomposition" OR "carcass decomposition" OR scaveng*). To improve the cost-efficiency of our review process, we filtered the initial search by the categories “Entomology”, “Ecology”, “Zoology”, “Environmental Sciences”, “Biodiversity Conservation”, “Medicine Legal”, “Biology”, and “Microbiology” in Web of Science, while the categories “Agricultural and Biological Sciences”, “Environmental Science”, “Immunology and Microbiology”, and “Medicine” were applied in Scopus. This filtered search returned

2185 results considering both databases, which after removing the duplicates resulted in 1557 unique studies. Our search mainly returned studies in English, but we also reviewed some results in Spanish and French.

From the identified studies, we selected those that reported any use of vertebrate carcasses by a single invertebrate species or the entire visiting community (including indirect uses such as predation on carcass larvae), based on empirical data (rather than modeled ones or laboratory studies) focused on colonization, succession patterns, interactions between scavenger species, and removal experiments in terrestrial habitats. We also reviewed studies in terrestrial habitats nearby aquatic environments (e.g. estuaries, rocky shores, and beaches) to only compile records of carcass use by terrestrial species. We did not consider studies based on small baited-traps (e.g. minced meat and artificial proteins), but only studies that used entire carcasses or parts from large carcasses (e.g. entire legs or offal of ungulates). Finally, data from studies or carcass inputs that experimentally reduced or prevented the presence of invertebrates on carrion were not compiled, such as burning, chemical additions, and drowning. We applied these criteria in both screening procedures (abstract and full-text). After this, we selected 107 studies. Finally, we combined the data from different studies conducted at the same sampling sites ("redundant studies", n=16) to obtain a single dataset per each habitat type in each site, such as a unique species list per site. If available, numeric data was averaged across these redundant studies. In total, 91 unique studies were used in this review, covering 104 sites across 29 countries (Fig. 1 and see Appendix A for the complete review workflow and references, including the "redundant studies").

2.2. Data extraction

The 91 selected studies resulted in a large dataset encompassing field data from 1984 to 2020, totaling 7475 monitored carcass inputs (ranging from one to 3700 across studies), whose masses ranged from tiny lizard carcasses of ~0.002 kg to a large input of 2700 kg of pig carcasses. For each study (including their supplementary materials), we extracted information about habitat types (e.g. forests and croplands), site coordinates, sampling effort (number of carcasses), and study main focus (e.g. colonization record and succession patterns). To address our questions, we extracted unique data for each habitat type sampled in each site across studies. Thus, each

unique combination of habitat type and carcass species/taxon per site was considered an independent replicate in our analyses.

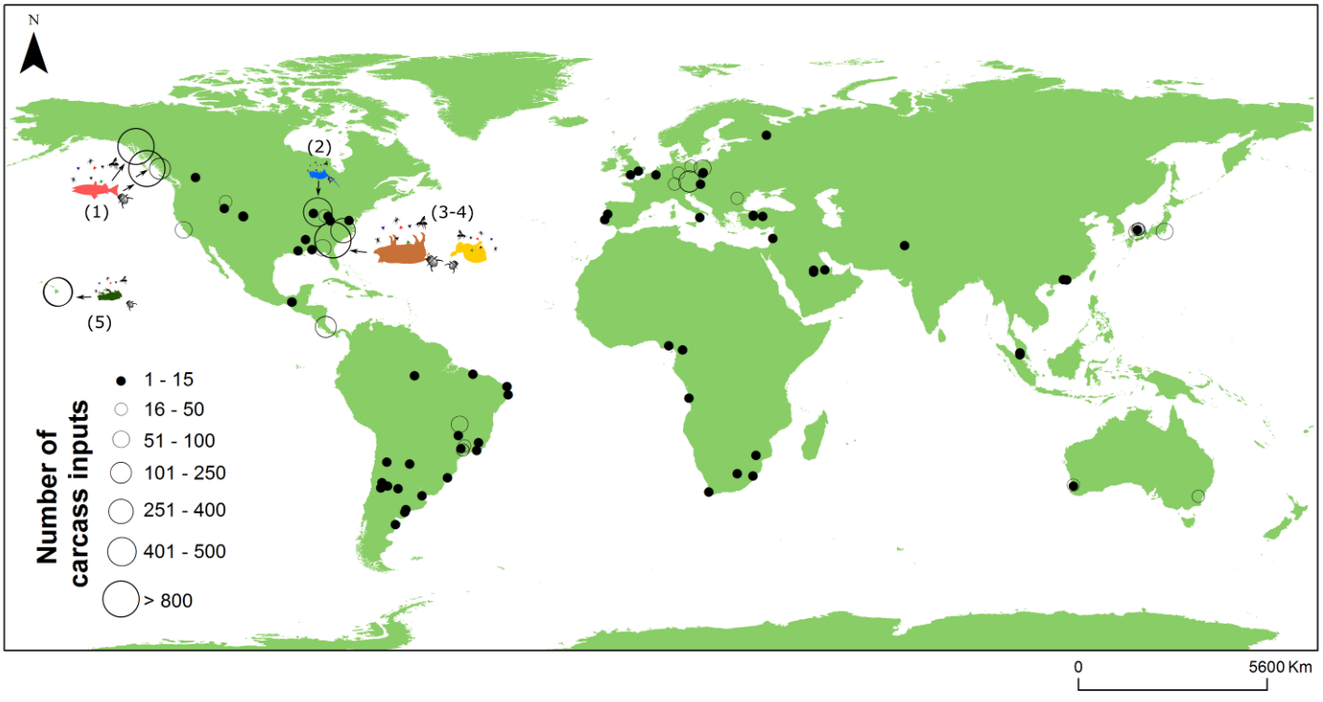


Fig. 1 –Sampling sites where the studies considered in this review were carried out (Appendix A). The circle size shows the sampling effort (number of used carcasses) for each sampling site. Colored silhouettes highlight the sites with the largest carcass inputs to each of the five main carcass models: (1) salmon, (2) mouse/rat, (3) domestic pig, (4) rabbit, and (5) amphibians.

We compiled a global species list of invertebrates visiting the carcass inputs using the data from each habitat in the sites, considering individuals identified at the level of species, genus, or family (question A). Also, the uses of carcasses by invertebrate species (e.g. flesh feeding, nestling, and maggot predation; question B) were recorded based on the observations or inferences provided by the original studies. The full dataset is available in Appendix B.

To address our questions on scavenging efficiency, we distinguished the carcass inputs into two groups: (i) available to vertebrate scavengers, and (ii) not available to vertebrates (i.e. inputs from which their activities were

prevented by using cages or other exclusion devices). Thus, we considered each replicates as a unique combination of study sites × habitat types × carcass species/taxon × presence/absence of vertebrates (Table B.2 in Appendix B). For each replicate, we compiled the mean biomass of carcass inputs per species/taxon (kg) and their respective elapsed mean removal times in days, when available. Based on 60 studies that reported these variables, as well as the number of carcasses, two variables were defined to evaluate scavenging efficiency by invertebrates (including microorganisms) in the presence and absence of vertebrates: mean elapsed removal time of carcass inputs and the mean daily carcass consumption rate (in kg/day; question C). The consumption rate (*cr*) for each replicate was calculated as $cr = (w_{mean} \times nc) / rt_{mean}$, where: w_{mean} is the overall mean carcass biomass, *nc* is the number of carcasses, and rt_{mean} is the mean removal time. Finally, the removal time refers to the reported mean elapsed time from carcass placement until the onset of the dry stage (i.e. when all used carcasses were reduced to bones, skin, fur, and other hard tissues or when >95% of the consumable biomass was removed).

2.3. Modeling the interaction between invertebrates and vertebrates on scavenging efficiency

The presence/absence of vertebrates on scavenger efficiency was evaluated through two linear mixed-effect models by restricted log-likelihood (REML) using the study ID as a random effect. We fitted two independent models, one for carcass consumption rate and another for carcass removal time. The carcass consumption rate was log-transformed to improve the normality and homoscedasticity of residuals, which were checked by graphical inspection in both models (Appendix B). The presence or absence of vertebrates on carcass inputs per each habitat type was used as an explanatory categorical variable in both models.

We obtained 65 independent carcass inputs available to the entire scavenger community across habitats (n=26 studies), and 56 inputs not available to vertebrate scavengers (37 studies). Also, we added three covariates in both models to control their likely effects on scavenging efficiency: 1) total carcass biomass (i.e. overall mean carcass biomass in the study × number of carcasses per species/taxon), given that it is expected that smaller carcasses are removed faster; 2) annual temperature, given that the activity of scavenging invertebrates and microorganisms increase towards warmer regions or in higher temperatures (Iancu et al., 2018; Jordan and

Tomberlin, 2017); 3) the number of carcasses in the inputs (sampling effort compiled from studies), given that both responses may be biased toward inputs with more carcasses. We used the WorldClim data at the 30-s resolution (~1 km², Fick & Hijmans 2017) to estimate the mean annual temperature (bio1) for each site within a 5-km-buffered area around the central point of each site (according to the study coordinates). We ran the models using the R package *nlme* (version 3.1-140; Pinheiro et al., 2019). All analyses were run in the R Programming Environment (R Core Team 2015).

3. Results

Studies addressing interactions between invertebrates and vertebrates carcasses were mostly conducted to evaluate succession patterns in forensic approaches (Fig. 2; ~65% of the selected studies), followed by studies focused on the colonization of species or groups on carcasses, as well as records of feeding interactions and/or nestling. Studies addressing carrion removal efficiency accounted for about 20% of the studies (Fig. 2). Domestic pigs (n=47 studies), mouse/rat (19 studies), and domestic rabbits (n=12; Fig. 3) were the most common carcass models across studies. Despite the largest number of salmon carcasses observed in this review, they represented only three studies focused on some spawning events in North America (Figs. 1 and 2; Hocking et al., 2009; Pechal and Benbow, 2016; Reimchen, 2017). The use of wild carcasses, such as amphibians, birds, and large ungulates represented no more than 4% of the total carcass inputs in this review (Fig. 3). Finally, the majority of the studies were conducted in urban and agricultural habitats (52%), followed by well-conserved forest habitats (32%; Fig. 2).

3.1. Invertebrate species and functions on carrion

We recorded 1576 invertebrate species (mainly arthropods) on carcasses belonging to 20 taxonomic groups (Table B.1 in Appendix B). Non-arthropod invertebrates comprised only a few records of terrestrial mollusks (Gastropoda, three species) and annelids (Haplotaxida, three species). Coleoptera was the species-richest group across studies with 870 species (55% of all recorded species), followed by Diptera (455 species, 29%), Hymenoptera (192 species, 12%), Lepidoptera (14; 0.9%), and Orthoptera (seven, 0.4%).

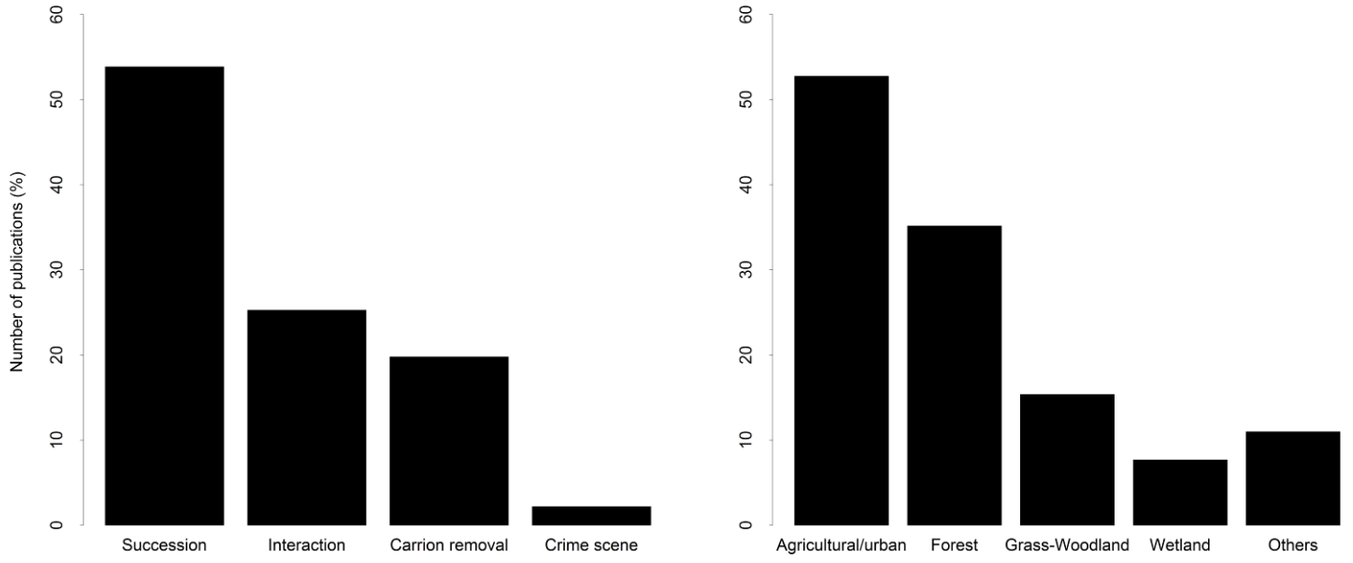


Fig. 2 – Main aims and sampling habitats of each study used in this review (n=48). "Others" includes transitional zones and/or non-specified habitats (Appendix B). "Succession" refers to the arrival order and colonization patterns, which are often considered succession patterns across studies.

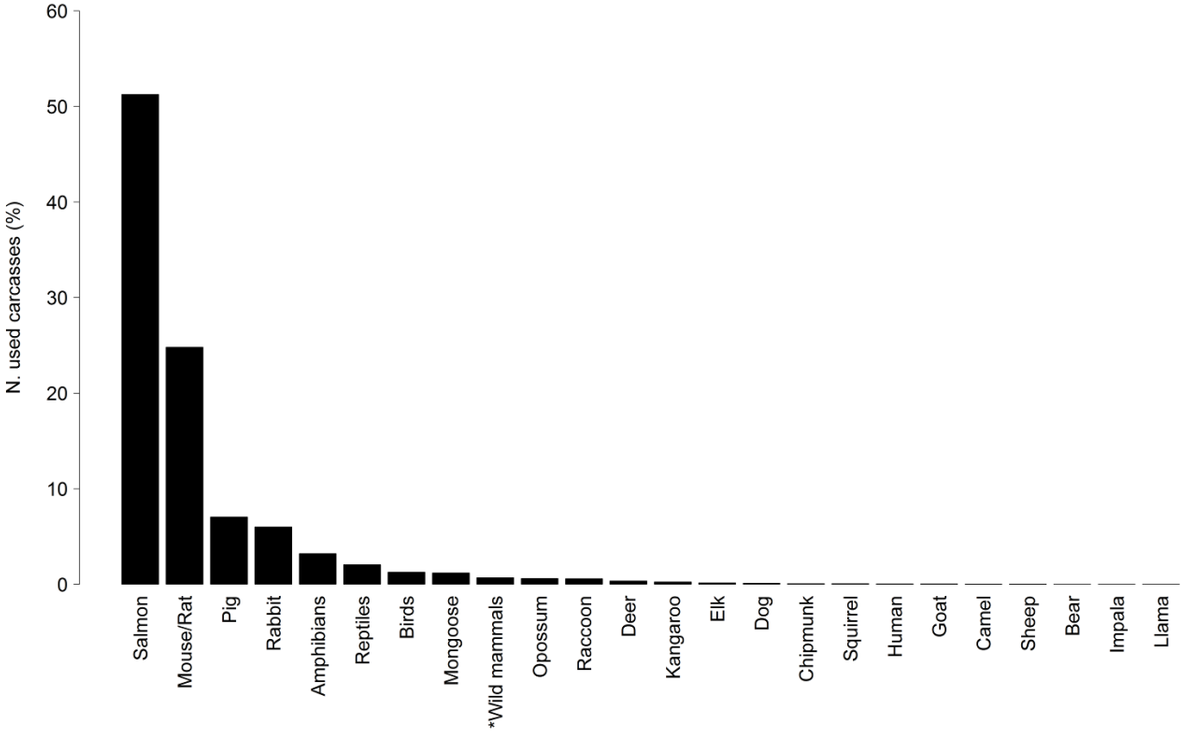


Fig. 3 – Experimental carcasses used in the studies of this review (n=91). "*Wild mammals" represents a mix of wild deer and boar carcasses (Raw data in Appendix B).

Invertebrate species were recorded mainly feeding (or likely feeding) on carcass tissues (73.24% of all recorded species), highlighting again the predominance of Coleoptera and Diptera species (71.10% of all carrion-eating species). The second most common use of carcasses by invertebrates was predation (including parasitodism) on carcass maggots (104 species; 6.62%). This function was mainly played by beetles (58 species; 3.70%), ants, wasps (Hymenoptera; 37 species, 2.35%), and spiders (Araneae; four species, 0.25%). Some species used the carcasses as nesting sites or substrate, i.e. *Coprophanaeus corythus* (Coleoptera) and *Musca domestica* (Diptera) in carcasses at the fresh or advanced decay decomposition stage, as well as *Apis mellifera* (Hymenoptera), *Paravespula vulgaris* (Hymenoptera), and four Lepidoptera species in dry or mummified remains (Chin et al., 2008; Romero, 2020; Singh et al., 2020b; Szleszkowski et al., 2018). Finally, nine species were recorded drinking on carcass fluids, i.e. *Sepsis* spp. (Diptera), six wasps/bees (Hymenoptera), and two Lepidoptera species (Chin et al., 2008; Gomes et al., 2007). In addition, 336 species (21.40%) were observed on carcasses, but their specific carcass use was not clearly defined or observed by the original studies (see Appendix B).

3.2. Scavenging efficiency by invertebrates in the presence or absence of vertebrates

A total of about 3065 kg of 420 carcasses (from 0.03 to 918 kg) were recorded being removed by invertebrates in the absence of vertebrates in 29.81 days on average (±32.31 SD; see Table B.2), showing a mean carcass consumption rate of 3.04 kg/day (±7.96). Studies focused on the entire scavenger community accounted for total biomass of ~7405 kg (ranging from 0.03 to 3720 kg across 2870 carcasses), which were removed in 20.80 days on average (±29.97). The carcass consumption rate in the presence of vertebrates showed a mean of 3.41 kg/day (±6.98), showing that vertebrate presence did not affect this measure of removal efficiency (Table 1). On the other hand, we found a significant effect of the vertebrate presence on carcass removal times, in which carcasses were removed, on average, almost nine days faster (30% more) in the presence of vertebrates (20.97 days ±29.97 SD) compared to the carcasses removed exclusively by invertebrates (29.81 days ±32.31 SD).

4. Discussion

Our review showed that invertebrates visiting vertebrate carcasses are primarily carrion-eaters. This function contributes to the removal of carrion in almost all types of ecosystems across the globe, from well-conserved tropical or temperate forests to urban environments, including arid areas and habitats nearby freshwater and marine ecosystems. Interest in carrion-visiting invertebrates remains biased toward estimates of post-mortem intervals and colonization patterns with direct forensic applications, while the role of invertebrates in removing carrion from the ecosystems still represents a secondary interest in the literature.

TABLE 1 - Global linear mixed-effect models to evaluate the effects of the presence/absence of vertebrates on carcass inputs* on scavenging efficiency, together with three covariates, total carcass biomass (mean biomass per carcass input × N. carcasses), temperature, and sampling effort (N. of carcasses). We used the study ID as a random effect (intercepts). All data used in the models are available in Appendix B.

