LETTER

Farmer Perceptions of the Ecosystem Services Provided by Scavengers: What, Who, and to Whom

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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.

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; Bennet et al. 2016). One of the reasons for mainstreaming the social dimensions (i.e., perceptions, values, beliefs, or attitudes) in biodiversity conservation (Bennet et al. 2016; 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 (*Ursus arctos*) and gray wolves (*Canis lupus*; 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)?

Methods

Study areas

The investigation was performed at seven study areas in Spain (Figure 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 Figure 1 for sampling points, and Appendices S1-S3 and Tables S2 and S3 for additional details). 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 S4 and S5 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.

First, we used nonparametric comparison tests to identify differences in farmer perceptions of the capacity of
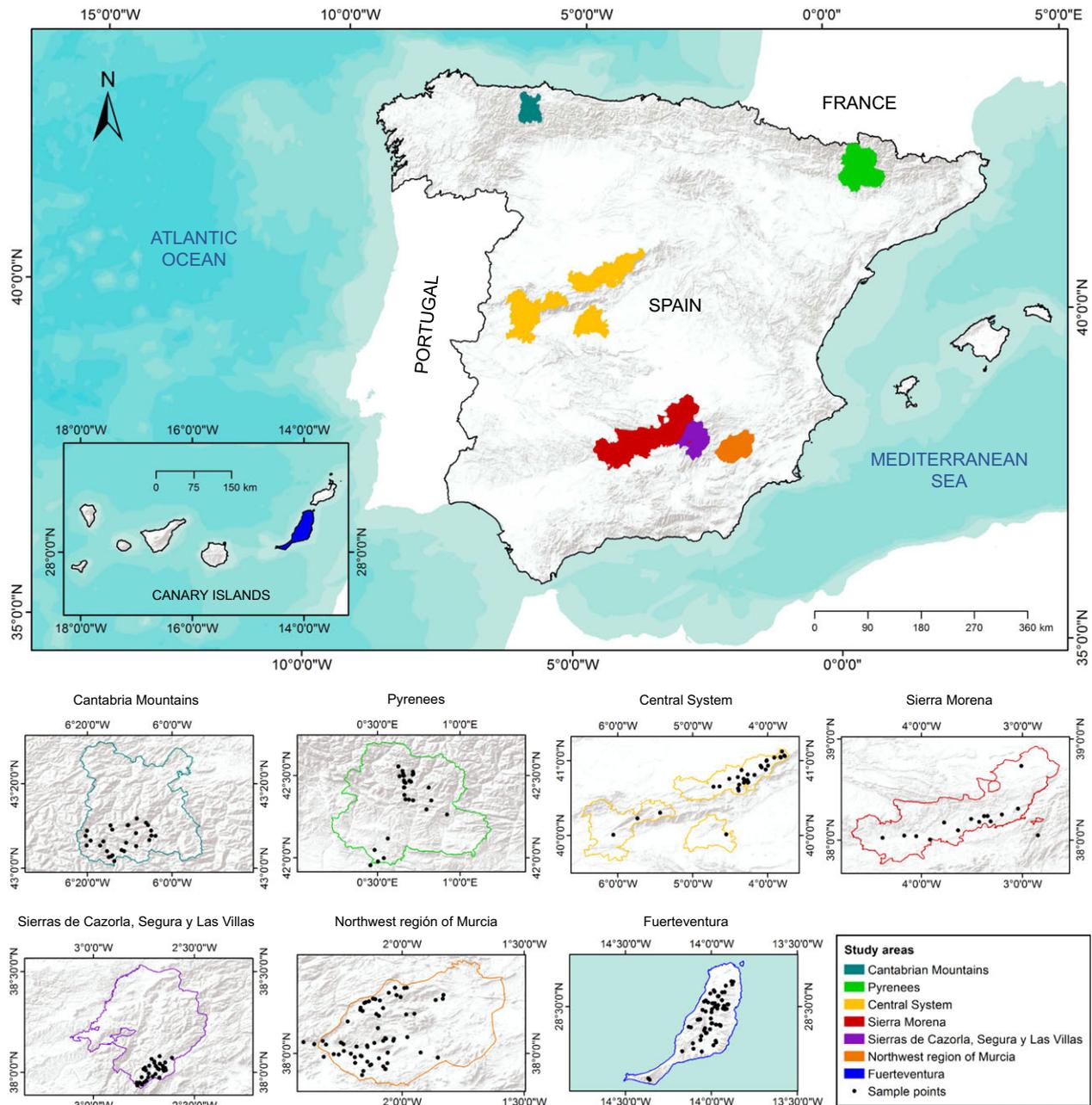
Figure 1 Map of the locations of study areas. Study areas are indicated with colored lines. Sampling points are indicated with black circles. Overall, sample points represent the farms, but occasionally surveys were conducted in other places (e.g., the main square of the village or in the field). Map was generated using ArcGIS 10.1.

