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A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision, globally

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Abstract
Land use and cover change (LUCC) is the main cause of natural ecosystem degradation and biodiversity loss and can cause a decrease in ecosystem service provision. Animal populations are providers of some key regulation services: pollination, pest and disease control and seed dispersal, the so-called faunal ecosystem services (FES). Here we aim to give an overview on the current and future status of regulation FES in response to change from original habitat to agricultural land globally. FES are much more tightly linked to wildlife populations and biodiversity than are most ecosystem services, whose determinants are largely climatic and related to vegetation structure. Degradation of ecosystems by land use change thus has much more potential to affect FES. In this scoping review, we summarise the main findings showing the importance of animal populations as FES providers and as a source of ecosystem disservices; underlying causes of agriculturalisation impacts on FES and the potential condition of FES under future LUCC in relation to the expected demand for FES globally. Overall, studies support a positive relationship between FES provision and animal species richness and abundance. Agriculturalisation has negative effects on FES providers due to landscape homogenisation, habitat fragmentation and loss, microclimatic changes and development of population imbalance, causing species and population losses of key fauna, reducing services whilst enhancing disservices. Since evidence suggests an increase in FES demand worldwide is required to support increased farming, it is imperative to improve the understanding of agriculturalisation on FES supply and distribution. Spatial conservation prioritisation must factor in faunal ecosystem functions as the most biodiversity-relevant of all ecosystem services and that which most closely links sites of service provision of conservation value with nearby sites of service use to provide ecosystem services of agricultural and economic value.

Keywords
crop raiding, disease control, providers, invasive species, pest control, pollination, seed dispersal

Introduction

Biodiversity is recognised as a key support for stable life on Earth (Hautier et al. 2015) and plays an essential and complex role in all levels of ecosystem services production (Pimentel et al. 1997, Balvanera et al. 2006, Mace et al. 2012). To properly manage, value and conserve ecosystem services (ES), it is essential to have an accurate definition and characterisation of the services and the traits that underpin them. Ecosystem service providers are the species or entities on which the service provision depends and identifying and characterising their functional relationships are amongst the key research areas to increase understanding of the link between biodiversity and ecosystem services production (Luck et al. 2003, Kremen 2005, Duncan et al. 2015).

Animals are key ecosystem services providers; therefore, we denominate faunal ecosystem services (FES) as those services that rely heavily on animal population. Fauna is a source of provisioning (e.g. Henchion et al. 2014), cultural (e.g. Villamagna et al. 2014) and regulation (e.g. Kremen et al. 2007) services. For the latter, animals perform functions that allow ecosystem maintenance and thus production of other services, such as food or fibre provision. Conserving animal populations that provide FES is essential to maintain the correct functioning of ecosystems to provide ecosystem services where there is demand for them.

An imbalance of animal populations may be the cause of reduced FES production and/or the generation of faunal ecosystem disservices, such as the occurrence of crop pests (e.g. Rasmussen et al. 2017) and the spread of zoonotic diseases to humans (e.g. McCauley et al. 2015). Evidence suggests that such an imbalance can result from land use and cover change (LUCC), the dominant form of which globally is agriculturalisation of natural ecosystems (e.g. Wilby and Thomas 2002, McCauley et al. 2015). LUCC is considered the most important driving force of biodiversity and ecosystem function loss (MA 2005, Bastian 2013).

Regulation FES occur mostly at the local scale (Kremen et al. 2007) and the assessment of their provision and effects of LUCC has been evaluated at this scale (e.g. Kremen et al. 2002, Levey et al. 2008, Chaplin-Kramer et al. 2011). Although many studies have focused on finding spatial congruence between faunal diversity and regulation ecosystem services at large scales (Naidoo et al. 2008, Luck et al. 2009), these studies assess groups unlikely to produce a direct influence on the regulation services, e.g. linking diversity of vertebrates to carbon storage (Strassburg et al. 2010) or threatened species to freshwater provision (Larsen et al. 2011). This research is limited to describing spatial patterns of biodiversity and ecosystem services but does not assess the underlying role of faunal diversity in providing regulation ecosystem services. The direct relationship between animal diversity and regulation FES beyond the local scale and understanding the effects of LUCC on FES provision globally remains to be evaluated.

In this scoping review, we aim to give an overview of the current and future situation of regulation FES in response to agriculturalisation globally. We summarise the most relevant evidence addressing the following topics: a) the relevance of animal populations as providers of regulation services; b) the role of species richness and of abundance of providers in regulation FES provision; c) animal populations as a source of ecosystem disservices, d) the effects of agriculturalisation on FES providers, e) the mechanisms underlying the observed negative impact of provider loss on regulation FES provision, f) the potential condition of regulation FES under future LUCC and g) the expected demand of regulation FES worldwide.

Rationale

First, we summarise the evidence available to support the FES concept, which highlights animal populations as essential providers of animal pollination, biological control (including pest and disease control) and seed dispersal, as fundamental regulation services operating in both natural ecosystems and agriculture. Hereafter, the topics included in the review are addressed per service, in the order given.

ES provision has been used as a strong argument for biodiversity conservation (e.g. Balmford et al. 2002, Balvanera et al. 2006, Cardinale et al. 2011, Bastian 2013) and, simultaneously, this idea has been widely debated (e.g. Schwartz et al. 2000, Balvanera et al. 2001, Kleijn et al. 2015). Ecosystem services are by definition a function of supply and demand (there is no service without demand for it) and for many services proximity to demand is key. Many non-FES services are as much a function of climate, landscape and ecosystem structure as they are of biodiversity or species abundance. We give an overview of the role of richness and abundance in regulation FES provision to assess if FES provision can more directly support faunal conservation than other types of ecosystem service provision.

This is followed by the evidence showing the negative impacts on human well-being that can be produced by animal populations under agriculturalisation, which are referred to as faunal ecosystem disservices (Lyytimäki and Sipilä 2009, Shackleton et al. 2016). Like all the components of ecosystems, animal populations can be a source of benefit or can undermine human well-being (Zhang et al. 2007, von Döhren and Haase 2015; Figure 1). It has been recognised that the occurrence of services and disservices is part of a continuum and must be examined together to improve the understanding of their relationship with biodiversity (Shackleton et al. 2016). We address the faunal disservices caused by both invasive and native species including spread of human diseases, crop pests and crop raiding.

Finally, we synthesise evidence indicating the causes of loss of FES providers in response to the consequences of agriculturalisation: landscape homogenisation, habitat fragmentation and loss, microclimatic changes, proliferation of pests and use of pesticides. We describe the impacts of loss of FES providers on provision. It is worth mentioning that we make a distinction between the effects on providers and on provision because the former indicates the causes of loss and the latter its consequences.

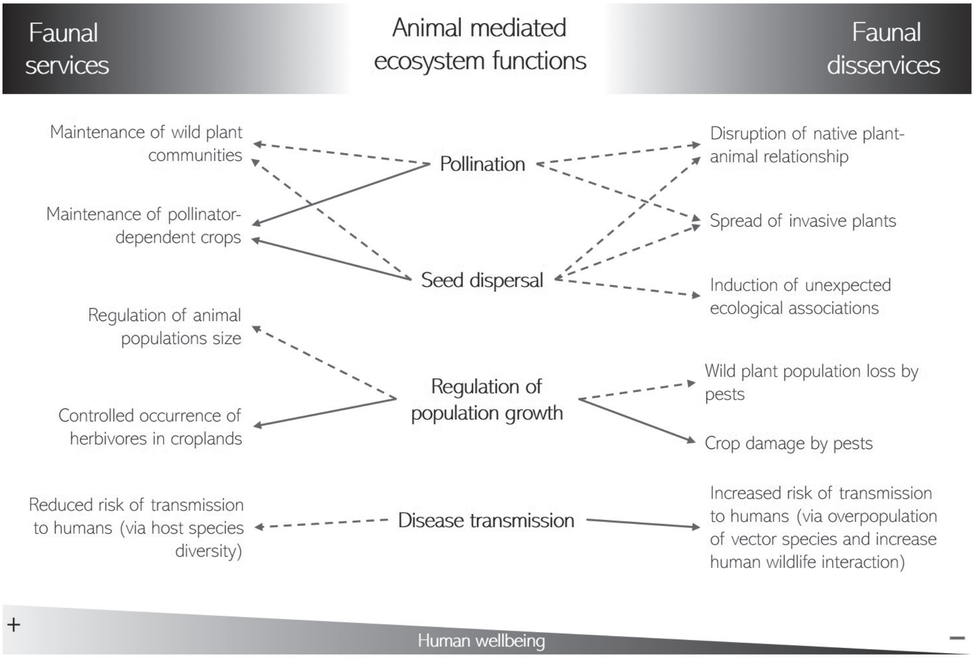

Figure 1. Animal populations as source of services and disservices. The same ecosystem function mediated by animal populations may enhance (faunal service) or undermine (faunal disservice) human wellbeing and it can manifest directly (solid arrows) or indirectly (dashed arrows).

Having addressed the present situation of FES and impacts of agriculturalisation, we address the potential trajectories for FES in the future based on the few studies that have used modelling to project agriculturalisation over the next decades and which have also assessed the impact on regulation services. Finally, we assess the expected demand for FES worldwide, given projected population growth and agricultural expansion since service provision cannot be assessed unless changes in demand are understood.

Regulation faunal ecosystem services

Ecosystem functions can produce ecosystem services (benefits or goods) where there is human demand. A key suite of these services are the regulation services (Haines-Young and Potschin 2011). Animal populations are essential providers of the following regulation services: 1) animal pollination, for which insects, especially bees, are the major providers (e.g. Kremen et al. 2002, Klein et al. 2007); 2) natural pest control, provided mainly by vertebrate predators (e.g. Mols and Visser 2007, Maas et al. 2016) and parasitoid invertebrates (e.g. Letourneau et al. 2015); 3) human disease control provided by vertebrates (e.g. tick-borne diseases, Ostfeld and LoGiudice 2003, McCauley et al. 2015); and 4) seed dispersal, where providers are mostly birds and flying mammals (e.g. McConkey and Drake 2006, García and Martínez 2012).

The assessment of regulation FES provision is complex, since populations of providers form intricate ecological relationships (e.g. Perfecto and Vandermeer 2006). It requires identification of the community structure that influences ecosystem function and assessment of the key factors affecting such provision, along with the spatial and temporal scale at which providers and services operate (Kremen 2005). FES providers can include a single population (e.g. Hougner et al. 2006), multilevel taxonomic groups (e.g. Blanche and Cunningham 2005, Maas et al. 2013) and different functional groups (e.g. Letourneau et al. 2015). Since service provision assumes a demand for the service, we must also understand the drivers and spatial distribution of that demand.

Most studies in which animal pollination and biological control are evaluated have been carried out in agroecosystems (Table 1), due to the relevance of these FES on crop yield, food supply and the role of providers in agricultural economy (Ricketts et al. 2004, Blanche and Cunningham 2005, Morandin and Winston 2006), while seed dispersal has been evaluated mostly in natural ecosystems, where it is fundamental to understand plant community composition (Wenny et al. 2016). These studies have been carried out throughout the world, mostly at the local scale.

There is a wide range of measures used to assess FES provider contributions to different services (Table 1) and methods vary from purely observational (i.e. natural conditions, e.g. McConkey and Drake 2006) or experimental (i.e. controlled conditions, e.g. Maas et al. 2013, Garratt et al. 2016) to a combination of both (e.g. Hougner et al. 2006, Egerer et al. 2018). Below, we summarise the evidence per service, showing the relevance of animals as FES providers.

Animal pollination

Animal pollination is a fundamental process in terrestrial ecosystems and is essential for maintenance of wild plant communities and agricultural systems (Potts et al. 2010). Faunal pollination is a key ecosystem service in agricultural productivity. In contrast with the other regulation FES, the contribution of animal pollination has been widely quantified.

According to Klein et al. (2007), 35% of crops depend on pollinators globally, while Kremen et al. (2002) estimated 66% for the 1,500 crop species of the world amounting to between 15 and 30% of food production. Williams (1996) estimated for European crops that over 80% of the 264 species assessed require animal pollination. Roubik (1995) estimated that productivity of approximately 70% of tropical crops is improved by animal pollinators. Regarding wild plant species, 80% of flowering plants are directly dependent on insect pollination for fruit and seed set globally (Klein et al. 2007, Ollerton et al. 2011).

Given the morphological diversity of plants, the degree of self-compatibility and the diversity of reproductive organs in the flowers of crops, a great diversity of vectors is required for efficient animal pollination (Williams 2002, Blüthgen and Klein 2011). Insects are the most important animal pollinators by virtue of their abundance and foraging behaviour (Williams 2002). Thousands of species of bees, flies, wasps, beetles,

Table 1. Faunal ecosystem services. Selected examples of studies where regulation ecosystem services provided by fauna are assessed, describing the providers, ecosystem benefited by the service and service quantification measure.

Ecosystem service	Service provider	Ecosystem	Measure	Study site	Reference
Pollination	Native bees	Agroecosystem (watermelon crops)	Pollen deposition	Yolo County, California, USA	Kremen et al. (2002)
	Exotic and native bees	Agroecosystem (coffee plantation)	Seed mass, fruit set, peaberry frequency, pollen deposition, bee species richness	Finca Santa Fe, Valle General, Costa Rica	Ricketts et al. (2004)
	Nitidulid and Staphylinid beetles	Agroecosystem (atemoya crops)	Beetle species richness	Atherton Tableland, Queensland, Australia	Blanche and Cunningham (2005)
	Wild bees	Agroecosystem (canola crops)	Bee abundance, seed set	La Crete, Alberta, Canada	Morandin and Winston (2006)
	Ceratopogonids midges	Agroecosystem (cocoa and plantain crops)	Midges abundance, pod set, intercropping proportion	Kubease, Abrafo-Ebekawopa and Edwenease, Ghana	Frimpong et al. (2011)
	Hoverfly, solitary mason bee and bumblebee	Agroecosystem (apple orchards)	Flower visitation, fruit set	Reading and Leeds experimental farms, UK	Garratt et al. (2016)
Pest control	Parasitoid eggs (Mirid bug, Wolf spider, Tetragnathid spiders)	Agroecosystem (rice crops)	Plant- and leaf-hoppers abundance	Luzon, Ifugao, Philippines	Drechsler and Settele (2001)
	Aztec ant and Green scale (mutualism avoids occurrence of coffee berry borer)	Agroecosystem (coffee plantation)	Ant activity, green scales abundance	Finca Irlanda, Chiapas, Mexico	Perfecto and Vandermeer (2006)
	Great Tits	Agroecosystem (apple orchards)	Percentage of caterpillar damage per apple tree	Netherlands	Mols and Visser (2007)
	Birds and bats	Agroecosystem (cacao plantations)	Herbivorous insect abundance, final crop yield	Napu Valley, Central Sulawesi, Indonesia	Maas et al. (2013)
	Birds and bats	Agroecosystem (coffee plantation)	Herbivorous arthropod abundance and leaf damage proportion	Finca San Antonio and Hacienda Rio Negro, Coto Brus Valley, Costa Rica	Karp and Daily (2014)
	Parasitoid wasps and flies	Agroecosystem (cruciferous crops)	Parasitoid richness, abundance of parasitised cabbage by aphids and loopers	Monterey, Santa Cruz, and San Benito Counties, California, USA	Letourneau et al. (2015)
	Leaf beetles, root and flower-feeding weevils	Wetland	Purple loosestrife cover, occurrence of feeding damage and abundance of biological control agents	Minnesota, USA	Wilson et al. (2004)
Human diseases control	Mammals, birds and reptiles	Temperate forest	Infected ticks with Lyme disease proportion	Southern New York State, USA	Ostfeld and LoGiudice (2003)
	Birds	Forested urban to rural areas	Bird diversity, mosquitoes and humans infected West Nile virus	St Tammany Parish, Louisiana, USA Ozark forest, Missouri, USA	Ezenwa et al. (2006)Allan et al. (2009)

Ecosystem service	Service provider	Ecosystem	Measure	Study site	Reference
Human diseases control	Small wild mammals	Desert (Caatinga) Tropical forest (Amazon) Wetland (Pantanal)	Small mammal diversity and abundance, dogs infected with Chagas disease	Amazon Basin, Brasil	Xavier et al. (2012)
	Rodents	Evergreen forest and Agroecosystem (mainly maize crops)	Infected rodents with bubonic plague abundance	Tloma village, Kambi ya Nyoka village and Manyara region, Tanzania	McCauley et al. (2015)
Seed dispersal	Eurasian jay	Oak forest (National Urban Park)	Oak saplings abundance	National Urban Park of Stockholm, Sweden	Hougner et al. (2006)
	Flying fox	Tropical forest	Flying fox abundance, chewed diaspores	Vava'u Islands, Tonga	McConkey and Drake (2006)
	Thrushes	Temperate secondary forest	Seed abundance and richness and frugivorous abundance and richness	Cantabrian Range, Spain	García and Martínez (2012)
	Native frugivore birds	Tropical forest (Wild chillies)	Seedling emergence of gut passed seeds vs. non-gut passed seeds	Guam, Mariana Islands	Egerer et al. (2018)

butterflies and moths contribute to pollination of many crops, such as gourds, oilseeds, berries and tobacco, amongst many others (Roubik 1995, Williams 2002, Blanche and Cunningham 2005), as well as a countless number of wild plant species. Bees are probably the most recognised pollinators (>12,000 species; e.g. Kremen et al. 2002, Larsen et al. 2005, Morandin and Winston 2005, Potts et al. 2010, Kerr et al. 2015).

Biological control of pests and human diseases

Biological control is the natural process responsible for the regulation of species' population growth through ecological interactions –mutualism, parasitism and predation. This has been highlighted as a relevant regulation FES given the key role in restraining the spread of crop pests and diseases (Wilby and Thomas 2002, Fiedler et al. 2008, Karp and Daily 2014).

Oerke (2006) made an estimation of potential and actual losses due to pests for wheat, rice, maize, potatoes, soybeans and cotton, between 2001 and 2003, worldwide. Arthropod pests destroy 8–15% of these crops and without natural biological control and pesticides, this figure could reach 9–37%. According to the estimation done by Losey and Vaughan (2006), crop damage due to the absence of arthropod native predators might cost approximately US $4.5 billion more than the actual cost given pest control services.

Predation is one of the best-known mechanisms of biological control for agricultural pests and birds and bats have been identified as the main contributors, by their predation of species responsible for crop damage (Mols and Visser 2007, Maas et al. 2013, Karp and Daily 2014, Railsback and Johnson 2014). Increasing knowledge of the relevance of predators for pest control has increased the concern to conserve the conditions required to maintain these predators (e.g. Williams-Guillén and Perfecto 2010, Railsback and Johnson 2014).

Parasitoidism is considered another important mechanism of agricultural pest control (Drechsler and Settele 2001, Letourneau et al. 2015). The main providers identified are flies and parasitoid wasps, which lay eggs on or in the body of a host, in this case pest insects, eventually killing the hosts and diminishing the spreading of the pest.

Mutualism has been identified as another mechanism that can contribute to pest control. Perfecto and Vandermeer (2006) provided evidence that the mutualistic relationship between the Aztec ant and a coccid has a positive effect on coffee plants by reducing the numbers of the coffee borer beetle, coffee's main pest. This exemplifies the complexity of biological control mechanisms and how an imbalance in ecological condition can negatively impact this FES.

Disease control is also recognised as a relevant FES (Ostfeld and LoGiudice 2003, Foley et al. 2005, McCauley et al. 2015). Wild and domestic animals are vectors for a wide range of infectious diseases that are potentially transmitted to humans (see Molyneux et al. 2008, Civitello et al. 2015). Healthy populations of animals (i.e. populations with the minimum number of sexually mature individuals required to secure their viability) and high diversity provide less risk of human infection, since the probabilities of vectors (e.g. flies and ticks) targeting humans as hosts decreases with higher availability of other host species (Keesing et al. 2006, Civitello et al. 2015). Disease control is a FES directly related to human health and well-being.

Seed dispersal

Animals are also relevant actors in seed dispersal. They drive plant gene flow, population dynamics and spatial structure in undisturbed habitats and contribute to regeneration of deforested habitats, by moving seeds from one site to another (Russo et al. 2006, García and Martínez 2012). Animals are considered long-distance vectors; they contribute to seed dispersal mainly by defecation and epizoochory (seeds adhere to the outside of animal bodies). These include ants, frugivorous terrestrial, arboreal and flying mammals and frugivorous and/or caching birds (Greene and Calogeropoulos 2002). Animal seed dispersal is an essential mechanism in the maintenance of temperate and tropical ecosystems (García and Martínez 2012) and are particularly important for large-seeded plants (Greene and Calogeropoulos 2002, McConkey and Drake 2006, Wenny et al. 2016). Approximately one-half of seed plant species are dispersed by animals (Wenny et al. 2016, Egerer et al. 2018).

The ecological value of faunal dispersal is well known (Russo et al. 2006, Wenny et al. 2016). However, in comparison with animal pollination and pest control, the quantitative assessment of the seed dispersal service by fauna is scarce. Seed dispersal benefits are spatially and temporally distant from the mother plant, making them difficult to measure, especially for tree species and species not used directly by humans (Wenny et al. 2016) and further quantitative assessment is required for this FES.

The economic value of animals for seed dispersal is even less well known than their ecological value (Wenny et al. 2016). Some studies have indirectly estimated the value of animal seed dispersal through the economic valuation of associated food and fibre consumed by humans (e.g. Fujita and Tuttle 1991, Paoli et al. 2001). However, studies on direct valuation are scarce. A direct economic valuation is made by Hougner et al. (2006), who value seed dispersal carried out by the Eurasian Jay in an oak forest, through the estimation of the cost of replacing birds by human force.

Some of the studies where the role of animals in seed dispersal has been assessed are in tropical ecosystems. McConkey and Drake (2006) highlighted the relevance of flying foxes to sustain Pacific island forests, since these are the only existing animals capable of dispersing large seeds over long distances in such isolated habitats. Egerer et al. (2018) showed that bird dispersal provides a benefit to wild chilli plants in Guam through increased seedling emergence of gut-passed seeds in comparison to depulped seeds and whole fruits.

The role of richness and abundance of regulation faunal ecosystem service providers

Species richness (i.e. the number species present in a certain area) is considered the most simple and direct measure of biodiversity (Gotelli and Colwell 2001) and has been considered an important trait to evaluate the ecosystem services-biodiversity relationship (e.g. Egoh et al. 2009, Schneiders et al. 2012). There is the assumption that high species richness has a strong positive relationship with ES production and by conserving biodiversity, ES can be secured and improved (de Groot et al. 2010, Cardinale et al. 2011, Cimon-Morin et al. 2013, Isbell et al. 2015). However, this idea has been widely debated (Schwartz et al. 2000, Ridder 2008, Kleijn et al. 2015).

An empirical literature review by Schwartz et al. (2000) found little support for the hypothesis that there is a strong dependence of ecosystem function on species richness. They describe a curvilinear response where ecosystem function reaches saturation at low levels of species richness, indicating that few species can be enough to fulfil ecosystem functions. Equally, Ridder (2008) pointed out that most ES are not provided by all the extant species in a given ecosystem, but by any group of species that meet certain basic functional criteria or by species that are dominant and especially resilient in the face of change. In this sense, they highlight that using this argument could be counterproductive for both biodiversity and multiple ES conservation, since it would focus only on the conservation of a few "functional" species.

In contrast, Hector and Bagchi (2007) concluded that large numbers of species are necessary to fulfil the inherent multi-functionality of ecosystems. As more ecosystem functions were included in their analysis, more species were found to affect the overall functioning. Isbell et al. (2011) argued that species may appear functionally redundant when only one function is considered under one set of environmental conditions, but many species are needed to maintain multiple functions at multiple times and places. Bastian (2013) argued that species are embedded in an ecosystem and the loss of a single species (or population) and/or ecosystem function might have unpredictable effects. Therefore, conservation of all ES does imply conservation of biodiversity, even though many services are unrelated to species diversity or abundance and more related to climatic and structural properties of vegetation and landscape as well as human demand for them (Mulligan 2018).

Regarding regulation FES, there is evidence that, by increasing species richness, FES provision is improved. For instance, Larsen et al. (2005) showed how a decrease in bee species diversity considerably disrupts the pollination service. The meta-analysis carried out by Civitello et al. (2015), provided evidence that host diversity inhibits wildlife and human parasite abundance. Concerning seed dispersal, García and Martínez (2012) described a positive relationship between frugivorous birds richness and all the indicators of dispersion evaluated.

Abundance (i.e. number of individuals per species), rather than species richness, has been suggested as the most important trait that influence FES occurrence (Harrison et al. 2014, Winfree et al. 2015), particularly for pest regulation and pollination. According to the analysis carried out by Winfree et al. (2015), abundance of the dominant species is the main driver of ES delivery, while rare species are important for species richness but have little contribution to ecosystem functioning.

Some studies have evidenced the relevance of abundance of beetles (Blanche and Cunningham 2005), midges (Frimpong et al. 2011) and bees (Morandin and Winston 2005,2006) for crop pollination. Equally, predator abundance appears to be a determinant for the pest control service (Koh 2008, Crowder et al. 2010, Maas et al. 2013). The evidence above suggests that, unlike for many other classes of ecosystem service, animal species richness and abundance is required to secure regulation FES provision.

Faunal ecosystem disservices

Ecosystem disservices were recently defined as the ecosystem generated functions, processes and attributes that result in perceived or actual negative impacts on human well-being (Shackleton et al. 2016). Although there is literature addressing ecosystem disservices across several scientific disciplines, such as natural disaster management, agriculture and public health (Lyytimäki and Sipilä 2009, von Döhren and Haase 2015, Shackleton et al. 2016), the concept and theoretical framework around it are relatively new and undeveloped compared to that of ecosystem services (Shackleton et al. 2016) and associated literature is scarce (von Döhren and Haase 2015).

For many years, the assessment of the links between ecosystems and human well-being has been focused only on ecosystem services (Lyytimäki and Sipilä 2009). However, there are strong links between services and disservices: the same ecosystem function or component can be a source of service or disservice simultaneously (Zhang et al. 2007, Limburg et al. 2010, Escobedo et al. 2011; Figure 1).

The designation as service or disservice depends on the perceived influence on human well-being (Lyytimäki and Sipilä 2009). For example, a pollinator insect population can act as service provider by pollinating native plants and act as disservice provider by pollinating invasive plants in the same ecosystem. Therefore, to enhance our understanding of the ecosystem-human well-being relationship, we should aim for an integrative examination of ecosystem services and disservices (Ninan and Inoue 2013, Shackleton et al. 2016).

An integrative and balanced approach to services and disservices provides a better foundation for environmental management and conservation efforts (Lyytimäki 2015). With this aim in mind, Shackleton et al. (2016) proposed a working definition, characterisation and first categorisation for ecosystem disservices. They recognise that manifestation of disservices can be direct, i.e. impacting directly on human well-being (e.g. crop raiding by medium or large sized mammals) or indirect, by diminishing the flow or causing the loss or impairment of ecosystem services (e.g. invasive species altering native pollinator-plant relationships). Regarding categorisation, they consider two main aspects: origin of the disservice as biotic or abiotic and nature of the impact, as economic, health (health and safety) and cultural (aesthetic and cultural). According to this typology, the disservices related to agriculturalisation here termed faunal ecosystem disservices, belong to Shackleton et al's (2016) bio-economic and bio-health categories (Table 2). The disservices addressed here are: impacts of invasive species, spread of human diseases, crop pests and crop raiding.

Invasive species

Effects of invasive species on native species are well documented (e.g. D'Antonio et al. 2004, Alpert 2006) and, more recently, their effects on ecosystem services has also drawn attention (Pejchar and Mooney 2009, Pyšek and Richardson 2010, Peh et al. 2015, Walsh et al. 2016). According to Pejchar and Mooney (2009), the impact of alien species is usually well quantified for provisioning services (food, fibre and fuel). However, impacts on regulation FES are rarely calculated, but are likely to be substantial.

Amongst the reported effects of invasive species on animal pollination services are: the disruption of mutualism between native bees and plants by invasive bees, the range expansion in pollinator-limited invasive plants and consequent distraction of pollinators from native plant species (Stokes et al. 2006, Traveset and Richardson 2006). According to the review made by Morales et al. (2017), the impacts of invasive pollinators on pollination are predominantly negative for native plants, mixed for crops and positive for invasive plants. Although invasive pollinators can be beneficial for some native plants in highly disturbed habitats and some crops in intensively modified agroecosystems (e.g. Ricketts et al. 2004), they cannot replace the role of a diverse pollinator assemblage for wild plant reproduction and crop yield.

Table 2. Faunal ecosystem disservices. Selected examples of disservices related to agriculturalisation caused by fauna, describing providers, type of manifestation: direct or indirect (when causes decrease or loss of a service), category (according to Shackleton et al. 2016) and impact on human well-being.

Provider	Manifestation	Category	Disservice	Reference
Invasive pollinators	Indirect (pollination)	Bio-economic	Disruption of native pollinator-plant relationship, spreading of invasive plants	Traveset and Richardson (2006), Morales et al. (2017)
Herbivore insects	Direct (herbivory)	Bio-economic	Damage to crops	Pimentel et al. (2005)
Birds and mammals	Direct (crop riding)	Bio-economic	Damage to crops	Naughton-Treves and Treves (2005), Ango et al. (2016)
Invasive hosts	Indirect (disease control)	Bio-health	Novel hosts increase incidence of diseases, decrease of vertebrate population increases the risk of transmission to humans	Pejchar and Mooney (2009), McCauley et al. (2015)
Invasive frugivores and herbivores	Indirect (seed dispersal)	Bio-economic	Disruption of native seed disperser-plant relationship, spreading of invasive plants, emergence of new ecological associations	Richardson et al. (2000), Gosper et al. (2005)

Invasive species like weeds, insects and plant pathogens (mainly fungi) can become pests and have major impacts on crops. For instance, a well-documented case is the Mediterranean fruit fly, native from West Africa, but now found worldwide, which causes damage to over 250 types of crops. The cost estimated for California reaches US $1 billion (Mooney 2005). Similarly, Pimentel et al. (2005) made a detailed review of the environmental and economic costs associated with alien species in the United States. Related to crops, pasture and forest losses, they identify 500 weed species, feral pigs, European starlings, over 900 insect species and 20 plant pathogen species, as the main agents. The cost of losses, damages and control techniques reaches an annual value of approximately US $50,000 million.

Animal seed dispersal can be a disservice when this involves the spread of invasive plants. Just like the service, the knowledge on how animals contribute to the success of invasive plants is limited (Gosper et al. 2005). However, several mechanisms have been identified: the invasive plant species rely on common native disperser species with generalist diets; the invasive plant is reunited with the disperser species of its native range — like the case of *Rubus* spp. and blackbirds (*Turdus merula*) in Australia; and a new association between plant and animal can occur — like the case of the accidental spread of seeds of wind dispersed pines, *Pinus* spp., by seed predating cockatoos, *Calyptorhynchus* spp., in Australia (Richardson et al. 2000). Additionally, the dispersal of native plants is affected by the competition of dispersal service from invasive plant species (Gosper et al. 2005).

Equally relevant is the effect of invasive species on disease control: invasive plants and animals can act as novel hosts for diseases. Pyšek and Richardson (2010) provided detailed examples of how several invasive species affect human health, acting as vectors (e.g. rodents and bats as vectors of rabies, leptospirosis and hepatitis) or acting directly (e.g. snake bites).

Spread of human diseases

Overpopulation of disease organisms or disease vector organisms and/or the absence of defence organisms can increase the risk of spread for human disease. Many cases of disease outbreaks in human history have been related with invasive pathogens, due to the continual expansion and interchange of human population worldwide (Dobson and Carper 1996, Pejchar and Mooney 2009). For instance, the introduction of smallpox, measles and typhus with European arrivals to the New World increased mortality of the native human population at unprecedented rates (Dobson and Carper 1996). More recently, the increase of mosquito-borne diseases, like yellow fever and dengue, has been attributed to invasive mosquitoes in America and Asia (Pejchar and Mooney 2009). The negative effect can also be indirect, for example, the invasion of the American plant *Lantana camara* in East Africa. *L. camara* is now the habitat of the tsetse fly, vector of sleeping sickness.

Native species may also represent a risk for human health if the natural control of population growth is altered or if human contact with vectors increases. For instance, Ostfeld and LoGiudice (2003) evidenced how the risk of human exposure to Lyme disease increases due to the decrease in diversity of other hosts for ticks (Lyme disease vectors). Equally, McCauley et al. (2015) showed how changes in rodent and flea community composition due to LUCC, increase the abundance of *Mastomys natalensis*, transmitter of plague, in agricultural habitats in Tanzania.

Crop pests

Since the beginning of agriculture, humans have faced crop pests (Oerke 2006), which have had major impacts in human history. Pests, such as rusts on wheat, ergot on rye potato blight, gypsy moth and the boll weevil, have had deep social and economic consequences (Horsfall 1983). Currently 10–16% of global crop production is lost due to pests (Bebber et al. 2013).

Amongst the known causes of occurrence of crop pests is the imbalance of natural biological control, produced by a change in the abundance of natural enemy populations. For instance, a decrease in predator populations allows the increase of prey population (e.g. Drechsler and Settele 2001, Wilby and Thomas 2002, Karp and Daily 2014). Other causes are the absence of indigenous populations which facilitates the success of invasive species with similar ecological requirements (Pejchar and Mooney 2009) and the concentration of food resources, especially in perennial monocultures (Risch 1981, Altieri 2018). Although crop pests have been present since the appearance of agriculture, modern agricultural practices, like agricultural intensification (e.g. Wilby and Thomas 2002), manipulation of soil fertility and irrigation (e.g. Fuller et al. 2012) and use of chemical pesticides (Rosenzweig et al. 2001) have exacerbated these causes (Tilman 1999).

Crop raiding

Crop raiding is the term used to describe the action of wild animals foraging or trampling crops (Hill 2016). In this context, wildlife is considered a pest. However, this is not produced by an imbalance in wildlife populations, but by the increasing overlap of human and wildlife niches, due to continuous human population growth and the anthropogenic transformation of habitat (Hill 1997, Campbell et al. 2000). The most commonly identified actors are medium and large sized mammals (e.g. monkeys, wild pigs, hippopotamus, elephants; Naughton-Treves 1998, Engeman et al. 2010, Ango et al. 2016), but some studies also refer to small mammals and birds (e.g. Naughton-Treves and Treves 2005). Amongst the identified factors influencing crop raiding are the distance from cropland to natural habitat patches, the crop type and hunting practices (Naughton-Treves 1998). Drought, leading to paucity of production in (non-irrigated) natural lands, can also act as a push factor alongside the pull factor of higher productivity in irrigated or improved agricultural areas (Mulligan 2018).

Literature on this subject is extensive and mostly consists of case studies. The approaches to quantify losses vary considerably and are not comparable from site to site (McGuinness and Taylor 2014). The impacts have been assessed in human settlements adjacent to natural protected areas, where the raiding occurs frequently (e.g. Sekhar 2002, Linkie et al. 2007, Hedges and Gunaryadi 2010). However, there are also studies that address this phenomenon outside of protected areas (e.g. Ango et al. 2016, Chaves and Bicca-Marques 2017).

The extent of damage varies widely depending on where the raiding occurs and the type of crops and wildlife species involved. For instance, the socioeconomic impact might be higher in developing countries in non-protected areas with farmers losing their livelihood and rarely being compensated for the losses, thereby creating antagonism towards wildlife (Linkie et al. 2007). In contrast, in protected areas, prevention and compensation measures are more frequently enforced (Sekhar 2002, Davies et al. 2011).

The approaches to estimate monetary losses are variable, varying in unit of measurement and spatial scale. For example, Chakravarthy and Thyagaraj (2005) estimated a loss of US $8 per kilogram of dry capsules of cardamom caused by the Bonnet macaque (*Macaca radiate*), while Engeman et al. (2010) estimated that Rhesus macaque (*Macaca mulatta*) and Patas monkey (*Erythrocebus patas*), both invasive species, causes a nationwide economic impact of US $1.46 million per year in Puerto Rico.

Human-driven environmental changes strongly influence the occurrence of faunal disservices. Simultaneously, these environmental changes have an adverse effect on faunal services through the negative impact on the providers, mainly caused by the loss or transformation of habitat.

Effect of agriculturalisation on regulation faunal ecosystem service providers

Agriculturalisation is considered to be the main driver of loss, modification and fragmentation of habitats, causing biodiversity loss and ES degradation globally (Gaston et al. 2003, MA 2005). Ramankutty and Foley (1999) estimated that nearly 10.7 million km^2 of forests/woodlands and savannahs/grasslands have been transformed to agricultural land globally between 1700 and 1990. Temperate regions of developed countries experienced the greatest changes during nineteenth century, whilst most tropical developing countries have faced the greatest change from the late twentieth century to the present (Goldewijk 2001). In the past, the change conversion was mostly natural grasslands, whilst currently forests are the agricultural frontier. During the period from 1990 to 2015, there was a net loss of 129 million ha of forests worldwide (FAO 2015). Tropical forests present the highest rates of LUCC (anual rate 0.13%; FAO 2015), mainly for industrial export agriculture, traditional shifting agriculture and cattle ranching (Grau and Aide 2008).

Landscape homogenisation and habitat fragmentation

Landscape heterogeneity refers to the variety of different landscape conditions within a landscape (i.e. area that is spatially heterogeneous in at least one factor of interest, Turner and Gardner 2015) as with mixed habitats or land cover types. A closely related concept is landscape complexity, which can be defined as the level of difficulty observed in understanding the interactions of the landscape components (Papadimitriou 2010). The relationship between these concepts is controversial. Heterogeneity has been described as a function of complexity (e.g. Chen and Xu 2015), at the same time, heterogeneity has been considered an attribute of complexity (e.g. Papadimitriou 2010); furthermore, the terms have been used interchangeably (e.g. Miles et al. 2012).