Response variables	Terms	Estimate	SE	DF	t-value	P
Removal time (days)	Intercept	42.363	12.780	53	3.315	0.002
	Vertebrate presence	-9.967	4.903	39	-2.033	**0.049**
	Total carcass biomass (kg)	0.947	0.169	39	5.608	<0.001
	Mean annual temperature (ºC)	-1.447	0.642	39	-2.255	0.030
	N. of carcasses	-0.034	0.064	39	-0.536	0.595
Carcass consumption rate (log kg/day)	Intercept	-2.701	0.509	53	-5.305	<0.001
	Vertebrate presence	0.226	0.385	39	0.587	0.560
	Total carcass biomass (kg)	0.054	0.011	39	5.125	<0.001
	Mean annual temperature (ºC)	0.097	0.027	39	3.664	0.001
	N. of carcasses	0.009	0.003	39	2.570	0.014

*Carcass inputs consider unique combinations of sampled habitat types (e.g. forest and urban) and carcass species (e.g. pig and salmon), in the presence or absence of vertebrates across sampling sites.

Studies in our review showed that invertebrates can outcompete vertebrate scavengers in small carcass inputs (< 2 kg), i.e. being the main consumers of >50% of the available carcasses and even more than 90% (Abernethy et al., 2017, 2016; De Jong and Chadwick, 1999; Sugiura and Hayashi, 2018). However, the presence of vertebrates seems to be a crucial factor to ensure a high scavenging efficiency when considering all carcass inputs (Abernethy et al., 2017; Olson et al., 2016; Turner et al., 2021, Young et al., 2014). Thus, the maintenance of scavenging efficiency across the globe relies on a high diversity of scavenger communities, including both invertebrates and vertebrates. Therefore, the functions played by both groups in the carrion removal process are mostly redundant, but somehow complementary in some contexts.

4.1. The roles of invertebrates in the carcass removal process

Invertebrates not only remove carcass tissues but also modulate the entire removal process by interacting with other scavenger and decomposer groups in each stage of the decay process. For instance, invertebrates affect the initial putrefaction by interacting with the endogenous carcass microorganisms (Ito, 2021; Pechal et al., 2013; Pechal and Benbow, 2016), direct nutrient inputs to the soil from surface breakdowns or burying of carcasses in intermediate stages (Fialho et al., 2018; Ito, 2021; Lashley et al., 2018; Parmenter and MacMahon, 2009), and carcass breakdown by vertebrates in intermediate-later stages (Olson et al., 2016; Ray et al., 2014; Sugiura and Hayashi, 2018).

Invertebrates show competitive and/or facilitative interactions with microorganisms, other invertebrates, and vertebrate scavengers. Firstly, studies have shown the activity of invertebrates on carcasses can reduce the abundance of some bacterial or fungal groups, while also changing the overall bacterial/fungal composition of carcasses via both microbial transfers from the invertebrate bodies or due to competitive exclusions mediated by chemical secretions (Iancu et al., 2015b, 2018; Ito, 2021; Pechal et al., 2013). Such changes in microbial compositions can reduce olfactory putrefaction cues from carcasses, due to a reduction of proteins such as cadaverine and putrescine produced by carcass bacteria and fungi (Shukla et al., 2018). This potentially increases the carcass detection time by vertebrates that rely on olfactory cues, such as reptiles, some vultures, and mammals

(DeVault et al., 2004; Romero, 2020; Turner et al., 2021). Also, changes in olfactory cues can affect the arrival of other invertebrate scavengers, given that the most common carrion-eaters, i.e. flies and beetles, find carcasses using their acute smell sense (Carvalho et al., 2017; Ito, 2021).

Invertebrates on carcasses can also regulate the occurrence and density of other carrion-visiting invertebrates acting as predators of carcass maggots. This function is provided mainly by beetles, ants, and wasps, which often affect fly larvae, but also adults. Wasps (Hymenoptera) act mainly as parasitoids of maggots (Ellison, 1990; Frederickx et al., 2013; Grassberger and Frank, 2004), while beetles and ants usually are true predators of larvae and adult species on carcasses (Andrade-Silva et al., 2015; Barton and Evans, 2017; Ries et al., 2021). As a result, the carrion removal process may be delayed, thus increasing the availability time of carcasses (Barton and Evans, 2017; Pereira et al., 2017). For instance, caged pig carcasses decomposing near nests of the predatory ant *Solenopsis saevissima* took three more days to reach the second decomposition stage in the control (i.e. bloated; Pereira et al., 2017). This role of invertebrate predators in controlling maggot density may be beneficial to other scavenger species, mainly vertebrate ones. In African forests, carrion insects can remove carcasses weighing up to 10 kg within three days (Houston, 1985). However, the same study has highlighted a different pattern in Neotropical forests, where the removal process can take more than two weeks. This extended time may be explained by the presence of predatory ants on carcasses, which can reduce larvae density by up to 90% (Houston, 1985). Despite this seminal study, there are few studies addressing interactions among invertebrate scavenger groups (but see Ito, 2021; Turner et al., 2021). For instance, the ecological impacts of parasitoid wasps on carrion flies are still poorly understood, although some species such as *Alysia manducator* and *Nasonia vitripennis* can parasitize up to 90% of the recorded fly species on 10 pig carcasses (Frederickx et al., 2013).

Another competitive mechanism played by invertebrates against other invertebrates and vertebrates consist in monopolizing entire carcasses by burying them (Sugiura and Hayashi, 2018; Ururahy-Rodrigues et al., 2008; Watson and Carlton, 2005). Total or partial burying of carcasses can prevent or delay other invertebrates and even vertebrates from consuming them (Abernethy et al., 2017; De Jong et al., 2021; Romero, 2020; Singh et al., 2020a). Despite that there is evidence in the literature that burials of carcasses decrease the decomposition process

compared to those on the soil surface (see Carter et al., 2007), we found records of burying species quickly removing a great number of small buried carcasses compared to those on surface microsites (Parmenter and MacMahon, 2009; Romero, 2020). Ultimately, these burials may quickly transfer moisture and nutrients to the soils, improving their fertility (Hoback et al., 2020).

On the soil surface, invertebrates can also open entire carcasses, including the creation of wounds, making them accessible to other invertebrate and vertebrate scavengers (De Jong et al., 2021; Kadej et al., 2020; Morton and Lord, 2006; Olson et al., 2016). The activity and movement of maggots can spread carcass tissues to the soil and transport microorganisms away from the initial carcass site (Fialho et al., 2018; Mariani et al., 2014; Singh et al., 2020a). Thus, invertebrates contribute to carcass removal (direct feeding or nestling), especially for small carcass inputs, while also establishing facilitative (carcass opening and then smell release) and/or competitive interactions (burial or inhibition of olfactory cues) with vertebrates and other invertebrates, controlling also microbial growth and its dispersion away from the carcasses.

4.2. Effects of the presence or absence of vertebrates on the carrion removal process

The scavenging efficiency provided by invertebrates (including microorganisms) in the absence of vertebrates varies strongly across the globe. Both small (e.g. <10 kg) and large (>90 kg) inputs of carrion can be removed at a similar time, e.g. about two weeks on average (Alvarado-Montero et al., 2021; Carvalho et al., 2017; Farwig et al., 2014; Parmenter and MacMahon, 2009). The faster removal time in the presence of vertebrate scavengers means that their functional loss is not fully compensated by invertebrates. Also, this finding underpins that more diverse scavenger communities (i.e. with both invertebrates and vertebrates) are more efficient in removing tons of carrion in both natural well-conserved, and human-altered habitats around the globe.

The absence of vertebrates on carcasses can also trigger increases in the daily carcass consumption rate by invertebrates. It is possible to assume that this higher consumption is due to increases in fly densities on carcasses (Hocking et al., 2009; Mashaly et al., 2019). In other words, the availability of carcasses increases, favoring colonization by invertebrates. This facilitated colonization may also intensify competitive and/or predatory

interactions among invertebrate species on carcasses, generating dominance or exclusion of some groups, as well as a reduction in the use by other ones (Hocking et al., 2009; Ito, 2021). Calliphoridae flies can be favored by the absence of vertebrates on large carcasses due to their higher competitive ability compared to other fly species (Hocking et al., 2009). For instance, one or two Calliphoridae species can represent more than half of all recorded individuals in studies using caged carcasses (Jales et al., 2021; Sebastião and Prado e Castro, 2019; Vasconcelos et al., 2013). Again, our results suggest that a higher diversity of scavengers (both invertebrates and vertebrates) improves the removal efficiency across ecosystems.

4.3. Future research in Carrion Ecology

It is remarkable the lack of studies addressing the ecological importance of invertebrates and their interactions in the carrion removal process, as pointed out recently by carrion ecologists (Olea et al., 2019). Given the many roles of invertebrate scavengers on carcasses, including as predators, parasitoids, and mycophages, there are many possibilities of experimental approaches focusing on interactions among invertebrate species and microbes, as well as their effects on scavenging efficiency. For instance, evaluating whether a scavenger species or group can competitively exclude other carrion visitors (as in Ito, 2021); what factors determine the richness, abundance, or arrival of Diptera species, such as Calliphoridae, on carcasses; how parasitoid species affect the scavenging efficiency of their insect hosts; how the initial composition of endogenous microbes affects the colonization of scavenger species. Of course, there is also an open avenue to evaluate interactions between invertebrates and vertebrates, such as the likely “decoy effect” provided by invertebrates, which enhances carcass detection by the vertebrates.

5. Concluding Remarks

This review shows that invertebrate scavenger assemblages across numerous ecosystems can remove a variety of vertebrate carcasses ranging from small (<2 kg) to large (>90 kg) biomasses in less than 30 days. At the same time, we found solid evidence that the presence of vertebrates reduces the removal time of carcasses by about 30%. Of course, invertebrates are the key scavengers for those carrion inputs that are not accessible to

vertebrates, such as the carcasses of small animals in enclosed spaces (e.g. burrows, cavities, and trashcans) (DeVault et al., 2003; Lutz et al., 2019; Parmenter and MacMahon, 2009). Thus, scavenging efficiency at the community level seems to rely on the diversity of both scavenger groups.

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References

Abernethy, E.F., Turner, K.L., Beasley, J.C., DeVault, T.L., Pitt, W.C., Rhodes Jr, O.E., 2016. Carcasses of invasive species are predominantly utilized by invasive scavengers in an island ecosystem. Ecosphere 7, e01496. doi:10.1002/ecs2.1496

Abernethy, E.F., Turner, K.L., Beasley, J.C., Rhodes Jr, O.E., 2017. Scavenging along an ecological interface: utilization of amphibian and reptile carcasses around isolated wetlands. Ecosphere 8, e01989. doi:10.1002/ecs2.1989

Alvarado-Montero, S., Boesing, A.L., Metzger, J.P., Jaffé, R., 2021. Higher forest cover and less contrasting matrices improve carrion removal service by scavenger insects in tropical landscapes. J. Appl. Ecol. 58, 2637–2649. doi:10.1111/1365-2664.13991

Andrade-Silva, J., Pereira, E.K.C., Silva, O., Santos, C.L.C., Delabie, J.H.C., Rebêlo, J.M.M., 2015. Ants (Hymenoptera: Formicidae) associated with pig carcasses in an Urban Area. Sociobiology 62, 527–532. doi:10.13102/sociobiology.v62i4.795

Barton, P.S., Cunningham, S.A., Macdonald, B.C.T., McIntyre, S., Lindenmayer, D.B., Manning, A.D., 2013.

Species Traits Predict Assemblage Dynamics at Ephemeral Resource Patches Created by Carrion. PLoS ONE 8, e53961. doi:10.1371/journal.pone.0053961

Barton, P.S., Evans, M.J., 2017. Insect biodiversity meets ecosystem function: differential effects of habitat and insects on carrion decomposition. Ecol. Entomol. 42, 364–374. doi:10.1111/een.12395

Barton, P.S., McIntyre, S., Evans, M.J., Bump, J.K., Cunningham, S.A., Manning, A.D., 2016. Substantial long-term effects of carcass addition on soil and plants in a grassy eucalypt woodland. Ecosphere 7, e01537.

Benbow, M.E., Barton, P.S., Ulyshen, M.D., Beasley, J.C., DeVault, T.L., Strickland, M.S., Tomberlin, J.K., Jordan, H.R., Pechal, J.L., 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecol. Monogr. 89, e01331. doi:10.1002/ecm.1331

Benbow, M.E., Lewis, A.J., Tomberlin, J.K., Pechal, J.L., 2013. Seasonal Necrophagous Insect Community Assembly During Vertebrate Carrion Decomposition. J. Med. Entomol. 50, 440–450. doi:10.1603/ME12194

Bump, J.K., Peterson, R.O., Vucetich, J.A., 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90, 3159–3167.

Carter, D.O., Yellowlees, D., Tibbett, M., 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94, 12–24.

Carvalho, R.P., Azevedo, W.T.A., Figueiredo, A.L., Lessa, C.S.S., Aguiar, V.M., 2017. Dipterofauna Associated With Rat Carcasses in the Atlantic Forest, Southeastern Brazil. J. Med. Entomol. 1–12. doi:10.1093/jme/tjx118

Charabidze, D., Vincent, B., Pasquerault, T., Hedouin, V., 2016. The biology and ecology of *Necrodes littoralis*, a species of forensic interest in Europe. Int. J. Leg. Med. 130, 273–280. doi:10.1007/s00414-015-1253-8

Chin, H.C., Marwi, M.A., Salleh, A.F.M., Jeffery, J., Kurahashi, H., Baharudin, O., 2008. Study of insect succession and rate of decomposition on a partially burned pig carcass in an oil palm plantation in Malaysia. Trop. Biomed. 25, 202–208.

De Jong, G.D., Chadwick, J.W., 1999. Decomposition and arthropod succession on exposed rabbit carrion during summer at high altitudes in Colorado, USA. J. Med. Entomol. 36, 833–845. doi:10.1093/jmedent/36.6.833

De Jong, G.D., Meyer, F., Goddard, J., 2021. Relative Roles of Blow Flies (Diptera: Calliphoridae) and Invasive Fire Ants (Hymenoptera: Formicidae: *Solenopsis* spp.) in Carrion Decomposition. J. Med. Entomol. 58, 1074–1082. doi:10.1093/jme/tjab014

DeVault, T.L., Brisbin, I.L., Rhodes Jr, O.E., 2004. Factors influencing the acquisition of rodent carrion by vertebrate scavengers and decomposers. Can. J. Zool. 82, 502–509. doi:10.1139/z04-022

DeVault, Travis L, Rhodes Jr, O.E., Shivik, J.A., Rhodes, Olin E, Shivik DeVault, J.A., DeVault, T L, Rhodes, O E, 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102, 225–234. doi:10.1034/j.1600-0706.2003.12378.x

Ekanem, M.S., Dike, M.C., 2010. Arthropod succession on pig carcasses in southeastern Nigeria. Pap. Avulsos Zool. 50, 561–570.

Ellison, G.T.H., 1990. The effect of scavenger mutilation on insect succession at impala carcasses in southern Africa. J. Zool. 220, 679–688. doi:10.1111/j.1469-7998.1990.tb04742.x

Eubanks, M.D., Lin, C., Tarone, A.M., 2019. The role of ants in vertebrate carrion decomposition. Food Webs 18, e00109. doi:10.1016/j.fooweb.2018.e00109

Farwig, N., Brandl, R., Siemann, S., Wiener, F., Müller, J., 2014. Decomposition rate of carrion is dependent on composition not abundance of the assemblages of insect scavengers. Oecol. 175, 1291–1300. doi:10.1007/s00442-014-2974-y

Fialho, V.S., Rodrigues, V.B., Elliot, S.L., 2018. Nesting strategies and disease risk in necrophagous beetles. Ecol. Evol. 8, 3296–3310. doi:10.1002/ece3.3919

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.

Frederickx, C., Verheggen, F., Haubruge, E., 2013. The community of Hymenoptera parasitizing necrophagous Diptera in an urban biotope. J. Insect Sci. 13, 1–14.

Gomes, L., Gomes, G., Oliveira, H.G., Morlin Jr, J.J., Desuo, I.C., Queiroz, M.M.C., Giannotti, E., Von Zuben, C.J., 2007. Occurrence of Hymenoptera on *Sus scrofa* carcasses during summer and winter seasons in southeastern Brazil. Rev. Bras. Entomol. 51, 394–396. doi:10.1590/S0085-56262007000300019

Grassberger, M., Frank, C., 2004. Initial study of arthropod succession on pig carrion in a central European urban habitat. J. Med. Entomol. 41, 511–523. doi:10.1603/0022-2585-41.3.511

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecol. Evol. 8, 2518–2526. doi:10.1002/ece3.3840

Hoback, W.W., Freeman, L., Payton, M., Peterson, B.C., 2020. Burying beetle (Coleoptera: Silphidae: *Nicrophorus fabricius*) brooding improves soil fertility. Coleop. Bull. 74, 427–433.

Hocking, M.D., Ring, R.A., Reimchen, T.E., 2009. The ecology of terrestrial invertebrates on Pacific salmon carcasses. Ecol. Res. 24, 1091–1100. doi:10.1007/s11284-009-0586-5

Houston, D.C., 1985. Evolutionary Ecology of Afrotropical and Neotropical vultures in forests. Ornithol. Monogr. 36, 856–864.

Iancu, L., Carter, D.O., Junkins, E.N., Purcarea, C., 2015a. Using bacterial and necrophagous insect dynamics for post-mortem interval estimation during cold season: Novel case study in Romania. Forensic Sci. Int. 254, 106–117. doi:10.1016/j.forsciint.2015.07.024

Iancu, L., Junkins, E.N., Purcarea, C., 2018. Characterization and microbial analysis of first recorded observation of *Conicera similis* Haliday (Diptera: Phoridae) in forensic decomposition study in Romania. J. Forensic Leg. Med. 58, 50–55. doi:10.1016/j.jflm.2018.04.012

Iancu, L., Sahlean, T., Purcarea, C., 2015b. Dynamics of necrophagous insect and tissue bacteria for postmortem interval estimation during the warm season in Romania. J. Med. Entomol. 53, 54–66. doi:10.1093/jme/tjv156

Ito, M., 2021. Mechanisms of succession between two Silphidae, *Necrophila japonica* and *Nicrophorus concolor*

on small vertebrate carcasses. Ecol. Entomol. 47, 1–10. doi:10.1111/een.13084

Jales, J.T., Barbosa, T.M., Soares, V.P., Gama, R.A., 2021. Effect of terbufos (organophosphate) on the cadaveric colonization process: implications for postmortem interval calculation. J. Med. Entomol. 58, 1056–1063. doi:10.1093/jme/tjaa284

Jordan, H.R., Tomberlin, J.K., 2017. Abiotic and Biotic Factors Regulating Inter-Kingdom Engagement between Insects and Microbe Activity on Vertebrate Remains. Insects 8, 54. doi:10.3390/insects8020054

Joy, J.E., Liette, N.L., Harrah, H.L., 2006. Carrion fly (Diptera: Calliphoridae) larval colonization of sunlit and shaded pig carcasses in West Virginia, USA. Forensic Sc. Int. 164, 183–192. doi:10.1016/j.forsciint.2006.01.008

Kadej, M., Szleszkowski, Ł., Thannhäuser, A., Jurek, T., 2020. A mummified human corpse and associated insects of forensic importance in indoor conditions. Int. J. Leg. Med. 134, 1963–1971. doi:10.1007/s00414-020-02373-2

Lashley, M.A., Jordan, H.R., Tomberlin, J.K., Barton, B.T., 2018. Indirect effects of larvae dispersal following mass mortality events. Ecology 99, 491–493. doi:10.1111/ijlh.12426

Lutz, L., Moreau, G., Czuprynski, S., Bernhardt, V., Amendt, J., 2019. An empirical comparison of decomposition and fly colonisation of concealed carcasses in the Old and New World. Int. J. Leg. Med. 133, 1593–1602.