scavengers of different taxonomic (i.e., vultures, raptors [excluding vultures], nonraptors birds, and mammals) and functional groups (i.e., obligate and facultative scavengers) to provide ecosystem services (see Table S1 for additional details). Second, ordinary least squares regression models were performed to predict the effect of variables representing the abundance of species (i.e., *distribution* of species and farmer *perceptions of species' pop-*ulation trends) on farmer perceptions about the services provided by scavengers. Simple linear regression was used to estimate the effect of the scavengers' community (i.e., *richness* of species, *functional evenness*, and *functional dispersion*) on farmer perceptions. Third, 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

A

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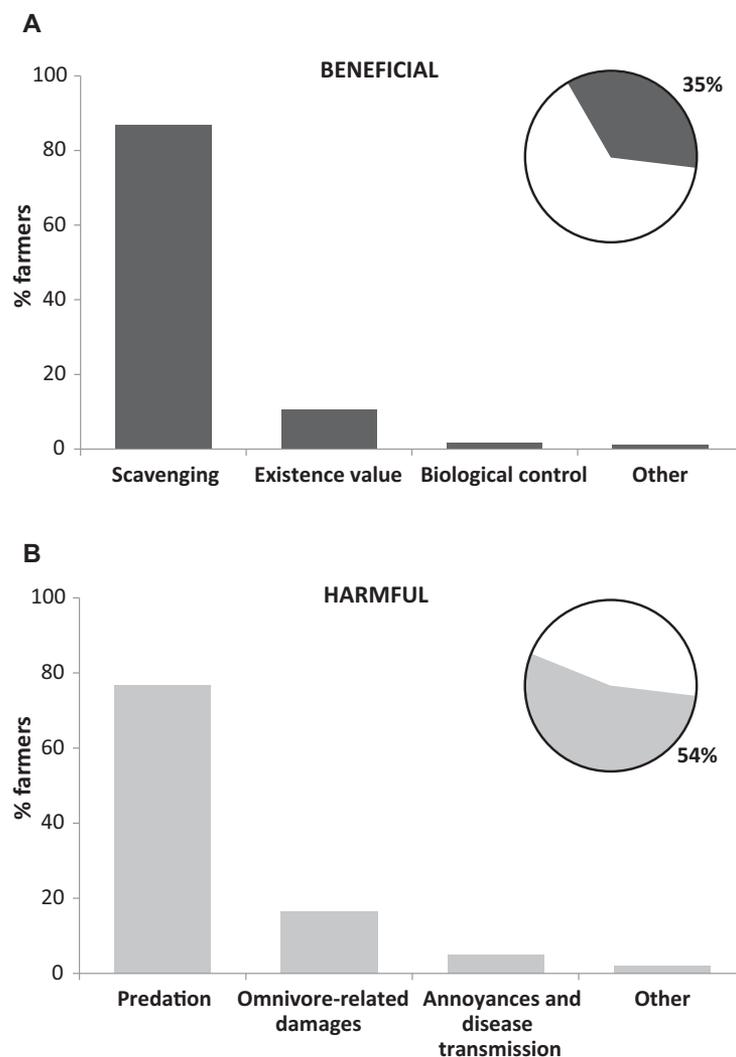
Figure 2 Perception of ecosystem services provided by scavengers. Pie charts show percentage of surveyed farmers that perceived ecosystem services provided by scavengers as beneficial (A) or harmful (B). A total of 10.5% of surveyed farmers considered the role of scavengers as irrelevant. Bar diagrams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

ecosystem services. Full details of statistical analyses are provided in Appendix S4.