The inconsistency in the use of terms makes the comparison and synthesis of studies difficult (Reyes Sandoval 2017). However, for practical purposes, we consider that loss of complexity/heterogeneity or landscape homogenisation/simplification refers to the same phenomenon: loss of components and/or loss of the interaction amongst components in a landscape.

The idea that the diversity of landscape components is a key determinant for biodiversity is widely accepted (Fahrig et al. 2011, Katayama et al. 2014). Increased landscape heterogeneity is generally associated with increased biodiversity, since high habitat and resource diversity allows high diversity of species, while the opposite, i.e. landscape homogeneity, is associated with low biodiversity (Parks and Mulligan 2010, Stein et al. 2014).

A consequence of LUCC due to agriculture is landscape homogeneity, as different land cover and habitat types are converted to more uniform agricultural land. Therefore, the proportion of agricultural land is the most commonly used indicator of homogenisation in studies where the relationship between biodiversity and landscape heterogeneity is assessed (e.g. Letourneau et al. 2015, Maas et al. 2016, Jonason et al. 2017). Other indicators include distance from original habitat (e.g. Blanche and Cunningham 2005, Ricketts et al. 2008) and diversity and management indices (Gardiner et al. 2009, Williams-Guillén and Perfecto 2010, Chaplin-Kramer et al. 2011).

Several studies support a positive relationship amongst landscape heterogeneity, species diversity and abundance of FES providers (Table 3). Although neutral or mixed relationships have also been evidenced (Jonsen and Fahrig 1997, Chaplin-Kramer et al. 2011), due mostly to species' particular ecological traits and range sizes (Katayama et al. 2014), landscape heterogeneity has proven to be a relevant factor in ecosystem functioning and population dynamics. Sustainable landscape management is suggested as the most important means of maintaining healthy populations of FES providers (Ricketts et al. 2008, Maas et al. 2013, Letourneau et al. 2015). There is also evidence that homogenised landscapes favour the occurrence of disservices by reducing the diversity and abundance of beneficial arthropods, such as pollinators and parsitoid insects and vertebrate predators (e.g. Letourneau et al. 2015, Senapathi et al. 2015, Maas et al. 2016) and thus increasing the outbreaks of herbivore and diseases pests (e.g. Altieri 1999, McCauley et al. 2015).

Along with landscape homogenisation, agricultural intensification has led to original habitat loss and concurrently to habitat fragmentation. Habitat fragmentation refers to the reduction of continuous tracts of habitat to smaller, spatially distinct remnant patches (Wilson et al. 2016). Fragmentation alters habitat connectivity and quality, affecting biodiversity and ecosystem functioning negatively (Haddad et al. 2015). Equally, reduction of the original habitat of animal populations has increased the conflict between humans and wildlife and the risk of disease transmission (Campbell et al. 2000, Xavier et al. 2012).

The degradation of ecosystems by landscape homogenisation, habitat loss and fragmentation results in decreased carrying capacity to sustain all the organisms that inhabit these ecosystems, leading to continued population losses. The loss of populations precedes species extinction and, therefore, the reduction of biodiversity (Ceballos and Ehrlich 2002).

Several studies have suggested that the loss of genetically distinct populations globally is both absolutely and proportionally several times greater than the rate of extinction of species (Hughes et al. 1997, Ceballos and Ehrlich 2002, Gaston et al. 2003). Genetic variation amongst and within populations confers resilience to environmental change whereas the loss of individuals or populations increases the vulnerability of species, destabilises ecosystem functions and affects ES provision (Luck et al. 2003).

Population losses through habitat loss

Habitat loss and fragmentation are the main causes of population decline (Fahrig 1997, He and Hubbell 2011, Wilson et al. 2016). Hughes et al. (1997) estimate the population diversity, defined as the number of populations on the planet, for 82 species (35 vertebrates, 23 plants, 19 arthropods, four molluscs and one platyhelminth) in the range 1.1–6.6 billion populations. By using the midrange estimation (3 billion populations), assuming a linear function between population and habitat loss and that two-thirds of all populations exist in tropical regions, they estimate that 16 million populations are lost annually across these 82 species alone.

Table 3. Faunal ecosystem service providers and landscape heterogeneity. Examples of studies evaluating the relationship of landscape heterogeneity and FES providers richness and abundance, including the definition of heterogeneity as described by the studies' authors.

Group	Study type	Description of landscape heterogeneity	Relationship	Reference
Native bees	Original	Watermelon farms with gradient of agricultural intensification, 1% to ≥30% natural habitat within a 1-km radius	Positive	Kremen et al. 2002
Nitidulid and Staphylinid beetles	Original	Atemoya orchards with gradient of decreasing distance (0.1–24 km) from tropical rain forest	Positive	Blanche and Cunningham 2005
Bees, bumblebees and beetles	Meta-analysis	Isolation of several crops from natural habitats	Positive	Ricketts et al. 2008
Coccinellid beetles	Original	Soybean and corn crops with gradient of agriculturally dominated to forest and grassland dominated within a 3.5-km radius, landscape diversity measured as Simpson's D	Positive	Gardiner et al. 2009
Pollen beetles, stem weevils	Original	Various crops with gradient ranging from structurally poor to complex landscape at several spatial scales (250–2000 m radius), landscape diversity measured with Shannon-Wiener index	Mixed (Scale-dependent)	Zaller et al. 2008
Leaf-Nosed Bats	Original	Coffee plantations and forest fragments along a gradient of management intensity, landscape diversity measured with Management Index	Mixed (Trophic guild-dependent)	Williams-Guillén and Perfecto (2010)
Natural enemies of pests	Meta-analysis	Landscape complexity metric consider % natural habitat, % non-crop habitat, % crop, habitat diversity measured using Shannon and Simpson indices	Positive	Chaplin-Kramer et al. (2011)
Birds	Original	Coffee farms in sites of mixed cropland and habitat vs. separate areas of intensive agriculture and habitat	Positive	Railsback and Johnson (2014)
Parasitic wasps and flies	Original	Rotatory organic crop fields ranging from homogenous cover of annual crops to primarily forest trees and native shrubs within 500 m and 1500 m radius	Positive	Letourneau et al. (2015)
Bees and wasps	Original	Historical land cover change using spatial analysis within 1, 2, 5 and 10 km radii	Positive	Senapathi et al. (2015)
Birds and bats	Review	Cacao, coffee and mixed fruit orchards and tropical forest sites, comparison among forest, agroforestry and agricultural systems	Mixed (Taxa-dependent)	Maas et al. (2016)
Arthropods enemies of aphids	Meta-analysis	Proportion of cultivated land within a 1 km radius around each plot	Positive	Rusch et al. (2016)
Wild bees	Original	50 ha landscape plots in agricultural areas with increasing cover of semi-natural and natural vegetation patches	Positive	Bukovinszky et al. (2017)
Butterflies and farmland birds	Original	Proportion of arable field cover	Positive	Jonason et al. (2017)

Ceballos and Ehrlich (2002) made an indirect estimation of mammal population loss globally, by comparing present and historic ranges of 173 declining species, reaching a collective loss of 50% of range area. Regarding bird populations, Gaston et al. (2003) estimated a loss of approximately 22% of breeding bird individuals so that an average of 87 billion breeding bird individuals remain from approximately 112 billion estimated before 1700, which is considered the starting date for development of the current pattern of LUCC due to agriculture.

Global declines in pollinator populations are widely recognised (Biesmeijer et al. 2006, Gallai et al. 2009, Potts et al. 2010) and habitat loss is considered the main threat, particularly for habitat and plant specialists (Ricketts et al. 2008, Potts et al. 2010, Winfree et al. 2015). Equally, decline in predator and parasitoid populations due to habitat loss has been reported (Williams-Guillén and Perfecto 2010, Letourneau et al. 2015).

Population losses through microclimatic changes and edge effects

LUCC causes microclimatic changes in the remaining patches of ecosystem related to temperature, wind and humidity (Meyer and Turner 1992). There is evidence that deforestation can modify local rainfall and droughts pattern, changes in moisture and humidity can also negatively affect canopy, understorey and litter organisms and can increase fire frequency in tropical and arid ecosystems (Goldammer and Seibert 1990, Rao 2009), increasing the mortality of animal populations.

Along with climatic modification, physical changes diminish animal habitat suitability by reducing the quantity and quality of nesting, sheltering, and foraging sites (Frumhoff 1995). These changes can affect ecological interactions, survivorship, reproductive fitness and distribution of populations, particularly for highly specialised organisms (Dale 1994, Afrane et al. 2006, Rao 2009). Finally, the decrease in population sizes at the interface between two land cover types, known as the edge effect, is also enhanced by habitat fragmentation, caused by deforestation (Levin et al. 2009).

Population losses through pest proliferation and chemical pest control

Environmental changes caused by LUCC may adversely affect biological control processes. Spatial and temporal distribution and proliferation of insects, weeds and pathogens is largely determined by climate, therefore microclimatic changes in temperature, light and water supply can drive overpopulation of pests (Rosenzweig et al. 2001). Pest proliferation has detrimental consequences for ecosystems (Chapin et al. 2000, Wilby and Thomas 2002, Foley et al. 2005). For example, *Imperata cylindrica*, an aggressive indigenous grass, which colonises forest lands of Asia that are cleared for slash-and-burn agriculture, forms a monoculture grassland with no vascular plant diversity and few mammalian species in comparison with the native forest (Chapin et al. 2000).

Crop pests produce major losses for crop yields, therefore, farmers have resorted to the use of pesticides as a means of control. In the last six decades, there has been a dramatic increase in the use of pesticides. Along with agricultural intensification, herbicides, insecticides and fungicides have produced highly negative effects on species abundance and diversity (Geiger et al. 2010, Isenring 2010) and also threaten water quality (Vymazal and Březinová 2015) and human health directly (see Budzinski and Couderchet 2018) . There is evidence of the adverse effect of chemical pest control on farmland and wildlife populations worldwide (e.g. amphibians and reptiles, Gibbons et al. 2000, farmland birds, Boatman et al. 2004, benefitial arthropods, Desneux et al. 2007). Direct adverse effects include higher mortality due to poisoning, reduced fecundity and detrimental changes in physiology and behaviour. Indirect effects include reduction of habitat, due to destruction of non-invasive vegetation, reduction of food resources for predators by indiscriminate elimination of arthropod populations and imbalance in ecological interactions.

Impacts of biodiversity losses on provision of regulation faunal ecosystem services

It is sensible to assume that, by losing populations of providers, the production of ES might be compromised. However, it is crucial to understand the mechanisms that affect provision first. Several studies have evidenced the underlying reasons for the negative effect of population losses on FES production as outlined below.

Species richness loss

Regarding animal pollination, the high diversity in morphology and reproductive strategies of plants requires a similar diversity of pollinators (Blüthgen and Klein 2011). Therefore, a decrease in pollinator diversity potentially causes a decline in wild plant and crop diversity (Biesmeijer et al. 2006, Potts et al. 2010), as well as reduced crop productivity. Blanche and Cunningham (2005) observed a highly significant reduction in fruit set due to pollinator exclusion in atemoya crops. The risk is greater for wild or crop species that rely on a narrow range of pollinator species. Although the threshold of diversity, required to maintain pollination stability, depends on the biology and variety of crops, landscape structure and regional pollinator community, the evidence suggests that stability is higher with a diverse and abundant pollinator community (Klein et al. 2007).

Equally, a detrimental effect on natural pest control in crops has been identified due to a reduction in natural enemy diversity (e.g. rice crops, Drechsler and Settele 2001, Wilby and Thomas 2002, cacao plantations, Maas et al. 2013, coffee plantations, Karp and Daily 2014). Straub et al. (2008) indicated that higher diversity of predators implies higher complementarity on functional roles: feeding on different pest species, at different life stages of the pest, using diverse strategies and differential partitioning of space and/or time (e.g. eating pest insects from different parts of the plant or during different seasons). This explanation could also be applied to parasitoid species.

Human disease control can be affected by reduction in species richness. A 'dilution effect' (*sensu* Keesing et al. 2006), where increased species diversity reduces disease risk for individual species, has been described for some diseases (e.g. tick-borne diseases, Norman et al. 1999, Ostfeld and LoGiudice 2003, viral pulmonary disease, Ruedas et al. 2004, mosquito-borne diseases, Ezenwa et al. 2006, Allan et al. 2009). This indicates richness loss can lead to more disease. Keesing et al. (2006) provides a detailed explanation of the mechanisms through which higher species richness decreases disease risk, including: reducing the rate of encounter between susceptible and infectious individuals, reducing the probability of transmission given an encounter, decreasing the density of susceptible individuals, increasing the recovery rate and increasing the death rate of infected individuals.

Seed dispersal is also affected by diversity loss. García and Martínez (2012) found a clear positive relationship between richness of frugivorous birds and all components of seed dispersal (i.e. seed richness and abundance and arrival and colonisation rates). Just like pollination and biological control, this suggests the existence of functional complementarity and/or facilitation amongst dispersers.

In general, even though initial species loss can be compensated by remaining species with similar functions, significant species loss will eventually reduce provisioning of FES. Therefore, to secure FES production, it is essential to conserve species richness.

Population loss

Along with species richness, population size or abundance, are determining factors for FES provision. Since population losses are higher than diversity losses (Ceballos and Ehrlich 2002, Gaston et al. 2003), these can have major implications on the magnitude and quality of FES provision.

Losses in pollinator populations produce a negative impact in wild plant communities, affecting the integrity of natural vegetation (Williams 2002, Biesmeijer et al. 2006). Additionally, population declines reduce crop production (Kremen et al. 2002, Larsen et al. 2005, Klein et al. 2007), causing important economic losses (Losey and Vaughan 2006, Gallai et al. 2009) and jeopardising food sufficiency worldwide (Aizen et al. 2009).

Equally affected is the pest control service, where abundance of natural enemies, predators and parasitoid species, largely determines the abundance of species that can become pests (Drechsler and Settele 2001, Mols and Visser 2007, Railsback and Johnson 2014). Like pollinators, losses in natural enemy populations cause losses in natural and agricultural systems (Losey and Vaughan 2006, Oerke 2006).

Regarding the disease control service, population size of hosts has a complex effect on transmission dynamics. Through model-based analysis, Norman et al. (1999), and

Gilbert et al. (2001) suggested that intermediate abundances of non-viraemic hosts (i.e. where pathogens do not enter the bloodstream) allow persistence in viraemic hosts, whereas high or low abundances lead to vector fadeout. Keesing et al. (2006) provided an example of how variation of population sizes of two rodent species through time affects disease spread: when there is a high density of chipmunks, there is a reduction in tick burdens on white-footed mice (the most competent reservoir for the Lyme bacterium). Losses in populations can lead to unpredictable effects on spread of vector transmitted diseases.

Decline in frugivorous populations reduce availability and quality of seed dispersal services (McConkey and Drake 2006, Peres and Palacios 2007). McConkey and Drake (2006) demonstrated that there is a threshold in population size for service provision; this is when the functionality of dispersers is lost, even before the individuals become rare. Therefore, the losses in disperser populations should not be dramatic to have a great impact on the seed dispersal service.

Thus, a decrease in abundance of FES providers has a negative impact on FES provision. Even though the reduction is small, the consequences on FES production can be significant given the complex interactions amongst the providers and the ecosystem functioning. Population losses imply more immediate effects than the loss of richness.

Potential impacts of future land use and cover change on faunal ecosystem service provision

While the understanding of the effects of current LUCC on ES provision has increased (Nelson et al. 2010), few studies have assessed the potential effects in the future (Nelson and Daily 2010). One of these is the assessment made by Lawler et al. (2014). They used LUCC models to assess the effects on the provision of carbon storage, timber production, food production and wildlife habitat. They projected LUCC from 2001 to 2051 for the United States under two scenarios: 1) a large increase in croplands (28.2 million ha) due to a high crop demand, mirroring conditions starting in 2007; and 2) a loss of cropland (11.2 million ha) mirroring conditions in the 1990s. These scenarios result in large differences in land-use trajectories that generate increases in ES from increased yields (even with declines in cropland area) and >10% decreases in wildlife habitat.

Mulligan (2015a) assessed the effects of agriculturalisation in Brazil and Colombia on carbon storage and sequestration, water services, hazard mitigation and species richness and endemism. He projected LUCC forward to 2100, using historic rates of conversion with new areas of agricultural growth based on agricultural suitability, proximity to current deforestation fronts and current and likely new transport routes, under two scenarios: 1) change is excluded from occurring in current protected areas and 2) change occurs both within and outside of protected areas. In both scenarios, there is a decrease in services, although it is lower in the first scenario. Similarly, Mulligan (2015b) assessed the effects of the same scenarios on these same services pantropically from 2010 to 2050. Results suggest rapid agriculturalisation in the tropics implying considerable threats to the remaining natural capital and ES provision.

Regarding FES, Aizen et al. (2009) modelled the potential expansion of cropland and the resultant decline of pollinator populations. Based on annual data compiled for 45 years (1961–2006), they estimated a decrease of 8% in agricultural production due to loss of pollinator population. Crops with the least yield growth over the last five decades generally had the greatest expansion of cultivated area – including avocado, blueberry, cherry, plums and raspberry, which are highly pollinator-dependent. Therefore, they predict an increase in cultivated area, particularly in the developing world – mostly distributed in the tropics. Potential effects of future agriculturalisation on other FES remain to be evaluated.

Although there is still much to know about the future impacts of LUCC on FES provision, it seems possible to assess changes in supply in relation to agriculturalisation.

Expected demand for regulation faunal ecosystem services

ES demand is the sum of ecosystem goods and services currently consumed or used in a certain area over a given time of period (Burkhard et al. 2012). Therefore, to assess demand for ES – or FES – we need to know the factors determining their use in order to infer changes in demand as these factors change with agriculturalisation. For instance, the increasing demand for food, derived from population growth, the growing diversification of human diet, particularly in industrialised nations and globalisation in food trade have increased demand for many animal-pollinated crops. This is likely to continue in the future (Aizen et al. 2009).

World population is expected to reach 9 billion people by 2050 and would require raising overall food production by 70% (FAO 2009). Production in the developing countries would need to almost double. This implies significant increases in the production of several commodities, including crops (Alexandratos and Bruinsma 2012). Since agricultural land has a high demand for regulation ES and FES (Burkhard et al. 2012), such as pollination, natural pest control or nutrient regulation, an increase in demand for these services is expected.

Today, the developing world represents more than two thirds of global agricultural production and cultivated land and supports agriculture, which per unit of production, is 50% more pollinator-dependent than that of the developed world (Aizen et al. 2009). Along with the increase in food demand, the shortage in pollinator population might result in an increase in demand for agricultural land (Aizen et al. 2009), since per unit area crop yield may be reduced in the absence of pollinators (Morandin and Winston 2005, Aizen et al. 2009), causing, in turn, more extensive demand of FES provision.

Human induced changes might increase the demand for natural disease control. For instance, the development of irrigation systems is likely to increase the risk of contracting diseases such as dengue and malaria, by favouring the breeding of vectors, like flies and mosquitoes, in areas where they were absent or rare (Fuller et al. 2012). Irrigated cropland has expanded considerably since 1970 and is projected to increase a further 20% worldwide by 2030, reaching almost 2,500,000 km^2 (Turral et al. 2010). Therefore, an increase in vector-disease outbreaks may be expected, as vectors may disperse to newly irrigated areas (Fuller et al. 2012).

Global forest area is projected to continue to decrease over the next years, although at a lower rate compared with the beginning of the century, declining from 0.13% to 0.06% per year by 2030 (d'Annunzio et al. 2015). This projection of forest area is the net result of increase in some regions and decrease in others. Faunal seed dispersal is a service that might help to regenerate and shape the forest structure in these areas, by allowing the seed movement of animal-dependent tree species. However, in general, based on the past and current information, the projections suggest an increase in FES demand due to agricultural expansion at the same times as there is a reduction in FES supply.

Conclusions

Ecosystem functions deliver final benefits or goods through the provision of ecosystem services where there is demand for them. To achieve proper management, conservation and valuation of such functions or of regulation ecosystem services and FES, an accurate characterisation is essential and understanding the providers of these services is a significant part. Animal populations are key providers of regulation services and simultaneously can be source of disservices. To secure the service provided and minimise disservices, it is imperative to continue studying their role, to understand the potential implications of their loss and to use this evidence base to advise conservation and sustainable land use.

We identified two components of faunal diversity as influential to FES provision, richness and abundance. Richness brings functional diversity and complementarity, improving the range of FES provision, while a higher number of species improves the magnitude and spatial distribution of provision, since it is abundance that determines the occurrence of these services. Speciose systems with low species abundance may have low or null FES provision.

Animal species may also be a source of disservices to people. We identified invasive and native species pest outbreaks as the most common sources of disservice. Animal populations can be the main actors or can act as vectors of viral, bacterial or fungal pests. The evidence suggests that invasive species can be an indirect source of disservice when disrupting the service provision by native species, while native species may impact directly as crop pests, human disease vectors or crop raiders.

Several studies suggest that agriculturalisation has negative effects on FES providers due to landscape homogenisation, habitat loss and fragmentation, microclimatic changes and population imbalance, causing species and population losses. This increases the occurrence of disservices, impacting FES production through the decrease of functional complementarity — in the case of pollination, seed dispersal and pest control — or dilution effect — for human disease control and increasing crop and disease pest populations and wildlife-human conflict.

Few studies have addressed potential effects of LUCC on FES provision under different scenarios of agricultural change. LUCC models can be used to drive models for current and future FES provision. Such analyses are particularly important given the expected concomitant increase in demand for FES as land continues to be converted for agriculture.

The effects of land use change on FES providers have been assessed mostly at the local scale, using a range of approaches. To improve understanding of these effects at wider scales, it is desirable to develop a common approach to allow comparison and to identify land use configurations that maximise FES provision. For this, further research is required; first, to know the spatial distribution of FES providers; second, to identify the suitable conditions that allow FES providers to provide the FES and third, to relate these conditions to characteristics of land use and cover. Moreover, to date, the different FES have been evaluated independently: analysing them together can provide valuable information about distribution patterns, synergies and trade-offs amongst them.

Conservation prioritisation must factor in faunal ecosystem services (and disservices) as the most biodiversity-relevant of all ecosystem services and those which most closely links sites of conservation value that provide services with nearby sites of service use of agricultural and economic value. This will require the development of spatial models of faunal ecosystem services and disservices to compliment the ecosystem service models in existing tools such as Co$ting Nature (Mulligan et al. 2010, Mulligan 2015b) and InVEST (Tallis and Polasky 2009) and to drive these for baseline and scenarios of land use using LUCC models.

Maximum robustness of modelling results for policy formulation is achieved by using an ensemble of ecosystem service models, as has been common practice with climate models for decades. Each rigorous new approach to modelling faunal ecosystem services that is globally applicable and inter-operable or capable of comparison with existing models, can be a valuable contribution to improving our understanding of this important class of ecosystem services.

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References

Afrane YA, Zhou G, Lawson BW, Githeko AK, Yan G (2006) Effects of microclimatic changes caused by deforestation on the survivorship and reproductive fitness of Anopheles gambiae in Western Kenya highlands. The American journal of tropical medicine and hygiene 74: 772–778. doi:http://www.ajtmh.org/content/74/5/772.abstract

Aizen MA, Garibaldi LA, Cunningham SA, Klein AM (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. Annals of Botany 103(9): 1579–1588. https://doi.org/10.1093/aob/mcp076

Alexandratos N, Bruinsma J (2012) World agriculture towards 2030/2050: the 2012 revision. ESA Working paper Rome, FAO, 147 pp. http://www.fao.org/docrep/016/ap106e/ap106e.pdf

Allan BF, Langerhans RB, Ryberg WA, Landesman WJ, Griffin NW, Katz RS, Oberle BJ, Schutzenhofer MR, Smyth KN, de St. Maurice A, Clark L, Crooks KR, Hernandez DE, McLean RG, Ostfeld RS, Chase JM (2009) Ecological correlates of risk and incidence of West Nile virus in the United States. Oecologia 158: 699–708. https://doi.org/10.1007/s00442-008-1169-9

Alpert P (2006) The advantages and disadvantages of being introduced. Biological Invasions 8(7): 1523–1534. https://doi.org/10.1007/s10530-005-5844-z

Altieri MA (1999) The ecological role of biodiversity in agroecosystems. In: Paoletti MG (Ed.) Invertebrate Biodiversity as Bioindicators of Sustainable Landscapes. Elsevier, Amsterdam, 19–31. https://doi.org/10.1016/B978-0-444-50019-9.50005-4

Altieri MA (2018) Ecological management of insect pests, pathogens and weeds. In: Altieri MA (Ed.) Agroecology: the science of sustainable agriculture. CRC Press, 16. https://www.taylorfrancis.com/books/9780429964015

Ango TG, Börjeson L, Senbeta F (2016) Crop raiding by wild mammals in Ethiopia: Impacts on the livelihoods of smallholders in an agriculture-forest mosaic landscape. Oryx 51(03): 527–537. https://doi.org/10.1017/S0030605316000028

Balmford A, Bruner A, Cooper P, Costanza R, Farber S, Green RE, Jenkins M, Jefferiss P, Jessamy V, Madden J, Munro K, Myers N, Naeem S, Paavola J, Rayment M, Rosendo S, Roughgarden J, Trumper K, Turner RK (2002) Economic Reasons for Conserving Wild Nature. Science 297(5583): 950–953. https://doi.org/10.1126/science.1073947

Balvanera P, Daily GC, Ehrlich PR, Ricketts TH, Bailey S-A, Kark S, Kremen C, Pereira H (2001) Conserving Biodiversity and Ecosystem Services. Science 291(5511): 2047. https://doi.org/10.1126/science.291.5511.2047

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9(10): 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Bastian O (2013) The role of biodiversity in supporting ecosystem services in Natura 2000 sites. Ecological Indicators 24: 12–22. https://doi.org/10.1016/j.ecolind.2012.05.016

Bebber DP, Ramotowski MAT, Gurr SJ (2013) Crop pests and pathogens move polewards in a warming world. Nature Climate Change 3(11): 985–988. https://doi.org/10.1038/nclimate1990

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. Science 313(5785): 351–354. https://doi.org/10.1126/science.1127863

Blanche R, Cunningham SA (2005) Rain Forest Provides Pollinating Beetles for Atemoya Crops. Journal of Economic Entomology 98(4): 1193–1201. https://doi.org/10.1603/0022-0493-98.4.1193

Blüthgen N, Klein A-M (2011) Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. Basic and Applied Ecology 12(4): 282–291. https://doi.org/10.1016/j.baae.2010.11.0011

Boatman ND, Brickle NW, Hart JD, Milsom TP, Morris AJ, Murray AWA, Murray KA, Robertson PA (2004) Evidence for the indirect effects of pesticides on farmland birds. The Ibis 146: 131–143. https://doi.org/10.1111/j.1474-919X.2004.00347.x

Budzinski H, Couderchet M (2018) Environmental and human health issues related to pesticides: From usage and environmental fate to impact. Environmental Science and Pollution Research International 25(15): 14277–14279. https://doi.org/10.1007/s11356-018-1738-3

Bukovinszky T, Verheijen J, Zwerver S, Klop E, Biesmeijer JC, Wäckers FL, Prins HHT, Kleijn D (2017) Exploring the relationships between landscape complexity, wild bee species richness and reproduction, and pollination services along a complexity gradient in the Netherlands. Biological Conservation 214: 312–319. https://doi.org/10.1016/j.biocon.2017.08.027

Burkhard B, Kroll F, Nedkov S, Müller F (2012) Mapping ecosystem service supply, demand and budgets. Ecological Indicators 21: 17–29. https://doi.org/10.1016/j.ecolind.2011.06.019

Campbell DJ, Gichohi H, Mwangi A, Chege L (2000) Land use conflict in Kajiado District, Kenya. Land Use Policy 17(4): 337–348. https://doi.org/10.1016/S0264-8377(00)00038-7

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. American Journal of Botany 98(3): 572–592. https://doi.org/10.3732/ajb.1000364

Ceballos G, Ehrlich PR (2002) Mammal Population Losses and the Extinction Crisis. Science 296(5569): 904–907. https://doi.org/10.1126/science.1069349

Chakravarthy AK, Thyagaraj NE (2005) Coexistence of bonnet macaques (*Macaca radiata radiata* Geoffroy) with planters in the cardamom (*Elettaria cardamomum* Maton) and coffee (*Coffea arabica* Linnaeus) plantations of Karnataka, South India: hospitable or hostile. In: Paterson JD, Wallis J (Eds) Commensalism and conflict: the human-primate interface. The American Society of Primatologists, Norman, OK, 271–293

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 405(6783): 234–242. https://doi.org/10.1038/35012241

Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecology Letters 14(9): 922–932. https://doi.org/10.1111/j.1461-0248.2011.01642.x

Chaves ÓM, Bicca-Marques JC (2017) Crop Feeding by Brown Howlers (Alouatta guariba clamitans) in Forest Fragments: The Conservation Value of Cultivated Species. International Journal of Primatology 38(2): 263–281. https://doi.org/10.1007/s10764-016-9927-88

Chen B, Xu B (2015) A Novel Method for Measuring Landscape Heterogeneity Changes. IEEE Geoscience and Remote Sensing Letters 12(3): 567–571. https://doi.org/10.1109/LGRS.2014.2351575

Cimon-Morin J, Darveau M, Poulin M (2013) Fostering synergies between ecosystem services and biodiversity in conservation planning: A review. Biological Conservation 166: 144–154. https://doi.org/10.1016/j.biocon.2013.06.023

Civitello DJ, Cohen J, Fatima H, Halstead NT, Liriano J, McMahon TA, Ortega CN, Sauer EL, Sehgal T, Young S, Rohr JR (2015) Biodiversity inhibits parasites: Broad evidence for the dilution effect. Proceedings of the National Academy of Sciences of the United States of America 112(28): 8667–8671. https://doi.org/10.1073/pnas.1506279112

Crowder DW, Northfield TD, Strand MR, Snyder WE (2010) Organic agriculture promotes evenness and natural pest control. Nature 466(7302): 109–112. https://doi.org/10.1038/nature09183

D'Antonio CM, Jackson NE, Horvitz CC, Hedberg R (2004) Invasive plants in wildland ecosystems: Merging the study of invasion processes with management needs. Frontiers in Ecology and the Environment 2(10): 513–521. https://doi.org/10.1890/1540-9295(2004)002[0513:IPIWEM]2.0.CO;2

d'Annunzio R, Sandker M, Finegold Y, Min Z (2015) Projecting global forest area towards 2030. Forest Ecology and Management 352: 124–133. https://doi.org/10.1016/j.foreco.2015.03.014

Dale V (1994) Effects of Land-Use Change on Atmospheric CO2 Concentrations. Springer New York, 1–14. https://doi.org/10.1007/978-1-4613-8363-5_1

Davies TE, Wilson S, Hazarika N, Chakrabarty J, Das D, Hodgson DJ, Zimmermann A (2011) Effectiveness of intervention methods against crop-raiding elephants. Conservation Letters 4(5): 346–354. https://doi.org/10.1111/j.1755-263X.2011.00182.x

de Groot RS, Alkemade R, Braat L, Hein L, Willemen L (2010) Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. Ecological Complexity 7(3): 260–272. https://doi.org/10.1016/j.ecocom.2009.10.006

Desneux N, Decourtye A, Delpuech J-M (2007) The Sublethal Effects of Pesticides on Beneficial Arthropods. Annual Review of Entomology 52(1): 81–106. https://doi.org/10.1146/annurev.ento.52.110405.091440

Dobson AP, Carper ER (1996) Infectious diseases and human population history. Bioscience 46(2): 115–126. https://doi.org/10.2307/1312814

Drechsler M, Settele J (2001) Predator-prey interactions in rice ecosystems: Effects of guild composition, trophic relationships, and land use changes — a model study exemplified for Philippine rice terraces. Ecological Modelling 137(2–3): 135–159. https://doi.org/10.1016/S0304-3800(00)00423-3

Duncan C, Thompson JR, Pettorelli N (2015) The quest for a mechanistic understanding of biodiversity-ecosystem services relationships. Proceedings of the Royal Society of

London. Series B, Biological Sciences 282(1817): 20151348. https://doi.org/10.1098/rspb.2015.1348

Egerer MH, Fricke EC, Rogers HS (2018) Seed dispersal as an ecosystem service: Frugivore loss leads to decline of a socially valued plant, Capsicum frutescens. Ecological Applications 28(3): 655–667. https://doi.org/10.1002/eap.1667

Egoh B, Reyers B, Rouget M, Bode M, Richardson DM (2009) Spatial congruence between biodiversity and ecosystem services in South Africa. Biological Conservation 142(3): 553–562. https://doi.org/10.1016/j.biocon.2008.11.009

Engeman RM, Laborde JE, Constantin BU, Shwiff SA, Hall P, Duffiney A, Luciano F (2010) The economic impacts to commercial farms from invasive monkeys in Puerto Rico. Crop Protection (Guildford, Surrey) 29(4): 401–405. https://doi.org/10.1016/j.cropro.2009.10.021

Escobedo FJ, Kroeger T, Wagner JE (2011) Urban forests and pollution mitigation: Analyzing ecosystem services and disservices. Environmental Pollution 159(8–9): 2078–2087. https://doi.org/10.1016/j.envpol.2011.01.010

Ezenwa VO, Godsey MS, King RJ, Guptill SC (2006) Avian diversity and West Nile virus: Testing associations between biodiversity and infectious disease risk. Proceedings. Biological Sciences 273(1582): 109–117. https://doi.org/10.1098/rspb.2005.3284

Fahrig L (1997) Relative Effects of Habitat Loss and Fragmentation on Population Extinction. The Journal of Wildlife Management 61(3): 603–610. https://doi.org/10.2307/3802168

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology Letters 14(2): 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

FAO (2009) How to feed the world in 2050. Food and Agriculture Organization of the United Nations, Rome.

FAO (2015) Global Forest Resources Assessment 2015 How are the world's forests changing? Food and Agriculture Organization of the United Nations, Rome.

Fiedler AK, Landis DA, Wratten SD (2008) Maximizing ecosystem services from conservation biological control: The role of habitat management. Biological Control 45(2): 254–271. https://doi.org/10.1016/j.biocontrol.2007.12.009

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global Consequences of Land Use. Science 309(5734): 570–574. https://doi.org/10.1126/science.1111772

Frimpong EA, Gemmill-Herren B, Gordon I, Kwapong PK (2011) Dynamics of insect pollinators as influenced by cocoa production systems in Ghana. Journal of Pollination Ecology. http://www.pollinationecology.org/index.php?journal=jpe&page=article&op=view&path%5B%5D=111&path%5B%5D=16

Frumhoff PC (1995) Conserving Wildlife in Tropical Forests Managed for Timber. Bioscience 45(7): 456–464. https://doi.org/10.2307/1312789

Fujita MS, Tuttle MD (1991) Flying Foxes (Chiroptera: Pteropodidae): Threatened Animals of Key Ecological and Economic Importance. Conservation Biology 5(4): 455–463. https://doi.org/10.1111/j.1523-1739.1991.tb00352.x

Fuller DO, Parenti MS, Hassan AN, Beier JC (2012) Linking land cover and species distribution models to project potential ranges of malaria vectors: An example using Anopheles arabiensis in Sudan and Upper Egypt. Malaria Journal 11(1): 264. https://doi.org/10.1186/1475-2875-11-264

Gallai N, Salles J-M, Settele J, Vaissière BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics 68(3): 810–821. https://doi.org/10.1016/j.ecolecon.2008.06.014

García D, Martínez D (2012) Species richness matters for the quality of ecosystem services: A test using seed dispersal by frugivorous birds. Proceedings of the Royal Society of London. Series B, Biological Sciences 279(1740): 3106–3113. https://doi.org/10.1098/rspb.2012.0175

Gardiner MM, Landis DA, Gratton C, DiFonzo CD, O'Neal M, Chacon JM, Wayo MT, Schmidt NP, Mueller EE, Heimpel GE (2009) Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. Ecological Applications 19(1): 143–154. https://doi.org/10.1890/07-1265.1

Garratt MPD, Breeze TD, Boreux V, Fountain MT, McKerchar M, Webber SM, Coston DJ, Jenner N, Dean R, Westbury DB, Biesmeijer JC, Potts SG (2016) Apple Pollination: Demand Depends on Variety and Supply Depends on Pollinator Identity. PLoS One 11(5): e0153889. https://doi.org/10.1371/journal.pone.0153889

Gaston KJ, Blackburn TM, Goldewijk KK (2003) Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society of London. Series B, Biological Sciences 270(1521): 1293–1300. https://doi.org/10.1098/rspb.2002.2303

Geiger F, Bengtsson J, Berendse F, Weisser WW, Emmerson M, Morales MB, Ceryngier P, Liira J, Tscharntke T, Winqvist C, Eggers S, Bommarco R, Pärt T, Bretagnolle V, Plantegenest M, Clement LW, Dennis C, Palmer C, Oñate JJ, Guerrero I, Hawro V, Aavik T, Thies C, Flohre A, Hänke S, Fischer C, Goedhart PW, Inchausti P (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic and Applied Ecology 11(2): 97–105. https://doi.org/10.1016/j.baae.2009.12.001

Gibbons JW, Scott DE, Ryan TJ, Buhlmann KA, Tuberville TD, Metts BS, Greene JL, Mills T, Leiden Y, Poppy S, Winne CT (2000) The Global Decline of Reptiles, Déjà Vu Amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. Bioscience 50: 653–666. https://doi.org/10.1641/0006-3568(2000)050[0653:TGDORD]2.0.CO;2

Gilbert L, Norman R, Laurenson KM, Reid HW, Hudson PJ (2001) Disease persistence and apparent competition in a three-host community: An empirical and analytical study of large-scale, wild populations. Journal of Animal Ecology 70(6): 1053–1061. https://doi.org/10.1046/j.0021-8790.2001.00558.x

Goldammer JG, Seibert B (1990) The impact of droughts and forest fires on tropical lowland rain forest of East Kalimantan. In: Goldammer JG (Ed.) Fire in the tropical biota. Springer, 11–31.

