




Viewpoint

Top-down limitation of mesopredators by avian top predators: a call for research on cascading effects at the community and ecosystem scale

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The global human footprint currently impacts all ecosystems, from the upper atmosphere to the deep sea (Steffen *et al.* 2015). Direct human exploitation combined with other indirect impacts such as habitat loss and alteration, pollution or the introduction of invasive species commonly affect keystone species worldwide, driving potentially complex interaction chains that remain mostly unexplored (Worm & Paine 2016), although they have critical consequences. For instance, in many temperate systems, humans have dramatically altered predator assemblages, in three different ways. First, from the 18th century, accelerated large-scale land-use change, prey loss and, most importantly, extensive persecution campaigns have led to the extinction of almost all top predator species from important parts of their former distribution range, particularly from lowland farmland areas (Linnell *et al.* 2001). Secondly, mesopredator communities have also been profoundly modified. On the one hand, they may have increased in areas thanks to top predator eradication and subsequent mesopredator release (Pasanen-Mortensen *et al.* 2017). On the other hand, mammalian mesopredators have been heavily persecuted since the 19th century in Western Europe and USA, mainly as a management tool to increase small game hunting bags or protect poultry. Institutionalized predator persecution has probably

caused large-scale mesopredator declines in abundance, although few empirical data are available (Reynolds & Tapper 1996). Finally, a new variable to this equation is the increasing predation pressure exerted by feral domestic predators on small vertebrate populations in all human-transformed systems (Loss *et al.* 2013), in particular feral cats *Felis catus* but also feral dogs *Canis lupus familiaris*, which may have an overlooked impact on biodiversity (Doherty *et al.* 2017). Feral domestic predators may further interact with the functional role of mesopredators through interspecific antagonistic interactions (Krauze-Gryz *et al.* 2012). What are the consequences of all these changes in terms of food-web structure and ecosystem processes? Did these modified trophic interactions cascade to lower trophic levels, i.e. herbivore abundance and behaviour and thus to vegetation composition and structure? Indeed, in many temperate systems, predator assemblages have been so dramatically altered that it is no longer possible to quantify trophic network changes and past signatures will be difficult to find (but see Sallan *et al.* 2011, Svenning *et al.* 2016, Van Valkenburgh *et al.* 2016).

In anthropized landscapes, however, recent shifts in wildlife population trends and the consequent restructuring of predator communities offer the unique opportunity for researchers to take advantage of these landscape-scale natural experiments, perhaps providing a way to answer these questions. Indeed, starting in the second half of last century, a triple simultaneous change has affected the predator community. First, generalist mesopredators have bounced back as a result of lower hunting pressure and adaptation to anthropogenic resources in modified landscapes (Bino *et al.* 2010), sometimes at the expense of the vulnerable specialist mesopredators (Lindström *et al.* 1995, Henden *et al.* 2010, Elmhagen *et al.* 2015). In parallel, several top predators, including large carnivorous mammals and avian top predators, have recolonized previously deserted areas (Fasce *et al.* 2011, Chapron *et al.* 2014, Graciá *et al.* 2015). In quite a few cases, recolonization has been assisted by reinforcement or reintroduction programmes (Dalbeck & Heg 2006, Evans *et al.* 2009, Morandini *et al.* 2017). Despite strong scientific interest, empirical or theoretical approaches aimed at understanding potential trophic cascades triggered by the recovery of avian top predators have been extremely rare (but see Harvey *et al.* 2012). By considering natural or assisted recolonization of avian top predators as natural experiments, we have a unique opportunity to better understand their role in ecosystem structure and functioning.

Secondly, humans have extensively impacted ecosystem functioning, possibly changing mechanisms of bottom-up regulation by increasing the productivity of systems used by herbivores. This has resulted from increased agricultural nitrogen subsidies and by planting nutrient-rich crops (Vitousek *et al.* 1997). Therefore, we

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argue here that human agricultural practices may have oversimplified ecosystem dynamics, shifting from top-down effects of predators to bottom-up effects of plant biomass availability on upper trophic levels, highlighting a possibly hidden and overlooked effect of human influence on ecosystem functioning (Kuijper *et al.* 2016).