Results

Ecosystem services provided (what)

Overall, a higher percentage of farmers perceived scavengers as harmful (54.2%) than beneficial (35.3%; Figure 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%; Figure 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 (*Sus scrofa*) 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%; Figure 2B).
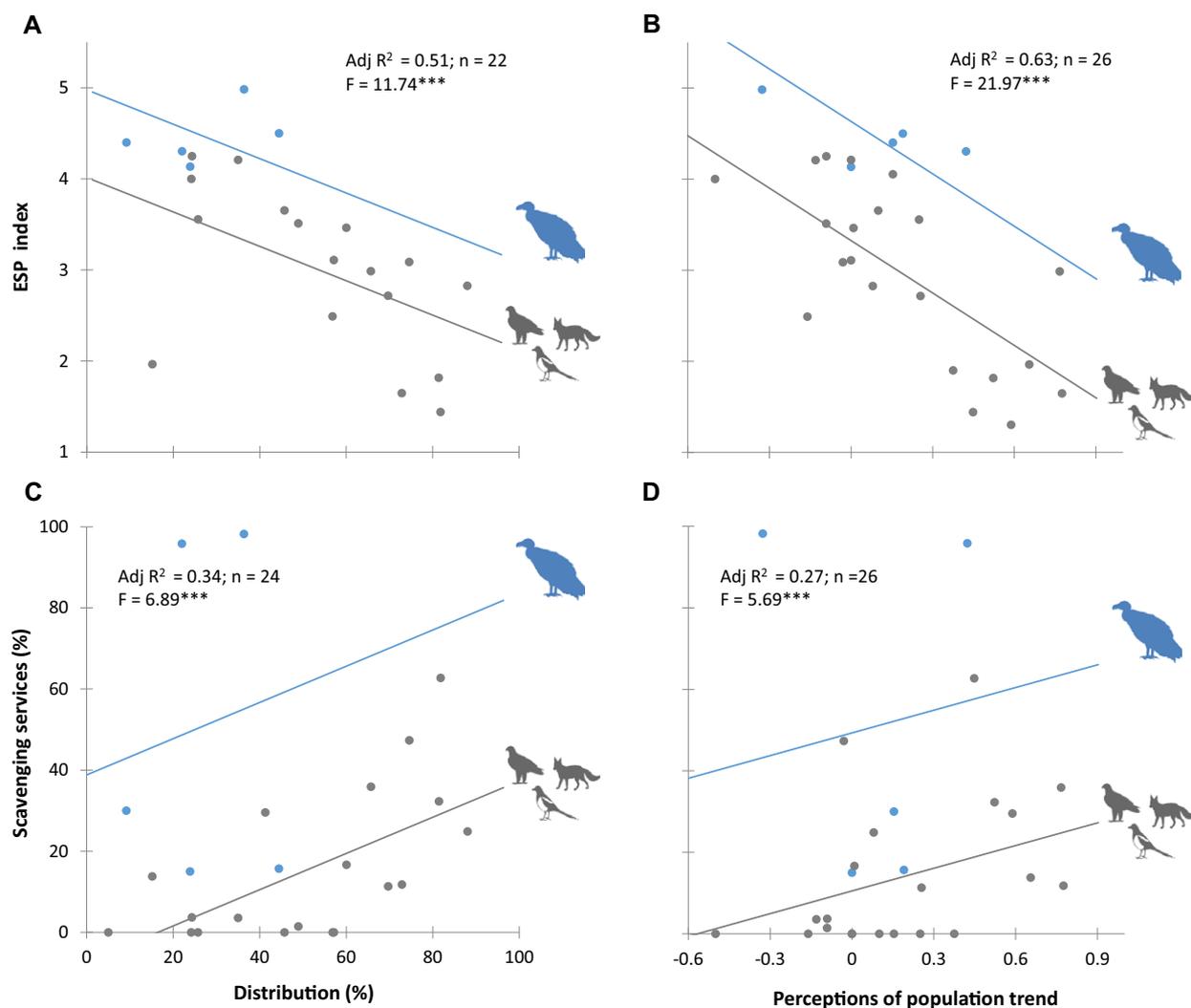
Ecosystem service providers (who)