Goldewijk KK (2001) Estimating global land use change over the past 300 years: The HYDE Database. Global Biogeochemical Cycles 15(2): 417–433. https://doi.org/10.1029/1999GB001232

Gosper CR, Stansbury CD, Vivian-Smith G (2005) Seed dispersal of fleshy-fruited invasive plants by birds: Contributing factors and management options. Diversity & Distributions 11(6): 549–558. https://doi.org/10.1111/j.1366-9516.2005.00195.x

Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4(4): 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Grau HR, Aide M (2008) Globalization and land-use transitions in Latin America. Ecology and Society 13(2): 16. https://doi.org/10.5751/ES-02559-130216

Greene DF, Calogeropoulos C (2002) Measuring and modelling seed dispersal of terrestrial plants. In: Bullock J, Kenward R, Hails R (Eds) Dispersal Ecology: The 42nd Symposium of the British Ecological Society. Blackwell Publishing (Oxford), 3–23.

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song D-X, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1(2): e1500052. https://doi.org/10.1126/sciadv.1500052

Haines-Young R, Potschin M (2011) Common international classification of ecosystem services (CICES): 2011 Update. Report to the European Environmental Agency, Nottingham.

Harrison PA, Berry PM, Simpson G, Haslett JR, Blicharska M, Bucur M, Dunford R, Egoh B, Garcia-Llorente M, Geamănă N, Geertsema W, Lommelen E, Meiresonne L, Turkelboom F (2014) Linkages between biodiversity attributes and ecosystem services: A systematic review. Ecosystem Services 9: 191–203. https://doi.org/10.1016/j.ecoser.2014.05.006

Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348(6232): 336–340. https://doi.org/10.1126/science.aaa1788

He F, Hubbell SP (2011) Species-area relationships always overestimate extinction rates from habitat loss. Nature 473: 368–371. doi:http://www.nature.com/nature/journal/v473/n7347/abs/10.1038-nature09985-unlocked.html#supplementary-information

Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. Nature 448: 188–190.

Hedges S, Gunaryadi D (2010) Reducing human-elephant conflict: Do chillies help deter elephants from entering crop fields? Oryx 44(01): 139–146. https://doi.org/10.1017/S0030605309990093

Henchion M, McCarthy M, Resconi VC, Troy D (2014) Meat consumption: Trends and quality matters. Meat Science 98(3): 561–568. https://doi.org/10.1016/j.meatsci.2014.06.007

Hill CM (1997) Crop-raiding by wild vertebrates: The farmer's perspective in an agricultural community in western Uganda. International Journal of Pest Management 43(1): 77–84. https://doi.org/10.1080/096708797229022

Hill CM (2016) Crop Raiding. The International Encyclopedia of Primatology. John Wiley & Sons, Inc. https://doi.org/10.1002/9781119179313.wbprim0109

Horsfall JG (1983) Impact of introduced pests on man. In: Graham CLWL (Ed.) Exotic Plant Pests and North American Agriculture. Academic Press, London, 1–13. https://doi.org/10.1016/B978-0-12-757880-4.50006-3

Hougner C, Colding J, Söderqvist T (2006) Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden. Ecological Economics 59(3): 364–374. https://doi.org/10.1016/j.ecolecon.2005.11.007

Hughes JB, Daily GC, Ehrlich PR (1997) Population Diversity: Its Extent and Extinction. Science 278(5338): 689–692. https://doi.org/10.1126/science.278.5338.689

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. Nature 477: 199–202. http://www.nature.com/nature/journal/v477/n7363/abs/nature10282.html#supplementary-information

Isbell F, Tilman D, Polasky S, Loreau M (2015) The biodiversity-dependent ecosystem service debt. Ecology Letters 18(2): 119–134.https://doi.org/10.1111/ele.12393

Isenring R (2010) Pesticides and the loss of biodiversity: How intensive pesticide use affects wildlife populations and species diversity. In: Network PA (Ed.) Pesticides News, London, 2–12.

Jonason D, Ekroos J, Öckinger E, Helenius J, Kuussaari M, Tiainen J, Smith HG, Lindborg R (2017) Weak functional response to agricultural landscape homogenisation among plants, butterflies and birds. Ecography 40(10): 1221–1230. https://doi.org/10.1111/ecog.02268

Jonsen I, Fahrig L (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. Landscape Ecology 12(3): 185–197. https://doi.org/10.1023/A:1007961006232

Karp DS, Daily GC (2014) Cascading effects of insectivorous birds and bats in tropical coffee plantations. Ecology 95(4): 1065–1074. https://doi.org/10.1890/13-1012.1

Katayama N, Amano T, Naoe S, Yamakita T, Komatsu I, Takagawa S-i, Sato N, Ueta M, Miyashita T (2014) Landscape Heterogeneity-Biodiversity Relationship: Effect of Range Size. PLoS One 9(3): e93359. https://doi.org/10.1371/journal.pone.0093359

Keesing F, Holt RD, Ostfeld RS (2006) Effects of species diversity on disease risk. Ecology Letters 9(4): 485–498. https://doi.org/10.1111/j.1461-0248.2006.00885.x

Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweiger O, Colla SR, Richardson LL, Wagner DL, Gall LF, Sikes DS, Pantoja A (2015) Climate change impacts on bumblebees converge across continents. Science 349(6244): 177–180. https://doi.org/10.1126/science.aaa7031

Kleijn D, Winfree R, Bartomeus I, Carvalheiro LG, Henry M, Isaacs R, Klein A-M, Kremen C, M'Gonigle LK, Rader R, Ricketts TH, Williams NM, Lee Adamson N, Ascher JS, Báldi A, Batáry P, Benjamin F, Biesmeijer JC, Blitzer EJ, Bommarco R, Brand MR, Bretagnolle V, Button L, Cariveau DP, Chifflet R, Colville JF, Danforth BN, Elle E, Garratt MPD, Herzog F, Holzschuh A, Howlett BG, Jauker F, Jha S, Knop E, Krewenka KM, Le Féon V, Mandelik Y, May EA, Park MG, Pisanty G, Reemer M, Riedinger V, Rollin O, Rundlöf M, Sardiñas HS, Scheper J, Sciligo AR, Smith HG, Steffan-Dewenter I, Thorp R, Tscharntke T, Verhulst J, Viana BF, Vaissière BE, Veldtman R, Ward KL, Westphal C, Potts SG (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature Communications 6(1): 7414. https://doi.org/10.1038/ncomms8414

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London. Series B, Biological Sciences 274(1608): 303–313. https://doi.org/10.1098/rspb.2006.3721

Koh LP (2008) Birds defend oil palms from herbivorus insects. Ecological Applications 18(4): 821–825. https://doi.org/10.1890/07-1650.1

Kremen C (2005) Managing ecosystem services: What do we need to know about their ecology? Ecology Letters 8(5): 468–479.https://doi.org/10.1111/j.1461-0248.2005.00751.x

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Packer L, Potts SG, Roulston T, Steffan-Dewenter I, Vázquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein A-M, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. Ecology Letters 10(4): 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences of the United States of America 99(26): 16812–16816. https://doi.org/10.1073/pnas.262413599

Larsen FW, Londoño-Murcia MC, Turner WR (2011) Global priorities for conservation of threatened species, carbon storage, and freshwater services: Scope for synergy? Conservation Letters 4(5): 355–363. https://doi.org/10.1111/j.1755-263X.2011.00183.x

Larsen TH, Williams NM, Kremen C (2005) Extinction order and altered community structure rapidly disrupt ecosystem functioning. Ecology Letters 8(5): 538–547. https://doi.org/10.1111/j.1461-0248.2005.00749.x

Lawler JJ, Lewis DJ, Nelson E, Plantinga AJ, Polasky S, Withey JC, Helmers DP, Martinuzzi S, Pennington D, Radeloff VC (2014) Projected land-use change impacts on ecosystem services in the United States. Proceedings of the National Academy of Sciences of the United States of America 111(20): 7492–7497. https://doi.org/10.1073/pnas.1405557111

Letourneau DK, Bothwell Allen SG, Kula RR, Sharkey MJ, Stireman JO III (2015) Habitat eradication and cropland intensification may reduce parasitoid diversity and natural pest control services in annual crop fields. Elementa. Science of the Anthropocene 3: 69. https://doi.org/10.12952/journal.elementa.000069

Levey DJ, Tewksbury JJ, Bolker BM (2008) Modelling long-distance seed dispersal in heterogeneous landscapes. Journal of Ecology 96(4): 599–608. https://doi.org/10.1111/j.1365-2745.2008.01401.x

Levin SA, Carpenter SR, Godfray HCJ, Kinzig AP, Loreau M, Losos JB, Walker B, Wilcove DS (2009) The Princeton guide to ecology. Princeton University Press. https://doi.org/10.1515/9781400833023

Limburg KE, Luzadis VA, Ramsey M, Schulz KL, Mayer CM (2010) The good, the bad, and the algae: Perceiving ecosystem services and disservices generated by zebra and quagga mussels. Journal of Great Lakes Research 36(1): 86–92. https://doi.org/10.1016/j.jglr.2009.11.007

Linkie M, Dinata Y, Nofrianto A, Leader-Williams N (2007) Patterns and perceptions of wildlife crop raiding in and around Kerinci Seblat National Park, Sumatra. Animal Conservation 10(1): 127–135. https://doi.org/10.1111/j.1469-1795.2006.00083.x

Losey JE, Vaughan M (2006) The Economic Value of Ecological Services Provided by Insects. Bioscience 56(4): 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Luck GW, Daily GC, Ehrlich PR (2003) Population diversity and ecosystem services. Trends in Ecology & Evolution 18(7): 331–336. https://doi.org/10.1016/S0169-5347(03)00100-9

Luck GW, Harrington R, Harrison PA, Kremen C, Berry PM, Bugter R, Dawson TP, de Bello F, Díaz S, Feld CK, Haslett JR, Hering D, Kontogianni A, Lavorel S, Rounsevell M, Samways MJ, Sandin L, Settele J, Sykes MT, van den Hove S, Vandewalle M, Zobel M (2009) Quantifying the Contribution of Organisms to the Provision of Ecosystem Services. Bioscience 59(3): 223–235. https://doi.org/10.1525/bio.2009.59.3.7

Lyytimäki J (2015) Ecosystem disservices: Embrace the catchword. Ecosystem Services 12: 136. https://doi.org/10.1016/j.ecoser.2014.11.008

Lyytimäki J, Sipilä M (2009) Hopping on one leg – The challenge of ecosystem disservices for urban green management. Urban Forestry & Urban Greening 8(4): 309–315. https://doi.org/10.1016/j.ufug.2009.09.003

MA (2005) Ecosystems and Human Well-being: Synthesis. Millennium Ecosystem Assessment, Island Press, Washington, DC.

Maas B, Clough Y, Tscharntke T (2013) Bats and birds increase crop yield in tropical agroforestry landscapes. Ecology Letters 16(12): 1480–1487. https://doi.org/10.1111/ele.12194

Maas B, Karp DS, Bumrungsri S, Darras K, Gonthier D, Huang JCC, Lindell CA, Maine JJ, Mestre L, Michel NL, Morrison EB, Perfecto I, Philpott SM, Şekercioğlu ÇH, Silva RM, Taylor PJ, Tscharntke T, Van Bael SA, Whelan CJ, Williams-Guillén K (2016) Bird and bat predation services in tropical forests and agroforestry landscapes. Biological Reviews of the Cambridge Philosophical Society 91(4): 1081–1101. https://doi.org/10.1111/brv.12211

Mace GM, Norris K, Fitter AH (2012) Biodiversity and ecosystem services: A multilayered relationship. Trends in Ecology & Evolution 27(1): 19–26. https://doi.org/10.1016/j.tree.2011.08.006

McCauley DJ, Salkeld DJ, Young HS, Makundi R, Dirzo R, Eckerlin RP, Lambin EF, Gaffikin L, Barry M, Helgen KM (2015) Effects of land use on plague (*Yersinia pestis*) activity in rodents in Tanzania. The American Journal of Tropical Medicine and Hygiene 92(4): 776–783. https://doi.org/10.4269/ajtmh.14-0504

McConkey KR, Drake DR (2006) Flying Foxes Cease to Function as Seed Dispersers Long before They Become Rare. Ecology 87(2): 271–276. https://doi.org/10.1890/05-0386

McGuinness S, Taylor D (2014) Farmers' Perceptions and Actions to Decrease Crop Raiding by Forest-Dwelling Primates Around a Rwandan Forest Fragment. Human Dimensions of Wildlife 19(2): 179–190. https://doi.org/10.1080/10871209.2014.853330

Meyer WB, Turner BL II (1992) Human Population Growth and Global Land-Use/Cover Change. Annual Review of Ecology and Systematics 23(1): 39–61.https://doi.org/10.1146/annurev.es.23.110192.000351

Miles A, Wilson H, Altieri M, Nicholls C (2012) Habitat Diversity at the Field and Landscape Level: Conservation Biological Control Research in California Viticulture. In: Bostanian NJ, Vincent C, Isaacs R (Eds) Arthropod Management in Vineyards: Pests, Approaches, and Future Directions. Springer Netherlands, Dordrecht, 159–189. https://doi.org/10.1007/978-94-007-4032-7_8

Mols CMM, Visser ME (2007) Great Tits (*Parus major*) Reduce Caterpillar Damage in Commercial Apple Orchards. PLoS One 2(2): e202. https://doi.org/10.1371/journal.pone.0000202

Molyneux DH, Ostfeld RS, Bernstein A, Chivian E (2008) Ecosystem disturbance, biodiversity loss, and human infectious disease. In: Chivian E, Bernstein A (Eds) Sustaining life, how human health depends on biodiversity. Oxford University Press, New York, 287–323

Mooney HA (2005) Invasive alien species: the nature of the problem. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage J (Eds) Invasive Alien Species: A New Synthesis. Island Press, Washington DC, 1–15.

Morales CL, Sáez A, Garibaldi LA, Aizen MA (2017) Disruption of Pollination Services by Invasive Pollinator Species. In: Vilà M, Hulme PE (Eds) Impact of Biological Invasions on Ecosystem Services. Springer International Publishing, Cham, 203–220. https://doi.org/10.1007/978-3-319-45121-3_13

Morandin LA, Winston ML (2005) Wild bee abundance and seed production in conventional, organic, and genetically modified canola. Ecological Applications 15(3): 871–881. https://doi.org/10.1890/03-5271

Morandin LA, Winston ML (2006) Pollinators provide economic incentive to preserve natural land in agroecosystems. Agriculture, Ecosystems & Environment 116(3–4): 289–292. https://doi.org/10.1016/j.agee.2006.02.012

Mulligan M (2015a) Trading off agriculture with nature's other benefits, spatially. In: Zolin CA, Rodrigues RdAR (Eds) Impact of climate change on water resources in agriculture. CRC Press, Boca Raton, 184–204. https://doi.org/10.1201/b18652-10

Mulligan M (2015b) Tropical agriculturalisation: Scenarios, their environmental impacts and the role of climate change in determining water-for-food, locally and along supply chains. Food Security 7(6): 1133–1152. https://doi.org/10.1007/s12571-015-0506-1

Mulligan M (2018) Realised wildlife disservice. Co$ting Nature Policy Support System [0.3] http://www.policysupport.org/costingnature

Mulligan M, Guerry A, Arkema K, Bagstad K, Villa F (2010) Capturing and quantifying the flow of ecosystem services. In: Silvestri S, Kershaw F (Eds) Framing the flow: innovative approaches to understand, protect and value ecosystem services across linked habitats. UNEP World Conservation Monitoring Centre (Cambridge), 26–33. https://portals.iucn.org/library/sites/library/files/documents/Bios-Eco-Mar-Cst-007.pdf

Naidoo R, Balmford A, Costanza R, Fisher B, Green RE, Lehner B, Malcolm TR, Ricketts TH (2008) Global mapping of ecosystem services and conservation priorities. Proceedings of the National Academy of Sciences of the United States of America 105(28): 9495–9500. https://doi.org/10.1073/pnas.0707823105

Naughton-Treves L (1998) Predicting Patterns of Crop Damage by Wildlife around Kibale National Park, Uganda. Conservation Biology 12(1): 156–168. https://doi.org/10.1046/j.1523-1739.1998.96346.x

Naughton-Treves L, Treves A (2005) Socio-ecological factors shaping local support for wildlife: Crop-raiding by elephants and other wildlife in Africa. Conservation Biology Series Cambridge 9: 252.

Nelson E, Sander H, Hawthorne P, Conte M, Ennaanay D, Wolny S, Manson S, Polasky S (2010) Projecting Global Land-Use Change and Its Effect on Ecosystem Service Provision and Biodiversity with Simple Models. PLoS One 5(12): e14327. https://doi.org/10.1371/journal.pone.0014327

Nelson EJ, Daily GC (2010) Modelling ecosystem services in terrestrial systems. F1000 Biology Reports 2: 53. https://doi.org/10.3410/B2-53

Ninan KN, Inoue M (2013) Valuing forest ecosystem services: What we know and what we don't. Ecological Economics 93: 137–149. https://doi.org/10.1016/j.ecolecon.2013.05.005

Norman R, Bowers RG, Begon M, Hudson PJ (1999) Persistence of Tick-borne Virus in the Presence of Multiple Host Species: Tick Reservoirs and Parasite Mediated Competition. Journal of Theoretical Biology 200(1): 111–118. https://doi.org/10.1006/jtbi.1999.0982

Oerke EC (2006) Crop losses to pests. The Journal of Agricultural Science 144(01): 31–43. https://doi.org/10.1017/S0021859605005708

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120(3): 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Ostfeld RS, LoGiudice K (2003) Community disassembly, biodiversity loss, and the erosion of an ecosystem service. Ecology 84(6): 1421–1427. https://doi.org/10.1890/02-3125

Paoli GD, Peart DR, Leighton M, Samsoedin I (2001) An Ecological and Economic Assessment of the Nontimber Forest Product Gaharu Wood in Gunung Palung National Park, West Kalimantan, Indonesia. Conservation Biology 15(6): 1721–1732. https://doi.org/10.1046/j.1523-1739.2001.98586.x

Papadimitriou F (2010) Conceptual Modelling of Landscape Complexity. Landscape Research 35(5): 563–570. https://doi.org/10.1080/01426397.2010.504913

Parks KE, Mulligan M (2010) On the relationship between a resource based measure of geodiversity and broad scale biodiversity patterns. Biodiversity and Conservation 19(9): 2751–2766. https://doi.org/10.1007/s10531-010-9876-z

Peh KS-H, Balmford A, Birch JC, Brown C, Butchart SHM, Daley J, Dawson J, Gray G, Hughes FMR, Mendes S, Millett J, Stattersfield AJ, Thomas DHL, Walpole M, Bradbury RB (2015) Potential impact of invasive alien species on ecosystem services provided by a tropical forested ecosystem: A case study from Montserrat. Biological Invasions 17(1): 461–475. https://doi.org/10.1007/s10530-014-0743-9

Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. Trends in Ecology & Evolution 24(9): 497–504.https://doi.org/10.1016/j.tree.2009.03.016

Peres CA, Palacios E (2007) Basin-Wide Effects of Game Harvest on Vertebrate Population Densities in Amazonian Forests: Implications for Animal-Mediated Seed Dispersal. Biotropica 39(3): 304–315. https://doi.org/10.1111/j.1744-7429.2007.00272.x

Perfecto I, Vandermeer J (2006) The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. Agriculture, Ecosystems & Environment 117(2–3): 218–221. https://doi.org/10.1016/j.agee.2006.04.007

Pimentel D, Wilson C, McCullum C, Huang R, Dwen P, Flack J, Tran Q, Saltman T, Cliff B (1997) Economic and Environmental Benefits of Biodiversity. Bioscience 47(11): 747–757. https://doi.org/10.2307/1313097

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52(3): 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: Trends, impacts and drivers. Trends in Ecology & Evolution 25(6): 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Pyšek P, Richardson DM (2010) Invasive Species, Environmental Change and Management, and Health. Annual Review of Environment and Resources 35(1): 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

Railsback SF, Johnson MD (2014) Effects of land use on bird populations and pest control services on coffee farms. Proceedings of the National Academy of Sciences of the United States of America 111(16): 6109–6114. https://doi.org/10.1073/pnas.1320957111

Ramankutty N, Foley JA (1999) Estimating historical changes in global land cover: Croplands from 1700 to 1992. Global Biogeochemical Cycles 13(4): 997–1027. https://doi.org/10.1029/1999GB900046

Rao AS (2009) Climate and Microclimate Changes Influencing the Fauna of the Hot Indian Arid Zone. In: Sivaperuman C, Baqri QH, Ramaswamy G, Naseema M (Eds) Faunal Ecology and Conservation of the Great Indian Desert. Springer Berlin Heidelberg, 13–23. https://doi.org/10.1007/978-3-540-87409-6_2

Rasmussen LV, Christensen AE, Danielsen F, Dawson N, Martin A, Mertz O, Sikor T, Thongmanivong S, Xaydongvanh P (2017) From food to pest: Conversion factors determine switches between ecosystem services and disservices. Ambio 46(2): 173–183.https://doi.org/10.1007/s13280-016-0813-6

Reyes Sandoval WM (2017) Landscape Heterogeneity and Complexity: Implications for Terrestrial Carbon and Water Cycles. North Carolina State University, Raleigh. http://www.lib.ncsu.edu/resolver/1840.20/33660

Richardson DM, Allsopp N, D'antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions—The role of mutualisms. Biological Reviews of the Cambridge Philosophical Society 75(1): 65–93. https://doi.org/10.1017/S0006323199005435

Ricketts TH, Daily GC, Ehrlich PR, Michener CD (2004) Economic value of tropical forest to coffee production. Proceedings of the National Academy of Sciences of the United States of America 101(34): 12579–12582. https://doi.org/10.1073/pnas.0405147101

Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA, Ochieng' A, Viana BF (2008) Landscape effects on crop pollination services: Are there general patterns? Ecology Letters 11(5): 499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Ridder B (2008) Questioning the ecosystem services argument for biodiversity conservation. Biodiversity and Conservation 17(4): 781–790. https://doi.org/10.1007/s10531-008-9316-5

Risch SJ (1981) Insect Herbivore Abundance in Tropical Monocultures and Polycultures: An Experimental Test of Two Hypotheses. Ecology 62(5): 1325–1340. https://doi.org/10.2307/1937296

Rosenzweig C, Iglesias A, Yang XB, Epstein P, Chivian E (2001) Climate Change and Extreme Weather Events; Implications for Food Production, Plant Diseases, and Pests. Global Change and Human Health 2(2): 90–104.https://doi.org/10.1023/A:1015086831467

Roubik DW (1995) Pollination of cultivated plants in the tropics. Food & Agriculture Organization, 193 pp.

Ruedas LA, Salazar-Bravo J, Tinnin DS, Armién B, Cáceres L, García A, Diaz MÁ, Gracia F, Suzán G, Peters C (2004) Community ecology of small mammal populations in Panama following an outbreak of Hantavirus pulmonary syndrome. Journal of Vector Ecology 29: 177–191.

Rusch A, Chaplin-Kramer R, Gardiner MM, Hawro V, Holland J, Landis D, Thies C, Tscharntke T, Weisser WW, Winqvist C, Woltz M, Bommarco R (2016) Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agriculture, Ecosystems & Environment 221: 198–204. https://doi.org/10.1016/j.agee.2016.01.039

Russo SE, Portnoy S, Augspurger CK (2006) Incorporating animal behaviour into seed dispersal models: Implications for seed shadows. Ecology 87(12): 3160–3174. https://doi.org/10.1890/0012-9658(2006)87[3160:IABISD]2.0.CO;2

Schneiders A, Van Daele T, Van Landuyt W, Van Reeth W (2012) Biodiversity and ecosystem services: Complementary approaches for ecosystem management? Ecological Indicators 21: 123–133. https://doi.org/10.1016/j.ecolind.2011.06.021

Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: Implications for conservation ecology. Oecologia 122(3): 297–305. https://doi.org/10.1007/s004420050035

Sekhar NU (2002) Crop and livestock depredation caused by wild animals in protected areas: The case of Sariska Tiger Reserve, Rajasthan, India. Environmental Conservation 25(2): 160–171. https://doi.org/10.1017/S0376892998000204

Senapathi D, Carvalheiro LG, Biesmeijer JC, Dodson C-A, Evans RL, McKerchar M, Morton RD, Moss ED, Roberts SPM, Kunin WE, Potts SG (2015) The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. Proceedings of the Royal Society of London B: Biological Sciences 282: 20150294. https://doi.org/10.1098/rspb.2015.0294

Shackleton CM, Ruwanza S, Sinasson Sanni GK, Bennett S, De Lacy P, Modipa R, Mtati N, Sachikonye M, Thondhlana G (2016) Unpacking Pandora's Box: Understanding and Categorising Ecosystem Disservices for Environmental Management and Human Wellbeing. Ecosystems (New York, N.Y.) 19(4): 587–600. https://doi.org/10.1007/s10021-015-9952-z

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17(7): 866–880. https://doi.org/10.1111/ele.12277

Stokes KE, Buckley YM, Sheppard AW (2006) A modelling approach to estimate the effect of exotic pollinators on exotic weed population dynamics: Bumblebees and broom in Australia. Diversity & Distributions 12(5): 593–600. https://doi.org/10.1111/j.1366-9516.2006.00239.x

Strassburg BBN, Kelly A, Balmford A, Davies RG, Gibbs HK, Lovett A, Miles L, Orme CDL, Price J, Turner RK, Rodrigues ASL (2010) Global congruence of carbon storage and biodiversity in terrestrial ecosystems. Conservation Letters 3(2): 98–105. https://doi.org/10.1111/j.1755-263X.2009.00092.x

Straub CS, Finke DL, Snyder WE (2008) Are the conservation of natural enemy biodiversity and biological control compatible goals? Biological Control 45(2): 225–237. https://doi.org/10.1016/j.biocontrol.2007.05.013

Tallis H, Polasky S (2009) Mapping and Valuing Ecosystem Services as an Approach for Conservation and Natural-Resource Management. Annals of the New York Academy of Sciences 1162(1): 265–283. https://doi.org/10.1111/j.1749-6632.2009.04152.x

Tilman D (1999) Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. Proceedings of the National Academy of Sciences of the United States of America 96(11): 5995–6000. https://doi.org/10.1073/pnas.96.11.5995

Traveset A, Richardson DM (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution 21(4): 208–216. https://doi.org/10.1016/j.tree.2006.01.006

Turner MG, Gardner RH (2015) Introduction to landscape ecology and scale. Landscape ecology in theory and practice: pattern and process. Springer-Verlag, New York. https://doi.org/10.1007/978-1-4939-2794-4

Turral H, Svendsen M, Faures JM (2010) Investing in irrigation: Reviewing the past and looking to the future. Agricultural Water Management 97(4): 551–560. https://doi.org/10.1016/j.agwat.2009.07.012

Villamagna AM, Mogollón B, Angermeier PL (2014) A multi-indicator framework for mapping cultural ecosystem services: The case of freshwater recreational fishing. Ecological Indicators 45: 255–265. https://doi.org/10.1016/j.ecolind.2014.04.001

von Döhren P, Haase D (2015) Ecosystem disservices research: A review of the state of the art with a focus on cities. Ecological Indicators 52: 490–497. https://doi.org/10.1016/j.ecolind.2014.12.027

Vymazal J, Březinová T (2015) The use of constructed wetlands for removal of pesticides from agricultural runoff and drainage: A review. Environment International 75: 11–20. https://doi.org/10.1016/j.envint.2014.10.026

Walsh JR, Carpenter SR, Vander Zanden MJ (2016) Invasive species triggers a massive loss of ecosystem services through a trophic cascade. Proceedings of the National Academy of Sciences of the United States of America 113(15): 4081–4085. https://doi.org/10.1073/pnas.1600366113

Wenny DG, Sekercioglu C, Cordeiro NJ, Rogers HS, Kelly D (2016) Seed dispersal by fruit-eating birds. Why birds matter: avian ecological function and ecosystem services: 107–145

Wilby A, Thomas MB (2002) Natural enemy diversity and pest control: Patterns of pest emergence with agricultural intensification. Ecology Letters 5(3): 353–360. https://doi.org/10.1046/j.1461-0248.2002.00331.x

Williams-Guillén K, Perfecto I (2010) Effects of Agricultural Intensification on the Assemblage of Leaf-Nosed Bats (Phyllostomidae) in a Coffee Landscape in Chiapas, Mexico. Biotropica 42(5): 605–613. https://doi.org/10.1111/j.1744-7429.2010.00626.x

Williams IH (1996) The dependence of crop production within the European Union on pollination by honey bees. Agricultural Science Reviews 6: 229–257.

Williams IH (2002) Insect Pollination and Crop Production: A European Perspective. In: Kevan P, Imperatriz Fonseca V (Eds) Pollinating Bees – The Conservation Link Between Agriculture and Nature Ministry of Environment, Brasília, 59–65

Wilson LM, Schwarzlaender M, Blossey B, Randall CB (2004) Biology and biological control of purple loosestrife. USDA Forest Service/UNL Faculty Publications, 112 pp. http://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1111&context=usdafsfacpub

Wilson MC, Chen X-Y, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu J, Pimm SL, Robinson SK, Russo SE, Si X, Wilcove DS, Wu J, Yu M (2016) Habitat fragmentation and biodiversity conservation: Key findings and future challenges. Landscape Ecology 31(2): 219–227. https://doi.org/10.1007/s10980-015-0312-3

Winfree RW, Fox J, Williams NM, Reilly JR, Cariveau DP (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18: 626–635. https://doi.org/10.1111/ele.12424

Xavier SCC, Roque ALR, Lima VS, Monteiro KJL, Otaviano JCR, Ferreira da Silva LFC, Jansen AM, Xavier SCdC (2012) Lower Richness of Small Wild Mammal Species and Chagas Disease Risk. PLoS Neglected Tropical Diseases 6(5): e1647. https://doi.org/10.1371/journal.pntd.0001647

Zaller J, Moser D, Drapela T, Schmöger C, Frank T (2009) Parasitism of stem weevils and pollen beetles in winter oilseed rape is differentially affected by crop management and landscape characteristics. BioControl 54(4): 505–514. https://doi.org/10.1007/s10526-009-9212-2

Zhang W, Ricketts TH, Kremen C, Carney K, Swinton SM (2007) Ecosystem services and disservices to agriculture. Ecological Economics 64(2): 253–260. https://doi.org/10.1016/j.ecolecon.2007.02.024

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Assessing the potential distribution of invasive alien species *Amorpha fruticosa* (Mill.) in the Mureș Floodplain Natural Park (Romania) using GIS and logistic regression

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Abstract

The assessment of invasive terrestrial plant species in the Romanian protected areas is an important research direction, especially since the adventive species have become biological hazards with significant impacts on biodiversity. Due to limited resources being available for the control of the invasive plants, the modelling of the spatial potential distribution is particularly useful in order to find the best measures to eliminate them or prevent their introduction and spread, as well as including them in the management plans of protected areas. Thus, the present paper aims to assess one of the most disturbing invasive terrestrial plant species in Europe – *A. fruticosa* in one of the most important natural protected area in Romania, i.e. Mureş Floodplain Natural Park (V IUCN category and RAMSAR –Wetlands of International Importance). The current study is a geographical approach seeking to explain the spatial relationships between this invasive species and several explanatory factors (soil type, depth to water, vegetation cover, forest fragmentation and distance to near waters, roads and settlements) and to assess its potential distribution by integrating GIS and logistic regression into spatial simulation. The resultant probability map can be used by the park's administration in implementing the Management Plan in terms of identifying the areas with the highest occurrence potential of *A. fruticosa* according to the primary habitats and ecosystems and setting up actions for its eradication/limitation.

Keywords
A. fruticosa (Mill.), spatial assessment, GIS, logistic regression, Mureş Floodplain Natural Park, Romania

Introduction

Invasive species are acknowledged as economic, environmental or social threats (Charles and Dukes 2006; Bailey et al. 2007; Mcgeochm et al. 2010), becoming key components of global change (Shea and Chesson 2002; Arim et al. 2006) through their high adaptive capacity which enables them to penetrate natural geographic barriers or political boundaries (Richardson et al. 2000; Anastasiu and Negrean 2005; Anastasiu et al. 2008; Andreu and Vila 2010). As a result, invasive species are characterised by remarkable spatio-temporal dynamics, thus becoming successfully established and spread over extended areas in Europe, triggering significant environmental and socio-economic damages (Pyšek and Hume 2005; Lambdon et al. 2008). It is estimated that only 0.1% of the introduced species became invasive (Williamson 1996). However, at European level, in the last two centuries, an increasing number of species have become capable of spreading on an annual average of 6.2 neophytes (Lambdon et al. 2008, Pyšek et al. 2009). In protected areas, in particular, biological invasions are disturbing drivers for ecosystem functioning and structure, as well as for species, species communities or habitats (De Poorter et al. 2007). The site features that have been associated with invasibility include both environmental and anthropogenic factors such as disturbance (Almasi 2000; Silveri et al. 2001), proximity to roads (Harrison et al. 2002), soil nutrients, topographic position and forest fragmentation (Brothers and Spingarn 1992; Cadanasso and Pickett 2001, Mortensen et al. 2009).

A. fruticosa is considered one of the most invasive species, native to the south-eastern part of North America, widely introduced in North Asia and Europe (Weber and Gut 2004). In Romania, the species has been cultivated prior to the nineteenth century (Sîrbu and Oprea 2011; Sîrbu et al. 2012). Since 1975, it has become invasive and after 1985, it has spread over broader areas proving the high capacity for widening its habitat (Stănescu et al. 1997). However, it became adapted to different types of habitats such as: river banks (poplar or willow galleries, almond willow-osier scrubs), unvegetated or sparsely vegetated shores, water-fringing reed-beds, riverine and lake-shore scrubs (Anastasiu et al. 2008), as well as mesophyle and xeromesophyle meadows in western Romania (Sărăţeanu 2010). Recent studies consider that *A. fruticosa* is one of the worst invaders in wetland habitats (Doroftei 2009), a real competitor to native plant or riverine scrubs (Anastasiu and Negrean 2006) with high capacity to remove indigenous species (Sîrbu et al. 2016a).

Recent interdisciplinary studies conducted in the framework of FP7 enviroGRIDS project – *Building Capacity for a Black Sea Catchment Observation and Assessment supporting Sustainable Development* (WP5 – Impacts on Selected Societal Benefit; Subtask 5.6.2: *Terrestrial Invasive Plant Species in Romanian Protected Areas*) have identified and assessed *A. fruticosa* in the Danube Delta Biosphere Reserve, Comana and Mureş

Floodplain Natural Parks in relation to species preference for different natural and human-induced conditions (Dumitraşcu and Grigorescu 2016). Thus, large areas covered with *A. fruticosa* were spotted in wetlands, along forest roads, in arable lands, in the proximity of transport routes etc. (Anastasiu et al. 2008; Dumitraşcu et al. 2013; Dumitraşcu et al. 2014). In 2016, a first synthesis work, representing a geographical approach of the invasive terrestrial plant species in the Romanian protected areas, was elaborated. The volume includes various aspects connected with the *A. fruticosa* and its impact on the protected ecosystems, as well as relevant environmental and anthropogenic driving factors which influence its potential spread (Dumitraşcu and Grigorescu 2016). As a result, a first methodology, aiming to assess the spatial potential distribution of *A. fruticosa* in important wetland protected areas, was elaborated. Hence, based on the GIS spatial and statistical analysis, the frequency of the invasive species in relation to its natural and human-induced driving factors was calculated in order to identify different ecological requirements in various habitat types aimed at modelling the areas with different potential distribution (Kucsicsa et al. 2016).

Limited resources are available for the control of these plants (Goslee et al. 2006). Given this constraint, the mapping and assessment of invasive species' potential distribution can provide a useful tool for investigating its dynamics at different spatial scales. Thus, numerous studies use logistic regression to identify and quantify the strength of association between invasive plant presence and environmental and anthropogenic factors and to model their potential spread in new areas (e.g. Panetta and Dodd 1987; Franklin 1995; Higgins et al. 1999; Rouget et al. 2001; Dirnbock et al. 2003; Rew et al. 2005; Goslee et al. 2006; Fukasawa et al. 2009; Joly et al. 2011). In this respect, based on GIS spatial and statistical analysis, within the current research, two objectives have been achieved: (1) to identify which of the analysed explanatory driving factors better contribute to the explanation of *A. fruticosa* occurrence and (2) to generate a probability map in order to identify the areas with different potential for *A. fruticosa* spreading in the Mureș Floodplain Natural Park. The results of the current study might be useful for the administration of Mureș Floodplain Natural Park in terms of directing the management efforts towards monitoring the areas at high risk of being affected by invasive species and as support for thorough future research at finer spatial scales.

Materials and methods

The study-area

Mureş Floodplain Natural Park is located in the western part of Romania (20°53'E; 46°07'N) in the Panonic biogeographic region (Fig. 1). The study-area covers 17,455 ha and overlaps the lower part of the Mureş River (tributary of Tisa River), occupying the embanked enclosure of the river between the city of Arad and the state border with Hungary (Bălteanu et al. 2016).

