Ecosystem services and scavengers: ecological and socio-cultural assessment

Servicios ecosistémicos y carroñeros: valoración ecológica y socio-cultural

Zebensui Morales Reyes

PhD Thesis

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and Griffon vulture by Manuel J. de la Riva Pérez

Programa de Doctorado en Medio Ambiente y Sostenibilidad

Ecosystem services and scavengers: ecological and socio-cultural assessment

Servicios ecosistémicos y carroñeros: valoración ecológica y socio-cultural

Director: José Antonio Sánchez Zapata
Codirector: Marcos Moleón Paiz

Tesis Doctoral presentada por **Zebensui Morales Reyes** en la Universidad Miguel Hernández de Elche para la obtención del título de Doctor del Programa de Doctorado en Medio Ambiente y Sostenibilidad

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La presente Tesis Doctoral está sustentada por un compendio de trabajos previamente publicados o aceptados para publicación. La Tesis Doctoral queda constituida por los siguientes artículos científicos:

Chapter 2

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Chapter 4

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Chapter 5

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AUTORIZACIÓN PARA LA PRESENTACIÓN DE LA TESIS DOCTORAL POR COMPENDIO DE PUBLICACIONES

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CERTIFICA

Que la tesis doctoral presentada por D. Zebensui Morales Reyes, titulada "*Ecosystem services and scavengers: ecological and socio-cultural assessment*", que ha sido dirigida por Dr. José Antonio Sánchez Zapata de la Universidad Miguel Hernández de Elche y codirigida por Dr. Marcos Moleón Paiz de la Universidad de Granada y se ha desarrollado dentro del Programa de Doctorado en Medio Ambiente y Sostenibilidad, se encuentra en condiciones de ser leída y defendida ante el correspondiente tribunal en la Universidad Miguel Hernández de Elche.

Lo que firmo en Elche, a los efectos oportunos, a 23 de Marzo de 2018.

José Navarro Pedreño

Coordinador del Programa de Doctorado en Medio Ambiente y Sostenibilidad

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GOBIERNO DE ESPAÑA MINISTERIO DE EDUCACIÓN, CULTURA Y DEPORTE

GOBIERNO DE ESPAÑA MINISTERIO DE ECONOMÍA Y COMPETITIVIDAD

A mis padres,

a mis abuelas,

a Margarita

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

E. Abbey, *Desert Solitaire*

"The wild beasts are not our problem, the problem is we can't sell our products and the prices are too low […] Even beasts […] 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 M. Roué & Z. Molnar, *Knowing our Lands and Resources*

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PHOTOGRAPH CREDITS: Egyptian vulture *Neophron percnopterus* in Sierras de Odèn y Port del Comte,

Lérida, Spain (Eugenio Martínez Noguera)

SUMMARY

The relationship between biodiversity and ecosystem functioning in supporting human well-being through the provision of ecosystem services is broadly recognized. In recent decades, there has been an increase in the research on the crucial role of carrion and scavengers in ecosystem functioning. Vertebrate scavengers are providers of multiple ecosystem services such as nutrient cycling, disease and pest control, and recreational services such as ecotourism. Nevertheless, obligate scavengers (i.e., vultures) and many large facultative scavengers (e.g., apex predators) constitute one of the most threatened functional group worldwide. Interestingly, Spain still holds a relatively healthy population of vultures and a wide array of facultative scavengers. Thus, Spain becomes one of the main responsibles for the conservation of European scavengers.

This thesis focuses on the ecosystem services provided by vertebrate scavengers in Spain from a social-ecological perspective. Specifically, this thesis aims: i) to review the state of the art on the research on carrion, scavenging and associated ecosystem functions and services, social perceptions and attitudes toward scavengers, as well as indigenous and local knowledge (ILK) on carrion and scavenging (*Chapter 1*); ii) to spatially quantify the greenhouse gases (GHG) emitted by supplanting the natural removal of livestock carcasses by scavengers through the artificial carcass collection and transport from extensive farms to processing plants (*Chapter 2*); iii) assess the conservation and environmental consequences of the protection areas for the feeding of necrophagous species of European interest (PAFs) in Spain (*Chapter 3*); iv) to examine farmer perceptions of the ecosystem services provided by scavenging vertebrates in Spain (*Chapter 4*); v) to evaluate the similarities and contradictions between ILK and scientific knowledge (SK) regarding the scavenging service provided by vertebrates in extensive livestock farming systems (*Chapter 5*); and vi) to discuss the main results of the previous chapters, with special emphasis on the conservation implications and future perspectives (*Chapter 6*).

Chapter 1 presents an overview of the main research topics addressed through the rest of the thesis. This introductory chapter revealed that the ecosystem function and services provided by scavengers have been scarcely studied until very recently. Moreover, research on social perceptions and attitudes towards scavengers, as well as indigenous and local knowledge on carrion and scavenging, remains virtually unexplored.

In *Chapter 2*, we assessed the novel source of GHG emissions emerged following the implementation of a controversial European sanitary regulation (EC 1774/2002). After the mad cow crisis in Europe, the sanitary regulation required the collection of livestock carcasses from farms and their transformation or destruction in authorized plants. This situation had not only negative impacts on the conservation of scavengers but it also generated an unprecedented source of GHG

emissions through the artificial elimination of livestock carcasses. To spatially calculate the GHG emissions, first, peninsular Spain was divided into 10 x 10 km UTM grids and the carcasses biomass generated per year was estimated for each grid. Second, we calculated the distance covered by trucks in the transport of carcasses from the center of each grid to intermediate and/or processing plants. Third, the GHG emissions associated with the transport of livestock carcasses were estimated according to the Intergovernmental Panel on Climate Change (IPCC) methodology. In addition, information from the National Biodiversity Inventory was used to analyze the relationship between the estimated GHG emissions with the distance from the center of each grid to the nearest breeding site of the four Spanish species of vultures, and with vulture richness per grid. Results showed that supplanting the natural removal of dead extensive livestock by scavengers with carcass collection and transport to intermediate and processing plants meant the emission of 77,344 metric tons of CO_2 equivalent to the atmosphere per year, in addition to annual payments of ca. $50 million to insurance companies. Paradoxically, the areas with the highest levels of GHG emissions coincided with areas holding the highest densities of vultures. Thus, findings from this chapter support the return to a traditional and natural scenario in which scavengers freely remove livestock carcasses.

In *Chapter 3*, the network of protection areas for the feeding of necrophagous species of European interest (PAFs) was evaluated. In Europe, in an attempt to mitigate the negative impacts of the abovementioned, restrictive sanitary regulation (EC 1774/2002), a new regulation was approved (EC 142/2011) to allow farmers to leave the carcasses of extensive livestock within PAFs. To evaluate the Spanish PAFs network, first, all the Spanish autonomous communities were contacted to gather information about the characteristics of the PAFs. Second, we calculated the extensive livestock carrion biomass available inside PAFs. Third, data from the National Biodiversity Inventory were used to quantify the percentage of breeding distribution of the targeted and non-targeted scavenger species as well as the threatened and non-threatened species falling within PAFs. Fourth, we calculated the overlap between PAFs and the home range of 71 GPS-tracked vultures of four species, determining the use of the different administrative units by individuals and populations. Additionally, published studies on the home range of GPS-marked vultures in Spain were reviewed. Fifth, the potential savings in GHG emissions associated with the transport of livestock carcasses in relation to the pre-PAF scenario were estimated. The results displayed that the majority of the autonomous communities established PAFs in their territories, although the design criteria were variable. The extensive livestock carrion biomass potentially available for scavengers within PAFs was 33,474 tons per year, which represented 35% of the annual extensive livestock biomass generated in peninsular Spain. The breeding distribution of the targeted species was better represented within PAFs than that of the non-targeted species. Similarly, breeding distribution of threatened species was better represented than the one of non-threatened species. The overlap between

PAFs and the home range of GPS-tracked vulture populations ranged between 63% and 100%, whereas at the individual level, it ranged between 21% and 100%. The home area of these and other populations of GPS-marked vultures in peninsular Spain covered 3–14 autonomous communities and 1–4 countries. At the individual level, vultures used an average of 3.4 autonomous communities and 1.5 countries. The implementation of the PAF network implied a potential reduction of ca. 56% of GHG emissions compared to the previous scenario. Thus, the implementation of PAFs was potentially an important improvement compared to the previous scenario. However, the new regulation could be improved by considering the overall distribution of additional scavenger species and by supra-regional and supra-national coordination and management.

In *Chapter 4*, the farmer perceptions about the ecosystem services provided by vertebrate scavenger in Spain were assessed. To do this, 276 face-to-face surveys with farmers in 7 large extensive livestock systems were conducted. The findings indicated that the scavenging service (i.e., carrion consumption) was perceived by farmers as the most important service provided by scavengers. Interestingly, a "Dr. Jekyll and Mr. Hyde" paradox was detected, since the same species and species within the same guild can be dually perceived as beneficial or harmful depending on their consideration as primarily as scavengers or predators, respectively. Vultures were perceived by farmers as the most beneficial taxonomic group, followed by other raptors, non-raptor birds, and mammals. Farmers perceived the importance of scavengers as providers of ecosystem services when species had a more restricted distribution and their populations were perceived as declining. By contrast, farmers perceived that the provision of scavenging services increased with broader scavenger distributions. Moreover, in the scavenger communities with higher functional diversity, farmers perceived a higher capacity of the scavenger guild to provide ecosystem services. Farmers performing traditional livestock practices such as transhumance and the abandonment of livestock carcasses in the field had higher knowledge on scavengers and positive perception of them. In contrast, farmers having a higher livestock numbers, whether there were any attacks on livestock by scavengers, and having carcass removal insurance in the past, showed more negative perceptions of scavengers. In general, results from this chapter support the implementation of conservation policies in Europe that favor traditional extensive farming systems and strengthen the link between farmers and scavengers.

In *Chapter 5*, we examined the similarities and contradictions between shepherds' ILK and SK on the scavenging service provided by the vertebrate scavengers in Spain. To do so, 73 face-to-face surveys with livestock farmers of 2 extensive livestock systems were conducted. In addition, we carried out the monitoring of the consumption of 45 livestock carcasses by scavengers with camera traps. The level of consistency between the two knowledge systems was evaluated for three categories of shepherds' age and experience and at different levels of ecological organization (i.e., species and community). Overall, a high consistency between ILK and SK was found, particularly at the species level, which was also consistent over the range of shepherd ages and experience. At the species level, the scavengers' occurrence at carcasses observed by shepherds was highly correlated with the occurrence calculated from camera traps in both study areas. Likewise, the shepherds' consideration of each species as provider of the scavenging service and the carrion biomass consumed by the species calculated from camera traps were also highly related in both study areas. At the community level, no differences were found between ILK and SK regarding the mean detection time of carcasses by scavengers, whereas there were differences in the mean consumption time of carcasses, being lower for ILK than the calculated with trap cameras. In general, these results support the integration of ILK and SK into the management strategies of vertebrate scavengers.

Finally, *Chapter 6* discusses the main results obtained in the previous chapters, including conservation and policy implications, limitations and caveats, and future perspectives. Overall, through addressing some important gaps regarding carrion, scavenging and associated ecosystem services, as well as social perceptions and ILK on vertebrate scavengers in Spain from a social-ecological perspective, this thesis emphasizes the need to i) link sanitary and environmental policies, ii) support the implementation of policies that favor traditional extensive farming systems, and iii) integrate ILK and SK into the conservation strategies of vertebrate scavengers.

Resumen

PHOTOGRAPH CREDITS: Bearded vulture *Gypaetus barbatus* (Antoni Margalida Vaca)

RESUMEN

La relación entre biodiversidad, funcionamiento de los ecosistemas y bienestar humano a través de la provisión de servicios ecosistémicos es ampliamente reconocida. En las últimas décadas, ha aumentado notablemente la investigación sobre el papel crucial de la carroña y los carroñeros en el funcionamiento de los ecosistemas. Los carroñeros vertebrados son proveedores de múltiples servicios ecosistémicos tales como el ciclo de nutrientes, el control de plagas y enfermedades, y servicios recreativos como el ecoturismo. Sin embargo, los carroñeros estrictos (i.e., los buitres) y muchos carroñeros facultativos (e.g., los grandes depredadores) constituyen uno de los grupos funcionales más amenazados en todo el mundo. De manera interesante, España todavía posee una población relativamente sana de buitres y una amplia diversidad de carroñeros facultativos. Por lo tanto, España se convierte en uno de los principales responsables de la conservación de los carroñeros europeos.

*Esta tesis se centra en los servicios ecosistémicos que proporcionan los carroñeros vertebrados en España, desde una perspectiva socio-ecológica. Específicamente, esta tesis pretende: i) revisar el estado del arte en la investigación sobre carroña, funciones y servicios ecosistémicos asociados al consumo de carroña, percepciones sociales y actitudes hacia los carroñeros, así como el conocimiento indígena y local (CIL) sobre los procesos relacionados con el consumo de carroña. (*Capítulo 1*); ii) cuantificar espacialmente los gases de efecto invernadero (GEI) emitidos al suplantar la eliminación natural de los cadáveres de ganado por los carroñeros a través de la recogida y el transporte artificial de los cadáveres desde las explotaciones ganaderas en extensivo hasta las plantas de transformación (*Capítulo 2*); iii) evaluar las consecuencias de conservación y ambientales de las zonas de protección para la alimentación de especies necrófagas de interés comunitario (ZPAEN) en España (*Capítulo 3*); iv) examinar las percepciones de los ganaderos y ganaderas sobre los servicios ecosistémicos proporcionados por los carroñeros vertebrados en España (*Capítulo 4*); v) evaluar las similitudes y contradicciones entre el CIL y el conocimiento científico (CC) con respecto al servicio de consumo de carroña proporcionado por los carroñeros vertebrados en los sistemas ganaderos en extensivo (*Capítulo 5*); y vi) discutir los principales resultados de los capítulos anteriores, con especial énfasis en las implicaciones para la conservación y las perspectivas futuras (*Capítulo 6*).*

El Capítulo 1 *presenta una descripción general de los principales temas de investigación abordados en el resto de la tesis. Este capítulo introductorio reveló que las funciones y los servicios proporcionados por los carroñeros han sido poco estudiados hasta hace muy poco. Por otra parte, la investigación sobre las percepciones sociales y las actitudes hacia los carroñeros, así como el CIL sobre los procesos relacionados con el consumo de carroña, permanece prácticamente inexplorada.*

En el Capítulo 2*, se evaluó una nueva fuente de emisiones de GEI surgida tras la implementación de una controvertida regulación sanitaria europea (CE 1774/2002). Después de la crisis de las vacas locas en Europa, una regulación sanitaria exigía que los cadáveres de ganado se recogieran de las explotaciones ganaderas y se transformaran o destruyeran en plantas autorizadas. Esta situación no solo tuvo impactos negativos en la conservación de los carroñeros, sino que también generó una fuente sin precedentes de emisiones de GEI a través de la eliminación artificial de los cadáveres de ganado. Para calcular espacialmente las emisiones de GEI, primero, se dividió la España peninsular en cuadrículas UTM de 10 x 10 km y, para cada una, se estimó la biomasa de cadáveres generados por año. En segundo lugar, se calculó la distancia recorrida por los camiones en el transporte de los cadáveres desde el centro de cada cuadrícula hasta las plantas intermedias y/o de transformación. En tercer lugar, se calcularon las emisiones de GEI asociadas con el transporte de los cadáveres de ganado según la metodología del Grupo Intergubernamental de Expertos sobre el Cambio Climático (IPCC). Además, se utilizó información del Inventario Nacional de Biodiversidad para analizar la relación entre las emisiones estimadas de GEI y la distancia desde el centro de cada cuadrícula hasta el sitio de cría más cercano de las cuatro especies de buitres españoles, y con la riqueza de buitres por cuadrícula. Los resultados mostraron que suplantar la eliminación natural del ganado en extensivo muerto por los carroñeros con la recogida y el transporte de los cadáveres a plantas intermedias y de transformación supuso la emisión de 77.344 toneladas métricas de* CO_2 *equivalente a la atmósfera por año, además de pagos anuales de alrededor de 40 millones de euros a compañías de seguros. Paradójicamente, las áreas con los niveles más altos de emisiones de GEI coincidieron con las áreas con mayor abundancia de buitres. En consecuencia, los hallazgos de este capítulo apoyan el retorno al escenario tradicional y natural en el que los carroñeros eliminan libremente los cadáveres de ganado.*

En el Capítulo 3*, se evaluó la red de zonas de protección para la alimentación de especies necrófagas de interés comunitario (i.e., ZPAEN). En Europa, como un intento de mitigar los impactos negativos de la restrictiva regulación sanitaria antes mencionada (CE 1774/2002), se aprobó una nueva regulación (CE 142/2011) para permitir a los ganaderos dejar los cadáveres de ganado en extensivo dentro de las ZPAEN. Para evaluar la red española de ZPAEN, primero se contactó con todas las comunidades autónomas para recabar información sobre sus ZPAEN. En segundo lugar, se calculó la biomasa de carroña de ganado en extensivo disponible dentro de las ZPAEN. En tercer lugar, se utilizaron datos del Inventario Nacional de Biodiversidad para cuantificar el porcentaje del área de distribución de la población reproductora de las especies carroñeras objetivo y no-objetivo, así como de las especies amenazadas y no amenazadas incluido en las ZPAEN. En cuarto lugar, se analizó la superposición entre las ZPAEN y el área de campeo de 71 buitres de cuatro especies seguidos vía GPS, determinando el uso de las diferentes unidades administrativas por individuos y poblaciones. Además, se revisaron los estudios publicados sobre el área de campeo de buitres seguidos por GPS en España. En quinto lugar, se estimaron los* *ahorros potenciales en emisiones de GEI asociadas con el transporte de los cadáveres de ganado en relación con el escenario pre-ZPAEN. Los resultados mostraron que la mayoría de las comunidades autónomas establecieron las ZPAEN en sus territorios, aunque los criterios de diseño fueron variables. La biomasa de carroña de ganado en extensivo potencialmente disponible para los carroñeros dentro de las ZPAEN fue de 33.474 toneladas por año, lo que representó el 35% de la biomasa anual generada en la España peninsular. El área de distribución de las especies objetivo estuvo mejor representada en las ZPAEN que el de las especies no-objetivo. De manera similar, el área de distribución de las especies amenazadas estaba mejor representado que el de las especies no amenazadas. La superposición entre las ZPAEN y el área de campeo de las poblaciones de buitres seguidos vía GPS osciló entre un 63% y 100%, mientras que a nivel de individuo varió entre el 21% y 100%. El área de campeo de estas y otras poblaciones de buitres seguidos por GPS en la España peninsular abarcó de 3 a 14 comunidades autónomas y de 1 a 4 países. A nivel de individuo, los buitres utilizaron un promedio de 3,4 comunidades autónomas y 1,5 países. La implementación de la red ZPAEN supuso una reducción potencial de alrededor del 56% de las emisiones de GEI en comparación con el escenario anterior. Por lo tanto, la implementación de las ZPAEN significó una mejora potencial importante en comparación con el escenario anterior. Sin embargo, la nueva regulación podría mejorarse si se considera todo el área de distribución de especies carroñeras adicionales y una coordinación y gestión a escalas suprarregional y supranacional.*

En el Capítulo 4*, se evaluaron las percepciones de los ganaderos sobre los servicios ecosistémicos proporcionados por los carroñeros vertebrados en España. Para ello, se realizaron 276 encuestas cara a cara con ganaderos en 7 grandes sistemas ganaderos en extensivo. Los resultados indicaron que el servicio de consumo de carroña fue percibido por los ganaderos como el servicio más importante proporcionado por los carroñeros. Curiosamente, se detectó una paradoja del "Dr. Jekyll y Mr. Hyde", ya que las mismas especies y especies dentro del mismo gremio pueden ser percibidas doblemente como beneficiosas o dañinas dependiendo de si son consideradas principalmente como carroñeros o depredadores, respectivamente. Los buitres fueron percibidos por los ganaderos como el grupo taxonómico más beneficioso, seguidos de otras rapaces, aves no rapaces y mamíferos. Los ganaderos percibieron la importancia de los carroñeros como proveedores de servicios ecosistémicos cuando las especies tenían una distribución más restringida y su población se percibía como decreciente. Por el contrario, los ganaderos percibieron que la provisión del servicio de consumo de carroña aumentó con distribuciones más amplias de los carroñeros. Además, en las comunidades de carroñeros con mayor diversidad funcional, los ganaderos percibieron una mayor capacidad del gremio de carroñeros para proporcionar servicios ecosistémicos. Los ganaderos que realizan prácticas ganaderas tradicionales, como la trashumancia y el abandono de los cadáveres de ganado en el campo, tienen un mayor conocimiento de los carroñeros y una percepción positiva de ellos. Por el contrario, los ganaderos que tienen un mayor número de cabezas de ganado, que habían sufrido algún ataque al ganado por parte* *de carroñeros y que hayan tenido contratado un seguro de retirada de cadáveres en el pasado, mostraron percepciones más negativas de los carroñeros. En general, los resultados de este capítulo apoyan la implementación de políticas de conservación en Europa que favorezcan los sistemas ganaderos tradicionales en extensivo y fortalezcan el vínculo entre los ganaderos y los carroñeros.*

En el Capítulo 5*, se examinaron las similitudes y contradicciones entre el CIL de los pastores y el CC respecto al servicio de consumo de carroña proporcionado por los carroñeros vertebrados en España. Para ello, se realizaron 73 encuestas cara a cara con los pastores de dos sistemas ganaderos en extensivo. Además, se llevó a cabo el monitoreo del consumo de 45 cadáveres de ganado por los carroñeros con cámaras trampa. El nivel de consistencia entre los dos sistemas de conocimiento se evaluó para tres categorías de edad y experiencia de los pastores y en diferentes niveles de organización ecológica (i.e., especies y comunidad). En general, se encontró una alta consistencia entre el CIL y el CC, particularmente a nivel de especie, que también fue consistente en el rango de edades y experiencia de los pastores evaluado. A nivel de especie, las frecuencias de aparición de los carroñeros en los cadáveres observadas por los pastores y calculadas a partir de las cámaras trampa estaban altamente correlacionadas en ambas áreas de estudio. Del mismo modo, la consideración de los pastores de cada especie como proveedoras del servicio de consumo de carroña y la biomasa de carroña consumida por cada especie calculada usando cámaras trampa también estaban muy relacionadas en ambas áreas de estudio. A nivel de comunidad, no se encontraron diferencias entre el CIL y el CC con respecto al tiempo medio de detección de los cadáveres por los carroñeros, mientras que hubo diferencias en el tiempo medio de consumo de los cadáveres, siendo más bajo para el CIL que el calculado con cámaras trampa. En general, estos resultados apoyan la integración del CIL y el CC en las estrategias de gestión de los carroñeros vertebrados.*

Finalmente, el Capítulo 6 *discute los principales resultados obtenidos en los capítulos anteriores, incluidas las implicaciones de conservación y políticas, las limitaciones y advertencias, y las perspectivas futuras. En general, al abordar algunas lagunas importantes con respecto a la carroña y los servicios ecosistémicos asociados al consumo de carroña, así como las percepciones sociales y el CIL sobre los carroñeros vertebrados en España desde una perspectiva socio-ecológica, esta tesis enfatiza la necesidad de i) vincular políticas sanitarias y ambientales, ii) apoyar la implementación de políticas que favorezcan los sistemas ganaderos tradicionales en extensivo, e iii) integrar el CIL y el CC en las estrategias de conservación de los carroñeros vertebrados.*

Resumen global de los materiales y métodos y resultados

PHOTOGRAPH CREDITS: Bearded vulture *Gypaetus barbatus* in Sierras de Odèn y Port del Comte, Lérida, Spain

(Eugenio Martínez Noguera)

RESUMEN MATERIALES Y MÉTODOS

*En la introducción general de la tesis (*Capítulo 1*) se realizaron dos búsquedas bibliográficas para evaluar las publicaciones existentes sobre los dos siguientes temas: i) funciones y servicios ecosistémicos relacionados con el consumo de carroña por parte de los carroñeros y ii) percepciones sociales y actitudes hacia los carroñeros, así como conocimiento local sobre los procesos relacionados con el consumo de carroña. De los artículos seleccionados se extrajo la siguiente información: año de publicación, país de la investigación, tipo de ecosistema, grupo taxonómico y grupo funcional de las especies de carroñeros objeto de estudio. Además, en la primera búsqueda, se registró el grupo taxonómico al que pertenecían los cadáveres estudiados; en la segunda búsqueda, también se registró el tipo de agente implicado (e.g., ganaderos o cazadores) incluido en el estudio. Posteriormente, se utilizaron los artículos revisados para crear redes semánticas con los términos que aparecían en el título y resumen de los artículos seleccionados.*

En el Capítulo 2 *se estimaron las emisiones de gases de efecto invernadero (GEI) asociadas al transporte de los cadáveres de ganado. Para ello, se dividió la España peninsular en cuadrículas UTM de 10 x 10 km. En primer lugar, en cada cuadrícula se calculó la biomasa de cadáveres generados por año usando el número, el peso medio y la tasa anual de mortalidad para cada clase de edad de las diferentes especies de ganado en extensivo (i.e., bovino, ovino, caprino y porcino). En segundo lugar, se calculó la distancia recorrida en el transporte de los cadáveres desde el centro de cada cuadrícula hasta la planta intermedia y/o de procesamiento más cercana. En tercer lugar, se estimaron las emisiones de GEI asociadas con el transporte de cadáveres según la metodología indicada por el Grupo Intergubernamental de Expertos sobre el Cambio Climático (IPCC). Adicionalmente, se utilizó información del Inventario Nacional de Biodiversidad para analizar la relación entre las emisiones de GEI en cada cuadrícula con la distancia desde el centro de cada cuadrícula al sitio de cría de las cuatro especies de buitres presentes en España más cercano, y con la riqueza de especies por cuadrícula. Esta relación se analizó mediante modelos lineales generalizados y pruebas no paramétricas, respectivamente.*

En el Capítulo 3 *se evaluó la red de zonas de protección para la alimentación de especies necrófagas de interés comunitario (ZPAEN). Primero, se contactó con todas las comunidades autónomas de España para recabar información sobre las ZPAEN de su territorio. En segundo lugar, se calculó la biomasa de carroña de ganado en extensivo potencialmente disponible en las ZPAEN usando la metodología del Capítulo 2. En tercer lugar, se evaluó el porcentaje del área de distribución de la población reproductora de las especies carroñeras objetivo y no-objetivo así como de especies amenazadas y no amenazadas incluido en las ZPAEN, usando datos del Inventario Nacional de Biodiversidad sobre la presencia de las especies en cuadrículas UTM de 10 x 10 km. En cuarto lugar, se estudió el solapamiento entre las ZPAEN y el área de campeo de 71 buitres de cuatro especies seguidos por GPS, determinando el uso de las* *diferentes unidades administrativas por parte de individuos y poblaciones. De forma adicional, se revisaron estudios publicados sobre el área de campeo de buitres equipados con GPS en España. En quinto lugar, se estimaron los ahorros potenciales en las emisiones de GEI asociados con el transporte de los cadáveres de ganado en relación al escenario previo a las ZPAEN, mediante la comparación entre las emisiones de GEI asociadas a la normativa anterior (CE 1774/2002; i.e., Capítulo 2) y las emisiones de GEI después de la implementación de las ZPAEN (CE 142/2011).*

En el Capítulo 4 *se evaluó la percepción de los ganaderos y ganaderas sobre los servicios ecosistémicos proporcionados por los carroñeros vertebrados en España. Para ello, se realizaron 276 encuestas cara a cara con los ganaderos de siete grandes sistemas ganaderos en extensivo. Para testar las diferencias en la percepción de los ganaderos acerca de los diferentes grupos taxonómicos y funcionales de carroñeros se usaron pruebas no paramétricas. Se usaron regresiones lineales para ver la relación entre diferentes variables ecológicas (e.g., abundancia, riqueza, diversidad funcional) y la percepción de los ganaderos. Finalmente se realizó un análisis de correspondencia canónica para evaluar la influencia de diferentes variables socioeconómicas y características de las explotaciones ganaderas sobre la percepción de los ganaderos.*

En el Capítulo 5 *se examinaron las similitudes y contradicciones entre el conocimiento de los pastores y el conocimiento científico acerca del servicio de consumo de carroña proporcionado por los carroñeros vertebrados. Para ello, se llevaron a cabo 73 encuestas cara a cara con las pastoras y pastores de dos sistemas ganaderos en extensivo en España. Adicionalmente, se estudió el consumo de 45 cadáveres de ganado por parte de los carroñeros mediante el uso de cámaras trampa. Finalmente, se utilizó un enfoque mixto que incluye pruebas no paramétricas, correlaciones y análisis de la covarianza con el objetivo de comparar ambos sistemas de conocimiento. El nivel de consistencia entre ambos conocimientos se evaluó para tres categorías de edad y experiencia de los pastores y a diferentes niveles de organización ecológica (i.e., especies y comunidad).*

RESUMEN RESULTADOS

En el Capítulo 1, *la revisión bibliográfica mostró una escasa atención científica sobre las funciones y servicios ecosistémicos proporcionados por los carroñeros hasta muy recientemente. Además, la revisión reveló que las percepciones y actitudes sociales hacia los carroñeros, así como el conocimiento local sobre los procesos relacionados con el consumo de carroña, permanecen prácticamente inexplorados.*

En el Capítulo 2 *se calculó que la suplantación del servicio ecosistémico de eliminación de cadáveres de ganado en extensivo proporcionado por los carroñeros por la recogida y transporte de los cadáveres hasta las plantas intermedias y de transformación supuso la emisión de 77.344 toneladas métricas de* CO_2 *equivalente a la atmósfera cada año, además de pagos anuales a las compañías de seguros de* *alrededor de 40 millones de euros por parte de los ganaderos y las administraciones. Paródicamente, las áreas con mayores niveles de emisiones coincidían con áreas que albergan importantes poblaciones de buitres. Por lo tanto, los resultados del capítulo apoyan la vuelta al escenario natural en el que los carroñeros eliminan los cadáveres de ganado.*

En el Capítulo 3 *se observó que la mayoría de las comunidades autónomas establecieron las ZPAEN en sus territorios, aunque los criterios de diseño fueron variables. La biomasa de carroña de ganado en extensivo potencialmente disponible para los carroñeros dentro de las ZPAEN fue de 33.474 toneladas al año, lo cual representó el 35% de la biomasa anual de ganado en extensivo generada en la España peninsular. El área de distribución de la población reproductora de las especies objetivo estaba mejor representado dentro de las ZPAEN que el de las especies no-objetivo. De forma similar, se encontró que las especies amenazadas estaban mejor representadas en las ZPAEN que el resto de especies. El solapamiento entre el área de campeo de las poblaciones de buitres seguidos con GPS y las ZPAEN osciló entre el 63% y el 100%, mientras que a nivel de individuo osciló entre un 21% y 100%. El área de campeo de estas y otras poblaciones de buitres seguidos vía GPS en la España peninsular abarcó entre 3 y 14 comunidades autónomas y de 1 a 4 países. A nivel de individuo, el área de campeo de los buitres incluyó un promedio de 3,4 comunidades autónomas y 1,5 países. La implementación de las ZPAEN supuso una reducción potencial de aproximadamente el 56% de las emisiones de GEI en comparación con el escenario previo. A pesar de la significativa mejora tras la implementación de las ZPAEN, la nueva regulación podría mejorarse al considerar todo el área de distribución de especies carroñeras adicionales y a través de una coordinación y gestión a escalas suprarregional y supranacional.*

En el Capítulo 4 *se observó que el servicio de consumo de carroña fue percibido por los ganaderos como el más positivo. De manera interesante, se detectó una paradoja del "Dr. Jekyll y Mr. Hyde" ya que las mismas especies y especies dentro del mismo gremio pueden ser doblemente percibidas por los ganaderos como beneficiosas o dañinas según si son considerados principalmente como carroñeros o depredadores, siendo los buitres el grupo taxonómico percibido más positivamente y los mamíferos considerados como los menos beneficiosos. Los ganaderos consideraron más importantes los servicios ecosistémicos proporcionados por los carroñeros con áreas de distribución más restringida y aquellos cuyas tendencias poblaciones fueron percibidas en diminución, mientras que de manera contraria, el servicio de consumo de carroña fue considerado más importante para los carroñeros con áreas de distribución más amplias. Además, en las comunidades de carroñeros con mayor diversidad funcional, los ganaderos percibieron una mayor capacidad del gremio de carroñeros para proporcionar servicios ecosistémicos. Se observó que las prácticas ganaderas tradicionales tales como la trashumancia vinculadas al conocimiento local y basadas en la experiencia lleva a percepciones positivas de los ganaderos. Por el contrario, los ganaderos con mayor número de cabezas de ganado, que habían sufrido* *ataques de los carroñeros al ganado o habían contratado un seguro de retirada de cadáveres mostraron percepciones más negativas de los carroñeros. Por consiguiente, estos resultados apoyan la implementación de políticas de conservación que favorezcan los sistemas ganaderos tradicionales en extensivo y fortalezcan el vínculo entre los ganaderos y los carroñeros.*

En el Capítulo 5 *se encontró una alta consistencia entre el conocimiento local (CIL) de los pastores y el conocimiento científico (CC) con respecto al servicio de consumo de carroña proporcionado por los carroñeros vertebrados, siendo, en general, constante para todas las categorías evaluadas de edad y experiencia de los pastores. Se encontró una elevada correlación entre ambos sistemas de conocimiento, especialmente al nivel de especies. En concreto, la frecuencia de aparición de carroñeros en las carroñas percibida por los pastores y calculada a partir de las cámaras trampa fue altamente correlacionada. Además, la biomasa de carroña consumida por cada especie medida a partir de cámaras trampa y la percepción de los pastores de las especies como proveedoras del servicio de consumo de carroña estuvieron altamente relacionadas. A nivel de comunidad, no se encontraron diferencias entre el CIL y el CC en cuanto al tiempo medio de detección de las carroñas por los carroñeros. Por el contrario, sí se encontraron diferencias en cuanto al tiempo medio de consumo de las carroñas, siendo menor para el CIL que para el CC. De manera que, estos resultados apoyan la integración del CIL y el CC en las estrategias de gestión de los carroñeros vertebrados.*

LIST OF CO-AUTHORS AND THEIR AFFILIATIONS

Co-authors	Affiliations	Chapters
Ainara Cortés-Avizanda	Doñana Biological Station-CSIC (Spain)*	3
	Universidade de Lisboa (Portugal)	
	Universidade do Porto (Portugal)	
Antoni Margalida	University of Lleida (Spain)*	2, 3, 4
	University of Bern (Switzerland)*	
Berta Martín López	Leuphana University of Lüneburg (Germany)*	4, 5
Carolina Lazcano	Universidad Miguel Hernández (Spain)*	2
Eneko Arrondo	Doñana Biological Station-CSIC (Spain)*	3, 5
Francisco Botella	Universidad Miguel Hernández (Spain)*	2, 3, 4
Guillermo Blanco	National Museum of Natural Science-CSIC (Spain)*	4
Irene Pérez	Columbia University in the City of New York (USA)*	4
José A. Donázar	Doñana Biological Station-CSIC (Spain)*	2, 3, 4, 5
José A. Sánchez-Zapata	Universidad Miguel Hernández (Spain)*	2, 3, 4, 5
José Jiménez	Institute of Research in Game Resources-CSIC (Spain)*	3
Juan M. Pérez García	University of Lleida (Spain)*	2, 3
	Universidad Miguel Hernández (Spain)	
Marcos Moleón	University of Granada (Spain)*	2, 3, 4, 5
	Universidad Miguel Hernández (Spain)	
	Doñana Biological Station-CSIC (Spain)	
Martina Carrete	Pablo de Olavide University (Spain)*	2, 3
	Doñana Biological Station-CSIC (Spain)	
Patricia Mateo-Tomás	University of Coimbra (Portugal) *	4, 5
Pedro P. Olea	Universidad Autónoma de Madrid (Spain)*	5
Rubén Moreno-Opo	University Complutense of Madrid (Spain)*	2, 3

*Current address

ABBREVIATIONS AND ACRONYMS

ABPs	Animal by-products not intended for human consumption
BSE	Bovine spongiform encephalopathy
CBD	The Convention on Biological Diversity
CC	*Conocimiento científico*
CE	*Comisión Europea*
CES	Cultural ecosystem services
CIL	*Conocimiento indígena y local*
EC	European Community
ESP	Ecosystem service provider
EU	European Union
GEI	*Gases de efecto invernadero*
GHG	Greenhouse gases
GPS	Global Positioning System
GWP	Global warming potential
ILK	Indigenous and local knowledge
IPBES	Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
MCP	Minimum convex polygon
MEB	Multiple Evidence Base
NCP	Nature's contributions to people
nvCJD	New variant Creutzfeldt-Jakob disease
PAFs	Protection areas for the feeding of necrophagous species of European interest
PA	Protected area
PES	Payments for Ecosystem Services
SK	Scientific knowledge
UD	Utilization distributions
UNFCCC	United Nations Framework Convention on Climate Change
UTM	Universal Transverse Mercator
vCJD	Variant Creutzfeldt-Jakob disease
WDPA	World Database on Protected Areas
ZPAEN	*Zonas de protección para la alimentación de especies necrófagas de interés comunitario*

GLOSSARY

Carrion: any type of dead animal tissue. This includes carcasses, corpses and cadavers[1].

Ecosystem functioning: the flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem. It includes many processes such as biomass production, trophic transfer through plants and animals, nutrient cycling, water dynamics and heat transfer[2].

Ecosystem services: the benefits (and occasionally losses or detriments) that people obtain from ecosystems. These include provisioning services such as food and water; regulating services such as flood and disease control; and cultural services such as recreation, ethical and spiritual, educational and sense of place[2].

Facultative scavenger: an animal that scavenges at variable rates but that can subsist on other food resources in the absence of carrion. All mammalian predators (e.g., foxes, wolves, and bears), numerous birds of prey (e.g., most large eagles and kites), and corvids (e.g., ravens, crows), as well as other non-raptor birds (e.g., gulls)[1].