Mariani, R., García-Mancuso, R., Varela, G.L., Inda, A.M., 2014. Entomofauna of a buried body: study of the exhumation of a human cadaver in Buenos Aires, Argentina. Forensic Sci. Int. 237, 19–26. doi:10.1016/j.forsciint.2013.12.029

Mashaly, A.M., Al-Ajmi, R.A., Rady, A., Al-Musawi, Z., Farrukh, A., 2019. Species richness of scavenger insects on different carcass types. Trop. Biomed. 36, 630–639.

Morton, R.J., Lord, W.D., 2006. Taphonomy of child-sized remains: A study of scattering and scavenging in Virginia, USA. J. Forensic Sci. 51, 475–479. doi:10.1111/j.1556-4029.2006.00134.x

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2011. Effects of vulture declines on facultative

scavengers and potential implications for mammalian disease transmission. Conserv. Biol. 26, 453–460. doi:10.1111/j.1523-1739.2012.01827.x

Olea, P.P., Mateo-Tomás, P., Barton, P.S., 2019. Invertebrate scavengers matter. Science 363, 1161–1162.

Olson, Z.H., Beasley, J.C., DeVault, T.L., Rhodes Jr, O.E., 2012. Scavenger community response to the removal of a dominant scavenger. Oikos 121, 77–84. doi:10.1111/j.1600-0706.2011.19771.x

Olson, Z.H., Beasley, J.C., Rhodes, O.E., 2016. Carcass type affects local scavenger guilds more than habitat connectivity. PLoS ONE 11, e0147798. doi:10.1371/journal.pone.0147798

Parmenter, R.R., MacMahon, J.A., 2009. Carrion decomposition and nutrient cycling in a semiarid shrub- steppe ecosystem. Ecol. Monogr. 79, 637–661. doi:10.1890/08-0972.1

Payne, J.A., 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology 46, 592–602.

Pechal, J.L., Benbow, M.E., 2016. Microbial ecology of the salmon necrobiome: evidence salmon carrion decomposition influences aquatic and terrestrial insect microbiomes. Env. Microbiol. 18, 1511–1522. doi:10.1111/1462-2920.13187

Pechal, J.L., Crippen, T.L., Tarone, A.M., Lewis, A.J., Tomberlin, J.K., Benbow, E., 2013. Microbial community functional change during vertebrate carrion decomposition. PLoS ONE 8, e79035. doi:10.1371/journal.pone.0079035

Peisley, R.K., Saunders, M.E., Robinson, W.A., Luck, G.W., 2017. The role of avian scavengers in the breakdown of carcasses in pastoral landscapes. Emu 117, 68–77. doi:10.1080/01584197.2016.1271990

Pereira, E.K.C., Andrade-Silva, J., Silva, O., Santos, C.L.C., Moraes, L.S., Bandeira, M.C.A., Silva, C.R.R., Rebêlo, J.M.M., 2017. *Solenopsis saevissima* (Smith) (Hymenoptera: Formicidae) activity delays vertebrate carcass decomposition. Sociobiology 64, 369–372. doi:10.13102/sociobiology.v64i3.1266

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Willigen, B.V., 2019. Package nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-140.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Ray, R.-R., Seibold, H., Heurich, M., 2014. Invertebrates outcompete vertebrate facultative scavengers in simulated lynx kills in the Bavarian Forest National Park, Germany. Anim. Biodivers. Conserv. 37, 77–88. doi:10.32800/abc.2014.37.0077

Reimchen, T.E., 2017. Diverse ecological pathways of salmon nutrients through an intact marine-terrestrial interface. Can. Field Nat. 131, 350–368. doi:10.22621/cfn.v131i4.1965

Ries, A.C.R., Costa-Silva, V., Dos Santos, C.F., Blochtein, B., Thyssen, P.J., 2021. Factors affecting the composition and succession of beetles in exposed pig carcasses in Southern Brazil. J. Med. Entomol. 58, 104–113. doi:10.1093/jme/tjaa175

Romero, A., 2020. The fate of small-mammal carrion is affected by carcass size and visual conspicuousness in a neotropical rainforest. Therya 11, 423–431. doi:10.12933/therya-20-988

Sebastião, M., Prado e Castro, C., 2019. A preliminary study of carrion insects and their succession in Luanda, Angola. J. Med. Entomol. 56, 378–383. doi:10.1093/jme/tjy203

Shukla, S.P., Plata, C., Reichelt, M., Steiger, S., Heckel, D.G., Kaltenpoth, M., Vilcinskas, A., Vogel, H., 2018. Microbiome-assisted carrion preservation aids larval development in a burying beetle. PNAS 115, 11274–11279. doi:10.1073/pnas.1812808115

Singh, S., Abdullah, N.A.B., Carbaugh, J., Heo, C.C., 2020a. Ants associated with a rat carcass: its implications in forensic entomology with special emphasis on *Carebara diversa* (Hymenoptera: Formicidae). Int. J. Trop. Insect Sci. 40, 703–706. doi:10.1007/s42690-020-00110-1

Singh, S., Yong, S.K., Jalaludin, N.H., Brau, E., Shamsudin, N.N., Keawbaingam, N., Heo, C.C., 2020b. Preliminary observation on the lepidopteran colonization on rat and rabbit carcasses in Malaysia. Trop. Biomed. 37, 1146–1151. doi:10.47665/TB.37.4.1146

Sugiura, S., Hayashi, M., 2018. Functional compensation by insular scavengers: the relative contributions of

vertebrates and invertebrates vary among islands. Ecography 41, 1173–1183. doi:10.1111/ecog.03226

Szleszkowski, Ł., Kadej, M., Thannhäuser, A., Tarnawski, D., Jurek, T., 2018. Ecological aspects of unusual findings of animals nesting inside a mummified human corpse in natural conditions. Forensic Sci. Int. 289, 390–396. doi:10.1016/j.forsciint.2018.06.002

Trumbo, S.T., 1990. Reproductive Success, Phenology and Biogeography of Burying Beetles (Silphidae, Nicrophorus). Am. Midl. Nat. 124, 1–11.

Turner, K.L., Conner, L.M., Beasley, J.C., 2021. Effects of red imported fire ant (Solenopsis invicta) control on carrion use by vertebrate scavengers. Food Webs 29, e00212. doi:10.1016/j.fooweb.2021.e00212

Ururahy-Rodrigues, A., Rafael, J.A., Wanderley, R.F., Marques, H., Pujol-Luz, J.R., 2008. *Coprophanaeus lancifer* (Linnaeus, 1767) (Coleoptera, Scarabaeidae) activity moves a man-size pig carcass: Relevant data for forensic taphonomy. Forensic Sci. Int. 182, e19–e22. doi:10.1016/j.forsciint.2008.09.009

Vasconcelos, S.D., Cruz, T.M., Salgado, R.L., Thyssen, P.J., 2013. Dipterans associated with a decomposing animal carcass in a rainforest fragment in Brazil: notes on the early arrival and colonization by necrophagous species. J. Insect Sci. 13, 145.

Wang, Y., Ma, M., Jiang, X., Wang, J., Li, L., Yin, X., Wang, M., Lai, Y., Tao, L., 2017. Insect succession on remains of human and animals in Shenzhen, China. Forensic Sci. Int. 271, 75–86. doi:10.1016/j.forsciint.2016.12.032

Watson, E.J., Carlton, C.E., 2005. Insect succession and decomposition of wildlife carcasses during fall and winter in Louisiana. J. Med. Entomol. 42, 193–203. doi:10.1093/jmedent/42.2.193

Young, A., Stillman, R., Smith, M.J., Korstjens, A.H., 2014. An experimental study of vertebrate scavenging behavior in a northwest European woodland context. J. Forensic Sci. 59, 1333–1342. doi:10.1111/1556-4029.12468

SUPLEMENTARY MATERIALS

APPENDIX A – Review workflow and references of the selected studies;

FIGURE A.1 – Workflow showing the steps of the systematic review;

APPENDIX B – General database, including Tables B.1 and B.2.

Available online at drive.google.com/drive/folders/1iswjIKdz4jOiDrgxo3nL38M8cuO7kNXz?usp=sharing

CAPÍTULO IV

How many species can sustain the carrion removal function? A global review and reappraisal on the diversity of scavenging vertebrates

"Vultures are the "soap of the savannah", quickly and efficiently removing waste, controlling pests, and preventing disease outbreaks — all free of charge**"**

Evan R. Buechley & Cagan H. Sekercioglu (2016) – *Current Biology*, p.R561.

ABSTRACT

Tons of dead organic matter are generated annually due to human activities and ecological processes worldwide. In urban and agricultural landscapes, the accumulation of carrion and other detritus triggers a need to better understand the functions provided by scavenger communities. Over the past two decades, interest in vertebrate scavengers has increased substantially. Thus, there is a need for synthesis, reappraisal, and a better understanding of the diversity, structure, and composition of vertebrate scavenger communities. Here, we assembled a large global database of monitored carcasses to compile a global scavenger list, as well as to evaluate scavenger richness and composition of key groups (birds and mammals). We also estimated patterns of visitation and arrival on carcasses for each recorded species. We observed at least 374 vertebrate species on carrion, mostly birds. On average, scavenger communities were composed of less than 10 vertebrate species, suggesting that carrion removal is a function provided by a few species worldwide. Each scavenger species can visit more than 24% of the available carcasses, as well as detect carcasses within about four days on average. Birds and mammals showed similar patterns for both metrics. Given that only 18% of the communities were composed only of mammals, vultures, corvids and other raptors appear as the main carrion visitors worldwide.

Keywords: apex predator, apex scavenger, carnivores, carrion ecology, corvid, necrophagous, vultures.

INTRODUCTION

Dead organic matter and its role in ecosystem functioning have been largely studied by ecologists, mainly those derived from plant decomposition (Kampichler & Bruckner 2009). Despite the main contribution of organic vegetal matter to the ecosystems (Swift et al. 1979), scientists have also recognized the value of dead animals, i.e. carrion, to the dynamics, functioning and maintenance of biodiversity in the ecosystems, mainly in the last two decades (Moleón & Sánchez-Zapata 2015; Benbow et al. 2019). Carrion encompasses any animal-derived dead organic matter, but the term often refers to decaying vertebrate carcasses (Benbow et al. 2016). Vertebrate deaths

create a local disturbance that attracts a plethora of consumers, including microbes, insects, birds, and mammals (DeVault et al. 2003; Carter et al. 2007).

Human activities largely contribute to the accumulation of carrion and other types of dead organic matter in the ecosystems, mainly due to food production. For instance, more than seven million tons of fish are discarded in the world, as well as hunting in the USA can also subside about $6.9 \cdot 10^5$ tons of carcasses annually to the ecosystems (see Oro et al. 2013 for a review). Besides, ecological processes such as predation by large carnivores can also generate tons of carrion in many ecosystems (Bump et al. 2009; Elbroch et al. 2017; Barry et al. 2019). The high availability of carrion and other detritus in both well-conserved and human-altered habitats creates scavenging opportunities for several vertebrate species. The accumulation of carrion in human-dominated landscapes underpins the importance of scavengers to improve human and ecosystem healthy (Moleón et al. 2014; DeVault et al. 2016; O'Bryan et al. 2018).

Historically, the role of scavengers in structuring food webs, as well as communities was largely underestimated (Wilson & Wolkovich 2011; Moleón & Sánchez-Zapata 2015). Recent evidence has considered vertebrate scavengers as highly efficient in removing carrion, given that they can find the majority of the available carcasses and remove them within a few days (DeVault et al. 2003; Benbow et al. 2019). For instance, the continental population of the turkey vulture (*Cathartes aura*) can remove up to 1000 tons of organic matter annually (Grilli et al. 2019). Indeed, New and Old World vultures are unique terrestrial species specialized in carrion consumption, a fact that justifies an increasing body of interest in these birds (Moleón & Sánchez-Zapata 2015). However, corvids, other raptors (e.g. eagles and hawks), and carnivorous mammals also play complementary contributions in the carrion removal process (Inger et al. 2016; Mateo-Tomás et al. 2017). For instance, some facultative scavengers can act as providers of carrion, such as wolves and pumas (Bump et al. 2009; Barry et al. 2019).

Almost all carnivorous birds and mammals are considered facultative scavengers (Benbow et al. 2019). Despite this, the total number of potential scavenger species worldwide is uncertain. Some recent evidence has

estimated the number of fewer than 100 species (e.g. Mateo-Tomás et al. 2015; Pain et al. 2019). Given this number and the fact that birds are often considered as main scavengers (Sebastián-González et al. 2013; Inger et al. 2016; Peisley et al. 2017), carrion removal is likely an ecological function provided by fewer species compared to other ones such as seed dispersal and pest control (Sekercioglu 2006). Thus, there is a need to determine how many species can sustain carrion removal efficiently, as well as whether the composition of the scavenger community can affect patterns of carrion removal worldwide.

Here, we conducted a literature review to i) compile a global scavenger list, focused on birds and mammals, ii) describe and measure species richness and composition of key scavenger groups (birds and mammals) in communities worldwide, and iii) estimate global patterns of visitation and arrival time of vertebrate scavengers on carcasses.

METHODS

Data Search

We used the Web of Science database to search for studies that addressed interactions between carrion and vertebrate scavengers from the title, abstracts, and keywords. Given that birds and carnivorous mammals are the most common visitors on carcasses, we focused our search on these groups. We searched for studies published between 2010 and 2019 (papers, notes, and reviews in English) using the following combination of terms: (bird* OR avian OR mammal* OR carnivor* OR raptor*) AND (carcass* OR carrion OR scaveng* OR corpse OR roadkill). The result of this search was refined to the Web of Science categories Ecology, Zoology, Environmental Sciences, Biodiversity Conservation, Ornithology, Biology, and Environmental Studies. Thus, we obtained 1483 studies for the initial title and abstract screening.

In both abstract and full-text screening, studies were selected if they reported consumption or visitation of vertebrates on carrion (mainly birds and mammals), considering only empirical data (rather than modeled ones). We also considered studies with indirect evidence of carrion feeding, such as the occurrence of necrophagous

insects in scats or pellets (diet studies). In the full-text screening stage, we also considered any information about carrion consumption by vertebrates in any article part, including the introduction and supplementary materials. We did not consider studies using captive animals. Some regional (e.g. country and continental scale) and global reviews were compiled by providing a list of scavengers not documented in the other empirical studies. In total, we obtained 298 studies for this review (see the complete review workflow in Figure 1). These studies encompassed 444 sites in 78 countries and 19 regional or global lists (Figure 2), which were used to generate a global scavenger list using data collected from 1846 to 2018.

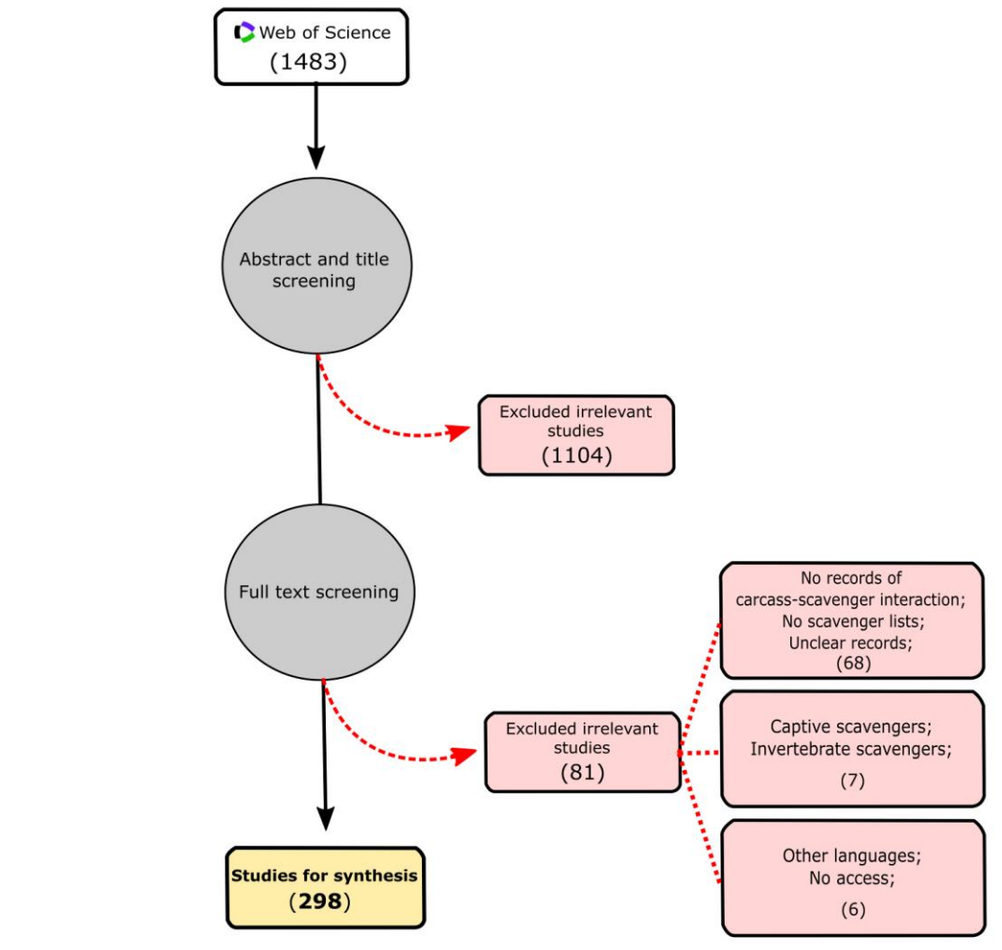

Figure 1 – Systematic review workflow showing all the steps to acquire the studies in this study. Red boxes and arrows indicate the exclusion of studies after each screening process.

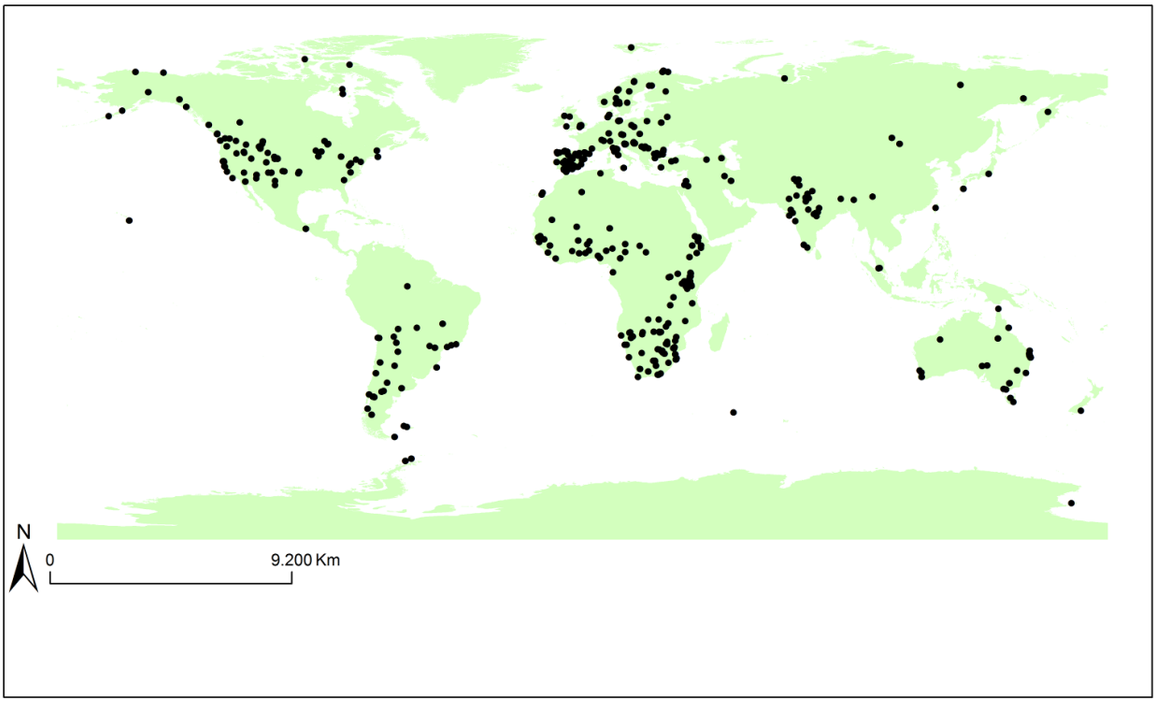

Figure 2 – Global distribution of sites (general database) where the empirical or observed records of scavenging by vertebrates were documented in this review.