According to the *ESP index*, farmers perceived vultures as the most beneficial scavengers providing ecosystem services, followed by other raptors, nonraptor birds, and mammals (Kruskal–Wallis test, $P = 0.001$; Figure 3A).
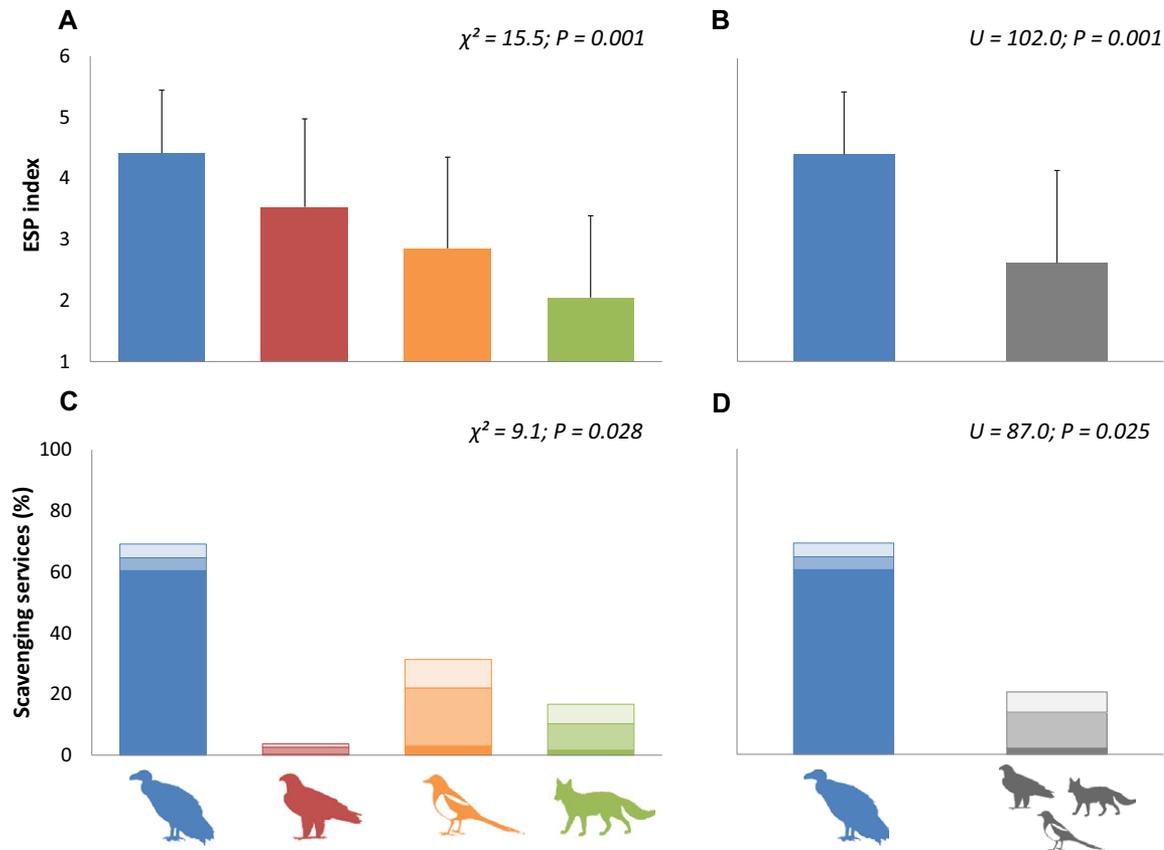
Figure 3 Perception of scavengers' capacity to provide ecosystem services. Top bar diagrams (A-B) show the surveyed farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) by taxonomic groups (A) vultures (blue), raptors (red), nonraptor birds (orange), and mammals (green); 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 ($\alpha = 0.05$). Differences between functional groups (B and D) were calculated through the nonparametric Mann–Whitney U test ($\alpha = 0.05$). Description of the variables is provided in Table S4. Details regarding the results per species are shown in Figure S1A and B.

Additionally, obligate scavengers (i.e., vultures) were significantly perceived as providers of more beneficial ecosystem services than facultative scavengers (Mann–Whitney U test, $P = 0.001$; Figure 3B). For the particular case of *scavenging services*, we also found differences in the farmer perceptions about the different taxonomic groups (Kruskal–Wallis test, $P = 0.028$; Figure 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, $P = 0.025$; Figure 3D). It is noteworthy that some species weakly perceived as providers of benefits (e.g., low *ESP index* for *Corvus corax canariensis* and *Canis lupus*; Figure S1A), were highly valued for their provision of scavenging services (i.e., high *Scavenging services [%]*; Figure S1B).