Indigenous and local knowledge: a cumulative body of knowledge, practice and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment. It is also referred to by other terms such as, for example, Indigenous, local or traditional knowledge, traditional ecological/environmental knowledge (TEK), farmers' or fishers' knowledge, ethnoscience, indigenous science, folk science[2].

Obligate scavenger: an animal that relies entirely or near entirely on carrion as food resource. Only vultures (both Old and New World species—families *Accipitridae* and *Cathartidae*, respectively) are considered obligate[1].

Perceptions: the way an individual observes, understands, interprets, and evaluates a referent object, action, experience, individual, policy, or outcome[3].

Predation: an interaction in which one animal kills and eats all or part of another[1].

Scavenging: an interaction in which one animal eats all or part of a dead animal. Scavenging is active (also called confrontational, aggressive, or power scavenging) when the predator that was responsible for the kill is chased away and most of the meat on the carcass is procured, or it is passive when the bones, which may contain fragments of meat, marrow, and skull contents, are collected[1].

Social-ecological systems: complex and adaptive systems, in which social (human) and ecological (biophysical) subsystem interact[4].

[1]Moleón, M., Sánchez-Zapata, J.A., Margalida, A., Carrete, M., Owen-Smith, N., & Donázar, J.A. (2014) Humans and scavengers: The evolution of interactions and ecosystem services. *BioScience*, **64**, 394–403.

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COLLAGE LAYOUT by Zebensui Morales Reyes

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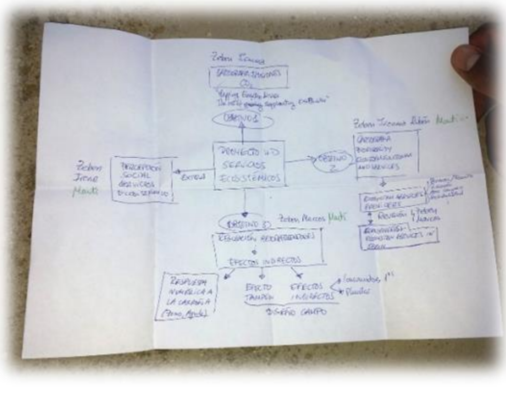

que pregunta "¿Qué tal?, ¿estás bien?... ¿seguro?", no es más que otra muestra de tu implicación en la tesis. A Marcos lo conocí un día en Pozo Alcón, y desde entonces de manera desinteresada me ha guiado acertadamente por el camino de mi carrera investigadora. No me importaría heredar tu perfeccionismo y capacidad para trabajar milimétricamente hasta convertir un texto normal en uno brillante o una figura corriente en una sorprendente. Da igual lo complicado que parezca, tú siempre contestas con optimismo y motivación, haciendo fácil el reto de la tesis. Pero no solo académicamente sois un lujo, también como personas sois de admirar. Bajo vuestra tutela he aprendido muchísimo, pero además me llevo dos amigos. De corazón, ¡¡gracias por vuestra entrega y por todo lo compartido!!

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Griffon vulture *Gyps fulvus* (Margarita Yécora Molina)

Chapter 1

General Introduction

PHOTOGRAPH CREDITS: Cow *Bos taurus* in Parque Natural de los Alcornocales, Cádiz, Spain

Griffon vultures *Gyps fulvus* in The Bardenas Reales of Navarre, Spain

(Manuel J. de la Riva Pérez)

BACKGROUND

The global biodiversity crisis

In the last 500 million years, five mass extinctions have occurred on Earth. Since the beginning of the industrialization, the alarming humanization of the planet has led to a new era, the Anthropocene, in which human impacts are at least as important as natural processes (Corlett 2015). In fact, scientists are recognizing a new global biodiversity crisis, the so-called "sixth extinction", which is driven by anthropogenic impacts on nature (Barnosky et al. 2011; Dirzo et al. 2014; Isbell et al. 2017). Although recognizing this human-driven, large-scale biodiversity loss is the first step towards biodiversity conservation, we need a global, multidisciplinary response to this concern of paramount importance for the future of nature and humans themselves (Johnson et al. 2017; Ripple et al. 2017).

Ecosystem services framework: strengths and weaknesses

Given that social and ecological systems are closely interlinked and therefore their separation is arbitrary and artificial (Berkes & Folke 1998), biodiversity conservation should be approached from a social-ecological perspective (Liu et al. 2007; Ban et al. 2013; Palomo et al. 2014; Martín-López et al. 2012; Martín-López & Montes 2015; Bennett 2016; Bennett et al. 2017). Within this context, the concept of ecosystem services arises as a key component for connecting both ecological and social systems. Ecosystem services are the benefits (and occasionally losses or detriments) that humans obtain from ecosystems (Díaz et al. 2015). These include three types: *provisioning services* such as food and water; *regulating services* such as flood and disease control; and *cultural services* such as recreation, ethical and spiritual, educational and sense of place (Díaz et al. 2015).

The role of biodiversity in ecosystem functioning and in supporting human well-being through the provision of ecosystem services is widely known (e.g., Balvanera et al. 2001; MA 2005; Mace et al. 2012; Cardinale et al. 2012). The concept of ecosystem services is increasingly used as a popular tool for encouraging nature conservation and quantifying human benefits from nature. It has been used by environmental managers, scientists, policy makers and other stakeholders to understand and communicate the consequences of biodiversity loss for human well-being (see review in Costanza et al. 2017).

Nonetheless, the ecosystem services concept as a conservation tool has been questioned in recent years (see e.g., Lele et al. 2013; Schröter et al. 2014; Gunton et al. 2017). First, the concept is criticized for being based on an anthropocentric view (e.g., McCauley 2006; Redford & Adams 2009), whereas some authors have pointed out that nature conservation should be based on the intrinsic value of nature (e.g., Jax et al. 2013). Second, the concept could stimulate an exploitative human–nature relationship (e.g., Brockington et al. 2008), but it can also be used to reinforce the idea that humanity depends on the ecosystems (e.g., Folke et al. 2011; Raymond et al. 2013). Third, previous research suggests that ecosystem services might both hinder (e.g., McCauley 2006; Vira & Adams 2009) and support (e.g., Balvanera et al. 2006; Armsworth et al. 2007) biodiversity conservation. Fourth, the concept is often criticized because of the monetary quantification of ecosystem services to communicate the value of biodiversity (see e.g., Goméz-Baggethun & Ruiz-Pérez 2011), but economic valuations provide extra information for decision-making processes (De Groot et al. 2012). Interestingly however, ecosystem services assessments do not necessarily include monetary valuations, there are other types of assessment such as sociocultural (e.g., Chan et al. 2012). Fifth, the concept is contested because it is based on commodification of nature and Payments for Ecosystem Services (PES) (e.g., Redford & Adams 2009; Turnhout et al. 2013), whereas it is also argued that ecosystem services are not necessarily associated with marketization (e.g., Skroch & López-Hoffman 2010). Sixth, there is an ambiguity around the definition and classifications of ecosystem services (e.g., Nahlik et al. 2012; Gunton et al. 2017), but this vagueness can be used to foster transdisciplinary research (see e.g., Jahn et al. 2012). Seventh, some studies discuss the normative nature of the concept for involving that all ecosystems outputs are beneficial to humans (e.g., McCauley 2006), whereas others claim that it should not be a problem if this is acknowledged (Schröter et al. 2014).

Scavenger ecological importance and conservation

The relationship between biodiversity and ecosystem functioning has been subject of broad scientific attention (e.g., Hooper et al. 2005; Cardinale et al. 2012). During the last years, there has been a recent, noticeable increase in the research and awareness on the key role that carrion and scavengers plays in the stability, structure and dynamics of food webs, as well as on ecosystem functioning (Wilson & Wolkovich 2011; Moléon & Sánchez-Zapata 2015). Recent studies have shown that species richness and composition enhance ecosystem functioning and stability in vertebrate scavenger networks (Sebastián-González et al. 2016; Mateo-Tomás et al. 2017). In fact, scavenger networks with obligate scavengers and top predators show a higher scavenging efficiency (Sebastián-González et al. 2016; Mateo-Tomás et al. 2017; Morales-Reyes et al. 2017). Therefore, the general decline of major scavengers such as vultures and top predators, across the planet could lead to negative impacts on ecosystem functioning. For instance, vulture loss may increase scavenging opportunities for facultative scavengers (Moleón et al. 2014a; Morales-Reyes et al. 2017), which could not only decrease the scavenging efficiency but also led to negative impacts such as disease transmission among scavengers, wild and domestic animals and even humans (Ogada et al. 2012a).

In many terrestrial ecosystems, a wide diversity of vertebrate scavengers rather than microbes or arthropods consume the majority of available carcasses (see e.g., DeVault et al. 2003). Vertebrate scavenging assemblages are represented by two major functional groups: obligate scavengers, i.e., Old– and New–World vultures (*Accipitridae* and *Cathartidae* family, respectively), which depend totally on carrion, and facultative scavengers, e.g., mammalian carnivores, suids, raptors and most corvids, which exploit carrion opportunistically (DeVault et al. 2003; Selva et al. 2003; Mateo-Tomás et al. 2015, 2017; Moleón et al. 2014a; Pereira et al. 2014). Whilst facultative scavengers constitute a ubiquitous group, obligate scavengers are among the most threatened functional group worldwide (Şekercioğlu et al. 2004; Ogada et al. 2012b, 2016; Buechley & Şekercioğlu 2016). In the world, there are 23 vulture species (16 Old World vultures and 7 New World vultures; Donázar 1993). Nevertheless, most vulture populations have suffered sharp declines worldwide. In fact, nine vulture species are critically endangered (CR), three are endangered (EN) and four are near threatened (NT) (Fig. 1). The main non-natural threats for vultures include dietary toxins (mostly intended and unintended poisoning and, occasionally, veterinary drugs such as diclofenac), electrocution and collision with electric infrastructures (wind farms and electric pylons), food shortage due to sanitary legislations, decline or abandonment of traditional farming practices and human persecution (Carrete et al. 2009, 2012; Olea & Mateo-Tomás 2009; Margalida et al. 2010; Mateo-Tomás et al. 2012; Ogada et al. 2012b; Margalida et al. 2014a, 2014b; Buechley & Şekercioğlu 2016; Green et al. 2016; Margalida & Moleón 2016; Sánchez-Zapata el al. 2016; Santangeli et al. 2016). In addition, many large facultative scavengers (e.g., apex predators) are also widely threatened worldwide (Estes et al. 2011).

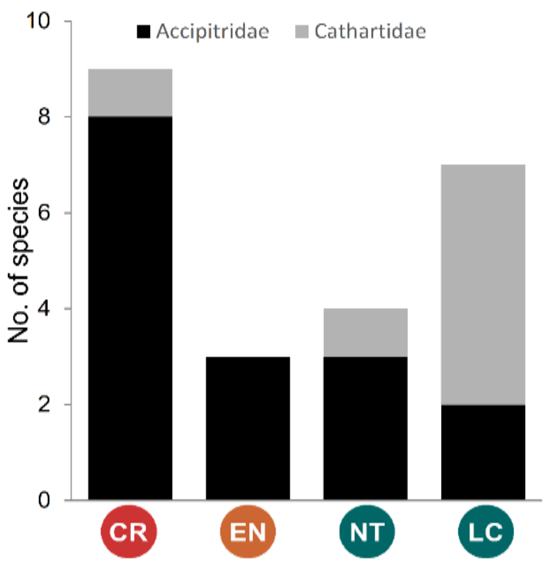


Figure 1. IUCN threat status for all vulture species (IUCN 2017) by family (i.e., *Accipitridae* and *Cathartidae*).

Whilst Asian and African vulture populations have suffered important declines during the last decades (Ogada et al. 2016; Buechley & Şekercioğlu 2016), Western Europe, and Spain in particular, still maintains a relatively healthy population of obligate scavengers (Margalida et al. 2010). In Spain there are four vulture species: griffon (*Gyps fulvus*), cinereous (*Aegypius monachus*), Egyptian (*Neophron percnopterus*) and bearded vultures (*Gypaetus barbatus*). Spanish vultures have noticeably recovered in the last decades after strong declines since the 1950s (del Moral 2009; Donázar et al. 2016; see Table 1), but three of the four species are still classified as threatened at the national level: Egyptian and bearded vultures are CR, and cinereous vulture is listed as vulnerable (VU) (Madroño et al. 2004). Spain is also home to a wide array of facultative avian scavengers (see Table 1), including apex predators such as the golden eagle (*Aquila chrysaetos*) and the Spanish imperial eagle (*A. adalberti*), other raptors such as black kites (*Milvus migrans*), red kites (*M. milvus*), common buzzards (*Buteo buteo*) and Western marsh harriers (*Circus aeruginosus*), corvids such as common ravens (*Corvus corax*), carrion crows (*Corvus corone*), Eurasian jays (*Garrulus glandarius*) and common magpies (*Pica pica*), and seabirds such as yellow-legged gulls (*Larus michahellis*). Among mammalian facultative scavengers, apex predators such as brown bears (*Ursus arctos*), gray wolves (*Canis lupus*) and Iberian lynxes (*Lynx pardinus*), mesocarnivores such as red foxes (*Vulpes vulpes*), stone martens (*Martes foina*), pine martens (*M. martes*), common genets (*Genetta genetta*), Eurasian badgers (*Meles meles*) and Egyptian mongooses (*Herpestes ichneumon*), and omnivores such as wild boars (*Sus scrofa*), are also present in Spain (Mateo-Tomás et al. 2015, 2017).

In Europe, after the sanitary crisis that arose with the outbreak of bovine spongiform encephalopathy, restrictive sanitary policies were applied. These regulations caused an important food shortage for scavengers (Donázar et al. 2009a; Margalida et al. 2010). This situation led to a negative impact for the conservation of vultures (Margalida & Colomer 2012) and it also affected facultative scavengers such as kites or wolves (Blanco 2014; Lagos & Bárcena 2015; Llaneza & López-Bao 2015). Considering that Spain hosts the largest European vulture population and many of the largest populations of large carnivores in Western Europe (Chapron et al. 2014), we are responsible for the conservation of these species in the European continent.

Table 1. Conservation status (according to IUCN Red List categories) and breeding population trend of main scavenger species present in Spain (species selection based on Mateo-Tomás et al. (2015)) at the global and national scales. Trends are reported as: increasing (+); decreasing (–); stable (0); or unknown (?). Conservation status: CR: Critically Endangered; EN: Endangered; VU: Vulnerable; NT: Near Threatened; LC: Least concerned. Own representation based on: (Madroño et al. 2004; Palomo et al. 2007; Wilson et al. 2009; Deinet et al. 2013; Chapron et al. 2014; BirdLife International 2015; IUCN 2017).

Species name	Scavenger group	Functional group	Conservation status (Global)	Population trend (Global)	Conservation status (Spain)	Population trend (Spain)
Gypaetus barbatus	Vulture	Obligate	NT	–	EN	+
Gyps fulvus	Vulture	Obligate	LC	+	LC	+
Neophron percnopterus	Vulture	Obligate	EN	–	EN*; CR**	0*; +**
Aegypius monachus	Vulture	Obligate	NT	–	VU	+
Aquila chrysaetos	Apex predator	Facultative	LC	0	NT	+
Aquila adalberti	Apex predator	Facultative	VU	+	EN	+
Milvus migrans	Generalists	Facultative	LC	?	NT	+
Milvus milvus	Generalists	Facultative	NT	–	EN	–
Buteo buteo	Generalists	Facultative	LC	0	LC*; NT**	–*; +**
Circus aeruginosus	Predator	Facultative	LC	+	LC	+
Corvus corax	Corvids	Facultative	LC	+	LC; EN**	–
Pica pica	Corvids	Facultative	LC	0	LC	0
Corvus corone	Corvids	Facultative	LC	+	LC	–
Garrulus glandarius	Corvids	Facultative	LC	0	LC	+
Larus michahellis	Seabirds	Facultative	LC	+	LC	+
Canis lupus	Apex predator	Facultative	LC	0	NT	+
Ursus arctos	Apex predator	Facultative	LC	0	CR	+‡; –‡‡
Lynx pardinus	Apex predator	Facultative	EN	+	CR	+

Vulpes vulpes	Generalists	Facultative	LC	0	LC	0
Martes foina	Generalists	Facultative	LC	0	LC	0
Martes martes	Generalists	Facultative	LC	0	LC	0
Genetta genetta	Generalists	Facultative	LC	0	LC*; VU***	0
Meles meles	Generalists	Facultative	LC	0	LC	0
Herpestes ichneumon	Generalists	Facultative	LC	0	LC	0
Sus scrofa	Omnivore	Facultative	LC	?	LC	+

*Spain populations.

**Canary Islands populations.

***Balearic Islands populations.

‡Cantabrian populations.

‡‡Pyrenean populations.

Scavengers as providers of ecosystem services

Humans and vertebrate scavengers have been closely related since the origin of the earliest hominids, especially since the emergence of agriculture and animal domestication around 10,500 years ago (Agudo et al. 2010; Moleón et al. 2014b). Since then, scavengers have provided multiple provisioning, regulating and cultural services to humans (Moleón et al. 2014b; Cortés-Avizanda et al. 2015; DeVault et al. 2016). For instance, vultures have been revered and incorporated into numerous human cultures (Ferrari et al. 2009; Morelli et al. 2015). Today, the Indian Parsi community depend upon funeral services provided by vultures, which consume the bodies of their dead relatives placed in the 'Towers of Silence' (Pain et al. 2003; Markandya et al. 2008; Ogada et al. 2012b). Tibetans Buddhists also carry out a traditional funerary practices ("Sky Burials") in which they expose their dead to scavengers (Ogada et al. 2012b). Also, the Socotra's Egyptian vultures provide an important service by means of the disposal of waste, carrion, and human excrements in villages and towns (Gangoso et al. 2013). In recent times, scavengers are important providers of recreational services, such as ecotourism (Becker et al. 2005). Nonetheless, the most evident ecosystem service provided by scavengers is the hygienic service through the removal of carrion from ecosystems, including wild animal carcasses, livestock carcasses and even human corpses (Dupont et al. 2012; Moleón et al. 2014b; Ćirović et al. 2016; DeVault et al. 2016; Donázar et al. 2016). Worldwide, vertebrate scavengers remove an important fraction of the carrion biomass available (see e.g., DeVault et al. 2003; Mateo-Tomás et al. 2015, 2017), and thus contribute to pest and disease regulation (Ogada et al. 2012a) and nutrient cycling (Wilson & Wolkovich, 2011; Beasley et al. 2015).

Despite the vertebrate scavenger guild is globally threatened (e.g., Ogada et al. 2012b, 2016; Buechley & Şekercioğlu 2016), the ecosystem services associated with them have received little scientific attention until recently (Moleón et al. 2014b). In fact, only a few articles have quantified the regulating ecosystem services (in particular, the very relevant hygienic role) provided by vertebrate scavengers (see Markandya et al. 2008; Dupont et al. 2012; Margalida & Colomer 2012, Ćirović et al. 2016).

Among vertebrate scavengers, obligate scavengers, are highly efficient in locating and consuming carcasses (Cortés-Avizanda et al. 2014; Moleón et al. 2014a; Sebastián-González et al. 2016; Morales-Reyes et al. 2017). Thus, the negative population trends of vultures could have negative effects not only on ecosystem functioning, but also on their capacity for providing ecosystem services. The catastrophic decline of vulture populations that took place in the 1990s in the Indian subcontinent (see e.g., Pain et al. 2003; Ogada et al. 2012b) is a "classical" example of consequences of obligate scavenger loss because of anthropogenic actions. This scenario led to numerous negative impacts for local people such as increases of livestock and human diseases due to an increase in reservoirs of pathogens such as rats (*Rattus sp.*) and feral dogs (*Canis lupus familiaris*), water pollution and the subsequent health expenditure in medical and pharmaceutical treatments (Markandya et al. 2008; Ogada et al. 2012a). Vulture declines also had a huge negative impact on recreational activities such as ecotourism, existence and cultural values of the vultures for local community (specially the Parsees; Pain et al. 2003; Markandya et al. 2008; Ogada et al. 2012b).

Traditional extensive livestock farming systems and scavengers

In Mediterranean ecosystems, traditional extensive livestock farming systems (i.e., pasture-based farming) are intimately linked to biodiversity conservation and ecosystem processes (Bernués et al. 2014). These livestock farming systems provide with numerous ecosystem services including provisioning services such as food (e.g., meat or dairies; Harrison et al. 2010), regulating services such as recovery or maintenance of grazing areas (Benthien et al. 2016), tree regeneration (Carmona et al. 2013), seed dispersal (Manzano & Malo 2006), disturbance prevention (e.g., forest fires; Strand et al. 2014), and cultural services such as the aesthetic and recreational values of the landscape, indigenous and local knowledge or cultural identity (e.g., Pereira et al. 2005; Oteros-Rozas et al. 2013a; López-Santiago et al. 2014). Therefore, the study of the sustainability of these systems is of great interest to the conservation of European natural ecosystems deeply linked to human activities (Bernués et al. 2011).

The link between extensive livestock farming systems and the community of vertebrate scavengers is a good example of the vital importance of traditional livestock farming systems to nature conservation (Moleón et al. 2014b). This interaction has allowed, on the one hand, the maintenance of the main populations of a globally threatened taxonomic group and, on the other hand, the functioning of ecological processes and the provision of essential ecosystem services to farmers and society in general (see e.g., Moleón et al. 2014b; Cortés-Avizanda et al. 2015). Although wild ungulates from culling and big game hunting are an important source of food for vultures and other facultative scavengers in Mediterranean environments (Mateo-Tomás et al. 2015), scavengers largely rely on the carcasses of domestic ungulates (Donázar et al. 2009b; Margalida & Colomer 2012). For this reason, traditional livestock farming practices in extensive and semi-extensive regimes such as transhumance are key to guarantee the long-term conservation of vertebrate scavengers (Olea & Mateo-Tomás 2009). Nonetheless, traditional farming practices such as transhumance in Europe have suffered a progressive decline, especially during the last decades (Olea & Mateo-Tomás 2009; Oteros-Rozas et al. 2013b).

Indigenous and local knowledge hold by shepherds

The importance of incorporating local perspectives and knowledge to understand the relationships between humans and nature and to provide essential information for biodiversity conservation have been recognized in social-ecological approaches (Huntington 2000; Berkes 2004). Indigenous and local knowledge (ILK) –also referred to as indigenous, local or traditional knowledge, traditional ecological/environmental knowledge, farmers' or fishers' knowledge, ethnoscience, indigenous science or folk science– is defined as "the cumulative body of knowledge, practices, and beliefs regarding the relationships of living things to their environment" (Díaz et al. 2015). The Intergovernmental Science-Policy Platform of Biodiversity and Ecosystem Services (IPBES) and the Convention on Biological Diversity (CBD) have recognized the role of ILK to gain understanding about biodiversity and ecosystem services and to provide information for biodiversity conservation and sustainable use of ecosystems (Tengö et al. 2014, 2017). The potential of ILK include understanding of environmental changes such as climate (Reyes-García et al. 2016), animal distribution (Danielsen et al. 2014; Parry & Peres 2015), coastal communities after a disturbance (Aswani & Lauer 2014), vegetation dynamics (Sop & Oldeland 2013) or perceiving population trends and abundance of different species (Anadón et al. 2009). Likewise, the integration of ILK and scientific knowledge for sustainable management of biodiversity and ecosystem services through the Multiple Evidence Base (MEB) approach has been suggested recently by IPBES (Tengö et al. 2017).

In Europe, ILK research on extensive farming systems has been documented mostly in the Mediterranean area (Hernández-Morcillo et al. 2014), where Spain is considered one of the research hotspots (see e.g., Gómez-Baggethun et al. 2010; Oteros-Rozas et al. 2013a; Iniesta-Arandia et al. 2015). In Mediterranean farming systems, studies have mostly focused on the importance of ILK for improving the management practices and its trends (e.g., Gómez-Baggethun et al. 2010; Oteros-Rozas et al. 2013a). Additionally, the value of ILK held by shepherds has broadly been indicated for the sustainable management of biodiversity and ecosystem services (e.g., Fernández-Giménez 2000; Anadón et al. 2009; Knapp & Fernández-Giménez 2009; Fernández-Giménez & Fillat Estaque 2012; Oteros-Rozas et al. 2013a). In this sense, the ILK held by shepherds in the Mediterranean extensive livestock farming systems about the role of vertebrate scavengers in providing scavenging services to humans may contribute to their conservation.

ECOSYSTEM SERVICES, SOCIAL PERCEPTIONS AND INDIGENOUS AND LOCAL KNOWLEDGE: STATE OF THE ART

Research on the role of carrion in ecosystems and its consumption by scavengers (i.e., scavenging) has increased markedly in recent years (see Moleón & Sánchez-Zapata 2015). By contrast, studies related to ecosystem services provided by scavengers and regarding social perceptions of scavengers and ILK on carrion and scavenging are relatively recent and quite scarce. Thus, we conducted a literature review to describe the existing scientific publications (see below).

Ecosystem services research

In order to describe the existing publications on carrion, scavenging and associated ecosystem functions and services in the scientific literature, we reviewed 83 articles (see Appendix 1.1 for methodological details). Among the terms related to carrion and scavenging, 'scaveng*' was the most frequent in the title, abstract and keywords of reviewed articles (this term appeared in 69% of the articles); this figure was lower for 'carrion' (48%), 'carcass' (41%), 'vulture' (15%), 'cadaver' (1%) and 'corpse' (1%; Fig. 2a). Among the terms related to ecosystem functions and services, 'ecosystem function*' was more frequent (77%) than 'ecosystem service' (39%; Fig. 2b).

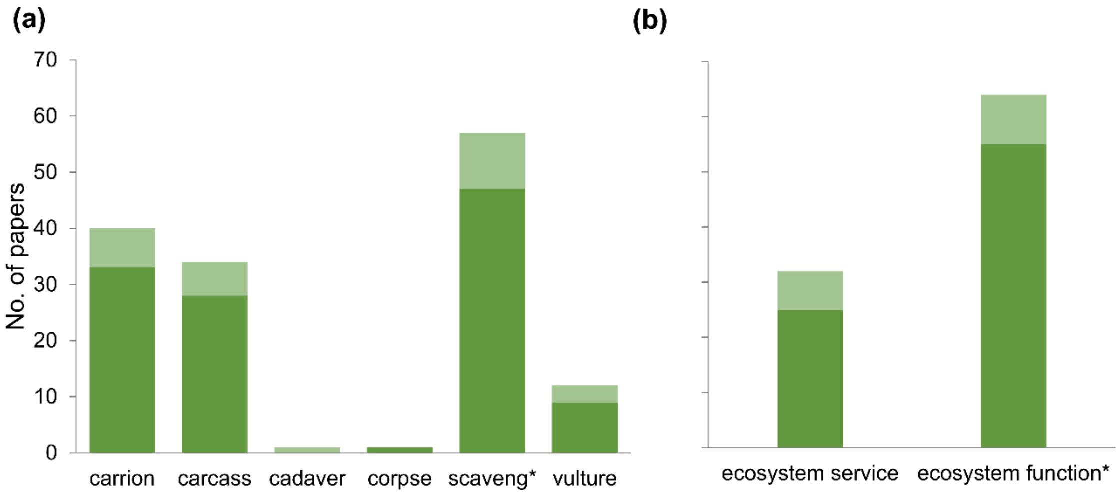


Figure 2. Number of reviewed articles (n = 83) containing the terms (a) 'carrion', 'carcass', 'cadaver', 'corpse', 'scaveng*', 'vulture', and (b) 'ecosystem service' and 'ecosystem function*'. Full color: research articles; light color: review articles.

Research on carrion, scavenging and ecosystem functions and services has received little scientific attention until very recently (Fig. 3a). The majority of research has been conducted in North America (mainly in United States), followed by Oceania (mainly in Australia), Western Europe (mainly in Spain and United

Kingdom), East and Southeast Asia (mostly in Japan and Malaysia), South America (principally in Brazil) and Africa (mainly in South Africa) (Fig. 3b).

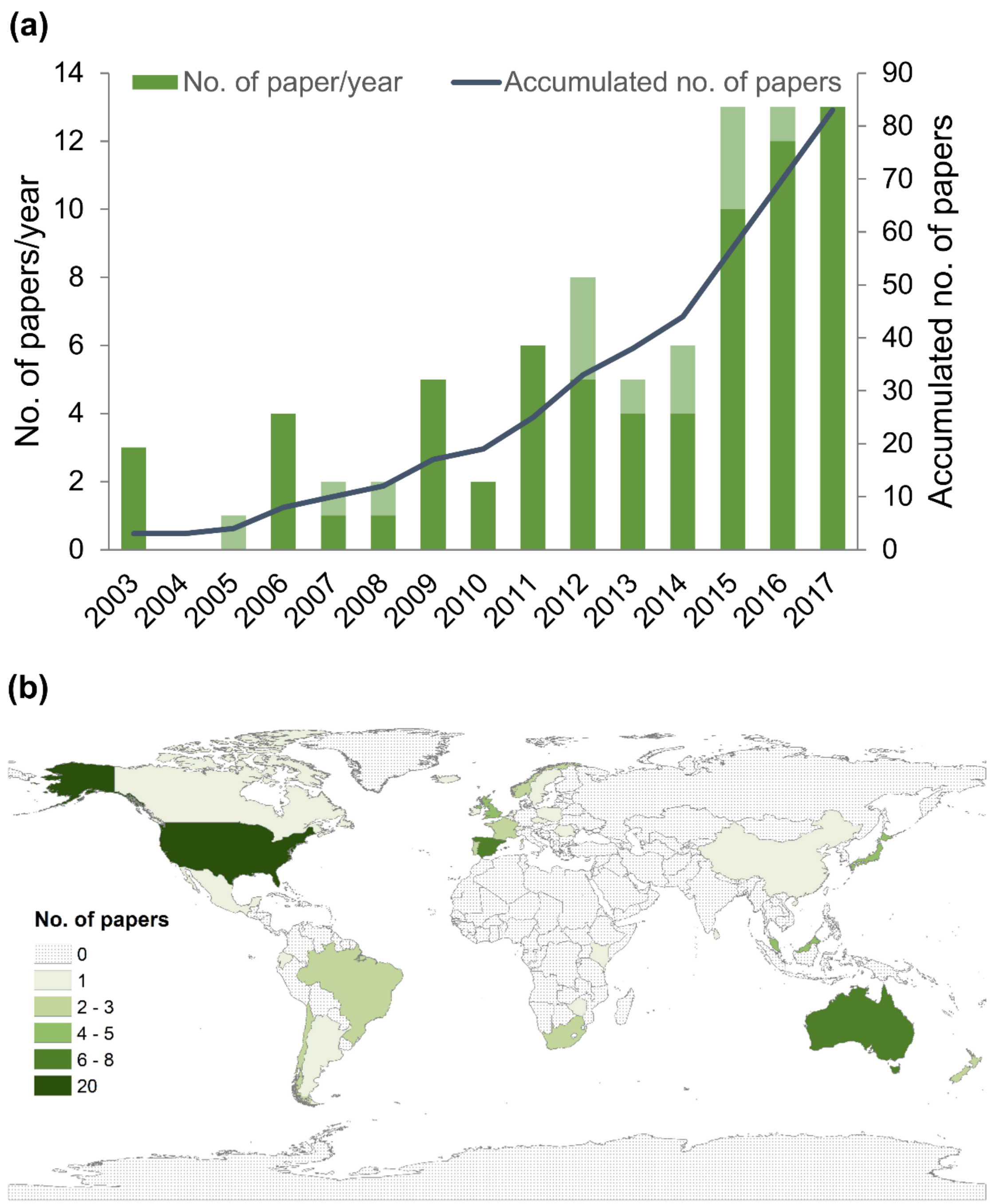


Figure 3. Number of articles on carrion, scavenging and associated ecosystem functions and services published (a) per year (full color: research articles; light color: review articles) and (b) by country (total n = 83).

The majority of articles were performed in terrestrial ecosystems (74%), followed by marine ecosystems (13%), freshwater ecosystems (8%), both terrestrial and marine ecosystems (4%) and both terrestrial and freshwater ecosystems (1%; Fig. 4).

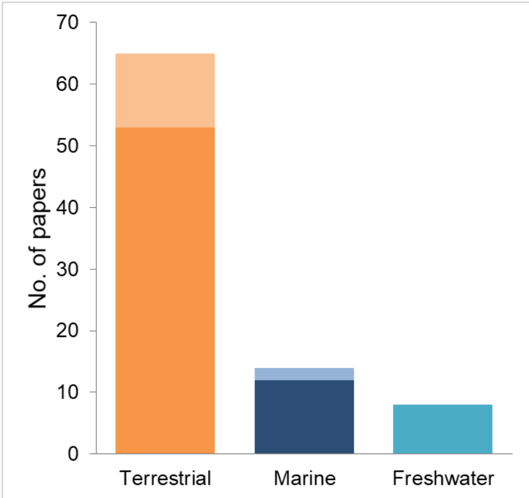


Figure 4. Number of articles on carrion, scavenging and associated ecosystem functions and services published according to ecosystem (i.e., terrestrial, marine and freshwater; n = 83). Full color: research articles; light color: review articles.

Within the articles dealing with scavengers (n = 64), most of them focused on invertebrates (53% of the articles), followed by mammals (33%), non-raptor birds (30%), raptors (excluding vultures; 20%), vultures (17%), reptiles (8%) and fish (5%; Fig. 5a). In addition, facultative scavengers were more frequent (88% of the articles) than obligate scavengers (31%; Fig. 5b).

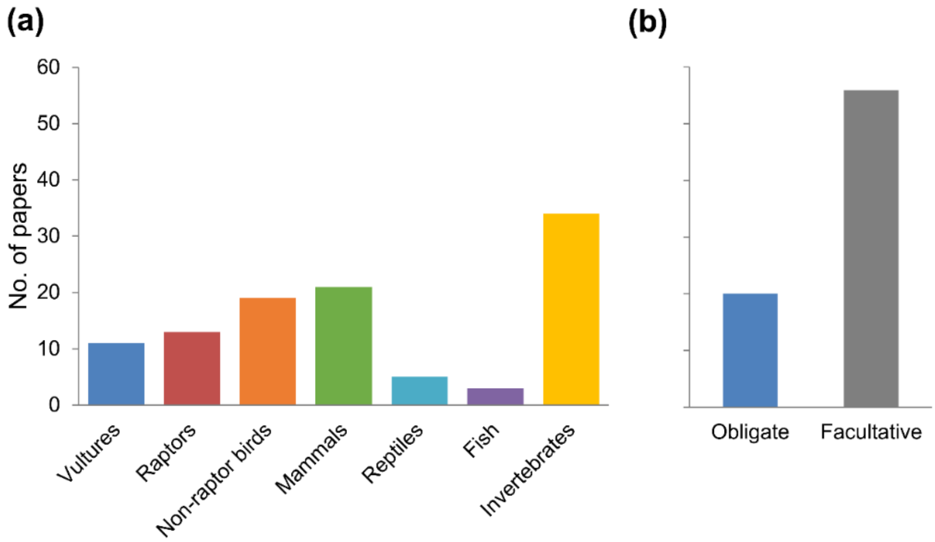


Figure 5. Number of articles on carrion, scavenging and associated ecosystem functions and services according to (a) scavenger taxonomic groups and (b) functional groups. Only research articles were considered for this purpose (n = 64).

Within the articles studying carcass consumption patterns (n = 47), mammals were the most frequent type of carcass (55% of the articles), followed by fish (26%), invertebrates (19%), birds (15%), amphibians (2%) and reptiles (2%; Fig. 6).

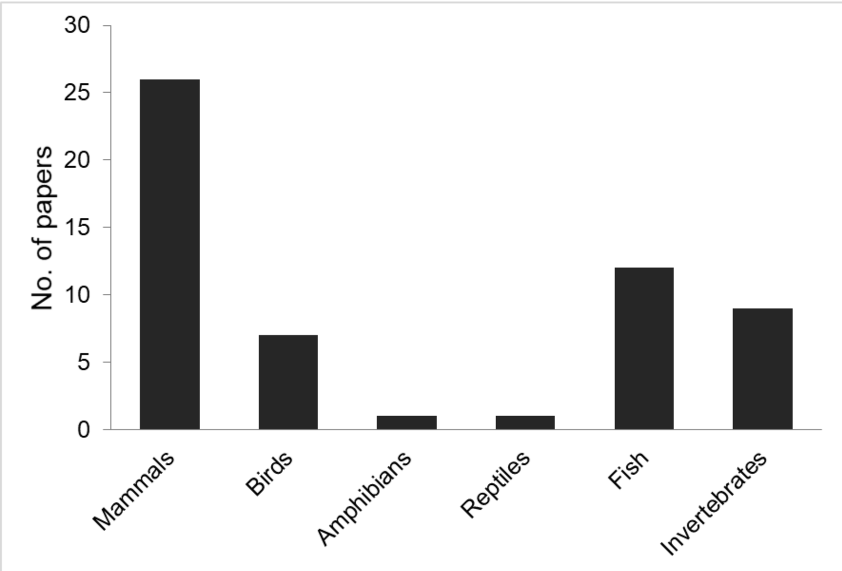


Figure 6. Number of articles on carrion, scavenging and associated ecosystem functions and services according to the taxonomic identity of the studied carcasses. Only research articles were considered for this purpose (n = 47).