Database assembly

We extracted general information about all selected studies (n=298), i.e. the main land uses (e.g. temperate forest and grassland), type of study (i.e. diet, community-based, occasional feeding notes, survey, and scavenger list/records from reviews), carcass source (e.g. roadkill, market, or predation-based kills), type of carcass used or consumed in each site per study (e.g. mammals and birds), and method to record scavengers (e.g. camera-trap, direct observation, and pellets). Finally, we compiled the number of carcasses visited/consumed by each recorded scavenger, expressing as a percentage of all carcasses used/observed in the study. Furthermore, the minimum elapsed time (days) for each species to find, at least, one carcass was used to measure the mean arrival time of each scavenger.

Richness and composition of scavenger communities

From studies focused on monitored carcasses (e.g. those with motion-trigged cameras; 132 communities/sites from 124 studies), we described the observed communities by quantifying the total richness and scavenger taxon composition (i.e. the proportion of birds and mammals) per community. For birds, we quantified the number of species and some morphospecies ("species" hereafter for convenience) of vultures, corvids, and other raptors (e.g. eagles and owls); while for mammals we classified the species as Carnivora mammals (mainly apex predators such as foxes and wolves), rodents, and other mammalian taxa (e.g. marsupials and boars). We pulled together different studies carried out in the same areas/sites to acquire only a species list per site.

Carcass visitation rate and arrival time

To measure visitation and arrival patterns of scavenger species, we considered the same data from studies that documented and/or surveyed scavenger communities on monitored carcasses, as described above. This dataset accounts for at least 10431 carcass inputs monitored between 1976 and 2018 (some studies did not report the total number of inputs, and we considered at least one input to estimate the total sampling effort). We quantified the number of carcasses visited or scavenged partially or totally by each vertebrate on each carcass input in the studies (i.e. % of all used carcasses, separating by carcass species or taxon). We obtained 34 studies to measure this variable, totaling 43 communities (details in Supplementary Materials - Dataset A). For the arrival time, we obtained 10 studies in 11 communities (Dataset B). From these studies, 38 independent carcass inputs were used to measure the mean time (in days) that avian and mammalian scavengers take to find carcasses. Studies carried out at the same site were pulled together, considering mean values among them for both variables.

RESULTS

Most of the studies only provided occasional or literature-cited records of scavenging by vertebrates (101 studies with observed records or mentions from the literature, 33.89% from the total selected studies), followed by diet studies (27.51%) and community surveys (26.51%). Temperate forests, grasslands, and agricultural areas were the most common land uses in the studies (Figure 3). Inland wetlands (e.g. nearby rivers and mangroves) and tropical forests were the less explored habitats across sampling sites. Studies on scavenger communities were mostly

experimental approaches using carcasses placed in the study area by the researchers (Figure 4), which were acquired in markets, local farms, and other sources. Also, many studies used carcasses that died of natural causes and were found near the study area. Interestingly, the use of predation remains (kills) provided by large carnivorous mammals was the third most common carcass source (e.g. lion kills; Figure 4). Consumption of urban garbage and marine discards were also observed or used as a model in the studies. By far the most common carcass type reported as a resource for scavengers (or used as a carrion model) was wild and/or domestic mammals (present in 183 studies), followed by birds (80 studies) and invertebrates (54 studies; Figure 4). Also, plant matter was often observed in the diet of scavenging birds and mammals (36 studies), such as fruits, leaves, and seeds. There are records of garbage consumption (cited in 20 studies), including excrement, human food remains, glass, honey, plastic, paper, meat, and fabrics.

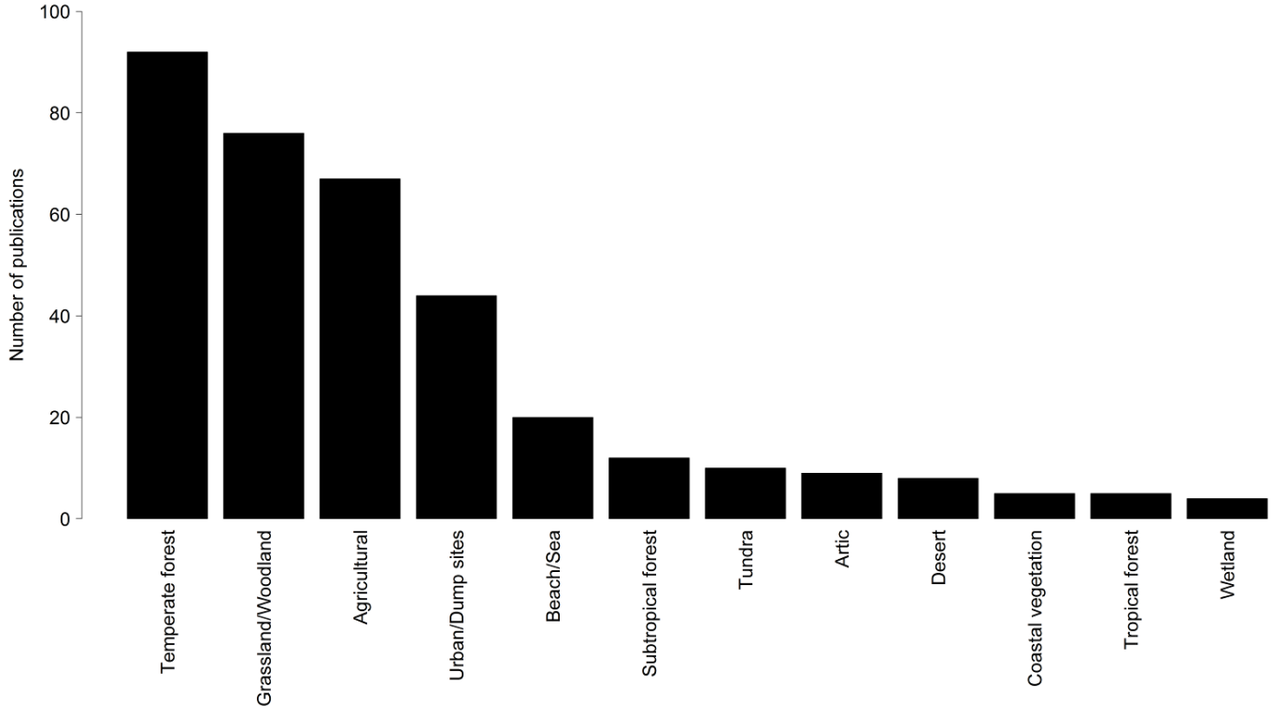

Figure 3 – The main land uses of the sites where empirical studies dealing with interactions between carcasses and vertebrates were carried out in this review.

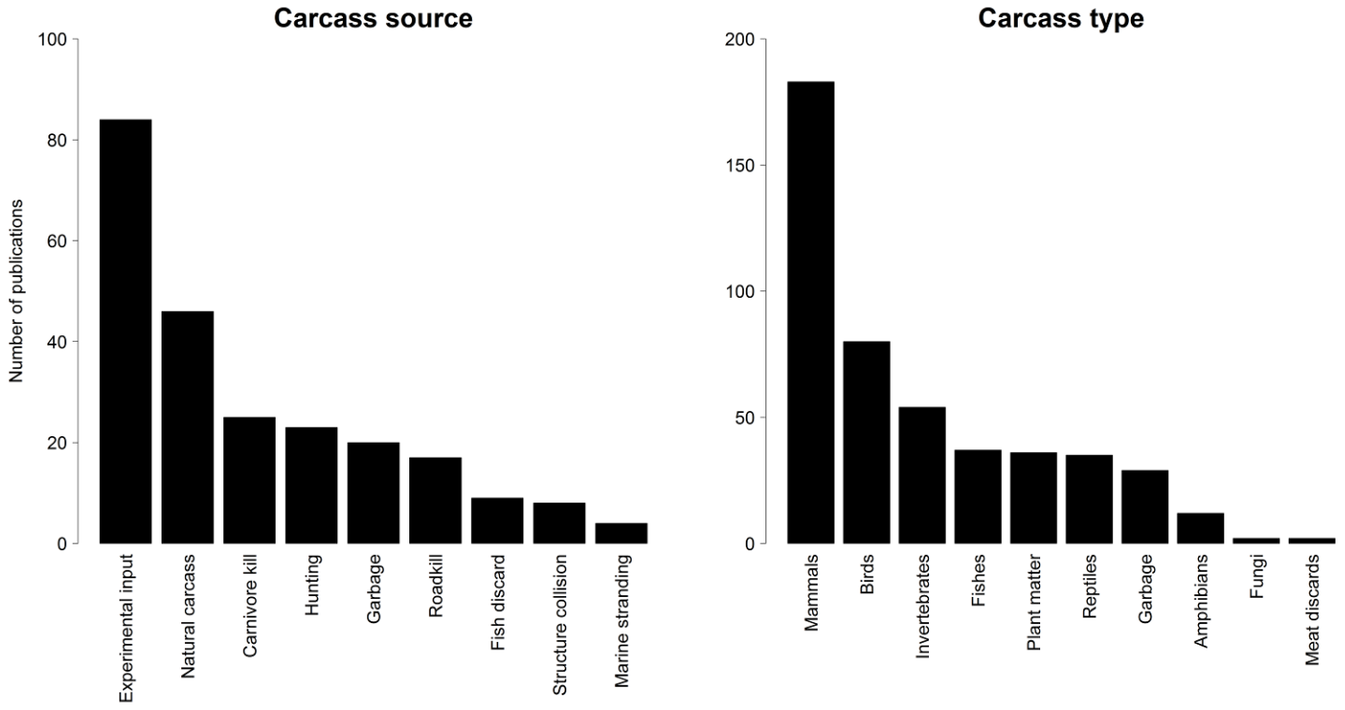

Figure 4 – Carcass models information of the studies observed in this review. Experimental input refers to experimental carcasses purchased or acquired locally by researchers, not including the relocation of carcasses found in the study area ("natural carcasses") or on nearby roads (roadkills). For carcass types, plant matter includes seeds, entire fruits, pulps, flowers, and leaves; while garbage includes plastic, paper, human food, and other urban waste. "Meat discards" refers to animal-based materials without clear identification.

Vertebrates recorded on carrion

We found at least 374 confirmed vertebrate species on carrion (i.e. excluding a few morphospecies at family and genera level) belonging to four groups, birds (243 species), mammals (123), reptiles (6), and amphibians (2) (Table S1). As expected, birds were the most common group documented on carrion. We found that 128 bird species from terrestrial environments were documented as carrion-eaters at least in one study, as well as 77 marine birds. We also recorded 38 birds typically insectivores visiting carrion (Supplementary materials - Table S1). The most cited avian scavengers were *Corvus corax* (42 studies), *Gyps fulvus* (39), *Neophron percnopterus* (37), *Aquila chrysaetos* (30), and *Cathartes aura* (28). Many typical scavenger birds such as vultures were poorly cited or studied, e.g. *Gymnogyps californianus* (five studies), *Cathartes burrovianus* (four), *Gyps bengalensis* (four),

Gyps indicus (three), *Sarcoramphus papa* (three), and *Cathartes melambrotus* (two). For mammals, 115 species were recorded feeding on carcass tissues, including domestic species such as dogs and cats (cited in 27 and 20 studies, respectively), rodents (e.g. *Rattus* spp. and *Apodemus* spp.), and large carnivores (e.g. *Ursus arctos* and *Panthera leo*). Also, one study documented the use of carrion by humans. Some herbivore species such as rabbits and deer were also documented on carrion (Table S1). The most commonly cited mammalian scavengers were *Vulpes vulpes* (cited in 65 studies), *Canis familiaris* (27), *Canis lupus* (25), *Canis latrans* (22), and *Felis catus* (20). Finally, the most cited reptile in our data was *Varanus varius* (cited in five studies), a well-documented large lizard on carrion, while the other species were cited in only one study.

Vertebrate scavenger communities

Considering all recorded visiting species on monitored carcasses, we observed a mean of 6.40 scavenger species across communities (ranging from 1 to 30 species; Figure 5). However, the majority of the communities were composed of less than 10 species (n=95 out of 132 communities, 71.96%; Figure 5). Overall, scavenger communities were composed of a greater proportion of birds on average (53.28% ±34.88 SD), followed by mammals (45.46% ±34.76) and other vertebrates (1.26% ±4.34; Figure 6). Also, more than half of the communities (n=70, 53.03%) were composed of more birds than mammals, while 31 communities (23.48%) were composed only of birds. About 18% of the communities were composed only of mammals.

Vultures were recorded on carcasses in 47 communities worldwide (35.60%), while corvids in 71 (53.78%) and other raptors in 88 (66.66%; Figure 6; Table S2). Overall, the main bird contribution in the global community compositions was provided by facultative scavenger raptors other than corvids (mean proportion of 26.37% ±29.91). For mammals, Carnivora order was the most common group across communities, occurring in 92 ones (~70%), followed by other non-Carnivora species (n=35; 26.51%) and rodents (i.e. 21; 15.90%). Overall, Carnivora species were the main visiting mammals on carcasses, representing 33.43% (±30.90 SD) of the scavenger communities on average. All data used in Figures 5 and 6 and the detailed information about the scavenger communities is available in Table S2.

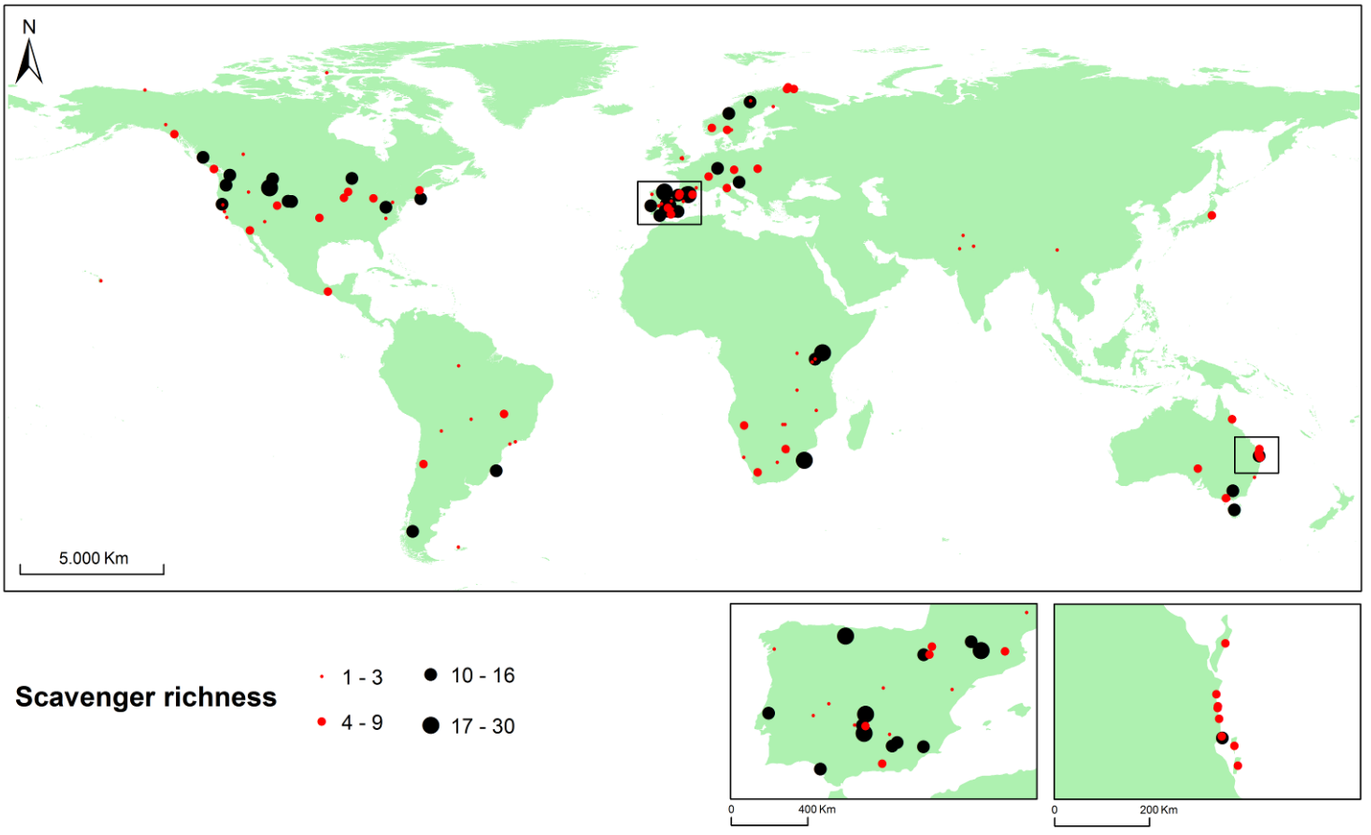

Figure 5 – Species richness of scavenger communities that used monitored carcasses in the sampling method. Red points highlight communities composed of less than 10 species, a pattern discussed in the review. The two inserts below the main map represent the Iberian Peninsula and the Australian east coast, which concentrate a large number of studies. All data used to generate this figure are available in Table S2.

Vertebrate scavengers visiting carcasses

Considering all recorded vertebrate scavengers, we observed that each species visited 24.74% (±28.20 SD) of the available carcasses across the studies, ranging from 0.30 to 100%. Each avian scavenger visited a mean of 23.60% (±27.56 SD) of the carcasses, while mammals showed mean values of 25.95% (±28.98). Eleven birds were documented visiting more than 80% of the deployed carcasses across studies (range: 7-115 carcasses in 20 sites), i.e. three vultures (*Vultur gryphus*, *Gyps fulvus*, and *Neophron percnopterus*), five corvids (*Garrulus glandarius*, *Pica pica*, *Corvus corax*, *Corvus cornix*, and *Pica hudsonia*), and three other raptors (*Phalcoboenus australis*, *Haliaeetus leucocephalus*, and *Aquila chrysaetos*). For mammals, five species showed a similar pattern of

attending (range: 11-28 carcasses in seven sites), i.e. *Vulpes vulpes*, *Sus scrofa*, *Nyctereutes procyonoides*, *Canis latrans*, and *Crocruta crocruta*.