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* ($t = -2.56$, $P = 0.019$; Figure 4A and Table S6) and their populations were perceived as declining ($t = -4.74$, $P < 0.0001$; Figure 4B and Table S7). In contrast, farmers perceived that the provision of scavenging services increased with broader distributions of scavengers ($t = 2.09$, $P = 0.049$; Figure 4C and Table S6). However, farmer *perceptions of species' population trends* did not influence their perceptions of provision of scavenging services ($t = 1.26$, $P = 0.219$; Figure 4D and Table S7). The four regressions showed that facultative scavengers were perceived by famers as less important in
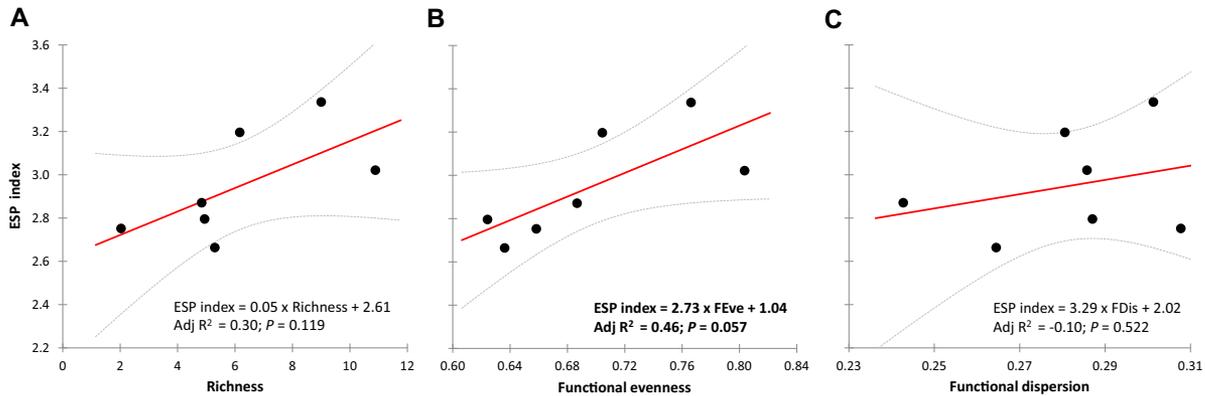
Figure 4 Influence of the abundance of scavengers on the perception of scavengers' capacity to provide ecosystem services. Scatterplots on the top (A-B) indicate the relationship between the surveyed farmer perceptions of scavengers as providers of ecosystem services (*ESP index*) and the *distribution* 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 ($\alpha \leq 0.01$). 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 S4. Additional information on regression models is shown in Tables S6 and S7.

providing ecosystem services (*ESP index*) and scavenging services than vultures (Figure 4).

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*; Figure 5). In particular, *functional evenness* was positive related to *ESP index* ($t = 2.46$, $P = 0.057$; Figure 5B and Table S8). We did not find any relationship for species *richness* and *functional dispersion* (Figure 5 and Table S8).

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 1). 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

Figure 5 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 S4. Additional information on regression models is shown in Table S8.

Table 1 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
Sociodemographic 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., sociodemographic 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 S3. Full names and description of the variables are provided in Table S5.

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.

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 (Figure 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 (Figure 3), (2) *distribution* of species and *perceptions of species' population trends* (Figure 4A and B) at the species level, and (3) *functional evenness* (Figure 5B) at the community level. First, vultures and nonraptor birds were mainly perceived as beneficial species because of their capacity to provide scavenging services (Figure 3C), whereas other raptors were appreciated primarily for their importance in biological control and their existence value (Figure 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 (Figure 4A 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 (Figure 4C 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* (Figure 5B). 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 1). 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 (Figure S1) 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.

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.* 2016). 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.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1. Details on data collection.

Appendix S2. Calculation of representative sample sizes.

Appendix S3. Potential biases associated with the data collection process.

Appendix S4. Detailed description of the statistical analyses.

Table S1. Species included in the questionnaires in each study area.

Table S2. Population size, sample size, and margin of error in each study area.

Table S3. Main sociodemographic and farming characteristics of the farmers for the set of study areas and in each study area.

Table S4. Overview of the variables used in the section "ecosystem service providers (who)".

Table S5. Overview of the variables obtained from the questionnaires and used in the section "ecosystem service beneficiaries (to whom)".