Finally, there is now some evidence that climate change may also affect predator–prey relationships in various ways (reviewed by Bretagnolle & Gillis 2010). Further research is urgently needed to understand how ecological networks respond to changes in predator community composition, particularly in anthropogenic systems undergoing rapid environmental changes. In the particular case of top avian predators, we argue here that we need experimental evidence as well as long-term empirical data on their role in food webs. Worm and Paine (2016) have suggested that food webs provide a useful conceptual platform on which ecological consequences of such global environmental changes can be mapped, knowledge gaps identified and predictions generated. Among the most significant patterns already identified, the disruption of trophic cascades by changing animal and plant communities in human-transformed ecosystems critically needs further research to predict the robustness or fragility of ecosystem states (Montoya *et al.* 2006). We first provide some theoretical background, then detail from our point of view the four most important research areas in this field.

THEORETICAL BACKGROUND

Top-down processes in terrestrial food webs

Superpredation

In terrestrial ecosystems, trophic cascade theory predicts that top predators structure ecosystems by regulating sympatric carnivorous and herbivorous populations via interactions such as predation or the generation of fear (Beschta & Ripple 2009). It is well known that the decline in density or distribution of a top predator can induce the expansion in density or distribution, or the change in behaviour of a middle-rank predator, the ‘mesopredator release’ (Prugh *et al.* 2009, Brashares *et al.* 2010). The relative strength of top-down forces in food webs therefore depends in part on the efficiency with which top predators can suppress mesopredators and exploit their prey, and thus varies spatially (Power 1992). Recent empirical and experimental advances have highlighted the potential for top predators to help restore ecosystems and confer resilience against environmental challenges, e.g. biological invasions (Ritchie *et al.* 2012, Suraci *et al.* 2016). For example, the recolonization of the White-tailed Eagle *Haliaeetus albicilla* in the Finnish archipelago reduced American mink *Neovision vison* movements, potentially mitigating their impact on

native species (Salo *et al.* 2008). Most recent research on trophic cascades has focused on determining how top predators shape and drive community structure (Terborgh & Estes 2010, Estes *et al.* 2011, Ritchie *et al.* 2012), leading to widespread predictions that the loss of large predators will release populations of smaller predators, as depicted by the mesopredator release hypothesis (Crooks & Soulé 1999, Ritchie & Johnson 2009). Newsome *et al.* (2017) have shown, consistently across three continents, that mammalian top predators can suppress sympatric mesopredators to the point of complete exclusion, but only when top predators occur at high densities over large areas. Their results further suggest that these conditions are more likely to occur at the core than on the margins of top predator ranges. Gordon *et al.* (2017) also provided evidence that the removal of a top predator, the dingo *Canis lupus dingo*, facilitated shrub encroachment in arid Australian ecosystems by triggering a four-level trophic cascade. Increased mesopredator abundance in the absence of dingoes results in suppressed abundance of consumers of shrub seeds and seedlings, rodents and rabbits, respectively. In turn, suppressed abundances of rodents and rabbits in the absence of dingoes resulted in increased seedling survivorship and decreased seed removal by rodents.

Predator–prey interactions

If, as seen above, predator–predator interactions can affect trophic network structure, predator–prey interactions are also important, as complex lethal and non-lethal interactions between predators and prey can further shape ecosystem structure. Predators impact prey through two key processes, first by directly killing and removing individuals from the population (*density-mediated effects*) and secondly through the indirect effects of predation risk that result in prey species modifying their behaviour (*behaviourally mediated effects*; Lima 1998, Brown *et al.* 1999). These non-lethal effects have a strong influence on prey fitness, with evidence suggesting substantial impacts at the population level possibly equal to, or even greater than, the removal of individuals through direct predation (Creel *et al.* 2007, Matassa & Trussell 2011). Furthermore, the risk of predation varies across time and space, with herbivores constantly balancing foraging effort against the need for safety from predators (Lima & Dill 1990, Verdolin 2006). Prey species therefore inhabit ranges of shifting predation risk that have been termed the ‘ecology or landscape of fear’ (Ripple & Beschta 2004, 2007). The landscape of fear is specific to the prey species and will depend on the predators to which they are exposed, the encounter rate, predatory defence and the effectiveness of vigilance (Lima 1998, Brown & Kotler 2004). However, bottom-up factors, such as food availability and habitat structure, can also

influence predator–prey interactions (Ritchie & Johnson 2009). For example, resource abundance can temporarily allow prey populations to escape predator regulation and decouple interactions between predators (Letnic & Dickman 2010).

Is top-down control ubiquitous in terrestrial food webs?