Vertebrate arrival in carcass sites

We found that vertebrate scavengers can detect carcasses in 4.17 days (±3.38 SD), ranging from <0.5 to 16 days. On average, birds arrive on carcasses in 3.68 days (±3.31), while mammals take a little more time, 4.63 days (±3.41). The most efficient species in locating carrion were 12 scavenging birds, which took less than one day to find carcasses on average. For instance, *Phalcoboenus australis* showed the shortest time to locate carcasses (just 2.4 minutes), followed by *Corvus capensis* (13 minutes), *Melierax canorus* (9 hours), *Gymnorhina tibicen* (14 hours), and *Pica hudsonia* (15 hours).

DISCUSSION

Scavenger vertebrates compose widespread species-poor communities in almost all types of habitats and ecosystems worldwide, such as forests, grasslands, deserts, beaches, open seas, urban, and even polar areas. In these natural and urban environments, vertebrate scavenger communities were mainly assembled by a few species, typically <10 species. This result supports findings in other broader-scale studies (Inger et al. 2016; Mateo-Tomás et al. 2017). Even species-poor communities can contribute to the removal of tons of dead organic matter, which is not limited to terrestrial vertebrate carcasses, but also invertebrates, plant matter, marine discards, and urban wastes. For instance, we found that a community composed of three scavenger species was able to remove seven mule deer carcasses (~56 kg on average) in 5.5 days on average (Grubb et al. 2019). Although our data consider the contributions of other non-vertebrate scavengers in the removal process, such as insects, large vertebrates are often considered the main carrion-eaters (DeVault et al. 2003; Olson et al. 2012; Hill et al. 2018). Thus, few vertebrate species are highly efficient in removing carrion, given that each vertebrate scavenger sustains high consumption rates (e.g. Grilli et al. 2019), finds carcasses in a few days (less than five), and feeds on most of the available carcasses, such as 80-100% of them.

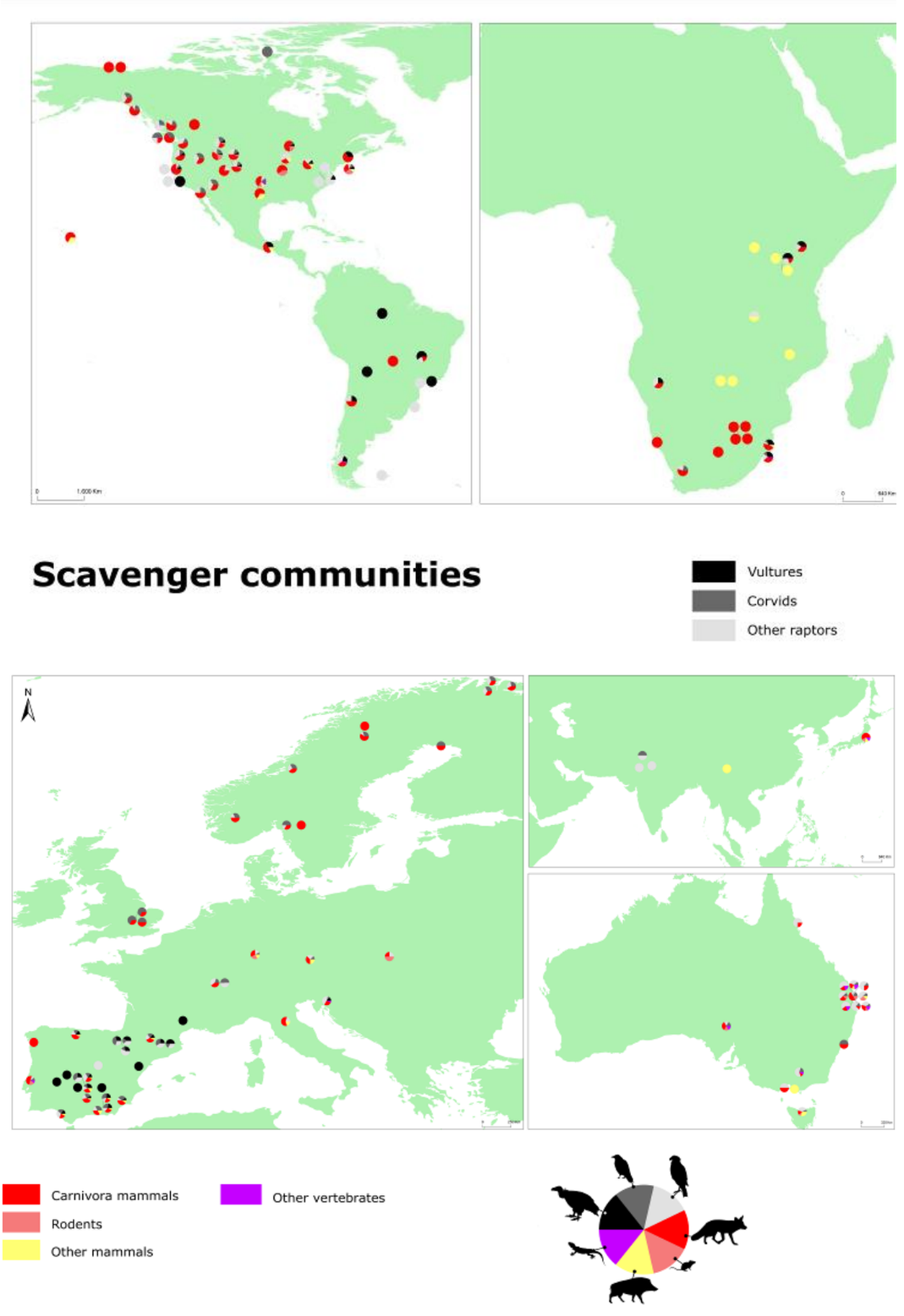

Figure 6 – Composition of the scavenger communities used in this study. The observed richness in each site is available in Figure 5. All data used to generate this figure are available in Table S2.

Although the presence of vultures is indeed outstanding in the carrion removal process, the maintenance of this function seems to be dependent on local communities mainly assembled by a similar mean proportion of birds and mammal species. Birds include the well-known obligate avian scavengers (New and Old World vultures), which often are considered more efficient in removing carrion than other facultative species, such as mammals (Ogada et al. 2011; Sebastián-González et al. 2013; Hill et al. 2018). In this review, some vulture species were documented feeding on almost all deployed carcasses in the studies (Cortés-Avizanda et al. 2012; Arrondo et al. 2019; Méndez et al. 2019). However, vultures do not occur in the entire world, which highlights the importance of other facultative scavengers such as corvids, eagles, and hawks. Some corvid species showed high scavenging efficiencies, such as visitation patterns in more than 80% of carcasses and very quickly arrivals (within minutes or hours) on carcasses. Thus, the dominance of birds in scavenger communities, mainly vultures and corvids, seems to improve the carrion removal process, as pointed out in some experimental studies (Ogada et al. 2011; Sebastián-González et al. 2013; Inger et al. 2016; Hill et al. 2018).

Despite the importance of scavenging birds, we also demonstrated that mammalian scavengers play a similar function alongside birds. Visitation rates of mammals on carcasses were slightly higher than birds on average. For instance, species such as red fox (*Vulpes vulpes*) and wild boar (*Sus scrofa*) were commonly recorded in many sites worldwide visiting a high proportion of carcasses (>80%). Also, more than 45% of the selected communities were dominated by mammals. Therefore, our findings underpin a need for diverse vertebrate communities, composed of obligate and facultative scavengers, to maintain the keystone function of removing animal-derived dead organic matter from both human-altered and well-conserved areas worldwide (Mateo-Tomás et al. 2017; Benbow et al. 2019).

Our review highlights another key function provided by mammals in the carrion dynamic, the provision of carcasses to scavengers. Predation remains were the second most common carcass source in the original studies. For instance, pumas (*Puma concolor*) killed more than 1000 prey weighing on average of 135 kg in a study in the USA, which provided food resources for at least 38 vertebrate scavengers (Elbroch et al. 2017). Also, at least 18 scavengers in an area of Slovenia fed on prey killed by the Eurasian lynx (*Lynx lynx*) (Krofel et al. 2019). Thus,

large carnivores can act as an ecosystem engineer species (*sensu* Barry et al. 2019). However, in the context of carrion ecology, we prefer to call these species "butcher species", given that they play upon many large preys, breakdown their carcasses, and abandon most of the carcasses in the environments, beneficing many scavengers and other predators.

Many studies recorded domestic species such as dogs and cats on carrion. Interactions between domestic species and wild carcasses may expose humans to harmful pathogens. For instance, domestic dogs on carcasses may expose humans to spongiform encephalopathy from deer carcasses (Jennelle et al. 2009). Also, the decline of vultures in India is correlated with an increase of dogs and other facultative scavengers in livestock carcasses, which can enhance the spread of rabies in urban areas (Markandya et al. 2008). Wild and domestic rodents (e.g. *Rattus rattus* and *Apodemus* spp.) often visit carrion, but the role of this group in carrion ecology has been poorly studied. However, rodents may contribute to the removal of hard tissues, such as bones (Haglund 1992). Thus, the majority of wild mammals play an important role in removing carrion, but the presence of domestic species on carrion should be carefully investigated in actions of carcass disposal management worldwide.

CONCLUDING REMARKS

Carrion inputs in natural and anthropogenic environments account for tonnes annually (Mateo-Tomás et al. 2015; Grilli et al. 2019), which feed up to 374 vertebrate species worldwide. Our estimates stress the unique and crucial role of vertebrate scavengers in removing carrion, but also plant matter, urban garbage, and marine discards. Also, we provided a comprehensive global list of vertebrate scavengers, as well as communities (Table S1 and S2). Finally, our study supports that, a) ecosystem functions provided by scavengers rely on few species in local communities (typically <10), b) birds are the main vertebrate scavengers (mainly vultures and corvids), and dominate the majority of the scavenger communities, c) mammals have a secondary role in carrion removal (e.g. later arrivals), but complementary with other scavengers, given that most efficient communities (therefore, more stable) are composed by a similar proportion of birds and mammals; d) predation by mammals can provide large inputs of carrion to the environments ("butcher species"); e) domestic mammals (dogs and cats) are frequent

visitors of carcasses, and f) other vertebrate groups, such as Amphibia and reptiles, are rarely documented on carcasses.

REFERENCES

Arrondo E, Morales-Reyes Z, Moleón M, Cortés-Avizanda A, Antonio J, Sánchez-Zapata JA. 2019. Rewilding traditional grazing areas affects scavenger assemblages and carcass consumption patterns. Basic and Applied Ecology 41:56–66. Elsevier GmbH. Available from https://doi.org/10.1016/j.baae.2019.10.006.

Barry JM, Elbroch LM, Aiello-Lammens ME, Sarno R, Seelye L, Kusler A, Quigley H, Grigione M. 2019. Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. Oecologia 189:577–586. Springer Berlin Heidelberg. Available from https://doi.org/10.1007/s00442-018-4315-z.

Benbow ME, Barton PS, Ulyshen MD, Beasley JC, DeVault TL, Strickland MS, Tomberlin JK, Jordan HR, Pechal JL. 2019. Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89:e01331.

Benbow ME, Tomberlin, JK, Tarone, AM. 2016. Introduction to Carrion Ecology, Evolution, and Their Applications. In: Benbow, M.E., Tomberlin, J.K. & Tarone, A.M (eds). *Carrion Ecology, Evolution, and their Applications*. CRC Press, Taylor & Francis Group, Boca Raton, USA, p.13-30.

Bump JK, Peterson RO, Vucetich JA. 2009. Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90:3159–3167.

Carter DO, Yellowlees D, Tibbett M. 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94:12–24.

Cortés-Avizanda A, Jovani R, Carrete M, Donázar JA. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. Ecology 93:2570–2579.

DeVault TL, Beasley JC, Olson ZH, Moleón M, Carrete M, Margalida A, Sánchez-zapata JA. 2016. Ecosystem Services Provided by Avian Scavengers. Pages 235–270 in C. H. Şekercioğlu, D. G. Wenny, and C. . Whelan, editors. Why Birds Matter: Avian Ecological Function and Ecosystem Services. Chicago, USA.

DeVault TL, Rhodes Jr OE, Shivik JA, Rhodes OE, Shivik DeVault JA, DeVault TL, Rhodes OE. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234.

Elbroch LM, Malley CO, Peziol M, Quigley HB. 2017. Vertebrate diversity benefiting from carrion provided by pumas and other subordinate, apex felids. Biological Conservation 215:123–131. Elsevier. Available from http://dx.doi.org/10.1016/j.biocon.2017.08.026.

Grilli M, Bildstein K, Lambertucci S. 2019. Nature's clean-up crew: Quantifying ecosystem services offered by a migratory avian scavenger on a continental scale. Ecosystem Services 39:100990. Elsevier B.V. Available from https://doi.org/10.1016/j.ecoser.2019.100990.

Grubb TG, Lopez RG, Ellis MM. 2019. Winter Scavenging of Ungulate Carrion by Bald Eagles, Common Ravens, and Coyotes In Northern Arizona. Journal of Raptor Research 52:471–483.

Haglund WD. 1992. Contribution of rodents to postmortem artifacts of bone and soft tissue. J Forensic Sci. **37**:1459–1465.

Hill JE, DeVault TL, Beasley JC, Rhodes OE, Belant JL. 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecology and Evolution 8:2518–2526.

Inger R, Per E, Cox DTC, Gaston KJ. 2016. Key role in ecosystem functioning of scavengers reliant on a single common species. Scientific Reports 6:2–6. Nature Publishing Group. Available from http://dx.doi.org/10.1038/srep29641.

Jennelle CS, Samuel MD, Nolden CA, Berkley EA. 2009. Deer Carcass Decomposition and Potential Scavenger Exposure to Chronic Wasting Disease. Journal of Wildlife Management 73:655–662. Available from http://www.bioone.org/doi/abs/10.2193/2008-282.

Kampichler C, Bruckner A. 2009. The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. Biological Reviews 84:375–389.

Krofel M, Skrbinšek T, Mohorović M. 2019. Using video surveillance to monitor feeding behaviour and kleptoparasitism at Eurasian lynx kill sites. Folia Zoologica 68:274–284.

Markandya A, Taylor T, Longo A, Murty MN, Murty S, Dhavala K. 2008. Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. Ecological Economics 67:194–204.

Mateo-Tomás P, Olea PP, Moleón M, Selva N, Sánchez-Zapata JA. 2017. Both rare and common species support ecosystem services in scavenger communities. Global Ecology and Biogeography 26:1459–1470.

Mateo-Tomás P, Olea PP, Moleón M, Vicente J, Botella F, Selva N, Viñuela J, Sánchez-Zapata JA. 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. Diversity and Distributions 21:913–924.

Méndez D, Marsden S, Lloyd H. 2019. Assessing population size and structure for Andean Condor Vultur gryphus in Bolivia using a photographic 'capture-recapture' method. Ibis 161:867–877.

Moleón M, Sánchez-Zapata JA, Margalida A, Carrete M, Owen-Smith N, Donázar JA. 2014. Humans and scavengers: The evolution of interactions and ecosystem services. BioScience 64:394–403.

Moleón M, Sánchez-Zapata JA. 2015. The Living Dead: Time to Integrate Scavenging into Ecological Teaching. BioScience 65:1003–1010.

O'Bryan CJ, Braczkowski AR, Beyer HL, Carter NH, Watson JEM, McDonald-Madden E. 2018. The contribution of predators and scavengers to human well-being. Nature Ecology and Evolution 2:229–236.

Ogada DL, Torchin ME, Kinnaird MF, Ezenwa VO. 2011. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. Conservation Biology 26:453–460.

Olson ZH, Beasley JC, DeVault TL, Rhodes Jr OE. 2012. Scavenger community response to the removal of a dominant scavenger. Oikos 121:77–84.

Oro D, Genovart M, Tavecchia G, Fowler M, Martínez-Abraín A. 2013. Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16:1501–1514.

Pain DJ, Mateo R, Green RE. 2019. Effects of lead from ammunition on birds and other wildlife: A review and update. Ambio 48:935–953. Springer Netherlands.

Peisley RK, Saunders ME, Robinson WA, Luck GW. 2017. The role of avian scavengers in the breakdown of carcasses in pastoral landscapes. Emu 117:68–77.

Sebastián-González E, Sánchez-Zapata JA, Donázar JA, Selva N, Cortés-Avizanda A, Hiraldo F, Blázquez M, Botella F, Moleón M. 2013. Interactive effects of obligate scavengers and scavenger community richness on lagomorph carcass consumption patterns. Ibis 155:881–885.

Sekercioglu CH. 2006. Increasing awareness of avian ecological function. TREE 21:464–471.

Swift MJ, Heal OW, Anderson JM. 1979. Decomposition in terrestrial ecosystems. University of California Press, Berkeley.

Wilson EE, Wolkovich EM. 2011. Scavenging: How carnivores and carrion structure communities. Trends in Ecology and Evolution 26:129–135.

SUPPLEMENTARY MATERIALS

General database, Table S1, Table S2, Dataset A and B are available online at drive.google.com/drive/folders/1iswjIKdz4jOiDrgxo3nL38M8cuO7kNXz?usp=sharing

CAPÍTULO V

Modeling the effect of vertebrate scavengers on the transmission of zoonotic diseases in the wildlife-livestock interface

“Even beasts are made by God and have a purpose, even the bad ones like wolves, they have their own role, they eat the corpses of dead animals, they cleanse the landscape**”**

Stefan Dunca, 50 years old, shepherd.

(In: Roué & Molnar (eds), 2016. Knowing our lands and resources [...] UNESCO, Paris, p. 34)

ABSTRACT

Zoonotic diseases often arise from wildlife to humans, such as past and current pandemics. In the complex and multifaceted dynamic of these diseases, an interface between wild fauna and domestic animals is commonly associated with outbreaks and spillover of several zoonoses. A key and underestimated component of this interface is the presence of vertebrate scavengers, which may contribute to decreasing the prevalence of some diseases by removing infected carcasses in the wild and human-altered landscapes, as well as by regulating the encounters among infected carcasses and potential hosts. However, scavengers have also been associated with the transmission of infectious diseases. Here, we fitted a global model to understand the role of different facets of scavenger diversity on the prevalence of anthrax disease. We found that vulture diversity and scavenger community composition (i.e. mammal-to-bird ratio) are not associated with anthrax cases. However, we detected a positive relationship between the diversity of facultative scavengers and anthrax cases. Our findings suggest that the prevalence of anthrax can be enhanced in regions with species-rich communities of facultative scavengers, given that these species can act as mechanical hosts of the disease. However, another likely explanation is that anthrax-generated carcasses provide food resources for scavengers, which may contribute to the attraction of scavengers to both wild and domestic carcasses.

Keywords: *Bacillus anthracis*, carcass removal, carrion, disease ecology, wildlife diseases, zoonosis.

INTRODUCTION

In the past and the present, humanity has faced several outbreaks of infectious diseases. From the Black Death (plague) in the fourteenth century to the recent coronavirus disease (COVID-19), several diseases continue to spread from wildlife to humans (Mohan and Vinod, 2020; Salkeld et al., 2016). Over recent decades, outbreaks of novel diseases are strongly associated with the demand for animal-based food products and alterations of natural landscapes by the human population (FAO, 2013). Deforestation, human population density, and conversions of natural areas into pastures and croplands are common drivers of zoonotic diseases, i.e. those transmitted among animals, especially vertebrates (FAO, 2013; Martin et al., 2011).