Table S6. Standardized coefficients, *P* values, and regression statistics of ordinary least squares regression models of the effect of distribution of species on the farmer perceptions of scavengers as providers of ecosystem services and on the percentage of farmers that perceived the provision of scavenging services.

Table S7. Standardized coefficients, *P* values, and regression statistics of ordinary least squares regression models of the effect of the farmer perceptions of species' population trends on the farmer perceptions of scavengers as providers of ecosystem services and on the percentage of farmers that perceived the provision of scavenging services.

Table S8. Standardized coefficients, *P* values, and regression statistics of simple linear regressions of species richness and functional diversity metrics against the farmer perceptions of scavengers as providers of ecosystem services.

Table S9. List of functional traits for which data were collected on the scavenger species present in each study area.

Table S10. Values of functional traits per species which were used to calculate the functional diversity metrics in each study area.

Table S11. Distribution of species and total number of grids in each study area.

Figure S1. Perception of scavenger species' capacity to provide ecosystem services.

References

Ament, J.M., Moore, C.A., Herbst, M. & Cumming, G.S. (2017). Cultural ecosystem services in protected areas: understanding bundles, trade-offs and synergies. *Conserv. Lett.*, **10**, 439-449. https://doi.org/10.1111/conl.12283

Balvanera, P., Quijas, S., Martín-López, B. *et al.* (2016). The links between biodiversity and ecosystem services. Pages 45-61 in M. Potschin, R. Haines-Young, R. Fish, R.K. Turner, editors. *Routledge Handbook of Ecosystem Services*. Routledge, London and New York.

Ban, N.C., Mills, M., Tam, J. *et al.* (2013). A social-ecological approach to conservation planning: embedding social considerations. *Front. Ecol. Environ.*, **11**, 194-202.

Bandara, R. & Tisdell, C. (2005). Changing abundance of elephants and willingness to pay for their conservation. *J. Environ. Manage.*, **76**, 47-59.

Bennett, N.J. (2016). Use of perceptions to improve conservation and environmental management. *Conserv. Biol.*, **30**, 1-5.

Bennett, E.M., Cramer, W., Begossi, A. *et al.* (2015). Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability. *Curr. Opin. Environ. Sustain.*, **14**, 76-85.

Bennett, N.J., Roth, R., Klain, S.C. *et al.* (2016). Mainstreaming the social sciences in conservation. *Conserv. Biol.*, **31**, 56-66.

Berkes, F., Colding, J. & Folke, C. (2000). Rediscovery of traditional ecological knowledge as adaptive management. *Ecol. Appl*, **10**, 1251-1262.

Cáceres, D.M., Tapella, E., Quétier, F. & Díaz, S. (2015). The social value of biodiversity and ecosystem services from the perspectives of different social actors. *Ecol. Soc.*, **20**, 62. https://doi.org/10.5751/ES-07297-200162.

Cardinale, B.J., Duffy, J.E., Gonzalez, A. *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, **486**, 59-67.

Chapron, G., Kaczensky, P., Linnell, J.D.C. *et al.* (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, **346**, 1517-1519.

Díaz, S., Fargione, J., Chapin III, F.S. & Tilman, D. (2006). Biodiversity loss threatens human well-being. *PLoS Biol*, **4**, e277.

Díaz, S., Quétier, F., Cáceres, D.M. *et al.* (2011). Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. *Proc. Natl. Acad. Sci. USA*, **108**, 895-902.

Díaz, S., Demissew, S., Carabias, J. *et al.* (2015). The IPBES conceptual framework—connecting nature and people. *Curr. Opin. Environ. Sustain.*, **14**, 1-16.

Donázar, J.A., Cortés-Avizanda, A., Fargallo, J. *et al.* (2016). Roles of raptors in a changing world: from flagships to providers of key ecosystem services. *Ardeola*, **63**, 181-234.

Gangoso, L., Agudo, R., Anadón, J.D. *et al.* (2013). Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. *Conserv. Lett.*, **6**, 172-179.

García-Llorente, M., Martín-López, B., Díaz, S. & Montes, C. (2011). Can ecosystem properties be fully translated into service values? An economic valuation of aquatic plant services. *Ecol. Appl.*, **21**, 3083-3103.