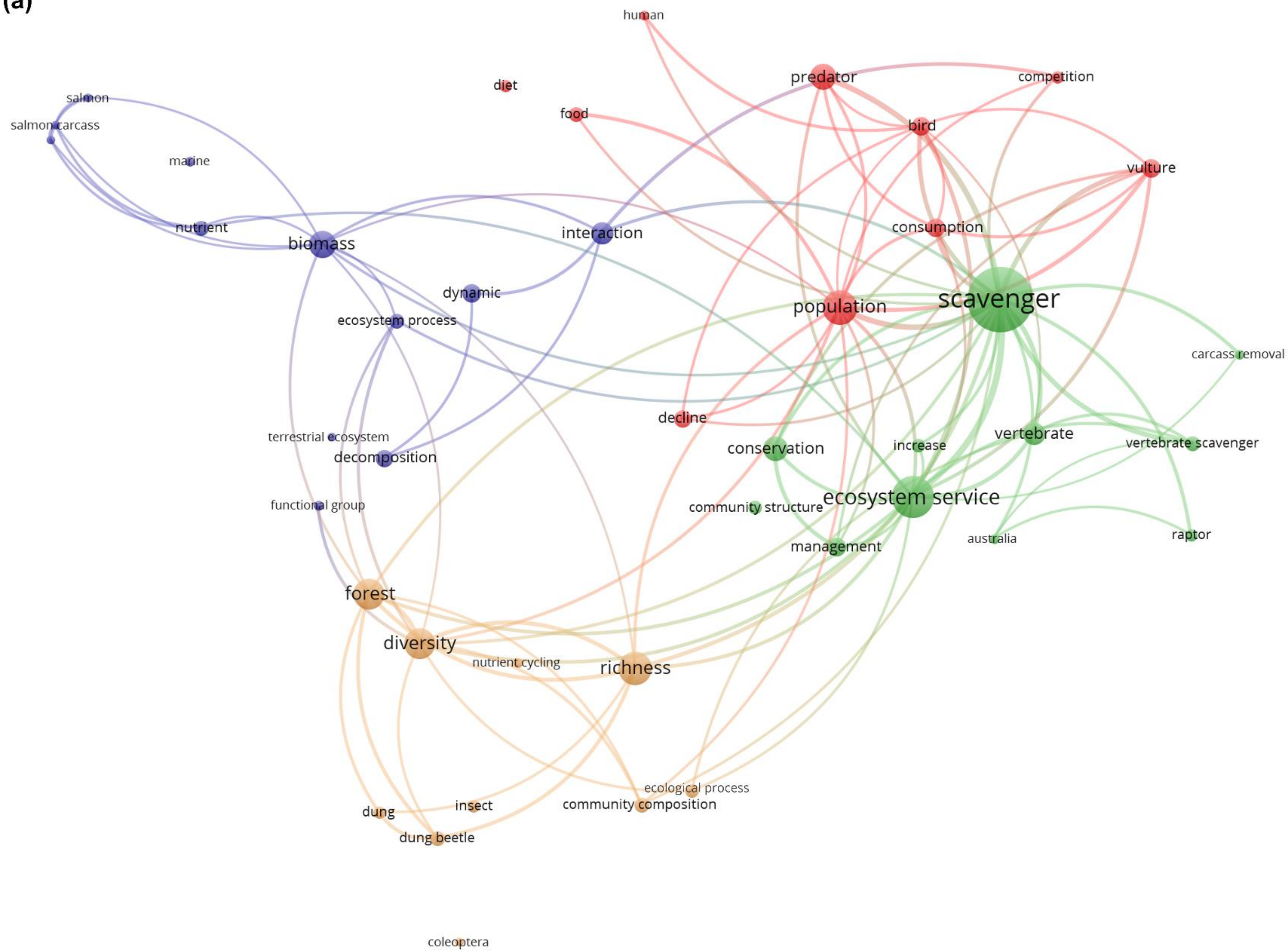
In order to show the terminology associated with carrion, scavenging and ecosystem functions and services, we examined the terms included in the title and abstract of the 83 reviewed articles (see more details in Appendix 1.1). We obtained 3,204 terms from which 112 co-occurred in more than 5 articles. From these, we removed general terms that randomly co-occur in articles, such as 'case', 'finding', 'proportion' or 'year'. A final subset of 43 terms were finally integrated in a semantic network (Table S1) that identified four major clusters (Fig. 7a).

The first cluster (blue cluster; Fig. 7a) included studies on food web dynamics, carcasses decomposition and transport of nutrients among marine, terrestrial and freshwater ecosystems (see e.g., Watts et al. 2011; Beasley et al. 2012). Research regarding the role of marine-derived nutrients from salmon carcasses in ecosystems deserves to be mentioned (e.g., Zhang et al. 2003; Merz & Moyle 2006; Levi et al. 2013). The second cluster (orange cluster; Fig. 7a) covered research on community composition of invertebrate scavengers and their role in nutrient cycling, which were mainly conducted in forest (see e.g., Nichols et al. 2007; Dangles et al. 2012; Fusco et al. 2017). Among insects, dung, burying and carrion beetles were the most studied organisms (Sugiura et al. 2013; Stavert et al. 2014; Iida et al. 2016), but other insects such as ants or flies were also studied (Fayle et al. 2011; Martín-Vega & Baz 2011; Pechal et al. 2014; Gray et al. 2016 ; Barton & Evans

2017). The third cluster (red cluster; Fig. 7a) referred to studies on ecology and population monitoring of predators and facultative scavengers including reptiles, mammals or birds (Schindler et al. 2013; Karunarathna et al. 2017). Furthermore, this cluster concerned vulture population declines worldwide (Ogada et al. 2012b; Buechley & Şekercioğlu 2016), ecosystem services provided by vultures (Moleón et al. 2014b; Morales-Reyes et al. 2015; Whelan et al. 2008, 2015) and management strategies for vulture conservation (e.g., Olea & Mateo-Tomás 2009; Mateo-Tomás & Olea 2010; Dupont et al. 2011). The fourth cluster (green cluster; Fig. 7a) mainly included studies on ecosystem services provided by vertebrate scavengers, both facultative (including mammals, birds or reptiles) and obligate, through carcass removal from the environment (e.g., Moleón et al. 2014b; Morales-Reyes et al. 2015; Inger et al. 2016a; Mateo-Tomás et al. 2017; Peisley et al. 2017). Works about monitoring of the carcass consumption by vertebrate scavengers were remarkable (e.g., DeVault et al. 2011; Olson et al. 2012, 2016; Inger et al. 2016b; Mateo-Tomás et al. 2015). In this cluster, research on vertebrate scavenger communities in Australia was highlighted (e.g., Schlacher et al. 2015; Huijbers et al. 2015, 2016; Peisley et al. 2017; Twining et al. 2017). Moreover, studies on the conservation and management of scavenger vertebrates in different regions such as South America (Lambertucci et al. 2014), Australia (Schlacher et al. 2015; Peisley et al. 2017) or Western Europe (e.g., Olea & Mateo-Tomás 2009; Dupont et al. 2011) are remarkable in the green cluster.

Overall, despite the four clusters were highly interconnected, the green (conservation and ecology of vertebrate scavenger, and ecosystem services) and red (ecology and population monitoring of predators and vultures) were the most interlinked clusters. The most recent interest was related to the terms in the green and orange (ecology of invertebrate scavengers and their role in nutrient cycling) clusters. By contrast, the blue cluster (food web dynamics, carcasses decomposition and nutrient transport) was mostly related to terms of lower interest in recent years (Fig. 7b).

(a)


human
diet
food
predator
competition
bird
vulture
consumption
salmon
salmon carcass
marine
nutrient
biomass
interaction
dynamic
ecosystem process
population
scavenger
carcass removal
decline
terrestrial ecosystem
decomposition
conservation
increase
vertebrate
vertebrate scavenger
functional group
community structure
ecosystem service
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forest
diversity
nutrient cycling
richness
ecological process
community composition
dung
insect
dung beetle
coleoptera

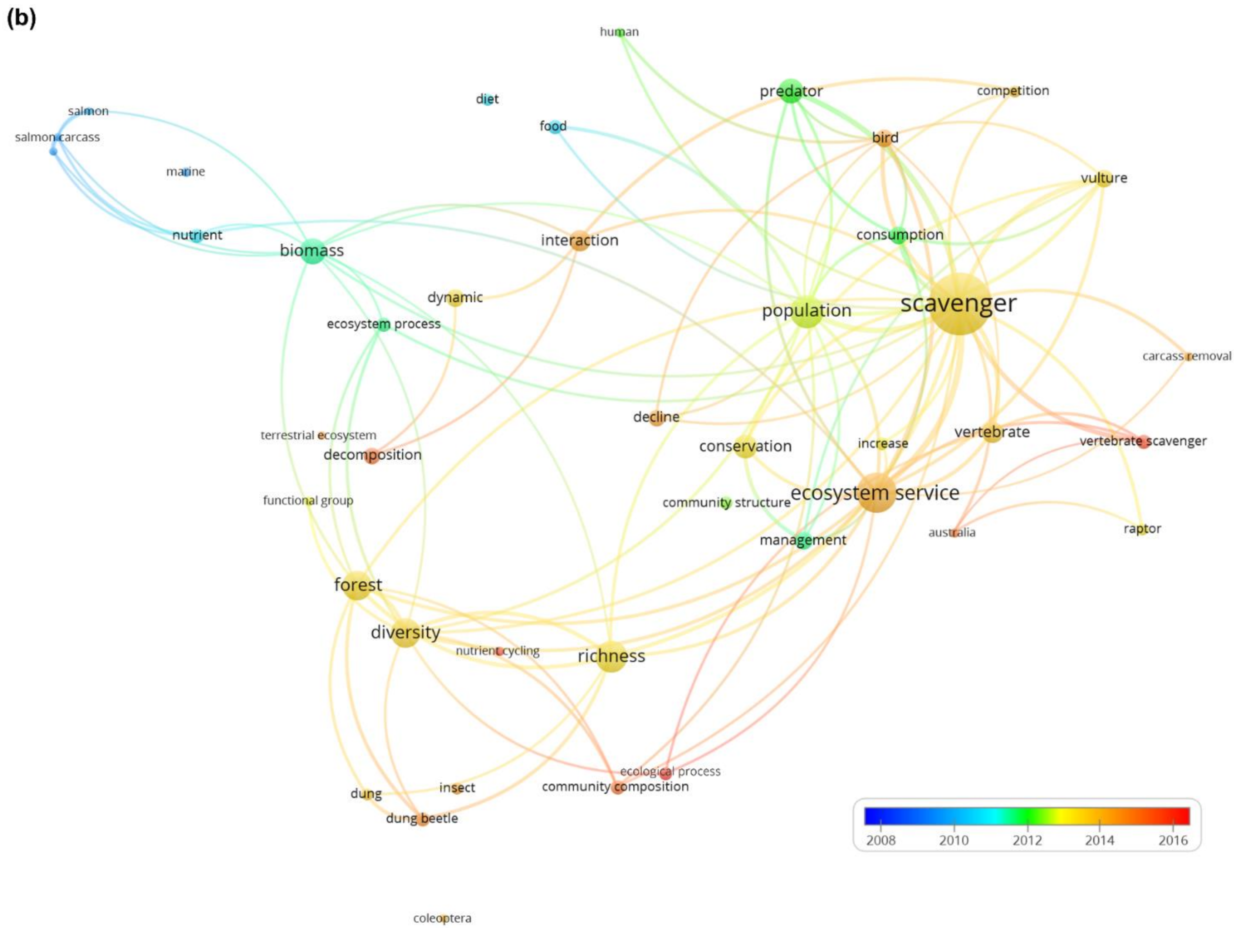


Figure 7. Research landscape on carrion, scavenging and associated ecosystem functions and services. (a) Semantic network of literature review showing the most relevant terms extracted from the reviewed articles (n = 83) and indicating four clusters: food web dynamics, carcasses decomposition and nutrient transport (blue), ecology of invertebrate scavengers and their role in nutrient cycling (orange), ecology and population monitoring of predators and vultures (red), and conservation and ecology of vertebrate scavenger, and ecosystem services (green). The size of a term indicates the number of publications in which the term occurs in the title/abstract. (b) Semantic network of the literature review according to the average publication year of the papers in which a term occurs.

Social perceptions and indigenous and local knowledge

We also conducted a review to characterize the existing publications on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging in the scientific literature (n = 16 reviewed articles; see Appendix 1.1). Among the terms related to carrion and scavenging, 'vulture' was the most frequent in the title, abstract and keywords of reviewed articles (56% of the articles), followed by 'scaveng*' (50%), 'carcass' (38%) and 'carrion' (19%); whereas we did not find articles including the terms 'cadaver' and 'corpse' (Fig. 8a). Among the terms related to social perceptions, attitudes and ILK, 'perception' was the most frequent term (69%), followed by 'perceive' (25%), 'attitude' (13%), 'traditional ecological knowledge' (13%), 'traditional knowledge' (6%) and 'local ecological knowledge' (6%; Fig. 8b).

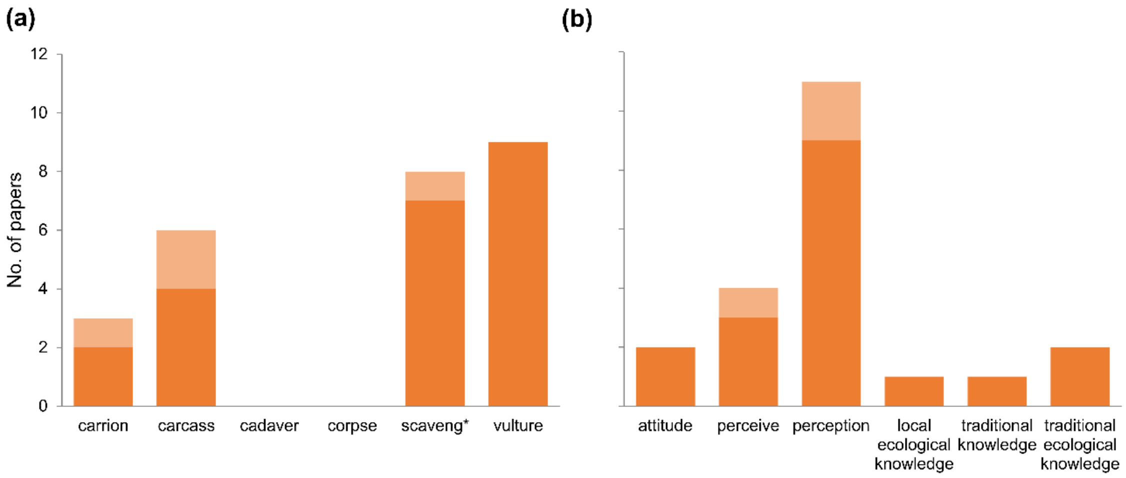


Figure 8. Number of reviewed articles (n = 16) containing the terms (a) 'carrion', 'carcass', 'cadaver', 'corpse', 'scaveng*', 'vulture', and (b) 'attitude', 'perceive', 'perception', 'local ecological knowledge', 'traditional knowledge' and 'traditional ecological knowledge'. Full color: research articles; light color: review articles.

Although the first article on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging was published in 2002, the number of articles has especially increased since 2013 (n = 16; Fig. 9a). The largest proportion of research was conducted in North America (mainly in United States), Africa (principally in Namibia) and South America (Fig. 9b).

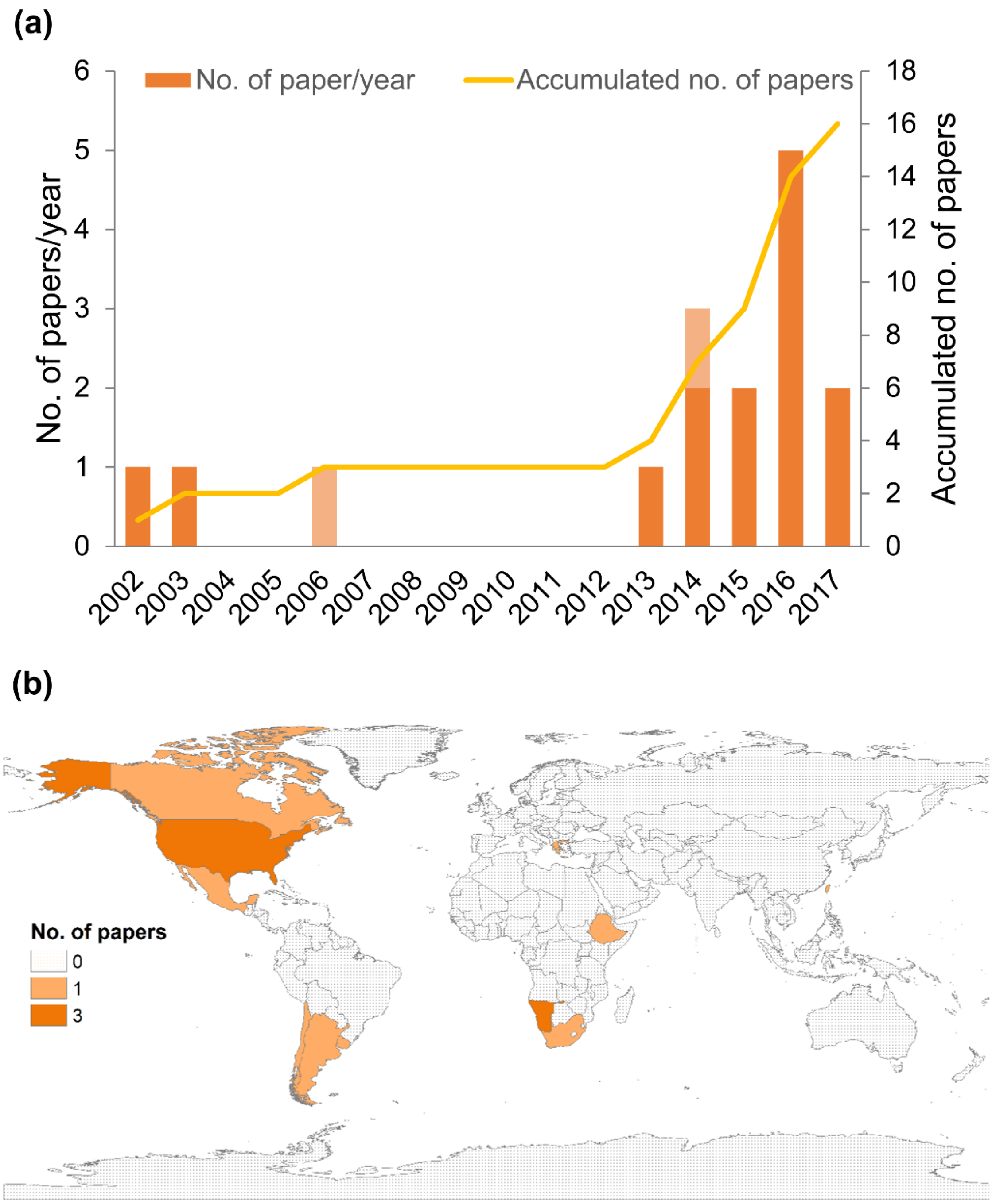


Figure 9. Number of articles on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging published (a) per year (full color: research articles; light color: review articles) and (b) by country (total n = 16).

The vast majority of articles were performed in terrestrial ecosystems (88%), followed by one article including both terrestrial and marine ecosystems (6%) and another including terrestrial, marine and freshwater ecosystems (6%; Fig. 10).

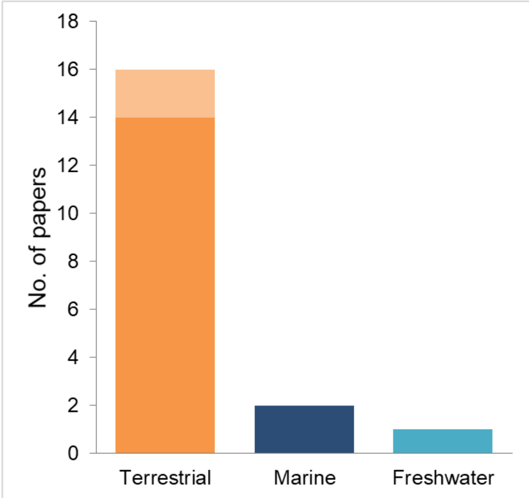


Figure 10. Number of articles on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging published according to ecosystem (i.e., terrestrial, marine and freshwater; n = 16). Full color: research articles; light color: review articles.

Within the articles dealing with scavengers (n = 15), most of them focused on vultures (60%), followed by mammals (53%), raptors (excluding vultures; 20%), non-raptor birds (20%) and fish (7%), whereas we did not find articles on reptiles and invertebrates (Fig. 11a). Furthermore, facultative scavengers were slightly more studied (73%) than obligate scavengers (60%; Fig. 11b).

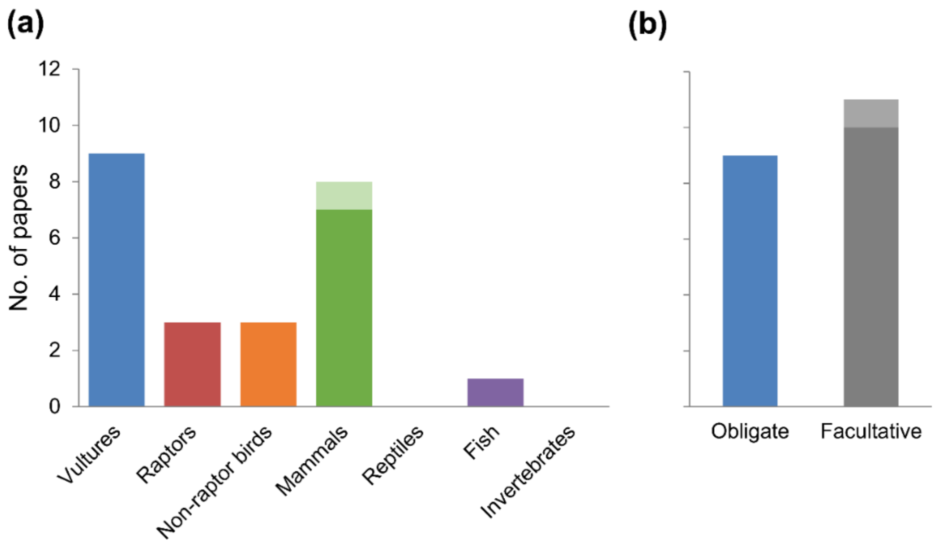


Figure 11. Number of articles on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging according to (a) scavenger taxonomic groups and (b) functional (n = 15). Full color: research articles; light color: review articles.

Within the articles including stakeholders in the study (n = 14), farmers or shepherds were the most included in the research (43% of the articles), followed by hunters (21%), rural residents (21%) and environmental managers (14%) among others (7% for all other stakeholders; Fig. 12).

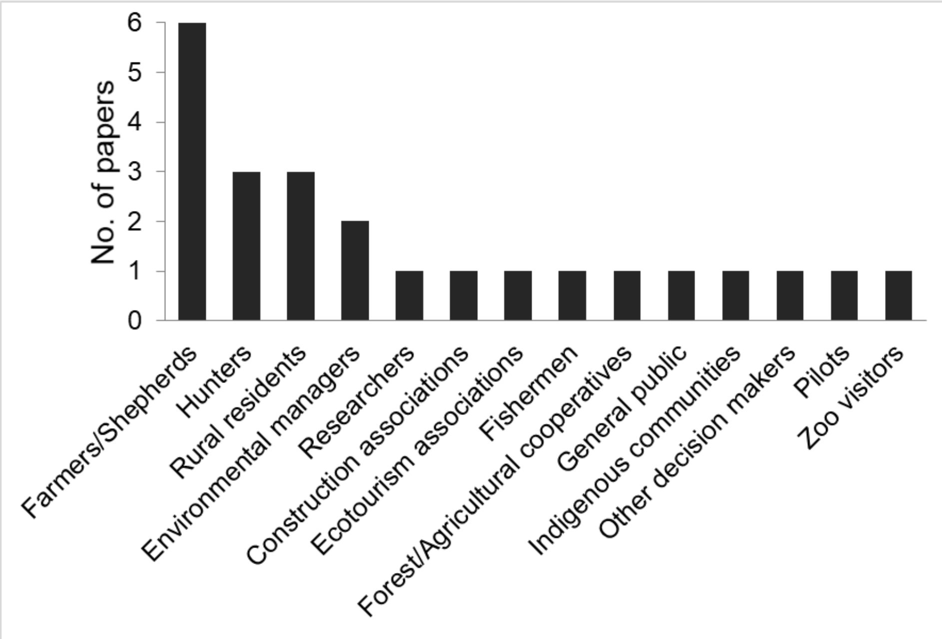


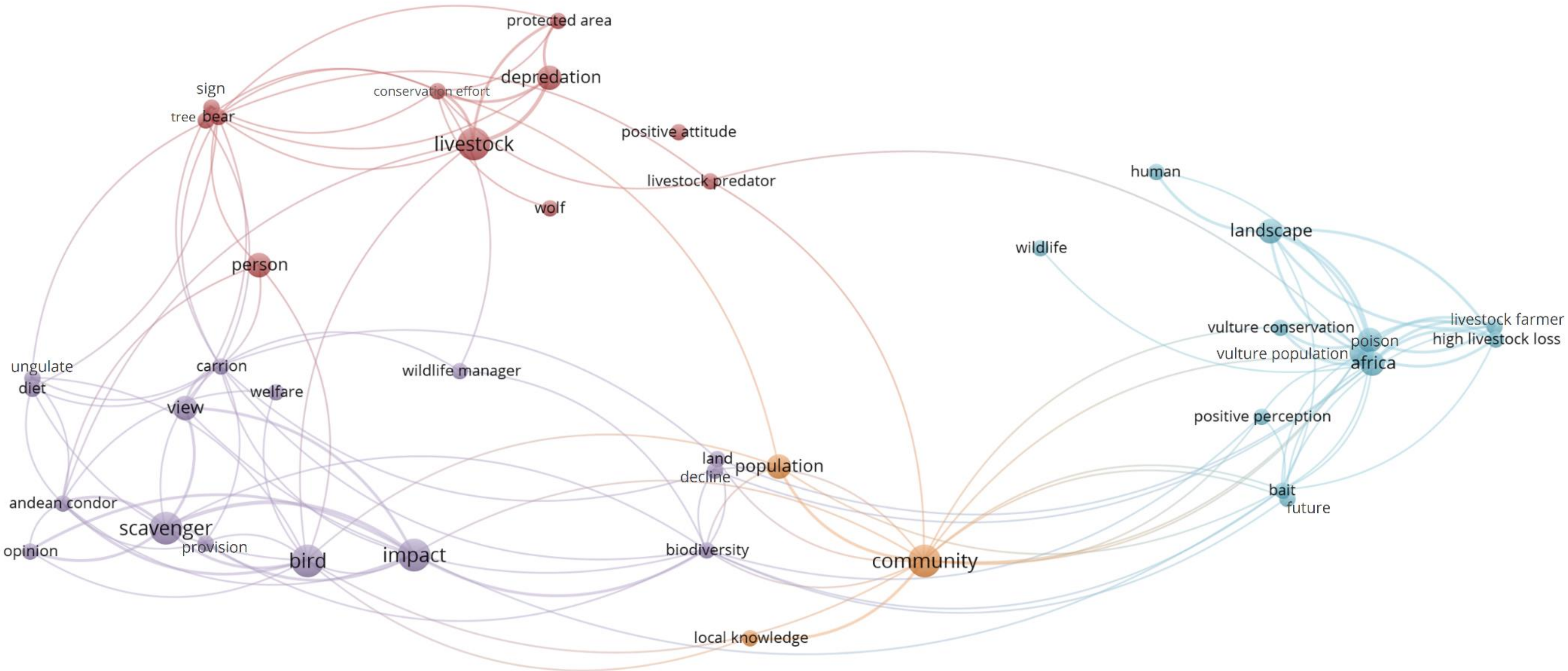
Figure 12. Number of articles on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging according to type of stakeholder included in the study. Only research articles were considered for this purpose (n = 14).

In order to review the terminology associated with social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging, we examined the terms included in the tittle and/or abstract of the 16 reviewed articles (see more details in Appendix 1.1). We obtained 657 terms from which 88 co-occurred in more than 2 articles. From these terms, we removed general terms that randomly co-occur in articles, such as 'little information, 'mean', or 'research. A final subset of 41 terms were finally integrated in a semantic network (Table S2) that identified four major clusters (Fig. 13a).

The first cluster (purple cluster; Fig. 13a) covered research on conservation and management strategies for scavengers. For instance, it was highlighted research on people's perception of the Andean condor (*Vultur gryphus*) in order to ensure the conservation of Condors and other scavengers (Cailly Arnulphi et al. 2017). Besides, this cluster included the discussion about the motivations and controversies around the practice of provisioning carcasses of ungulates to reverse scavenger declines (Fielding et al. 2014). Similarly, Gaengler & Clum (2015) evaluated the impact of carcass feeding for welfare of captive Andean condor and the opinion of zoo visitors about these practices. The second cluster (red cluster; Fig. 13a) mostly focused on human-predator conflicts as influenced by livestock depredation and its implications to conservation efforts (Goldstein et al. 2006; Yirga et al. 2014; Parks & Messmer 2016). This cluster included articles on bears and wolves depredation of domestic livestock (Goldstein et al. 2006; Parks & Messmer 2016), but also on perceptions of wild boars as predators (Herrero & Fernández de Luco 2003). Nevertheless, an article showed the importance of ecological knowledge of indigenous people to obtain information about bear diets (Hwang et al. 2013). Moreover, a paper evaluated the changes in attitudes towards animals including predators and vultures in recent decades (George et al. 2016). The third cluster (blue cluster; Fig. 13a) included studies on social perceptions of vulture populations and its implications on their conservation in Africa, mostly in Namibia (Santangeli et al. 2016, 2017) but also in South Africa (Pfeiffer et al. 2015) or Ethiopia (Yirga et al. 2014). Most articles focused on farmers' perception towards vultures and the identification of anthropogenic threats to vultures (mainly poison; Pfeiffer et al. 2015; Santangeli et al. 2016, 2017). Furthermore, this cluster also concerned human tolerance towards African predators in relation to livestock loss caused by them (Yirga et al. 2014; Santangeli et al. 2016, 2017). In addition, a study evaluated pilot perceptions of collision risk with birds including vultures at Namibian airports (Hauptfleisch & Avenant 2016). The fourth cluster (orange cluster; Fig. 13a) mainly referred to studies on local communities' knowledge on scavengers and how local knowledge might be incorporated into conservation of these endangered species (Haenn et al. 2014; Stara et al. 2016). For instance, Suazo et al. (2013) suggested that conservation of seabird populations may improve by including fishermen's perceptions regarding their interaction with seabirds and their knowledge in policy decisions.

Overall, all clusters were highly interlinked each other. The most recent interest was mainly related to the terms in the blue (social perceptions of vultures in Africa) and orange (local communities' knowledge on scavengers) clusters. In contrast, the red cluster (human-predator conflicts related to livestock) was related to terms of lower interest in recent years. The purple cluster (conservation and management strategies of scavengers) included terms of relatively old interest, but it also comprised terms of recent interest (Fig. 13b).

(a)


protected area
depredation
sign
conservation effort
tree bear
livestock
positive attitude
livestock predator
wolf
human
landscape
wildlife
person
livestock farmer
vulture conservation
poison
high livestock loss
vulture population
africa
ungulate
diet
carrion
wildlife manager
welfare
view
positive perception
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andean condor
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provision
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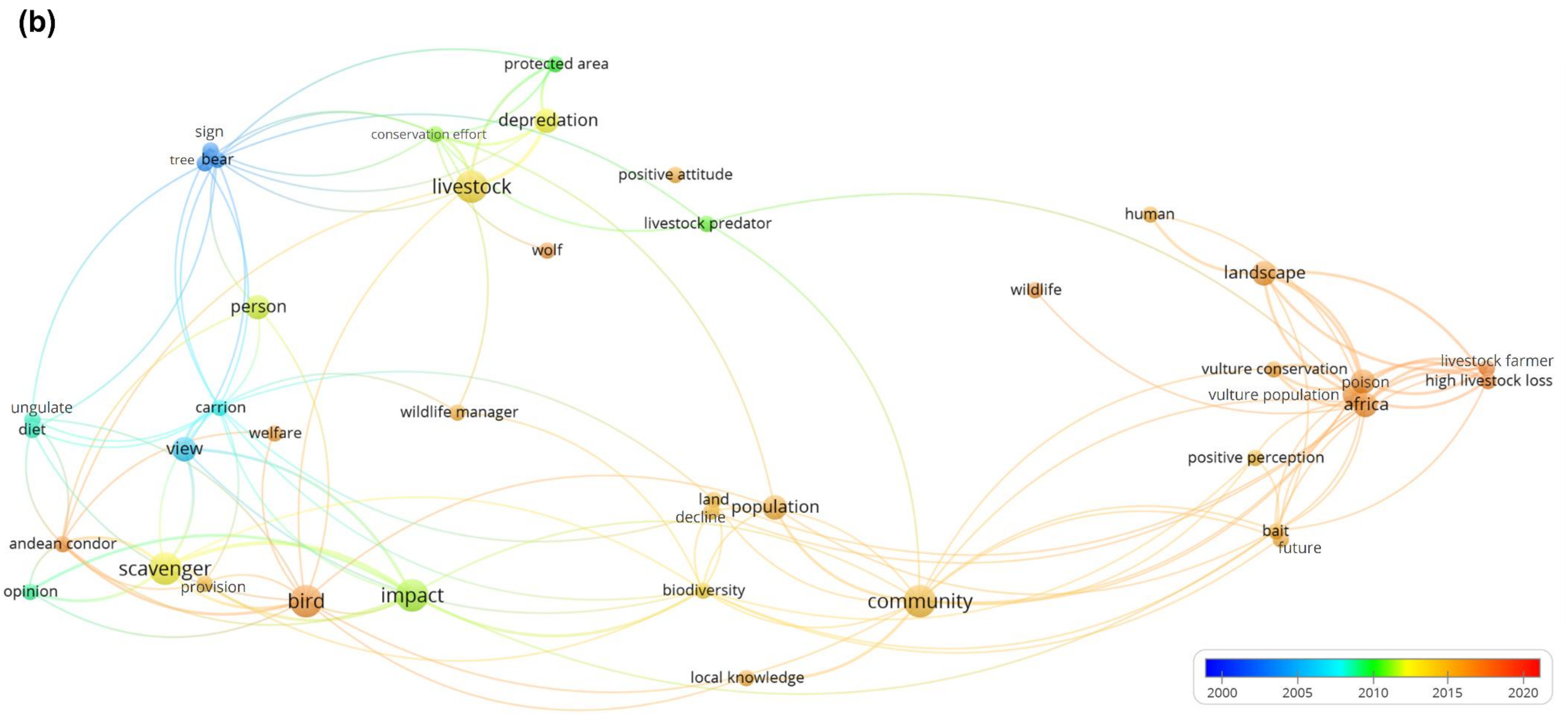

Figure 13. Research landscape on social perceptions and attitudes toward scavengers, and ILK on carrion and scavenging. (a) Semantic network of literature review showing the most relevant terms extracted from the reviewed articles (n = 16) and indicating four clusters: conservation and management strategies of scavengers (purple), human-predator conflicts related to livestock depredation (red), social perceptions of vultures in Africa (blue), and local communities' knowledge on scavengers (orange). The size of a term indicates the number of publications in which the term occurs in the title/abstract. (b) Semantic network of the literature review according to the average publication year of the papers in which a term occurs.

On the one hand, the literature review shows a scarce scientific attention on the ecosystem function and services provided by scavenging species until very recently. Moreover, the majority of research focused on ecosystem functions rather than ecosystem services. Spain stands out as one of the pioneer countries in the study of scavenging services. The review also exposed a notable lack of research dealing with freshwater and marine scavengers. Despite invertebrate scavengers were the most studied taxonomic group, research focused on their ecology and their role in nutrient cycling rather than on the valuation of the ecosystem services provided by them. On the other hand, the review reveled that social perceptions and attitudes towards scavengers, as well as ILK on carrion and scavenging, remain virtually unexplored. Most studies in this regard have focused on social perceptions of vertebrate scavengers (mainly vultures), the identification of anthropogenic threats to vultures and human-predator conflicts related to livestock predation. The present thesis aims to address some of these important knowledge gaps by exploring several scavenger-rich systems in which traditional extensive livestock farming still features prominently (see below).

STRUCTURE, OUTLINE AND AIMS OF THE DISSERTATION

This PhD dissertation includes a compilation of several scientific papers. It contains a general introduction (*Chapter 1*), four research chapters in the format of scientific articles (*Chapters 2-5*), a general discussion (*Chapter 6*), and a final section which synthesizes the main conclusions (*Conclusions*). Finally, several *Appendices* including additional information can be found at the end of this thesis. Research chapters are divided into two broad parts: *Part I* (*Chapters 2* and *3*) includes an ecological assessment of ecosystem services provided by scavengers; *Part II* (*Chapters 4* and *5*) includes a socio-cultural evaluation of the ecosystem services provided by scavengers. *Chapters 2-5* were structured following the conventionally accepted sections for a scientific publication: "introduction", "material and methods", "results" and "discussion". With the aim of favoring the reading of each chapter separately, all chapters conclude with a list of the references cited in their respective text. Thus, references can be repeated in different chapters. Likewise, to favor self-understanding of *Chapters 2-5*, each chapter includes an abstract (and a summary –*resumen*– in Spanish), in which a general introduction, the main objectives, methods, results and conclusions are presented, followed by several keywords (and the corresponding *palabras clave* in Spanish).

This introductory chapter (*Chapter 1*) has presented an overview of the main research topics addressed through the rest of the thesis. The current state of the research regarding carrion, scavenging and associated ecosystem functions and services, social perceptions and attitudes towards scavengers, and indigenous and local knowledge on carrion and scavenging has been deeply analyzed. It also enumerates the main aims of the thesis. *Chapter 2* explores the consequences of supplanting the ecosystem services provided by vertebrate scavengers in Spain. In particular, we map the greenhouse gases emissions linked to the artificial removal of livestock carcasses. *Chapter 3* investigates the conservation effectiveness of a recent sanitary regulation that allowed farmers to abandon extensive livestock carcasses in certain areas important for the feeding of scavengers. In particular, the greenhouse gases emission savings in relation to the previous scenario (i.e., *Chapter 2*) are estimated. *Chapter 4* deals with the social dimensions of biodiversity conservation through the evaluation of farmer perceptions of the ecosystem services provided by scavenging vertebrates. In addition, we identify the social and ecological factors determining these farmer perceptions. *Chapter 5* explores shepherds' knowledge on the scavenging service provide by vertebrate scavengers in extensive livestock farming systems, assessing the similarities and contradictions between shepherds' ILK and the scientific evidence. Based on our results, the importance of integrating both shepherds' ILK and scientific knowledge into conservation and management practices of scavengers is discussed. *Chapter 6* presents a general discussion of the main results of this research, with special emphasis on the conservation implications and future perspectives. Finally, I present the conclusions of this PhD project.