Many zoonotic diseases arise due to spillover events from wildlife to domestic animals, before any contact with humans, such as avian influenza, rabies, and leptospirosis (Wiethoelter et al., 2015). Thus, human actions to acquire animal-sourced products, such as hunting, massive transhumances, and agricultural intensification alongside natural habitats have increased the spreading of zoonoses in the interface wildlife-livestock (Jones et al., 2013; Martin et al., 2011; Wiethoelter et al., 2015). In addition, the climate can affect this interface, illustrating the complex and multifaceted dynamics of these diseases (Salkeld et al., 2016; Zhang et al., 2022). Therefore, spillover events and outbreaks of zoonoses are difficult to predict, which creates a challenge for governments to implement control and surveillance strategies. As part of the strategies to mitigate the impacts of zoonotic emergencies, there is a need to understand what factors control the persistence of wildlife diseases in their "cryptic phases" (Salkeld et al., 2016), such as in the natural reservoir before any spillover to livestock areas.

Livestock density across the globe comprises a key driver of environmental degradation and disease spreading (FAO, 2013). In regions that suffered declines in their native biodiversity via the intensification of agriculture and livestock, the likelihood of contact among domestic and wild animals is highly intensified (Jones et al., 2013). More livestock in the human-altered landscapes means a high density of potential hosts for many infectious parasites, as well as increases the generation of animal wastes, chemical and biological pollution in the nearby natural ecosystems (FAO, 2013; Jones et al., 2013).

The livestock presence and their wastes (e.g. carcasses) near natural ecosystems attract both predators and scavengers (wild and domestic) to human-altered landscapes (FAO, 2013; Rocha et al., Capítulo IV). In particular, the widespread availability of dead animals (carrion) may represent an additional infection risk for wildlife and livestock. Several pathogens of zoonotic diseases remain active or transmissible in host carcasses, such as chronic wasting diseases (CWD), plague, African swine fever, and anthrax (Escobar et al., 2020; Hugh-Jones and Vos, 2002; Probst et al., 2019; Salkeld et al., 2016). For instance, after severe outbreaks of bovine spongiform encephalopathy (a prion disease like CWD) in rural areas of Europe, strict sanitary policies were implemented to mechanically remove potentially infected carcasses. This example illustrates the concerning problem of carcasses

as foci of zoonotic diseases. Given that where there are carcasses, there are scavengers to consume them; these animals may play an important role in the dynamics of wildlife diseases, such as those that affect wild-domestic hosts and humans, given that they are strongly associated with the interface wildlife-livestock (Rocha et al., Capítulo IV).

The role of vertebrate scavengers in the dynamic of zoonoses is an open debate in the ecological and epidemiological literature (O'Bryan et al., 2018; Plaza et al., 2020). For some diseases, scavengers as often pointed out as disseminators by acting as mechanical vectors or hosts, such as for rabies and CWD (Borchering et al., 2017; Escobar et al., 2020), while there is also evidence of a control effect by reducing the pathogen density (or vectors) in carcass sites, such as for diarrhea and African swine fever (Lim et al., 2020; Probst et al., 2019). In general, vertebrate scavengers are pointed out as controllers of wildlife diseases due to two main factors: i) the consumption of infected carcasses can reduce risk zones, given that their acid stomachs can neutralize pathogens (Blumstein et al., 2017); ii) the higher competitive ability of obligate against facultative scavengers can prevent the arrival of potential hosts or vectors from carcasses (see Plaza et al., 2020 for a review). In both factors, it is important to note that vultures, the only obligate scavengers in terrestrial habitats, are often considered the main carrion removers, given that studies have shown that their absence on carcasses cannot be fully replaced by facultative scavengers, such as other bird of prey and mammals (Hill et al., 2018; Ogada et al., 2011). Given that most wild carnivores (e.g. mammals) are facultative scavengers, a disease associated with their prey (e.g. large wild herbivores) may have its transmission affected by the movement of these animals and the competition among scavenger species. This is the case of anthrax disease, which is highly prevalent in large domestic and wild herbivores (e.g. cattle and zebra), but rare in wild carnivorous mammals and birds (Bellan et al., 2012; Hugh-Jones and Vos, 2002).

Anthrax is a severe and lethal disease caused by the spore-forming bacteria *Bacillus anthracis*, affecting several vertebrate hosts such as wild and domestic herbivores, wild carnivores, and humans (Shafazand et al., 1999). The disease causes high mortality of wild herbivores, and the pathogen can spillover from its natural

reservoir (infected carcasses, soil, and vegetation around carcasses) to carrion visitors or grazing animals, as well as spillovers to livestock close to natural areas are common (Hoffmann et al., 2017; Hugh-Jones and Vos, 2002; Nannozi et al., 2022). Scavengers, mainly carnivorous mammals, are often considered potential mechanical vectors of anthrax spores (Alexander et al., 2018; Hugh-Jones and Vos, 2002). However, a recent review has emphasized that there is no solid evidence supporting the role of scavengers as anthrax disseminators (Plaza et al., 2020), especially when considering vultures. Indeed, the increasing number of anthrax and rabies cases in some parts of the world is assumed to be a consequence of the local extinction of vultures, such as in India (Markandya et al., 2008; Mudur, 2001). This conflicting evidence about the role of scavengers in spreading or controlling wildlife diseases, such as anthrax disease, demands a better understanding of transmission drivers in the wildlife-livestock interface.

Here, we aimed to understand and evaluate whether the diversity and composition of vertebrate scavenger communities are associated with the prevalence of anthrax worldwide. Considering the conflicting evidence on the effects of scavengers on the transmission of infectious diseases, we discuss a) the role of facultative scavengers (e.g. non-vulture birds and mammals) as potential natural reservoirs or vectors of anthrax spores, which can transmit the pathogen to living hosts via predation or scavenging; b) the role of obligate scavengers (vultures) as controller of anthrax spillovers, given their higher scavenging efficiency in detecting and removing carcasses, preventing the arrival of facultative scavengers such as wild mammals (potential hosts or mechanical vectors); c) a compositional effect of the scavenger pool, i.e. whether mammals are potential hosts of the disease so that where there are more mammals than birds visiting carrion, more cases are expected to be observed.

METHODS

Conceptual and empirical model

To understand the importance of vertebrate scavengers in the transmission of anthrax disease in both wild and domestic hosts, we first assembled a conceptual model based on the general epidemiological framework discussed by Alexander et al. (2018) and an ecological model proposed by Walsh et al. (2019). Both approaches consider

two interactive components to explain spillovers of the disease among the reservoir component (soil and natural vegetation), wildlife (intermediary component), livestock, and humans. In addition, we used the term anthropogenic ecotone (*sensu* Walsh et al., 2019) to denote the intermediary component connecting the interface wildlife-livestock, i.e. from the natural reservoir component to the human-altered landscape. Our conceptual model is represented in Figure 1. Based on this model, we selected explanatory variables to address the effect of all components and their interactive elements, as well as the diversity of scavengers, on the frequency of anthrax cases in the world by fitting an empirical model.

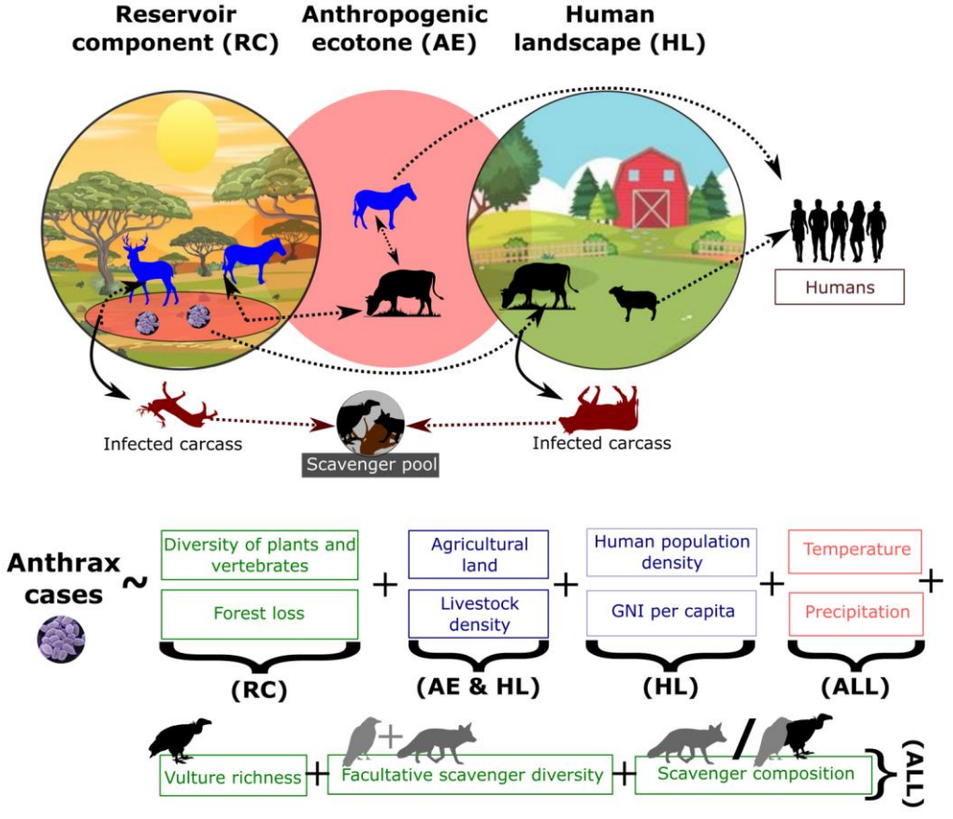

Figure 1 – Our conceptual model is based on Alexander et al. (2018) and Walsh et al. (2019), which considers the interaction among three spatial compartments (RC-HL). Dashed arrows represent anthrax transmission directions among potential hosts or mechanical vectors. We also illustrated anthrax-infected carcasses as potential reservoirs of the disease. Below, we show the selected variables to fit our empirical model, as well as the main transmission compartment explained by them. Here, we considered that vertebrate scavengers interact with all components, as well as the global-scale climate variables. Facultative scavengers comprise non-vulture birds and mammals, while scavenger composition is the ratio of mammal and bird species.

Our empirical model was conducted considering a scale of the global administrative area as sampling units, i.e. mainland country areas and their self-governing territories were considered separately. This administrative scale follows the Global Administrative Areas database (GADM; www.gadm.org), in which all spatial polygons (*shapefile*) can be directly downloaded using the function "getData" from the R package raster (Hijmans, 2019).

Anthrax data source

Our response variable comprises the total number of cases reported from 1996 to 2021 in each jurisdiction across the globe. We considered all cases reported in both domestic and wild vertebrate hosts (not including human cases). Data was obtained from immediate notifications and follow-up reports, six-monthly reports, and annual reports in the OIE World Animal Health Information System, which is maintained by the World Organization for Animal Health (WOAH, 2020).

Correlates of the number of anthrax cases

Climate

We used the WorldClim data at the 30-s resolution (~1 km², Fick and Hijmans, 2017) to measure the mean annual temperature and the total annual precipitation (bio1 and bio12, respectively) for each administrative area. From the spatial polygon obtained using the GADM data, we averaged the values captured by the polygon using the function "exact_extract" from the R package exactextractr (Baston, 2021).

Anthropogenic habitat changes

We measured the livestock density (head/km²) by considering average counts for cattle, goats, horses, and sheep (domestic groups with a widespread prevalence of anthrax; WOAH, 2020) from 1961 to 2020 divided by the total land area. Data were obtained from the FAOSTAT database, maintained by the Food and Agriculture Organization of the United Nations (FAO, 2022). Also, we measured the total agricultural lands per year as a percentage of the total administrative land area (mean proportion from 1960 to 2018; FAO, 2022). We downloaded the data using

the World Bank Open Data (https://data.worldbank.org/). Both variables were used as a measure of habitat changes by anthropogenic actions, which can increase the likelihood of encounters between domestic and wild animals.

Biodiversity and landscape changes

We used the national biodiversity index (NBI) provided by the Convention on Biological Diversity website for most countries and their dependencies (Global Biodiversity Outlook 1; www.cbd.int/gbo1/annex.shtml). The index is based on estimates of country richness for terrestrial vertebrates and vascular plants, ranging from 0.0 to 1.0. Also, we measured the total forest area lost between 1990 and 2020 (in km^2) by calculating the difference between the forest cover that was present in each year. Historical and recent forest lands (in km^2) in our areas were obtained using the World Bank Open Data (https://data.worldbank.org/). High biodiversity and well-conserved ecosystems are often associated with decreases (or even increases in some cases) in infectious diseases, e.g. due to a reduction of host densities mediated by competitive pressures (see Keesing et al., 2010 for a review).

Human economy and population

Regulations, financial investments in health surveillance, and other actions taken by governments to manage wildlife diseases strongly affect the prevalence of zoonoses. Given that these actions are associated with a country's population and economy, we used the mean gross national income per capita (GNI in current US$, data from 1960-2020) and the current human population density (in individual/km^2) as proxies for general human influences in the outbreaks and frequency of infectious diseases in natural and anthropogenic habitats. The second variable was calculated by dividing the most recent estimate of the total population by the total land area of the administrative area. All variables were also downloaded using the World Bank Open Data (https://data.worldbank.org/).

Scavenger pool

To determine the list of scavenger birds and mammals in each administrative area, we performed a systematic review using the following combination of terms: (bird* OR avian OR mammal* OR carnivor* OR raptor*) AND (carcass* OR carrion OR scaveng* OR corpse OR roadkill) in Web of Science. We searched for studies published between 2010 and 2019 (papers, notes, and reviews in English). By considering the title, abstract, and keywords (topic), the search results were refined to the Web of Science categories Ecology, Zoology, Environmental Sciences, Biodiversity Conservation, Ornithology, Biology, and Environmental Studies. In total, we obtained 1483 studies for the initial title and abstract screening. In the full-text screening stage, we considered any information about carrion consumption by vertebrates in any article part, including the introduction and supplementary materials. We did not consider studies using captive animals. Some regional (e.g. country and continental scale) and global reviews were compiled by providing a list of scavengers not documented in the other empirical studies. From the 298 resulting studies, we recorded a global list of 366 confirmed vertebrate species feeding on carrion, 243 birds (including vultures, crows, eagles, and hawks), and 123 mammals (including large carnivores such as bears and foxes, small mammals such as rodents, and domestic dogs and cats). More details in "Capítulo IV".

After removing species with unclear records, marine species (e.g. gulls and albatrosses), and insectivores, we obtained the global range spatial polygon of each species. We considered all occurrences of the species, including non-native ones, which were merged into a single spatial polygon if applicable. Each polygon was converted into raster files (cell size: 1500 x 1500 m) and reclassified to contain only values 0 for absence and 1 for presence in a UTM-projected world map. All reclassified rasters were summed to generate a global distribution map of a) all New World and Old World vultures, b) all scavenger birds, and c) all scavenger mammals (Figures 2-4). These maps were generated using the ArcGIS© software (ESRI, 2012; version 10.1), and the original range maps of scavengers were provided by the IUCN (2018) and Birdlife International and HBW (2019). From each distribution map, we extracted the maximum scavenger richness for each administrative area using the function "exact_extract" from the R package exactextractr.

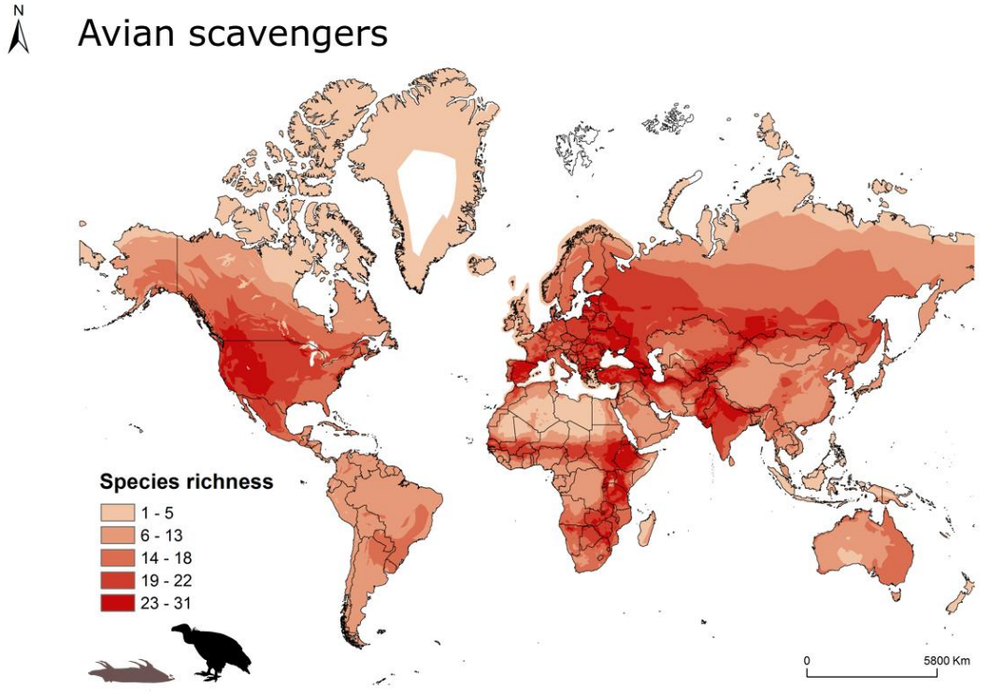

Figure 2 – Global distribution of avian scavengers, including obligate (vultures) and facultative species (e.g. eagles, hawks, and owls). The map was generated by overlapping the range of species documented visiting carrion (BirdLife International and HBW, 2019).

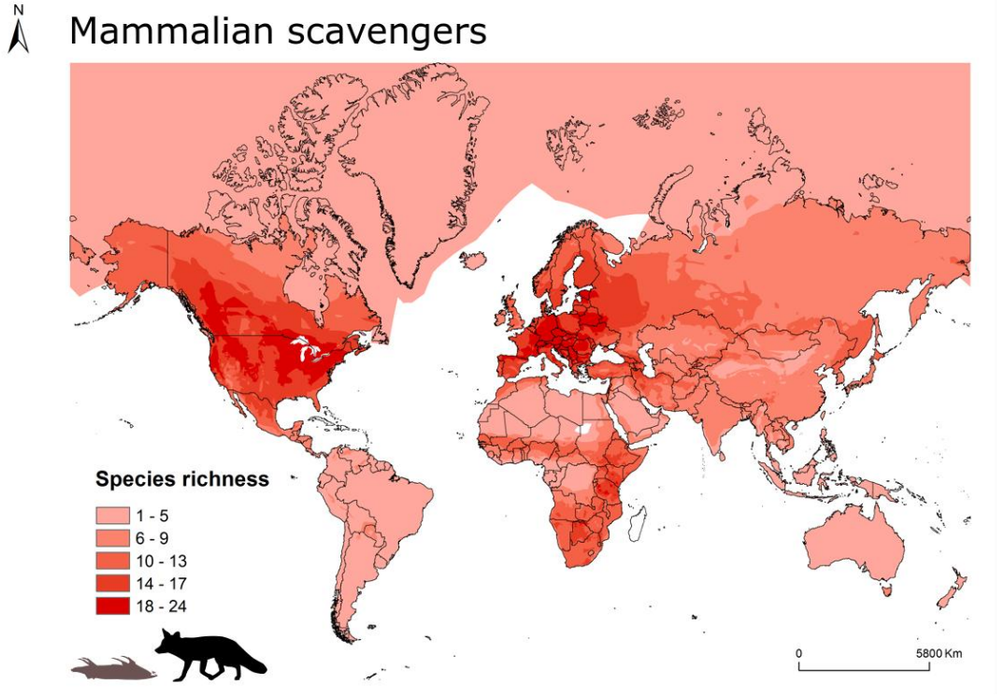

Figure 3 – Global distribution of mammalian scavengers (all facultative species). The map was generated by overlapping the range of species documented visiting carrion (IUCN, 2018). The shaded area in the north represents the polar bear's range.