Lescureux, N. & Linnell, J.D.C. (2010). Knowledge and perceptions of Macedonian hunters and herders: the influence of species specific ecology of bears, wolves, and lynx. *Hum. Ecol.*, **38**, 389-399.

López-Santiago, C.A., Oteros-Rozas, E., Martín-López, B., Plieninger, T., Martín, E.G. & González, J.A. (2014). Using visual stimuli to explore the social perceptions of ecosystem services in cultural landscapes: the case of transhumance in Mediterranean Spain. *Ecol. Soc.*, **19**, 27. https://doi.org/10.5751/ES-06401-190227.

Luck, G.W., Daily, G.C. & Ehrlich, P.R. (2003). Population diversity and ecosystem services. *Trends Ecol. Evol.*, **18**, 331-336.

MA (Millennium Ecosystem Assessment). (2005). *Ecosystems and human well-being: biodiversity synthesis*. World Resources Institute, Washington, DC.

Margalida, A., Donázar, J.A., Carrete, M. & Sánchez-Zapata, J.A. (2010). Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *J. Appl. Ecol.*, **47**, 931-935.

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

Martín-López, B. & Montes, C. (2015). Restoring the human capacity for conserving biodiversity: a social–ecological approach. *Sustain. Sci.*, **10**, 699-706.

Martín-López, B., Montes, C. & Benayas, J. (2007). The non-economic motives behind the willingness to pay for biodiversity conservation. *Biol. Conserv.*, **139**, 67-82.

Martín-López, B., Iniesta-Arandia, I., García-Llorente, M. *et al.* (2012). Uncovering ecosystem services bundles through social preferences. *PLoS One*, **7**, e38970.

Mascia, M.B., Brosius, J.P., Dobson, T.A. *et al.* (2003). Conservation and the social sciences. *Conserv. Biol.*, **17**, 649-650.

Mateo-Tomás, P. & Olea, P.P. (2010). Diagnosing the causes of territory abandonment by the endangered Egyptian vulture *Neophron percnopterus*: the importance of traditional pastoralism and regional conservation. *Oryx*, **44**, 424-433.

Mateo-Tomás, P., Olea, P.P., Sánchez-Barbudo, I.S. & Mateo, R. (2012). Alleviating human-wildlife conflicts: identifying the causes and mapping the risk of illegal poisoning of wild fauna. *J. Appl. Ecol.*, **49**, 376-385.

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.

Morales-Reyes, Z., Pérez-García, J.M., Moleón, M. *et al.* (2015). Supplanting ecosystem services provided by scavengers raises greenhouse gas emissions. *Sci. Rep.*, **5**, 7811. https://doi.org/10.1038/srep07811.

Ogada, D.L., Keesing, F. & Virani, M.Z. (2012). Dropping dead: causes and consequences of vulture population declines worldwide. *Ann. N. Y. Acad. Sci.*, **1249**, 57-71.

Olea, P.P. & Mateo-Tomás, P. (2009). The role of traditional farming practices in ecosystem conservation: the case of

transhumance and vultures. *Biol. Conserv.*, **142**, 1844-1853.

Oteros-Rozas, E., Ontillera-Sánchez, R., Sanosa, P., Gómez-Baggethun, E., Reyes-García, V. & González, J.A. (2013). Traditional ecological knowledge among transhumant pastoralists in Mediterranean Spain. *Ecol. Soc.*, **18**, 33. https://doi.org/10.5751/ES-05597-180333.

Pooley, S., Barua, M., Beinart, W. *et al.* (2017). An interdisciplinary review of current and future approaches to improving human–predator relations. *Conserv. Biol.*, **31**, 513-523.

Richardson, L. & Loomis, J. (2009). The total economic value of threatened, endangered and rare species: an updated meta-analysis. *Ecol. Econ.*, **68**, 1535-1548.

Saunders, M.E. & Luck, G.W. (2016). Limitations of the ecosystem services versus disservices dichotomy. *Conserv. Biol.*, **30**, 1363-1365.

Sebastián-González, E., Moleón, M., Gibert, J.P. *et al.* (2016). Nested species-rich networks of scavenging vertebrates support high levels of interspecific competition. *Ecology*, **97**, 95-105.

Wilson, E.E. & Wolkovich, E.M. (2011). Scavenging: how carnivores and carrion structure communities. *Trends Ecol. Evol.*, **26**, 129-135.

Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.*, **18**, 626-635.