The overall outcomes of interactions between predators may thus vary with resource availability, habitat structure and the complexity of predator communities (Elmhagen & Rushton 2007, Ritchie & Johnson 2009). Engeman *et al.* (2017) pointed out recently that studies on the role and function of mammalian top predators continue to struggle to implement study designs that have the potential to generate the necessary reliable evidence, many with flawed or too limited experimental designs and an overall lack of standardized and repeated observations of populations over time, seasons, habitats and geographical space. Allen *et al.* (2017) highlighted that theories of the effects of large mammalian carnivores on food webs, as developed in relatively pristine areas, may not be readily transferable or applicable to the human-modified landscapes that make up the majority of the Earth's surface (Haswell *et al.* 2017, Morgan *et al.* 2017). This is because the direct and indirect effects of humans (e.g. increased primary productivity through fertilization) on all trophic levels may simply overshadow any carnivore effects (Kuijper *et al.* 2016).

Trophic cascades driven by avian top predators

There is increasing evidence that avian top predators can limit sympatric populations of medium- and small-sized birds of prey through lethal and non-lethal effects, and can structure whole raptor assemblages under certain circumstances (Sergio & Hiraldo 2008, Lourenço *et al.* 2011).

For instance, Mueller *et al.* (2016) showed that the recolonization of an avian top predator, the Eurasian Eagle-Owl *Bubo bubo* (hereafter Eagle-Owl), negatively influenced two sympatric mesopredator species, the Common Buzzard *Buteo buteo* and the Northern Goshawk *Accipiter gentilis*, through increased brood failure rates. This was induced by both superpredation effects, as Eagle-Owls not only take over Goshawk and Buzzard nests, but also kill and eat chicks and adults (Chakarov & Krüger 2010), and non-lethal effects, as mesopredators shifted to alternative breeding sites (spatial avoidance of the top predator by the dominant mesopredator, i.e. Northern Goshawk) or changed their behaviour (the subdominant mesopredator, i.e. the Buzzard, showed increased aggressiveness towards the top predator). Further evidence of multi-level intraguild

predation and superpredation exists in bird of prey assemblages (Hoy *et al.* 2015, 2017, Björklund *et al.* 2016, Morosinotto *et al.* 2017); however, research on the top-down limitation of other mesopredator species (e.g. Corvidae) by avian top predators is scarce and the potential cascading effects at the ecosystem level have rarely been investigated (Box 1; Fig. 1).

Evidence from island ecosystems has shown that raptors can have strong structuring effects on animal communities. For instance, Roemer *et al.* (2002) showed that introduced pigs *Sus scrofa domestica* enabled Golden Eagles *Aquila chrysaetos* to colonize the California Channel Islands by providing abundant food. Eagles preyed heavily on the Island Fox *Urocyon littoralis*, whose resulting decline toward extinction released populations of the competitively inferior Channel Island Spotted Skunk *Spilogale gracilis amphiala*. This study highlighted how indirect predator–prey interactions between exotic introduced species and top predators could cause major ecological shifts in island communities. American Barn Owls *Tyto furcata* (previously classified *Tyto alba*) were also able to induce a behaviourally mediated cascade on Santa Barbara Island, California, such that Owls had a positive indirect effect on Scripps's Murrelet *Synthliboramphus scrippsi* egg survival by reducing the foraging activity of Deer Mice *Peromyscus maniculatus elusus* and thus reducing nest predation in this threatened seabird species (Thomsen & Green 2016). However, only a handful of studies have investigated the role of avian predators in structuring continental food webs that are more complex than isolated island systems. Recent research in boreal ecosystems has further shown that large raptors such as Golden Eagle and Northern Goshawk seem to have a positive effect on the breeding success of Black Grouse *Lyrurus tetrix* and Hazel Grouse *Tetrastes bonasia* by enhancing fear effects on small carnivores (Red Fox *Vulpes vulpes* and Pine Marten *Martes martes*, respectively; Lyly *et al.* 2015, 2016) and reducing the pressure from corvid populations (Tornberg *et al.* 2016), thus increasing juvenile grouse survival. Finally, Greeney *et al.* (2015) demonstrated that hawk territory occupancy in Arizona (USA) had a positive indirect effect on the reproductive success of Black-chinned Hummingbirds *Archilochus alexandri*, mediated by predator avoidance shifts in foraging behaviour of Mexican Jay *Amphelocoma wollweberi*, one of the main predators of hummingbird nests. Even though the same logistical difficulties posed by carnivore food web studies are applicable to raptor studies, a combination of well-designed experiments and long-term observational studies in a variety of ecosystems would bring much-needed essential insights to our understanding of the influence of avian top predators on the structure and stability of ecological networks.