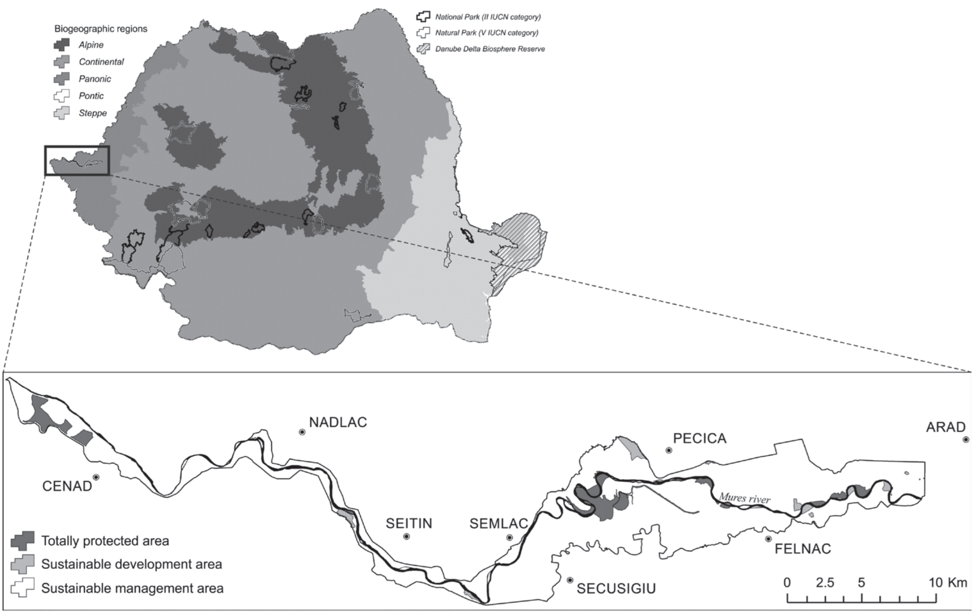

Figure 1. Location of the Mureş Floodplain Natural Park in Romania.

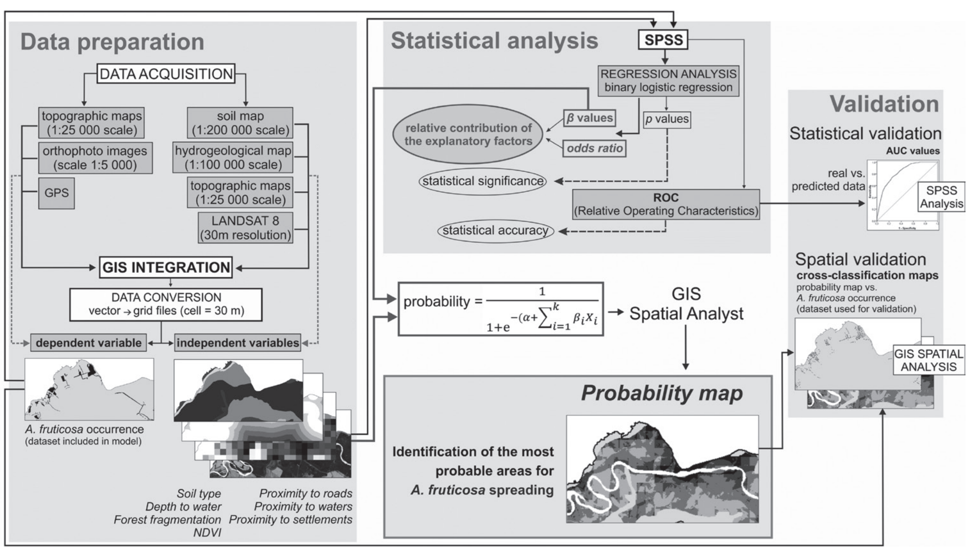

Figure 2. The flowchart showing the methodology used to assess *A. fruticosa* in Mureş Floodplain Natural Park.

The Mureş Floodplain Natural Park, established in 2004 through Government Decision no. 2151/2004, falls into *V IUCN category - Protected Landscape (Natural Park)* and Natura 2000 European Network, both *SPA – Special Protection Areas* and *SCI - Site of Community Importance*. Furthermore, since 2006, the area was included on the RAMSAR list as *Wetlands of International Importance*. The Park is a typical wetland area with running and still waters, alluvial forests, as well as an important place for nesting and passage for a large number of bird species of international importance (Dumitraşcu et al. 2013), hosting specific wetland habitats and species of conservation interest within four nature reserves: *Prundu Mare-Pecica, Igriş Isles, Insula Mare Cenad* and *Cenad Forest* (Bălteanu et al. 2016).

Generally, the area is a floodplain with altitudes decreasing from about 110 m (in east) to about 80 m (in west). The climate is temperate-continental with oceanic humid influences (Bogdan 2004), with almost 10–11 °C mean annual air temperature and 500–600 mm mean annual precipitation (Bogdan et al. 2016). Forests (in the eastern half) and agricultural land (mainly arable) represent the main land use/cover category of the Park.

According to the geographical distribution of habitats, the importance of the species and management, the Park is divided into three different zones: (1) the totally protected area (6%) which includes the most valuable natural elements, (2) the sustainable management area (92%), also called the buffer zone, which makes the transition between the totally protected area and (3) the sustainable development area (2%) which includes built-up areas or natural resources exploitation sites that existed prior to the designation of the protected area. Within the totally protected area, any form of use of natural resources, construction or investments which do not meet the sustainable management of the protected natural area and/or scientific research activities is forbidden. In the buffer zone, it is prohibited to build new constructions, except for those that strictly serve the protected natural area, the scientific research activities or those meant to ensure national safety or the prevention of natural disasters. Investments or development activities are accepted in the sustainable development area, priority being given to tourism, albeit respecting the sustainable use of natural resources and the prevention of any significant negative effects on biodiversity (Mureş Floodplain Natural Park Administration 2016).

Methodology

The current study aims to explain the relationships between *A. fruticosa* occurrence and its explanatory driving forces, on one hand and to model the probability of the potential distribution using spatial analysis and binary logistic regression (BLR), on the other. The methodology, used in the present study, includes three main stages: the extraction of the geospatial datasets, the spatial analysis using GIS and the statistical analysis using SPSS (Statistical Package for the Social Sciences) software package. Synthetically, Figure 2 describes the methodology applied to calibrate, simulate and validate the model in order to assess the potential distribution of *A. fruticosa* in Mureş Floodplain Natural Park.

Data and data processing

Based on field research findings, as well as on data availability, eight spatial datasets representing the dependent and the independent variables (Fig. 3) were employed to model

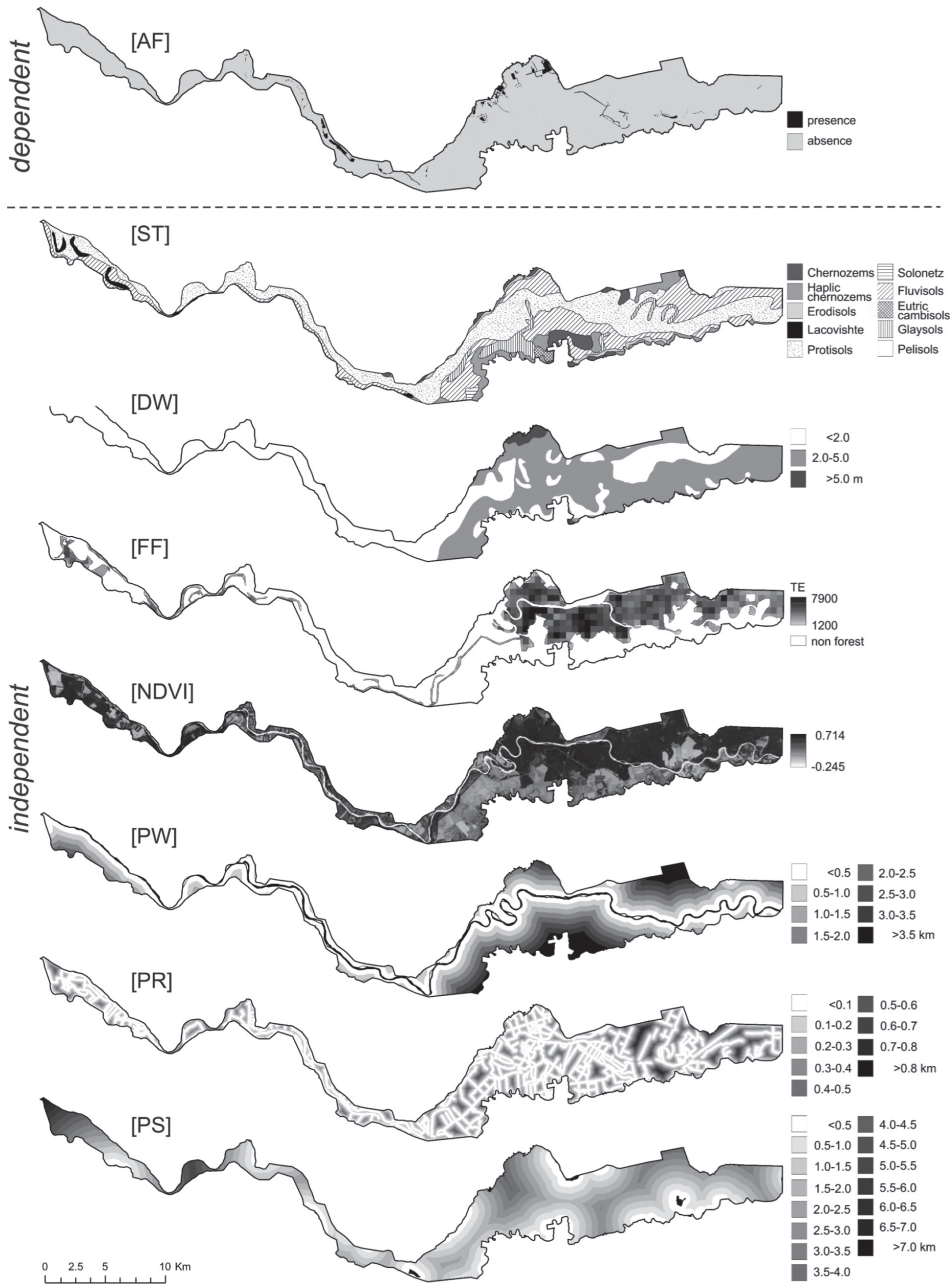

Figure 3. Raster layers representing the dependent and independent variables.

the probability of *A. fruticosa*'s potential distribution: *A. fruticosa* presence/absence (AF), soil type (ST), depth to water (DW), proximity to water (PW), Normalised Difference Vegetation Index (NDVI), proximity to near roads (PR), forest fragmentation (FF) and proximity to near settlements (PS). Due to the relative homogenous topographical characteristics with rather insignificant altitudinal difference (about 30 m), as well as to its longitudinal and latitudinal low extension (00°47' and 00°07', respectively), the explanatory factors related to climate and relief were not considered. Moreover, the scale of the study area, coupled with the particular local environmental features, makes this research a valuable local-scale approach, allowing a better understanding of the environmental issues and an increased potential for being included into the decision-making process. Thus, we consider that such an approach can be replicated to other geographical areas with similar environmental conditions or extrapolated from local to regional scales.

Dependent variable: *A. fruticosa* occurrence

The layer of *A. fruticosa* presence/absence in the Mureş Floodplain Natural Park was derived from the data collected during the field surveys which were carried out between 2012 and 2016. The mapping was realised using topographic maps (1:25000 scale) and, for more accuracy, using orthophoto images (scale 1:5000) and GPS measurements. The species was identified in various habitat types where field relevés with over 20% coverage (according to Braun – Blanquet scale) and frequency (according to Raunkiaer scale) were taken into consideration (Grigorescu et al. 2014). Thus, the total mapped area covers a surface of 363 ha, including polygons with different coverage of *A. fruticosa.*

With respect to the dataset used to model the probability map, a binary raster with the categories "presence" (coded with 1) and "absence" (coded with 0) was generated (Fig. 3), in order to discriminate the cells with *A. fruticosa* occurrence from the non-occurrence.

Explanatory factors

After processing different maps (topographic, soil and hydrogeological) and orthophoto images, six thematic layers were extracted and analysed: soil characteristics, piezometric level, surface waters, forests, built-up areas and roads from where soil type, depth to water, forest fragmentation, distance to roads, distance to waters and distance to settlements were derived.

In order to assess the occurrence of *A. fruticosa* within the dominant vegetation cover, the NDVI *(Normalised Difference Vegetation Index)* was used. This index was calculated using the Landsat 8 OLI_TIRS (Operational Land Imager_Thermal Infrared Sensor, accessed July 18, 2017) acquired from the United States Geological Survey – USGS (portal available at http://www.usgs.gov/). This index, developed by Rouse et al. in 1974 and widely used for the remote sensing of vegetation, is a measure of surface reflectance and gives a quantitative estimation of vegetation growth and biomass (Hall et al. 1995). The NDVI values were obtained by employing the following formula:

$$NDVI = \frac{NIR - RED}{NIR + RED}, \qquad \text{(Eq.1)}$$

where *NIR* = reflectance in the near infrared band; *RED* = reflectance in the red (visible) band.

Table 1. The input independents variables used to assess *A. fruticosa* potential occurrence.

Data layer	Meaning	Source	Data type	Assumption
Soil type (ST)	chernozems; haplic chernozems; erodisols; lacovishte; protisols; solonetz; fluvisols; eutric cambisols; glaysols; pelisols	National Research & Development Institute for Pedology, Agrochemistry and Environment Protection) (scale 1:200 000)	categorical	specific characteristics (e.g. soil moisture, nutrient availability, microorganisms, humus quality and quantity, pH) which play an important role in the occurrence of the invasive species
Depth to water (DW)	low piezometric level (<2 m); medium piezometric level (2–5 m) high piezometric level (>5 m)	Hydrogeological map (Geological Institute of Romania) (scale 1:100 000)	categorical	lower piezometric levels are assumed to be more suitable for invasive species occurrence due to the better connectivity to groundwater
Forest fragmentation (FF)	slightly fragmented forests (TE <2000 m) moderate fragmented forests (TE 2000–5000 m) highly fragmented forests (TE >5000 m)	derived from orthophoto images (scale 1: 5 000)	categorical	forest fragmentation could increase ecosystems' vulnerability to invasive species
Normalised Difference Vegetation Index (NDVI)	no vegetation areas (NDVI <0) crop lands (NDVI = 0–0.25) grasslands (NDVI = 0.25–0.40) transitional woodland-scrub (NDVI = 0.40–0.55) forests (NDVI = >0.55)	derived from LANDSAT 8 satellite image (30 m resolution)	categorical	vegetation cover can lead to spatial heterogeneity in invasive species distribution
Proximity to roads (PR)	distance to nearest roads (buffer = 0.1 km)	derived from topographic map (scale 1:25 000)	continuous	influence of roads in ecosystems fragmentation role of roads in facilitating the movement of the invasive species road traffic can favour invasive species' expansion (tolerance to polluting environments)
Proximity to settlements (PS)	distance to nearest settlements (buffer = 0.5 km)	derived from topographic map (scale 1:25 000)	continuous	the invasive species could be facilitated by human activities (e.g. plantation as ornamental species, natural habitat disturbance)
Proximity to waters (PW)	distance to nearest waters (buffer = 0.5 km)	derived from topographic map (scale 1:25 000)	continuous	water is considered as one of the main vectors for invasive species dissemination fluvial processes can generate natural disturbances that create suitable sites for invasive species expansion water can generate a microclimate with potential influence on the invasive species expansion

The resultant NDVI values ranged between –0.245 and 0.714. After the visual interpretation of orthophoto images, the NDVI values were considered as representing: no vegetation areas (aquatic surface, bare soils, built-up areas, recent riverbed deposits) (NDVI <0); agricultural crops (NDVI = 0…0.25); herbaceous vegetation (NDVI = 0.25…0.4); transitional woodland-scrub (0.40…0.55); forest vegetation (NDVI >0.55).

Total edge (TE), calculated as the sum of the lengths (m) of all edge segments in a class or landscape (McGarigal and Marks 1995) was used to quantify the forest fragmentation. In this case, the TE was calculated just for the forested class, in a 25 ha window size, using Patch Analyst (Rempel et al. 2012), a GIS tool developed to analyse spatial landscape patches and model the attributes associated with patches, according to numerous statistical metrics. The resultant values were categorised in: slightly fragmented forests (TE <2000 m); moderate fragmented forests (TE = 2000…5000 m); highly fragmented forests (TE >5000 m). Moreover, based on the *Euclidean multiple ring* buffers, maps depicting the distance to roads (buffer = 0.1 km), waters (buffer = 0.5 km) and settlements (buffer = 0.5 km) were created. Twenty-one binary rasters were generated to distinguish the ten soil type classes, three piezometric levels, three forest fragmentation classes and five NDVI classes. Finally, twenty-four categorical and continuous independent variables were prepared and homogenised as raster with 30×30 m cell (equivalent to the spatial resolution of the Landsat image used to derive NDVI) for further spatial and statistical analyses (Table 1). For these variables, several assumptions related to location suitability were presumed in order to explore the relationship between the invasive species and its explanatory factors.

Statistical analysis

In the present study, to assess the relationships of the site characteristics and *A. fruticosa* presence/absence, BLR was applied. This method is the most commonly used parametric model aimed at determining the empirical relationships between a dependent and several independent variables (McCullagh and Nelder 1989), where the dependent variable is a binary presence (1) or absence event (0) and the independent variables are categorical and/or continuous variables. If binary values 1 and 0 are used to represent *A. fruticosa* occurrence and no occurrence, respectively, the probability of the presence of the species for any specific grid cell was calculated using the logistic curve as described by the logistic function (Kleinbaum 1994):

$$f(z) = \frac{1}{1 + \mathrm{e}^{-z}}, \tag{Eq.2}$$

then the probability of occurrence can be estimated with the following logistic regression model:

$$P(Y = 1|X_1, X_2, \ldots, X_i) = \frac{1}{1 + \mathrm{e}^{-(\alpha + \sum_{i=1}^{k} \beta_i X_i}}, \tag{Eq.3}$$

where $P(Y = 1|X_1, X_2, \ldots, X_i)$ is the probability of the dependent variable Y being 1 given ($X_1, X_2, \ldots, X_i$), i.e. the probability of a cell of being invaded by invasive species; X_i is an independent variable representing the explanatory factors of *A. fruticosa* and β_i is the coefficient for variable X_i.

The response of these regression functions is visualised into the raster probability map based on the location suitability, given the probability of the occurrence of *A. fruticosa* in each resultant raster cell.

In order to reduce the effects of multi-collinearity, before the logistic regression analysis, *Pearson* correlations between each pair of independent variables were conducted and examined. In case of strong correlations (min. ±0.7), the better predictor variable (in univariate trials) was retained. Furthermore, to verify the explanatory power of the variables included in the sub-model, the *Cramer's V* statistics tool was used. *Cramer's V* is a statistic that transforms chi-square (for a contingency table larger than two rows by two columns) to a range of 0–1, where unit value indicates complete agreement between the two nominal variables (Liebetrau 1983). The test procedure is based on contingency table analysis which can test the strength of the association between the dependent variable and both continuous and categorical independent variables.

Model calibration and assessment of potential distribution

The BLR was performed using the backward stepwise method in SPSS in order to obtain the best-fit combination for predictors. Thus, the variables, which collectively best explain *A. fruticosa* occurrence, were adopted by the regression model. To indicate the effectiveness of the each sets, a Nagelkerke pseudo R square (Nagelkerke 1991) was determined. Furthermore, ROC/AUC (Relative Operating Characteristic/Area Under Curve) was used to test the "goodness of fit" (Pontius and Schneider 2001). In the standard ROC approach, the predictive probability map is compared with the map of the true binary event in order to assess the spatial coincidence between the event and the probability values (Mas et al. 2013). This graph displays the predictive accuracy of the logistic model, which can be evaluated using the area under the ROC curve (AUC). A completely random model gives a ROC value of 0.5, while a perfect fit results in a ROC value of 1.0. For the best-fit combination for resultant predictors, the maximum likelihood estimator (Hosmer and Lemeshow 1989) was determined. In the BLR, the model is considered to fit if the value of the Hosmer-Lemeshow test shows a value higher than p-value (0.05).

Based on the corresponding coefficients of the best fit predictor set, the relative contribution of the explanatory variables of the *A. fruticosa* occurrence was assessed and the potential distribution probability map was generated. To categorise the resultant map, five classes were used to classify the probability values: very high, high, medium, low and very low probability. The classification was performed by *Natural breaks (Jenks)*, a method that seeks to reduce the variance within classes and to maximise the variance between classes (Jenks 1967), commonly used in GIS techniques for grouping spatial values that are not evenly distributed.

Spatial validation

Usually, in the analysis and modelling of spatial data, real datasets are used to validate the performance using different techniques. A typical procedure is splitting data into two parts (Kanevski and Maignan 2004): training set (used to develop the model) and validation set (used to estimate the ability of the model). The proportions of data included in each dataset are somewhat arbitrary and dependent on the total mapped area available, 70% for calibration and 30% for validation being commonly used (Pearson 2010). According to the available datasets representing *A. fruticosa* occurrence (mapped) and to build the model with a significant percent for the training set, in the present study a 70%/30% training/validation split was considered. Furthermore, to eliminate sampling biases and associated subjectivism, the random-partition was used to extract the data for validation. Then, based on the cross-classification technique, the analysis between validation dataset and probability map was achieved and the frequency of the *A. fruticosa* occurrence was identified and quantified for each probability class.

Results

The occurrence of *A. fruticosa* in relation to the analysed explanatory variables

In terms of the analysed explanatory factors, *A. fruticosa* distribution across the park has a relative spatial heterogeneity. The frequency analysis (Fig. 4) shows that *A. fruticosa* occurs in various conditions but with differences mainly according to the soil type, vegetation cover and distance to roads. In relation to soil type, *A. fruticosa* overlaps largely protisols and fluvisols (92% of the total mapped area). Similar to the soil particularities, the roads appear to have the most important role in facilitating the establishment of *A. fruticosa*. In detail, the frequency of species related to distance to nearest roads, calculated for 0.1 km buffer rings, shows that 68% of the mapped area is identified in the first 0.1 km and 91% in the first 0.2 km. In relation to the depth to water, the most significant areas with *A. fruticosa* (58%) were mapped in the high floodplain, the sand banks and floodplain terraces where the aquifer level is situated at 2.0–5.0 m depth. In relation to the forest fragmentation, *A. fruticosa* was mainly found (69%) in the moderate fragmented forests (TE = 2000–5000 m/25 ha). Related to NDVI values, the large occurrence of *A. fruticoasa* (46%) is mainly related to values ranging between 0.40 and 0.55, thus indicating a preference of the invasive species for transitional woodland-scrub. Furthermore, the notable occurrence (25%), in relation to the highest NDVI values (>0.55) and 17% in relation to the medium positive NDVI values (0.25–0.40), indicate also a preference for forest vegetation and grasslands. In relation to the water's vicinity, 55% of the total mapped areas with *A. fruticosa* are situated close to the Mureș River, within the first 0.5 km buffer ring. The

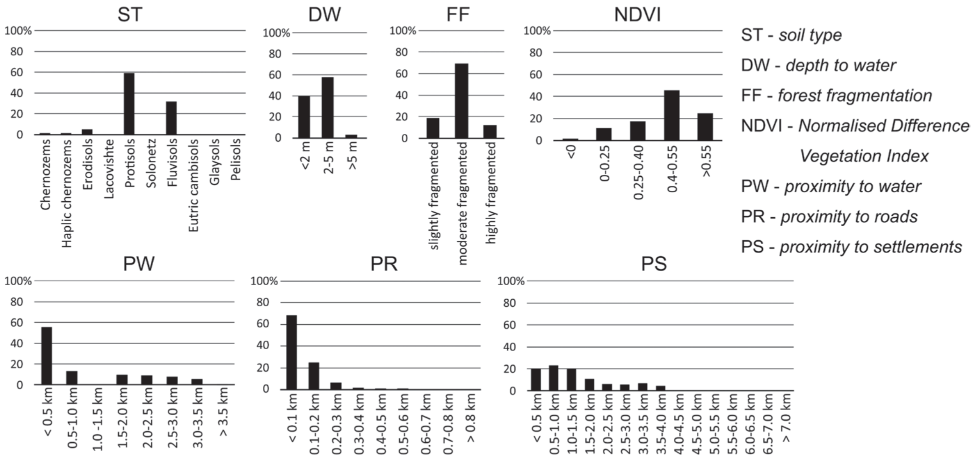

Figure 4. The distribution of *A. fruticosa* (mapped) in relation to the analysed explanatory factors.

frequency distribution of *A. fruticosa* indicates also an increasing occurrence in relation to the distance to settlements. Thus, 43% of the total mapped areas are distributed in the first 1 km and 73% in the first 2 km buffer rings.

Correlation analysis amongst the explanatory variables

The *Pearson* correlation analysis between the independent variables showed that the variables were not highly inter-correlated (max. ±0.30), which suggests the absence of multicollinearity. The highest values were found between NDVI (>0.55) and slightly fragmented forests (0.298), depth to water (<2 m) and protisols (0.255). The lowest coefficients (0.001) were found between slightly fragmented forests and chernozems soil type, moderate fragmented forests and depth to water (>5 m), NDVI (0–0.25) and lacovishte soil type.

Association between dependent variable and explanatory variables using *Cramer's V* test

The explanatory power of the independents' variables was tested based on the *Cramer's V* statistics. According to this method, the analysed explanatory factors were not strongly associated with *A. fruticosa* occurrence. Overall, continuous and few categorical variables were found to have better association with *A. fruticosa* occurrence with *Cramer's V* values between 1.5 and 2.3: proximity to roads (V = 0.224), proximity to settlements (V = 0.221), proximity to waters (V = 0.193), piezometric level <2 m (V = 0.151), moderate forest fragmentation (V = 0.161) and NDVI values between 0 and 0.25 (V = 0.152). Furthermore, except for erodisols (V = 0.143), protisols (V = 0.122), fluvisols (V = 0.113), piezometric level between 2 and 5 m (V = 0.114), highly fragmented forests (V = 0.105) and NDVI values between 0.25 and 0.40 (V = 0.11), remaining variables have values less than 0.1, indicating a weakly association with the *A. fruticosa* occurrence.

Logistic regression modelling

Setting the backward stepwise in the BLR, eight steps for the best predictor sets resulted (Table 2). Variables that were not statistically significant, associated with *A. fruticosa* occurrence within the 95% confidence interval, were identified and automatically excluded by the model. Thus, the best-fit combination for predictors was found in step eight, which includes seventeen explanatory factors (Table 3).

Table 2. Regression coefficients, indicating the effectiveness of eight sets of predictors, resulted after setting the backward method in BLR.

set	Nagelkerke R^2	AUC
1	0.161	0.648
2	0.195	0.743
3	0.220	0.769
4	0.228	0.777
5	0.237	0.790
6	0.241	0.794
7	0.242	0.797
8	0.243	0.798

Table 3. Estimated coefficients for the logistic regression model.

Independents' variables	*β*	*p*	*Odds ratio (OR)*
Erodisols (soil type)	2.923	0.000	18.588
Protisols (soil type)	2.101	0.000	8.171
Fluvisols (soil type)	1.940	0.000	6.961
Depth to water (0–2 m)	1.587	0.000	4.891
Depth to water (2–5 m)	0.867	0.000	2.381
Depth to water (>5 m)	–1.065	0.000	0.345
Forest fragmentation (low)	0.193	0.000	1.213
Forest fragmentation (medium)	0.672	0.000	1.959
Forest fragmentation (high)	1.167	0.000	3.211
NDVI (< 0)	0.202	0.035	1.224
NDVI (0–0.25)	0.415	0.032	1.515
NDVI (0.25–0.40)	0.872	0.039	2.392
NDVI (0.40–0.55)	0.833	0.049	2.301
NDVI (>0.55)	0.326	0.043	1.385
Proximity to roads	–0.694	0.000	0.500
Proximity to settlements	–0.155	0.000	0.857
Proximity to waters	0.006	0.018	1.006
Constant	–13.056	0.074	

For set-8, the regression "goodness of fit" measured by the Nagelkerke R^2 is -0.243 which, according to Clark and Hosking (1986), indicates that the model is a good fit for the data. Therewith, Hensher and Johnson (1981) also stated that pseudo R^2 value between 0.2 and 0.4 can be considered as an extremely good fit. The predictor set-8 also attained the highest accuracy (AUC=0.798) showing a prediction ability of 79.8% of the model. Furthermore, the Hosmer-Lemeshow significance test resulted in Chi-square = 13.39 and p = 0.063 (>0.05), indicating a good fit of the model.

The relative contribution of the explanatory factors was evaluated using the corresponding coefficients in the BLR (Table 3). Based on the coefficients' values, all the explanatory variables were ranked. Thus, amongst all variables, erodisols, protisols and luvisols were found as the most significant predictors for *A. fruticosa* occurrence in the study area. All values of OR are greater than one, indicating a higher probability of *A. fruticosa* occurrence in those areas comparing to other soil type classes. The probability of *A. fruticosa* occurrence in areas with erodisols is larger than the probability in areas covered with protisols. The areas with protisols present more suitability for *A. fruticosa* occurrence than areas with luvisols. This can be seen from the odds ratio values of 18.59, 8.17 and 6.96 in a decreasing order for erodisols, protisols and luvisols, respectively.

The regression model showed a positive relationship between *A. fruticosa* occurrence and depth to water for piezometric level less than 2 m and between 2 and 5 m and negative relation with respect to a piezometric level higher than 5 m. This means that, with the increase in depth to water, the *A. fruticosa* occurrence decreases due to less connectivity to groundwater. This can be seen in the odds ratio values (4.89, 2.38 and 0.35) in a decreasing order for the piezometric level. Furthermore, the positive values of β and OR show that *A. fruticosa* tends to spread in moderate and mainly highly fragmented forests. However, the positive values of β (0.19) and the value of OR greater than one (1.21) for slightly fragmented forests also demonstrate that the species can spread in rather compacted afforested areas.

The model also demonstrates that *A. fruticosa* is in relation to vegetation cover, the positive β coefficients and OR values for NDVI values >0.25 showing the tendency of species to spread in areas with grasslands, transitional woodland-scrub and afforested areas. The estimated β value (–0.694) and OR (0.50) for the proximity to roads indicates that the probability of *A. fruticosa* occurrence further away from roads is less expected. Specifically, the probability of species occurrence would decrease 2 times if distance to roads increases by 0.1 km. The model demonstrates that *A. fruticosa* occurrence is not significantly controlled by the proximity to settlements, however the negative value of β (–0.16) indicates that, with the increase in distance to settlements, the probability of this invasive terrestrial species to occur decreases. Thus, the odds of *A. fruticosa* occurrence in an area 0.5 km closer to settlements is estimated to be 1.17 as large as that in areas further away from settlements.

The regression results for proximity to waters (β = 0.006; OR = 1.006) revealed that they have no significant influence on *A. fruticosa* occurrence.

The probability map of *A. fruticosa* occurrence

The probability of *A. fruticosa* occurrence was assessed by plugging the β coefficients of the logistic regression model containing the 17 significant predictors (Table 3) into Eq. (3). Thus, the probability map (Fig. 5) indicated that 24.9% of the grid cells have high and very high suitability for *A. fruticosa* occurrence, largely in the eastern half of the Park, close to Felnac, Pecica and Semlac localities. Here, the suitability is mainly characterised by the favourable soil type, the presence of numerous agricultural and forestry roads and the large extension of the pastures and transitional woodland-scrub vegetation. On the other hand, the lowest probability values are in the western (near Cenad locality), north-eastern and southern parts of the protected area (near Arad and Secusigiu localities) where the unsuitable soil type classes and piezometric level ranking between 2 and 5 m or arable lands and compacted forests are predominant.

In order to conduct the spatial validation of the model, the map of *A. fruticosa* occurrence probability, computed using the logistic regression model, was compared with the actual *A. fruticosa* occurrence (reference datasets used for validation). Thus, the cross-classification map reveals a relatively good spatial fit between the observed data and the predicted data (Fig. 6). Both very high and high probability classes include 69.9% of total cells, representing the real *A. fruticosa* location used as the validation dataset. Furthermore, only 10% of the total pixels, representing the real *A. fruticosa* used as the validation dataset, overlap the very low and low probability classes.

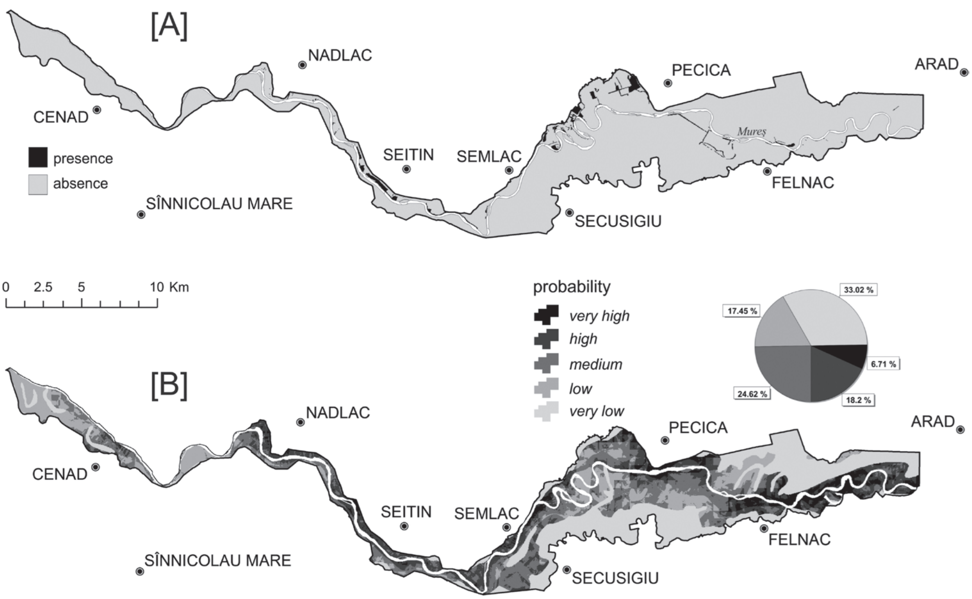

Figure 5. The mapped areas (**A**) and the probability of *A. fruticosa* occurrence, based on the BLR (**B**).

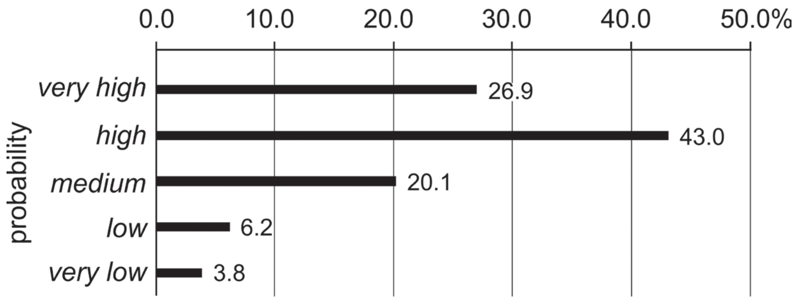

Figure 6. The frequency of *A. fruticosa* occurrence (datasets used for validation) in the probability classes.

Discussion

A. fruticosa location in the Mureș Floodplain Natural Park

The field surveys in the Mureș Floodplain Natural Park have shown *A. fruticosa* occurrence in different ecosystems and habitats, significantly affecting the native vegetation. The species were identified mainly along the forest roads edges and forest glades (especially north to Mureș River), as well as along the edges of arable lands (mainly abandoned, unused) with a tendency to invade them in the west and north-west of Felnac locality. The largest area was identified in the western part of Pecica locality and north-west of Fenlac, along the forest roads and at the contact between forested areas and pastures or arable lands. Therewith, the species has a significant spread south-west of Şeitin locality on arable lands and along Mureş River (Fig. 7). Selected biological indices (coverage, frequency, abundance) computed in six representative sites during the field research, indicate a preference mainly for the riparian habitats (with *Salix alba* and *Populus alba*), alluvial forest (with *Alnus glutinosa* and *Fraxinus excelsior*), riparian mixed forests (with *Quercus robur*, *Ulmus laevis*, *U. minor*, *Fraxinus excelsior*, *F. angustifolia*) and muddy banks (with *Chenopodium rubri* pp and *Bidention* vegetation).

In relation to park zoning, out of the total mapped surface, 1.7% is located in the totally protected area (Felnac, Libus), 13.6% in the sustainable development area (largely in Pecica locality), while the remainder (84.7%) is in the sustainable management area, mainly spreading along the left bank of Mureş River.

The main explanatory factors of *A. fruticosa* occurrence. Expected invasion

The driving factors of *A. fruticosa* occurrence may vary from place to place. Many factors can affect the establishment and spread of invasive species (Underwood et al. 2004). They include the interaction of multiple environmental variables, such as elevation, precipitation and soil type, which constitute the species' fundamental niche (Hutchinson 1957; Pysek et al. 2003). Invasive species have also been associated with areas of distur-

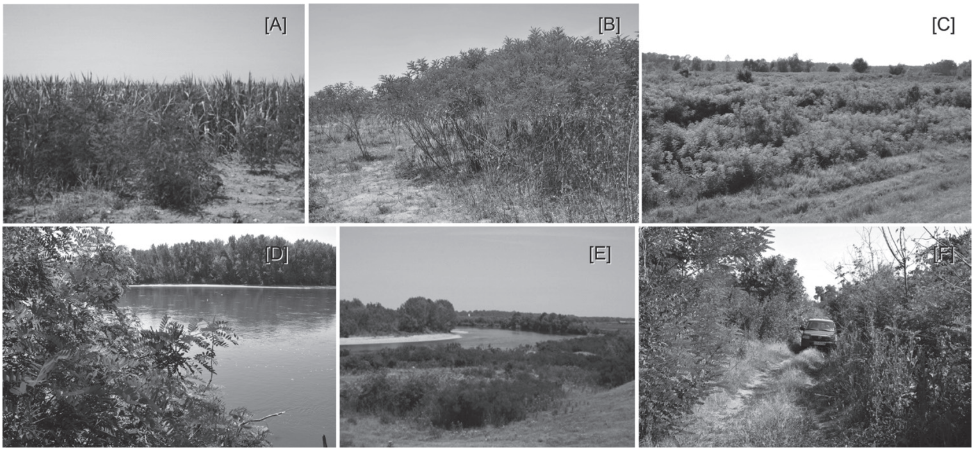

Figure 7. *A. fruticosa* invading: **A** crop lands **B** grasslands **C** abandoned agricultural land west of Pecica locality **D, E** Mureș River riverbed **F** forest roads.

bance, either natural (e.g. fire or floods; Rejmánek 1989; Mack and D'Antonio 1998) or human related (Macdonald et al. 1988; Cowie and Werner 1993) and influenced by abiotic factors, such as historical land use and management (Mack et al. 2000).