The main aim of the present dissertation is to assess the ecosystem services provided by vertebrate scavengers from a social-ecological perspective, and finally to provide some insight for scavengers conservation. In order to achieve the general objective, four specific aims are proposed:

1. To spatially quantify the greenhouse gases generated by supplanting the natural systems in which scavengers freely remove livestock carcasses through carcass collection and transport from extensive farms to processing plants (*Chapter 2*).

2. To evaluate the conservation and environmental consequences of the protection areas for the feeding of necrophagous species of European interest (PAFs) in Spain (*Chapter 3*). It includes five specific aims:
   - (i) To quantify the proportion of breeding distribution of targeted scavenger species falling within PAFs.
   - (ii) To estimate the extensive livestock carrion biomass available inside PAFs.
   - (iii) To calculate the proportion of the breeding distribution of other major, non-targeted scavenger species falling within PAFs.
   - (iv) To evaluate the overlap between the home range of GPS-tracked vultures, PAFs and to determine the use of different administrative units by particular individuals and populations.
   - (v) To estimate the potential savings in greenhouse gases emissions and economic savings associated with livestock carcass transport in relation to the pre-PAF scenario.

3. To analyze farmer perceptions of ecosystem services provided by scavenging vertebrates in Spain (*Chapter 4*). It includes three specific aims:
   (i) To assess the ecosystem services provided by scavenging vertebrates that are perceived by farmers.
   (ii) To evaluated the perception of scavenging vertebrates as providers of ecosystem services.
   (iii) To identify the social and ecological factors determining farmer perceptions of scavengers as providers of ecosystem services.

4. To assess the similarities and contradictions between indigenous and local knowledge and scientific knowledge regarding the scavenging service provided by vertebrates in extensive livestock farming systems (*Chapter 5*).

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PART I

Ecological assessment

Chapter 2

Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions

Zebensui Morales-Reyes, Juan M. Pérez-García, Marcos Moleón, Francisco Botella, Martina Carrete, Carolina Lazcano, Rubén Moreno-Opo, Antoni Margalida, José A. Donázar & José A. Sánchez-Zapata

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Incineration plant of Darmstadt, Germany (Armin Kübelbeck, CC-BY-SA, Wikimedia Commons)

Griffon vultures *Gyps fulvus* in The Bardenas Reales of Navarre, Spain (Manuel J. de la Riva Pérez)

ABSTRACT

Global warming due to human-induced increments in atmospheric concentrations of greenhouse gases (GHG) is one of the most debated topics among environmentalists and politicians worldwide. In this paper we assess a novel source of GHG emissions emerged following a controversial policy decision. After the outbreak of bovine spongiform encephalopathy in Europe, the sanitary regulation required that livestock carcasses were collected from farms and transformed or destroyed in authorized plants, contradicting not only the obligations of member states to conserve scavenger species but also generating unprecedented GHG emission. However, how much of this emission could be prevented in the return to traditional and natural scenario in which scavengers freely remove livestock carcasses is largely unknown. Here we show that, in Spain (home of 95% of European vultures), supplanting the natural removal of dead extensive livestock by scavengers with carcass collection and transport to intermediate and processing plants meant the emission of 77,344 metric tons of CO_2 equivalent to the atmosphere per year, in addition to annual payments of ca. $50 million to insurance companies. Thus, replacing the ecosystem services provided by scavengers has not only conservation costs, but also important and unnecessary environmental and economic costs.

KEYWORDS: air pollution; carcass removal; climate change; EU sanitary policies; extensive livestock; traditional farming practices; vultures

RESUMEN

El calentamiento global debido a incrementos inducidos por los humanos en las concentraciones atmosféricas de gases de efecto invernadero (GEI) es uno de los temas más debatidos entre ambientalistas y políticos de todo el mundo. En este trabajo evaluamos una nueva fuente de emisiones de GEI surgida a raíz de una decisión política controvertida. Después del brote de encefalopatía espongiforme bovina en Europa, la normativa sanitaria exigía que los cadáveres de ganado se recogieran de las explotaciones ganaderas y fueran transformados o destruidos en plantas autorizadas, contradiciendo no solo las obligaciones de los Estados miembros de la Unión Europea de conservar las especies carroñeras, sino también generando emisiones de GEI sin precedentes. Sin embargo, se desconoce en gran parte la cantidad de emisiones que se podrían evitar con la vuelta al escenario tradicional y natural en el que los carroñeros eliminan libremente los cadáveres de ganado. Aquí nosotros mostramos que en España (hogar del 95% de los buitres europeos), la suplantación de la eliminación natural de los cadáveres de ganado en extensivo por los carroñeros con la recogida y el transporte de los cadáveres hasta las plantas intermedias y de transformación supuso la emisión de 77.344 toneladas métricas de CO_2 equivalente a la atmósfera al año, además de pagos anuales a las compañías de seguros de alrededor de 40 millones de euros. Por lo tanto, la sustitución de los servicios ecosistémicos proporcionados por los carroñeros no sólo tiene costes de conservación, sino también importantes e innecesarios costes ambientales y económicos.

PALABRAS CLAVE: buitres; cambio climático; contaminación del aire; eliminación de cadáveres; ganado extensivo; políticas sanitarias de la UE; prácticas ganaderas tradicionales

INTRODUCTION

Global warming is one of the most debated topics among environmentalists and politicians because of its implications in biodiversity conservation and human welfare (Hughes et al. 2000; Moss et al. 2010). Scientific evidence supports a link between this unequivocal and continuing rise in average temperatures over the last 130 years and human-induced increments in atmospheric concentrations of some gases such as carbon dioxide, methane or nitrous oxide (globally called GHG) (Meehl et al. 2005; Meinshausen et al. 2009). Thus, in 1997 the United Nations Framework Convention on Climate Change (UNFCCC) developed the Kyoto Protocol, committing parties to setting internationally binding emission reduction targets. However, although the initiative is outstanding, policies have been weakly applied, and attempts to improve them have seen little success (Victor 2011). In fact, global GHG emissions have accelerated since 2000 (Raupach et al. 2007). The future is even more uncertain as some new human activities may be leading to novel pathways for GHG emissions.

An example of a new source of GHG emerged after the recent mad cow crisis in Europe. On this continent, the outbreak of bovine spongiform encephalopathy (BSE) in 2001 and the detection of the variant (vCJD) and new variant (nvCJD) of Creutzfeldt-Jakob disease in humans led to the passing of sanitary legislation (Regulation EC 1774/2002) that greatly restricted the use of animal by-products not intended for human consumption (ABPs). Under this legislation, carcasses of domestic animals had to be collected from farms and transformed or destroyed in authorized plants, not only contradicting the obligations and efforts of member states to conserve scavenger species (Tella 2001; Donázar et al. 2009a; Margalida et al. 2010), but also potentially generating an unprecedented source of GHG emissions through carcass transportation, transformation and incineration. Thus, while the European Commission is attempting to reduce GHG emissions by applying an assortment of policies and technologies (ECCP 2003), it is also potentially putting policies in place that increase emissions by replacing an ecological service that has been provided by scavengers for millennia (Moleón et al. 2014). Moreover, as vultures (specialized or obligate scavengers) in Europe have traditionally relied on domestic livestock carcasses for feeding (Donázar 1993; Olea & Mateo-Tomás 2009), the implementation of the European sanitary legislation – with the associated reduction in food supply and/or the change in its temporal and spatial availability, has had negative impacts on vulture behavior, ecology and conservation at both the individual and guild levels (Donázar et al. 2009b; Cortés-Avizanda et al. 2012; Margalida & Colomer 2012; Margalida et al. 2014).

Although new and encouraging legislation was approved in March 2011 (Regulation EC 142/2011), allowing farmers to abandon extensive livestock carcasses in certain ‘‘free areas’’ in the field and at feeding stations (Margalida et al. 2012), it is far from implementation and an important portion of livestock carcasses is still removed from the field by authorized companies as mandated by the previous regulation. Moreover, some regions lack the specific legislation required to apply the European guidelines at the local scale, and future reversion to more restrictive rules due to new sanitary pressures cannot be ruled out. Thus, modelling the current scenario of GHG emissions linked to the artificial removal of livestock carcasses may help to broaden our understanding of the dimensions of supplanting this ecosystem service provided by scavengers. Mapping ecosystem services, or the consequences of their suppression, has been suggested as an essential step to minimize the anthropogenic footprint through the implementation and improvement of ''win-win'' strategies –those benefiting both biodiversity conservation and human welfare, as well as the reconciliation of conflicting policies (Naidoo et al. 2008; Kareiva et al. 2011). Until now, however, how vertebrate animals might be allied in the fight against climate change, hence benefiting humanity through preventing the release of carbon and nitrogen stored in terrestrial ecosystems to the atmosphere is largely unknown (Dupont et al. 2012), and never has been spatially assessed.

Here, (Fig. 1). Briefly, this regulation mandates that livestock carcasses be collected from farms within 24 (cattle) or 48 h (other livestock) after death and moved to processing plants, where they are subjected to different treatments depending on their risk to public and animal health (i.e., if they are ruminant or non-ruminant carcasses). However, due to the long distance at which these plants are located, most livestock collected is first stored, unprocessed, at intermediate plants. At the end, carcasses can be used for industrial purposes (e.g., to produce organic fertilizers) or be transported to incineration plants or approved landfills (MAPA 2007). Fossil fuel combustion associated with the transport sector is one of the main sources of GHG emissions worldwide (Davis et al. 2010), and thus our goal is to demonstrate how much of this emission could be prevented in the return to traditional and natural systems in which scavengers freely remove livestock carcasses, or conversely, how much GHG is generated by supplanting this ecological service. We recreated the process of carcass collection and transport and the associated generation of GHG in peninsular Spain, where the majority of European vulture populations is located (ca. 95%) (Tella 2001; Margalida et al. 2010).

To spatially estimate GHG emission, we divided the entire area into 10 x 10 km grids and, for each, estimated the biomass of carcasses generated per year using the total number of extensive livestock (i.e., cattle, sheep, goat and pig), their weight and annual mortality rates. We calculated the distance covered in the transport of carcasses to intermediate and/or processing plants by twice simulating the displacement (using the main national road network) of a truck from the nearest plant to the center of each grid (empty and full truck; Fig. 1). We calculated GHG emissions associated with carcass transport according to IPCC (2006). GHG emissions are quantified as metric tons of CO_2 equivalents. As an indicator of the capacity of the environment to provide the supplanted ecosystem service, we used information from the National Biodiversity Inventory to cross the estimated GHG emissions with the distance of each grid center to the nearest breeding site, and with the richness per grid of obligate scavengers (griffon, cinereous, Egyptian and bearded vultures).

MATERIAL AND METHODS

Livestock and carcass availability

We obtained the number of head of livestock per municipality in 2012 from the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA 2012). We included the most important extensive livestock species: cattle, sheep, goat and pig. From the same source, we obtained the average weight of each livestock age class. Numbers, weight, and the annual mortality rate of each type of livestock per age class (Decree 17/2013 of the region of Castilla y León; Government of Castilla y León 2013; Table 1) were used to calculate the biomass of carcasses generated per year. We generated one map with the biomass of carcasses per municipality per day, as carcass collection should occur within 24–48 h after livestock death. This map was then divided into 10 x 10 km grids using the Universal Transverse Mercator (UTM) system.

Table 1. Number, average weight and annual mortality rate of the major extensive livestock species in Spain.

Species	Age class	Total number	Average weight (kg)	Annual mortality rate
Sheep	< 4 months	1,415,222	8	3%
	4–12 months	632,640	15	3%
	Breeding male	678,125	75	5%
	Breeding female	9,487,430	40	5%
Goat	< 4 months	81,840	8	3%
	4–12 months	56,829	15	3%
	Breeding male	35,360	75	5%
	Breeding female	670,009	40	5%
Pig	Suckling	287,670	6	6.4%
	Fattening	642,919	60	7.7%
	Rearing/transition	354,056	14	3.7%
	Reposition	11,169	140	3.7%
	Breeding male	14,679	180	3.7%
	Breeding female	146,734	220	3.7%
Cattle	< 6 months	425,222	100	4.6%
	6–12 months	375,929	200	4.6%
	12–24 months	257,500	300	4.6%
	> 24 months	1,843,827	700	4.6%

Carcass transport

We simulated the movement of carcasses from farms to processing plants directly or indirectly, through intermediate plants, following the scheme shown in the Fig. 1. We estimated the distance travelled by carcasses using the main national paved road network and the network analysis extension in ArcGIS 10.1. As the location of each farm was not available, we considered the center of each 10 x 10 km grid to be the point of origin (i.e., the farm) from which carcasses were moved. From these points, we calculated the distance travelled by trucks to the nearest plant. If this plant was a processing plant, then carcass movement was considered complete. If this plant was an intermediate plant, another truck was used to complete the transport of the carcasses to processing plants. In our analysis, movements from farms (i.e., grid centers) to intermediate or processing plants were performed daily, using 7.5 t rigid trucks of 230 hp, while movements from intermediate to processing plants occurred weekly and used 24 t articulated trucks of 340 hp. Vehicle types were determined by direct information from companies and regional regulations. We assumed that daily trucks collected all the carcasses generated within a grid cell until they reached their full load (7.5 t). Trucks moving carcasses from intermediate to processing plants were also completely loaded. Typically, more than one truck per week moved from an intermediate plant to a processing plant. All trips were calculated twice, as trucks must make the same trip in both directions. Intermediate and processing plants were geographically located using information provided by the Spanish Ministry of Agriculture, Food and Environment and the Autonomous Communities (SANDACH 2014). Distance calculations were made using the shortest road between origin and destination points (i.e., farms to intermediate or processing plants, and intermediate plants to processing plants), and prioritizing road type from highest to lowest speed (i.e., highways, national roads, autonomic roads, streets, and unpaved roads) (IDEE 2014).

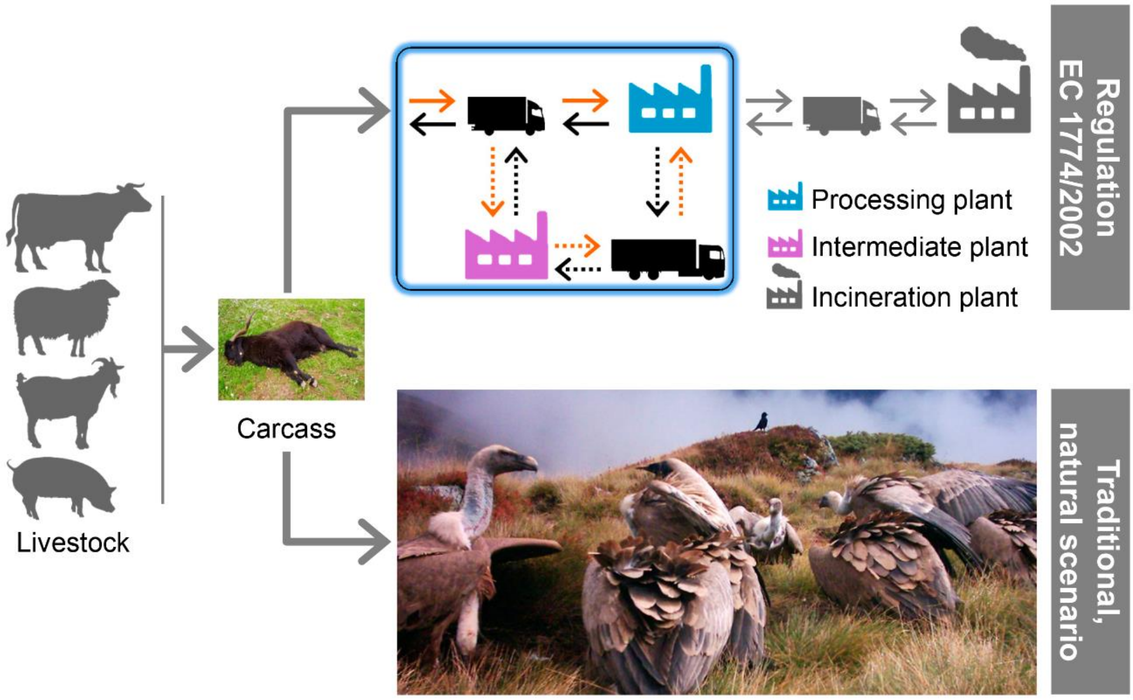

Figure 1. Schematic representation of the application of the European sanitary regulation 1774/2002 and the natural system of extensive livestock carcass removal. Following this regulation, carcasses are collected from extensive livestock farms and moved to the nearest processing plant within 24– 48 h after death. However, as some regions are too far from these processing plants and trucks would thus cover long distances without a full load, some intermediate plants have been established as storage points. From there, carcasses are then moved to processing plants using larger trucks. Carcasses may then be transported to incineration plants. The route done by full and empty trucks is shown by orange and black arrows, respectively. In the traditional, natural scenario, vultures and other scavengers efficiently remove carcasses in situ, normally in <24 h (Cortés-Avizanda et al. 2012). The activities modelled in this article are included in the blue box. Photographs were taken by José A. Donázar (goat) and José A. Sánchez-Zapata (vultures).

GHG emissions

During the combustion process, most carbon is immediately emitted as CO_2, although other GHG such as N_2O and CH_4 are also produced. Thus, we calculated the emissions of these three gases separately as $E(i) = AD * EF(i)$, where i is the gas type (CO_2, CH_4 or N_2O), AD is activity data and EF is the emission factor, 73.7 t/TJ for CO_2 (MAGRAMA 2013) and 0.0039 t/TJ for CH_4 and N_2O (IPCC 2006). Activity data (AD) was calculated as $FC * FD * LHV$, where FC is fuel consumption, FD is fuel density and LHV is lower heat value. FD (0.845 kg/l) and LHV (0.0424 TJ/t) were obtained from the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA 2012). FC was calculated by multiplying the distance covered by each truck by the expected average fuel consumption per km expected by each type of truck (IPCC 2006). We considered that all trucks of the same type consumed the same quantity of fuel per km regardless of their load (0.21 l/km for trucks used to move carcasses from farms to the nearest plant and 0.26 l/km for trucks used to move carcasses from intermediate plants to processing plants; IDAE 2006). We assumed that all trucks used oil/diesel fuel and were 11 years old, such that motors are thermally stabilized and do not have catalysts. These assumptions are based on the fact that in 2011, ca. 90% of trucks and vans in Spain were diesels, and their average age was 11 years old (ANFAC 2011). As fuel combustion is not perfect and a small portion may lead to residuals (ash and soot), we included an ''oxidation factor'' which expresses the ratio of CO_2 emitted per fuel unit (0.99) (MAGRAMA 2013). Results are presented as CO_2 equivalents (CO_2 eq.), a quantity that describes, for a given mixture and amount of GHG, the amount of CO_2 that would have the same global warming potential (GWP) when measured over a specified timescale (100 years; IPCC 2006). GWP values for CH_4 and N_2O were 34 and 298, respectively, with climate-carbon feedback values and lifetimes taken from Myhre et al. (2013). CO_2 eq. is expressed as parts per million by volume and referred to the 10 x 10 km grid cell where carcasses originated.

Scavenger distribution

We used data available from the Spanish National Biodiversity Inventory to map the distribution of obligate scavengers (i.e., griffon, cinereous, Egyptian and bearded vultures) across Spain. We focused on the breeding population, which represents approximately two-thirds of the total vulture population. We calculated the distance of each 10 x 10 km grid center to the nearest breeding site (i.e., nest or colony) of any obligate scavenger. Because of the high daily mobility of these species (griffon vultures: up to 70 km from breeding sites; cinereous vultures: up to 86 km from breeding sites; bearded vultures: up to 45 km from breeding sites; Egyptian vultures: up to 70 km from breeding sites) (Donázar 1993; Carrete & Donázar 2005), we also calculated their richness (i.e., number of species) in a 100 km buffer around each 10 x 10 km grid cell. We used Generalized Linear Models ($1/mu^2$ link function and inverse Gaussian error distribution) to explore the relationship between metric tons of CO_2 eq. per grid and distance to the nearest obligate scavenger breeding site. Metric tons of CO_2 eq. in a 100 km buffer around grids with different species richness (from 0 to 4) were compared using a Kruskal-Wallis test. All analyses were performed in R (R Core Team 2014). We used ArcGIS 10.1 to generate maps.

RESULTS

Supplanting the removal of dead livestock by scavengers through carcass collection and transport to intermediate and processing plants represented trips by 49,808,685 km and the consequent emission of 77,344 metric tons of CO_2 eq. to the atmosphere per year. Our estimates of CO_2 eq. should be considered as a minimum, as GHG emitted during carcass processing and incineration has not been included. This calculation is a challenge, as collected carcasses might follow very different industrial processes subjected to different sources of energy consumption and GHG emissions.

Mountainous and remote areas such as the Pyrenees or western Spain showed the highest levels of GHG emissions (Fig. 2), mainly due to their higher numbers of livestock but also to their location far from intermediate and/or processing plants. Paradoxically, those areas are also among the best conserved regions in Europe, showing the highest densities of vultures. Indeed, we found a strong association between CO_2 emissions and the distribution and richness of obligate scavengers (Fig. 3).

DISCUSSION

After the implementation of the European sanitary legislation approved in 2002, many contradictions between biodiversity conservation and sanitary policies arose. The removal of livestock carcasses from the field and their disposal at only a few authorized feeding points proved to have more negative than positive effects for the long-term viability of vulture and other scavenger populations (Donázar et al. 2009a; Donázar et al. 2010). Our findings suggest an additional argument in favor of traditional, more natural systems of livestock carcass removal. In Spain, emissions from the transport sector increased by 43.7% between 1990 and 2012, and currently account for 23.7% of total GHG emissions. According to our results, the emissions associated with the transport of extensive livestock carcasses represented 0.1% of the total national transport emissions in 2012 (EEA 2014). For comparison, our estimate signifies 25, 15, 8 and 4% of total national emissions arising from rice cultivation, burning of agricultural residuals in the field, the chemical industry and sewage treatment, respectively (MAGRAMA 2014a). It is worth to remark that this estimate corresponds only to one part of livestock carcass treatment, such that emissions would increase with the inclusion of the transformation and incineration of carcasses. Thus, further research is needed to complete the estimation of the total GHG emission linked to whole application of the actual sanitary regulation.

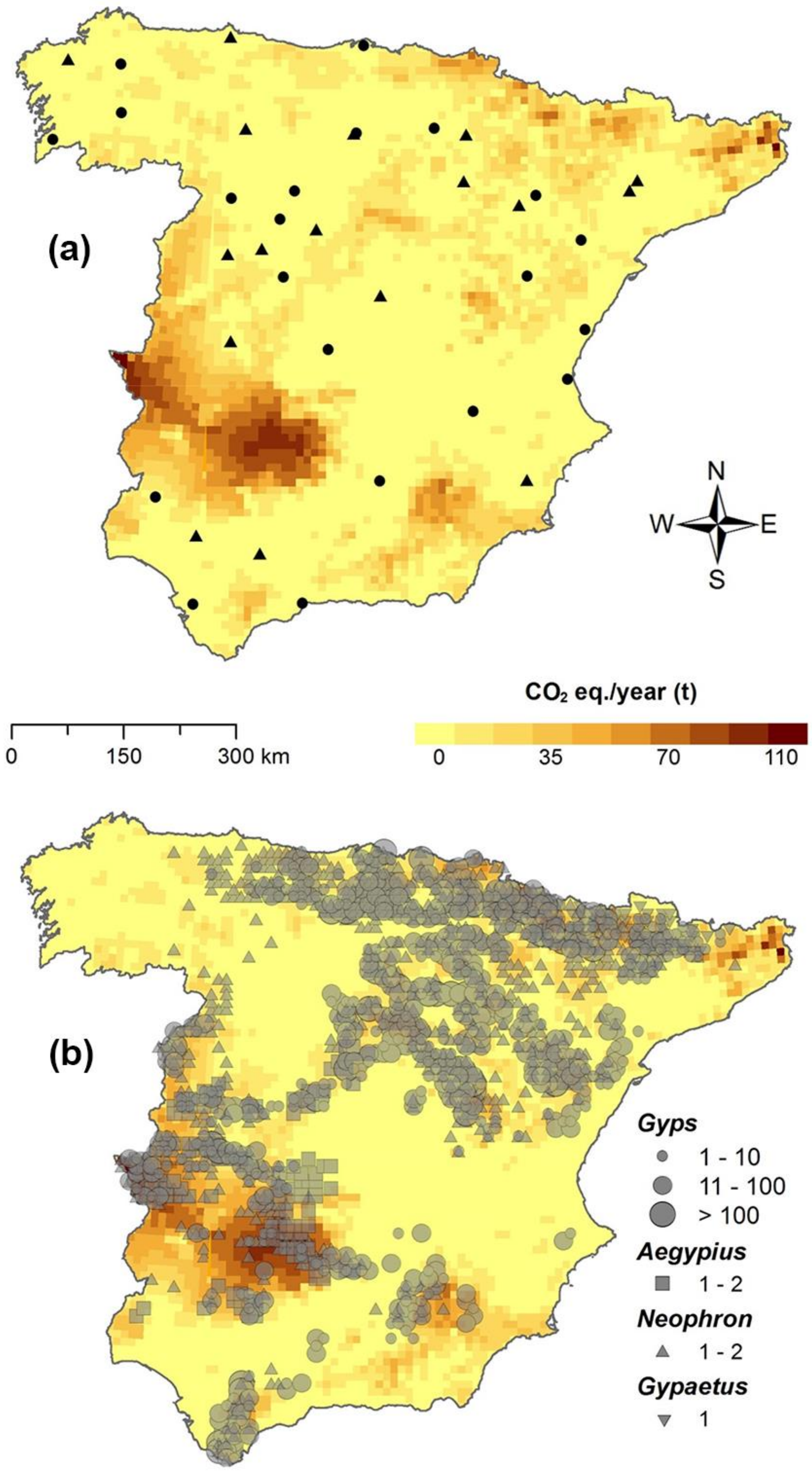

Figure 2. Estimated CO_2 emissions (in metric tons of CO_2 eq. per 10 x 10 km grid per year) associated with the transport of extensive livestock carcasses from farms to processing plants in continental Spain. The location of intermediate (circles) and processing (triangles) plants is shown in (a), and vulture breeding sites are shown in (b). Legend values represent the number of breeding pairs. Maps were generated with ArcGIS 10.1.

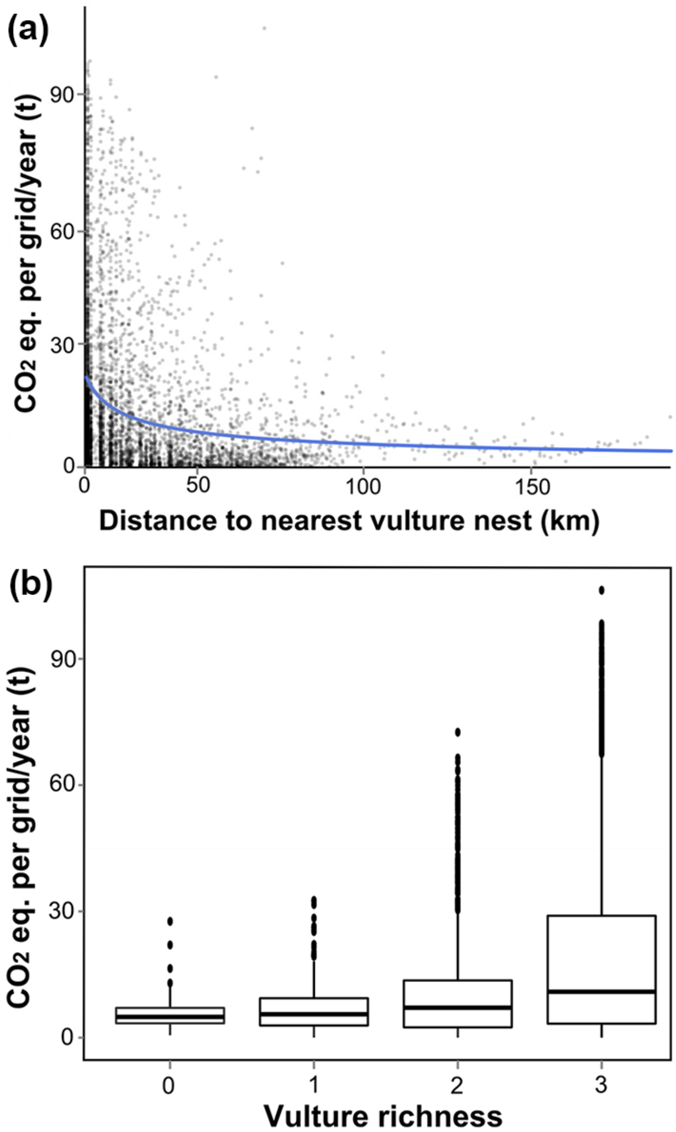

Figure 3. Relationships between CO_2 emissions and vulture distribution and richness in continental Spain. Metric tons of CO_2 eq. per grid per year were (a) negatively associated with distance to the nearest vulture nest/ colony (estimate = 2.80E-07, SE =1.60E-08; χ^2 = 482.7, $p < 0.0001$) and (b) higher in areas with higher richness of vulture species (Kruskal-Wallis test, χ^2_3 = 187.8, $p < 0.001$).

Given that Spain is one of European countries that has to pay more to comply with the Kyoto protocol (UNFCCC 2013), this is an unnecessary increment in GHG emission that should be considered, mainly when scavengers –and vultures in particular– are highly efficient in removing carcasses from the field (DeVault et al. 2003; Wilson & Wolkovich 2011). Indeed, the removal rate of livestock carcasses by scavengers in Spain (median: 166 min for predictable and 182 min for unpredictable carcasses; Cortés-Avizanda et al. 2012) is faster than figures depicted in the legislation. Strikingly, regions with the largest amounts of CO_2 emissions are also those supporting the largest vulture populations, suggesting that, in the absence of sanitary constraints, vultures would have removed most of the extensive livestock carcasses from the field without unnecessary environmental costs. In addition, this

EC regulation also entails economic costs other than those previously mentioned (i.e., derived from the excess of CO_2). The annual payment made by farmers and regional and national administrations to Spanish insurance companies for the artificial removal and processing of extensive livestock carcasses was ca. $50 million in 2012 (MAGRAMA 2014b). Environmental and economic savings associated to natural carcass removal have also been identified in other European countries hosting vultures, such as France, in which livestock carcass management strategies differ. However, due to the restricted geographic distribution of the main scavenger species, the griffon vulture (720 breeding pairs at one reintroduction site in the Grands Causses region, Massif Central, France), figures are substantially lower than those calculated in Spain (8.42–33.11 tons of CO_2 per year, depending on the simulated scenario; Dupont et al. 2012).

In 2013, no cases of BSE were reported in Spain, and European statistics show that the number of reported cases in farmed cattle is anecdotal (OIE 2013), so the sanitary risk associated with the natural removal of carcasses could be considered negligible. Therefore, the return to the traditional system in which vultures and other scavengers freely exploit the carcasses of extensive livestock is highly recommended from multiple points of view. Humans and scavengers have coexisted for millennia, and vultures have traditionally provided important ecosystem services such as disease and pest control, nutrient cycling, cultural inspiration and recreational activities (Moleón et al. 2014). Replacing some of these services, as shown here, not only has conservation costs but also unnecessary environmental and economic costs, which can be saved if we simply let nature do its job.

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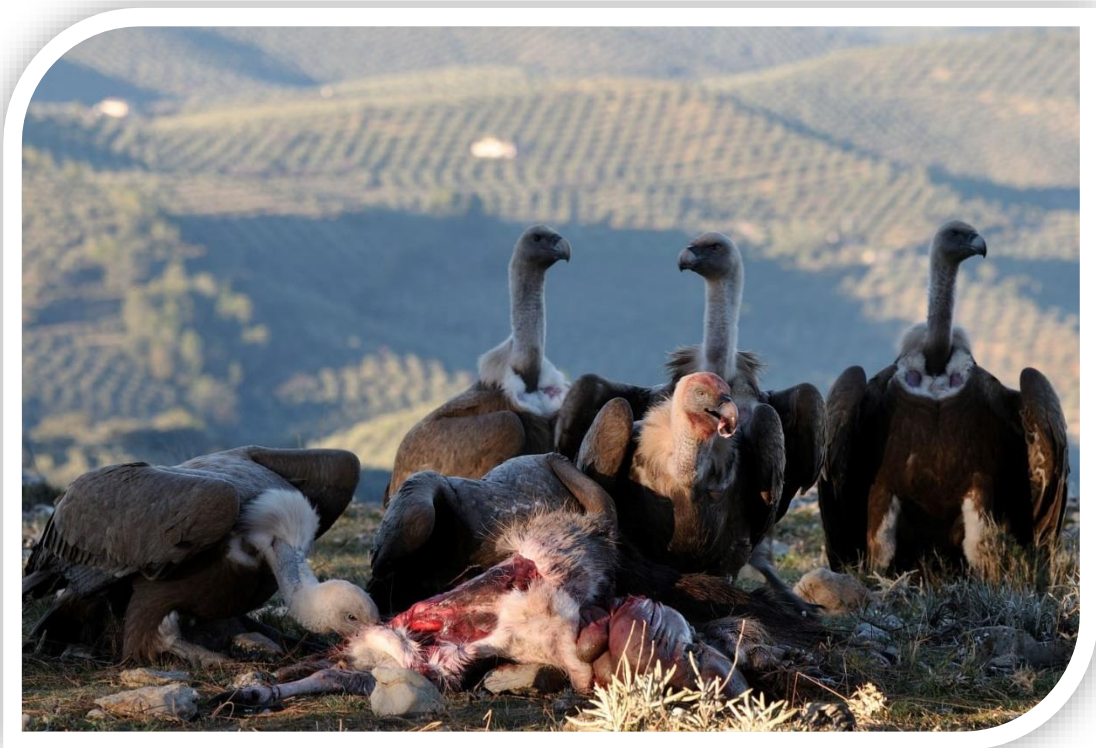
Chapter 3

Evaluation of the network of protection areas for the feeding of scavengers in Spain: from biodiversity conservation to greenhouse gas emission savings

Zebensui Morales-Reyes, Juan M. Pérez-García, Marcos Moleón, Francisco Botella, Martina Carrete, José A. Donázar, Ainara Cortés-Avizanda, Eneko Arrondo, Rubén Moreno-Opo, José Jiménez, Antoni Margalida & José A. Sánchez-Zapata



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PHOTOGRAPH CREDITS: Griffon vultures *Gyps fulvus* in Sierras de Cazorla, Segura y Las Villas, Jaén, Spain

(Manuel J. de la Riva Pérez)

ABSTRACT

Protected areas are one of the most common strategies for wildlife conservation worldwide. However, their effectiveness is rarely evaluated. In Europe, after the outbreak of bovine spongiform encephalopathy, a restrictive sanitary regulation (EC 1774/2002) prohibited the abandonment of dead livestock in extensive farming (extensive livestock) in the field, which led to negative consequences for scavengers. As an attempt to mitigate this negative impact, a new regulation was approved (EC 142/2011) to allow farmers to leave extensive livestock carcasses in the so-called 'Protection areas for the feeding of necrophagous species of European interest' (PAFs). Our general aims were to quantify (i) the proportion of breeding distribution of targeted scavenger species overlapping PAFs; (ii) the extensive livestock carrion biomass available inside PAFs; (iii) the proportion of breeding distribution of non-targeted scavenger species falling within PAFs; (iv) the overlap between the home range of vultures and PAFs, as well as the extent to which vultures move through different administrative units; and (v) the savings in greenhouse gas (GHG) emissions in relation to the pre-PAF scenario. After assessing the status of PAF implementation in every region of peninsular Spain, we analyzed the large-scale spatial information of extensive livestock carrion availability and scavenger breeding distribution, movement data of GPS-tracked vultures, and the annual GHG emissions associated with the transport of livestock carcasses. Most regions established PAFs in their territories, although design criteria were variable. The breeding distribution of targeted species was better represented within PAFs than that of non-targeted species. The extensive livestock carrion biomass potentially available for scavengers within PAFs represented 34.9% of the annual extensive livestock biomass generated in peninsular Spain. The overlap between the home range of GPS-marked vulture populations and PAFs ranged between 63.4% and 100%. The minimum convex polygon of these and other GPS-tracked vulture populations in peninsular Spain encompassed 3–14 Spanish regions and 1–4 countries. Post-PAF there was a potential reduction of c. 55.7% of GHG emissions compared to pre-PAF. The implementation of the new sanitary regulation by means of areas for the feeding of scavengers could mean an important improvement in scavenger conservation and a noteworthy reduction in greenhouse gas emissions: in Spain, extensive livestock carrion availability might increase to 33,474 t per year, and 43,344 t of CO_2 equivalent might be saved annually. However, we identified some gaps related to the distribution of endangered facultative scavengers. Moreover, given that vultures are highly mobile organisms, the design and management of these feeding areas should be coordinated at both the supra-regional and supra-national scales.