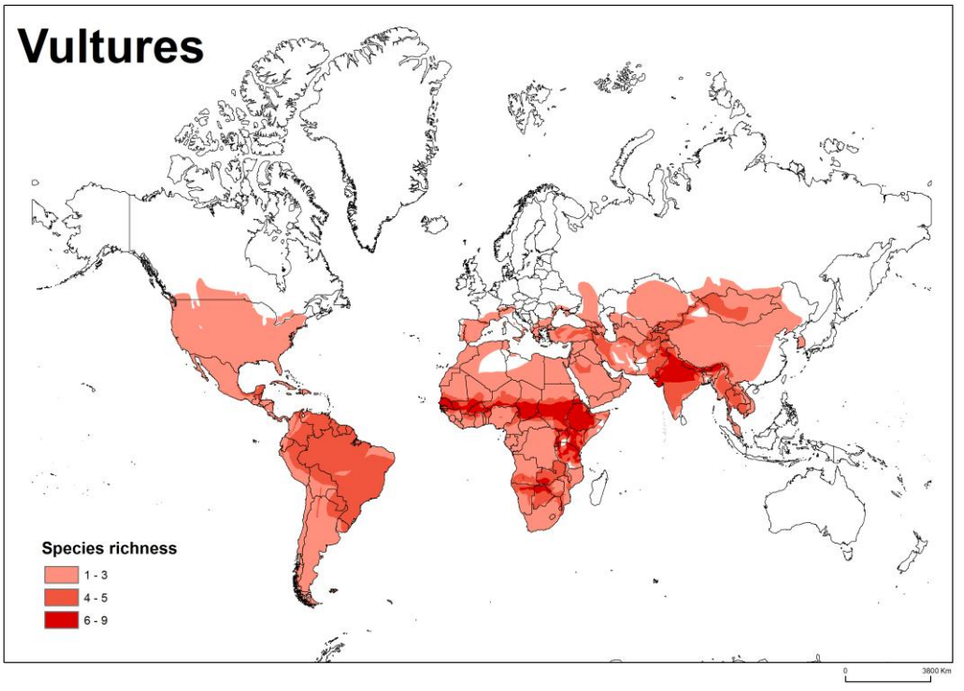

Figure 4 – Global distribution of vultures (obligate scavengers). The map was generated by overlapping the range of species documented visiting carrion (BirdLife International and HBW, 2019).

Model fitting

We fitted a generalized additive model (GAM) to measure the effect of our predictor variables on the anthrax cases worldwide, given that some predictors show nonlinear relationships, such as those with counts and proportion data. The response variable was modeled as a binary variable, i.e. areas with no cases vs. areas with at least one case, using the binomial family, given that our data show also many zeros (~45% of the observations) and large count values. Thus, the probability of anthrax cases (response) was fitted with 11 smoother fixed effects (i.e. thin-plate spline smooths; Figure 1, Appendix S1). To account for the effect of scavenger groups (birds or mammals), we considered three complementary variables: vulture species richness (obligate scavengers), species richness of facultative scavengers (non-vulture birds plus mammal species), and a compositional variable, i.e. the ratio of the number of mammal species to the number of birds (% scavenger mammals). All predictors were standardized to a mean of zero and a standard deviation of one before entering the models ("decostand" function in R package vegan; Oksanen et al., 2019). The model was fitted using the "gam" function in the R package mgcv

(Wood, 2011; model R code is available in Appendix S1). We checked the concurvity assumption (i.e. generalization of co-linearity among variables for GAM models) using the mgcv function "concurvity". Graphical representations were implemented using the visreg package (Breheny and Burchett, 2017). All analyses were conducted in the R environment (R Core Team, 2015).

RESULTS

We observed a nonlinear and non-significant effect of vulture richness on the probability of anthrax cases in wild and domestic animals across the world (χ^2=9.058, edf=4.220, p=0.115; Figure 5), as well as for scavenger composition (% mammals; χ^2=0.262, p=0.610), which showed a linear relationship (Figure 5). The richness of facultative scavengers was positively associated with the occurrence of anthrax cases (χ^2=4.263, p=0.039). Together with this variable, annual mean temperature and GNI per capita were the best linear predictors for disease occurrence. Intriguingly, the biodiversity index showed a non-monotonic relationship, given that the probability of anthrax cases dropped towards moderate values, but increased towards higher values of the index.

DISCUSSION

Our model is a first look at understanding the role of vertebrate scavengers in the frequency of zoonotic outbreaks in wildlife and livestock areas alongside other well-known drivers of infectious diseases. Thus, the prevalence of anthrax seems to be associated with the species-rich communities of facultative vertebrate scavengers in poorer and colder global regions. Surprisingly, livestock density and the agricultural land area did not affect the probability of anthrax cases, despite the high prevalence of anthrax in domestic mammals in agricultural areas across the globe (CDC and NCEZID, 2022). Despite the difficulty in recording the disease in the wild carcasses due to scavenger activity and poor surveillance approaches (Mukarati et al., 2020; Walsh et al., 2019), the frequency of anthrax outbreaks between wildlife and livestock varies across global regions, but often affects mainly large wild and domestic ungulates of the Bovidae family (Hugh-Jones and Vos, 2002; Mukarati et al., 2020; Mwakapeje et al., 2018). Thus, the weak relationship between livestock density with anthrax cases may be explained by aggressive sanitary and epidemiological regulations in richer areas of the globe, such as livestock

vaccination (Shafazand et al., 1999). In fact, we observed higher livestock densities in high-income countries, such as New Zealand, the United Kingdom, the Netherlands, and Uruguay.

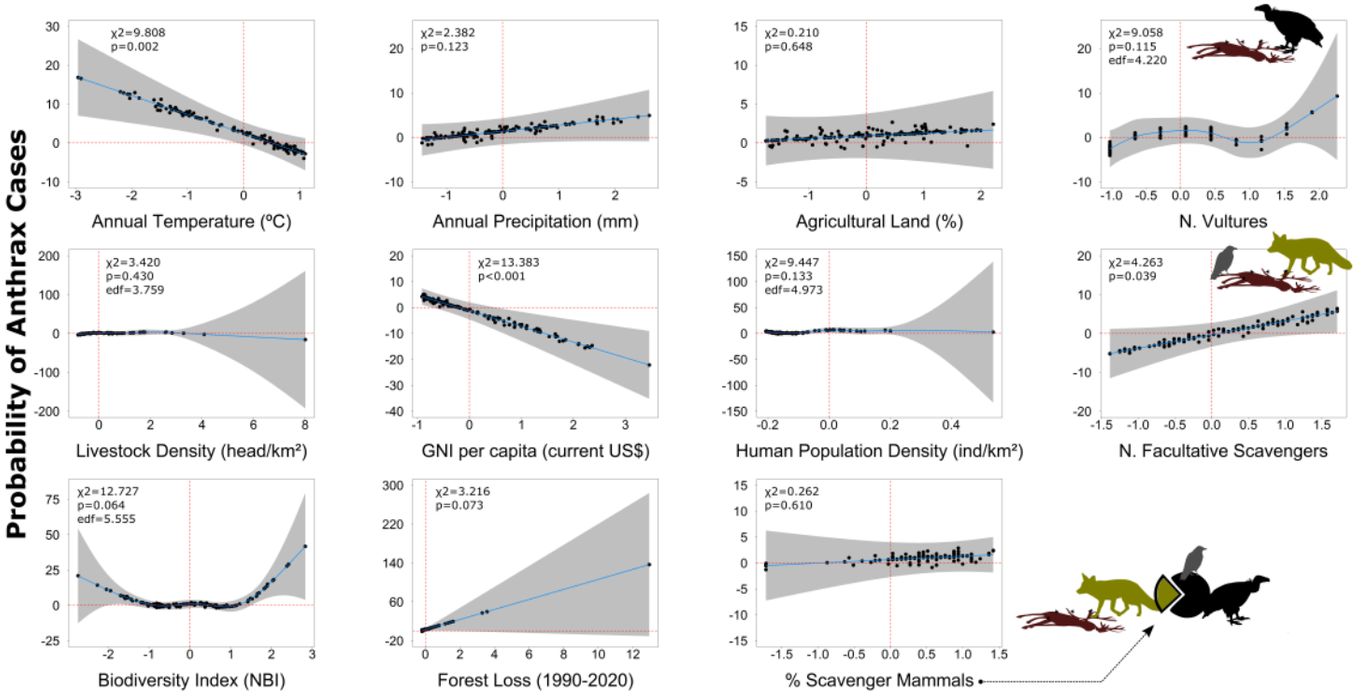

Figure 5 - Relationships of the 11 predictor variables with the probability of anthrax cases worldwide. Scatter plots represent the partial residuals of each smoothed variable when controlling for other variables (visreg package). Blue lines show the predicted function of each variable with the shaded area as the 95% confidence band based on GAM function (mgcv package). The response variable is treated as a binary probability of occurrence (at least one case) and no occurrence in our data series. All predictor variables were standardized (to a mean of zero and standard deviation of one) before entering the model, and those without the edf value (effective degrees of freedom) represent linear relationships (i.e. edf=1). The model code is available in Appendix S1.

In human landscapes, adequate vaccination of livestock and safe disposal of infected dead animals are considered key strategies to control the prevalence of anthrax (Hugh-Jones and Vos, 2002; Mukarati et al., 2020; Mwakapeje et al., 2018). In low- and middle-income nations, where these strategies are often reduced or inadequate, a higher probability of cases is expected. For instance, India showed the fourth highest prevalence of anthrax in our data, a middle-income country with several problems with carcass disposal near human settlements and deficits of vaccines for livestock (Mudur, 2001). Thus, these sanitary approaches can attenuate the occurrence of the disease in livestock and potentially in zones nearby natural landscapes, but not directly in the environment

near the natural reservoir of the disease. Thus, anthrax-generated carcasses in the wild and the interface wildlife-livestock (anthropogenic ecotone) seem to be a key component in the transmission risk of the disease across global regions, due to a likely higher probability of encounters with potential hosts (wild and domestic herbivores) and the attraction of mechanical vectors via carcasses, such as wild carnivores and scavengers (Alexander et al., 2018; Walsh et al., 2019).

In natural landscapes (including the disease reservoir), the mortality of wild herbivores from anthrax can create hotspots of pathogens in the landscapes even after the removal of carcass hosts (Turner et al., 2014). Thus, the likelihood of contact of large carnivores with *anthracis*-laden carrion may be intensified (Borchering et al., 2017), which potentially contributes to punctual spillovers across the landscapes. Also, infected carcasses from livestock can create these hotspots and attract scavengers to the anthropogenic ecotone and human landscape (as represented in Figure 1). Despite that scavengers are often pointed out as resistant or less likely to be infected by many pathogens from carcasses (Blumstein et al., 2017; Borchering et al., 2017; Hugh-Jones and Vos, 2002), a high diversity of scavengers (both obligate and facultative) seems to not decrease the probability of anthrax outbreaks, at least, in a broader scale, such as for countries. However, facultative scavengers seem to play a role in becoming potential anthrax reservoirs or mechanical vectors in wild, which would explain the strong relationship with anthrax cases. In addition, the effect of facultative scavengers is not related to a higher proportion of scavenger mammals, i.e. if a region has more mammal species visiting carrion, it is not expected to have more cases of anthrax. Thus, the functional identity concerning the degree of carcass dependency in the scavenger community (i.e. facultative vs. obligate) seems to be a more important factor for the prevalence of the disease in the interface wildlife-livestock, instead of the taxonomic identity (i.e. mammals vs. birds).

Mammal biodiversity is often pointed out as an important driver of the emergence of infectious diseases worldwide (Allen et al., 2017). Especially, wild carnivores and rodents are often considered spillover hosts or reservoirs of many infectious diseases, such as rabies, toxoplasmosis, plague, and even anthrax (Zhang et al., 2022). Given that vertebrate carnivores and rodents are often facultative scavengers in agricultural zones, they can translocate some pathogens from wild carcasses to areas close to humans. For instance, several typical wild

scavenger mammals prey on livestock or scavenge their carcasses (e.g. cattle, donkeys, goats, and sheep), such as hyenas, jackals, foxes, bears, and coyotes (Rocha et al., Capítulo IV). However, it is important to note that the magnitude of these potential effects on spreading wildlife diseases by large scavengers is often speculative or unknown. On the other hand, it is a fact that scavengers are strongly associated with disease-generated carcasses. Indeed, an intriguing ecological relationship between the anthrax bacteria and scavengers (including invertebrates) occurs in wild, i.e. when a host dies from anthrax, the sporulation start right after the opening of carcasses by scavengers, followed by a potential transport of spores via both avian and mammalian species (Hugh-Jones and Vos, 2002; Vicente and VerCauteren, 2019). Based on two mathematical models focused on the relationship between vertebrates and *anthracis*-laden carcasses (Borchering et al., 2017; Mackey and Kribs, 2021), three consequences can arise from this relationship, i) carcasses of anthrax hosts benefit scavengers by providing food resources for them, ii) carcass sites visited by scavengers reduce infection zones for other herbivores due to inactivation of vegetative cells (e.g. carrion consumption neutralizes pathogens due to stomach pH), iii) anthrax favors aggregations of scavengers in carcass sites, thus increasing its persistence in the environment (i.e. more hosts or vectors). In summary, anthrax disease is closely related to carcasses and scavengers, but mostly with facultative scavengers, as pointed out in our model. However, the persistence of the bacteria in the environment seems not to depend strongly on scavengers in some conditions that set its basic reproductive number (R_0) to be greater than one, i.e. the prevalence will not be affected by the presence of scavengers (Mackey and Kribs, 2021). Thus, even considering scavenger mammals as potential anthrax reservoirs, vertebrate scavengers seem to be a minor risk factor for spreading the disease. Therefore, the relationship between the disease and scavengers seems to be an ecological interaction mediated by the carcass availability provided by the pathogen.

Anthrax disease manifestation is very rare in scavenger mammals, and even more in birds. In facultative scavenging birds, such as caracaras, hawks, and owls, the prevalence of anthrax spores after passing through their digestive tracts appears to be very low compared to mammals (Saggese et al., 2007). In vultures, the only terrestrial obligate scavengers, some seminal evidence has shown that spores or vegetative cells of anthrax are poorly recovered in their feces in comparison with mammals (Houston and Cooper, 1975; Lindeque and Turnbull,

1994). Despite this, vultures have often been pointed out as disseminators of anthrax to some degree (Hugh-Jones and Vos, 2002; Vicente and VerCauteren, 2019). However, we did not find any solid empirical evidence supporting this dissemination hypothesis. In contrast, the decline of vultures in some parts of the world is often correlated with outbreaks of wildlife diseases, including anthrax, rabies, and canine distemper (Markandya et al., 2008; Mudur, 2001; Ogada et al., 2011). Given that vultures can detect carcasses quickly and remove them before the arrival of facultative scavengers such as wild carnivores (Ogada et al., 2011; Plaza et al., 2020), they can reduce infection zones for herbivorous hosts of anthrax, as well as the presence of mechanical vectors such as wild and domestic mammals. Finally, our model showed that a high diversity of vultures is not associated with a high probability of anthrax cases when considering a broader scale of global administrative zones.

Concluding Remarks

It is important to note that the anthrax bacteria infect many vertebrate species (mainly wild and domestic herbivores, but also some carnivorous mammals, monkeys, and humans; Bellan et al., 2012; Hoffmann et al., 2017; Alexander et al., 2018) and there is a multi-source of infections, such as directly from the natural reservoir, via infected carcasses, and contact with spillover hosts or mechanical vectors (Figure 1; Alexander et al., 2018). In addition, spores can persist for decades in the soil (CDC and NCEZID, 2022). Thus, strategies to control outbreaks of anthrax are very difficult, especially in wildlife. Vaccination, safe disposal of carcasses from agricultural areas, and avoidance of grazing livestock nearby wildlife are key strategies in human landscapes (Nannozi et al., 2022). On the other hand, strategies to avoid the presence of scavengers seem not to be effective to control the disease but can create a conservation problem for them. For instance, strict policies for the mechanical removal of carcasses in rural areas of Europe reduce the availability of food for vultures, affecting the conservation of their populations (Arrondo et al., 2018). Furthermore, vultures can help to find anthrax foci due to their ability in detecting carcasses in a broader area (Walker et al., 2021), thus acting as a surveillance tool. Therefore, the role of vultures in anthrax-generated carcass sites deserves better attention in experimental approaches. Finally, we argue that increases in biodiversity across nations may contribute to the control of the disease in the wild, given that we detected a

downward trend in the likelihood of anthrax cases in regions with intermediate-high levels of plant and vertebrate diversity.

REFERENCES

Alexander, K.A., Carlson, C.J., Lewis, B.L., Getz, W.M., Marathe, M.V., Eubank, S.G., Sanderson, S.E., Blackburn. J.K., 2018. The Ecology of Pathogen Spillover and Disease Emergence at the HumanWildlife-Environment Interface, in: Olea, P., Mateo-Tomás, P., Sánchez-Zapata, J. (Eds.), Carrion Ecology and Management. Wildlife Research Monographs. Springer, Cham, pp. 267–298.

Allen, T., Murray, K.A., Zambrana-Torrelio, C., Morse, S.S., Rondinini, C., Di Marco, M., Breit, N., Olival, K.J., Daszak, P., 2017. Global hotspots and correlates of emerging zoonotic diseases. Nature Communications 8, 1124. doi:10.1038/s41467-017-00923-8

Arrondo, E., Moleón, M., Cortés-Avizanda, A., Jiménez, J., Beja, P., Sánchez-Zapata, J.A., Donázar, J.A., 2018. Invisible barriers: Differential sanitary regulations constrain vulture movements across country borders. Biological Conservation 219, 46–52. doi:10.1016/j.biocon.2017.12.039

Baston, D., 2021. Exactextractr: Fast Extraction from Raster Datasets using Polygons. R package version 0.6.1. https://CRAN.R-project.org/package=exactextractr.

Bellan, S.E., Cizauskas, C.A., Miyen, J., Ebersohn, K., Küsters, M., Prager, K.C., van Vuuren, M., Sabeta, C., Getz, W.M., 2012. Black-backed jackal exposure to rabies virus, canine distemper virus, and Bacillus anthracis in Etosha National Park, Namibia. Journal of Wildlife Diseases 48, 371–381. doi:10.7589/0090-3558-48.2.371

BirdLife International, HBW-Handbook of the Birds of the World, 2019. Bird species distribution maps of the world. Version 2019.1. Available at http://datazone.birdlife.org/species/requestdis.

Blumstein, D.T., Rangchi, T.N., Briggs, T., De Andrade, F.S., Natterson-Horowitz, B., 2017. A Systematic

Review of Carrion Eaters' Adaptations to Avoid Sickness. Journal of Wildlife Diseases 53, 577–581. doi:10.7589/2016-07-162

Borchering, R.K., Bellan, S.E., Flynn, J.M., Pulliam, J.R.C., McKinley, S.A., 2017. Resource-driven encounters among consumers and implications for the spread of infectious disease. Journal of the Royal Society Interface 14, 20170555.

Breheny, P., Burchett, W., 2017. Visualization of Regression Models using visreg. The R Journal 9, 56–71.