FUTURE RESEARCH DIRECTIONS

Combining experimental and long-term observational approaches to decipher the role of avian top predators in terrestrial ecosystems

Top predators occur naturally at low densities and are often endangered and elusive. Recent advances in camera trap technology and animal-borne sensors (Wilmers *et al.* 2015, Caravaggi *et al.* 2017) have opened new research opportunities to overcome these logistical difficulties and answer questions related to the ecological role of top predators in terrestrial ecosystems. For instance, the fine-scale spatial response of subordinate predators to the presence of a top predator has been documented among guilds of mammalian carnivores (Swanson *et al.* 2014, Ramesh *et al.* 2017). Integrating GPS telemetry data of large raptor movements and camera trap surveys of sympatric mammalian mesopredators would help to determine how the latter respond to spatial variation in predation risk, controlling for landscape heterogeneity (see Davies *et al.* 2016 for a similar approach with

mammalian top predators) and predator foraging mode (Preisser *et al.* 2007).

Recent research showed that experimental manipulations of fear in free-living mammalian mesopredators using month-long playbacks of intraguild top predator vocalizations caused cascading effects, reducing mesopredator foraging to the benefit of the mesopredator's prey, which in turn positively influenced multiple trophic levels in an intertidal food web (Suraci *et al.* 2016). Similar experimental manipulations using visual (e.g. taxidermied raptors with small servo motors to move their heads, see Billings *et al.* 2017) or acoustic (call playbacks) cues of different large raptor species (Billings *et al.* 2017) would make it possible to determine whether mesopredators (mammalian mesopredators and corvids) alter their foraging behaviour in the presence of avian top predators, show reduced foraging time and success, or change habitat use and how this reverberates throughout food webs in diverse ecosystems varying in their level of anthropization.

Additionally, accounting for variation in ecosystem productivity (Pasanen-Mortensen *et al.* 2017) would allow better capture of the dynamics of response variability to the presence of avian top predators. In

Box 1

Case study: anthropogenic impact, small mammals and changing predator communities in European agro-systems

Top predators are particularly vulnerable to anthropogenic disturbance due to their slow life histories (low reproductive rates) and low population density. In addition, they often are a source of human-wildlife conflict. This results in a worldwide population decline of top predators in both marine and terrestrial ecosystems. The loss of top-order predators has been identified as a key factor contributing to continuing species extinctions and the global biodiversity-loss crisis (Johnson *et al.* 2007, Estes *et al.* 2011).

Previous studies focusing on trophic cascades in terrestrial ecosystems have often been carried out in boreal ecosystems with limited land-use change (Ripple & Beschta 2012; Lyly *et al.* 2015, 2016). As the impact of predators on prey populations depends to a large extent on the productivity of the landscape, which determines the growth rates and abundance of prey populations (Elmhagen *et al.* 2010), human management regimes and human-mediated food subsidies may, in particular, be expected to interact with the impact of mammalian or avian predators on prey populations (Gagné *et al.* 2016). Therefore, the functional role of predators could be modified under varying levels of resource conditions. The interactive effects between human-induced productivity and 'natural' productivity deserve attention because these may be key factors determining the impact of predators on ecosystem processes in anthropogenic landscapes.

Further research is therefore urgently needed in European agro-ecosystems, which cover 56% of total ecosystems in Europe, as extensive human influence on vegetation and predator communities in these systems may disrupt predator-prey interactions, which has important consequences in terms of conserving ecosystem structure and function. For instance, recent research found large-scale dampening of population cycles in keystone small rodents (Cornulier *et al.* 2013). The causes of this change and its cascading effects on food webs remain poorly understood. Thus, understanding how populations of avian top predators may limit populations of specialist and generalist mesopredators in these ecosystems and how this could reverberate throughout the community to impact lower trophic levels appears to be a clear global priority (see Fig. 1).