KEYWORDS: carrion availability; conservation effectiveness; ecosystem services; EU sanitary policies; facultative scavengers; home range; movement ecology; PAFs; protected areas; vultures

RESUMEN

Las áreas protegidas son una de las estrategias más comunes para la conservación de vida silvestre en todo el mundo. Sin embargo, su eficacia rara vez se evalúa. En Europa, después del brote de encefalopatía espongiforme bovina, una restrictiva normativa sanitaria (CE 1774/2002) prohibió el abandono del ganado en extensivo muerto en el campo, lo que tuvo consecuencias negativas para los carroñeros. Como un intento de mitigar dicho impacto negativo, se aprobó una nueva normativa (CE 142/2011) para permitir a los ganaderos dejar los cadáveres de ganado en extensivo en las denominadas "Zonas de protección para la alimentación de especies necrófagas de interés comunitario" (ZPAEN). Nuestros objetivos generales consistieron en cuantificar (i) la proporción del área de distribución de las especies carroñeras objetivo que se superpone a las ZPAEN; (ii) la biomasa de carroña de ganado en extensivo disponible en las ZPAEN; (iii) la proporción del área de distribución de las especies carroñeras no-objetivo incluida en las ZPAEN; (iv) la superposición entre el área de campeo de los buitres y las ZPAEN, así como el grado en que los buitres se mueven a través de las diferentes unidades administrativas; y (v) los ahorros en emisiones de gases de efecto invernadero (GEI) en relación con el escenario previo a las ZPAEN. Después de evaluar el estado de la implementación de las ZPAEN en todas las comunidades autónomas peninsulares de España, analizamos la información espacial a gran escala de la disponibilidad de carroña de ganando en extensivo y el área de distribución de la población reproductora de las especies carroñeras, los datos de los movimientos de buitres seguidos por GPS, y las emisiones anuales de GEI asociadas al transporte de cadáveres de ganado. La mayoría de las comunidades autónomas establecieron las ZPAEN en sus territorios, aunque los criterios de diseño fueron variables. El área de distribución de las especies objetivo estaba mejor representado dentro de las ZPAEN que el de las especies no objetivo. La biomasa de carroña de ganado en extensivo potencialmente disponible para los carroñeros dentro de las ZPAEN representó el 34,9% de la biomasa anual de ganado en extensivo generada en la España peninsular. La superposición entre el área de campeo de las poblaciones de buitres marcados con GPS y las ZPAEN osciló entre el 63,4% y el 100%. El mínimo polígono convexo de estas y otras poblaciones de buitres seguidos por GPS en la España peninsular abarcó entre 3 y 14 comunidades autónomas y de 1 a 4 países. El escenario posterior a las ZPAEN supuso una reducción potencial de aproximadamente el 55,7% de las emisiones de GEI en comparación con el escenario previo. La implementación de la nueva normativa sanitaria mediante áreas para la alimentación de los carroñeros podría significar una importante mejora en la conservación de los carroñeros y una notable reducción de las emisiones de gases de efecto invernadero: en España, la disponibilidad de carroña de ganado en extensivo podría aumentar a 33.474 t/año, y 43.344 t de CO_2 equivalente podrían ser ahorradas anualmente. Sin embargo, identificamos algunas brechas relacionadas con la distribución de los carroñeros facultativos amenazados. Además, dado que los buitres son organismos altamente móviles, el diseño y la gestión de estas áreas de alimentación deben ser coordinados a escalas tanto supra-autonómica como supra-nacional.

PALABRAS CLAVE: área de campeo; áreas protegidas; buitres; carroñeros facultativos; disponibilidad de carroña; ecología del movimiento; eficacia de la conservación; políticas sanitarias de la UE; servicios ecosistémicos; ZPAEN

INTRODUCTION

The establishment of protected areas (PAs) is one of the most common strategies for wildlife conservation worldwide (e.g., Ervin 2003; Gaston et al. 2008a). According to the World Database on Protected Areas (WDPA), 20.6 million square kilometers (15.4%) of terrestrial areas are covered by PAs (UNEP-WCMC 2014). However, despite the numerous international agreements to protect the natural world, global biodiversity continues to decline (e.g., Butchart et al. 2010; Craigie et al. 2010; Regan et al. 2015). This may be partly due to a deficient design and implementation of management guidelines within PAs, as well as to a spatial mismatch between PAs and conservation priorities (Rodrigues et al. 2004). For instance, many PAs have focused on a few emblematic threatened species (Bonn et al. 2002), while other species of conservation concern have been ignored. Moreover, PA limits have often been demarcated around breeding areas of target species. However, movements outside the breeding distribution during key ecological and behavioral activities (e.g., foraging and social interactions; Bennett et al. 2009) have often been neglected. In addition, trans-jurisdictional conservation strategies that reconcile PA limits beyond jurisdictional (regions and countries) borders are largely missing. This may have important consequences for highly mobile organisms such as large predators and soaring birds (e.g., Block et al. 2011; Lambertucci et al. 2014). Therefore, the continuous scientific evaluation of conservation effectiveness to provide corrective feedback to policy makers should be a key ingredient of PAs' management strategies (e.g., Ervin 2003; Chape et al. 2005; Gaston et al. 2008b; Leverington et al. 2010). However, this critical step has rarely been taken (McLain & Lee 1996).

The PA network should recognize the changing socio-economic context (Walters 1986). The outbreak of the bovine spongiform encephalopathy that occurred in Europe in 2001 led to the approval of a sanitary regulation (EC 1774/2002) that forced farmers to remove livestock carcasses from the field and transport them to authorized plants for their transformation (for industrial purposes, e.g., to produce organic fertilizers) or incineration. In Spain, which is home to >90% of European vulture population (Tella 2001; Margalida et al. 2010), this regulation caused a food shortage for these and other scavengers of conservation concern (e.g., Donázar et al. 2009; Margalida et al. 2010), which largely rely on domestic ungulates in Mediterranean landscapes (Donázar 1993). This, in turn, affected their behavior (Donázar et al. 2010; Margalida et al. 2011; Cortés-Avizanda et al. 2012), demographic parameters (Margalida et al. 2014) and the ecosystem services they provide (Margalida & Colomer 2012; Moleón et al. 2014). This conflicting sanitary regulation originated a new source of GHG emissions, associated with the carcass transport of livestock in extensive farming (hereafter, extensive livestock; Morales-Reyes et al. 2015).

To ensure sufficient food supply to sustain the breeding populations of vultures and other avian scavengers (bearded vultures, cinereous vultures, Egyptian vultures, griffon vultures, golden eagles, Spanish imperial eagles, black kites and red kites), a new regulation was recently approved (EC 142/2011) to allow farmers to abandon extensive livestock carcasses in certain areas ('Protection areas for the feeding of necrophagous species of European interest'; hereafter, PAFs) at the place of death or at nearby fenced feeding stations (Margalida et al. 2012). This legislation was applied in Spain through the Royal Decree 1632/2011, which urged every autonomous community (hereafter, region) to design their own PAF network, with implementation in 2013. PAFs must be included in Natura 2000 spaces with the presence of necrophagous species of European interest, areas devoted to conservation plans of such species and/or important areas for the feeding of these species. Once PAFs are approved, every farm within their limits must apply for permission to abandon carcasses in the field; also, farms have to meet several technical (e.g., only livestock in extensive farming) and sanitary requirements (see Royal Decree 1632/2011 for more details). This new regulation was well received among conservationists and wildlife managers (Margalida et al. 2012). However, no evaluation has been conducted to assess the adequacy of the PAF network to improve target scavenger conservation, or minimizing other negative impacts associated with the original, highly restrictive sanitary regulation.

Our main goal was to assess the conservation and environmental consequences of the Spanish PAF network. First, we evaluated the main criteria used to define PAFs. For this purpose, we quantified (i) the proportion of breeding distribution of targeted scavenger species falling within PAFs and (ii) the extensive livestock carrion biomass available inside PAFs. Second, we identified major gaps that need to be taken into account to improve the current PAF network. For this purpose, we calculated (iii) the proportion of breeding distribution of other major, non-targeted scavenger species falling within PAFs and (iv) the overlap between the home range of GPS-tracked vultures and PAFs, with special emphasis on determining the use of different administrative units by particular individuals and populations. Third, we assessed indirect, unintended benefits of PAF implementation by (v) estimating the potential savings in GHG emissions associated with livestock carcass transport in relation to the pre-PAF scenario (Morales-Reyes et al. 2015).

MATERIAL AND METHODS

PAFs

We contacted every region of peninsular Spain (n = 15 regions; Fig. 1) to gather information about their PAFs. As of October 2015, 11 of these regions had approved specific PAF legislation, whereas three regions had drafted the spatial limits of their PAFs and one region showed no progress in PAF establishment (Table 1). For each region, we extracted the area occupied by PAFs, the criteria used for their design, and the livestock species permitted to be abandoned in these areas (Table 1).

Figure 1. Map of regions of peninsular Spain, indicating if they have approved or drafted specific regulations regarding PAFs

Overlap between PAFs and the breeding distribution of targeted scavenger species

To assess the spatial overlap between PAFs and the breeding distribution of the scavenger species included in the new European regulation (EC 142/2011), we used maps from the Spanish National Biodiversity Inventory (MAGRAMA 2012), which represent species occurrence according to a UTM 10 x 10 km grid square. For each species, we used ArcGIS 9.3 (ESRI 2009) to calculate the overlap as the percentage of the breeding distribution included inside the PAFs.

Table 1. Livestock species permitted to be abandoned inside PAFs, total area of the region (km^2), percentage of the area occupied by PAFs and PAFs design criteria for each region in peninsular Spain. Regions with legislation approved are shown in bold. Regions without legislation approved but with a draft of the limits of distribution of the PAFs are underlined. All were used to map the PAFs.

Region	**Livestock species**	**Area**	**% of the area with PAFs**	**Design criteria**
Andalusia[1]	Sheep and goat	87,268	53	Distribution area of scavengers *Gypaetus barbatus*, *Gyps fulvus*, *Aegypius monachus*, *Neophron percnopterus* and partially Aquila chrysaetos, *Aquila adalberti*, *Milvus milvus* and *Milvus migrans*
Aragon[2]	All extensive livestock species (PAFs type 1) Sheep and goat (PAFs type 2)	47,719	59	List of municipalities
Asturias	NA	10,604	-	NA
Basque Country[3]	Sheep, goat, pig, cattle and/or horse†	7,234	19	Special Protection Areas (SPAs) and Sites of Community Importance (SCIs) of the Natura 2000 and other protected areas and lands above 500 or 700 metres altitude (depending on the region)
Cantabria[4]	Not specified	5,326	41	Public Utility Forest
Castile La Mancha[5]	Preferentially sheep and species different from cattle	79,463	80	List of regions and municipalities
Castile and Leon[6]	Preferentially sheep, goat, horse† or species different from cattle (< 48 months)	94,226	88	List of municipalities
Catalonia[7]	Sheep, goat, cattle and horse†	32,107	13	Public forests or other lands above 1400 metres altitude and list of municipalities
Extremadura[8]	Sheep and horse† (horse if it includes cattle, sheep, goat or pig in extensive)	41,635	100	All municipalities of the Region
<u>Galicia</u>	Sheep and goat*	29,574	16	NA
La Rioja[9]	Sheep, goat, cattle or horse†	5,045	59	List of municipalities fully or partially included in the Natura 2000 and municipalities not included in the Natura 2000
<u>Madrid</u>	Sheep and goat*	8,022	17	NA
<u>Murcia</u>	Sheep and goat*	11,313	20	NA
Navarre[10]	Sheep, goat, cattle and horse†	10,391	87	All municipalities, except those within the area of influence of the Pamplona-Noáin airport
Valencian Community[11]	Ruminant (sheep, goat, cattle)	23,255	20	Special Protection Areas (SPAs) of the Natura 2000

* In these regions, which had only drafted the limits of the PAFs, we assumed that the livestock species permitted to be disposed in the field within PAFs are sheep and goat. † Some regional legislation included horses.

[1]Boletín Oficial de la Junta de Andalucía (BOJA). Available at: https://www.juntadeandalucia.es/boja/.

[2]Boletín Oficial de Aragón (BOA). Available at: https://www.boa.aragon.es/.

[3]Boletín Oficial del País Vasco (BOPV). Available at: https://www.euskadi.eus/r48-bopv2/es/bopv2/datos/Ultimo.shtml/.

[4]Boletín Oficial de Cantabria (BOC). Available at: https://boc.cantabria.es/boces/.

[5]Diario Oficial de Castilla-La Mancha (DOCM). Available at: https://docm.castillalamancha.es/portaldocm/sumario.do/.

[6]Boletín Oficial de la Junta de Castilla y León (BOCYL). Available at: https://bocyl.jcyl.es/.

[7]Diari Oficial de la Generalitat de Catalunya (DOGC). Available at: https://dogc.gencat.cat/ca/.

[8]Diario Oficial de Extremadura (DOE). Available at: https://doe.gobex.es/.

[9]Boletín Oficial de La Rioja (BOR). Available at: https://www.larioja.org/npRioja/default/defaultpage.jsp?idtab=449881/.

[10]Boletín Oficial de Navarra (BON). Available at: https://www.navarra.es/home_es/Actualidad/BON/.

[11]Diari Oficial de la Comunitat Valenciana (DOCV). Available at: https://www.docv.gva.es/portal/.

Livestock carrion biomass availability in relation to PAFs

We obtained the abundance of the most important extensive livestock species (i.e., cattle, sheep, goat and pig) per municipality of peninsular Spain in 2012 and the average weight per age class from the Spanish Ministry of Agriculture, Food and Environment (MAGRAMA 2012). We used this information, together with the annual mortality rate of each species of livestock per age class (Government of Castilla y León 2013; see Table 1 in Chapter 2), to calculate the carrion biomass available for scavengers per year across peninsular Spain and within PAFs. For this purpose, we took into account the legislation specified in each region (Table 1). For the three regions that had only drafted the limits of the PAFs, we assumed that sheep and goats were the livestock species permitted to be disposed in the field within PAFs, i.e., the most commonly authorized species in the other regions (Table 1). Our calculations represent the maximum carrion biomass available because not all the farmers are actually permitted to abandon their livestock carcasses, i.e., each farm within the PAFs must request the corresponding permit from the regional administration. We represented the spatial distribution of maximum carrion biomass availability (t per year) according to the UTM 10 x 10 km grid square. When a grid belonged to more than one region, the biomass availability was distributed according to their areas.

Overlap between PAFs and the breeding distribution of non-targeted scavenger species

We evaluated several major avian (common ravens and carrion crows) and mammalian (gray wolves, brown bears, red foxes and stone martens; Mateo-Tomás et al. 2015) facultative scavengers not included in the abovementioned European regulation (EC 142/2011). We assessed the spatial overlap between PAFs and the breeding distribution of these scavengers in peninsular Spain using the same approach as for targeted species (see above; MAGRAMA 2012). We then compared the scavenger breeding distribution-PAF overlap between targeted and non-targeted species, as well as between vultures and facultative scavengers. We compared the scavenger breeding distribution-PAF overlap between endangered (i.e., listed as 'Critically Endangered', 'Endangered' or 'Vulnerable') and non-endangered species (i.e., listed as 'Near Threatened' or 'Least Concern') according to Spanish (Madroño et al. 2004; Palomo et al. 2007) and global lists (IUCN 2016). Comparisons were made by means of Mann–Whitney tests.

Vulture movements in relation to PAFs and administrative boundaries

To analyze vulture movements, we tracked 71 birds equipped with GPS transmitters from different Spanish PAFs: 30 griffon vultures from Sierras de Cazorla, Segura y Las Villas Natural Park (south-eastern Spain), 11 cinereous vultures from Cabañeros

National Park (central Spain), 19 bearded vultures from the Pyrenees (northern Spain) and 11 Egyptian vultures from Cádiz (southern Spain). We selected these cases because they offer the most complete information, i.e., a higher number of GPS-marked individuals in a single population, for each species in Spain. Sex, age and the number of fixes of each tracked vulture, as well as tracking period, are detailed in Table 2. Migratory movements of Egyptian vultures (from Europe to Africa) were excluded.

We used movement data for two purposes. First, we calculated the home range sizes of each tracked bird using kernel h reference models as the activity utilization distributions (UD; Worton 1989) at the 50% and 90% level (hereafter k50% and k90%, respectively). We selected these kernel levels because they provide information on conservative home ranges (Börger et al. 2006). UD surface maps were created using the 'adehabitatHR' package (Calenge 2006) of R (R Core Team 2014) in combination with ArcGIS 9.3 (ESRI 2009). We then evaluated the overlap between PAFs and home ranges (k50% and k90%; excluding marine areas), both at the population (i.e., considering all tracked individuals of a given species together) and individual levels.

Second, we estimated the 100% minimum convex polygon (MCP) to calculate the number of administrative units, i.e., countries and regions within peninsular Spain, used by each tracked population and individual. Additionally, we reviewed the published studies on the home range of vultures (MCP) equipped with GPS tracking systems in Spain that provided enough spatial information to assess the number of regions and countries included in their home ranges (Table 2).

Greenhouse gas emissions savings

We quantified the annual GHG emissions associated with the transport of extensive livestock carcasses from farms to authorized plants in peninsular Spain according to IPCC (2006) and following the methodology described in Morales-Reyes et al. (2015). Calculations included the transport of carcasses from outside the PAFs, as well as from inside the PAFs in the case of those livestock species not permitted to be left in the field (i.e., those which must collected and transported to plants) according to each regional legislation (see Table 1). We assumed that all extensive farms inside PAFs are authorized to abandon their livestock carcasses in the field, so the resulting figure is a maximum estimate. We then compared the national GHG emissions per year associated with the previous regulation (EC 1774/2002; Morales-Reyes et al. 2015) with the estimated annual GHG emissions after the implementation of the PAF regulation (EC 142/2011).

Table 2. Number of individuals tracked (N), sex (F=female; M=male), age class (Ad=adults, i.e., birds showing typical adult plumage; Non-ad=non-adults, i.e., birds exhibiting juvenile, immature or sub-adult plumages; Forsman 2003; Ferguson-Lees & Christie 2006), tracking period, total number of GPS fixes used, place of capture and tracking devices used for the monitoring of four vulture populations from different PAFs within peninsular Spain.

Vulture species	N	F/M	Age class	Period	Fixes	Place of capture	Tracking device	References
Gypaetus barbatus	19	10/9	9 Ad, 10 Non-ad	2006-2014	66,674	The Pyrenees	Solar-powered 70g Argos/GPS PTTs[1]	This study
	13	6/7	13 Non-ad	2006-2012	32,838	Sierras de Cazorla, Segura y Las Villas N.P.	Solar-powered 70g Argos/GPS PTTs[1]	Margalida et al. 2013
Aegypius monachus	11	4/7	11 Non-ad	2006-2009	29,735	Cabañeros N.P.	Solar-powered 70g Argos/GPS PTTs[1]	This study
	12	2/8	12 Non-ad	2010-2013	47,785	Montes de Toledo, Sierras in the Guadiana Valley, Sierra de Canalizos and Sierra Madronal-Alcudia	Solar-powered 70g Argos/GPS PTTs[1]	Castaño et al. 2015
Gyps fulvus	30	11/19	30 Ad	2014-2015	322,893	Sierras de Cazorla, Segura y Las Villas N.P.	Bird Solar GSM/GPRS 90g[3]	This study
	8	NA	7 Ad, 1 Non-ad	2007-2010	2,122	Castellón	Solar-powered 70g Argos/GPS PTTs[1]	García-Ripollés et al. 2011
Neophron percnopterus	11	4/7	11 Non-ad	2009-2014	8,984	Cádiz	40g GPS PTT[2]	This study

[1]Microwave Telemetry Inc., Columbia, USA.

[2]North Star Science and Technology LLC, King George, USA.

[3]e-obs digital telemetry GmbH, Gruenwald, Germany.

RESULTS

PAFs

PAFs occupy an area of 300,997 km^2, representing 61.2% of peninsular Spain. The regional surface occupied by PAFs ranged between 13% and 100% (mean = 48.0%, SD = 31.4%). Guidelines for the design of PAFs were highly heterogeneous among the 11 regions that had approved specific legislation (Table 1). All regions (n = 11) allowed the abandonment of sheep carcasses in their PAFs; this figure was lower for goats (90.9%), cattle (81.8%), horses (81.8%) and pigs (45.5%) (Table 1).

Overlap between PAFs and the breeding distribution of scavenger species

The breeding distribution of targeted species (mean = 89.6%, SD = 9.3%) was better represented in PAFs than that of non-targeted species (mean = 77.0%, SD = 4.0%; W = 6, p = 0.02). The PAF network included >95% of the breeding distribution of all vulture species (mean = 95.5%, SD = 4.8%) and ≥70% of the facultative scavengers (mean = 79.7%, SD = 7.0%), showing a significantly better coverage for the first group than for the second (W = 1, p = 0.004). We found that endangered species were better represented within PAFs than the rest of the species considered in this study, according to both Spanish (90.9% vs. 79.2%; W = 6, p = 0.02) and global lists (IUCN 2016) of endangered species (89.8% vs. 83.2%; W = 6, p = 0.35; differences were non-significant in this case; Table 3).

Table 3. Proportion (%) of the breeding distribution of scavenger species included in PAFs and their conservation status (according to IUCN Red List categories).

Species	Breeding distribution	IUCN (Spain)	IUCN (Global)
*Gypaetus barbatus**	100	EN	NT
*Aegypius monachus**	98.7	VU	NT
*Gyps fulvus**	93.6	-	LC
*Neophron percnopterus**	89.6	EN	EN
Total vultures	95.5		
*Aquila adalberti**	90.0	EN	VU
*Aquila chrysaetos**	86.9	NT	LC
*Milvus milvus**	87.7	EN	NT
*Milvus migrans**	70.0	NT	LC
Total other raptors	83.7		
Corvus corax	77.0	-	LC
Corvus corone	75.1	-	LC
Total corvids	76.1		
Ursus arctos	79.2	CR	LC
Canis lupus	83.7	NT	LC
Vulpes vulpes	72.8	LC	LC
Martes foina	74.2	LC	LC
Total mammals	77.5		

*Targeted species according to EC 142/2011.

Livestock carrion biomass availability inside and outside of PAFs

The maximum extensive livestock carrion biomass potentially available to scavengers within PAFs was 33,474 t in 2012. This represented c. 35% of the annual extensive livestock biomass generated in peninsular Spain. The percentage of carrion biomass available in PAFs relative to the total in each region varied between 0.8% and 95.5% (mean = 36.9%, SD = 30.7%; Table 4). The highest amount of carrion biomass within PAFs was located in the central-west part of peninsular Spain (Fig. 2), mainly due to the presence of an important number of cattle.

Table 4. Total livestock carrion biomass available in each region (t), livestock carrion biomass available in PAFs relative to the total in each region (%), total GHG emissions after the implementation of PAFs in each region (metric tons of CO_2 equivalents to the atmosphere per year) and GHG emissions savings in relation to a pre-PAF scenario (%). Regions with legislation approved are shown in bold. Regions without legislation approved but with a draft of the limits of distribution of the PAFs are underlined.

Region	Total biomass	Biomass in PAFs	Total GHG emissions	GHG emissions savings
Andalusia	11,876	23.3	7,483	47.6
Aragon	5,066	59.7	2,607	67.7
Asturias	5,029	0.8*	1,143	2.3*
Basque Country	2,317	16.6	1,237	16.7
Cantabria	2,332	44.7	306	47.6
Castile La Mancha	5,562	95.5	333	95.7
Castile and Leon	21,659	49.9	1,975	78.4
Catalonia	3,275	20.7	4,396	14.4
Extremadura	23,852	23.6	9,578	53.6
<u>Galicia</u>	7,490	1.2	1,898	11.0
La Rioja	883	72.7	105	73.1
<u>Madrid</u>	1,640	5.1	409	14.2
<u>Murcia</u>	915	23.1	1,533	33.7
Navarre	2,701	90.0	253	88.8
Valencian Community	1,191	27.3	1,044	25.5

* Biomass available in PFAs and GHG emissions savings in Asturias were not equal to zero because both of them were calculated according to the UTM 10 x 10 km grid square, which do not exactly match with the regional boundaries

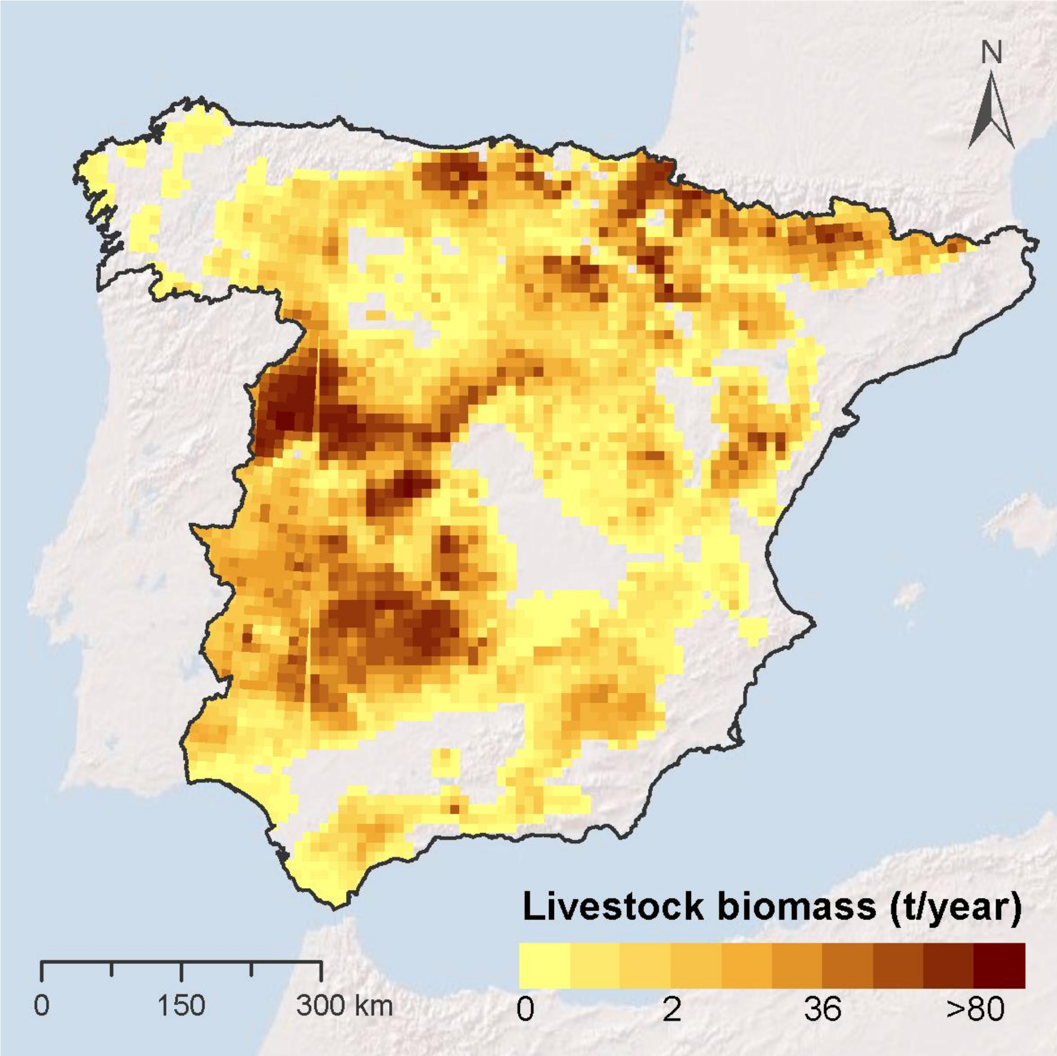

Figure 2. Spatial distribution of carrion biomass availability (t) per 10 x 10 km grid per year and protection areas for the feeding of necrophagous species (PAFs) in peninsular Spain.

Vulture movements in relation to PAFs and administrative boundaries

The home range of the four vulture species together, calculated using information from 428,086 locations, was 47,272 km^2 (k50%) and 285,908 km^2 (k90%). The overlap between the home range of each vulture population and PAFs was similar for k50% (mean = 85.4%, range = 63.4–100%) and k90% (mean = 80.2%, range = 64.9–97.2%; Table 5; Fig. 3). At the individual level, mean overlap of all species together was 92.9% (range = 20.7–100%) for k50% and 89.5% (range = 45.2–100%) for k90% (see Table 5 for data separated by species).

Table 5. Home range size (km²) of the GPS-tracked populations of the four obligate scavenger species estimated by kernel utilization density (k50% and k90%) and percentage of home range included inside Spanish protection areas for the feeding of necrophagous species (PAF coverage) at both the population and individual (mean ± SD) levels.

	k50%			k90%		
		PAF Coverage (%)			PAF Coverage (%)	
Vulture species	**km²**	**Population**	**Individual**	**km²**	**Population**	**Individual**
Gypaetus barbatus	3,240	63.4	80.3 ± 24.4	18,497	64.9	79.3 ± 15.4
Aegypius monachus	2,101	100	100 ± 0	41,688	97.2	97.1 ± 2.8
Gyps fulvus	4,146	99.8	99.1 ± 2.6	46,038	91.4	95.2 ± 4.4
Neophron percnopterus	37,785	78.4	90.8 ± 15.2	179,685	67.1	83.9 ± 15.3

Vulture populations (GPS-tracked either in this study or in the reviewed studies) moved across different Spanish peninsular regions (range = 3–14) and countries (range = 1–4; Spain, Portugal, Andorra and France; see Table 6). Vulture individuals used an average of 3.4 regions (range = 1–12) and 1.5 countries (range = 1–3; see Table 6 for data separated by species and studies).

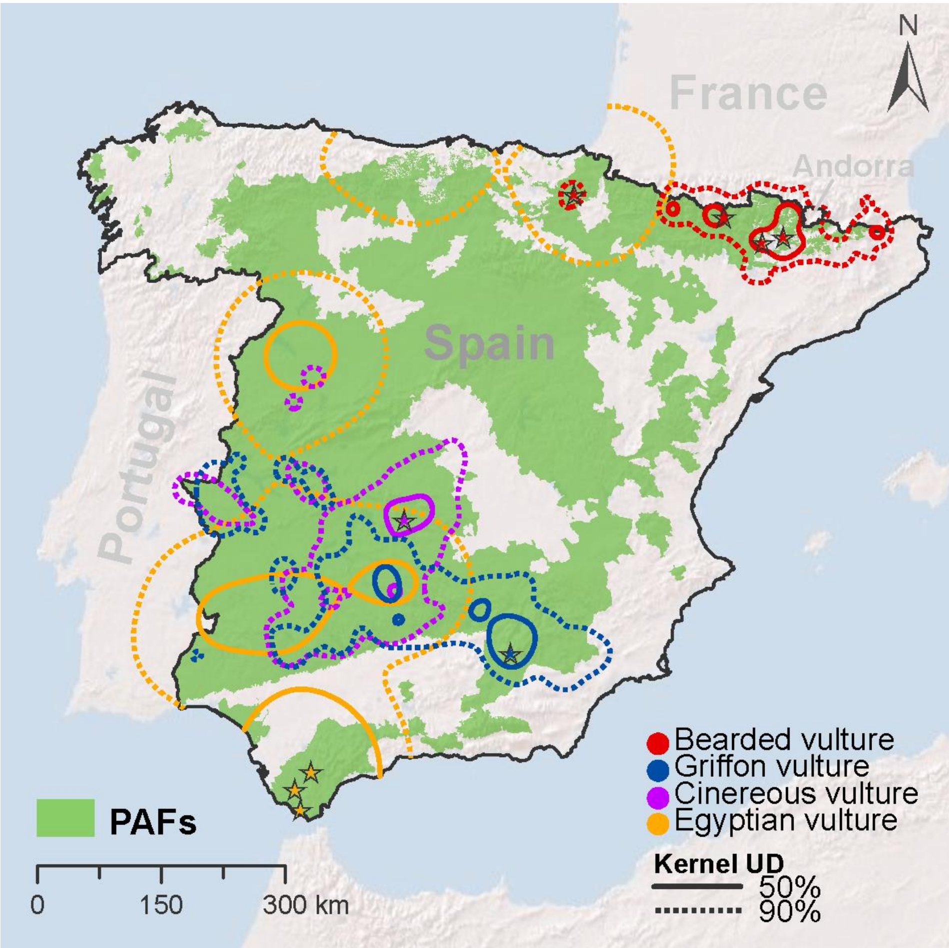

Figure 3. Spatial distribution of home ranges (k50% and k90% UD) of vultures and protection areas for the feeding (PAFs) of necrophagous species in peninsular Spain. Stars show places of capture.

Vulture populations (GPS-tracked either in this study or in the reviewed studies) moved across different Spanish peninsular regions (range = 3–14) and countries (range = 1–4; Spain, Portugal, Andorra and France; see Table 6). Vulture individuals used an average of 3.4 regions (range = 1–12) and 1.5 countries (range = 1–3; see Table 6 for data separated by species and studies).

Table 6. Regions and countries included in the minimum convex polygon (MCP) obtained for different vulture populations (total number of regions/countries) and individuals (mean number of regions/countries; range is shown in parenthesis). Information was compiled from studies performed using birds equipped with GPS tracking systems in peninsular Spain.

	Spanish regions		Countries		
Vulture species	**Population**	**Individual**	**Population**	**Individual**	**Reference**
Gypaetus barbatus	4	2.2 (1–4)	3	2.2 (1–3)	This study
	14	–	4	–	Margalida et al. (2013)
Aegypius monachus	10	5.8 (4–10)	3	1.7 (1–2)	This study
	9	4.1 (1–9)	2	1.5 (1–2)	Castaño et al. (2015)
Gyps fulvus	4	3.4 (2–4)	2	1.1 (1–2)	This study
	7	3.0 (2–6)	1	1.0 (1)	García-Ripollés et al. (2011)
Neophron percnopterus	12	2.9 (1–12)	3	1.5 (1–3)	This study

GHG emissions savings

The transport of dead livestock from farms to authorized plants after the new regulation (considering both the livestock outside of PAFs and the livestock species that must be collected inside PAFs according to each regional rule) meant a minimum emission of 34,300 metric tons of CO_2 equivalents to the atmosphere per year. The south-western and north-eastern extremes of peninsular Spain showed the highest levels of GHG emissions (Fig. 4). Considering that the GHG emissions in the pre-PAF scenario was 77,344 metric tons of CO_2 equivalents to the atmosphere per year (Morales-Reyes et al. 2015), the post-PAF scenario meant a potential reduction of c. 55.7% in GHG emissions. The percentage of reduction in GHG emissions ranged between 2.3% and 95.7% (mean = 44.7%, SD = 30.7%) depending on the region considered (Table 4).

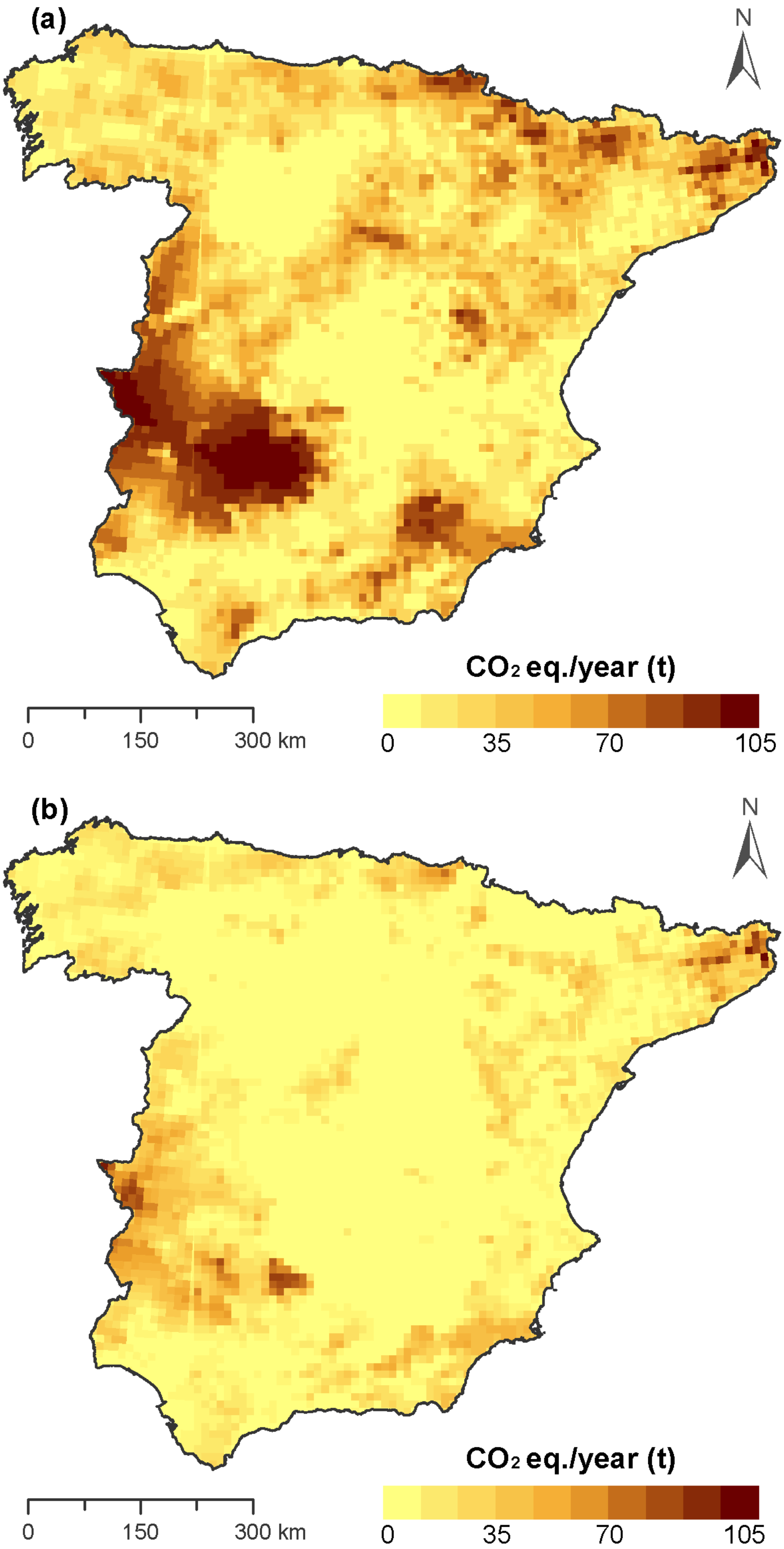

Figure 4. GHG emissions (in metric tons of CO_2 eq. per 10 x 10 km grid per year) before (a) and after (b) the implementation of the protection areas for the feeding (PAFs) of necrophagous species in peninsular Spain.

DISCUSSION

Our findings show that PAFs created specifically to ensure areas for the feeding of necrophagous species after the new European sanitary regulation (EC 142/ 2011) have resulted in significant improvements in relation to the previous regulation based on the percentage of the breeding distribution of the targeted species covered by these areas and the amount of feeding resources available within them. We also show that the implementation of the new regulation potentially leads to a considerable reduction in the GHG emissions associated with artificial carcass disposal. However, given the large movements performed by individual birds throughout the year as well as the by the targeted species considered, there are still several aspects that should be improved to properly ensure the long-term conservation of scavenger species.