CDC–Centers for Disease Control and Prevention, NCEZID–National Center for Emerging and Zoonotic Infectious Diseases, 2022. What is Anthrax? U.S. Department of Health & Human Services. Available at https://www.cdc.gov/anthrax/basics/index.html [accessed June 2022].

Escobar, L.E., Pritzkow, S., Winter, S.N., Grear, D.A., Kirchgessner, M.S., Dominguez-Villegas, E., Machado, G., Townsend Peterson, A., Soto, C., 2020. The ecology of chronic wasting disease in wildlife. Biological Reviews 95, 393–408. doi:10.1111/brv.12568

ESRI, 2012. ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

FAO–Food and Agriculture Organization of the United Nations, 2013. World Livestock 2013 – Changing disease landscapes. FAO, Rome.

FAO–Food and Agriculture Organization of the United Nations, 2022. FAOSTAT. Available at www.fao.org/faostat/en/#data [accessed June 2022].

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302–4315.

Hijmans, R.J., 2019. Raster: Geographic Data Analysis and Modeling. R package version 2.9-23. https://CRAN.R-

project.org/package=raster.

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Effects of vulture exclusion on carrion consumption by facultative scavengers. Ecology and Evolution 8, 2518–2526. doi:10.1002/ece3.3840

Hoffmann, C., Zimmermann, F., Biek, R., Kuehl, H., Nowak, K., Mundry, R., Agbor, A., Angedakin, S., Arandjelovic, M., Blankenburg, A., Brazolla, G., Corogenes, K., Couacy-Hymann, E., Deschner, T., Dieguez, P., Dierks, K., Düx, A., Dupke, S., Eshuis, H., Formenty, P., Yuh, Y.G., Goedmakers, A., Gogarten, J.F., Granjon, A.C., McGraw, S., Grunow, R., Hart, J., Jones, S., Junker, J., Kiang, J., Langergraber, K., Lapuente, J., Lee, K., Leendertz, S.A., Léguillon, F., Leinert, V., Löhrich, T., Marrocoli, S., Mätz-Rensing, K., Meier, A., Merkel, K., Metzger, S., Murai, M., Niedorf, S., De Nys, H., Sachse, A., Van Schijndel, J., Thiesen, U., Ton, E., Wu, D., Wieler, L.H., Boesch, C., Klee, S.R., Wittig, R.M., Calvignac-Spencer, S., Leendertz, F.H., 2017. Persistent anthrax as a major driver of wildlife mortality in a tropical rainforest. Nature 548, 82–85. doi:10.1038/nature23309

Houston, D.C., Cooper, J.E., 1975. The digestive tract of the whiteback griffon vulture and its role in disease transmission among wild ungulates. Journal of wildlife diseases 11, 306–313. doi:10.7589/0090-3558-11.3.306

Hugh-Jones, M., Vos, V. de, 2002. Anthrax and wildlife. OIE Revue Scientifique et Technique 21, 359–383. doi:10.1002/9781118829417.ch9

IUCN. Red List version 2018. The IUCN Red List of Threatened Species. <Red List version 2018.2>. https://www.iucnredlist.org. Downloaded on 01 September 2020.

Jones, B.A., Grace, D., Kock, R., Alonso, S., Rushton, J., Said, M.Y., McKeever, D., Mutua, F., Young, J., McDermott, J., Pfeiffer, D.U., 2013. Zoonosis emergence linked to agricultural intensification and environmental change. Proceedings of the National Academy of Sciences of the United States of America 110, 8399–8404. doi:10.1073/pnas.1208059110

Keesing, F., Belden, L.K., Daszak, P., Dobson, A., Harvell, C.D., Holt, R.D., Hudson, P., Jolles, A., Jones, K.E., Mitchell, C.E., Myers, S.S., Bogich, T., Ostfeld, R.S., 2010. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468, 647–652. doi:10.1038/nature09575

Lim, N.T.-L., Kelt, D.A., Lim, K.K.P., Bernard, H., 2020. Vertebrate Scavengers Control Abundance of Diarrhea-causing Bacteria in Tropical Plantations. Zoological Studies 59, 63. doi:10.6620/ZS.2020.59-63

Lindeque, P.M., Turnbull, P.C., 1994. Ecology and epidemiology of anthrax in the Etosha National Park, Namibia. The Onderstepoort Journal of Veterinary Research 61, 71–83.

Mackey, C., Kribs, C., 2021. Can scavengers save zebras from anthrax? A modeling study. Infectious Disease Modelling 6, 56–74. doi:10.1016/j.idm.2020.10.016

Markandya, A., Taylor, T., Longo, A., Murty, M.N., Murty, S., Dhavala, K., 2008. Counting the cost of vulture decline-An appraisal of the human health and other benefits of vultures in India. Ecological Economics 67, 194–204. doi:10.1016/j.ecolecon.2008.04.020

Martin, C., Pastoret, P.-P., Brochier, B., Humblet, M.-F., Saegerman, C., 2011. A survey of the transmission of infectious diseases / infections between wild and A survey of the transmission of infectious diseases / infections between. Veterinary Research 42, 70.

Mohan, B., Vinod, N., 2020. COVID-19: An Insight into SARS-CoV2 Pandemic Originated at Wuhan City in Hubei Province of China. Journal of Infectious Diseases and Epidemiology 6. doi:10.23937/2474-3658/1510146

Mudur, G., 2001. Human anthrax in India may be linked to vulture decline. British Medical Journal 322, 320.

Mukarati, N.L., Matope, G., de Garine-Wichatitsky, M., Ndhlovu, D.N., Caron, A., Pfukenyi, D.M., 2020. The pattern of anthrax at the wildlife-livestock-human interface in Zimbabwe. PLoS Neglected Tropical Diseases 14, e0008800. doi:10.1371/journal.pntd.0008800

Mwakapeje, E.R., Høgset, S., Fyumagwa, R., Nonga, H.E., Mdegela, R.H., Skjerve, E., 2018. Anthrax outbreaks in the humans - livestock and wildlife interface areas of Northern Tanzania: a retrospective record review 2006-2016. BMC public health 18, 106. doi:10.1186/s12889-017-5007-z

Nannozi, B., Kebirungi, P., Asiimwe, A., Mweheire, I., Ademun, A., Mugaya, H., Ndyamgayo, G., Ndyanabo, S., Ayebazibwe, C., Nizeyimana, G., Okuthe, S., Magona, J., 2022. Risk factors influencing the occurrence of anthrax outbreaks at the Livestock-Game interface in Katunguru, Rubirizi district, Uganda. International Journal of Veterinary Science and Research 8, 015–022. doi:10.17352/ijvsr.000106

O'Bryan, C.J., Braczkowski, A.R., Beyer, H.L., Carter, N.H., Watson, J.E.M., McDonald-Madden, E., 2018. The contribution of predators and scavengers to human well-being. Nature Ecology and Evolution 2, 229–236. doi:10.1038/s41559-017-0421-2

Ogada, D.L., Torchin, M.E., Kinnaird, M.F., Ezenwa, V.O., 2011. Effects of Vulture Declines on Facultative Scavengers and Potential Implications for Mammalian Disease Transmission. Conservation Biology 26, 453–460. doi:10.1111/j.1523-1739.2012.01827.x

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. Vegan: Community Ecology Package. R package version 2.5-5. https://CRAN.Rproject.org/package=vegan.

Plaza, P.I., Blanco, G., Lambertucci, S.A., 2020. Implications of bacterial, viral and mycotic microorganisms in vultures for wildlife conservation, ecosystem services and public health. Ibis 162, 1109–1124. doi:10.1111/ibi.12865

Probst, C., Gethmann, J., Amler, S., Globig, A., Knoll, B., Conraths, F.J., 2019. The potential role of scavengers in spreading African swine fever among wild boar. Scientific Reports 9, 1–13. doi:10.1038/s41598-019-47623-5

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Saggese, M.D., Noseda, R.P., Uhart, M.M., Deem, S.L., Ferreyra, H., Romano, M.C., Ferreyra-Armas, M.C., Hugh-Jones, M., 2007. First detection of Bacillus anthracis in feces of free-ranging raptors from central Argentina. Journal of Wildlife Diseases 43, 136–141. doi:10.7589/0090-3558-43.1.136

Salkeld, D.J., Stapp, P., Tripp, D.W., Gage, K.L., Lowell, J., Webb, C.T., Brinkerhoff, R.J., Antolin, M.F., 2016. Ecological Traits Driving the Outbreaks and Emergence of Zoonotic Pathogens. BioScience 66, 118–129. doi:10.1093/biosci/biv179

Shafazand, S., Doyle, R., Ruoss, S., Weinacker, A., Raffin, T.A., 1999. Inhalational anthrax: Epidemiology, diagnosis, and management. Chest 116, 1369–1376. doi:10.1378/chest.116.5.1369

Turner, W.C., Kausrud, K.L., Krishnappa, Y.S., Cromsigt, J.P.G.M., Ganz, H.H., Mapaure, I., Cloete, C.C., Havarua, Z., Küsters, M., Getz, W.M., Stenseth, N.C., 2014. Fatal attraction : vegetation responses to nutrient inputs attract herbivores to infectious anthrax carcass sites. Proceedings of the Royal Society B: Biological Sciences 281, 20141785.

Vicente, J., VerCauteren, K.C., 2019. The Role of Scavenging in Disease Dynamics, in: Olea, P., Mateo-Tomás, P., Sánchez-Zapata, J. (Eds.), Carrion Ecology and Management. Wildlife Research Monographs. Springer, Cham, pp. 161–182.

Walker, M.A., Uribasterra, M., Asher, V., Getz, W.M., Ryan, S.J., Ponciano, J.M., Blackburn, J.K., 2021. Anthrax Surveillance and the Limited Overlap between Obligate Scavengers and Endemic Anthrax Zones in the United States. Vector-Borne and Zoonotic Diseases 21, 675–684. doi:10.1089/vbz.2020.2747

Walsh, M.G., Mor, S.M., Hossain, S., 2019. The elephant-livestock interface modulates anthrax suitability in India. Proceedings of the Royal Society B: Biological Sciences 286, 20190179. doi:10.1098/rspb.2019.0179

Wiethoelter, A.K., Beltrán-Alcrudo, D., Kock, R., Mor, S.M., 2015. Global trends in infectious diseases at the wildlife–livestock interface. Proceedings of the National Academy of Sciences 112, 9662–9667.

doi:10.1073/pnas.1422741112

WOAH–World Organisation for Animal Health, 2020. OIE-WAHIS Quantitative data. Available at wahis.woah.org/#/dashboards/qd-dashboard [accessed February 2022].

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. Journal of the Royal Statistical Society (B) 73, 3–36.

Zhang, L., Rohr, J., Cui, R., Xin, Y., Han, L., Yang, X., Gu, S., Du, Y., Liang, J., Wang, X., Wu, Z., Hao, Q., Liu, X., 2022. Biological invasions facilitate zoonotic disease emergences. Nature Communications 13, 1762. doi:10.1038/s41467-022-29378-2

SUPPLEMENTARY MATERIAL

Appendix S1 – R code of the binomial GAM model

#Tested variables and abbreviations

Country_code: administrative area ISO3 code;

#Income: categorical income classification (low, middle, and high) based on the GNI per capita (World Bank);

#LandArea_km2: total land area in km² of each administrative unit;

#R1_Anthrax: mean of Anthrax cases from 1996-2021;

#Anthrax_total: total cases of Anthrax from 1996-2021 (response variable);

#Anthrax_d: density of Anthrax cases (cases/total land area);

#Temp: annual mean temperature (bio1, WorldClim);

#Rain: annual precipitation (bio12, WorldClim);

#Bird_rich: maximum scavenger bird richness per administrative area;

#Avian_index: scaled Bird_rich (0 to 1);

#Bird_d: density of bird species (Bird_rich /LandArea_km2);

#Mamm_rich: maximum scavenger mammal richness per administrative area;

#Mamm_index: scaled Mamm_rich (0 to 1),

#Mamm_d: density of mammal species (Mamm_rich /LandArea_km2),

Mamm_per: ratio of scavenger mammal richness to bird richness (converted into %);

ScaFacul: the total richness of facultative scavengers (non-vulture birds + mammals);

#Vulture: the total richness of vultures;

#Biodi: biodiversity index (0.000 to 1.000; NBI from Convention on Biological Diversity);

#PrtA: number of protected areas;

#PrtAk2: area covered by protected areas in km²;

#Agri: % agricultural land from the total land area;

#Fore: % forest cover from the total land area;

#For_loss: the difference between forest area in 1990 and 2020;

#GDP_USD: GDP total of the country or region in current USD, measured from 1960-2020;

#totalpop: mean total population of the country or region across 1960-2020;

#GDPp: GDP per capita measured from 1960-2020;

#GNIpc: GNI per capita in current USD, based on the data from 2019

#PopU: % urban population from the total population of the country or region;

#PopR: % rural population from the total population of the country or region;

#Live: mean livestock head counts (total of cattle, goats, horses, pigs, and sheep);

#Live_den: livestock density per land area (Live/ LandArea_km2);

#Sanit: percentage of the total population using at least basic sanitation services (%; WHO) per year

#Packages

require(mgcv)

require(visreg)

require(vegan)

require(corrplot)

#Raw data

disease<-read.csv2("disease_data.csv", dec=".", row.names=1)

#Renaming variables

names(disease)

names(disease)<-c("Country_code", "Income", "LandArea_km2", "R1_Anthrax" , "Anthrax_total", "Anthrax_d",
"Temp", "Rain", "Bird_rich", "Avian_index", "Bird_d", "Mamm_rich", "Mamm_index",
"Mamm_d", "Mamm_per", "ScaFacul" , "Vulture", "Biodi", "PrtA", "PrtAk2" ,
"PrtA_s" , "Agri", "Fore", "For_loss","GDP_USD", "totalpop", "GDPp", "GNIpc", "PopU",
"PopR", "Live", "Live_den","Sanit")

Calculating human population density

disease$PopDen<-(disease$totalpop/disease$LandArea_km2)

```
#Standardization of predictors to a mean of zero and standard deviation
disease.std<-round(decostand(disease[,-c(1:6)], "standardize"), 3)
#Add response variable
disease.std$Anthrax_total<-disease$Anthrax_total


#Correlations (Pearson), just for data exploration
cor1=cor(na.omit(disease.std))
windows()
corrplot(cor1, method ="square")
#

#Model fitting#####

dis_bin<-gam(I(Anthrax_total>0)~s(Temp, k=10)+
                                s(Rain, k=10)+
                                s(Agri, k=10)+
                                s(Live_den, k=10)+
                                s(GNIpc, k=10)+
                                s(PopDen, k=10)+
                               s(Mamm_per, k=10)+ #Scavenger component
                               s(ScaFacul,k=10)+ #Scavenger component
                               s(Vulture, k=10)+ #Scavenger component
                                s(Biodi, k=10)+
                                s(For_loss, k=10),
                                family=binomial(link="logit"),
                                method="REML",
                                data=disease.std)
```

```
#
summary(dis_bin)#Estimates and fit measures
plot(dis_bin,se=T)
visreg(dis_bin)#visualization of partial residuals
gam.check(dis_bin)#Check whether the k (basis dimensions) was enough to fit the smoothes (i.e. k index close to 1 and p >0.05)
dis_bin$outer.info#Check convergence
concurvity(dis_bin, full=F)#generalization of co-linearity
#

###Example of model visualization using visreg####

visreg(dis_bin,   xvar="Temp",
       xlab=c("Annual Temperature (ºC)"),
       cex.main=3,
       points.par=list(cex=3, col="black"),
       fill=list(col="gray75"),
       band=T, partial=T,
       ylab="",
       yaxt="n",
       ylim=c(-10,20),
       cex.axis=3,
       cex.lab=3)
at<-seq(-10, 20, 5)
axis(2, at=at, lab=at, las=1, cex.axis=3)
abline(h=0, col="red", lty=2, lwd=2)
abline(v=0, col="red", lty=2, lwd=2)
#End
```

CONSIDERAÇÕES FINAIS

Dentre as várias funções desempenhadas pela biodiversidade nos ecossistemas, a remoção de animais mortos destaca-se pela relação direta com a ciclagem de nutrientes para o solo, a sanitização de áreas naturais e antropizadas e a diversidade de uma complexa comunidade de espécies de quase todos os reinos da vida, incluindo fungos, bactérias, animais e plantas. Fato que evidencia uma necessidade de integrar o conhecimento da moderna área de "ecologia de carcaças" (*Carrion ecology*) nos currículos das ciências biológicas, sobretudo na área de ecologia. A presente tese gerou informações básicas, curiosidades e um entendimento preliminar de como a remoção de carcaças de vertebrados é mantida no bioma Cerrado, bem como comparou, sintetizou e revelou padrões globais, abarcando as principais funções ecossistêmicas providas pelas comunidades de vertebrados e invertebrados carniceiros.

Ao fim dessa tese, as principais mensagens são:

- No Cerrado, urubus e invertebrados mantêm a função de remoção de carcaças em áreas bem conservadas, destacando o papel de besouros rola-bostas (Scarabaeidae), que em condições chuvosas podem soterrar carcaças, inibindo assim o uso delas por vertebrados e outros insetos;

- Mesmo na ausência de vertebrados, a função de remoção pode ser mantida pelos invertebrados, considerando que esses organismos aparentemente intensificam suas atividades nas carcaças durante a estação chuvosa do Cerrado;

- O impacto inicial do processo de remoção de carcaças, i.e. logo após ser removida por invertebrados e/ou vertebrados, afetou fracamente a composição de nutrientes do solo, bem como a decomposição da serrapilheira;

- Carcaças decompondo no Cerrado não só atraem insetos carniceiros, como moscas, besouros e formigas, mas também uma gama de grupos oportunistas e predadores de insetos carniceiros, como vespas, abelhas, borboletas e hemípteros;

- A ausência total dos vertebrados nas carcaças pode aumentar a taxa de consumo pelos invertebrados, mas eles levam um tempo maior para removê-las (~30% a mais), se comparado com carcaças que ambos os grupos estão atuando em comunidades ao redor do mundo;

- Comunidades de carniceiros vertebrados ao redor do mundo são compostas, em média, por menos de 10 espécies, com predomínio de aves como corvos, gaviões e urubus/abutres;

- Mamíferos carnívoros contribuem para o processo de remoção de carcaças ao redor do mundo, destacando também sua função como um grupo provedor de carcaças via predação (“espécies açougueiras”);

- Regiões com uma maior riqueza de urubus e abutres (i.e. carniceiros obrigatórios) não apresentaram uma maior prevalência de anthrax. Apesar de espécies carniceiras serem comumente apontadas como propagadoras de doenças, esse resultado sugere que essas aves pouco afetam a disseminação dessa zoonose fortemente associada com as carcaças de seus hospedeiros (i.e. mamíferos herbívoros selvagens ou domésticos);

- Por outro lado, regiões com uma maior riqueza de carniceiros facultativos (principalmente mamíferos carnívoros) foram associadas com maiores prevalências de anthrax. Uma possível explicação seria que o

patógeno da doença (*Bacillus anthracis*) aumenta a disponibilidade de carcaças no ambiente, o que favorece a distribuição desses carniceiros, tratando-se assim de uma interação ecológica entre ambos os táxons. Assim, onde há mais carcaças (inclusive mortas por anthrax) haverá mais carniceiros para removê-las. No entanto, o modelo apresentado aqui não nos permite afirmar se essa interação com carcaças oriundas da doença pode afetar sua propagação pela paisagem ou se, de fato, mamíferos selvagens atuam como "vetores mecânicos" de *B. anthracis*.

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Fotos das capas:

Joedison Rocha