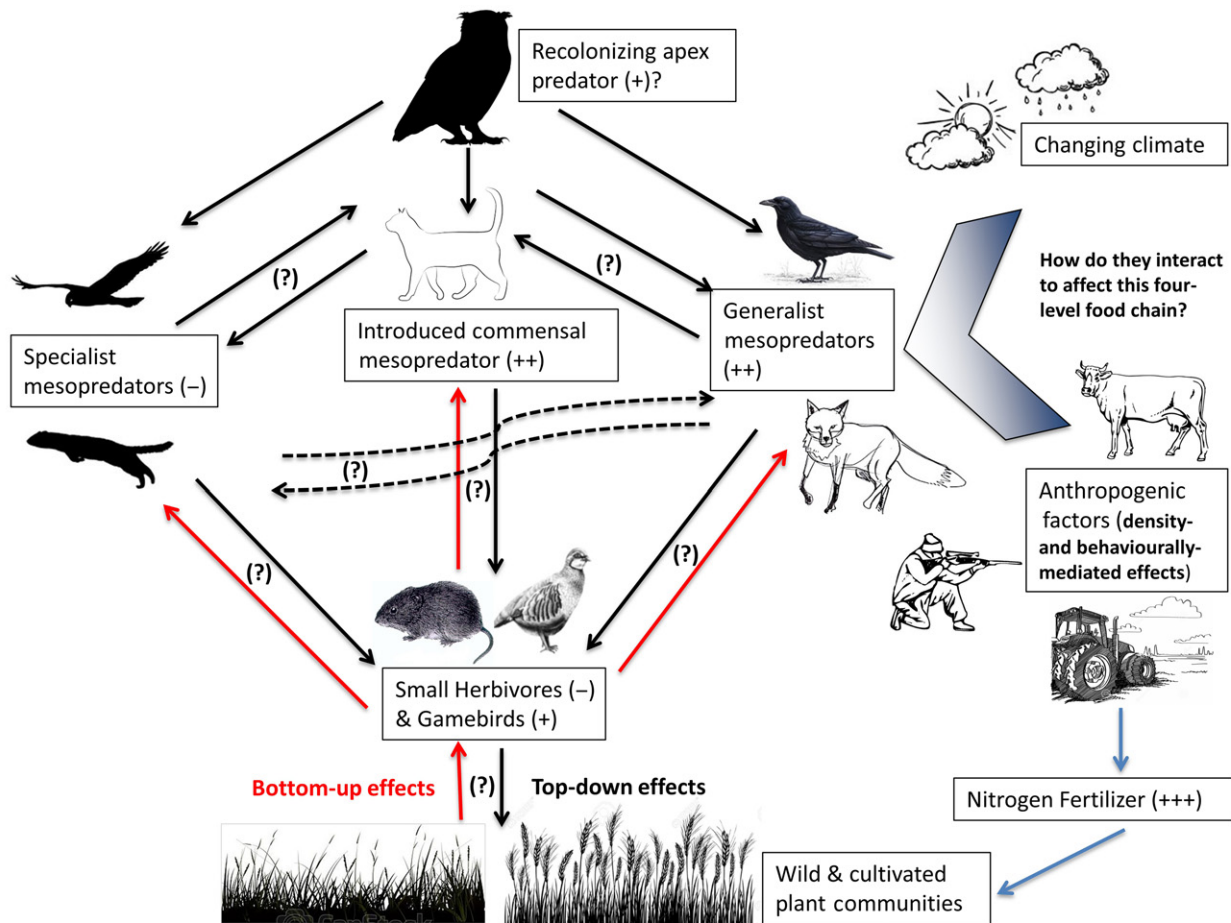


Figure 1. Diagram of hypothesized four-level trophic interactions in European intensive agro-ecosystems highlighting the potential role of recolonizing avian top predators and the anthropic factors affecting the structure of this ecological network (signs in parentheses describe European population trends or levels of resource use). [Colour figure can be viewed at [http://onlinelibrary.wiley.com/journal/10.1111/\(ISSN\)1474-919X](http://onlinelibrary.wiley.com/journal/10.1111/(ISSN)1474-919X)]

particular, further research is needed to understand how food subsidies to small herbivores (through the effects of nitrogen fertilization on primary productivity) could lead to a reduced potential for top-down density- or behaviourally mediated effects of an avian top predator on sympatric mesopredators and prey population size in anthropogenic landscapes (Muhly *et al.* 2013).

These effects of food subsidies may be particularly relevant for systems with low productivity because the top-down potential of predators seems to be especially limited in highly productive systems (Melis *et al.* 2009). Using the combined empirical and experimental approaches previously described, researchers could take better advantage of the spatial heterogeneity in primary productivity observed in agro-systems and created by variation in local levels of nitrogen fertilization to investigate the relative importance of bottom-up vs. top-down effects in four-level trophic chains (Box 1; Fig. 1).