PAFs performance in relation to targeted species and carrion availability

Importantly, the breeding distribution of priority species, particularly vultures, was better represented in PAFs than the distribution of other facultative scavengers not included as targeted species. In this sense, Spanish PAFs may meet their purpose reasonably well. However, there are still populations of targeted species outside PAFs. Efforts to protect these populations should be especially encouraged in the case of the most endangered species at the national and global scales, i.e., Egyptian vultures, Spanish imperial eagles and red kites.

As expected as a consequence of the application of the new European regulation permitting the disposal of carrion in the field, we found a significant increment in the availability of food resources for scavengers (measured as tons of carrion) within these areas. This may alone imply a significant step in the conservation of the Spanish and, by extension, European vulture populations. In particular, the Spanish PAF network could potentially provide c. 4–6 times the carrion needed annually by the whole Spanish vulture population (Margalida & Colomer 2012). However, calculations are not available for the rest of the species included in this study and we must recognize the spatial heterogeneity in both scavenger and carrion abundance. It is worth noting that our results are not exact figures of food availability as some regions do not fully apply the recently approved regulations while others, mainly those located in remote areas (i.e., high mountains, far from roads and trails), have never removed carcasses due to the logistic constraints in locating them. Moreover, to predict the carrying capacity of these areas to maintain healthy populations of vultures and other facultative scavengers in Spain, it is important to simultaneously assess the role played by wild ungulate carcasses as another source of food for these species (Mateo-Tomás et al. 2015).

How can be the PAF network be improved?

Non-targeted facultative scavengers can also benefit from the resources available within PAFs. For example, the application of the previous EU sanitary regulation led to changes in the diet of wolves (e.g., increased large domestic ungulate consumption; Lagos & Bárcena 2015; Llaneza & López-Bao 2015), possibly affecting their role in the ecosystem (Lagos & Bárcena 2015) and exacerbating human–wolf conflicts (Llaneza & López-Bao 2015). Regarding the brown bear, carrion is an important resource for this species (Clevenger & Purroy 1991; Naves et al. 2003; Mateo-Tomás et al. 2015), which is critically endangered in Spain. Its inclusion as a priority species in PAFs might significantly contribute to improving its conservation status. Thus, we encourage the inclusion of additional facultative scavengers of special conservation concern and those associated with outstanding human-wildlife conflicts when designing PAFs.

The most important failure of current PAF design is probably their focus on the breeding distribution of scavengers. Vultures are soaring birds that can travel several hundreds of km daily from breeding to foraging areas (see Table 5) across physical and political boundaries (see Table 6). Long-distance daily movements are common in seabirds that often cross different jurisdictions (Yorio 2009) or large carnivores that have large spatial requirements (e.g., Falcucci et al. 2013; Trouwborst et al. 2015). In these cases, conservation strategies that consider movements outside of breeding areas are highly desirable (Lambertucci et al. 2014). Previous studies have described vulture foraging movements related to the use of carrion resources (i.e., vulture restaurants) at the local scale through GPS tracking (e.g., Monsarrat et al. 2013; López-López et al. 2014), but not at a large scale as in this study. We observed that the breeding distribution of the four vulture species were well represented in PAFs, while the fit between their home ranges and PAFs was less adequate, especially for young birds. This clearly highlights another important avenue for the improvement of the new sanitary regulation, which should recognize the combination of breeding and foraging areas. However, although our case studies rely on a large number of individuals, expanding the number of GPS-tracked vultures (e.g., taking into account other areas and seasons, as well as individuals of different age classes and breeding status) would provide an improved, more comprehensive assessment of the new regulation. For instance, pre-adult bearded vultures from the Pyrenean population moved much less than individuals reintroduced in Andalusia, which may be related to the abundance and predictability of food resources (Margalida et al. 2013). In any case, our results offer an unprecedented starting point and reveal interesting hypotheses that can be further tested. Our findings indicate that PAFs may be more efficient for breeders than for floaters, whose home ranges can be considerably larger. In the case of bearded vultures in the Pyrenees, the overlap of core areas (k50%) of breeders with PAFs reached 90.6%, while the overlap was only 64.2% for floaters.

Collateral benefits of PAFs

The previous European sanitary regulation resulted in a new source of GHG emissions associated with carcass collection and transport to authorized plants (Morales-Reyes et al. 2015). The new regulation meant a substantial GHG emission reduction (see Fig. 4), although there is still c. 44% of the original emissions that could be saved. The areas that currently accumulate most of the GHG emissions are associated with a high number of livestock of species not included in the regional regulations and located far from authorized plants. For example, in south-western Spain, where there are many cattle and other extensive livestock species, the regional PAF regulation only allows farmers to abandon sheep carcasses in the field (see Table 1) and in north-eastern Spain, only lands above 1400 m are included within PAFs (Table 1). In parallel, the new regulation meant important economic savings to farmers and to regional and national administrations when compared to the previous situation in terms of payments to insurance companies for carcass transport (Morales-Reyes et al. 2015). Including all livestock species in the PAFs of all regions would further reduce these environmental and economic costs.

Management implications and conclusions

Our results show that the implementation of the new regulation regarding the management of extensive livestock debris may greatly improve the previous rules and have obvious positive effects on scavenger conservation. Also, the PAFs' scenario means an important tool to reduce the environmental (and economic) costs associated with the artificial removal and processing of livestock carcasses. However, the Spanish network of PAFs should be improved to cover the full distribution range of priority species and additional facultative scavengers of special conservation concern. Moreover, to maximize the effectiveness of PAFs in Spain, managers should recognize that vultures are highly mobile organisms that must move daily from breeding to foraging areas across physical and political boundaries. Thus, management should be performed, or at least coordinated, at a supra-regional scale. As a first step, regional administrations should avoid establishing how much carrion can be left in the field based only on the scavengers present in their region. Additionally, the design criteria of PAFs and the livestock species subject to regulation should be unified among Spanish regions at the national level. Supra-national coordination with neighboring European countries that support vulture populations is also desirable. PAFs should recognize that movements of scavengers are age-dependent and take into account the foraging strategies of floaters.

Protected areas have been the cornerstone of biodiversity conservation worldwide (e.g., Ervin 2003; Gaston et al. 2008a). Thus, the evaluation of their conservation effectiveness (e.g., Chape et al. 2005; Gaston et al. 2008b; Leverington et al. 2010) is an essential component of conservation strategies. The findings from our work support the utility of combining large scale information on biodiversity, movement ecology of target species and the evaluation of ecosystem services to inform political and technical decisions regarding environmental conservation policies.

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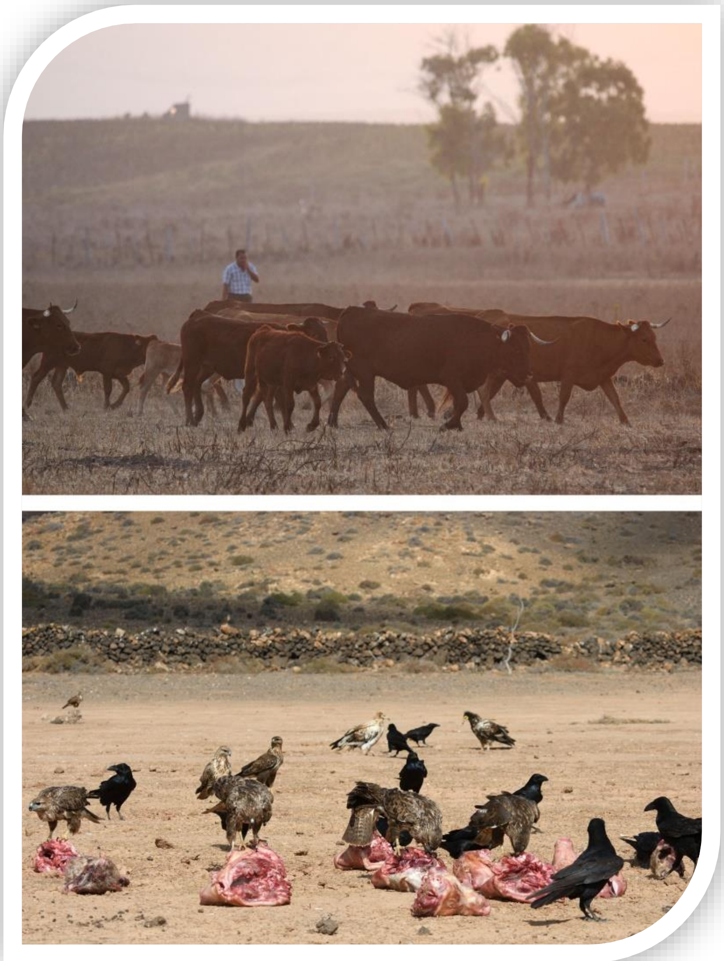
PART II

Socio-cultural assessment

Chapter 4

Farmer perceptions of the ecosystem services provided by scavengers: what, who, and to whom

Zebensui Morales-Reyes, Berta Martín-López, Marcos Moleón, Patricia Mateo-Tomás, Francisco Botella, Antoni Margalida, José A. Donázar, Guillermo Blanco, Irene Pérez & José A. Sánchez-Zapata



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PHOTOGRAPH CREDITS: Shepherd and cattle *Bos taurus* in El Prado de Castilobo, Cádiz, Spain

Common buzzards *Buteo buteo insularum*, common ravens *Corvus corax canariensis* and

Egyptian vultures *Neophron percnopterus majorensis* in Fuerteventura, Canary Islands, Spain

(Manuel J. de la Riva Pérez)

ABSTRACT

A socioecological approach to biodiversity conservation has recently been encouraged. We examined farmer perceptions of ecosystem services provided by scavenging vertebrates in Spain through face-to-face surveys with farmers in seven large extensive livestock systems. Scavenging services (i.e., carrion consumption) was the most perceived benefit whereas the role of some scavengers as predators was the most recognized damage. The most beneficial scavengers perceived were vultures. Overall, we detected a "Dr. Jekyll and Mr. Hyde" paradox as the same species and species within the same guild can be dually perceived as beneficial or harmful. Our findings provide evidence that traditional extensive farming linked to experience-based and local ecological knowledge drives positive perceptions of scavengers and their consideration as ecosystem services providers. Research on social perceptions can contribute to the conservation of scavengers by raising awareness about the ecosystem services provided by this functional group.

KEYWORDS: carrion removal; functional diversity; predators; traditional farming; transhumance; vultures

RESUMEN

Recientemente se ha fomentado un enfoque socioecológico para la conservación de la biodiversidad. En este trabajo examinamos las percepciones de los ganaderos sobre los servicios ecosistémicos proporcionados por los carroñeros vertebrados en España a través de encuestas cara a cara con los ganaderos en siete grandes sistemas ganaderos en extensivo. El servicio de consumo de carroña fue percibido como el más beneficioso, mientras que el papel de algunos carroñeros como depredadores fue el perjuicio más reconocido. Los buitres fueron percibidos como los carroñeros más beneficiosos. En general, detectamos una paradoja del "Dr. Jekyll y Mr. Hyde" ya que las mismas especies y especies dentro del mismo gremio pueden ser doblemente percibidas como beneficiosas o dañinas. Nuestros resultados proporcionan evidencia de que la ganadería extensiva tradicional vinculada al conocimiento ecológico local y basada en la experiencia conduce a percepciones positivas de los carroñeros y su consideración como proveedores de servicios ecosistémicos. La investigación sobre las percepciones sociales puede contribuir a la conservación de los carroñeros mediante una mayor conciencia acerca de los servicios ecosistémicos proporcionados por este grupo funcional.

PALABRAS CLAVE: buitres; depredadores; diversidad funcional; eliminación de carroña; ganadería tradicional; trashumancia

INTRODUCTION

Recognition about the need for approaching biodiversity conservation from a social-ecological perspective is now highlighted in the research agenda (Ban et al. 2013; Martín-López & Montes 2015; Bennett et al. 2017). One of the reasons for mainstreaming the social dimensions (i.e., perceptions, values, beliefs, or attitudes) in biodiversity conservation (Bennett et al. 2017; Pooley et al. 2017) is the acknowledgment of the crucial role of biodiversity in supporting human well-being through the provision of ecosystem services (e.g., MA 2005; Díaz et al. 2006; Cardinale et al. 2012), which are understood as the benefits (and occasionally detriments) that people obtain from ecosystems (Díaz et al. 2015). In this sense, it has recently been recognized that the same ecosystem service can be perceived as benign or harmful, depending on the social actors involved (Saunders & Luck 2016). Additionally, conservation policies and practices are a result of human decisions and behavior, either intended or unintended (Mascia et al. 2003). To foster societal change toward biodiversity conservation, there is a need to comprehend how biodiversity and its resulting ecosystem services are perceived by humans (Martín-López et al. 2012; Bennett 2016). Here, perceptions refer to the way humans understand, interpret, and value biodiversity and ecosystem services (Bennett 2016). However, understanding the links between biodiversity, ecosystem services, and human perceptions still remains a critical challenge. Indeed, most of the research in biodiversity and ecosystem services has not truly addressed this key challenge because it has mainly focused either on the links between biodiversity and ecosystem services (e.g., Díaz et al. 2006; Cardinale et al. 2012) or social preferences for ecosystem services (e.g., Martín-López et al. 2012; Ament et al. 2017). Only a few studies have aimed to understand the entwined links between biodiversity and social perceptions of ecosystem services through the analysis of functional diversity (Díaz et al. 2011; García-Llorente et al. 2011; Cáceres et al. 2015). Therefore, a scientific approach to assessing social perceptions of the ecosystem services provided by different functional groups and particular species may improve the understanding of this lack of knowledge and favor biodiversity conservation. For instance, the contrasting behavioral attributes of three large carnivore species in southeastern Europe led to species specific social perceptions of them and conservation implications (Lescureux & Linnell 2010).

In this study, we examined the social perceptions of those ecosystem services provided by scavenging vertebrate species in Spain, which is home to globally threatened scavenger species, including >90% of European vulture populations (Margalida et al. 2010) and the largest populations of large carnivores in Western Europe, such as brown bears and gray wolves (Chapron et al. 2014). It has been globally demonstrated that scavenging vertebrates are crucial for providing ecosystem services, such as disease and pest control (Markandya et al. 2008), nutrient cycling (Wilson & Wolkovich 2011), indirect greenhouse emissions regulation (Morales-Reyes et al. 2015) and cultural inspiration and recreational activities (Markandya et al. 2008; Gangoso et al. 2013). Despite the decline in their populations worldwide (Ogada et al. 2012) leading to the loss of ecosystem services (Markandya et al. 2008), this group of species has received little attention in ecosystem services research (Moleón et al. 2014).

To address this knowledge gap, we aim to analyze farmer perceptions of ecosystem services provided by scavenging vertebrates in Spain and to identify the social and ecological factors determining whether scavengers are considered by farmers as providers of benefits or sources of damage. In vertebrate scavenging guilds, two functional groups can be defined: facultative scavengers, i.e., animals that exploit carrion opportunistically but rely upon other food sources in the absence of carrion (e.g., mammalian carnivores, raptors and corvids), and obligate scavengers, i.e., animals that depend totally on carrion (i.e., vultures). We particularly explore the following research questions: What ecosystem services provided by scavenging vertebrates are perceived by farmers? Which scavenging vertebrates are perceived as providers of ecosystem services? To whom are the ecosystem services provided (i.e., farmers)?

MATERIAL AND METHODS

Study areas

The investigation was performed at seven study areas in Spain (Fig. 1): Fuerteventura on the Canary Islands, Sierras de Cazorla Segura y Las Villas Natural Park, the Sierra Morena, the northwest region of Murcia, the Central System, the Pyrenees and the Cantabrian Mountains on peninsular Spain. These areas represent the main traditional and large extensive and semiextensive livestock farming systems in Spanish mountainous areas, which maintain important populations of vertebrate scavengers, both facultative and obligate. Species considered in each study area are shown in Table S1.

Data collection

We conducted 276 face-to-face questionnaires with farmers from 2012 to 2016 (see Fig. 1 for sampling points). We designed a sampling strategy that consisted of three main stages: (i) for each study area, an initial set of extensively managed farms was randomly selected from the Spanish General Register of Livestock Farms; (ii) contact details of farmers in each study area with extensive livestock farms were obtained from the local sanitary authorities; (iii) we met farmers on or near their farms to conduct the survey. Occasionally, we identified additional farmers by using the snowball sampling technique (i.e., we asked farmers to name other farmers in the area), a technique commonly used when conducting social research in biodiversity conservation and ecosystem services (e.g., Pereira et al. 2005; Anadón et al. 2009; Newing 2010; Martín-López et al. 2011; Oteros-Rozas et al. 2013, 2014).

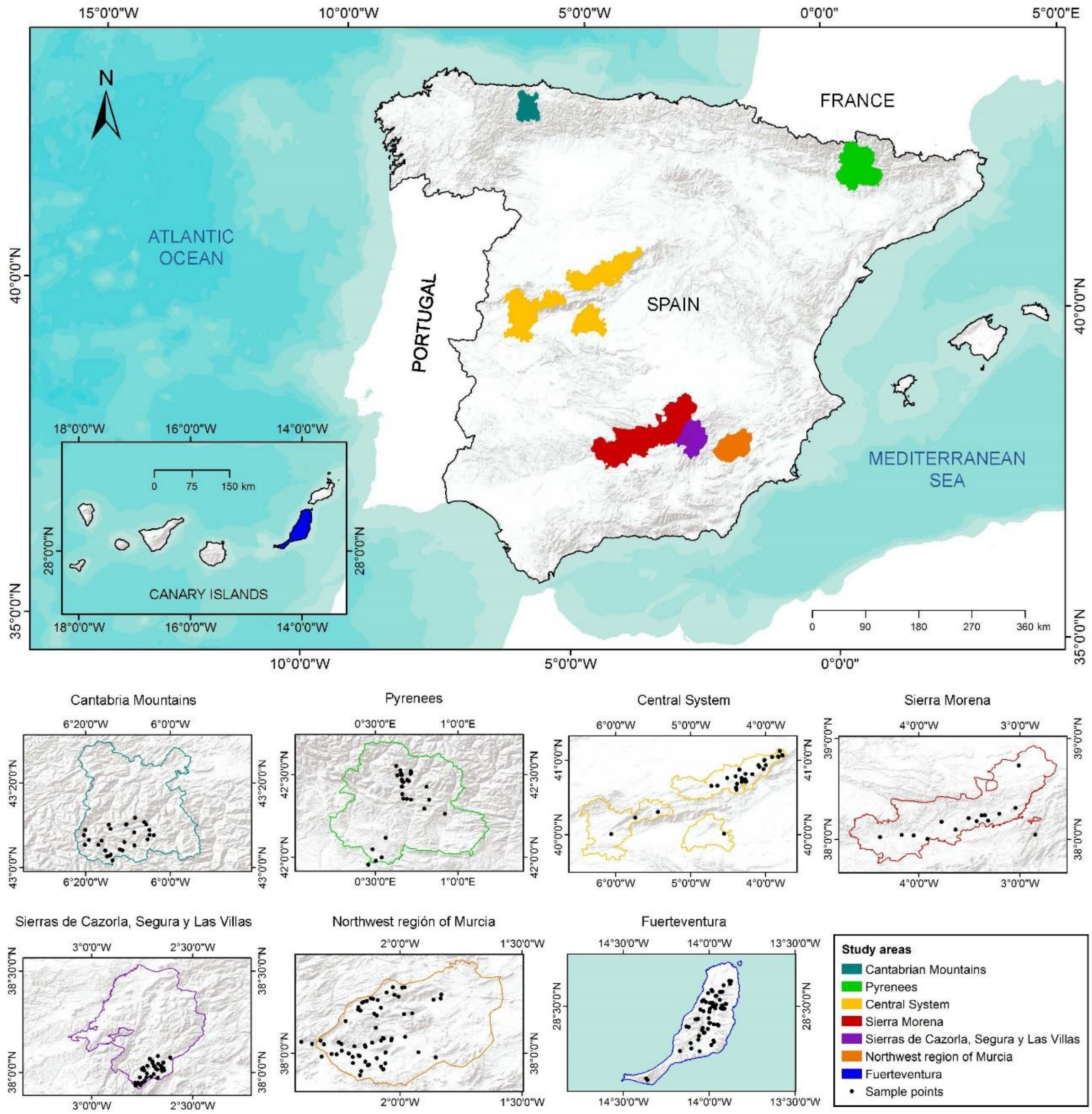

Figure 1. Map of the locations of study areas. Study areas are indicated with colored lines. Sampling points are indicated with black circles. Overall, sample points represent the farms, but occasionally surveys were conducted in other places (e.g., the main square of the village or in the field). Map was generated using ArcGIS 10.1.

The questionnaire was pre-tested on a small sample of farmers in the northwest region of Murcia to improve its readability and clarity. For each study area, we estimated a representative sample size of farmers at a 95% confidence level, with a sampling error ranging 10.6-15.1% depending on the study area (see Appendix 4.1 and Table S2 for additional details). Socio-demographic and farming characteristics were similar in all study areas, allowing analysis of the whole sample (see Table S2 for the total farmer population and sample size in each study area, and Table 1 for the socio-demographic and farming characteristics). In all cases, we followed ethical standards of social surveys by informing respondents that their participation was voluntary and that we would ensure their anonymity.

The questionnaire was structured in three sections: (1) perception of ecosystem services provided by scavengers (*what*), (2) perception of scavengers' capacity to provide different ecosystem services, scavenging services in particular, and the perception of their population trends (*who*), and (3) characteristics of farming and sociodemographic variables (*to whom*). Tables 2 and 3 present the variables used in sections "ecosystem service providers (who)" and "ecosystem service beneficiaries (to whom)," respectively. It is important to note that we are assessing *perceptions*, i.e., not the *reality*. Thus, we can appraise the mindset of farmers and how this can be shaped according to their experience-based knowledge.

Data analyses

To analyze the farmer perceptions about the capacity of scavenging species to provide services, we created two variables: (1) *ecosystem service provider (ESP) index*, i.e., average farmer perceptions of scavengers as providers of ecosystem services for each species using a five-point scale from very harmful (i.e., *ESP index* = 1) to very beneficial (i.e., *ESP index* = 5), and (2) *Scavenging services (%)*, i.e., percentage of farmers that selected each species as a provider of scavenging services (i.e., carcasses consumption) either in the first, second or third ranking of importance. Description of both variables is provided in Table 2.

Non-parametric comparison tests

We used the Kruskal-Wallis test ($\alpha = 0.05$) to identify differences in farmer perceptions of the capacity of scavengers of different taxonomic (i.e., vultures, raptors [excluding vultures], non-raptor birds, and mammals) and the Mann-Whitney U test ($\alpha = 0.05$) to recognize differences between functional groups (i.e., obligate and facultative scavengers) to provide ecosystem services (see Table S1 for additional details).

Table 1. Main socio-demographic and farming characteristics of the farmers for the set of study areas and in each study area. Mean ± SD are shown. Description of the variables are provided in Table 3.

Variable	**Fuerteventura**	**Cazorla**	**Sierra Morena**	**Murcia**	**Central System**	**Pyrenees**	**Cantabrian M.**	**National**
Socio-demographic characteristics								
Average age of farmers	49.3±11.3	47.2±6.9	45.3±7.0	53.4±11.2	56.6±13.7	49.2±11.3	50.4±13.9	51.1±11.8
Gender								
Male (%)	86.4	100	100	98.3	100	84.4	77.5	91.0
Female (%)	13.6	0	0	1.7	0	15.6	22.5	9.0
Farming characteristics								
Number of livestock	525.7±644.5	695.2±348.7	796.8±371.7	696.7±503.3	142.5±100.7	527.1±542.9	88.0±74.7	463.9±510.5
Number of sheep	45.3±105.5	660.0±337.9	751.9±360.0	635.7±527.7	15.2±71.2	470.0±562.2	2.6±7.7	295.2±447.9
Number of goats	466.9±586.3	29.1±55.7	39.9±67.3	60.6±128.5	0.3±1.7	17.2±36.2	18.1±55.6	131.5±345.4
Number of cattle	1.3±6.5	5.8±23.1	4.8±21.8	0.3±2.1	126.3±89.3	39.5±80.4	64.3±66.0	32.5±66.4
*Number of other livestock**	3.1±22.5	0.4±1.2	0.2±0.6	0	0.2±0.8	0.9±4.3	2.9±6.2	2.1±16.7
Selling other products (%)	91.5	48.5	47.6	41.4	0	62.5	0	44.7
Number of problems on farm	2.5±0.9	2.5±1.1	2.5±0.9	2.3±1.1	2.2±0.9	3.3±1.4	2.7±1.6	2.6±1.2
Attacked by scavengers (%)	93.2	84.8	95.2	34.5	24.2	62.5	95.0	66.3
Transhumance (%)	0	63.6	100	0	0	18.8	20.0	13.7
Carcass removal insurance in the past (%)	11.9	54.5	61.9	29.3	63.6	6.3	0	25.5
Carcasses left in field in the past (%)	54.2	3.0	4.8	74.1	24.2	75.0	2.5	42.7
Carcasses currently left in field (%)	55.9	100	100	93.1	63.6	96.9	95.0	82.4
Carcass removal insurance at present (%)	61.0	21.2	19.0	63.8	36.4	96.9	85.0	61.6

*Other livestock include horse, pig, donkey and dromedary.

Table 2. Overview of the variables used in the section 'Ecosystem service providers (Who)'.

Name of variable	Description
Response variables	
ESP index	Average farmer perceptions of scavengers as providers of ecosystem services for each species using a five-point scale from 1 to 5, where 1 is very harmful and 5 is very beneficial. Variable obtained through questionnaires. Question: Of the species you see in your area (see *Sighting index* in Table 3), could you assess how beneficial or harmful these species are to you? Using a five-point scale from 1 to 5, being 1 very harmful and 5 very beneficial
Scavenging services	Percentage of farmers that selected each species as a provider of scavenging services (i.e., carcasses consumption) either in the first, second or third ranking. It ranges from 0 to 100%. Variable obtained through questionnaires. Question: In your opinion, what species do you think are more involved in the elimination of your livestock carcasses? Could you order these species by their importance in the removal of your livestock carcasses?
Explanatory variables	
Perceptions of species' population trend	Average farmer perceptions of population trend for each species using the following values: -1 (decreasing), 0 (stable) and 1 (increasing). Variable obtained through questionnaires. Question: Of the species you see in your area (see *Sighting index* in Table 3), in the past, did you see them more, less or equal as today?
Distribution	Percentage of 10 x 10 km grids covered by each species (only breeding distribution) in the study areas based on the Spanish National Biodiversity Inventory (MAGRAMA 2012)
Richness	Average number of scavenger species per 10 x 10 km grids in the study areas based on the Spanish National Biodiversity Inventory (MAGRAMA 2012)
Functional evenness	The regularity with which species abundances are distributed along the minimum spanning tree which links all the species in the multidimensional functional space (Villéger et al. 2008). It was calculated based on species' traits (Table S3) and abundances (i.e., *distribution*; see Table S4) using the package 'FD' in R version 1.0-12 (Laliberté et al. 2014)
Functional dispersion	The weighted mean distance in multidimensional trait space of individual species to the centroid of all species. Weights are species' relative abundances (Laliberté & Legendre 2010). It was calculated based on species' traits (Table S3) and abundances (i.e., *distribution*; see Table S4) using the package 'FD' in R version 1.0-12 (Laliberté et al. 2014)

Table 3. Overview of the variables obtained from the questionnaires and used in the section 'Ecosystem service beneficiaries (To whom)'.

Name of variable	Description
Response variables	
Knowledge index	Number of species known by farmers relative to the total number of species asked about (see Table S1). Ranged from 0 to 1. Question: Of the species I am showing you in these photos, which ones do you know?
Sighting index	Number of species seen by farmers relative to the total number of species asked about (see Table S1). Ranged from 0 to 1. Question: Of the species I am showing you in these photos, which ones have you ever seen in the area?
Beneficial index	Number of species considered beneficial (i.e., *ESP index* ranged from 4 to 5) by farmers relative to the total of species seen. Ranged from 0 to 1
Harmful index	Number of species considered harmful (i.e., *ESP index* ranged from 1 to 2) by farmers relative to the total of species seen. Ranged from 0 to 1
Scavenging index	Number of species selected as a provider of scavenging services either in the first, second or third ranking by farmers, relative to the total of species seen. Ranged from 0 to 1. For the specific question, see *Scavenging services* in Table 2.
Explanatory variables	
Socio-demographic characteristics	
Age	Farmer's age (in years). Ln (x+1) transformation was applied to avoid heteroskedasticity
Female	When farmer was female. Dummy variable (1-0)
Male	When farmer was male. Dummy variable (1-0)
Farming characteristics	
Number of livestock	Head of livestock per farmer. Ln (x+1) transformation was applied to avoid heteroskedasticity
Selling other products	Other products sold different from livestock (e.g., cheese, milk, etc.). Dummy variable (1-0)
Number of problems on farm	Number of problems associated to the farm' sustainability (e.g., high livestock feed costs, selling products at low prices, etc.) perceived per farmer. Ln (x+1) transformation was applied to avoid heteroskedasticity
Attacked by scavengers	Whether livestock have been or not attacked by scavenger species. Dummy variable (1-0)
Transhumance	Farmer performs transhumance. Dummy variable (1-0)
Carcass removal insurance in the past	Farmer removed livestock carcasses from the farm using an insurance payment in the past. Dummy variable (1-0)
Carcasses left in field in the past	Farmer traditionally abandoned livestock carcasses in the field and the carcasses were removed by scavengers in the past. Dummy variable (1-0)
Carcasses currently left in field	Farmer abandons livestock carcasses in the field and the carcasses are removed by scavengers as current practice. They also might remove the livestock carcasses from the farm using insurance payments as current practice. Dummy variable (1-0)
Carcass removal insurance at present	Farmer removes livestock carcasses from the farm by using insurance payments as current practice. They also might abandon the livestock carcasses in the field as current practice. Dummy variable (1-0)

Regressions

Ordinary least squares regression models were performed to predict the effect of variables representing the abundance of species on farmer perceptions about the services provided by scavengers. *ESP index* and *Scavenging services (%)* were used as response variables in linear regression models. We used two explanatory variables: (i) the *distribution* of species and (ii) the *farmer perceptions of species' population trends*. Whether the species is obligate or facultative scavenger was used as covariate in the regression models.

Simple linear regression was used to estimate the effect of the scavengers' community on farmer perceptions of scavengers as providers of ecosystem services (*ESP index*). We used three diversity metrics (including taxonomic and functional diversity) as explanatory variables: (i) *richness* of scavenger species as taxonomic diversity metric, (ii) *functional evenness* and (iii) *functional dispersion* as functional diversity metrics. We selected these functional diversity metrics because they are little influenced by the species richness, are weighted by relative abundances of species and they do not require more species than traits (Villéger et al. 2008; Laliberté & Legendre 2010). Functional diversity metrics were calculated based on a list of functional traits related to scavenger species (Table 4) by using the package 'FD' in R (Laliberté et al. 2014; R Core Team 2016). Table S3 presents the values of traits for all species and Table S4 the estimated abundance of each species. Description of the variables is provided in Table 2. All data were checked to accomplish the assumptions of normality (Shapiro-Wilk's test), homoscedasticity and absence of outliers (Grubbs' test; Grubbs 1969).

Table 4. List of functional traits for which data were collected on the scavenger species present in each study area. Based on (Luck et al. 2012).

Trait	Description
Social	Foraging in large groups (*social*); foraging in family groups (*group*); foraging alone or in pairs (*solitary*)
Range	Adult home range normally <10 km^2 (*1*); 10-100 km^2 (*2*); 100-1000 km^2 (*3*); >1000 km^2 (*4*)
Scavenger	Depend totally on carrion (*obligate scavenger*); exploit carrion opportunistically (*facultative scavenger*)
Predator	<5% of preyed vertebrates in diet (*non-predator*); >5% of preyed vertebrates in diet (*mesopredator*); predator able to kill other scavengers at carcasses (*top predator*)
Diet	Diet consisting mainly or exclusively in animals (*carnivorous*); diet including both animals and other source of nutrients (*omnivorous*)
Body mass	Average adult (female and male) weight, in kg. Ln (x+1) transformation was applied to avoid heteroskedasticity
Fecundity	Maximum number of offspring per female and year. Ln (x+1) transformation was applied to avoid heteroskedasticity
Longevity	Maximum longevity according to AnAge (2016). Ln (x+1) transformation was applied to avoid heteroskedasticity
Activity	Mostly nocturnal (*nocturnal*); mostly diurnal (*diurnal*); both nocturnal and diurnal (*both*)
Color	Cryptic, uniform color (*plain*); spotted pattern (*spots*); presence of patches of contrasting and/or iridescent colors, black and white normally involved (*contrast*)

Canonical Correspondence Analysis

A canonical correspondence analysis (CCA) was used to determine those farmers and farming characteristics that are associated with the perceptions of scavengers as providers of ecosystem services. We used five variables related to farmer perceptions and knowledge of scavengers: (i) *knowledge index*, i.e., number of species known by farmers relative to the total number of species asked about in the area and showed to farmers in the questionnaires (see Table S1); (ii) *sighting index*, i.e., number of species seen by farmers relative to the total number of species asked about in the area; (iii) *beneficial index*, i.e., number of species considered beneficial by farmers relative to the total of species seen; (iv) *harmful index*, i.e., number of species considered harmful by farmers relative to the total of species seen; and (v) *scavenging index*, i.e., number of species selected as a provider of scavenging services by farmers relative to the total of species seen. Further, we identified which variables that characterized both the farming practice and socio-demographic characteristics of farmers are linearly related with the axes resulted from the ordination of aforementioned five variables. Description of the explanatory variables used is provided in Table 3; whereas percentage, mean and standard deviation are shown in Table 1. The significance of the CCA was tested with a Monte Carlo permutation test by using 500 iterations. XLSTAT software (version 2016.04, Addinsoft) was used to perform all statistical analyses.

RESULTS

Ecosystem services provided (what)

Overall, a higher percentage of farmers perceived scavengers as harmful (54.2%) than beneficial (35.3%; Fig. 2). Among the benefits identified by farmers, scavenging services (i.e., carcasses consumption) were the most often mentioned (86.8%), followed by the benefit people receive from knowing that scavengers exist (i.e., existence value; 10.5%), the benefit associated with biological control (e.g., predation of rodents and lagomorphs by raptors and mammals; 1.6%) and other beneficial ecosystem services (1.1%; Fig. 2a). Among damages, farmers perceived those related to the role of some species as predators (76.6%), as omnivores (16.4%), other harms to livestock besides predation (4.9%) and other damage, such as damage to farm infrastructure (2.0%). The damages related to the role of some scavengers as predators included predation on livestock (37.3%), game species and their hatchlings and eggs (27.5%), and nonspecified species (11.8%). Negative impacts associated with the role of certain scavengers as omnivores included wild boar rooting (8.1%), cropland damage (7.9%), and damage to beehives (0.5%). Other damage to livestock included annoyances to livestock (2.9%) and disease transmission (2.0%; Fig. 2b).

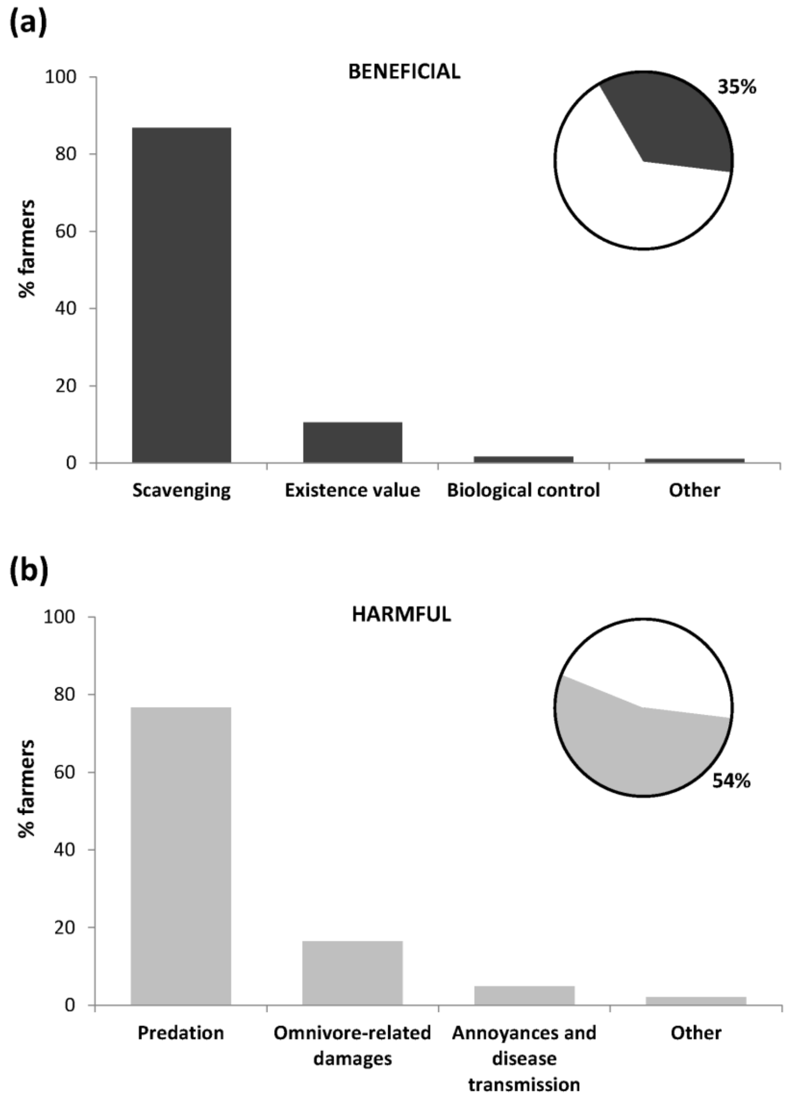

Figure 2. Perception of ecosystem services provided by scavengers. Pie charts show percentage of surveyed farmers that perceived ecosystem services provided by scavengers as beneficial (a) or harmful (b). A total of 10.5% of surveyed farmers considered the role of scavengers as irrelevant. Bar diagrams indicate the percentage of surveyed farmers who considered the ecosystem services as (a) benefits and (b) damages (see main text for added details).