In the present study, the selected explanatory variables encompass a significant share of the driving factors. Many studies have indicated that most of the analysed factors were also found to be important in other protected wetland areas in Romania (Dumitraşcu et al. 2011, Dumitraşcu et al. 2013, Kucsicsa et al. 2013; Dumitraşcu et al. 2014; Grigorescu et al. 2014), as well as in the other European countries (Blagojević et al. 2015; Radovanović et al. 2017; Delai et al. 2018). In the present study, the model shows that *A. fruticosa* is mainly controlled by the soil, groundwater's availability, predominant vegetation type in the invaded areas and human-induced disturbance (forest fragmentation, roads extension). Specifically, amongst all analysed explanatory factors, erodisols, protisols and luvisols were found as the most significant categorical predictors for *A. fruticosa* occurrence in the Mureş Floodplain Natural Park. It should be noted that, in the study area, these classes of soil types cover about 80% of the total area, thus indicating a significant potential for *A. fruticosa* to spread in large areas of the park. The model also proved a significant relationship between the piezometric level and *A. fruticosa* distribution indicating species' requirements for water availability in the soil.

A. fruticosa is considered a weak competitor in forests because it is usually excluded by tree species (Magyar 1960), but due to its fast growth, shading and probably its allelopathic effects (Elakowich and Wooten 1995) and nitrogen-fixing ability (Wang et al. 1999), it is a superior transformer in grasslands (Szigetvári 2002). In the present study, the model confirms the strong adaptability of *A. fruticosa* in grasslands areas. However, it can be noticed that the regression coefficients for highest values of NDVI also show the tendency of *A. fruticosa* to spread in the transitional woodland-scrub and afforested areas. This can indicate the adaptation capacity to any terrestrial ecosystems and, consequently, a tolerance for semi-shade. Furthermore, the model indicates the preference of *A. fruticosa* for fragmented forests, confirming that forest fragmentation could increase the ecosystems' vulnerability to invasive species and habitat decline (Turner 1989).

It is widely known that roads can serve as corridors for the movement of invasive species (Christen and Matlack 2006), as well as for providing main habitats for establishment (Mortensen et al. 2009). In other Romanian protected areas, large areas covered by *A. fruticosa* were spotted in wetlands, along the forest roads (Dumitraşcu et al. 2013; Dumitraşcu et al. 2014). This can be explained by their influence in ecosystems fragmentation through creating suitable areas for invasive species growth. For the present-study, the regression results indicate that the proximity to roads was the predictor that has the most important contribution for *A. fruticosa* occurrence amongst the continuous driving factors. On the other hand, the continuity and the patterns of *A. fruticosa* occurrence along the roads show the very important role of roads in facilitating the movement of this invasive plant. Moreover, the road traffic close to the Park's border can favour species' expansion, having been known for its tolerance to polluting environments (Seo et al. 2008; Marian et al. 2010; Xiang et al. 2011). The development of the invasive species on contaminated areas was confirmed within another protected area of Romania (Comana Natural Park), where the large spread of *A. fruticosa* along the main roads and non-electrified railroad was observed (Dumitraşcu et al. 2011). The model does not demonstrate that *A. fruticosa* occurrence is significantly controlled by the proximity to settlements. However, the negative value of regression coefficients shows that the presence of the invasive plant species could be facilitated by human activities, indicating that the disturbed habitats inside and close to the settlements are easier to invade. This study also revealed that the proximity of aquatic surfaces has no significant influence on *A. fruticosa* occurrence. However, the positive regression coefficients, as well as the mapped areas with *A. fruticosa* (59%) within the first 500 m distance to Mureş River, could be explained through the favourable specific microclimate or fluvial processes within the riverbed which can favour the growth of invasive species to the detriment of riparian vegetation. In addition, the occurrence of *A. fruticosa* along the riverbed could be also explained by the fact that rivers are regularly considered natural vectors for invasive species dissemination (Fenesi et al. 2009).

In this respect, the authors consider that the more ecosystems and habitats are affected by disturbance, the more likely they become invaded by *A. fruticosa*. Thus, future forest fragmentation and clearing, the extension of the transportation network and the abandonment of the agricultural lands will increase the potential spread of *A. fruticosa*. Furthermore, planting *A. fruticosa* for different purposes (on the degraded lands, protection of dams or roads) will facilitate species' invasion within the important habitats and ecosystems of the Park.

Importance of the study. Perspectives

Invasive species may cause cascading effects in communities and/or affect both biotic and abiotic components of ecosystems (Charles and Dukes 2006) bringing in substantial costs to agriculture, forest and human health (Sîrbu et al. 2016b), as well as to ecosystem services, affecting ecosystem structure and function (Charles and Dukes 2006), loss of biodiversity or unique habitats. Invasive plants may decrease the suitability of soil for native species (Callaway and Ridenour 2004), disturbing soil formation, nutrient components or altering microbial communities. As a result, detailed knowledge of species' ecological and geographic distribution is critical for effective conservation planning and modelling of its potential spread. However, data about most of species occurrence is sparse, resulting in incomplete information about species distribution, which leads to its difficult control and monitoring in sensitive areas (e.g. protected areas, wetlands). Hence, species distribution models attempt to provide detailed spatial data by relating presence of species to environmental predictors (Guisan and Thuiller 2005; Elith et al. 2006; Václavík and Meentemeyer 2009). In the current study, in order to identify and inventory *A. fruticosa,* as well as to develop a potential distribution model for the entire protected area, integrating GIS and logistic regression have been performed, given that we consider that the resultant map would provide the necessary information for the effective management of native ecosystems in the study area. Since the river systems are considered as main transport corridors for the invasive plants (Gallé et al. 1995), characterised by natural disturbances that create suitable sites for invasive species (Rood et al. 2010), it can be appreciated that *A. fruticosa* expansion could represent an important trans-border ecological issue given that Mureş River represents an important tributary of the Tisa River in the Danube Basin area. More than that, this can be critical given that the Danube is considered one of the most important routes for spreading invasive species, owing to its long distance, fluctuating water level and long-time anthropogenic presence, which facilitate these invasions (Pedashenko et al. 2012). Due to the resultant map indicating a significant susceptibility to invasion, we consider that, without careful management, the important habitats and essential ecosystem processes in large fluvial areas in the Mureş Floodplain Natural Park could be seriously disturbed in a relatively short time. Hence, the resultant outcomes could become important tools for the park's administration to adopt appropriate planning strategies for the eradication/limitation of *A. fruticosa* in view of conserving the biodiversity of native flora and, finally, to provide the sustainable development of this protected area. On the other hand, the database containing the spatial distribution of *A. fruticosa* can serve the park's administration and research as useful information about the location of the invasive species in order to monitor and carry out an assessment of the quantitative rates of dispersal in different habitats and ecosystems within the protected area, but also cross-boundary, knowing the relative continuity of the environmental conditions which provides suitable habitats for potential expansion. Furthermore, the results might be also used in other similar sites where *A. fruticosa* occurs in order to identify the areas that can be potentially invaded by this terrestrial invasive plant species. Given that this invasive plant is strongly associated with some landscape features such as soil type, depth to water, vegetation cover or roads, it is also essential to incorporate this knowledge into the assessment of potential spreading of other invasive terrestrial plant species in other sites. In addition, the probability map generated in this study can provide the basis for scenario analysis where independent variables can be improved and modified according to the specific biophysical and anthropogenic changes in an area.

Limitation of the results

Uncertainty is an inevitable component of invasion forecasts (Yemshanov et al. 2015) and modelling will always contain a level of errors resulting from a wide range of factors (Pearce et al. 2003), including insufficient sample size, measurements errors in the biological survey data or insufficient spatial resolution in the mapped environmental variables and impossibility or difficulty in integrating critical habitat variables and others factors (e.g. competition, dispersion). Hence, the resultant probability map should be used as a preliminary data on the potential distribution of *A. fruticosa* in order to identify regions with different probability and, consequently, to spot the areas that require more or less intensive monitoring of this invasive terrestrial plant species. Thus, important limitations and assumptions in the calibration of the model and generating the probability map have to be considered. The first is related to the *A. fruticosa* occurrence inventory dataset. In the present paper, we assume that all areas covered with *A. fruticosa* occurrence were not included in the analysis. However, several inconvenient factors (e.g. large extension of the area or inaccessibility in different sites) limited the mapping of all areas covered by *A. fruticosa*. We consider that the available datasets used to model the probability map were not sufficient to assess with the highest accuracy the potential occurrence *of A. fruticosa*. Thus, the estimated coefficients in the logistic regression models have associated estimation errors, the uncertainty decreasing by mapping more plant occurrence data and predictors (Horssen et al. 2002; Elith et al. 2006).

Another limitation refers to the unavailable datasets for the independent variables. Thus, the resulted pseudo R^2 values indicate that only 24.3% of *A. fruticosa* occurrence in the Mureş Floodplain Natural Park can be influenced by the analysed explanatory factors and the remaining percentage was influenced by other factors. Thus, in order to allow a better and realistic modelling of species' spreading potential in the future at a much finer scale, more information on the spatial distribution of *A. fruticosa* combined with other predictors (e.g. soil nutrients and heavy metals content, past land-use changes, existing plant community) must be integrated. Moreover, the coarse resolution of the available soils and depth to water data have also restricted the accuracy of the model. One more limitation is related to the final probability map which does not reflect its temporal probability. As it is difficult or impossible to model seed dispersal at a regional scale (Goslee et al. 2006), the current results only display the spatial distribution potential of *A. fruticosa* depending on the analysed explanatory factors, without considering the seed dispersal vectors. In addition, environmentally suitable sites within the native distributional area may remain free from invasion because of biotic interactions, dispersal limitations or historical constraints (Ricklefs and Schluter 1993; Pulliam 2000). On the other hand, these restrictive factors may, at least in theory, differ or even be lacking in invaded areas (Jiménez-Valverde et al. 2011). As a consequence, it can be appreciated that, in the future, the spread might affect more or less other areas indicated by the current research.

Conclusions

The present study is a geographical approach to assess spatial potential spreading of one of the most disturbing invasive terrestrial plant species in Europe *(A. fruticosa)* in one of the most important natural protected area in Romania (Mureş Floodplain Natural Park). Cross-referencing the scientific findings on the assessment of invasive species in Romania, revealed that the present study is one of the first attempts to explain the spatial relationships between this invasive terrestrial plant species and its explanatory factors and to assess potential distribution, integrating GIS and logistic regression into spatial simulation. Thus, the model shows that the explanatory factors of *A. fruticosa* occurrence are varied and have different influences, confirming previous findings of scientific literature and other current research on the increased tolerance and high adaptation capacity of this invasive species to a variety of conditions. The probability map, resulting from plugging the β coefficients of the logistic regression, indicates that spreading of *A. fruticosa* is expected to continue mainly in the areas where significant parcels were mapped (close to Pecica, Semlac and Seitin localities), but with extension into the eastern and central part of the Park, close to Arad, Felnac, Secusigiu and Nadlac localities. This could indicate a future strong adaptation capacity of *A. fruticosa* to many terrestrial ecosystems and, consequently, a serious threat for the native terrestrial plant species, requiring the inclusion of specific measures in the park's management plan.

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References

Almasi KN (2000) A non-native perennial invades a native forest. Biological Invasions 2(2): 219–230. https://doi.org/10.1023/A:1010009123469

Anastasiu P, Negrean G (2005) Alien plants in Romania. Analele ştiinţifice ale Universităţii "Alexandru Ioan Cuza" Iaşi Biologie vegetală, LI, 87–96.

Anastasiu P, Negrean G (2006) Alien vascular plants in Dobrogea (Romania) and their impact on different types of habitats. Plant, Fungal and Habitat Diversity Investigation and Conservation, Proceedings IV, BBC, Sofia, 590–596.

Anastasiu P, Negrean G, Bas C, Sîrbu C, Oprea A (2008) A preliminary study on the neophytes of wetlands in Romania. In: Rabitsch W, Essl F, Klingenstein F (Eds) Biological Invasions – from Ecology to Conservation. Neobiota 7: 181–192.

Andreu J, Vila M (2010) Risk analysis of potential invasive plants in Spain. Journal for Nature Conservation 18(1): 34–44. https://doi.org/10.1016/j.jnc.2009.02.002

Arim M, Abades SR, Neill PE, Lima M, Marquet PA (2006) Spread dynamics of invasive species. PNAS 103(2): 374–378. https://doi.org/10.1073/pnas.0504272102

Bailey J, Bimova K, Mandak B (2007) The potential role of polyploidy and hybridisation in the further evolution of the highly invasive *Fallopia* taxa in Europe. Ecological Research 22(6): 920–928. https://doi.org/10.1007/s11284-007-0419-3

Bălteanu D, Dumitraşcu M, Geacu S, Ciupitu D (2016) Ariile naturale protejate. In: Romania. Space, Society, Environment. Romanian Academy, Bucharest, 542-563.

Blagojević M, Konstantinović B, Samardžić N, Kurjakov A, Orlović S (2015) Seed Bank of Amorpha fruticosa L. on Some Ruderal Sites in Serbia. Journal of Agricultural Science and Technology B 5(2): 122–128. https://doi.org/10.17265/2161-6264/2015.02B.006

Bogdan O (2004) Regionarea climatică în: România. In: Calitatea solurilor şi reţeaua electrică de transport. Atlas geographic. Romanian Academy Publishing House, 6.

Bogdan O, Dragotă C, Micu D (2016) Potențialul climatic. In: In: Romania. Space, Society, Environment. Romanian Academy, Bucharest, 102–130.

Brothers TS, Spingarn A (1992) Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6(1): 91–100. https://doi.org/10.1046/j.1523-1739.1992.610091.x

Cadanasso ML, Pickett ST (2001) Effect of edge structure on the flux of species into forest interiors. Conservation Biology 15(1): 91–97. https://doi.org/10.1111/j.1523-1739.2001.99309.x

Callaway RM, Ridenour WM (2004) Novel weapons: Invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2(8): 436–443. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Charles H, Dukes JS (2006) Impacts of Invasive Species on Ecosystem Services in Ecological Studies. Biological Invasions 193: 9–15.

Christen D, Matlack G (2006) The role of roadsides in plant invasions: A demographic approach. Conservation Biology 20(2): 385–391. https://doi.org/10.1111/j.1523-1739.2006.00315.x

Clark WAV, Hosking PL (1986) Statistical Methods for Geographers. Wiley, New York.

Cowie ID, Werner PA (1993) Non-native plant species invasive in Kakadu National Park, tropical northern Australia. Biological Conservation 63(2): 127–135. https://doi.org/10.1016/0006-3207(93)90500-Z

Delai F, Kiss T, Nagy J (2018) Field-based estimates of floodplain roughness along the Tisza River (Hungary): The role of invasive *Amorpha fruticosa.* Applied Geography (Sevenoaks, England) 90: 96–105. https://doi.org/10.1016/j.apgeog.2017.11.006

De Poorter M, Pagad S, Ullah MI (2007) Invasive alien species and protected areas. A scoping report. Part I. Scoping the scale and nature of invasive alien species. Threats to protected areas, impediments to IAS. Management and means to address those impediments. Produced for the World Bank as a contribution to the Global Invasive Species programme (GISP). http://www.issg.org/pdf/publications/gisp/resources/ias_protectedareas_scoping_i.pdf

Dirnbock T, Greimler J, Lopez PS, Stuessy TF (2003) Predicting Future Threats to the Native Vegetation of Robinson Crusoe Island, Juan Fernandez Archipelago, Chile. Conservation Biology 17(6): 1650–1659. https://doi.org/10.1111/j.1523-1739.2003.00173.x

Doroftei M (2009) Chorology of *Amorpha fruticosa* in Danube Delta. Romanian Journal of Plant Biology 54(1): 61–67.

Dumitraşcu M, Grigorescu I, Kucsicsa G, Dragotă C, Năstase M (2011) Non-native and native invasive terrestrial plant species in Comana Natural Park. Case-studies: *Amorpha fruticosa* and *Crataegus monogyna*. Rev. Roum. Géogr. Rom. Journ. Geogr. 55(2): 81–89.

Dumitraşcu M, Grigorescu I, Doroftei M, Kucsicsa G, Mierlă M, Dragotă C, Năstase M (2013) *Amorpha fruticosa* in three wetland areas: Danube Delta Biosphere Reserve, Comana and Mureş Floodplain Natural Parks, The 13th International Multidisciplinary Scientific GeoConference SGEM, 16–22 iunie, 2013, Albena, Bulgaria, Ecology, Economics, Education and Legislation Conference Proceedings 1: 113–124. http://sgem.org/sgemlib/spip.php?article3268

Dumitraşcu M, Grigorescu I, Kuscicsa G, Doroftei M, Năstase M, Dragotă C (2014) Invasive terrestrial plant species in the Romanian protected areas. A geographical approach. Rev. Roum. Géogr. Rom. Journ. Geogr. 58(2): 145–160.

Elakowich SD, Wooten JW (1995) Allelopathyc woody plants I. *Abies alba* through *Lyonia lucida.* Allelopathy Journal 2: 117–146.

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29(2): 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Fenesi A, Ruprecht EK, Vincze E (2009) Aggressively spreading exotic plant species in Romania. Neobiota din Romania. Presa Universitara Clujeana.

Franklin J (1995) Predictive vegetation mapping: Geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19(4): 474–499. https://doi.org/10.1177/030913339501900403

Fukasawa K, Koike F, Tanaka N, Otsu K (2009) Predicting future invasion of an invasive alien tree in a Japanese oceanic island by process-based statistical models using recent distribution maps. Ecological Research 24(5): 965–975. https://doi.org/10.1007/s11284-009-0595-4

Gallé L, Margóczy K, Kovács E, Gyrffy G, Körmöczy L, Németh L (1995) River valleys: Are they ecological corridors? Tiscia 29: 53–58.

Goslee SC, Debra PC, Peters DPC, Beck GK (2006) Spatial prediction of invasion success across heterogeneous landscapes using an individual-based model. Biological Invasions 8(2): 193–200. https://doi.org/10.1007/s10530-004-2954-y

Grigorescu I, Dumitrascu M, Kucsicsa G, Doroftei M, Dragotă C, Năstase M (2014) Assessing Invasive Terrestrial Plant Species in the Mureş Floodplain Natural Park. Romania. The 14th International Multidisciplinary Scientific GeoConference SGEM, 17–26 iunie, 2014, Albena, Bulgaria, 1, Ecology & Environmental Protection, 51–58. https://doi.org/10.5593/SGEM2014/B51/S20.008

Guisan A, Thuiller W (2005) Predicting species distribution: Offering more than simple habitat models. Ecology Letters 8(9): 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Hall FG, Towhshend JR, Engman ET (1995) Status of remote sensing algorithms for estimation of land surface state parameters. Remote Sensing of Environment 51(1): 138–156. https://doi.org/10.1016/0034-4257(94)00071-T

Harrison S, Hohn C, Ratay S (2002) Distribution of exotic plants along roads in a peninsular nature reserve. Biological Invasions 4(4): 425–430. https://doi.org/10.1023/A:1023646016326

Hensher DA, Johnson LW (1981) Applied Discrete Choice Modeling. Croom Helm, London.

Higgins SI, Richardson DM, Cowling RM, Trinder Smith TH (1999) Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. Conservation Biology 13(2): 303–313. https://doi.org/10.1046/j.1523-1739.1999.013002303.x

Hosmer DW, Lemeshow S (1989) Applied logistic regression. Wiley, New York.

Horssen PW, Pebesma EJ, Schot PP (2002) Uncertainties in spatially aggregated predictions from a logistic regression model. Ecological Modelling 154(1–2): 93–101. https://doi.org/10.1016/S0304-3800(02)00060-1

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22(0): 415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Jenks GF (1967) The Data Model Concept in Statistical Mapping. International Yearbook of Cartography 7: 186–190.

Jiménez-Valverde J, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biological Invasions 13(12): 2785–2797. https://doi.org/10.1007/s10530-011-9963-4

Joly M, Bertrand P, White MC, Lavoie C, Gbangou RY, Dube J (2011) Paving the Way for Invasive Species: Road Type and the Spread of Common Ragweed (*Ambrosia artemisiifolia*). Environmental Management 48(3): 514–522. https://doi.org/10.1007/s00267-011-9711-7

Kanevski M, Maignan M (2004) Analysis and modelling of spatial environmental data. EPFL Press, 300 pp.

Kucsicsa G, Grigorescu I, Dumitraşcu M (2013) Integrated methodology for the assessment of Invasive Terrestrial Plant Species potential distribution in the Romanian Protected Areas. A GIS-based approach. Proceedings of 9th WSEAS International Conference on Energy, Environment, Ecosystems and Sustainable Development, Recent Advances in Environmental Science, 150–155.

Kucsicsa G, Grigorescu I, Dumitrascu M (2016) Integrated methodology and Data. In: Invasive Terrestrial Plant Species in the Romanian Protected Areas. A geographical approach. Romanian Academy Publishing House, 37–46.

Lambdon P, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Andriopoulos P (2008) Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. Preslia 80(2): 101–149.

Macdonald IAW, Graber DM, DeBenedetti S, Groves RH, Fuentes ER (1988) Introduced species in nature reserves in Mediterranean-type climatic regions of the world. Biological Conservation 44(1–2): 37–66. https://doi.org/10.1016/0006-3207(88)90004-3

Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution 13(5): 195–198. https://doi.org/10.1016/S0169-5347(97)01286-X

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10(3): 689–710. https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Magyar P (1960) Afforestation in Great Hungarian Plain. Akadémiai Kiadó, Budapest. [in Hungarian]

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Gen. Tech. Rep. PNW-GTR-351.U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 122 pp.

Mcgeochm MA, Stuart HM, Spear D, Marais E, Kleynhans EJ, Symes A, Chanson J, Hoffmann M (2010) Global indicators of biological invasion: Species numbers, biodiversity impact and policy responses. Diversity & Distributions 16(1): 95–108. http://www.cbd.int/sp/. https://doi.org/10.1111/j.1472-4642.2009.00633.x

Mortensen DA, Emily SJ, Rauschert ESJ, Nord AN, Jones BP (2009) Forest Roads Facilitate the Spread of Invasive Plants. Invasive Plant Science and Management 2(03): 191–199. https://doi.org/10.1614/IPSM-08-125.1

Mureş Floodplain Natural Park Administration (2016) Mureş Floodplain Natural Park Management Plan, National Forest Administration ROMSILVA, 193 pp.

Panetta FD, Dodd J (1987) Bioclimatic prediction of the potential distribution of skeleton weed *Chondrilla juncea* L. in Western Australia. Journal of the Australian Institute of Agricultural Science 53: 11–16.

Pearce JL, Venier LA, Ferrier S, McKenney DW (2003) Measuring prediction uncertainty in models of species distribution. Predicting Species Occurrences: Issues of Accuracy and Scale. The Auk 120(4): 1199–1200. https://doi.org/10.1642/0004-8038(2003)120[1199:PSOIOA]2.0.CO;2

Pearson RG (2010) Species' Distribution Modeling for Conservation Educators and Practitioners. Lessons in Conservation 3: 54–89.

Pedashenko HP, Apostolova II, Kiril V, Vassilev KV (2012) *Amorpha fruticosa* invasibility of different habitats in lower Danube. Phytologia Balcanica 18(3): 285–291.

Pulliam HR (2000) On the relationship between niche and distribution. Ecology Letters 33: 49–361. https://doi.org/10.1046/j.1461-0248.2000.00143.x

Pyšek P, Hume PE (2005) Spatio-temporal dynamics of plant invasions: Linking pattern to process. Ecoscience 12(3): 302–315. https://doi.org/10.2980/i1195-6860-12-3-302.1

Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kühn I, Tichý L, Danihelka J, Chrtek jun J, Sádlo J (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Diversity & Distributions 15(5): 891–903. https://doi.org/10.1111/j.1472-4642.2009.00602.x

Pysek P, Jarosik V, Kucera T (2003) Inclusion of native and alien species in temperate nature reserves: An historical study from Central Europe. Conservation Biology 17(5): 1414–1424. https://doi.org/10.1046/j.1523-1739.2003.02248.x

Radovanović N, Kuzmanović N, Vukojičić S, Lakušić D, Jovanović S (2017) Floristic diversity, composition and invasibility of riparian habitats with *Amorpha fruticosa*: A case study from Belgrade (Southeast Europe). Urban Forestry & Urban Greening 24: 101–108. https://doi.org/10.1016/j.ufug.2017.04.006

Rejmánek M (1989) Invasibility of plant communities. Biological invasions: a global perspective. John Wiley & Sons, Chichester, 369–388.

Rempel RS, Kaukinen D, Carr AP (2012) Patch Analyst and Patch Grid. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.

Rew LJ, Maxwell BD, Aspinall R (2005) Predicting the occurrence of nonindigenous species using environmental and remotely sensed data. Weed Science 53(2): 236–241. https://doi.org/10.1614/WS-04-097R

Richardson DM, Pysek P, Rejmánek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity & Distributions 6(2): 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Ricklefs RE, Schluter D (1993) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, 414 pp.

Rood SB, Braatne JH, Goater LA (2010) Favorable fragmentation: River reservoirs can impede downstream expansion of riparian weeds. Ecological Applications 20(6): 1664–1677. https://doi.org/10.1890/09-0063.1

Rouget M, Richardson DM, Milton SJ, Polakow D (2001) Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecology 152(1): 79–92. https://doi.org/10.1023/A:1011412427075

Rouse JW, Haas RH, Deering DW, Sehell JA (1974) Monitoring the vernal advancement and retrogradation (Green wave effect) of natural vegetation. Final Rep. RSC, 1978-4, Remote Sensing Center, Texas A&M Univ, College Station.

Sărăţeanu V (2010) Assessing the influence of *Amorpha fruticosa* L. invasive shrub on some grassland vegetation types from western Romania. Research Journal of Agricultural Science 42(1): 536–540.

Seo KW, Son Y, Rhoades CC, Noh NJ, Koo JW, Kim JG (2008) Seedling Growth and Heavy Metal Accumulation of Candidate Woody Species for Revegetating Korean Mine Spoils. Restoration Ecology 16(4): 702–712. https://doi.org/10.1111/j.1526-100X.2008.00485.x

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasion. Trends in Ecology & Evolution 17(4): 170–176. https://doi.org/10.1016/S0169-5347(02)02495-3

Silveri A, Dunwiddie PW, Michaels HJ (2001) Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. Biological Invasions 3(4): 379–389. https://doi.org/10.1023/A:1015898818452

Sîrbu C, Oprea A (2011) Plante adventive în flora Românei. Editura "Ion Ionescu de la Brad", Iaşi, 733 pp.

Sîrbu C, Oprea A, Eliáš P, Ferus P (2012) New data addition to the Romanian alien flora. Journal of Plant Development 19: 141–156.

Sîrbu C, Oprea A, Doroftei M (2016a) Invasive Terrestrial Plant Species in Romania. In: Invasive Terrestrial Plant Species in the Romanian Protected Areas. A geographical approach. Romanian Academy Publishing House, 17–29.

Sîrbu C, Oprea A, Doroftei M (2016b) Management and Control of Invasive Terrestrial Plant Species in Romania. Invasive Terrestrial Plant Species in the Romanian Protected Areas. A geographical approach. Romanian Academy Publishing House, 103–112.

Stănescu V, Şofletea N, Popescu O (1997) Flora forerstieră lemnoasă a României. Edit. Ceres, Bucureşti.

Szigetvári C (2002) Initial steps in the regeneration of a floodplain meadow after a decade of dominance of an invasive transformer shrub, *Amorpha fruticosa* L. TISCIA 33: 67–77.

Turner MG (1989) Landscape ecology: The effect of patterns on process. Annual Review of Ecology and Systematics 20(1): 171–197. https://doi.org/10.1146/annurev.es.20.110189.001131

Underwood EC, Klinger R, Moore PE (2004) Predicting patterns of non-native plant invasions in Yosemite National Park, California, USA. Diversity & Distributions 10(5–6): 447–459. https://doi.org/10.1111/j.1366-9516.2004.00093.x

Václavík T, Meentemeyer RK (2009) Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? Ecological Modelling 220(23): 3248–3258. https://doi.org/10.1016/j.ecolmodel.2009.08.013

Wang ET, van Berkum P, Sui XH, Beyene D, Chen WX, Martínez-Romero E (1999) Diversity of microbial associated with *Amorpha fruticosa* isolated from Chinese soils and description of *Mesorhizobium amorphae* sp. nov. International Journal of Systematic Bacteriology 49(1): 51–65. https://doi.org/10.1099/00207713-49-1-51

Weber E, Gut D (2004) Assessing the risk of potentially invasive plant species in central Europe. Journal for Nature Conservation 12(3): 171–179. https://doi.org/10.1016/j.jnc.2004.04.002

Williamson M (1996) Biological invasions. Chapman and Hall, London, 1–244.

Xiang S, Xiaolei Z, Guangcai C, Yitai C, Ling W, Xiaoquan S (2011) Seedling growth and metal accumulation of selected woody species in copper and lead/zinc mine tailings. Journal of Environmental Sciences (China) 23(2): 266–274. https://doi.org/10.1016/S1001-0742(10)60402-0

Yemshanov D, Koch FH, Ducey MJ (2015) Making invasion models useful for decision makers: incorporating uncertainty, knowledge gaps, and decision-making preferences. Pest Risk Modeling and Mapping for Invasive Alien Species. Wallingford, UK, CABI Publishing, 206–222. https://doi.org/10.1079/9781780643946.0206

Dumitrascu M, Grigorescu I. (Ed.) (2016) Invasive Terrestrial Plant Species in the Romanian Protected Areas. A geographical approach, Romanian Academy Publishing House, 155 pp.

McCullagh P, Nelder JA (1989) Generalized Linear Models. Chapman and Hall, New York. https://doi.org/10.1007/978-1-4899-3242-6

Kleinbaum D. (1994) Logistic regression: a self-learning text. SpringerVerlag, New York. https://doi.org/10.1007/978-1-4757-4108-7

Liebetrau AM (1983) Measures of association. Sage, Newbury Park, CA. https://doi.org/10.4135/9781412984942

Nagelkerke NJD (1991) A note on a general definition of the coefficient of determination. Biometrika*,* 78(3), 691–692. https://doi.org/10.1093/biomet/78.3.691

Pontius Jr RG, Schneider LC (2001) Land-cover change model validation by an ROC method for the Ipswich watershed, Massachusetts, USA. Agriculture, ecosystems and environment, 85(1–3), 239–248. https://doi.org/10.1016/S0167-8809(01)00187-6

Mas JF, Soares Filho B, Pontius RG, Farfán Gutiérrez M, Rodrigues H (2013) A suite of tools for ROC analysis of spatial models. ISPRS International Journal of Geo-Information, 2(3), 869–887. https://doi.org/10.3390/ijgi2030869

Marian M, Nicula C, Mihaly-Cozmuta L, Peter A, Mihaly-Cozmuta A (2010) Participation of the indigenous vs. alien herbaceous species to the constitution of vegetal layer on the Bozânta Mare tailing ponds*,* Analele Universităţii din Oradea – Fascicula Biologie, XVII, 1, pp. 134–141.

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Matching social-ecological systems by understanding the spatial scale of environmental attitudes

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Abstract
Mismatching in the spatial scales of social structures and ecological processes complicates the management of natural resources. Here we suggest the use of variance components to determine at which spatial scale variation in feelings, environmental attitudes and value orientation is largest and hence most exposed to conflicts. We estimated the variance components of the feeling of fear for large carnivores, environmental attitudes towards large carnivores and environmental value orientation at 3 scales (municipality, county and country) in Norway and Sweden. The feeling of fear for specific carnivores had the highest variance components at the municipality level, we found no specific scale that best explained the variance in attitudes towards carnivores in general, while attitudes based on environmental value orientation showed the highest variance components at the country level. To match the social-ecological systems, we conclude that management units have to be designed as the best possible trade-off between the social and ecological scales; i.e. largest possible to maintain ecological sustainability, but small enough to maintain a low degree of social conflicts.

Keywords
carnivores, conflict, human-wildlife, management, scale, variance components

Introduction

Scaling is an important issue in ecology as patterns and processes vary with scale. The most appropriate scale to study will depend on the species', or the individuals', perception of the landscape and the organisational level of interest. For instance, individuals, populations, ecological communities, ecosystems and landscapes will require different scales of the study (e.g. Wiens 1989, Gaillard et al. 2010). Scaling in the social sciences relates to individuals and social structures that govern jurisdictions, laws, policies, cultural norms and values, resource access rights, economics and management responsibilities (e.g. Gibson et al. 2000, Cumming et al. 2006). Most often, such structures have a spatial dimension and Gibson et al. (2000) defined the following spatial levels of political jurisdictions: household, community, regional, national and international. The different nature of social science and ecology makes it difficult to create common definitions or comparisons of scale (Gibson et al. 2000) resulting in the management of natural resources is functioning at a different scale than the ecological processes subjected to management interventions (Norton 1998, Cumming et al. 2006).

Ideally, management units should incorporate large enough areas to ensure sustainability of the ecological process, but, at the same time, avoid incorporating excessive attitudinal variation in order to avoid problems that are outside the powers of managers. This connection between the ecological and social scale is important as management policies are dynamic and to a large extent founded on public opinion (Butler et al. 2003). Management may thus make decisions at a scale that fits the public opinion, but not necessarily the ecological sustainability. In wildlife management, anything connected to public opinion is often labelled as attitudes and are most frequently studied using social-psychological approaches in which attitudes are thought to be psychological characteristics of individuals (Manfredo and Dayer 2004, Peterson et al. 2010). In scientific terms, attitudes may be defined as people's evaluation of their surroundings referring to an object, issue or an event (Eagly and Chaiken 2007, Manfredo 2008) and is a complex, but precise construct, made up of cognitive, emotional and behavioural components (Stern et al. 1995). Attitudes are assumed to be rather stable as the complex structures are difficult to break apart (Heberlein 2012).

Attitudes are part of the cognitive hierarchy together with norms and values (Manfredo and Dayer 2004). The complex structures of the cognitive hierarchy consist of an array of components that show different origin and stability. For instance, values are fundamental, achieved early in life and highly resistant to change (Bjerke and Kaltenborn 1999, Manfredo and Dayer 2004). In wildlife management, the value concept is often described as environmental value orientation ranging from ecocentric values (wildlife protection) to anthropocentric values (wildlife use) (Thompson and Barton 1994, Bjerke and Kaltenborn 1999). We therefore assume that environmental value orientation is an even more stable component than attitudes. On the other hand, attitudes consist of an emotional component which is more volatile (Scherer 2005). Emotions are also described as complex structures, amongst others, consisting of feelings which have a cognitive input and are the subjective mental associations to an emotion (Damasio 2000, Scherer 2005).

To approach a common social-ecological understanding of scale, we have taken some of the social responses connected to components of the cognitive hierarchy (i.e. feelings, attitudes and environmental value orientation) and analysed them in a typical physical way by using variance components to reveal at which spatial scale variability is being introduced to these components. We have based our analyses on the results from a questionnaire related to large carnivores. Large carnivores present a good opportunity for studying social-ecological scales since public opinion affects policy at multiple levels. The presence of carnivores changes locally, human-carnivore conflicts change locally and the management of carnivores changes from national authorities to more regional or local authorities and may also change over time (Bisi et al. 2007, Majic et al. 2011, Treves et al. 2013).

We assumed that the relatively stable components of the cognitive hierarchy develop slowly over time and expand into larger stable socio-spatial structures, e.g. at a regional or national level, rather than changing abruptly depending on changes in the local environment. Hence, we expected that feelings (here represented by fear towards specific carnivore species) were connected to local changes in the presence of the carnivore species and thus to have the highest variation at local scales (i.e. municipality). Furthermore, we expected attitudes towards carnivores to have the highest variation at an intermediate scale (i.e. county) and environmental value orientation to have the highest variation at a large scale (i.e. country).

Methods

Data on attitudes were collected in 2011 through a telephone survey carried out by a data collection company (www.norstat.no) from 4–5 respondents in each municipality in Norway and Sweden. The data collection company (NORSTAT) bases its sample on existing registers that are publicly available when they collect data by telephone interviews. When the respondents in our study were contacted, the interviewer followed a strict protocol as dictated by standard research ethics, including presenting the purpose of the study and the agency behind it, that participation is entirely voluntary, how long the interview would take and how the results would be used (see Gangaas et al. 2013 for a more detailed description of the questionnaire).

The survey provided answers from 2522 respondents (1508 in Norway and 1014 in Sweden) from 722 municipalities, which are combined into 40 counties from 2 countries (Norway and Sweden; Table 1). The sample was designed not to be representative of the population in the two countries, but to detect spatial patterns and facilitate analysis of differences between local, regional and national levels (Fig. 1).