Taking advantage of natural raptor recolonization or reintroduction programmes in Europe to assess the effect of large raptor return on ecosystems

The Golden Eagle and the Eagle-Owl, two top predators once eliminated from large parts of their European distribution range, have been recolonizing parts of their former range, including territories located at low altitudes in anthropogenic landscapes. Despite their large trophic spectrum and evidence that mammalian mesopredators are regular prey of both species (Lourenço *et al.* 2011), research has until now only focused on the effects of Eagle-Owl presence on intraguild avian predators. This natural recolonization process could be used as a before-after-control-impact (BACI) experimental design integrating methodological aspects described in the previous section (monitoring mesopredator spatial

use at the range edge of expanding Eagle-Owl and Golden Eagle populations or taking advantage of Golden Eagle reintroductions in some countries) to better understand how this top predator impacts mesopredator populations and how their return affects lower trophic levels (birds, small herbivores and primary productivity).

Developing research on the role of top avian predators in tropical ecological networks

Studies are being carried out on the ecology of Verreaux's Eagle *Aquila verreauxii*, Martial Eagle *Polemaetus bellicosus* and African Crowned Eagle *Stephanoaetus coronatus* in sub-Saharan Africa (McPherson *et al.* 2016, Murgatroyd *et al.* 2016, van Eeden *et al.* 2017) and the Harpy Eagle *Harpia harpyja* in South and Central America (Miranda 2015, Miranda *et al.* 2018). Further research is needed on the role of these large eagles on mesopredator habitat use and population dynamics in diverse ecosystems.

Retaliatory poaching linked to cases of poultry depredation is still an important cause of mortality in these species, particularly for the Vulnerable Martial Eagle (Birdlife International, 2017). Increased understanding of the potential benefits associated with the presence of these large eagles in terms of pest species control in tropical countries (monkey and medium-sized carnivore species) and communicating the results to local communities would potentially benefit the conservation of these species.

Towards a valuation of the regulatory services provided by top avian predators?

Most of the studies investigating the functional role of raptors have focused on rodent control and the potential benefits to society associated with a reduction in agriculture damage or the scavenging services provided by vultures (Paz *et al.* 2013, Morales-Reyes *et al.* 2015; Donazar *et al.* 2016). However, a broader understanding of the ecological functions of avian top predators, particularly of the trophic linkages between large raptors, mesopredators and game species and how they can be valued as regulatory services by the hunting sector, would bring potential conservation benefits to this guild.

Hunting has an important socio-economic role in the UK and several Southern European countries; for instance, income generated by Red-legged Partridge *Alectoris rufa* hunting has been roughly estimated at more than €1000 million per year in Spain (Garrido 2012, Arroyo *et al.* 2017). However, total expenses linked to management practices in hunting estates can reach €66 273 per km² in the most intensively managed estates, where one of the main costs is the salary of gamekeepers who typically undertake intensive predator

control (Díaz-Fernández *et al.* 2012). This practice has seemingly limited effectiveness on increasing Red-legged Partridge post-breeding abundance in comparison with other estate aspects such as provision or supplementary food or habitat (Díaz-Fernández *et al.* 2013), although it apparently has positive effects on other farmland birds, such as the Little Bustard *Tetrax tetrax* (Estrada *et al.* 2015). However, the influence of intraguild predation on the effectiveness of predator control in these rich predator communities has never been assessed. In particular, the potential impact of large predator presence on the effect of Red Fox and corvids on small game species is a research priority given the economic costs associated with predator control and the potential benefits in terms of conservation arising from changes in gamekeeper attitudes towards raptors (Red Fox and Eurasian Magpie *Pica pica* are the two main species targeted by predator control in Spain and also regular prey of several species of large eagles and of the Eagle-Owl). Similarly, in a recent study, Gilbert *et al.* (2016) revealed that recolonizing Cougars *Puma concolor* could reduce deer densities and deer-vehicle collisions by 22% in the Eastern United States, preventing 21 400 human injuries, 155 fatalities and \$2.13 billion in avoided costs within 30 years of establishment.

More studies using the same approach as Gilbert *et al.* (2016), coupling mesopredator population models to socio-economic valuation in order to assess the ecosystem services provided by large raptors through reduction in impact of mesopredators (through either direct trophic cascades or behaviourally mediated effects) on decreasing and economically important game species, would be extremely valuable.

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