Ecosystem service providers (who)

According to the *ESP index*, farmers perceived vultures as the most beneficial scavengers providing ecosystem services, followed by other raptors, non-raptor birds, and mammals (Kruskal–Wallis test, p = 0.001; Fig. 3a). Additionally, obligate scavengers (i.e., vultures) were significantly perceived as providers of more beneficial ecosystem services than facultative scavengers (Mann–Whitney U test, p = 0.001; Fig. 3b). For the particular case of scavenging services, we also found differences in the farmer perceptions about the different taxonomic groups (Kruskal–Wallis test, p = 0.028; Fig. 3c), with vultures considered the main providers of scavenging services. Accordingly, obligate scavengers were perceived as more important for providing scavenging services than facultative scavengers (Mann–Whitney U test, p = 0.025; Fig. 3d). It is noteworthy that some species weakly perceived as providers of benefits (e.g., low *ESP index* for the Canarian common raven and the gray wolf; Fig. 4a), were highly valued for their provision of scavenging services (i.e., high *Scavenging services [%]*; Fig. 4b).

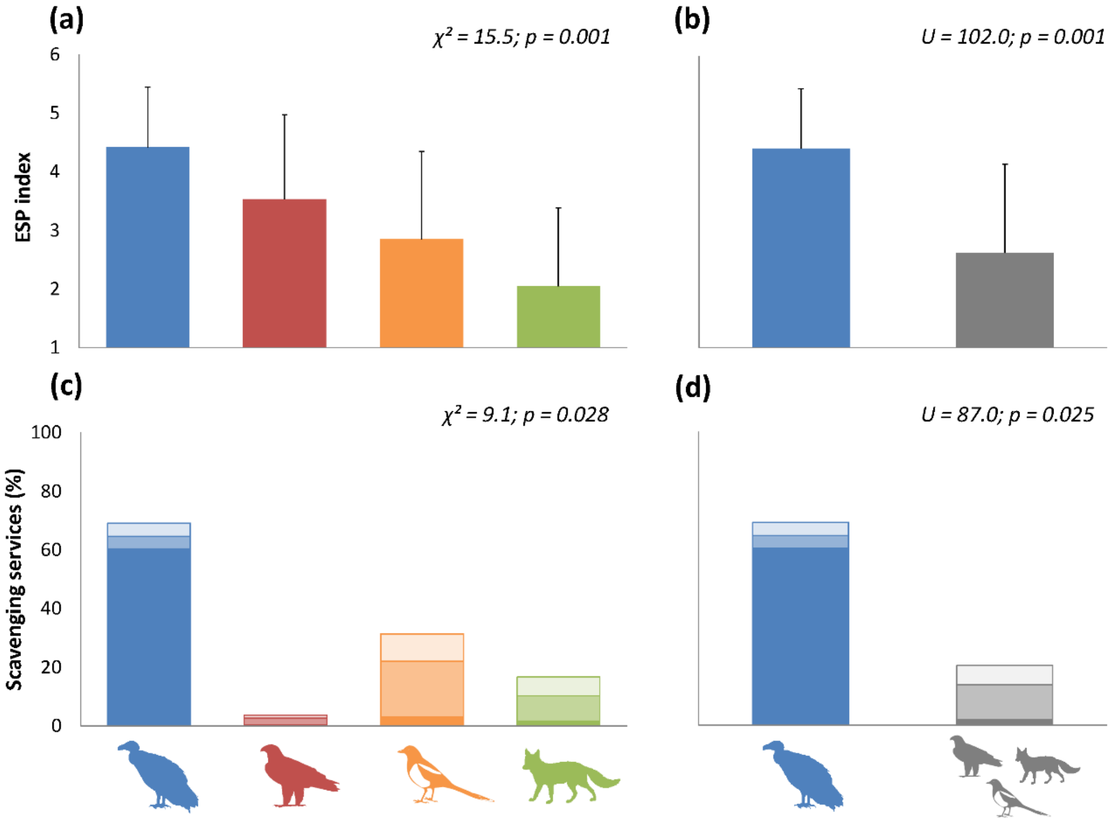

Figure 3. Perception of scavengers' capacity to provide ecosystem services. Top bar diagrams (a-b) show the surveyed farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) by taxonomic groups (a) vultures (blue), raptors (red), non-raptor birds (orange), and mammals (green); and functional groups (b) obligate (blue) and facultative scavengers (gray). Bars and whiskers indicate the mean value of *ESP index* ± SD. Bar diagrams on the bottom (c-d) present the percentage of surveyed farmers that perceived the provision of *scavenging services* provided by the aforementioned taxonomic (c) and functional groups (d). The different grade of colors in c-d show whether these species were ranked first (darkest color), second (middle), or third (lightest) as providers of scavenging services. Differences among taxonomic groups (a and c) were estimated by using the nonparametric Kruskal–Wallis test (α = 0.05). Differences between functional groups (b and d) were calculated through the nonparametric Mann–Whitney U test (α = 0.05). Description of the variables is provided in Table 2. Details regarding the results per species are shown in Fig. 4.

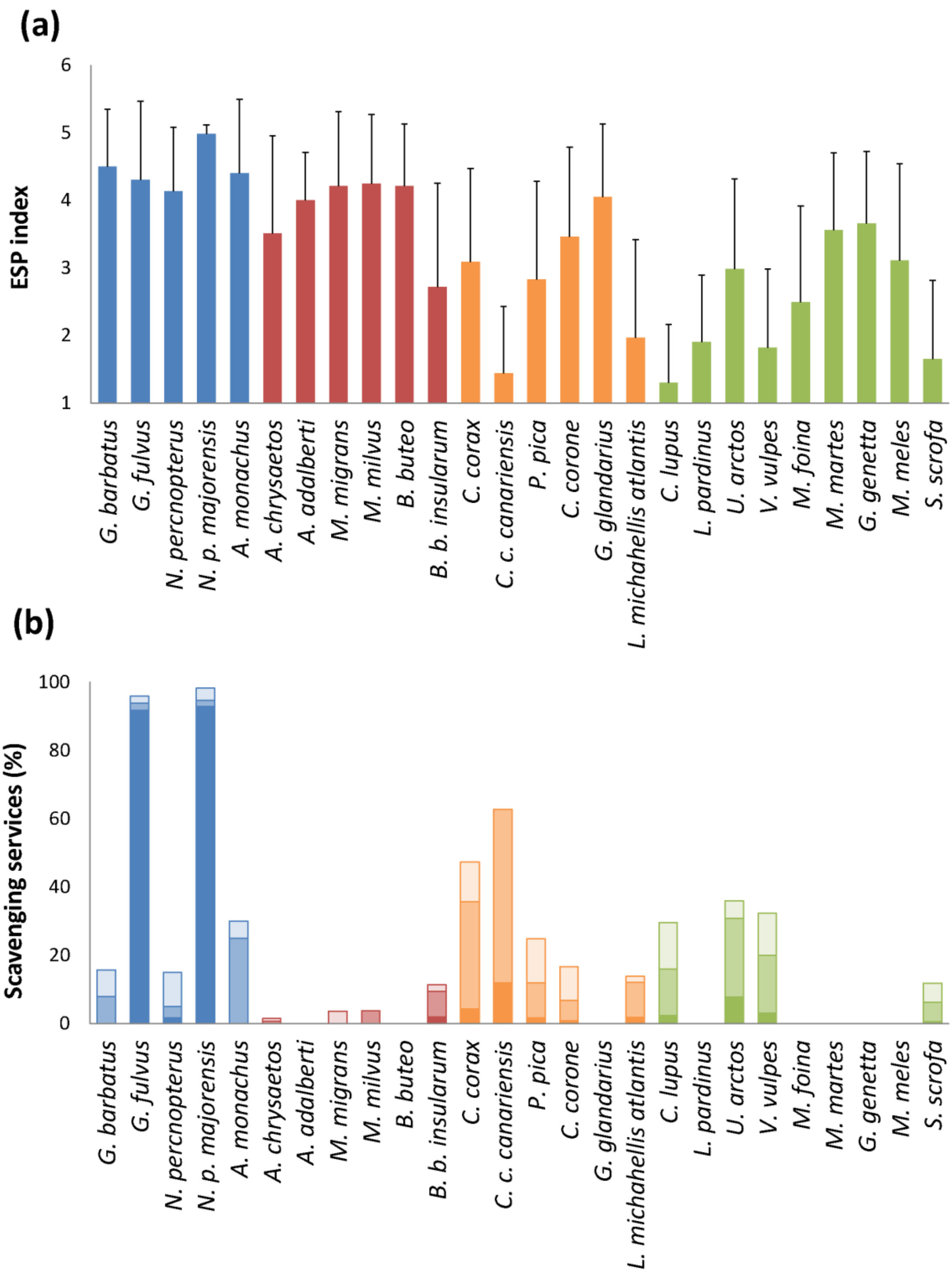

Figure 4. Perception of scavenger species' capacity to provide ecosystem services. Top bar diagram (a) show the farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) by species. The different colors display the taxonomic groups -i.e., vultures (in blue), raptors (red), non-raptor birds (orange) and mammals (green)-. Bars and whiskers indicate the mean value of *ESP index* ± SD. Bar diagram on the bottom (b) present the percentage of farmers that perceived the provision of scavenging services (*Scavenging services [%]*) provided by species. The different grade of colors in (b) show whether these species were ranked first (darkest color), second (middle) or third (lightest) as provider of scavenging services.

Linear regressions of the *ESP index* with variables representing the abundance of scavengers (i.e., *distribution* of species and farmer *perceptions of species' population trends*) suggest that farmers perceived the importance of scavengers in providing beneficial services when species had a more restricted *distribution* (t = -2.56, p = 0.019; Table 5 and Fig. 5a) and their populations were perceived as declining (t = -4.74, p < 0.0001; Table 6 and Fig. 5b). In contrast, farmers perceived that the provision of scavenging services increased with broader distributions of scavengers (t = 2.09, p = 0.049; Table 5 and Fig. 5c). However, farmer *perceptions of species' population trends* did not influence their perceptions of provision of scavenging services (t = 1.26, p = 0.219; Table 6 and Fig. 5d). The four regressions showed that facultative scavengers were perceived by famers as less important in providing ecosystem services (*ESP index*) and scavenging services than vultures (Fig. 5).

Table 5. Standardized coefficients (*t*), *p* values and regression statistics of ordinary least squares (OLS) regression models of the effect of *distribution* of species (measured as the % of 10 x 10 km grids covered by each species) on the farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) and on the percentage of farmers that perceived the provision of scavenging services (*Scavenging services [%]*). The regression lines are provided in Figs. 5a and c. Description of the variables are provided in Table 2. Outliers were identified based on Grubbs' test statistics (α ≤ 0.01) (Grubbs 1969).

	ESP index				**Scavenging services (%)**			
	Full sample		*Without outliers*		*Full sample*		*Without outliers*	
Variables	*t*	*p value*	*t*	*p value*	*t*	*p value*	*t*	*p value*
Constant	9.763	< 0.0001	13.297	< 0.0001	3.775	0.001	3.289	0.004
Distribution	0.067	0.947	-2.558	0.019	1.274	0.215	2.093	0.049
Facultative	-3.018	0.006	-2.337	0.031	-3.374	0.003	-3.652	0.001
OLS statistics								
Adjusted R^2	0.261		0.506		0.273		0.339	
F	5.408	0.012	11.744	< 0.001	5.703	0.010	6.892	0.005
n	26		22		26		24	

Table 6. Standardized coefficients (*t*), *p* values and regression statistics of ordinary least squares (OLS) regression models of the effect of the farmer *perceptions of species' population trends* on the farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) and on the percentage of farmers that perceived the provision of scavenging services (*Scavenging services [%]*). The regression lines are provided in Figs, 5b and d. Description of the variables are provided in Table 2.

	ESP index		**Scavenging services (%)**	
Variables	*t*	*p value*	*t*	*p value*
Constant	15.757	< 0.0001	4.615	< 0.001
Perceptions of population trend	-4.748	< 0.001	1.265	0.219
Facultative	-3.996	0.001	-3.260	0.003
OLS statistics				
Adjusted R^2	0.627		0.273	
F	21.974	< 0.0001	5.686	0.010
n	26		26	

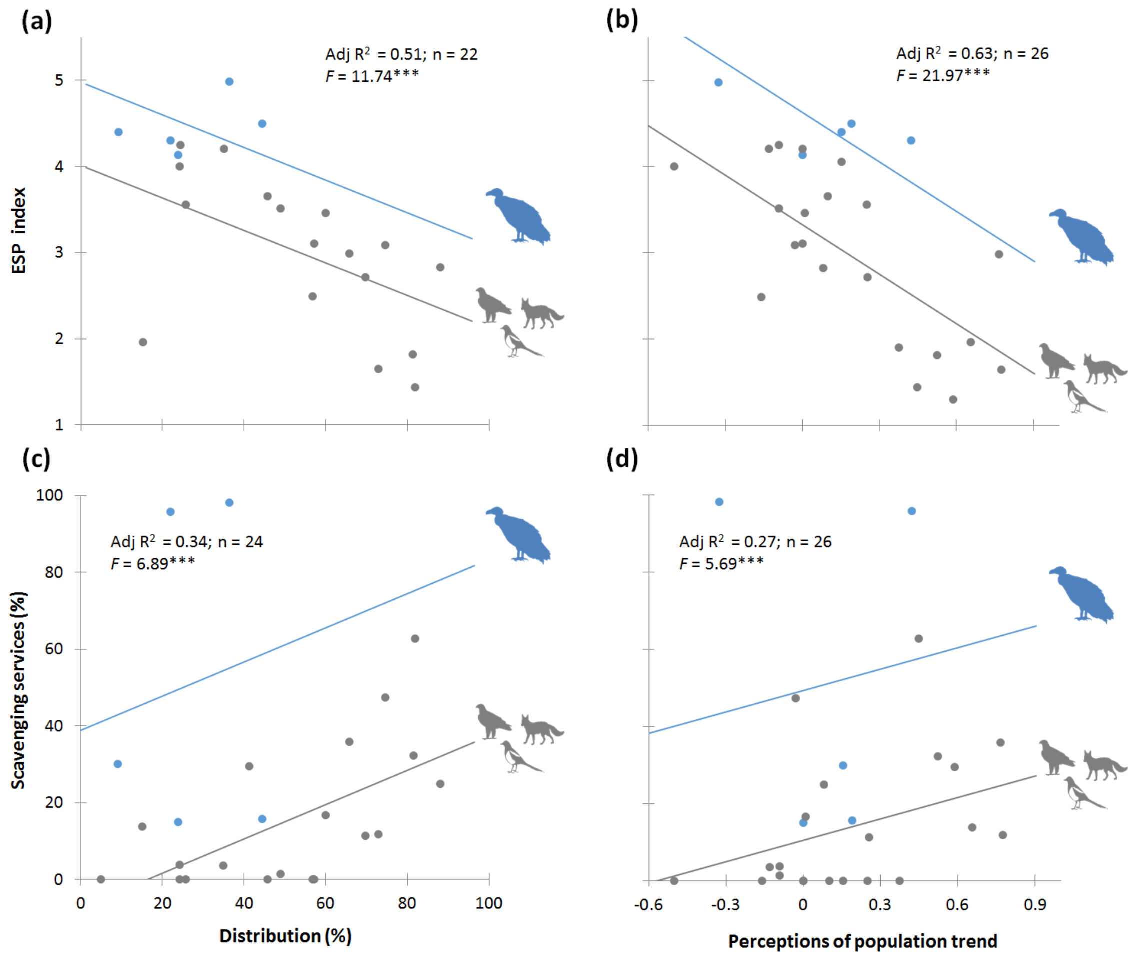

Figure 5. Influence of the abundance of scavengers on the perception of scavengers' capacity to provide ecosystem services. Scatterplots on the top (a-b) indicate the relationship between the surveyed farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) and the *distribution* of species—% of 10 km × 10 km grids covered by each species in each study area (a) and the surveyed farmer *perceptions of species' population trends* (b). Scatterplots on the bottom (c-d) show the association between the percentage of surveyed farmers that perceived the provision of *scavenging services* and the *distribution* of species (c) as well as the surveyed farmer *perceptions of species' population trends* (d). Ordinary least squares regressions are plotted for the different functional groups (i.e., obligate [blue] and facultative scavengers [gray]). Facultative and obligate scavengers were included as covariates. Adjusted R^2, sample size (n), and F-statistic of the entire model are shown. Outliers were removed based on Grubbs' test statistics (α ≤ 0.01). Asterisks indicate significant differences according to $*p \leq 0.10$, $**p \leq 0.05$, $***p \leq 0.01$. Description of the variables is provided in Table 2. Additional information on regression models is shown in Tables 5 and 6.

Furthermore, in the scavenger communities with higher functional diversity, farmers tended to perceive a higher capacity of the scavenger guild to provide multiple ecosystem services (i.e., higher *ESP index*; Fig. 6). In particular, *functional evenness* was positive related to *ESP index* (t = 2.46, p = 0.057; Fig. 6b and Table 7). We did not find any relationship for species *richness* and *functional dispersion* (Fig. 6 and Table 7).

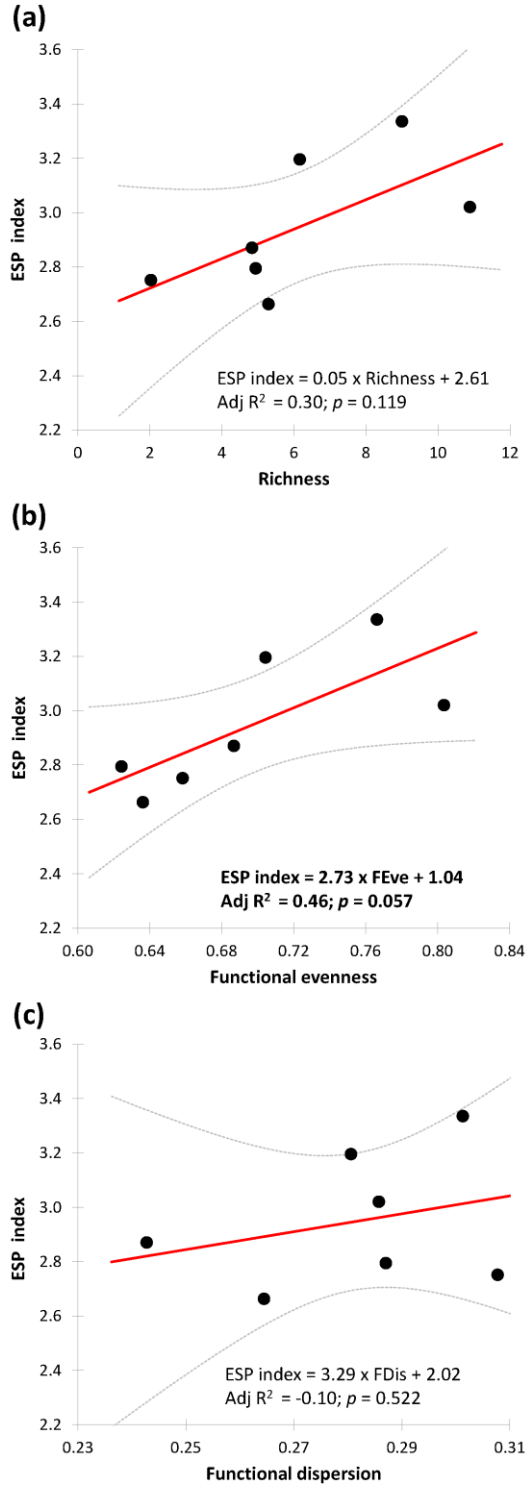

Figure 6. Influence of characteristics of the ecological community on the perception of scavengers' capacity to provide ecosystem services. Relationship between (a) species *richness*, (b) *functional evenness*, and (c) *functional dispersion* and the surveyed farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) across the seven study areas. Solid red lines are fit with simple linear regression models. Dashed gray lines symbolize the 95% confidence interval of regression models. Equation of the model, adjusted R^2 and p values are shown, when results were statistically significant, they are indicated in bold. Description of the variables is provided in Table 2. Additional information on regression models is shown in Table 7.

Table 7. Standardized coefficients (t), p values and regression statistics of simple linear regressions of species *richness* and functional diversity metrics (i.e., *functional evenness* and *functional dispersion*) against the farmer perceptions of scavengers as providers of ecosystem services (*ESP index*). The regression lines are provided in Figs. 6a–c. Full names and description of the variables are provided in Table 2.

Variables	ESP index – Richness *t*	*p value*	ESP index – Functional evenness *t*	*p value*	ESP index – Functional dispersion *t*	*p value*
Constant	13.436	< 0.0001	1.338	0.238	1.499	0.194
Richness	1.879	0.119				
Functional evenness			2.457	0.057		
Functional dispersion					0.688	0.522
OLS statistics						
Adjusted R^2	0.297		0.456		-0.096	
F	3.530	0.119	6.039	0.057	0.473	0.522
n	7		7		7	

Ecosystem services beneficiaries (to whom)

The CCA revealed significant effects of different variables associated with sociodemographic and farming characteristics on farmer perceptions and knowledge of scavengers (Table 8). The first axis of the CCA (46.4% of the variance) captured the farmer perceptions of beneficial services provided by scavengers (i.e., beneficial index). The beneficial index was positively related to the practice of transhumance and male farmers who have broadened the products of their farm beyond livestock production (e.g., milk or cheese production). In contrast, it was negatively related to the problems reported on their farms (e.g., high livestock feed costs or selling products at low prices). The second axis (29.8%) captured a gradient between the farmer knowledge about scavengers (i.e., knowledge and sighting indices, in negative scores) and the perception of these species as providers of scavenging services (i.e., scavenging index, in positive scores). Male farmers who traditionally abandoned livestock carcasses in the field had higher knowledge indices. The perception of the provision of scavenging services was associated with female farmers who have broadened the products of their farm beyond livestock production. The third axis (22.6%) captured the farmer perceptions of harms (i.e., harmful index) provided by scavengers, which was explained by having high livestock numbers, whether there were any attacks on livestock by scavengers, and having carcass removal insurance in the past.

Table 8. Summary statistics and results of CCA showing the influence of sociodemographic and farming characteristics on the perception and knowledge of scavengers as providers of ecosystem services.

	Axis 1	**Axis 2**	**Axis 3**
Indices of social perception			
Knowledge index	0.016	**−0.031**	−0.014
Sighting index	0.027	**−0.044**	−0.034
Beneficial index	**−0.194**	−0.006	0.040
Harmful index	0.079	0.033	**0.113**
Scavenging index	−0.002	**0.153**	−0.059
Socio-demographic characteristics			
Age	0.013	−0.008	−0.006
Female	**0.027**	**0.027**	0.003
Male	**−0.027**	**−0.027**	−0.003
Farming characteristics			
Number of livestock	−0.013	0.005	**0.019**
Selling other products	**−0.026**	**0.029**	−0.009
Number of problems on farm	**0.028**	0.014	0.010
Attacked by scavengers	0.009	−0.016	**0.028**
Transhumance	**−0.036**	−0.017	0.019
Carcass removal insurance in the past	0.015	0.013	**0.027**
Carcasses left in field in the past	**0.031**	**−0.014**	**−0.032**
Carcasses currently left in field	0.002	**−0.022**	0.014
Carcass removal insurance at present	0.012	**−0.020**	**−0.028**
CCA statistics			
Explained variation (%)	46.384	29.761	22.592
Cumulative explained variation (%)	46.384	76.146	98.738

Factor scores of response (i.e., indices of social perception) and explanatory variables (i.e., socio-demographic and farming characteristics) are shown in the first three axes. Bold font indicates the highest squared cosines for the response variables and the significant regression coefficients for the explanatory variables. Eigenvalues for the first three CCA axes were significant (Monte Carlo permutation test with 500 iterations; $p < 0.0001$). Additional information of sociodemographic and farming characteristics in each study area are shown in Table 1. Full names and description of the variables are provided in Table 3.

DISCUSSION

Despite extensive ecosystem services research in the last two decades, knowledge about the interlinkages between biodiversity, ecosystem services, and social perceptions remains unclear (Bennett et al. 2015; Balvanera et al. 2016), especially at the level of species and communities. Although functional diversity strongly impacts the provision of services, particularly for regulating services (Díaz et al. 2006), individual species and guilds can also play important roles (Luck et al. 2003). This work provides empirical evidence of the provision of ecosystem services by vertebrate scavenger species and the associated social perceptions by farmers.

First, results show that farmers perceived scavengers as harmful more often than beneficial (Fig. 2). Benefits were mainly related to the scavengers' capacity to remove carcasses from the field (i.e., scavenging services), whereas harms were associated with their role as predators. Second, our findings indicate that different species within the scavenger guild, or even a single species, can be dually perceived as beneficial and harmful by farmers. This "Dr. Jekyll and Mr. Hyde" hypothesis can be explained by the characteristics of the ecological community (*who*) and the socioeconomic characteristics of farmers (*to whom*).

Regarding ecological characteristics, our analyses demonstrated that three main factors determine the perception of scavengers as beneficial or harmful: (1) taxonomic and functional group (Fig. 3), (2) *distribution* of species and *perceptions of species' population trends* (Figs. 5a and b) at the species level, and (3) *functional evenness* (Fig. 6b) at the community level. First, vultures and non-raptor birds were mainly perceived as beneficial species because of their capacity to provide scavenging services (Fig. 3c), whereas other raptors were appreciated primarily for their importance in biological control and their existence value (Fig. 3a). In fact, the existence value of eagles has been identified as one of the main contributors to the increase in social support for its conservation (Martín-López et al. 2007; Richardson & Loomis 2009; Donázar et al. 2016). Second, we found that perceptions as beneficial beyond scavenging services (i.e., *ESP index*) are determined by the level of rareness of the species, in terms of both distribution range and perceived population trends (Figs. 5a and b). Although the influence of rareness on positive human attitudes toward species has been previously reported (e.g., Bandara & Tisdell 2005), this is the first study reporting a positive relationship between species' rareness (i.e., species' reduced distribution and the perception of declining populations) and the perception of species as providers of multiple ecosystem services. Paradoxically, when we focus on the particular service of scavenging, our results showed the opposite pattern: rare species are perceived as less important (Figs. 5c and d). This result is consistent with the fact that abundant species tend to contribute more to the provision of a particular ecosystem service than scarce species (Díaz et al. 2011; Winfree et al. 2015). Third, our results also revealed that farmers recognize a greater capacity to provide ecosystem services in those communities with higher levels of *functional evenness* (Fig. 6b). In agreement with farmer perceptions, the role of functional diversity is extensively recognized as a key factor for ensuring the provision of ecosystem services (e.g., Díaz et al. 2006, 2011). Moreover, farmer perceptions is in accordance with the findings in the field, since carcass consumption rates are higher in complex scavenging networks with the presence of obligate scavengers (Sebastián-González et al. 2016).

With regard to the socioeconomic characteristics of farmers (*to whom*), past and current experience in the field and farmer knowledge seem to influence farmer perceptions of scavengers as beneficial. Whereas transhumance determines the perception of scavengers as providers of beneficial ecosystem services, the past and current practice of leaving livestock carcasses in the field influence farmer knowledge about scavengers (Table 8). We argue that farmer experience in the field can be associated with local ecological knowledge (i.e., the cumulative body of knowledge, practices, and beliefs regarding the relationships of living things to their environment; Berkes et al. 2000; Díaz et al. 2015), and that this association could come together with farmer perceptions of scavengers as beneficial species. Consistently, previous studies have shown that shepherds who continue to develop transhumance by walking have higher levels of local ecological knowledge than those who are settled (Oteros-Rozas et al. 2013), and than those who have experience with transhumance highly appreciated the importance of ecosystem services (López-Santiago et al. 2014). Our results show that farmer experience-based and local ecological knowledge might relate to their capacity to identify species as providers of ecosystem services. Therefore, farmers with experience-based knowledge become important social actors for fostering the preservation of key species able to provide ecosystem services.

Our findings support the idea that perceptions of the benefits provided by species are crucial for enhancing biodiversity conservation (Bennett 2016). On the one hand, as social support for conservation can rely on the perceived ecosystem services provided by biodiversity (Bennett 2016), the long-term preservation of scavengers might benefit from a wider social recognition of the beneficial services they provide. Our results show that the perception of scavengers as providers of ecosystem services depends on preserving traditional livestock practices, such as transhumance and the abandonment of livestock carcasses in the field. This is consistent with previous studies that have demonstrated the role of traditional farming practices in the conservation of scavengers (Olea & Mateo-Tomás 2009; Mateo-Tomás & Olea 2010). On the other hand, it should be noted that the perception of some facultative scavengers as harmful (Fig. 4) could lead to illegal actions for their control (e.g., poisoning; Mateo-Tomás et al. 2012) which, in turn, may have unintended negative effects on other species in the guild.

We should recognize a potential source of bias in our procedure of farmer selection. We identified some farmers by the snowball sampling method (e.g., Oteros-Rozas et al. 2013), which may over-represent farmers with different perceptions than the randomly selected farmers. However, we feel that our results are robust and can be considered representative of the study population of farmers for several reasons. First, a large proportion of the farmer population was sampled (see Table S2) and only a small fraction of surveyed farmers were selected through the snowball technique. Second, the hypothetical bias caused by non-randomly selected farmers should be small because it is unlikely that the social network of farmers is influenced by their perception about scavengers because this is a minor issue in a farm business. Finally, we sampled a very homogeneous population of farmers, namely those in extensive and semi-extensive livestock systems.

Conclusions

By using social perceptions to understand the ecosystem services provided by scavenging vertebrates, this study contributes to the increasing recognition that omitting social considerations can be perilous for biodiversity conservation (Bennett et al. 2017). This study emphasizes the importance of experience-based and local ecological knowledge for preserving scavengers, the services they provide and the identification of management strategies able to contribute to their conservation. The findings from our work support the idea that the implementation of conservation policies in Europe that favor traditional extensive farming systems and strengthen the link between farmers and nature can foster positive perceptions of scavengers. Furthermore, we found that the dual perception of scavengers as both providers of beneficial ecosystem services and as harmful species should be addressed to preserve globally endangered vultures. Consequently, future conservation programs should target the social and ecological factors that promote the understanding of scavengers as beneficial species

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Chapter 6

General Discussion

PHOTOGRAPH CREDITS: Red fox *Vulpes vulpes* in Sierras de Cazorla, Segura y Las Villas, Jaén, Spain (Manuel J. de la Riva Pérez)

Sheep *Ovis aries* in Prioro, León, Spain (Patricia Mateo Tomás)

Overall, the findings presented in this dissertation have contributed to increase the global scientific understanding of the links between biodiversity, ecosystem services and human welfare and culture through the lens of the social-ecological perspective.

THEORETICAL AND METHODOLOGICAL CONTRIBUTIONS

Evaluating, quantifying and mapping ecosystem services

Mapping and valuing ecosystem services has been suggested as a useful approach for biodiversity conservation and decision making (e.g., Naidoo et al. 2008; Kareiva et al. 2011). The quantification and mapping of ecosystem services provided by scavengers have received little scientific attention until very recently. In fact, research on the importance of ecosystem services provided by scavengers has raised after vulture population declines worldwide, mostly in Asia and Africa (see e.g., Pain et al. 2003; Markandya et al. 2008; Ogada et al. 2012a, 2012b). For instance, in the Indian subcontinent, the total costs in terms of human health attributable to vulture declines over the period 1993 to 2006 were estimated in about $34 billion (Markandya et al. 2008). In addition, Ogada et al. (2012b) showed that, in the absence of vultures, carcass decomposition times were longer, which may facilitate disease transmission among mammalian carnivores.

In Europe, there are some studies that quantify the regulating services provided by vertebrate scavengers. The vast majority of the works on scavenging services are located in Western Europe, home of the largest populations of vultures (Margalida et al. 2010). For instance, in France, some studies have highlighted the carcass recycling service provided by vultures (see Deygout et al. 2009; Dupont et al. 2011, 2012). Particularly, in the Grands Causses region, Dupont et al. (2012) calculated that between 8.4 and 33.1 tons of carbon emissions per year could be saved thanks to the removal of the livestock carcasses by vultures. Furthermore, across Europe, golden jackals (*Canis aureus*) annually remove up to 8,800 tons of domestic animal remains and 4,300 tons of wild ungulate remains, with an estimated economic value of animal carcass removal of €2 million (Ćirović et al. 2016). Recently, the carcass removal by facultative scavengers from cities and towns has been recognized as a key urban ecosystem service in the United Kingdom (Inger et al. 2016).

In Spain, Margalida & Colomer (2012) estimated that, on average, vultures eliminate up to 200 tons of bones and 8,300 tons of meat from the ecosystem annually, which constitute annual savings for farmers and authorities estimated at 28,900–47,400€. Additionally, the findings from this dissertation show that supplanting the natural removal of extensive livestock carcasses by scavengers with artificial removal led to the emission of 77,344 metric tons of CO_2 eq. annually and the annual payments of about $50 million to insurance companies (*Chapter 2*;

Morales-Reyes et al. 2015). Thus, this thesis brings an important contribution by estimating the GHG emissions associated with the transport of carcasses at the large scale to show the environmental and economic costs of supplanting the regulating service provided by scavengers (*Chapter 2*; Morales-Reyes et al. 2015).

Previous studies have suggested the relevance of evaluating, mapping, and quantifying cultural ecosystem services (CES) for ecosystem management and to support decision-making (e.g., Kareiva et al. 2011; Chan et al. 2012; Plieninger et al. 2015). Nevertheless, only a few studies have recognized the CES provided by scavengers, such as spiritual and aesthetic inspiration (Markandya et al. 2008; Ferrari et al. 2009; Morelli et al. 2015) or recreational services and ecotourism (Becker et al. 2005; Markandya et al. 2008). The results presented in this thesis indicate that farmers attribute an existence value to some emblematic or iconic scavenger species (i.e., farmers showed satisfaction derived from knowing that a particular species exists; *Chapter 4*; Morales-Reyes et al. 2017a). However, in Spain, the CES provided by scavengers still remains virtually unexplored.

Integrating social perceptions and local knowledge of ecosystem services provided by scavengers

The incorporation of human dimensions (i.e., perceptions, values, beliefs, attitudes or knowledge) in biodiversity conservation is now widely accepted (e.g., Martín-López et al. 2012; Ban et al. 2013; Martín-López & Montes 2015; Bennett 2016; Bennett et al. 2017a, 2017b). Despite the importance of scavengers in supporting human welfare by providing ecosystem services, as well as the important impacts of human actions on scavenger conservation, social perceptions of scavengers have been poorly studied until very recently (see Pfeiffer et al. 2015; Santangeli et al. 2016; Cailly Arnulphi et al. 2017; Cortés-Avizanda et al. 2018; Henriques et al. 2018). For instance, social perceptions have been used to identify anthropogenic threats to vultures (e.g., Pfeiffer et al. 2015; Santangeli et al. 2016; Henriques et al. 2018), to evaluate pilot perceptions of risk of collision with vultures at airports (Hauptfleisch & Avenant 2016) or to identify the management strategies for vultures that would have social support from stakeholders (Cortés-Avizanda et al. 2018). Most research examining social perceptions of scavengers has mainly focused on a particular vulture or predator species, whereas the present dissertation examined perceptions of ecosystem services provided by scavengers from a multi-species perspective. Thus, we assessed different scavenging taxonomic groups, including vultures, other raptors non-raptor birds and mammals, at different levels (species, population and community; *Chapter 4*; Morales-Reyes et al. 2017a).

Overall, this thesis revealed that the same species and species within the same guild can be dually perceived as beneficial or harmful depending on their consideration as primarily scavengers or predators (“Dr. Jekyll and Mr. Hyde” paradox; *Chapter 4*; Morales-Reyes et al. 2017a). In addition, Cortés-Avizanda et al. (2018) found that perceptions about Egyptian vultures were not homogenous among stakeholders. For instance, hunters and livestock keepers perceived the importance of ecological role of vultures more often than tourists. In accordance to recent articles in Spain and Guinea-Bissau (Cortés-Avizanda et al. 2018; Henriques et al. 2018), this thesis showed that vultures were perceived by farmers as important providers of ecosystem services, mainly carcass removal. Interestingly, a recent article highlighted an increase in positive attitudes towards predators and vultures in recent decades in the United States (George et al. 2016). By contrast, most people in Argentina perceived Andean condors to be detrimental, mainly because they perceived that condors attack livestock (Cailly Arnulphi et al. 2017).

Only some research on social perceptions have identified the social factors and farming characteristics that might affect the social perceptions of scavengers. For instance, education level, along with people relationship with livestock ranching, were the main factors affecting people' perceptions of the Andean condor (Cailly Arnulphi et al. 2017). Stakeholders' knowledge about other endangered species and knowledge about the reasons by which the studied area was declared a protected area had a positive influence on the perceptions of the Egyptian vulture (Cortés-Avizanda et al. 2018). Additionally, results from this dissertation showed that preserving traditional livestock practices, such as transhumance, the abandonment of livestock carcasses in the field and delivering farm beyond livestock production could favor farmer perceptions about scavengers as providers of beneficial ecosystem services. By contrast, the negative farmer perception about scavengers was related to having high livestock numbers, having suffered any attacks on livestock by scavengers, and having had a carcass removal insurance in the past (*Chapter 4*; Morales-Reyes et al. 2017a). This is consistent with a study in Namibia that demonstrated that farmers having large numbers of small livestock (i.e., sheep and goats), large farms and suffering high livestock losses to predators were most likely to use poison to control them (Santangeli et al. 2016).

Our findings evidenced that traditional farming practices associated with experience-based and local ecological knowledge encourage positive perceptions of scavengers as ecosystem services providers (*Chapter 4*; Morales-Reyes et al. 2017a). Consistently, some studies demonstrated that increased stakeholders' ILK about species was positively related with positive perceptions of species and their support for species' conservation (Bandara & Tisdell 2003; Wilson & Tisdell 2005; Cortés-Avizanda et al. 2018). Similarly, our results agree closely with previous studies showing that experienced shepherds who have higher levels of ILK highly appreciated the provision of ecosystem services (Oteros-Rozas et al. 2013a; López-Santiago et al. 2014). Accordingly, there is a growing bulk of literature suggesting the important role of ILK for conservation practices (see Tengö et al. 2017).