The large carnivores in Norway and Sweden consist of brown bear *Ursus arctos*, wolverine *Gulo gulo*, lynx *Lynx lynx* and wolves *Canis lupus*. These large carnivores are managed at the national scale in both Norway and Sweden, while some of the management actions are delegated down to a local scale (county level or to local boards consisting of politicians from counties merged into specific management regions). There are differ-

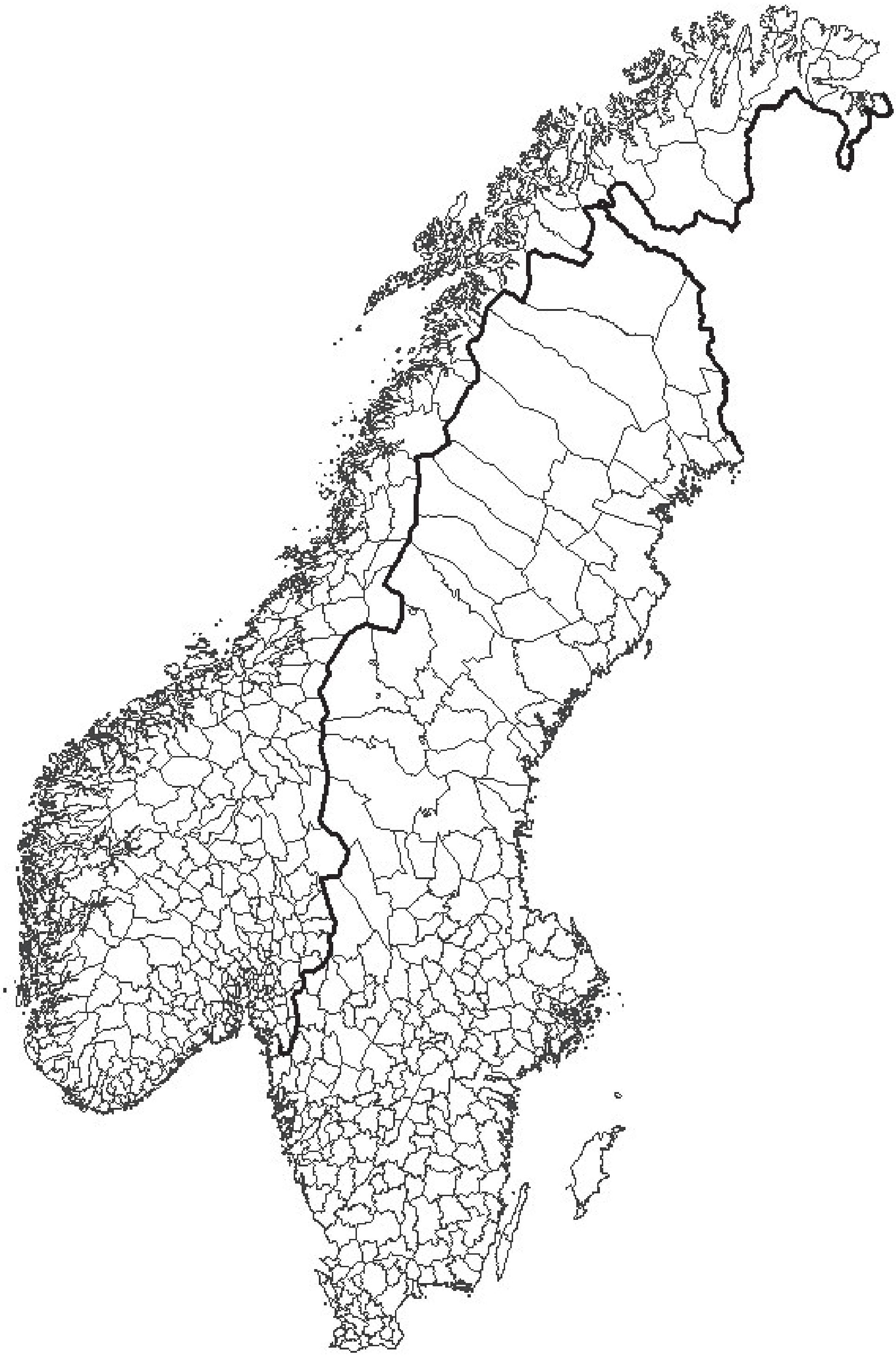

Figure 1. Map of Norway and Sweden split into the 722 municipalities.

Table 1. The number of municipalities, counties and countries analysed to describe the local, regional and national levels.

Level	Norway	Sweden
Municipality	431	291
County	19	21
Country	1	1

ences in the numbers of carnivores between the two countries, as Sweden houses much higher densities of all large carnivore species compared to Norway (Linnell et al. 2000).

The full questionnaire included questions characterising the respondent (e.g. sex and age), several questions that were given only to some respondents depending on whether their acceptance of carnivores was unconditional or not and questions related to management and expressions used to identify the respondents' general environmental attitudes (Gangaas et al. 2013). Here we analysed questions and statements that were asked of all respondents and that were not directly connected to management (Table 2). These questions and statements were answered with a 3 to 5-level scale as described in Table 2. Note that the direction of the answer (i.e. towards an anthropocentric or an ecocentric view) is not important in the present context as our focus is on the variance of the answers.

We expected that the presence of carnivores could cause local conflicts that could change humans' attitudes towards carnivores at a local scale and even more if the carnivore species were emphasised by species names. We classified *a priori* the following spatial scale expected to give highest variance for the given feeling/attitude stated in the questions and expressions:

- Small (i.e. municipality) scale to questions and expressions describing feelings or attitudes towards specific carnivore species
- Intermediate (i.e. county) scale to questions and expressions describing attitudes towards carnivores in general, without naming the carnivore species
- Large (i.e. country) scale to questions and expressions describing environmental value orientation.

All questions and the scale expected to have the highest variation are listed in Table 2. All analyses were done with the lme-function in R 3.0.1 (http://cran.r-project.org/) by extracting the variance components from random nested models (Country/County/Municipality) with the varcomp-function. We then estimated the percentage of each of the spatial scale component contributed to the random variance components.

Results

Our results did, to some extent, confirm our predictions. The very specific questions related to fear of specific carnivore species had largest variance components at a small scale (S1 – S4; Figs 2, 3). However, the variance components with regard to the other

Table 2. The questions and statements from the questionnaire included in the analyses, with the scale we *a priori* expected would explain most of the variation (small is municipality, medium is county and large is country). We registered replies to questions S1 – S4 as 1: not at all, 2: a little scared, 3: quite scared and 4: very scared; M1 as 1: too few, 2: just the right amount and 3: too many. All other questions were registered as: 1: highly disagree, disagree, 3: neither agree nor disagree, 4: agree; 5: highly agree. Note that agreement to the questions M2, M4, L4 and L6 indicates the anthropocentric view, while questions M3, M5, M6, L1–L5 and L7 are reversed and disagreement also indicates the anthropocentric view.

ID*	Expected scale	Question / Statement
Questions related to emotions		
S1	Small	How scared are you of wolverine?
S2	Small	How scared are you of wolf?
S3	Small	How scared are you of brown bear?
S4	Small	How scared are you of lynx?
Questions related to attitudes		
S5	Small	Poaching of wolverine is acceptable
S6	Small	Poaching of wolf is acceptable
S7	Small	Poaching of brown bear is acceptable
S8	Small	Poaching of lynx is acceptable
M1	Medium	Do you think there are too few, just the right amount or too many large carnivores in your country today?
M2	Medium	Fear is a good enough reason to remove large carnivores
M3	Medium	Large carnivores are an enrichment for my nature experience
M4	Medium	Large carnivores limit my use of nature
M5	Medium	Seeing large carnivores in nature is a privilege
M6	Medium	Norway/Sweden is a rich country that should take responsibility for large carnivores
Questions related to value orientation		
L1	Large	Seeing tracks and signs increase my quality of life
L2	Large	The balance in nature is delicate and easily upset
L3	Large	Humans are severely abusing the environment
L4	Large	The so-called “ecological crisis” facing human kind has been greatly exaggerated
L5	Large	Plants and animals have the same rights to life on earth as humans
L6	Large	The balance of nature is sufficiently stable to withstand the impacts from a modern industrial society
L7	Large	If things continue on their present course, we will soon experience a major ecological catastrophe

* ID is an identification of the question used in Fig. 1.

4 questions related to attitudes to specific carnivore species (S5–S8; acceptance of illegal hunting) were highest at the large country scale. Questions related to carnivores in general, without naming the carnivore species, were not related to any specific scale as the variance component was more evenly distributed between municipality, county and country. The general questions, related to environmental value orientation had, as expected, the largest variance components at the largest scale (country).

Discussion

Attitudes toward the environment have frequently been studied with questionnaires at one given spatial scale, e.g. at a national or regional level (Bjerke et al. 1998, Kalten-

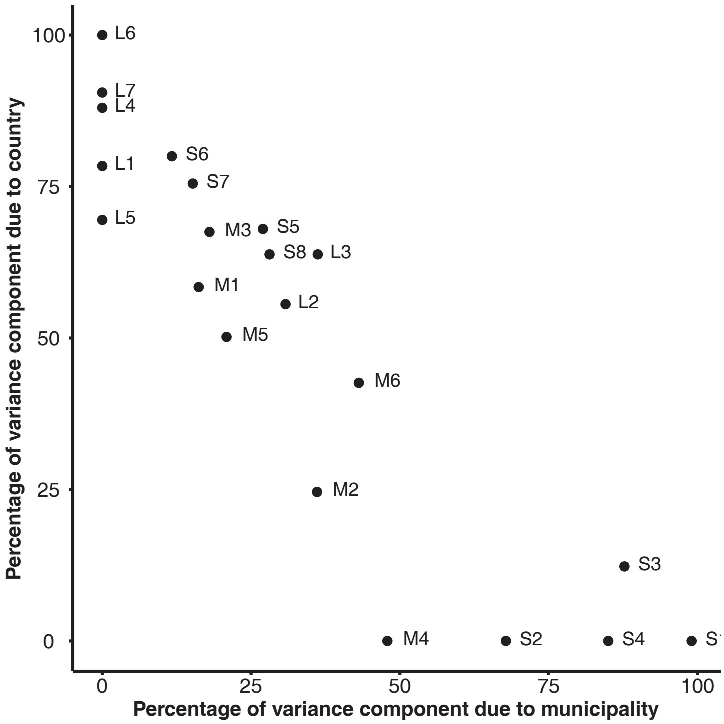

Figure 2. The location of the questions and statements (described in Table 2) depending on the percentage of the variance components explained by municipality (small scale) and country (large scale). Questions and statements located at the lower right of the plot are mainly explained by variations at smaller scales, while questions and statements at upper left of the plot are mainly explained by variation at larger scales.

born et al. 1998, Kaltenborn and Bjerke 2002, Butler et al. 2003, Roskaft et al. 2007, Heberlein and Ericsson 2008, Kaltenborn et al. 2008, Ardahan 2012, Heberlein 2012), while attitudinal variation in space has received less attention (Gangaas et al. 2013; 2014). Hence, even though the mismatch between social and ecological scale is evident, there have been few attempts to study at what spatial scale variation in feelings, attitudes and value orientation are introduced.

We need to understand the role of how attitudes are developed in conservation biology since attitudes heavily influence public opinion and policy-making (Manfredo et al. 1999). Even though measuring a subject's attitude from questionnaires does not imply that the respondent will behave in accordance with the attitudes expressed, attitudes explain a significant part of the variance in behaviour (Manfredo 2008, Heberlein 2012, Kaiser et al. 1999, Milfont and Duckitt 2010, Rodríguez-Barreiro et al. 2013, Armitage and Conner 2010, Rivis et al. 2009, Bamberg and Möser 2007)

Here, we broke down the variance in our responses from a broad spectrum of questions related to environmental feelings, attitudes and value orientation into various spatial scales. As expected, the variability in the responses depended on specific spatial scales. A large degree of the variation in fear for carnivores was connected to the

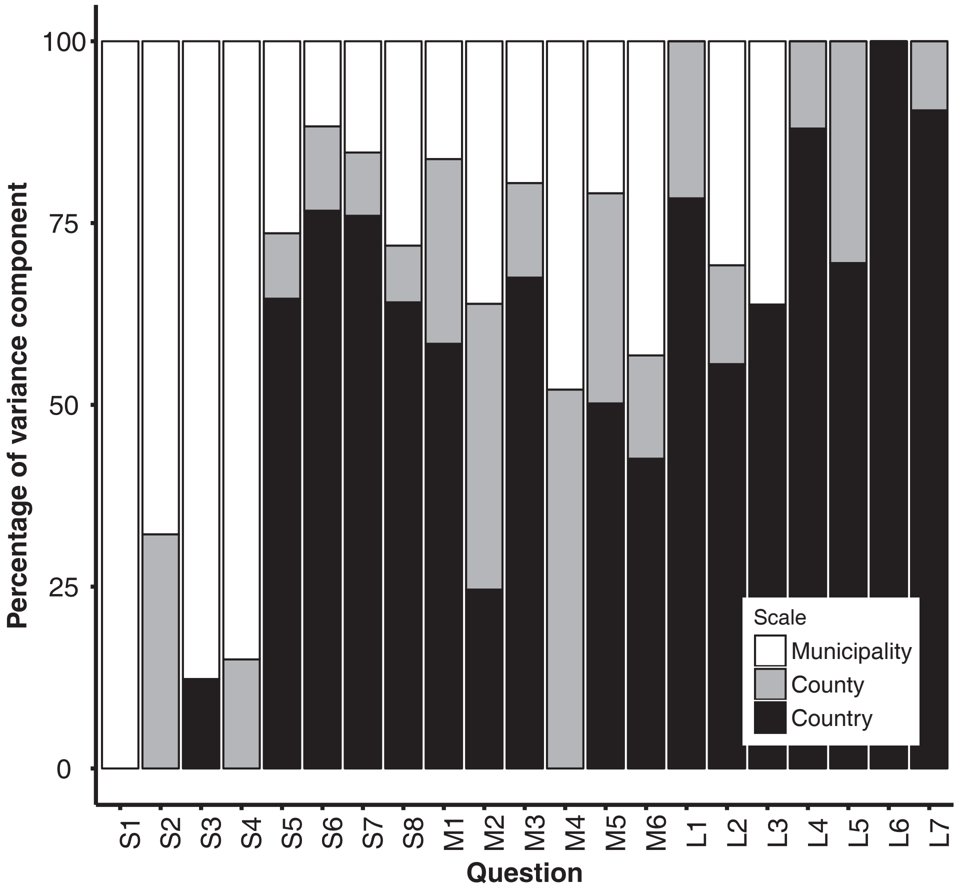

Figure 3. The percentage of the variance components explained by municipality (white), county (grey) and country (black) for each of the questions and statements in Table 2.

local scale. This connection appeared despite the low number of respondents per municipality. Contrary to our expectations, the variability in acceptance of illegal hunting of specific carnivore species was best described at the country level. General attitudes towards carnivores did not relate to any specific spatial scale, while most of the questions and expressions related to value orientation and environmental attitudes were best explained at the level of country as expected.

We argue that certain feelings or attitudes specifically related to carnivore species may be changeable and develop at local spatial scales, possibly as a result to environmental changes. For instance, Bisi et al. (2007) and Treves et al. (2013) showed that the fear of wolves decreased through time, but not the acceptance of wolves. Fear of animals represents complex emotional and somatic reactions to the experience of danger and is usually divided into a) expectations and beliefs about threats (cognition), b) physiological emergency reactions (somatic), c) feelings of dread or panic (emotion) and sometimes d) fleeing or fighting (behaviour) (Roskaft et al. 2003). Fear of large predators is usually considered as a rational, natural and adaptive response, but can be difficult to predict or treat considering its complexity and fundamental importance to human psyche and development. It is also, to some extent, conditioned by exposure. The feeling of fear for carnivores may be developed in as small a scale as a household and spread into the local community, being accelerated as a response to the new perception of the environment.

We may expect that environmental attitudes responding to the large spatial scale have developed over time and there seem to be national socio-spatial structures that are difficult to change (see also Heberlein 2012). We have previously shown that the presence of carnivores today or in historic times did not correlate with acceptance of illegal hunting or general environmental attitudes, but differs between countries (Gangaas et al. 2013). Consequently, these attitudes are not affected by local changes in the environment, for instance recolonising carnivores, at least not in a short to moderate time span. Despite Norway and Sweden sharing many national level policies, economies, education levels and, in many ways, a common history (Otterlei and Sande 2010), there seems to be national socio-cultural structures that introduce variability to illegal hunting and general environmental attitudes (Gangaas et al. 2013, 2014). One difference between the countries is that Swedes are used to a top-down and Norway a bottom-up governance system (Otterlei and Sande 2010), which result in that Swedes are more likely to accept centralised management decisions (Skogen 2001, Skogen 2003, Skogen and Thrane 2008, Otterlei and Sande 2010).

For several decades, it has been evident that environmental management requires integration of natural and social sciences. Such a multidisciplinary approach is complex as natural resource management always is somehow specified in space. Social sciences, on the other hand, typically operate with concepts that are difficult to define in spatial terms, such as processes and discourses related to institutions, power relations and macro-level socio-economic changes or psychological aspects of human-environment interactions. In addition, except for fear, the spatial scaling of environmental attitudes seems to be more or less disconnected from the ecological processes and rather linked to large scale socio-spatial structures (Treves and Karanth 2003, Bisi et al. 2007, Johansson et al. 2012).

Our approach for estimating the variance components of attitudes and feelings is, however, a way to link the social-ecological systems. For instance, from a purely ecological perspective, recolonisation of carnivores in the Scandinavian Peninsula would benefit from a joint Swedish-Norwegian management model. However, the potential for conflicts increases with increasing variation in attitudes (Manfredo et al. 2003, Vaske et al. 2010). If management increases its management units towards the scale of highest attitudinal variance components, it runs the danger of increasing environmental and social conflicts. In ecological terms, while it might be preferable to establish a common Scandinavian management model for large carnivores, the results from this study suggest that differences between the countries in socio-cultural traditions and attitudes linked to the carnivore situation might fuel increased societal conflicts. Another example would be that attempts to reduce fear of carnivores should direct attention to specific and local issues and recognise fear as a legitimate response to changing environments. Finally, attempts to influence environmental attitudes or value orientations correspond better to national level management policies.

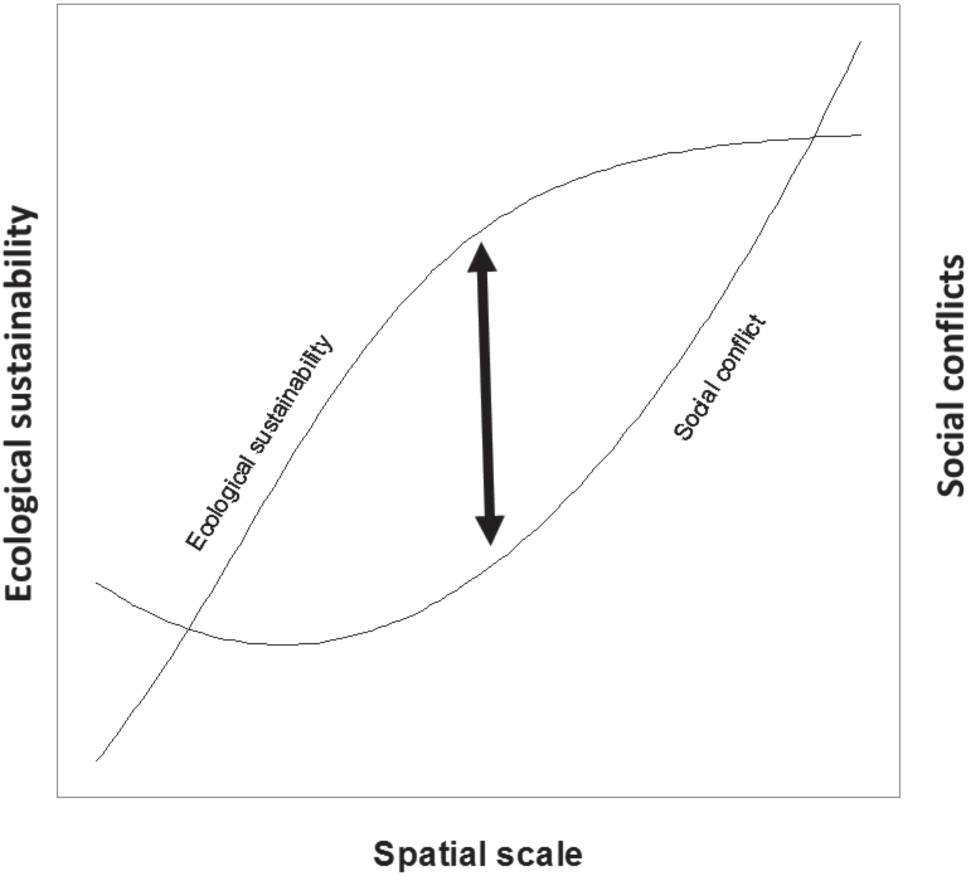

Figure 4. A conceptual model describing how spatial scale described as the extension of an area depends on the trade-off between ecological sustainability and social conflicts. Environmental management authorities should manage as large units as possible to maintain ecological sustainability, but at the same time keeping low conflict levels, here shown by the arrow.

Conclusion

In Figure 4, we have tentatively depicted the challenge related to these two disciplinary scales. Ecological sustainability requires as large areas as possible. Hence, as spatial scale increases, the ecological sustainability of a system will increase asymptotically. Social conflicts due to varying attitudes may be lowest at some kind of intermediate scale (e.g. municipality or county) and highest at large scales (international scales), while some social conflicts may also appear at local scales. Conservation policies need to design management units as the best possible trade-off between the social and ecological scales, by increasing management units to maintain sustainable ecological systems, while maintaining the lowest possible degree of social conflicts.

References

Ardahan F (2012) Comparison of the New Ecological Paradigm (NEP) Scale's Level of Participants and Non Participants of outdoor Sport with Respect to Some Demographic variables: Turkey CAse. The Online Journal of Recreation and Sport 1: 8–18.

Armitage CJ, Conner M (2010) Efficacy of the theory of planned behaviour: A meta-anlytical review. British Journal of Social Psychology 40(4): 471–499. https://doi.org/10.1348/014466601164939

Bamberg S, Möser B (2007) Twenty years after Hines, Hungerford and Tomera: A new meta-analysis of psycho-social determinants of proenvironmental behaviour. Journal of Environmental Psychology 27(1): 14–25. https://doi.org/10.1016/j.jenvp.2006.12.002

Bisi J, Kurki S, Svensberg M, Liukkonen T (2007) Human dimensions of wolf (*Canis lupus*) conflicts in Finland. European Journal of Wildlife Research 53(4): 304–314. https://doi.org/10.1007/s10344-007-0092-4

Bjerke T, Reitan O, Kellert SR (1998) Attitudes toward wolves in southeastern Norway. Society & Natural Resources 11(2): 169–178. https://doi.org/10.1080/08941929809381070

Bjerke T, Kaltenborn BP (1999) The relationship of ecocentric and anthropocentric motives to attitudes toward large carnivores. Journal of Environmental Psychology 19(4): 415–421. https://doi.org/10.1006/jevp.1999.0135

Butler JS, Shanahan J, Decker DJ (2003) Public attitudes toward wildlife are changing: A trend analysis of New York residents. Wildlife Society Bulletin 31: 1027–1036.

Cumming GS, Cumming DHM, Redman CL (2006) Scale mismatches in social-ecological systems: Causes, consequences, and solutions. Ecology and Society: 11. https://doi.org/10.5751/ES-01569-110114

Damasio A (2000). A second chance for emotion. In: Lane RD, Nadel L (Eds) Cognitice neuroscience of emotion. Oxford University Press, Oxford, UK, 12–23.

Eagly AH, Chaiken S (2007) The Advantages of an Inclusive Definition of Attitude. Social Cognition 25(5): 582–602. https://doi.org/10.1521/soco.2007.25.5.582

Gaillard JM, Hebblewhite M, Loison A, Fuller M, Powell R, Basille M, Van Moorter B (2010) Habitat-performance relationships: Finding the right metric at a given spatial scale. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 365(1550): 2255–2265. https://doi.org/10.1098/rstb.2010.0085

Gangaas KE, Kaltenborn BP, Andreassen HP (2013) Geo-spatial aspects of acceptance of illegal hunting of large carnivores in Scandinavia. PLoS One 8(7): e68849. https://doi.org/10.1371/journal.pone.0068849

Gangaas KE, Kaltenborn BP, Andreassen HP (2014) Environmental attitudes associated with large-scale cultural differences, not to local environmental conflicts. Environmental Conservation 42(01): 41–50. https://doi.org/10.1017/S0376892914000125

Gibson CC, Ostrom E, Ahn TK (2000) The concept of scale and the human dimensions of global change: A survey. Ecological Economics 32(2): 217–239. https://doi.org/10.1016/S0921-8009(99)00092-0

Heberlein TA (2012) Navigating environmental attitudes. Oxford University Press, Oxford, UK, 1–240. https://doi.org/10.1093/acprof:oso/9780199773329.001.0001

Heberlein TA, Ericsson G (2008) Public attitudes and the future of wolves *Canis lupus* in Sweden. Wildlife Biology 14(3): 391–394. https://doi.org/10.2981/0909-6396(2008)14[391:PAATFO]2.0.CO;2

Johansson M, Sjostrom M, Karlsson J, Brannlund R (2012) Is Human Fear Affecting Public Willingness to Pay for the Management and Conservation of Large Carnivores? Society & Natural Resources 25(6): 610–620. https://doi.org/10.1080/08941920.2011.622734

Kaiser FG, Wolfing S, Fuhrer U (1999) Environmental attitude and ecological behaviour. Journal of Environmental Psychology 19(1): 1–19. https://doi.org/10.1006/jevp.1998.0107

Kaltenborn BP, Andersen O, Nellemann C, Bjerke T, Thrane C (2008) Resident Attitudes Towards Mountain Second-Home Tourism Development in Norway: The Effects of Environmental Attitudes. Journal of Sustainable Tourism 16(6): 664–680. https://doi.org/10.1080/09669580802159685

Kaltenborn BP, Bjerke T (2002) Associations between environmental value orientations and landscape preferences. Landscape and Urban Planning 59(1): 1–11. https://doi.org/10.1016/S0169-2046(01)00243-2

Kaltenborn BP, Bjerke T, Strumse E (1998) Diverging Attitudes Towards Predators: Do Environmental Beliefs Play a Part? Human Ecology Review 5: 1–9.

Linnell JDC, Swenson JE, Andersen R (2000) Conservation of biodiversity in Scandinavian boreal forests: Large carnivores as flagships, umbrellas, indicators, or keystones? Biodiversity and Conservation 9(7): 857–868. https://doi.org/10.1023/A:1008969104618

Majic A, de Bodonia AMT, Huber D, Bunnefeld N (2011) Dynamics of public attitudes toward bears and the role of bear hunting in Croatia. Biological Conservation 144(12): 3018–3027. https://doi.org/10.1016/j.biocon.2011.09.005

Manfredo MJ (2008) Who cares about wildlife?: social science concepts for exploring human-wildlife relationships and conservation issues. Springer-Verlag New York, New York, 1–327.

Manfredo MJ, Pierce CL, Fulton D, Pate J, Gill BR (1999) Public acceptance of wildlife trapping in Colorado. Wildlife Society Bulletin 27: 499–508.

Manfredo MJ, Vaske JJ, Teel, TL (2003) The Potential for Conflict Index: A Graphic Approach to Practical Significance of Human Dimensions Research Human Dimensions of Wildlife 8: 219–228.

Manfredo MJ, Dayer AA (2004) Concepts for exploring the social aspects of human-wildlife conflicts in a global context. Human Dimensions of Wildlife 9(4): 1–20. https://doi.org/10.1080/10871200490505765

Milfont TL, Duckitt J (2010) The environmental attitudes inventory: A valid and reliable measure to assess the structure of environmental attitudes. Journal of Environmental Psychology 30(1): 80–94. https://doi.org/10.1016/j.jenvp.2009.09.001

Norton BG (1998) Improving ecological communication: The role of ecologists in environmental policy formation. Ecological Applications 8(2): 350–364. https://doi.org/10.1890/1051-0761(1998)008[0350:IECTRO]2.0.CO;2

Otterlei JB, Sande A (2010) Environmental policy and governing nature government or governance. Tidsskrift for Samfunnsforskning 51: 419–443.

Peterson MN, Birckhead JL, Leong K, Peterson MJ, Peterson TR (2010) Rearticulating the myth of human-wildlilfe conflict. Conservation Letters 3(2): 74–82. https://doi.org/10.1111/j.1755-263X.2010.00099.x

Rivis A, Sheeran P, Armitage CJ (2009) Expanding the affective and normative components of the theory of planned behavior: A meta-analysis of anticipated affect and moral norms. Journal of Applied Social Psychology 39(12): 2985–3019. https://doi.org/10.1111/j.1559-1816.2009.00558.x

Rodríguez-Barreiro LM, Fernandéz-Manzanal R, Serra LM, Carresquer J, Murillo MB, Morales MJ, Calvo JM, del Valle J (2013) Approach to a causal model between attitudes and environmental behaviour. A graduate case study. Journal of Cleaner Production 48: 116–125. https://doi.org/10.1016/j.jclepro.2012.09.029

Roskaft E, Bjerke T, Kaltenborn B, Linnell JDC, Andersen R (2003) Patterns of self-reported fear towards large carnivores among the Norwegian public. Evolution and Human Behavior 24(3): 184–198. https://doi.org/10.1016/S1090-5138(03)00011-4

Roskaft E, Handel B, Bjerke T, Kaltenborn BP (2007) Human attitudes towards large carnivores in Norway. Wildlife Biology 13(2): 172–185. https://doi.org/10.2981/0909-6396(2007)13[172:HATLCI]2.0.CO;2

Scherer KR (2005) What are emitions? And how can they be measured? Social Sciences Information. Information Sur les Sciences Sociales 44(4): 695–729. https://doi.org/10.1177/0539018405058216

Skogen K (2001) Who's afraid of the big, bad wolf? Young people's responses to the conflicts over large carnivores in eastern Norway. Rural Sociology 66(2): 203–226. https://doi.org/10.1111/j.1549-0831.2001.tb00064.x

Skogen K (2003) Adapting adaptive management to a cultural understanding of land use conflicts. Society & Natural Resources 16(5): 435–450. https://doi.org/10.1080/08941920309180

Skogen K, Thrane C (2008) Wolves in context: Using survey data to situate attitudes within a wider cultural framework. Society & Natural Resources 21(1): 17–33. https://doi.org/10.1080/08941920701460408

Stern PC, Dietz T, Kalof L, Guagnano GA (1995) Values, beliefs, and proenvironmental action – attitude formation toward emergent attitude objects. Journal of Applied Social Psychology 25(18): 1611–1636. https://doi.org/10.1111/j.1559-1816.1995.tb02636.x

Thompson SCG, Barton MA (1994) Ecocentric and anthropocentric attitudes toward the environment. Journal of Environmental Psychology 14(2): 149–157. https://doi.org/10.1016/S0272-4944(05)80168-9

Treves A, Karanth KU (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. Conservation Biology 17(6): 1491–1499. https://doi.org/10.1111/j.1523-1739.2003.00059.x

Treves A, Naughton-Treves L, Shelley V (2013) Longitudinal Analysis of Attitudes Toward Wolves. Conservation Biology 27(2): 315–323. https://doi.org/10.1111/cobi.12009

Vaske JJ, Beaman J, Barreto H, Shelby LB (2010) An Extension and Further Validation of the Potential for Conflict Index. Leisure Sciences 32(3): 240–254. https://doi.org/10.1080/01490401003712648

Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3(4): 385–397. https://doi.org/10.2307/2389612

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A socio-economic survey of pangolin hunting in Assam, Northeast India

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Abstract
India has been identified as a source country for the illegal international trade in endangered pangolins, "scaly mammalian anteaters", widely considered as the "world's most trafficked mammal". In this study, we investigated the involvement of hunters belonging principally to three locally prominent tribes (Biate, Dimasa and Karbi) in Assam State, Northeast India. Based on the results of interviews with 141 individuals, we conclude that all three tribal groups engaged in pangolin hunting between 2011 and 2016. Although pangolin meat is used locally, we found that hunters largely targeted pangolins for their scales and that substantial commercial gain via urban middlemen has now supplanted low-level traditional use as the primary driver for this activity. On average, each hunter captured one pangolin per year with the potential to earn 9,000 INR (135 USD) for a single animal (equating to approximately four months average income). The majority of hunters (89%) stated that pangolins were less abundant than they were five years ago, which suggests off-take is unsustainable. All hunters interviewed appeared to hunt pangolins occasionally, regardless of tribe, demography or income, which suggests that any mitigation strategy should focus on rural hunters. Whilst interventions to reduce poverty are no doubt required, we argue that such interventions alone are unlikely to be effective in reducing pangolin hunting. Rather, there is a need for co-ordinated packages of mutually reinforcing interventions to address this pangolin hunting in a more comprehensive manner. In particular, implementing a demand reduction strategy targeting urban consumers is urgently required.

Keywords
Bushmeat, *Manis crassicaudata*, *Manis pentadactyla*, traditional medicine, wildlife trade

Introduction

Pangolins ("scaly mammalian anteaters", belonging to the order Pholidota) are extensively hunted for their meat and for their scales (Baillie et al. 2014). Pangolin meat is considered a delicacy in some countries [notably in China and Vietnam (Challender 2011, Challender et al. 2015, Cheng et al. 2017)] and believed in some cultures to have health benefits [e.g. in eastern Nepal (Katuwal et al. 2015) and parts of India (Mohapatra et al. 2015, Aisher 2016 and references therein)]. Pangolin scales are used in Traditional Medicine, predominantly in China and Vietnam (Challender 2011, Challender et al. 2015, Xu et al. 2016), but also traditionally, amongst rural people, across South and Southeast Asia (e.g. Misra and Hanfee 2000, Katuwal et al. 2015, Aisher 2016) and Africa (Boakye et al. 2014, 2015, Soewu and Ayodele 2009, Soewu and Adekanola 2011, Soewu and Sodeinde 2015) although no reliable clinical efficacy of scales has been reported (Cheng et al. 2017). Pangolin scales are also used in rituals and as decorative items amongst local communities (e.g. Mahmood et al. 2012, Mohapatra et al. 2015). Ten years ago, relatively few people knew what a pangolin was (Zhang et al. 2017) but in recent years they have become an icon of the illegal wildlife trade in the media (Harrington et al. 2018) and are now widely reported to be the "world's most heavily trafficked mammal" (Sutter 2014, Aisher 2016).

The true extent of the numbers of pangolins hunted throughout their range is unknown, but it has been estimated that over a million individuals were taken from the wild between 2000 and 2013 (Challender et al. 2014a). Between 2010 and 2015, 1,270 reported seizures, in 67 countries and territories across six continents, involved a total of 120 tonnes in body parts, whole animals and scales of pangolins, plus an additional 46,000 individual pangolins (Heinrich et al. 2017) and this is believed to represent only the "tip of the iceberg" (Challender et al. 2015). As such, when key aspects of their biology [low reproductive output (e.g. Mahmood et al. 2015, Zhang et al. 2016), low density (e.g. Mahmood et al. 2014, 2018) and specialised niche requirements (Ma et al. 2017)] are also taken into account, the international trade of pangolins is now recognised as the most significant impediment for their conservation (Zhang et al. 2017).

There has been a notable shift in the sourcing of pangolins for the Chinese market, to other *Manis* species in Southeast Asia [predominantly Malaysia and Indonesia (Pantel and Chin 2008, Pantel and Anak 2010, Challender 2011, Gomez et al. 2017)]. A zero export quota for commercial trade in Asian species in 2000 (CITES 2017) led to a shift to target African species [*Phataginus* and *Smutsia* spp. (Challender 2011, Challender and Hywood 2012, Mambeya et al. 2018, Gomez et al. 2016, Heinrich et al. 2016, Ingram et al. 2017)]. In addition, it has also become clear that pangolins in other range states such as India (Mohapatra et al. 2015, Choudhary et al. 2018), Nepal (Katuwal et al. 2015, Thapa et al. 2014), Pakistan (Mahmood et al. 2017), Bangladesh (Trageser et al. 2017) and Myanmar (Zhang et al. 2017) are also being targeted by actors involved in the illegal international trade in these species. As such, all eight pangolin species are now listed as threatened on the IUCN Red List of Threatened Species (www.redlist.org) and, whilst the initial post-2000 trade from Africa was legal under CITES permits (CITES 2017), since 2016 (effective as of January 2017), all international commercial trade in wild-caught pangolins has been banned under their CITES Appendix I listing at the CITES Conference of the Parties 17 (https://cites.org/eng/app/appendices.php).

Understanding the scale and type of use of wildlife products, the drivers of commercial trade and what motivates people to hunt illegally, is crucial for developing effective interventions (TRAFFIC 2008, Duffy and St John 2013, Duffy et al. 2016, Nash et al. 2016). In the case of pangolins, the drivers of trade at a global scale are relatively well known (Heinrich et al. 2017). In contrast, information on what drives local people to hunt pangolins, and how this is connected with traditional cultural use, seems to be lacking for some communities. Local studies of pangolin hunting and trade (at the supply end of trade) have typically focused on market surveys (e.g. Nijman et al. 2016, Ingram et al. 2017), seizure data (e.g. Mohapatra et al. 2015, Nijman 2015, Cheng et al. 2017, Gomez et al. 2016, 2017) or questionnaires seeking local perceptions of hunting or trade activities (e.g. Katuwal et al. 2015, Nash et al. 2016, Zhang et al. 2017) rather than asking hunters directly about their own activities and beliefs. In Asia, exceptions are: Nash et al. (2016) who assessed local ecological knowledge across seven protected areas in Hainan, China; Zhang et al. (2017) who gathered data from 38 informants in the northwest of Kachin State, Myanmar; Mahmood et al. (2017) who interviewed an unreported number of local people in Pakistan; and Pantel and Anak (2010) who interviewed 13 individuals in Sabah, Malaysia.

Here, we present detailed data on the hunting activities of 141 male rural hunters, belonging to three local tribes (Biate, Karbi and Dimasa), living in the least populated district of Assam (Dima Hasao), located in Northeast India. The aim of our study was to: (1) quantify the extent to which local hunters hunt pangolins in this previously unstudied area; (2) describe the circumstances under which they hunt pangolins; and (3) their reasons for doing so. Ultimately, we aimed to identify what a pangolin is worth to a rural hunter in this region and thus to understand the drivers for such hunting activity, with a view to considering the nature and magnitude of intervention that might be required to reduce it.

Two species of pangolin, the Indian pangolin (*Manis crassicaudata*) and the Chinese pangolin (*M. pentadactyla*) currently occur in Northeast India. Both species are solitary, primarily nocturnal (sometimes crepuscular) and largely terrestrial (digging their own burrows) although they are fully capable of climbing trees (Baillie et al. 2014, Challender et al. 2014b). There is almost no information available on the population status of these two pangolin species at a local level in India; however, globally, populations are considered to be in significant decline and therefore the Indian pangolin is currently classified as Endangered and the Chinese pangolin as Critically Endangered, according to the IUCN Red List of Threatened Species (Baillie et al. 2014, Challender et al. 2014b).