Regarding scavengers, only a few recent studies have suggested the incorporation of local communities' ILK on scavengers into the conservation of these species (Haenn et al. 2014; Stara et al. 2016). To our knowledge, this thesis is the first study showing a high consistency between shepherds' ILK and scientific knowledge on the scavenging service provided by vertebrate scavengers (*Chapter 5*; Morales-Reyes et al. 2018a). Therefore, results from this thesis suppose an important starting point by revealing the importance of shepherds in extensive livestock farming systems as ILK holders for scavenger conservation. Nevertheless, sometimes ILK acquired in some contexts may negatively influence people attitudes toward scavengers. For instance, despite the low percentage of people that recognizes that they had actually seen an attack, most people in Argentinian rural areas perceived condors as detrimental animals because they believe that condors actively kill livestock, which have led to illegal actions such as killing or poisoning of condors (Cailly Arnulphi et al. 2017). Likewise, local sayings and beliefs in Greece relate vultures to curses and punishments (Stara et al. 2016).

BIODIVERSITY CONSERVATION AND POLICY IMPLICATIONS

The findings obtained in this thesis have several implications to scavenger and environmental conservation. *Chapter 2* highlighted that contradictions in the application of sanitary and environmental policies in Europe led to negative effects for the natural environment. Our contribution highlighted how the lack of coordination between the sanitary and environmental authorities led to substantial, largely unnecessary GHG emissions (Morales-Reyes et al. 2015). Thus, we show how apparently simple sanitary measures may be ultimately linked to complex ecological processes such as global climate change. Fortunately, thanks to a number of scientific arguments and coordinating efforts by ecologists and policy makers, a new sanitary regulation (EC 142/2011) was approved in Europe to allow farmers to leave extensive livestock carcasses in the field in certain areas that are important for the feeding of necrophagous species (i.e., PAFs). This means the return to more natural and traditional systems in which scavengers freely remove extensive livestock carcasses. The results of this thesis have contributed to the subsequent application in Spain of such a normative. Importantly, our results show that the application of this new European sanitary regulation supposed a significant step in the conservation of the European scavenger populations and an important tool to improve the environmental health through a considerable reduction of GHG emissions (see *Chapter 3*; Morales-Reyes et al. 2017b). The findings from *Chapter 2 and 3* highlight the utility of combining large scale ecological data such as movement data, breeding distribution of scavengers or livestock carcasses availability, and the evaluation of ecosystem services to help political and technical decisions regarding environmental conservation policies.

In a socio-cultural context, findings from this thesis have pointed out that research on stakeholders' perceptions and attitudes towards scavenger species can contribute to their conservation (*Chapter 4*; Morales-Reyes et al. 2017a). In addition, results of *Chapter 5* illustrate that the integration of ILK hold by shepherds in traditional extensive livestock farming systems with scientific knowledge on the ecosystem services provided by vertebrate scavengers may benefit the management and conservation strategies of these species and the ecosystem services they provide (*Chapter 5*; Morales-Reyes et al. 2018a). The findings from *Chapter 4 and 5* revealed that traditional livestock farming practices can benefit scavenger conservation in mainly two ways. First, shepherds performing traditional practices such as transhumance and the abandonment of livestock carcasses in the field displayed positive perceptions of scavengers as providers of ecosystem services (*Chapter 4*; Morales-Reyes et al. 2017a). Second, shepherds' ILK is fundamental for the maintenance of the livestock farming practices, on which the scavengers rely (*Chapter 5*; Morales-Reyes et al. 2018a).

In a review, Mace (2014) identified four main phases of nature conservation. First, before and throughout the 1960s, conservation biology focused on 'Nature for itself', with a special attention on species conservation and the management of protected areas. Second, in the 1970s and 1980s, emerged the 'Nature despite people' conservation paradigm, in which the focus was on human threats to species and habitats, and on management strategies to control them. Third, by the late 1990s, conservation thinking moved to 'Nature for people', in which the provision of ecosystem goods and services became the main driving force. Fourth, in recent years, 'People and Nature' thinking emphasizes a shift towards sustainable and resilient interactions between humans and the natural environment. Nowadays, these shifts in focus of nature conservation have led to multiple framings of conservation in practice. In general, the social-ecological evaluation of the ecosystem services provided by vertebrate scavengers conducted in this thesis shows the great potential for conserving scavengers by highlighting how human benefit from them. Nevertheless, we should recognize the intrinsic value of scavengers, so the ecosystem services concept should be a complementary rather than a substitute tool in biodiversity conservation.

LIMITATIONS AND CAVEATS

In this thesis, we have identified some limitations and caveats that should be taken into account in future research. First, in *Chapter 2* we calculated the GHG emissions associated with carcass collection and transport to intermediate and processing plants. However, GHG emitted during carcass processing and incineration were not included. Additionally, we calculated the distance travelled by trucks from each 10 x 10 km grid to the nearest plant, whilst the real distance covered by tracks could be longer in some cases (e.g., trans-regional movements). Therefore, the estimates correspond only to a part of the livestock carcass treatment process, so the GHG emissions here estimated should be considered as a minimum.

In *Chapter 3*, we calculated the maximum potential biomass available in PAFs and the potential GHG emission savings at the national level. Thus, it is worth taking into account that some regions have not allowed the abandonment of livestock carcasses in their PAFs or have not designed their PAFs, whereas others have never removed carcasses due to the logistic constraints in locating them (i.e., remote areas). Moreover, to improve the evaluation of the benefits of the new European regulation related to PAFs for the conservation of vultures and facultative scavengers, it would be important to consider other sources of food (i.e., wild ungulate carcasses; Mateo-Tomás et al. 2015). In addition, the analyses of the movements performed by GPS-tracked vultures in relation to PAFs could also be improved by including other areas and seasons, as well as more individuals of different age classes and breeding status (see Margalida et al. 2017).

Concerning *Chapter 4*, some potential biases in questionaries' design should be taken into account in the future. For instance, to avoid learning bias (i.e., prior questions can affect the respondent's answer to subsequent questions) it may be necessary to randomize the order of the questions for different respondents. In addition, it would be important to avoid variables with an odd number of categories in the scale. For instance, in this chapter, we used a five-point scale to analyze farmer perceptions of scavenger as providers of ecosystem services (i.e., *ESP index*). This variable, with an odd number of categories (i.e., five), could tend to result in neutral answers (i.e., 3), whereas a variable with an even number of categories, tends to force respondents to take sides. As we mentioned in the chapter, despite we only used the snowball sampling method occasionally, it could have biased the sample of selected farmers (but see discussion in *Chapter 4*). Furthermore, it would be useful to analyze additional social-ecological variables that can be related to the farmer perceptions of scavengers. In addition, further research on perceptions about scavengers of different stakeholders such as hunters and tourists are needed (see Cortés-Avizanda et al. 2018).

Regarding *Chapter 5*, in order to delve deeper into some topics (e.g., how ILK hold by shepherds sometimes can negatively influence their attitudes about scavengers), some direct face-to-face interviews could be done in addition to surveys. Overall, we examined the shepherds' ILK built through observation of scavengers and the shepherds' practical experience gained when leaving livestock carcasses in the field. However, it would have been interesting to look into other sources of knowledge (e.g., the media) and how they might influence shepherds' perception of scavengers. In addition, the consistency between scientific knowledge and ILK on the scavenging service could be assessed more deeply by comparing them at different levels of ecological organization (i.e., the population level).

FUTURE PERSPECTIVES

The recognition and evaluation of the ecological role of scavengers is relatively new. Most of the research on scavengers has focused on studying the functioning of the ecosystem, including movement ecology of vultures (e.g., Dodge et al. 2014; Lambertucci et al. 2014; Margalida et al. 2017; Arrondo et al. 2018), ecology of facultative and obligate scavenging vertebrates (e.g., Selva & Fortuna 2007; Cortes-Avizanda et al. 2014; Inger et al. 2016; Sebastián-González et al. 2016; Mateo-Tomás et al. 2017; Hill et al. 2018) and scavenger conservation measures such as supplementary feeding (see e.g., Moreno-Opo et al. 2015; Cortés-Avizanda et al. 2016). However, the provision of ecosystem services by vertebrate scavengers has received little scientific attention (e.g., Moleón et al. 2014). Next, I identify several key questions that could be addressed in future studies.

First, it would be very important to perform more studies aimed at quantifying and mapping the ecosystem services provided by vertebrates (see *Chapter 2*; Morales-Reyes et al. 2015), particularly CES. Additionally, the incorporation of CES provided by scavengers into decision-making would be desirable.

Second, valuing, quantifying and mapping the potential threats for the provision of regulating and cultural services by scavengers (e.g., poisoning, electric infrastructures) as well as the evaluation of conservation measures of scavengers (see *Chapter 3*; Morales-Reyes et al. 2017b) is an ambitious, though necessary, undertaking.

Third, additional research on indigenous and local knowledge and social perceptions of ecosystem services provided by scavengers would be very useful, since these studies can contribute to the conservation of scavengers (see *Chapters 4 and 5*; Morales-Reyes et al. 2017a, 2018a). For instance, an evaluation of farmer perceptions of scavengers in different livestock farming systems (e.g., traditional extensive vs. intensive systems) or farming practices (e.g., local vs. new peasant farmers) would be interesting to understand its implications for scavenger conservation.

Fourth, despite the wide recognition of the practical usefulness of the ecosystem services framework and its contribution to nature management (MA 2005; Costanza et al. 2017), there is no a complete scientific consensus (see reviews in Lele et al. 2013; Schröter et al. 2014). This thesis has used the ecosystem services framework, but new approaches have been recently proposed to analyze the link between people and nature. The nature's contributions to people (NCP) approach have been suggested by IPBES as an alternative to the term "ecosystem services" (Pascual et al. 2017; Díaz et al. 2018). Thus, the NCP approach could help to improve assessments of ecosystem services provided by vertebrates, especially by paying more attention to social and cultural aspects.

Fifth, important socio-cultural changes are taking place in the European traditional livestock farming systems, leading to the abandonment or the intensification of livestock practices such as transhumance (Olea & Mateo-Tomás 2009; Bernués et al. 2011; Cocca et al. 2012; Oteros-Rozas et al. 2013b; Plieninger & Bieling 2013). Thus, it is necessary further research regarding the sustainability of traditional extensive livestock farming systems (Bernués et al. 2011) and its consequences for the conservation of the scavenger guild (Olea & Mateo-Tomás 2009). For instance, according to the perceptions of farmers in extensive and semi-extensive livestock farming systems in Spain, the sustainability of their farms is greatly affected by market forces (e.g., low prices of selling products and high prices of livestock feed; Oteros-Rozas et al. 2013b; Morales-Reyes et al. 2018b). Moreover, more attention should be paid to the possible loss of ILK associated with the changes in traditional farming practices as well as its consequences on management practices and scavenger conservation.

Sixth, despite scavengers provide key hygienic services through the removal of carcasses, the potential risk of disease transmission *via* scavenging requires further research (Moleón et al. 2017). For instance, some facultative scavengers such as the red fox or the wild boar can act as potential vectors of pathogens affecting livestock, wildlife, and even humans (e.g., tuberculosis; Romero et al. 2008). Thus, additional research on disease ecology and epidemiology could provide useful information to the conservation of threatened species and to the management of domestic and wild animals. Complementarily, an evaluation of the sanitary benefits of scavengers would be highly welcome.

Seventh, livestock-scavenger conflict is an emerging topic in conservation that requires additional research (Avery & Cummings 2004; Margalida et al. 2011, 2014; Pfeiffer et al. 2015; Cailly Arnulphi et al. 2017). Overall, farmers' perception of ecosystem services provided by scavengers is positive (Morales-Reyes et al. 2017a). Nevertheless, the creation of a situation of social alarm about livestock attacks attributed to scavengers and the magnification of the problem by the media can seriously affect their conservation (Margalida et al. 2011), for instance, through intentional poisoning of scavenger species (Mateo-Tomás et al. 2012; Santangeli et al. 2016). In fact, the damages caused by predation, in general, do not seem to be very relevant in terms of the economic sustainability of the farms in relation to other causes perceived by the farmers such as market forces (Morales-Reyes et al. 2018b).

And eighth, it would be necessary to evaluate the ecosystem services provided by scavengers by integrating the role of invertebrate scavengers (Martín-Vega & Baz 2011; Moleón & Sánchez-Zapata 2015; Donázar et al. 2016) and marine and freshwater scavenging communities (Watts et al. 2011; Quaggiotto et al. 2016). Moreover, important efforts are needed to improve our understanding of how differences in scavenging patterns on different carcass types could affect the provision of scavenging services (DeVault et al. 2017; Mateo-Tomás et al. 2017; Moleón et al. 2017).

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Conclusions

PHOTOGRAPH CREDITS: Golden eagle *Aquila chrysaetos* in Sierra Espuña, Murcia, Spain

(Eugenio Martínez Noguera)

CONCLUSIONS

1 The literature review pointed out a scarce but increasing scientific attention on the ecosystem services provided by vertebrate scavengers, whereas the social perceptions and attitudes toward scavengers, as well as the local ecological knowledge on carrion and scavenging, remain virtually unexplored.

2 Replacing the ecosystem service of livestock carcasses removal by vertebrate scavengers through the artificial collection and transport of carcasses to intermediate and processing plants, as mandated by the EU sanitary regulation after the bovine spongiform encephalopathy crisis in 2001, meant not only a scavenger conservation concern but also a novel, substantial and largely unnecessary source of greenhouse gases emissions as well as important economic costs to farmers and regional and national administrations in terms of insurances.

3 The approval of a new European sanitary regulation in 2011 that allowed the establishment of protection areas for the feeding of necrophagous species has led to an important improvement of scavenger conservation, a substantial reduction in greenhouse gases emissions, and significant economic savings to farmers and administrations compared to the previous normative. Nevertheless, these areas should be further improved by taking into account the overall distribution range of additional scavenger species, and the design criteria and management strategies should be more coherent at the supra-regional and supra-national scales.

4 Farmer perceptions in Spanish traditional extensive livestock farming systems are characterized by a "Dr. Jekyll and Mr. Hyde" paradox in which scavenger species can be dually perceived as beneficial or harmful depending on whether they are mainly considered as scavengers or predators respectively. However, farmer perceptions varied to some extent according to several variables related to the ecology of the scavengers and the socio-economic characteristics of farmers.

5 The local knowledge on the scavenging service provided by vertebrate scavengers hold by shepherds in traditional extensive livestock farming systems was highly consistent with scientific data, especially regarding ecological processes taking place at the species level.

6 Overall, the first part of this thesis emphasizes that linking sanitary and environmental policies should be a conservation priority for the European Union, whereas the second part supports the implementation of policies that favor traditional extensive farming systems as well as the integration of local and scientific knowledge into the conservation strategies for vertebrate scavengers.

Conclusiones

PHOTOGRAPH CREDITS: Common buzzards *Buteo buteo insularum* in Fuerteventura, Canary Islands, Spain (Manuel J. de la Riva Pérez)

CONCLUSIONES

1 *La revisión de la literatura reveló una escasa pero creciente atención científica sobre los servicios ecosistémicos proporcionados por los carroñeros vertebrados, mientras que las percepciones y actitudes sociales hacia los carroñeros, así como el conocimiento ecológico local sobre los procesos relacionados con el consumo de carroña, permanecen prácticamente inexplorados.*

2 *La suplantación del servicio ecosistémico de eliminación de cadáveres de ganado por los carroñeros vertebrados a través de la recogida y el transporte artificial de los cadáveres hasta las plantas intermedias y de transformación, tal y como lo obligaban las regulaciones sanitarias de la UE después de la crisis de encefalopatía espongiforme bovina en 2001, supuso no solo un problema de conservación, sino también una nueva fuente, sustancial y en gran medida innecesaria de emisiones de gases de efecto invernadero, así como importantes costes económicos para los ganaderos y las administraciones autonómicas y nacionales en términos de pagos a las compañías de seguros.*

3 *La aprobación de una nueva regulación sanitaria europea en 2011 que permitía el establecimiento de zonas de protección para la alimentación de especies necrófagas ha llevado a una mejora importante en la conservación de los carroñeros, una reducción sustancial de las emisiones de gases de efecto invernadero y ahorros económicos significativos para los ganaderos y las administraciones respecto a la regulación anterior. Sin embargo, estas áreas deberían mejorarse aún más teniendo en cuenta toda el área de distribución de especies carroñeras adicionales, y los criterios de diseño y las estrategias de gestión deberían ser más coherentes a escalas supra-autonómica y supra-nacional.*

4 *Las percepciones de los ganaderos en los sistemas tradicionales de ganadería extensiva en España se caracterizaron por una paradoja del "Dr. Jekyll y Mr. Hyde" ya que las especies carroñeras pueden ser doblemente percibidas como beneficiosas o dañinas dependiendo de si se les considera principalmente como carroñeros o depredadores respectivamente. Sin embargo, las percepciones de los ganaderos variaron en cierta medida según varias variables relacionadas con la ecología de los carroñeros y las características socioeconómicas de los ganaderos.*

5 *El conocimiento local sobre el servicio de consumo de carroña proporcionado por los carroñeros vertebrados que tienen los pastores en los sistemas tradicionales de ganadería extensiva fue altamente consistente con los datos científicos, especialmente con respecto a los procesos ecológicos que tienen lugar a nivel de especie.*

6 *En general, la primera parte de esta tesis enfatiza que vincular las políticas sanitarias y medioambientales debe ser una prioridad de conservación para la Unión Europea, mientras que la segunda parte apoya la implementación de políticas que favorezcan los sistemas ganaderos extensivos tradicionales así como la integración del conocimiento local y científico en las estrategias de conservación de los carroñeros de vertebrados.*

Appendices

PHOTOGRAPH CREDITS: Golden eagle *Aquila chrysaetos* in Sierra Espuña, Murcia, Spain

(Eugenio Martínez Noguera)

Chapter 1

General Introduction

Appendix 1.1. Literature review.

We searched in the Web of Science (WOS) database to find publications related to carrion, including carcasses, corpses and cadavers, and its consumption by scavengers (i.e., scavenging). The search was limited to articles written in English (e.g., we excluded book chapters) for the period 1900-2017 (including any scientific category or discipline). We conducted two literature searches. The first search string combined different terms related to carrion and scavenging (i.e., 'carrion' OR 'carcass' OR 'cadaver' OR 'corpse' OR 'scaveng*' OR 'vulture') and associated ecosystem functions and services (i.e., AND 'ecosystem service' OR 'ecosystem function*'). We searched articles with these terms in the title, abstract and keywords, obtaining a total of 107 articles. Then, we discarded those articles that were unrelated to scavenger species and the process of carrion decomposition (e.g., we did not consider immunology and endocrinology studies dealing with 'scavenger receptors'), obtaining a final set of 83 articles. The second search string included the same terms mentioned above (i.e., 'carrion' OR 'carcass' OR 'cadaver' OR 'corpse' OR 'scaveng*' OR 'vulture'), but they were combined with additional terms related to social perceptions and attitudes toward scavengers and indigenous and local knowledge on carrion and scavenging (i.e., AND 'perception' OR 'perceive' OR 'attitude' OR 'indigenous and local knowledge' OR 'indigenous knowledge' OR 'local knowledge' OR 'traditional knowledge' OR 'traditional environmental knowledge' OR 'traditional ecological knowledge' OR 'ethnoscience' OR 'indigenous science' OR 'folk science'). Again, we focused on articles containing these terms in the title, abstract and keywords, obtaining a total of 1,133 articles. However, after restricting the search to articles focused on scavenger species and the process of carrion consumption, we obtained a final set of 16 articles.

We thoroughly examined the selected articles to record the following information: *year* of publication, *country* of the research, *ecosystem* (terrestrial, marine and freshwater), and *scavenger taxonomic group* (i.e., vultures, other raptors, non-raptor birds, mammals, reptiles, fish and invertebrates) and *functional group* (i.e., obligate and facultative). Additionally, in the first search, we recorded *carcass taxonomic group* (i.e., mammals, birds, amphibians, reptiles, fish and invertebrates), whereas in the second search, we recorded *type of stakeholder* included in the study (e.g., farmers and hunters).

In addition, we used the reviewed articles to create semantic networks of the terms occurring in the title and abstract of the selected articles. We used VOSviewer (http://www.vosviewer.com/), a freeware tool for constructing and visualizing semantic networks based on bibliography. This software offers text mining functionality and clustering functions to analyze co-occurrence networks of important terms extracted from a body of scientific literature (van Eck & Waltman 2010). We constructed two semantic network based on the articles obtained in the two searches: i) the first search (carrion, scavenging and associated ecosystem functions and services; n = 83 articles) and ii) the second search (carrion, scavenging and social perceptions and attitudes toward scavengers and indigenous and local knowledge on carrion and scavenging; n = 16 articles). To build the semantic networks, first, all the terms were extracted from the title and/or abstract of the selected articles. Second, the set of extracted terms were filtered for a minimum of 5 occurrences for the first network and a minimum of 2 occurrences for the second network. Third, the 60% most relevant terms were selected based on a relevance score. Fourth, unrelated terms were excluded (e.g., general terms such as institution names). Fifth, with the final set of selected terms, we used VOSviewer to create the semantic network and to identify thematic clusters based on co-occurrence of these terms. We used the binary counting method in which the occurrence of each term indicates the number of documents in which that term occurs at least once. Moreover, we explored the temporal evolution of the use of each term in the network by calculating the average publication year of the articles in which a term occurs.

Table S1. Terms included in the first semantic network (carrion, scavenging and associated ecosystem functions and services) with their occurrence in articles published between 1900 and 2017.

	Occurrence		Occurrence
Cluster 1 (blue)		***Cluster 2 (orange)***	
biomass	16	richness	19
interaction	13	diversity	18
dynamic	11	forest	18
decomposition	10	community composition	9
ecosystem process	9	dung beetle	9
nutrient	9	ecological process	8
functional group	6	dung	7
marine	6	insect	7
salmon	5	nutrient cycling	6
salmon carcass	5	coleoptera	5
stream	5		
terrestrial ecosystem	5		
Cluster 3 (red)		***Cluster 4 (green)***	
population	20	scavenger	37
predator	15	ecosystem service	24
bird	11	conservation	14
consumption	11	vertebrate	13
vulture	11	management	11
decline	10	vertebrate scavenger	9
food	9	community structure	8
competition	7	increase	8
diet	7	raptor	7
human	6	australia	6
		carcass remomal	6

Table S2. Terms included in the second semantic network (carrion, scavenging and social perceptions and attitudes toward scavengers and indigenous and local knowledge on carrion and scavenging) with their occurrence in articles published between 1900 and 2017.

	Occurrence		Occurrence
Cluster 1 (purple)		***Cluster 2 (red)***	
bird	4	livestock	4
impact	4	depredation	3
scavenger	4	person	3
view	3	bear	2
andean condor	2	conservation effort	2
biodiversity	2	livestock predator	2
carrion	2	positive attitude	2
decline	2	protected area	2
diet	2	sign	2
land	2	tree	2
opinion	2	wolf	2
provision	2		
ungulate	2		
welfare	2		
wildlife manager	2		
Cluster 3 (blue)		***Cluster 4 (orange)***	
africa	3	community	4
landscape	3	population	3
poison	3	local knowledge	2
vulture population	3		
bait	2		
future	2		
high livestock loss	2		
human	2		
livestock farmer	2		
positive perception	2		
vulture conservation	2		
wildlife	2		

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Chapter 4

Farmer perceptions of the ecosystem services provided by scavengers: what, who, and to whom

Appendix 4.1. Calculation of representative sample sizes.

We used Cochran's equation (1977) (Eq. 1), adjusted to finite populations (Bartlett et al. 2001) (Eq. 2), to calculate the size of representative samples in each of the study areas (see Table S2):

$$n_0 = \frac{Z^2pq}{e^2} \qquad \text{(Eq. 1)}$$

where n_0 is the sample size, Z^2 is the abscissa for the normal curve that cuts off an area α at the tails (1 – α equals the desired confidence level, e.g., for a confidence level of 95%, α is 0.05 and the critical value is Z^2= 1.96), *e* is the desired margin of error, *p* is the estimated proportion of an attribute that is present in the population, and q is 1-*p*. Since the *p* value in our population was unknown we used *p* = 0.5, which is conservative and gives the largest sample size.

For finite populations, the sample size (n_0) was adjusted using the following equation:

$$n = \frac{n_0}{1+\frac{(n_0-1)}{N}} \qquad \text{(Eq. 2)}$$

where *n* is the sample size and *N* is the population size.

Cochran's equation (1977) is widely used in socio-ecological studies to calculate survey sample size (e.g., Heitz et al. 2009; Perez et al. 2012; La Rosa & Privitera 2013; Mekasha et al. 2014). To calculate the sample size, we used 95% confidence level, margin of error between 10 and 15%, and *p* value of 0.5. The final margin of error was calculated using the following equation (Eq. 3):

$$e = \sqrt{\frac{N-n}{N-1}} * Z^2 \sqrt{\frac{pq}{n}} \qquad \text{(Eq. 3)}$$

where *e* is the margin of error, *N* is the population size, *n* is the sample size, Z^2 is the abscissa for the normal curve that cuts off an area α at the tails, *p* is the estimated proportion of an attribute that is present in the population, and q is 1-*p*. $\sqrt{\frac{N-n}{N-1}}$ is the correction factor for finite populations.

Table S2 shows the total farmer population (i.e., population size; *N*), total number of surveys (i.e., sample size; *n*) and final margin of error of the survey sample in each study area.

Table S1. Species included in the questionnaires in each study area. Vertebrate scavenger species detected in the monitoring of the consumption of carcasses using cameras traps and/or other scavenger species breeding in each study area were included. See García-Heras et al. 2011, Mateo-Tomás et al. 2015, Sebastián-González et al. 2016 for a more detailed description of the monitoring and the study areas.

Common name	Scientific name	Taxonomic group	Functional group	Fuerteventura	Cazorla	Sierra Morena	Murcia	Central System	Pyrenees	Cantabrian Mountains
Bearded vulture	*Gypaetus barbatus*	vultures	obligate	No	**Yes**	No	No	No	**Yes**	No
Griffon vulture	*Gyps fulvus*	vultures	obligate	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Egyptian vulture	*Neophron percnopterus*	vultures	obligate	No	**Yes**	**Yes**	No	**Yes**	**Yes**	**Yes**
Egyptian vulture*	*N. p. majorensis*	vultures	obligate	**Yes**	No	No	No	No	No	No
Cinereous vulture	*Aegypius monachus*	vultures	obligate	No	**Yes**	**Yes**	No	No	No	**Yes**
Golden eagle	*Aquila chrysaetos*	raptors	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Spanish imperial eagle	*Aquila adalberti*	raptors	facultative	No	No	**Yes**	No	No	No	No
Black kite	*Milvus migrans*	raptors	facultative	No	**Yes**	**Yes**	No	No	**Yes**	No
Red kite	*Milvus milvus*	raptors	facultative	No	**Yes**	**Yes**	No	No	**Yes**	**Yes**
Common buzzard	*Buteo buteo*	raptors	facultative	No	No	No	No	No	No	**Yes**
Common buzzard*	*B. buteo insularum*	raptors	facultative	**Yes**	No	No	No	No	No	No
Common raven	*Corvus corax*	non-raptor birds	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Common raven	*C. corax canariensis*	non-raptor birds	facultative	**Yes**	No	No	No	No	No	No
Common magpie	*Pica pica*	non-raptor birds	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Carrion crow	*Corvus corone*	non-raptor birds	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Eurasian jay	*Garrulus glandarius*	non-raptor birds	facultative	No	No	No	No	No	No	**Yes**
Yellow-legged gull*	*Larus michahellis atlantis*	non-raptor birds	facultative	**Yes**	No	No	No	No	No	No
Gray wolf	*Canis lupus*	mammals	facultative	No	No	**Yes**	No	No	No	**Yes**

Iberian Lynx	*Lynx pardinus*	mammals	facultative	No	No	**Yes**	No	No	No	No
Brown bear	*Ursus arctos*	mammals	facultative	No	No	No	No	No	No	**Yes**
Red fox	*Vulpes vulpes*	mammals	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Stone marten	*Martes foina*	mammals	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**
Pine marten	*Martes martes*	mammals	facultative	No	No	No	No	No	No	**Yes**
Common genet	*Genetta genetta*	mammals	facultative	No	No	No	No	No	No	**Yes**
Eurasian badger	*Meles meles*	mammals	facultative	No	No	No	No	No	No	**Yes**
Wild boar	*Sus scrofa*	mammals	facultative	No	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**	**Yes**

*Canary Islands subspecies.

Table S2. Population size (*N*), sample size (*n*), and margin of error (in %) in each study area. Population size refers to farms with >25 head of sheep or goats, and >10 head of cattle or other livestock.

Study area	***N***	***n***	**Margin of error**
Fuerteventura	287	59	11.4
Cazorla	122	33	14.6
Sierra Morena	30	21	11.9
Murcia	176	58	10.6
Central System	148	33	15.1
Pyrenees	86	32	13.8
Cantabrian Mountains	246	40	14.2
Total	*1,098*	*276*	*5.1*

Table S3. Values of functional traits per species which were used to calculate the functional diversity metrics (i.e., *functional evenness* and *functional dispersion*) in each study area.

	Traits*									
Species	*Social*	*Range*	*scavenger*	*Predator*	*Diet*	*Body mass*	*Fecundity*	*Longevity*	*Activity*	*Color*
Gypaetus barbatus	solitary	4	obligate	non-predator	carnivorous	1.95	1.10	3.71	diurnal	contrast
Gyps fulvus	social	4	obligate	non-predator	carnivorous	2.25	0.69	3.71	diurnal	plain
Neophron percnopterus	solitary	4	obligate	non-predator	carnivorous	1.10	1.10	3.64	diurnal	contrast
Aegypius monachus	group	4	obligate	non-predator	carnivorous	2.38	0.69	3.69	diurnal	contrast
Aquila chrysaetos	solitary	2	facultative	top predator	carnivorous	1.61	1.39	3.89	diurnal	plain
Aquila adalberti	solitary	2	facultative	top predator	carnivorous	1.39	1.61	3.81	diurnal	plain
Milvus migrans	group	1	facultative	mesopredator	carnivorous	0.56	1.61	3.22	diurnal	plain
Milvus milvus	group	1	facultative	mesopredator	carnivorous	0.69	1.61	3.66	diurnal	plain
Buteo buteo	solitary	1	facultative	mesopredator	carnivorous	0.55	1.79	3.37	diurnal	plain
Corvus corax	group	1	facultative	mesopredator	omnivorous	1.10	2.20	4.25	diurnal	contrast
Pica pica	group	1	facultative	mesopredator	omnivorous	0.22	2.30	3.09	diurnal	contrast
Corvus corone	group	1	facultative	mesopredator	omnivorous	0.47	2.08	3.00	diurnal	contrast
Garrulus glandarius	solitary	1	facultative	mesopredator	omnivorous	0.17	2.08	2.89	diurnal	contrast
Larus michahellis atlantis	group	3	facultative	mesopredator	omnivorous	0.77	1.39	3.00	diurnal	contrast
Canis lupus	group	3	facultative	top predator	carnivorous	3.43	2.40	3.04	nocturnal	plain
Lynx pardinus	solitary	2	facultative	top predator	carnivorous	2.48	1.61	3.18	nocturnal	spots
Ursus arctos	solitary	3	facultative	top predator	omnivorous	4.94	0.92	3.71	both	plain
Vulpes vulpes	solitary	2	facultative	mesopredator	omnivorous	1.95	2.56	3.09	both	plain
Martes foina	solitary	2	facultative	mesopredator	omnivorous	0.79	2.20	2.94	nocturnal	plain
Martes martes	solitary	2	facultative	mesopredator	omnivorous	1.06	2.20	2.94	nocturnal	plain
Genetta genetta	solitary	1	facultative	mesopredator	omnivorous	1.06	1.61	3.14	nocturnal	spots
Meles meles	solitary	2	facultative	mesopredator	omnivorous	2.12	1.79	2.94	nocturnal	contrast
Sus scrofa	group	2	facultative	mesopredator	omnivorous	3.99	2.30	3.33	nocturnal	plain

*Sources for species trait values: (del Hoyo et al. 1994, 1996, 2009; Wilson & Mittermeier 2009, 2011).

Table S4. *Distribution* of species (i.e., percentage of 10 x 10 km grids covered) and total number of grids (*n*) in each study area. Description of the variable is provided in Table 2.

Species	Fuerteventura	Cazorla	Sierra Morena	Murcia	Central System	Pyrenees	Cantabrian Mountains
Gypaetus barbatus	-	NA	-	-	-	44.44	-
Gyps fulvus	-	32.43	15.83	5.41	16.48	46.03	34.29
Neophron percnopterus	-	21.62	4.17	-	21.02	55.56	51.43
N. p. majorensis	36.36	-	-	-	-	-	-
Aegypius monachus	-	NA	9.17	-	-	-	NA
Aquila chrysaetos	-	64.86	45.00	54.05	41.48	68.25	42.86
Aquila adalberti	-	-	24.17	-	-	-	-
Milvus migrans	-	8.11	36.67	-	-	47.62	-
Milvus milvus	-	8.11	10.00	-	-	73.02	2.86
Buteo buteo	-	-	-	-	-	-	100
B. buteo insularum	69.70	-	-	-	-	-	-
Corvus corax	-	97.30	50.00	51.35	81.25	96.83	85.71
C. corax canariensis	81.82	-	-	-	-	-	-
Pica pica	-	83.78	77.50	89.19	95.45	85.71	94.29
Corvus corone	-	78.38	23.33	64.86	58.52	98.41	100
Garrulus glandarius	-	-	-	-	-	-	100
Larus michahellis atlantis	15.15	-	-	-	-	-	-
Canis lupus	-	-	33.33	-	-	-	68.57
Lynx pardinus	-	-	5.00	-	-	-	-
Ursus arctos	-	-	-	-	-	-	65.71
Vulpes vulpes	-	83.78	70.00	72.97	83.52	95.24	91.43

Martes foina	-	62.16	36.67	70.27	59.66	90.48	31.43
Martes martes	-	-	-	-	-	-	25.71
Genetta genetta	-	-	-	-	-	-	45.71
Meles meles	-	-	-	-	-	-	57.14
Sus scrofa	-	75.68	53.33	75.68	72.16	98.41	91.43
n	33	37	120	37	176	63	35

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Chapter 5

Shepherds' local knowledge and scientific data on the scavenging ecosystem service: insights for conservation

Appendix 5.1. Calculation of the biomass consumed (%) by each vertebrate scavenger species in each study area (see Mateo-Tomás et al. 2017 for further details).

First, for each study area (i.e., Cantabrian Mountains and Baetic Mountains), we estimated the carrion consumed by each vertebrate species scavenging at a carcass as:

$$Carrion\ consumed_i = \sum_{j=1}^{days} n_{ij} * DFI_i \quad \text{eq. (1)}$$

where n_{ij} is the abundance of species *i* recorded scavenging at a carcass (see above) on day *j*. This value was multiplied by the daily food intake of the species *i* (i.e., *DFIi*) as resulting from the following equation (Crocker et al. 2002):

$$Daily\ Food\ Intake\ (DFI) = \frac{Daily\ Energy\ Expenditure\ (kJ)}{Food\ Energy\ \left(\frac{kJ}{g}\right) * (1 - Moisture) * Assimilation\ Efficiency} \quad \text{eq. (2)}$$

Daily Energy Expenditure has a strong relationship with body weight:

$$Log\ (Daily\ Energy\ Expenditure) = Log\ a + b * (log\ Body\ weight) \quad \text{eq. (3)}$$

Log *a* and *b* are parameters separately obtained from Hudson et al. (2013). Mean body weights for the recorded scavengers were obtained from official databases (i.e., PanTHERIA, HBW Alive; Jones et al. 2009; del Hoyo et al. 2015). Energy and moisture content for mammal carrion were 22.6 kJ/g and 68.8% respectively (Crocker et al. 2002). Here, we assumed that each individual scavenger arriving at a carcass consumed the daily food intake.

Second, we estimated the percentage of biomass consumed per species *i* at each carcass *c* as:

$$Biomass\ consumed_i(\%) = \frac{Carrion\ consumed_{ci} * 100}{\sum_{i=1}^{N}(Carrion\ consumed_{ci})} \quad \text{eq. (4)}$$

Finally, we calculated the average biomass consumed (%) by each species at all the carcasses within each study area (i.e., the variable *biomass consumed SK*; see Table 3).

Table S1. Species included in the questionnaires in each study area. Vertebrate scavenger species detected in the monitoring of the consumption of carcasses using camera traps and/or other scavenger species breeding in each study area were included.

Scientific name	Common name	Cantabrian Mountains	Baetic Mountains
Birds			
Aegypius monachus	Cinereous vulture	**Yes**	**Yes**
Gypaetus barbatus	Bearded vulture	No	**Yes**
Gyps fulvus	Griffon vulture	**Yes**	**Yes**
Neophron percnopterus	Egyptian vulture	**Yes**	**Yes**
Aquila chrysaetos	Golden eagle	**Yes**	**Yes**
Buteo buteo	Common buzzard	**Yes**	No
Milvus migrans	Black kite	No	**Yes**
Milvus milvus	Red kite	**Yes**	**Yes**
Corvus corax	Common raven	**Yes**	**Yes**
Corvus corone	Carrion crow	**Yes**	**Yes**
Garrulus glandarius	Eurasian jay	**Yes**	No
Pica pica	Common magpie	**Yes**	**Yes**
Mammals			
Ursus arctos	Brown bear	**Yes**	No
Canis lupus	Gray wolf	**Yes**	No
Vulpes vulpes	Red fox	**Yes**	**Yes**
Genetta genetta	Common genet	**Yes**	No
*Martes foina**	Stone marten	**Yes**	**Yes**
*Martes martes**	Pine marten	**Yes**	No
Meles meles	Eurasian badger	**Yes**	No
Sus scrofa	Wild boar	**Yes**	**Yes**

* In Cantabrian Mountains, we considered stone marten (*Martes foina*) and pine marten (*M. martes*) together as *Martes spp.* because specific identification was not possible from the pictures at night (n = 1 carcass).

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Zebensui Morales Reyes **PhD Thesis**