Methods

Study area

Known as the "Gateway of Northeast India", Assam State comprises approximately 12.8% of the total tribal population of India (Census of India 2011). The Dima Hasao district (located at 92°37–93°17E, 25°3–25°27N, Fig. 1) covers an area of 4,890 km^2 and is inhabited by more than 12 ethnic tribes (including the Biate, Dimasa, Hmar, Hrangkhol, Jaintia, Karbi, Khelma, Kuki, Lushai, Rongmei, Vaiphei and Zeme) in addition to several other non-tribal groups (including Assamese, Bengali and Nepali communities). The physical geography of the region includes a mix of tropical semi-evergreen forests, tropical deciduous forests, secondary forests and crop fields (Choudhury 2013). It is the least populated district of Assam [with a population of 213,529 and a population density of 44 individuals per km^2 (Census of India 2011)], with most of the villages situated far from modern conveniences and inaccessible by road or rail (Betlu 2013).

Our study focussed on three of the predominant indigenous tribes of Assam State in Northeast India: (1) Biate; (2) Dimasa; and (3) Karbi. These tribes are characterised by unique traditions and cultures distinct from each other and from other ethnic groups of the region (Teronpi et al. 2012). However, broadly speaking, subsistence agriculture or hunting and gathering are practised by rural villagers belonging to all three groups (Sajem and Gosai 2006). A deep faith in, and preference for, their traditional healthcare system (based on surrounding flora and fauna) rather than the modern system of medicine has been reported across all three groups (e.g. Sajem and Gosai 2010, Teronpi et al. 2012, Betlu 2013). Similarly, although they are known to practise traditional religion (that is animistic in nature) to varying degrees, the prevalence of associated rituals has been affected by the advent of Christianity across all three groups (e.g. Sajem and Gosai 2010, Teronpi et al. 2012, Betlu 2013).

With regards to national legislation, selling pangolins for commercial gain in India is illegal under Schedule I of the Wildlife (Protection) Act 1972. However, it is important to note that hunting pangolins outside of Reserved Forests (i.e. protected areas) for personal use is sometimes permitted for certain native tribal communities (Aiyadurai 2011). Specifically, the state of Assam has several tribal majority areas recognised as Autonomous regions governed by laws framed by Regional Councils according to Schedule 6 of the Indian Constitution. As such, hunting of pangolins by Biate, Dimasa and Karbi tribal communities for personal use outside of Reserved Forests in areas of Dima Hasao district is technically permissible assuming: (1) there is no contravening law made by the Regional Council on hunting; (2) the Council's law prevails over the State's law; and (3) the State Governor has not passed any law to restrict any hunting (Government of India 2007). Nevertheless, the State Governor has the power to amend the laws of the Regional Council in any situation where conflict should occur (Government of India 2007).

Figure 1. Location of the Dima Hasao district in Northeast India. India map by Ganeshk (own work derived from Image: India-locator-map-blank.svg, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=801542). State map from d-maps.com (http://d-maps.com/m/asia/india/assam).

Data collection

We used semi-structured interviews for which participants were purposefully selected rather than randomly sampled. The questionnaire focused on meat consumption of hunters, pangolin hunting and attitudes towards pangolins. Key questions were related to personal and commercial use of both the meat and scales of hunted pangolins and, specifically, whether and where they were sold and for how much. We interviewed hunters in villages that self-identified as having hunted a pangolin and that were willing to participate in the study, through a process of chain referral (Newing 2011), whereby participants recommended other potential participants or persuaded others to take part. This snowball sampling approach (Babbie 2004) is useful when researchers are interested in the opinions of a particular hidden population (Potgieter et al. 2017) and, in this case, ensured that participants who could provide information pertinent to the study were selected as representatives of the pangolin hunting community. Our aim was not to extrapolate our results to the wider community but to understand what drives the hunters whom we interviewed to hunt pangolins.

Interviews were conducted by four local field staff asking a set of predetermined questions that included open-ended, closed and multiple choice questions (see Suppl. materials 1). Participants were initially asked some non-pangolin related questions (including what pets they kept) and what type of meat they preferred to eat before being asked about their use of pangolins; by asking sensitive questions at the end of the interview, our aim was to ensure that respondents were as comfortable and as relaxed as they could be (Newing 2011). Interviews were conducted in Hindi, Biate, Dimasa and Karbi and later translated into English. Surveys were carried out in 31 villages in the Dima Hasao district of Assam, between January and October 2017. In accordance with the British Sociological Association Statement of Ethical Practice (BSA 2017), informed consent was obtained verbally from every survey participant prior to the interview, participants were made aware of their rights to voluntarily participate or to decline, no identifying participant or household data were collected and the database collated was entirely anonymous. In addition, villages were coded in the database and village names not reported to further protect study participants from harm or discrimination (St John et al. 2016).

Data analysis

We used descriptive statistics to describe patterns and trends in the data and used chi-squared tests of association and non-parametric statistical tests to test for relationships between and differences in demographic and hunting parameters and amongst hunters of different ethnicity. For chi-square tests, we obtained simulated p values (based on 2000 replicates) for tests with low expected values. All statistical analyses were carried out in R (version 3.3.3, R Core Team 2017). Pairwise post hoc chi-squared tests were performed with the package fifer (Fife 2017), p values adjusted for multiple comparisons. All interviews were included in the analysis, even if they contained missing data, but some questions were omitted due to overlap and/or potential misinterpretation by participants.

Results

Interviews lasted between 30 minutes and two and a half hours. Individual questions were answered by between 57% and >90% of interviewees. All interviewees had captured at least one pangolin in the last five years. Some of the hunters interviewed took part in the same hunt, therefore the numbers reported do not represent the number of individual pangolins taken during the study, rather they represent the individual hunters that took part in these activities. Similarly, hunters did not distinguish between pangolin species so data refer collectively to "pangolins".

Hunter demographics

Interviewees, on average, were in their 30s (median age = 36, range 17–76), owned one or two houses [N = 4 (2.8%) owned three], with four to seven people per household (median = 6, range 1–12) including two to three children (median = 2, maximum = 8). Ninety percent (N = 102) were married. All but three interviewees were originally from the area and all but four belonged to either the Biate (N = 82), Dimasa (N = 33) or Karbi (N = 22) tribes (one belonged to the Nepali community and another to the Khasi tribe in the neighbouring state of Meghalaya, two were of unknown affiliation). Dimasa were all Hindu (as was the single Nepali), Biate (with the exception of one Hindu), Karbi and the Kashi were Christian (one Karbi described himself as animist). With the exception of education level and income (below), there were no apparent demographic differences amongst tribal/community members interviewed.

Education level of interviewees was variable: 53.2% (N = 75) went to middle/high school, but only 10% (N = 7) of those completed 10th class (10th grade in US or Year 11 in the UK); 19.9% (N = 28) had no education and none was educated at or beyond senior secondary school (12th grade in US or A levels in UK). Interviewees with no, or only primary, education, were older than those who attended middle or high school (K-W χ^2 = 12.38, DF = 4, p = 0.015) and Biate were significantly better educated than either Dimasa or Karbi [see Table 1; there were no differences in age amongst members of each tribe (K-W χ^2 = 3.93, DF = 3, p = 0.269)].

With the exception of one individual [who earned an estimated 300,000 INR (Indian Rupees), 4,644 USD, per year], all interviewees described themselves as farmers, farmers/labourers, or farmers/hunters/labourers, with an estimated annual household income of between 10,000 and 90,000 INR (median = 25,000 INR, or 387 USD; 1USD = 64.6 INR, 23/11/17). Dimasa reported significantly higher average incomes than did members of the other two tribes but there was considerable variation within tribes and overlap amongst them (Table 1).

Table 1. Differences in education and reported income amongst the three tribes.

	Ethnicity/tribe			Statistics	p
	Biate	Dimasa	Karbi		
Education				χ^2 = 21.79 DF=6	**0.002***
- Attended high school	33%	18%	5%	Biate vs. Dimasa	**0.005**†
- No school education	10%	42%	27%	Biate vs. Karbi	**0.007**†
Annual income (INR)					
- Median	21,500	32,500	27,500	K-W χ^2 = 26.55 DF=3	**<0.001**
- Maximum	70,000	90,000	60,000		

* = Simulated p value, † = post hoc adjusted p value.

Bush meat consumption

Interviewees reported eating wild meat between one and five times per week (median = 1, with no apparent difference amongst tribes; K-W χ^2 = 0.69, DF = 2, p = 0.710). Only 4.8% of interviewees relied primarily on wild meat (73.6% supplemented domestic meat with wild meat). Only one interviewee listed pangolin as their favourite wild meat; most said that deer (51.8%) or boar (44.7%) were their favourite wild meat. Ranked by preference (1st to 9th), 89.4% of 85 respondents who included pangolin as a wild meat that they might consume, ranked them 4th or lower and all respondents gave them low ranks significantly more often than either bear, bird, porcupine or primate (in addition to deer and boar that were most often ranked 1st or 2nd; post hoc chi-squared tests, all p = 0.020, with Bonferroni correction for 28 comparisons). Nevertheless, most interviewees said that when they did capture a pangolin, they ate it.

Pangolin hunting

Ninety-four percent (N = 133) of hunters described hunting pangolins as being dependent on finding field signs (footprints or marks in the mud or on the trees or fresh den holes). Field signs were sometimes detected opportunistically, when hunting in the forest for other animals or fishing. For example, one hunter remarked that (a pangolin hunt) was "not planned, if we see the pangolin footprints and new holes, then we change the plan and do a pangolin hunt". Sometimes pangolins were searched for deliberately. For example, one hunter described how five to six hunters spent several days systematically searching the forest for signs, another said that they "search every tree in the forest for fresh footprints" and another said "sometimes takes months to find them". It was not possible, however, to quantify from their descriptions of how they hunted pangolins to what extent either occurred. March to May was reported most frequently to be the best time for hunting pangolins (Fig. 2).

Hunters reported that pangolins were captured by being dug from their holes (> 2 m underground, usually with the help of several villagers or family members) or forced from tree holes with smoke or by cutting or burning down the tree. Escaping pangolins were picked up or caught with a spear. Only one hunter said that he used traps. Sometimes hunters accidentally came across pangolins in the open, in which case, when the animal rolled into a ball (documented defensive behaviour, Mohapatra and Panda 2014), they simply picked it up and put it in a bag. Pangolins captured alive were transported to hunters' homes in a bag and killed at home by "hitting on the head with knife" or by "cutting their head with a knife".

Frequency of hunting

Ninety-five percent (N = 134) of hunters reported hunting pangolins at least once in the last 12 months (median number of hunts in the last 12 months = 3, Fig. 3a).

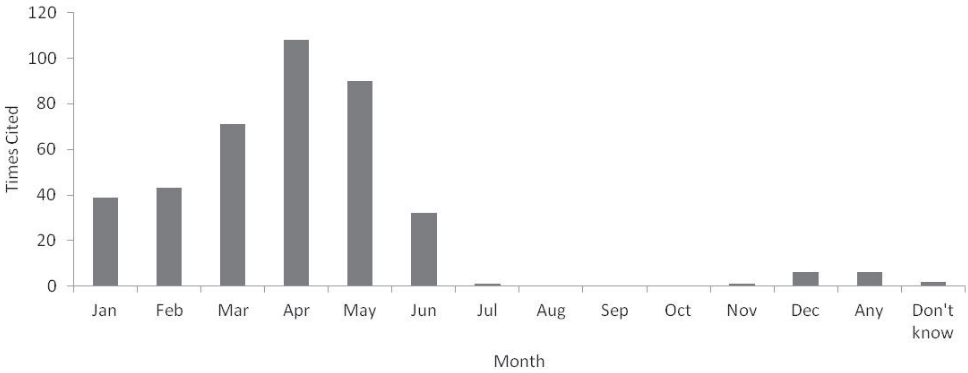

Figure 2. Reported best months for capturing pangolins (data are the number of times the month was cited). Note that most interviewees gave months as a range rather than a single optimal month so values sum up to more than the number of interviewees. Several hunters referred to signs being detectable "after the rain".

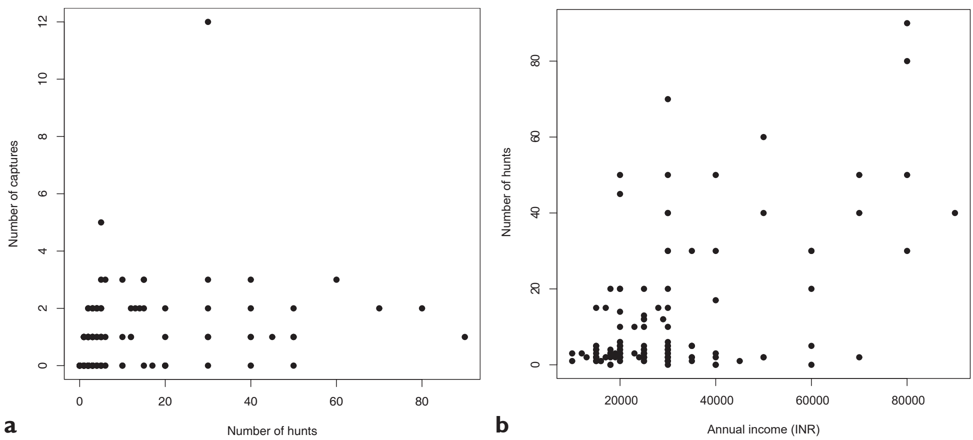

Figure 3. Reported number of pangolin captures in the last 12 months as related to reported number of hunts undertaken (**a**) (r = 0.418, p <0.001; excluding the reported capture of 12 pangolins: r= 0.307, p <0.001) and hunts in relation to reported annual income (**b**).

Twenty-seven percent (N = 38) of hunters reported hunting pangolins 12 or more times (once per month or more) and 6.4% (N = 9) 50 or more times (approximately once per week, Fig. 3a).

Hunting success

Fifty-six percent (N = 79) of hunters stated that they had captured a pangolin at least once in the last 12 months (Fig. 3a). Individuals who had gone hunting frequently (at least once per month in the last 12 months) were more likely to have captured at least one pangolin in that time than those who had gone hunting infrequently:

73.7% of those that hunted ≥12 times per year caught ≥1 pangolin compared with 49.5% of those that hunted <12 times (χ^2 = 5.058, DF = 1, p = 0.025). However, on average, the number of captures reported was low, regardless of the number of hunts undertaken (median number of captures in the last 12 months = 1, Fig. 3a). High capture rates were rare: only two interviewees reported capturing more than three pangolins in the last 12 months (Fig. 3a). Overall, the approximate average reported success rate (number of captures/number of hunts) per hunter was 21.6% but varied between 0 and 100%.

Demographic and tribal differences in hunting behaviour

There was no apparent relationship between reported number of hunts or reported number of captures in the last 12 months and hunter age or household size (number of people in the house or number of children; all r <0.2, p >0.05). There was also no apparent difference in either hunts or captures amongst hunters of different tribes (hunts: K-W χ^2 = 1.75, DF = 2, p = 0.416; captures: K-W χ^2 = 5.98, DF = 2, p = 0.050, excluding one high value of 12 pangolins reportedly captured by a Karbi hunter that we treated as an outlier – we suspected that this answer was not true and therefore did not include it in the analyses, see Fig. 3a). Across all hunters, there was a very weak positive correlation between the number of hunts undertaken and income (r = 0.297, p < 0.001; excluding the single high income of INR 300,000, Fig. 3b) but no such relationship for captures (r <0.2, p >0.05).

Drivers of pangolin hunting

When asked how pangolins were prepared, all hunters interviewed reported that the pangolin bodies were boiled in hot water and that they removed the scales after boiling or described how boiling softened the skin rendering the scales easy to remove while retaining their original shape. Only two interviewees described the use of spices prior to serving the meat or sharing the meat amongst those involved in the hunt. With the exception of two apparently atypical interviewees (one older man who suggested that he had once captured a pangolin incidentally, cooked the meat and gave away the scales and an individual from outside the area, who said that he was dependent on wild meat and ate pangolin meat but did not use pangolins for commercial purposes), all hunters said yes to both questions when asked if they hunted pangolins for personal use and if they hunted pangolins for commercial use.

Pangolin meat

Most (85.8%, N = 121) hunters reported that they used pangolin meat for food, relatively few (14.9%, N = 21) reported using it for medicine (including N = 6 who used it for both). One interviewee used the meat only for income; one said that they had no

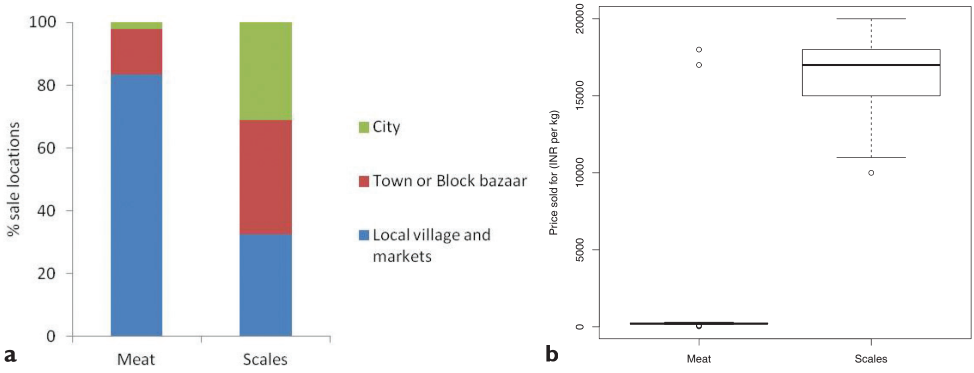

Figure 4. Sale locations (**a**) and price (**b**) for pangolin meat and scales as reported by interviewees (N = 90 locations given by 61 hunters and N = 249 locations given by 131 hunters, respectively, N = 81 and 134 prices given). Local includes the village within which the hunter lives, surrounding villages and the local market (which moves within the local area amongst the villages); Town or Block bazaar includes towns (approximately 10–20 km away) and large markets (e.g. the Block bazaar serves the 'block', which is an administrative unit within the district); City refers to is a major urban centre (approximately 50 km away by road).

use for the meat. Precise medical uses were not specifically asked for, but interviewees reported usage for "piles", malaria, the "nervous system", stomach problems or (for pangolin liver specifically) "stomach disease".

Half (50%, N = 71) of all hunters also sold the meat, mostly (83.3% locations) locally, in the village or at the local market (see Fig. 4a). With the exception of two interviewees who reported selling the liver and bile for medical purposes ("cancer medicine" and because it is "good for the nervous system") for 17,000 and 18,000 INR per kg (263 and 279 USD per kg, respectively), the price of meat per kg ranged between 80 and 300 INR per kg (1.2 – 4.6 USD, median = 200 INR or 3.1 USD per kg, N = 67, Fig. 4b). There was some evidence that the Dimasa obtained higher prices for the meat (median 250 INR, 3.9 USD, per kg) than did the Biate or Karbi (median 200 INR, 3.1 USD, per kg, for both; K-W χ^2 = 29.45, DF = 2, p <0.001). When asked what the meat that they sold would be used for, interviewees (42.6%, N = 60) listed a number of medical or health-related reasons, including the treatment of neurological disease, stomach ache and paralysis (liver and bile), use as massage oil, to "increase strength", "aid the digestive system" and that the liver and bile were "good for a weak person". One said that pangolin meat was "good for body, cure many diseases". Others thought that it would be used simply for food (27.0%, N = 38), did not know what it would be used for (17.7%, N = 25) or both (1.4%, N = 2).

Pangolin scales

Few (12.1%, N = 17) interviewees reported that they used the pangolin scales for medicine (those who gave precise medical uses referred only to "piles"); most (80.1%, N = 113) used them only for income (Fig 5a). Other minor uses included "protection

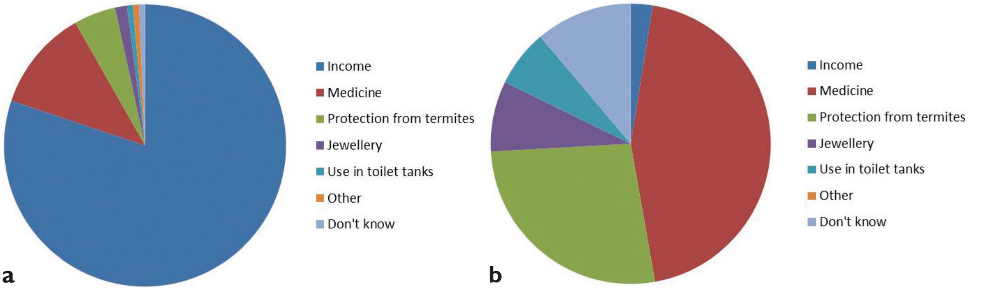

Figure 5. Percentage use of pangolin scales by interviewees (**a**) and buyers (as perceived by interviewees) (**b**) (note that interviewees listed up to four possible uses so the total number of uses was greater than the number of interviewees, N = 146 and 197, respectively; percentages in the text refer to percentage of interviewees, N = 141). Medicine refers almost exclusively to treatment for "piles" (see text), for which the prescribed use involved burning scales and inhaling (or squatting over) the smoke or boiling in water and drinking. "Protection from termites" referred to use in either houses or plantations and the belief that placing a scale under a pole or log would provide protection (four interviewees suggested that this was something that "older people" did). For perceived buyer uses, Jewellery was referred to exclusively as good luck charms or amulets, whereas interviewees referring to their own use used the term Jewellery without specifying any particular further purpose. "Use in toilet tanks" was explained as placing a scale/s in the toilet tank "to prevent it filling up too soon". Other = "protect house from fire" (N = 1).

from termites" (N = 7) and jewellery (N = 2, see Fig 5a). Two said that they gave them away (most likely to other villagers).

Almost all (96.5%, N = 136) hunters sold the scales. Scales were more likely than meat to be sold in large markets, towns or the city (χ^2 = 70.97, DF = 2, p <0.001, Fig. 4a). The price of pangolin scales ranged between 10,000 and 20,000 INR per kg (median = 17,000 INR, 263 USD, per kg, N = 135, Fig. 4b) with the highest prices obtained by the Biate (median 18,000 INR, 279 USD, per kg, compared with 16,000 INR, 248 USD, for the Karbi and 15,000 INR, 232 USD, per kg for the Dimasa; K-W χ^2 = 38.90, DF = 2, p <0.001). Over half (59.6%, N = 84) of hunters questioned thought that the scales they sold would be used for medicine (mostly to cure piles; three interviewees also referred to the use of scales to treat "stomach disease" or stomach problems and two to a pendant that a child can wear to "cure vomiting"). Other suggestions as to what buyers might use the scales for included predominantly "protection from termites", good luck charms or amulets or "use in toilet tanks" (Fig. 5b, further explanations in figure legend). Fifteen percent (N = 22) of hunters did not know what the scales would be used for, only that someone was willing to buy them.

Attitudes towards pangolins and perceived population trends

When asked how they felt about pangolins (on a scale of 1 to 5, with 1 being strongly dislike and 5 strongly like), there was a strong bias towards liking pangolins, with 61.7% (N = 87) of interviewees reporting that they strongly liked pangolins, 29.8%

Figure 6. A Indian pangolin (*Manis crassicaudata*) **B** Pangolin scale worn as a charm bracelet **C** a bag of pangolin scales intended for commercial sale **D** Pangolin scale and claw worn as talisman. Dima Hasao district, Assam.

(N = 42) quite liking them and none disliking them (nine said "neither like nor dislike", two did not answer the question and one said he did not know). The majority [63.8% (N = 90)] of interviewees said that the benefits provided by pangolins (to either themselves or to the forest) were "income from trade". Other benefits suggested were: medicinal benefits (N = 8), provision of a food source (N = 4), good luck (N = 5), killing termites or protecting trees from termites (N = 10), creating holes for other animals to live or shelter in (N = 7) and that they were considered "harmless" (to humans, animals, agricultural fields and the forest, N = 5). Seven interviewees said that pangolins provided no benefits (but also no disbenefits). Most interviewees [88.7% (N = 125)] believed that there were fewer pangolins than there were five years ago (although they were not asked why they thought this to be the case).

Of 105 hunters who described a memorable experience associated with hunting or catching a pangolin, some (*N* = 30) reported that hunting pangolins was always hard work, “hard labour” or “difficult” and described how they might have to dig all day or dig a hole over 2 m deep, whereas others (*N* = 33) seemed to have come across pangolins opportunistically (e.g. in the road, from where they could simply pick them up) or said that they caught them easily (e.g. by finding them in a log and “easily” taking them out or by setting a trap near the den hole). Twenty referred to being “lucky”, “happy” or it being a “good day”, when they captured the pangolin (or captured a particularly large pangolin). One interviewee said that it was “the happiest moment of [his] own life” when he caught a “big” (3 kg) pangolin and three others (two of whom appeared to hunt together) remarked that it was like “winning the lottery”. Very few interviewees revealed precisely why it was a particularly good day when they caught a pangolin or what they needed the income for, except for two who referred to covering their debts and two others who said they used the money to pay for medical treatment for their family.

Discussion

Our study represents the first socio-economic review of pangolin poaching being carried out by three of the tribal groups in Assam, Northeast India. Our approach permitted extensive data to be collected and provides a unique insight into the practices, drivers and impacts associated with this type of wildlife trade activity. Our findings clearly demonstrate that male rural hunters, belonging to the Biate, Dimasa and Karbi tribes in Dima Hasao district, are carrying out pangolin hunting, both for personal and commercial gain. The fact that more than 100 interviewees stated that they have hunted pangolins during the past twelve months (and captured at least one in the last five years) indicates that such activity is likely to be commonly practised by hunters of these communities throughout the district of Dima Hasao.

Why are rural hunters targeting pangolins in Assam?

The local use of pangolin derivatives in India is “steeped in tradition” and it is therefore unsurprising that, during our field study, hunters listed a number of medicinal and superstitious uses for both pangolin meat and scales that broadly reflected those previously described by Mohapatra et al. (2015). However, unlike some findings made elsewhere [e.g. Myanmar (Nijman et al. 2016)] the results of our study indicate that, broadly speaking, hunters in Dima Hasao are not currently targeting pangolins specifically for their meat. For example, with regards to personal use, only a minority of hunters reported using pangolin meat for medicinal purposes. Furthermore, although all hunters said that they ate the meat if they caught a pangolin, the fact that most disliked it (or ranked it very low compared with other bush meat) suggests that they ate it only because they could not afford not to. This was reflected in the stated prices obtained for pangolin meat [being less valuable than other types of domesticated meat sold in Dima Hasao e.g. chicken (approx. 200 INR, 3.1 USD, per kg) and goat approx. (450 INR, 7.0 USD, per kg)]. With regards to commercial use, although pangolin meat is a luxury product in China and Vietnam (Challender et al. 2015), hunters provided little indication that the meat was traded beyond the local area.

In contrast to pangolin meat, it is apparent from our study that rural hunters in Dima Hasao are specifically targeting pangolins for their scales and that commercial gain has supplanted traditional use as the primary driver for this type of activity. Specifically, hunter responses overwhelmingly indicate that, while relatively few might use some of the pangolin scales obtained from a hunt themselves, they actually go on to sell the vast majority. Unlike pangolin meat, it is likely that the pangolin scales are destined for urban and international consumers. For example, during our study, hunters were more likely to travel to the city to sell the scales and some hunters reported that buyers come from the city to buy scales directly from the rural villages or at local markets. These results are consistent with the study of Thapa et al. (2014) in Eastern Nepal, where pangolins were hunted primarily for trade and used occasionally by local people for food but rarely for traditional medicine. In both cases, hunters, in the context of the illegal wildlife trade, fall into a combined typology of subsistence/opportunistic harvesters (as defined by Phelps et al. 2016). However, similar to Challender (2011), our survey suggests that the external market may now be driving the opportunistic (economic) element of hunting, whilst the (local) subsistence element appears to be of relatively little importance. These types of commercially-motivated opportunistic behaviour, that are neither a primary nor a regular livelihood, are often overlooked in discussions of illegal wildlife trade (Phelps et al. 2016 and references therein).

Interestingly, 15% of hunters interviewed during our study stated that they did not know precisely what the scales they sold were being used for or why the market existed, rather only that consumers were willing to pay a substantial amount for them (see also Katuwal et al. 2015). An additional 8% of hunters did not provide any answer at all in this regard. This lack of knowledge on consumer demand amongst rural hunters may explain some of the more perplexing novel answers provided on intended use – for example, the use of pangolin scales to unblock toilet tanks. This also adds weight to concerns that more wealthy urban actors are exploiting rural hunters (see Duffy and St John 2013 and references therein), potentially taking advantage of both their ability to source pangolin scales and their lack of knowledge regarding their use and commercial value.

What is a pangolin worth to a rural hunter in Assam?

Our study also serves to demonstrate just how economically valuable a pangolin has become to rural hunters in the Dima Hasao district of Assam, India. We found that, on average, hunters capture one pangolin per year, receive an average of 200 INR (3.1 USD) per kg of meat (which for an approx. 3 kg animal is 600 INR, equivalent to 9.3 USD), plus an average of 17,000 INR per kg of scales (equivalent to 263 USD per kg of scales at the time of writing). Therefore, assuming that there are approximately 0.5 kg of scales per animal (Zhou et al. 2012), we estimate that hunters can potentially receive up to a total of around 9,000 INR per pangolin (for the meat and scales combined if they do not consume the meat themselves, equivalent to 139 USD). Even when divided by up to five people who might take part in a given hunt, this could amount to 1,800 INR (28 USD) each, in a one-off payment, that is likely to occur once per year. When compared to an average annual income of 25,000 INR (387 USD), this means that a single pangolin may be worth just less than one months' income to a hunter in this area, even when hunting with others. A hunter operating alone has the potential to obtain a far greater amount, closer to just under a full year's income for those on the lowest incomes.

Furthermore, the prices paid for pangolin scales in India are reported to have increased substantially in recent decades. For example, Chinlampianga et al. (2013) reported that scales sold for 1,000 INR per kg in 1996 increased to INR 13,000 per kg in 2012 across different locations in the State of Mizoram. In accordance with increasing value elsewhere (e.g. Zhou et al. 2014, Trageser et al. 2017), the price obtained for scales during our survey in 2017 (taking account of inflation in India over the intervening time period, obtained from http://calculatorstack.com/inflation-calculator-india.php) was ten times that reported by Misra and Hanfee (2000) in 1997–1998 for scales sold at collection points or at trading centres. As such, the potential economic value of a pangolin to a rural hunter is likely to increase further as pangolins become even more rare and demand continues to increase - a phenomenon that has been coined the anthropogenic Allee effect (Courchamp et al. 2006, see also Aisher 2016).

What are the impacts of hunting on pangolins?

For most hunters interviewed during our study, hunting pangolins, either for their meat and or their scales, did not appear to be a frequent activity. Rather it seemed that they came across pangolins or their signs accidentally and then decided to hunt the animal opportunistically. Alternatively, they only occasionally decided to go into the forest and search for a pangolin. However, the fact that most of the hunters interviewed identified pangolins as being less abundant than they were five years ago suggests that levels of off-take, although seemingly low, are unsustainable. The low reproductive rate of pangolins (one to two young per year, Mahmood et al. 2015, Zhang et al. 2016) is already recognised as a biological factor which makes wild populations particularly vulnerable to any level of hunting (CITES 2017). Furthermore, our study indicates that peak pangolin hunting activity in Dima Hasao took place between the months of March and May. This coincides with the period when female pangolins are reported to have their young [recorded in India as occurring between January and April (Mahmood et al. 2015)] that are also taken by hunters. The practice of destroying burrows, cutting down or burning hollow trees to capture pangolins may also have additional conservation impacts by reducing the availability of denning habitat (Newton et al. 2008). As in Mohapatra et al. (2015), we were unable to distinguish between pangolin species, but anecdotal reports of black and red pangolins, suggest that both species were involved.

In addition to conservation concerns, there are a number of animal welfare issues associated with hunting practices currently being applied in Dima Hasao. The duration of suffering is of particular concern given that hunters stated it can take several hours to successfully extricate a pangolin from its burrow or tree den during capture. Live transport after capture is also of concern (see e.g. Baker et al. 2013). Although we found no evidence of traditional or commercial use of live pangolins, hunters reported that pangolins are often carried in a bag until they reach a more suitable place for subsequent slaughter. The opportunity for animal suffering during slaughter is particularly apparent given that hunters reported placing pangolins into boiling water [a technique employed to aid scale removal (Mohapatra et al. 2015)]. Although 74% of hunters reported that a knife or club was used to kill the pangolins beforehand, concerns remain that a proportion may still be alive when the boiling process begins.

How can we protect pangolins and people?

We did not detect any particular demographic characteristics that appeared to dictate either hunting frequency or success, nor did we detect any particular differences amongst the three tribal communities (except for the small differences detected in the prices obtained for pangolin scales). There was also no evidence that individuals with lower incomes were more likely to resort to hunting pangolins. However, it is important to note that all rural hunters in this area can be considered to receive relatively low incomes and the monetary rewards that could be gained from capturing a pangolin and selling its scales were substantial relative to income. Furthermore, some comments and memorable experiences described by hunters anecdotally suggested that the money received was needed for necessities (medical treatment, schools) rather than for luxuries or to “get rich”.

Our study also serves as another useful case study which exemplifies the extent to which unsustainable consumer demand for pangolin scales and associated illegal trade activity can permeate remote rural communities involving many individuals who, most likely, do not fully understand the true ramifications of demand or even why the market exists (CBD – Subsidiary Body on Scientific, Technical and Technological Advice 2016).

What are the limitations of our study?

Caution is almost always required in interpreting data derived from hunter interviews, particularly when hunting involves some element of illegality (e.g. Newton et al. 2008). Given the sensitive nature of the information asked for in our surveys, interviewees might have been reluctant to be honest about the magnitude of illegal hunting activities and there is a risk that the data underestimate the impact of hunting. However, our aim was not to assess the extent of impact or the total number of people involved, rather we sought to understand the practices undertaken by those who were willing to admit that they hunted pangolins and their reasons for doing so. That over a hundred hunters were willing to talk to us and that almost all (those who sold the meat or scales) openly admitted to an illegal activity, suggests that they were being truthful (at least insofar as hunting one pangolin is as illegal as hunting several, so there is little reason not to be honest about the details). The overall similarity in the answers from hunters across 31 different villages (that might be up to 50 km from one another) in interviews carried out over a year, further suggests that the data are reliable.

Conclusion

The information that we obtained from hunters in this study was consistent with respect to existing knowledge of the pangolin trade (e.g. Mohapatra et al. 2015). However, it also provides new information that can help to further inform about existing and future initiatives to better protect pangolins and people being exploited by consumer demand for the most "trafficked mammal in the world". Our results suggested that commercial gain has supplanted traditional use as the primary driver for pangolin hunting, specifically as related to the use of pangolin scales. Pangolin meat was clearly only consumed or sold as a by-product of this activity and there was no evidence that it entered trade beyond perhaps sale within the hunters' village. That the value of pangolin scales from a single animal approximates to four months' of the average income of hunters in this region illustrates the substantial financial gains that are possible, even when hunting pangolins only occasionally. For this reason, whilst interventions to reduce poverty are no doubt required (Challender and MacMillan 2014), we suspect that such interventions alone are unlikely to be effective in reducing illegal and unsustainable wildlife trade in Dima Hasao. Rather, co-ordinated packages of mutually reinforcing interventions are required to address illegal and unsustainable wildlife trade in a more comprehensive manner (TRAFFIC 2008, Mohapatra et al. 2015). In particular, we agree with Challender et al. (2014a; see also Verissimo et al. 2012) that implementing a demand reduction strategy targeting urban consumers (particularly in China and Vietnam) is also crucial for addressing the welfare and conservation crisis facing pangolins, especially given that there is some encouraging evidence that similar reduction campaigns for other species have been successful (Cheng et al. 2017). Given that all hunters whom we interviewed seemed to hunt pangolins occasionally, regardless of tribe, demography or income, we suggest that any mitigation strategy should focus on all rural hunters in this region.

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References

Aisher A (2016) Scarcity, Alterity and Value: Decline of the Pangolin, the World's Most Trafficked Mammal. Conservation & Society 14(4): 317–329. https://doi.org/10.4103/0972-4923.197610

Aiyadurai A (2011) Wildlife hunting and conservation in Northeast India: A need for an interdisciplinary understanding. International Journal of Galliformes Conservation 2: 61–73.

Babbie E (2004) The Practice of Social Research (10th edn). Thomson/Wadsworth, Belmont.

Baker SE, Cain R, van Kesteren F, Zommers ZA, D'Cruze N, Macdonald DW (2013) Rough Trade: Animal Welfare in the Global Wildlife Trade. Bioscience 63(12): 928–938. https://doi.org/10.1525/bio.2013.63.12.6

Baillie J, Challender D, Kaspal P, Khatiwada A, Mohapatra R, Nash H (2014) *Manis crassicaudata*. The IUCN Red List of Threatened Species 2014: e.T12761A45221874. http://dx.doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12761A45221874.en

Betlu ALS (2013) Indigenous knowledge of zootherapeutic use among the Biate tribe of Dima Hasao District, Assam, Northeastern India. Journal of Ethnobiology and Ethnomedicine 9(1): 56. https://doi.org/10.1186/1746-4269-9-56

Boakye MK, Pietersen DW, Kotzé A, Dalton D-L, Jansen R (2015) Knowledge and uses of African pangolins as a source of traditional medicine in Ghana. PLoS One 10(1): e0117199. https://doi.org/10.1371/journal.pone.0117199

Boakye MK, Pietersen DW, Kotzé A, Dalton D-L, Jansen R (2014) Ethnomedicinal use of African pangolins by traditional medical practitioners in Sierra Leone. Journal of Ethnobiology and Ethnomedicine 10(1): 76. https://doi.org/10.1186/1746-4269-10-76

BSA [British Sociological Association] (2017) Statement of Ethical Practice. BSA Publications www.britsoc.co.uk/media/24310/bsa_statement_of_ethical_practice.pdf

CBD [Subsidiary Body on Scientific Technical and Technological advice] (2016) Beyond enforcement: involving indigenous peoples and local communities in combating illegal wildlife trade: regional workshop for West and Central Africa. Twentieth meeting Montreal, Canada, 25–30 April 2016 UNEP/CBD/SBSTTA/20/INF/59. https://www.cbd.int/doc/meetings/sbstta/sbstta-20/information/sbstta-20-inf-59-en.pdf

Census of India (2011) 2011 Census Data. Office of the Registrar General & Census Commissioner, India, Ministry of Home Affairs, Government of India. Available from: http://censusindia.gov.in/2011-Common/CensusData2011.html

Challender DWS (2011) Asian pangolins: Increasing affluence driving hunting pressure. Traffic Bulletin 23(3): 92–93.

Challender DWS, MacMillan DC (2014) Poaching is more than an Enforcement Problem. Conservation Letters 7(5): 484–494. https://doi.org/10.1111/conl.12082

Challender DWS, Hywood I (2012) African pangolins – under increased pressure from poaching and intercontinental trade. Traffic Bulletin 24(2): 53–55.

Challender DWS, Harrop SR, MacMillen DC (2015) Understanding markets to conserve trade-threatened species in CITES. Biological Conservation 187: 240–259. https://doi.org/10.1016/j.biocon.2015.04.015

Challender D, Baillie J, Ades G, Kaspal P, Chan B, Khatiwada A, Xu L, Chin S, KC R, Nash H, Hsieh H (2014b) *Manis pentadactyla*. The IUCN Red List of Threatened Species 2014: e.T12764A45222544. http://dx.doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12764A45222544.en

Challender DWS, Waterman C, Baillie JEM (2014a) Scaling up pangolin conservation. IUCN SSC Pangolin Specialist Group Conservation Action Plan. Zoological Society of London, London.

Cheng W, Xing S, Bonebrake TC (2017) Recent Pangolin Seizures in China Reveal Priority Areas for Intervention. Conservation Letters 10(6): 757–764. https://doi.org/10.1111/conl.12339

Chinlampianga M, Singh RK, Sukla AC (2013) Ethnozoological diversity of Northeast India: Emperical learning with traditional knowledge holders of Mizoram and Arunachal Pradesh. Indian Journal of Traditional Knowledge 12(1): 18–30.

Choudhary AN, Badola S, Fernandes M, Chhabra DB (2018) TRAFFIC Factsheet. Pangolins 2018. TRAFFIC India, New Delhi.

Choudhury A (2013) The mammals of North East India. Gibbon Books and the Rhino Foundation for nature in NE India, Guwahati.

CITES (2017) Consideration of proposals for amendment of Appendices I and II. Seventeenth meeting of the Conference of the Parties, Johannesburg (South Africa), 24 September – 5 October 2016. https://cites.org/eng/cop/17/prop/index.php

Courchamp F, Angulo E, Rivalan P, Hall RJ, Signoret L, Bull L, Meinard Y (2006) Rarity Value and Species Extinction: The Anthropogenic Allee Effect. PLoS Biology 4(12): e415. https://doi.org/10.1371/journal.pbio.0040415

Duffy R, St John FAV (2013) Poverty, poaching and trafficking: what are the links? Evidence on demand. UK DFID. http://dx.doi.org/10.12774/eod_hd059.jun2013.duffy

Duffy R, St John FA, Büscher B, Brockington D (2016) Toward a new understanding of the links between poverty and illegal wildlife hunting. Conservation Biology 30(1): 14–22. https://doi.org/10.1111/cobi.12622

Fife D (2017) Fifer: A Biostatisticians Toolbox for Various Activities, Including Plotting, Data Cleanup, and Data Analysis. R package version 1.1. https://CRAN.R-project.org/package=fifer

Gomez L, Leupen BTC, Krishnasamy K, Heinrich S (2017) Scaly nexus: mapping Indonesian pangolin seizures (2010–2015). TRAFFIC, Southeast Asia Regional Office, Petaling Jaya, Selangor.

Gomez L, Leupen BTC, Hwa TK (2016) The trade of African pangolins to Asia: A brief case study of pangolin shipments from Nigeria. Traffic Bulletin 28: 3–5.

Government of India (2007) The Constitution of India. Government of India, New Delhi. https://www.india.gov.in/my-government/constitution-india/constitution-india-full-text

Harrington LA, D'Cruze N, Macdonald DW (2018) Rise to fame: events. media activity and public interest in pangolins and pangolin trade, 2005–2016. Nature Conservation.

Heinrich S, Wittman TA, Ross JV, Shepherd CR, Challender DWS, Cassey P (2017) The global trafficking of pangolins: a comprehensive summary of seizures and trafficking routes from 2010 to 2015. TRAFFIC Southeast Asia, Petaling Jaya, Selangor, Malaysia.

Heinrich S, Wittmann TA, Prowse TAA, Ross JV, Delean S, Shepherd CR, Cassey P (2016) Where did all the pangolins go? International CITES trade in pangolin species. Global Ecology and Conservation 8: 241–253. https://doi.org/10.1016/j.gecco.2016.09.007

Ingram DJ, Coad L, Abernethy KA, Maisels F, Stokes EJ, Bobo KS, Breuer T, Gandiwa E, Ghiurghi A, Greengrass E, Holmern T, Kamgaing TOW, Ndong Obiang A-M, Poulsen JR, Schleicher J, Nielsen MR, Solly H, Vath CL, Waltert M, Whitham CEL, Wilkie DS, Scharlemann JPW (2017) Assessing Africa-wide pangolin exploitation by scaling local data. Conservation Letters 11(2): e12389. https://doi.org/10.1111/conl.12389

Katuwal HB, Neupane KR, Adhikari D, Sharma M, Thapa S (2015) Pangolins in eastern Nepal: Trade and ethno-medicinal importance. Journal of Threatened Taxa 7(9): 7563–7567. https://doi.org/10.11609/JoTT.o4202.7563-7

Ma J-E, Li L-M, Jiang H-Y, Zhang X-J, Li J, Li G-Y, Yuan L-H, Wu J, Chen J-P (2017) Transcriptomic analysis identifies genes and pathways related to myrmecophagy in the Malayan pangolin (*Manis javanica*). PeerJ 5: e4140. https://doi.org/10.7717/peerj.4140

Mahmood T, Kanwal K, Zaman IU (2018) Records of the Indian Pangolin (Mammalia: Pholidota: Manidae: Manis crassicaudata) from Mansehra District, Pakistan. Journal of Threatened Taxa 10(2): 11254–11261. https://doi.org/10.11609/jott.3314.10.2.11254-11261

Mahmood T, Akrim F, Irshad N, Hussain R, Fatima H, Andleeb S, Aihetasham A (2017) Distribution and illegal killing of the endangered Indian pangolin *Manis crassicaudata* on the Potohar Plateau, Pakistan. Oryx 2017: 1–6. https://doi.org/10.1017/S0030605317000023

Mahmood T, Irshad N, Hussain R, Akrim F, Hussain I, Anwar M, Rais M, Nadeem MS (2015) Breeding habits of the Indian pangolin (*Manis crassicaudata*) in Potohar Plateau, Pakistan. Mammalia 80(2): 231–234. https://doi.org/10.1515/mammalia-2014-0153

Mahmood T, Irshad N, Hussain R (2014) Habitat Preference and Population Estimates of Indian Pangolin (Manis crassicaudata) in District Chakwal of Potohar Plateau, Pakistan. Russian Journal of Ecology 45(1): 70–75. https://doi.org/10.1134/S1067413614010081

Mahmood T, Hussain R, Ishrad N, Akrim F, Nadeem MS (2012) Illegal mass killing of Indian pangolin (*Manis crassicaudata*) in Potohar region, Pakistan. Pakistan Journal of Zoology 44: 1457–1461.

Mambeya MM, Baker F, Momboua BR, Pambo AFK, Hega M et al. (2018) The emergence of a commercial trade in pangolins from Gabon. African Journal of Ecology 56(3): 601–609. https://doi.org/10.1111/aje.12507

Misra M, Hanfee F (2000) Pangolin distribution and trade in East and Northeast India. TRAFFIC Dispatches 14 (June 2000).

Mohapatra RK, Panda S (2014) Behavioural descriptions of Indian pangolins (*Manis crassicaudata*) in captivity. International Journal of Zoology 2014: 795062. https://doi.org/10.1155/2014/795062

Mohapatra RK, Panda S, Nair MV, Acharjyo LN, Challender DWS (2015) A note on the illegal trade and use of pangolin body parts in India. Traffic Bulletin 27(1): 33–40.

Nash HC, Wong MHG, Turvey ST (2016) Using local ecological knowledge to determine status and threats of the critically endangered Chinese pangolin (*Manis pentadactyla*) in Hainan, China. Biological Conservation 196: 189–195. https://doi.org/10.1016/j.biocon.2016.02.025

Newing H (2011) Conducting research in conservation: a social science perspective. Routledge, Abingdon, Oxford. https://doi.org/10.4324/9780203846452

Newton P, Van Thai N, Roberton S, Bell D (2008) Pangolins in peril: Using local hunters' knowledge to conserve elusive species in Vietnam. Endangered Species Research 6: 41–53. https://doi.org/10.3354/esr00127

Nijman V (2015) Pangolin seizures data reported. Traffic Bulletin 27(2): 44–46.

Nijman V, Zhang MX, Shepherd CR (2016) Pangolin trade in the Mong La wildlife market and the role of Myanmar in the smuggling of pangolins into China. Global Ecology and Conservation 5: 118–126. https://doi.org/10.1016/j.gecco.2015.12.003

Pantel S, Anak NA (2010) A preliminary assessment of pangolin trade in Sabah. TRAFFIC Southeast Asia, Petaling Jaya, Malaysia.

Pantel S, Chin SY (2008) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia. 30 June – 2 July 2008, Singapore Zoo, Singapore. TRAFFIC Southeast Asia, Petaling Jaya, Selangor, Malaysia.

Phelps J, Biggs D, Webb EL (2016) Tools and terms for understanding illegal wildlife trade. Frontiers in Ecology and the Environment 14(9): 479–489. https://doi.org/10.1002/fee.1325

Potgieter GC, Weise FJ, Wachter B, Melzheimer J, Wiesel I, Stratford K (2017) Comment on Rust et al.: Human-Carnivore Conflict in Namibia Is Not Simply About Black and White. Society & Natural Resources 30(10): 1299–1303. https://doi.org/10.1080/08941920.2017.1283077

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org

Sajem AL, Gosai K (2006) Traditional use of medicinal plants by the Jaintia tribes in North Cachar Hills district of Assam, northeast India. Journal of Ethnobiology and Ethnomedicine 2: 33. https://doi.org/10.1186/1746-4269-2-33

Sajem AL, Gosai K (2010) Ethnobotanical investigations among the Lushai tribes in North Cachar Hills district of Assam, North East India. Indian Journal of Traditional Knowledge 9(1): 108–113.

Soewu DA, Adekanola TA (2011) Traditional-medical knowledge and perception of pangolins (*Manis* spp.) among the Awori people, southwestern Nigeria. Journal of Ethnobiology and Ethnomedicine 7(1): 25. https://doi.org/10.1186/1746-4269-7-25

Soewu DA, Ayodele IA (2009) Utilisation of pangolin (*Manis sps*) in traditional Yorubic medicine in Ijebu province, Ogun State, Nigeria. Journal of Ethnobiology and Ethnomedicine 5(1): 39. https://doi.org/10.1186/1746-4269-5-39

Soewu DA, Sodeinde OA (2015) Utilization of pangolins in Africa: Fuelling factors, diversity of uses and sustainability. International Journal of Biodeversity and Conservation 7(1): 1–10. https://doi.org/10.5897/IJBC2014.0760

St. John FAV, Brockington D, Bunnefeld N, Duffy R, Homewood K, Jones JPG, Keane AM, Milner-Gulland EJ, Nuno A, Razafimanahaka JH (2016) Research ethics: Assuring anonymity at the individual level may not be sufficient to protect research participants from harm. Biological Conservation 196: 208–209. https://doi.org/10.1016/j.biocon.2016.01.025

Sutter JD (2014) The most trafficked animal you've never heard of. CNN: Change the list. http://edition.cnn.com/interactive/2014/04/opinion/sutter-change-the-list-pangolin-trafficking/ [Accessed 11th Jan 2018]

Teronpi V, Singh HT, Tamuli AK, Teron R (2012) Ethnozoology of the Karbis of Assam, India: Use of ichthyofauna in traditional health-care practices. Ancient Science of Life 32(2): 99–103. https://doi.org/10.4103/0257-7941.118547

Thapa P, Khatiwada AP, Nepali SC, Paudel S (2014) Distribution and conservation status of Chinese pangolin (*Manis pentadactyla*) in Nangkholyang VDC, Taplejung, Eastern Nepal. American Journal of Zoological Research 2(1): 16–21.

TRAFFIC (2008) What's driving the wildlife trade? A review of expert opinion on economic and social drivers of the wildlife trade and trade control efforts in Cambodia, Indonesia, Lao PDR and Vietnam. East Asia and Pacific Region Sustainable Development Discussion Papers. East Asia and Pacific Region Sustainable Development Department, World Bank, Washington DC.

Trageser SJ, Ghose A, Faisai M, Mro P, Mro P, Rahman SC (2017) Pangolin distribution and conservation status in Bangladesh. PLoS One 12(4): e0175450. https://doi.org/10.1371/journal.pone.0175450

Verissimo D, Challender DWS, Nijman V (2012) Wildlife trade in Asia: Start with the consumer. Asian Journal of Conservation Biology 1(2): 49–50.

Xu L, Guan J, Lau W, Xiao Y (2016) An overview of pangolin trade in China. TRAFFIC Briefing Paper (September 2016). TRAFFIC, Cambridge, UK

Zhang F, Wu S, Zou C, Wang Q, Li S, Sun R (2016) A note on captive breeding and reproductive parameters of the Chinese pangolin, *Manis pentadactyla* Linnaeus, 1758. ZooKeys 618: 129–144. https://doi.org/10.3897/zookeys.618.8886

Zhang M, Gouveia A, Qin T, Quan R, Nijman V (2017) Illegal pangolin trade in northernmost Myanmar and its links to India and China. Global Ecology and Conservation 10: 23–31. https://doi.org/10.1016/j.gecco.2017.01.006

Zhou Z-M, Zhou Y, Newman C, Macdonald DW (2014) Scaling up pangolin protection in China. Frontiers in Ecology and the Environment 12(2): 97–98. https://doi.org/10.1890/14.WB.001

Zhou Z-M, Zhao H, Zhang Z-X, Wang Z-H, Wang H (2012) Allometry of scales in Chinese pangolins (*Manis pentadactyla*) and Malayan pangolins (*Manis javanica*) and application in judicial expertise. Zoological Research 33(3): 271–275. http://www.zoores.ac.cn/EN/Y2012/V33/I3/271. https://doi.org/10.3724/SP.J.1141.2012.03271

Supplementary material 1

Hunter questionnaire

Authors: Neil D'Cruze, Bhagat Singh, Aniruddha Mookerjee, Lauren A. Harrington, David W. Macdonald

Data type: form

Explanation note: English translation of questions asked and information recorded.

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Rise to fame: events, media activity and public interest in pangolins and pangolin trade, 2005–2016

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Abstract

Attention focused on pangolins (Pholidota) and the threats posed to their survival and welfare by international trade (for use in Chinese Traditional Medicine and the Asian wild meat market) has skyrocketed across all digital information platforms over the last decade. Previously obscure and often referred to as the 'mammal you've never heard of', pangolins are now widely recognised as an icon of the illegal wildlife trade. We document the events that led to the pangolins' 'rise to fame', culminating in its Appendix I listing by CITES in September 2016 and a global commercial trade ban and explore temporal co-occurrence between events and peaks in media activity and public interest with the aim of identifying events (or types of events) that may have been influential in terms of awareness-raising. More broadly, our objective was to highlight lessons in public communication that might be applied to awareness campaigns for other lesser-known threatened species. We found no evidence that any particular type of event was more likely to generate a significant media/public response than any other, but peaks in public interest co-occurred with reports of pangolin seizures, highlighting the importance of news coverage of these incidents. Further, although neither editorial nor social media peaks were strongly correlated with the timing of events, they sometimes co-occurred with different events and each differed in their coverage of different types of events, suggesting that editorial and social media have independent and distinct roles to play in conservation communication. However, despite their iconic status, public interest in pangolins is still not equivalent to that directed at, for example, tigers, elephants or lions, so efforts need to be sustained. Finally, we note that, although attention can help to generate funds and influence policy, this alone will not be enough to achieve a favourable conservation status for pangolins – on-going and future work need to ensure that public enthusiasm for this species is translated into effective protection.

Keywords
Awareness, Facebook, Google trends, news, wildlife trade

Introduction

Public awareness of conservation and animal welfare issues at a global level can be hugely important in instigating, driving and supporting remedial action, largely through influences on policy change and funding (e.g. Lindemann-Matthies and Bose 2008, Tisdell 2006, Phillis et al. 2013, Wright et al. 2015). However, for some species, (particularly those not often seen in the wild, in zoos, sanctuaries or on television), the general public can be oblivious to the threats that they face. Ten years ago, this was true of pangolins for much of the public in the Western world (predominantly English-speaking countries in, for example, Europe and North America). Initially referred to in the media as the 'mammal you've never heard of' (e.g. Sutter 2014), pangolins are now widely portrayed as an icon of the illegal wildlife trade alongside the well-known 'charismatic megafauna' (elephants and rhinos) and their highly-publicised trade issues (poaching for ivory and rhino horn, respectively; e.g. Gao and Clark 2014, Haas and Ferreira 2016).

The precise mechanism underlying this 'rise to fame' is not well understood. Yet, whilst others have documented the conservation actions undertaken (e.g. Challender et al. 2012, 2014a, 2015, 2016) and the patterns of pangolin trade (e.g. Challender and Hywood 2012, Heinrich et al. 2016, 2017), there has been no comparable assessment of either the media or public response to this series of 'events'. By 'events' we mean here an action or incident concerning, or relevant to, pangolins, their conservation or trade. Events might, therefore, include public education campaigns run by NGOs that are designed specifically to raise awareness, but also conservation actions (by, for example, governments, government agencies or inter-governmental organisations) and/or trade-related incidents (such as animals poached, products [animals or their parts] seized or poachers/traffickers arrested), either of which may be covered in the news and thus picked up (directly or via social media) by the general public. Conservation actions may also be publicised directly online via group websites and Facebook pages. Media and/or public attention to such events varies and is not always predictable, but can be considerable. For example, the killing of 'Cecil the lion' in Hwange National Park, Zimbabawe, in 2015, was mentioned in almost 12,000 news articles and over 87,000 social media posts in a single day, largely (but not entirely) due to 'impassioned criticism' of the event by a popular US TV talk show host, although Cecil was not the only lion to have been hunted in Hwange either before or after this event (Macdonald et al. 2016).

Understanding of the types of events that are likely to be influential or to generate considerable public interest, would allow more efficient targeting of sustained awareness-raising strategies specifically for pangolins and, more broadly, would have benefits for conservation marketing for other similar little-known species where greater public awareness of their threats might be helpful. As a first step in this process, here we document and quantify 12 years of pangolin trade-related events and associated media activity and public interest. We hypothesised that there would be an underlying increase in the activity of all types of media and in public interest, related to pangolins and their trade, over this period. However, our specific focus in this analysis was to identify peaks in activity/interest and to explore temporal correlations amongst them and amongst media peaks and peaks in public interest and the occurrence of events. Our aim was to identify events, or types of events, that generated or attracted most public or media interest. Ultimately, our objective was to identify general patterns that could be applied to awareness-raising strategies targeted at similarly little-known threatened animal species.

Pangolins and their trade

There are eight species of pangolin (Order Pholidota, also known as 'scaly anteaters') that collectively range across Asia (where there are four *Manis* spp.) and Africa (where there are two *Phataginus* spp. and two *Smutsia* spp.; Hassanin et al. 2015). All eight species are listed by CITES as *Manis*. All pangolin species are unique amongst mammals in being covered in keratin scales, and all are traded, domestically and internationally, for their scales and their meat (UNODC 2016). Pangolin meat is consumed in Africa and Asia, and is considered a delicacy in many parts of China where it is available in high-end restaurants and desired because it is rare, wild, expensive and illegal and because of the status that it is perceived to impart on consumers (Challender et al. 2015). Their scales are sought after for use in traditional medicine in both Africa (particularly West Africa, see Boakye et al. 2015) and Asia (see Zhou et al. 2014) for their perceived effects in treating a range of physical and spiritual conditions (Challender et al. 2015). Pangolins (body mass 2–33 kg, depending on the species) are solitary, nocturnal, insectivorous mammals that exist almost entirely on ants and termites that they eat with their elongated tongues (Macdonald et al. 2004). They occur at low population densities (estimates of 0.2–1.0 individuals per km^2, Mahmood et al. 2014, Pietersen et al. 2014a) and reproduce slowly (usually giving birth to a single young once a year (Mahmood et al. 2015, Zhang et al. 2016) – life history characteristics that render them vulnerable to overexploitation (e.g. Sodhi et al. 2009). Commercial trade in wild-caught Asian pangolins has been illegal since 2000 (under a CITES zero export quota, Challender et al. 2015) and is now illegal for all pangolin species. Nevertheless, illicit trade in the period 2000 to 2013 is estimated to have involved over a million individual pangolins (IUCN PSG 2016, Heinrich et al. 2017), most of which were destined for China and Vietnam (UNODC 2016). Of the four Asian species, the Chinese pangolin (*M. pentadactyla*) and the Sunda pangolin (*M. javanica*) are Critically Endangered, the two other Asian species are Endangered and the four African species are Vulnerable (IUCN 2018). Hunting and poaching for trade is considered the greatest threat to the survival of all pangolin species (Baillie et al. 2014, Challender et al. 2014b, c, Lagrada et al. 2014, Pietersen et al. 2014b, Waterman et al. 2014a, b, c).

Methods

To provide a context for the analysis, we first described broadly the chronology of events associated with pangolin conservation and trade, beginning with the formation of SavePangolins.org in 2007 and culminating, in September 2016, with the voting of parties at the CITES CoP 17 (Convention of International Trade of Endangered Species of Wild Fauna and Flora, Conference of Parties) to list all eight species of pangolin under Appendix I, thus affording them the highest level of protection under the treaty. We then quantified patterns and trends in the volume of social and editorial media activity related to pangolins and their trade and in relative public interest in pangolins generally, between 2005 and 2016 (covering two years prior to the first prominent event). To quantify relative public interest, we used Google Trends data, which provides a measure of relative Google search activity associated with a specified keyword. The use of Google Trends in this context is well-established (Proulx et al. 2014) and has been used to gauge public awareness and interest in a number of other conservation contexts (e.g. Do et al. 2014, Kim et al. 2014, Nghiem et al. 2016, Soriano-Redondo et al. 2016, Braczkowski et al. 2018). Finally, we used outlier detection in time series analysis to identify (1) monthly peaks in public interest, 2005–2016 and (2) daily peaks in social and editorial media activity and weekly peaks in public interest, 2015–2016 and, for both, assessed temporal co-occurrence amongst datasets and with events. For the latter, we focused specifically on the final two years because this was a period when both events and media activity appeared to be particularly intense. The difference in resolution between datasets was due to limitations associated with Google Trends data.

Identification of events

Key events, related to pangolins and/or pangolin trade, were identified on the basis of personal observation (NC) and personal communication with pangolin experts, with additional events obtained from Challender et al. (2015), the Pangolin Specialist group website (https://www.pangolinsg.org), the WildAid website (a trade-related NGO known for their high-impact media campaigns, wildaid.org) and a Google (https://www.google.com) search for 'pangolin trade'. YouTube (http://www.youtube.com) was also searched for videos on pangolin trade and seizure data were obtained from the Pangolin Crime Dataset 2000–2017 (a dataset of poaching and seizure incidents derived from publicly available sources primarily in Chinese and English languages) held by the Environmental Investigation Agency (EIA) UK (https://eia-international.org/illegal-trade-seizures-pangolins). All events occurring between 2005 and 2016 were collated and categorised as governmental or inter-governmental, non-governmental, media/celebrity events, seizures or 'other' (e.g. zoo-related events). Online publication of a YouTube video was included as an event if the video received >10,000 views (the criteria used by YouTube for their partnership programme that allows users to carry adverts, BBC 2017). Seizures were defined as 'major' seizures and included as events, when the number of whole pangolins seized exceeded 1,000 individuals (or 4,000 kg where only total weight was reported; based on approximate equivalence indicated in the database where both number of individuals and total weight was given) or the weight of scales seized exceeded 3,000 kg (representing between 3,000 and 6,000 individuals based on an estimated 0.5–1.0 kg of scales per animal, depending on species, Choudhary et al. 2018). Our intention for including major seizures as events was not to describe trends in either trade or seizures (which has been covered adequately elsewhere, Heinrich et al. 2017), but to include a subset of the largest seizures on the basis that these were probably the most likely to have generated media coverage and thus public interest. The precise definition of a major seizure was somewhat arbitrary, but represented the top 2% of seizures (in terms of size) in the EIA database.

Social media activity

To quantify social media activity, we used Facebook (www.facebook.com, hereafter FB) as an indicator of social media rather than attempting to quantify all social media activity across multiple platforms. Although other social media platforms are reportedly gaining increasing popularity, especially amongst the younger generation (e.g. Instagram, WhatsApp), FB currently has the most active users worldwide of all social network sites (> 2 billion as of September 2017, Statista 2017) and in a recent survey was rated as the most popular social media platform for nature-related posts (Di Minin et al. 2015). We used the search term 'pangolin wildlife trade' and manually collated data on all posts to include date, original poster and reactions to posts (number of 'likes', comments and 'shares'). Number of posts (and number of 'new' posts, i.e. posts by individuals or organisations that had not posted on this subject previously), reactions to posts and total number of active FB users (from Statista 2017) were quantified per year from 2005 to 2016 (FB was launched in 2004) to provide a general overview of trends over a longer time period. The number of posts was also quantified per day for 2015–2016 to provide a more detailed exploration of the temporal links between social media activity, peaks in editorial media or public interest and the occurrence of events.

Editorial media

Traditional editorial media articles were obtained from Nexis UK (http://www.nexis.com), a 'media news' research service, licensed by LexisNexis for the academic market, covering global sources of news (including newspapers, newswires, blogs, reports and trade journals). We searched for all primary articles (where the search term – 'pangolin' – appeared in the headline or first paragraph), in all news held by Nexis UK, in all languages, published between 2005 and 2016. We manually screened any articles that did not contain the word 'pangolin' in the title prior to inclusion and included articles that focused specifically on pangolins or their conservation, but excluded those about wildlife trade or biodiversity generally that only mentioned pangolins in a list of other species. For comparability with social media data, we recorded the number of news articles (including the same articles published in different outlets to give an indication of the extent of news coverage) per year from 2005–2016 and per day from 2015–2016.

Public interest

We used Google Trends (hereafter GT) to obtain data on Google-based web searches for 'pangolins' (animal) as a topic (which automatically includes alternative forms of the search term), across the internet (web search), in all categories, worldwide, at a monthly resolution for 2005–2016 and separately (at a weekly resolution) for 2015–2016 (daily resolution data were not available). GT does not provide absolute counts of google searches, but gives relative search volume which represents searches relative to the peak in searches (arbitrarily assigned a value of 100) within the region and time period of interest (i.e. a value of 50 means that the term at that point in time was half as popular as at the peak) and is routinely corrected for the total number of web queries (Proulx et al. 2014). We also extracted data on the number of page views of Wikipedia's (en.wikipedia.org) pangolin page. Wikipedia page views have the advantage, compared with GT, of (1) being clearly indicative of people seeking information on pangolins (as opposed to, for example, potential confusion with people searching for 'Precise Pangolin', a computer operating system launched in 2012), (2) providing data on actual (rather than relative) number of page views and (3) providing data at daily resolution (Kämpt et al. 2015). Wikipedia page views were only available from July 2015 – we therefore used GT to obtain longer-term data on public interest but also used Wikipedia page views to verify and to further explore in finer detail, temporal patterns in public interest that occurred in the latter half of 2015 and in 2016.

Time series analysis

All statistical analyses were carried out in R (version 3.4.3, R Core Team 2017). To identify peaks in time series, statistical outliers were detected (in monthly GT data, 2005–2016 and in daily news articles, FB posts and weekly GT data, 2015–2016) using the tso function in the tsoutliers package (Lopez-de-Lacalle 2017) and peaks defined as positive, non-consecutive, statistical outliers of type AO (Additive Outlier, a single spike in the data) or TC (Temporary Change, a sudden increase followed by a gradual decline to baseline values). LS (Level Shift) outliers were also identified separately using the same function to identify points at which an overall increase in baseline activity occurred. Dates of peaks were extracted manually using the timestamps generated and temporal co-occurrence with dates of events recorded. For daily news articles and FB posts, the dates of daily peaks were used to generate binary time series and correlations between them assessed using the Ccf function in the forecast package (Hyndman 2017). Associations between media type, events and event type and the likelihood of co-occurring with peaks in interest, were tested using chi-squared tests or Fisher's exact test, as appropriate. For monthly GT, underlying trends in the data were described using the tslm function (also in the forecast package) and points at which trends changed identified using the breakpoints function in the struccchange package (Zeileis et al. 2002). We did not assess trends in media activity between 2005 and 2016 because, at an annual resolution, the dataset was too small for time series analysis. We also did not assess trends in the 2015–2016 data because the time period was short and we were primarily interested in peaks in the data.

Results

Chronology of events

Following the formation of SavePangolins.org in 2007, February 2012 saw the re-establishment of the IUCN Pangolin Specialist Group (PSG) and the first World Pangolin Day. Within this period (2007–2012), there were three key events, all of which involved conservation professionals: a TRAFFIC workshop in 2008, a CITES alert sent to Parties in 2010 and the formation of the African Working Group (preceding the IUCN PSG) in 2011. In addition, a rescued pangolin (later named 'Baba') was brought to San Diego zoo in 2007 and David Attenborough (a well-known naturalist TV presenter) named pangolins amongst his list of ten species that he would most like to 'save from extinction' in 2012. This was followed, through 2013 and 2014, by a number of events led by the IUCN, including the first international PSG conservation conference, publication of the updated pangolin Red List assessments and the launch of the IUCN Pangolin Action Plan. The first significant media event, where pangolins were featured for a week in a popular online game ('Angry Birds Friends', played by 200 million people worldwide), occurred in November 2014. The event was supported (in an online video interview) by Prince William in his role as president for United for Wildlife (Styles 2014). Pangolins also featured at the 2014 Montier-en-der film festival in a short film entitled 'Plight of the Pangolins'.

The number of pangolin-related events increased notably in 2015 and 2016. Events, at this time, initially involved predominantly governmental and non-governmental actions, including the formation of a trade coalition, the first pangolin range states meeting, a petition to list pangolins on the US Fish and Wildlife Endangered Species Act and an IUCN Resolution to provide greater protection for all pangolin species. From October 2015, there appeared to be an increasing media/celebrity involvement, beginning with the creation of the social media character 'Ollie the Pangolin' and including (through 2016) the appearance of a pangolin in the Disney movie 'The Jungle Book', the involvement of national celebrities in media campaigns in China and Vietnam, an event supported by Jane Goodall and a number of awareness-raising materials published online (e.g. the WildAid video infographic 'The Fight to Save Pangolins' and the National Geographic short video 'The Tragic Tale of a Pangolin'). In total, we identified 16 (non-seizure) key events between 2005 and 2014 and 26 in 2015 and 2016. Further details, additional events and references are given in Table 1.

Table 1. Pangolin-related events occurring between 2005 and 2016. Type of event coded as: governmental/intergovernmental G/IG, non-governmental NG, media/celebrity M, major seizures S, or 'other' (e.g. zoo-related events) O; YouTube videos were included as media events if they received ≥10K views (see text); seizures were defined as major seizures if they exceeded 1,000 whole pangolins (equivalent to c. 4,000 kg where weight of the seizure rather than numbers was given) or 3,000 kg pangolin scales (see text, this represents the top 2% of seizures in the source database). 2015–2016 events associated with peaks in editorial (marked as **N**) or social (**FB**) media, or with weekly GT peaks (**wGT**), are indicated in square brackets. (Note that the content of both news articles and Facebook posts suggest that the media peak on 5th October – see text – coinciding with publication of a YouTube video, was actually related to coverage of the CITES listing that occurred 7 days earlier – and that news coverage of this event continued until at least the 13th October 2016.)

Event	Date/Year	Type	Source [media/interest peak, shown for 2015–2016]
Hoi Ha Wan seizure of 1,800 whole pangolins, Hong Kong	2005	S	EIA database[11]
SavePangolins.org formed	2007	NG	www.savepangolins.org
'Baba' brought to San Diego Zoo[1]	2007	O	www.sandiegouniontribune.com/news/whats-now/sd-me-pangolin-dies-20160930-story.html
Seizure of whole pangolins (weight 21,000 kg) and 900 kg scales, Hai Phong, Vietnam	Mar 2008	S	EIA database[11]
Pangolin workshop in Singapore[2]	30th Jun-2nd Jul 2008	NG	Pantel and Chin 2009
Seizure of whole pangolins (weight 13,800 kg), Palembang, Indonesia	Aug 2008	S	EIA database[11]
Gaolan Island, Guangdong, seizure of 2,090 whole pangolins, China	13th Jul 2010	S	EIA database[11]
CITES alert sent to Parties[3]	2010	G/IG	Challender et al. 2015
African Pangolin Working Group (APWG) formed	27th Jun 2011	NG	www.africanpangolin.org/
Seizure of whole pangolins (weight 7,500 kg) and 65 kg scales, Tanjung Priok, Indonesia	26th May 2011	S	EIA database[11]
Seizure of 1,068 whole pangolins, Malaysia	7th Dec 2011	S	EIA database[11]
IUCN Pangolin Specialist Group (PSG) re-established	Feb 2012	G/IG	www.pangolinsg.org/about/
First World Pangolin Day	Feb 2012	NG*	www.pangolins.org/about-us/
INTERPOL Operation Libra[4]	Jun/Jul 2012	S	EIA database[7]; www.interpol.int/News-and-media/News/2012/N20120829
IUCN Pangolin SG website launched	17th Sept 2012	G/IG	www.pangolinsg.org/2012/06/14/hello-world-2/
Pangolin included in David Attenboroughs' ten favourite species	Nov 2012	M	www.telegraph.co.uk/news/9637972/Sir-David-Attenborough-picks-10-animals-he-would-take-on-his-ark.html
Huilai County seizure of 2,032 whole pangolins and 325 kg pangolin scales, China	23rd Dec 2012	S	EIA database[11]
YouTube 'Meet the Pangolin!' video published (22K views)	15th Feb 2013	M	www.youtube.com (uploaded by Annamiticus)
Seizure of whole pangolins (weight 10,000 kg), Tubbataha NP, Palawan, Phillippines	8th Apr 2013	S	EIA database[11]
1st International PSG conservation conference	Jun 2013	G/IG	portals.iucn.org/library/node/44947
Seizure of whole pangolins (weight 15,140 kg) and 990 kg scales, Hai Phong, Vietnam	Aug 2013	S	EIA database[11]
YouTube Born to be Wild video 'Doc Nielsen exposes the illegal pangolin trade' published (34K views)	4th Apr 2014	M	www.youtube.com (uploaded by GMA Public Affairs)
IUCN news release, Red List assessments published, launch of Action Plan	Jul 2014	G/IG	www.iucn.org/content/eating-pangolins-extinction; http://www.iucnredlist.org/; portals.iucn.org/library/node/44947
Range States requested to submit information on illegal trade at CoP16	Jul 2014	G/IG	Challender et al. 2015

Event	Date/Year	Type	Source [media/interest peak, shown for 2015–2016]
Pangolins featured in Angry Birds Friends[5]	Nov 2014	M	www.angrybirdsnest.com/angry-birds-friends-pangolins-tournament-on-now/
Plight of the Pangolins at Montier-en-Der film festival	Nov 2014	M	www.annamiticus.com/2014/11/28/french-wildlife-photography-festival-backs-pangolin-conservation/
Anti-pangolin poaching Public Service Announcement aired in Vietnam[6]	29th Jan 2015	M/NG	www.edition.cnn.com/2015/01/29/opinion/sutter-pangolin-psa-vietnam/index.html
Pangolin workshop in Brunei (sponsored by the British High Commission)[7]	16th-21st Feb 2015	G/IG	www.gov.uk/government/news/british-carnivore-and-pangolin-conservationist-to-support-bruneis-wildlife-conservation-efforts
World Pangolin Day 2015	21st Feb 2015	NG/M	**[FB]**
YouTube 'March of the Pangolins' video published (11K views)	6th Mar 2015	M	www.youtube.com (uploaded by WildAid)
Medan warehouse raid, seizure of 3,000-4,000 frozen pangolins, Indonesia	23rd Apr 2015	S	EIA database[11] **[wGT, see Fig. 2a]**
1st Pangolin Range States meeting	24th-26th Jun 2015	G/IG	www.fws.gov/news/blog/index.cfm/2015/7/2/Pangolins-Benefit-as-United-States-Range-States-Gather-to-Plan-Critical-Conservation
SOS and Foundation Segre announce International Pangolin Conservation Initiative	26th Jun 2015	NG	www.saveourspecies.org/news/sos-and-fondation-segre-announce-new-international-pangolin-conservation-initiative
NGOs petition USFWS to protect 7 pangolin species under the Endangered Species Act (ESA)	15th Jul 2015	NG	www.thepetitionsite.com/en-gb/790/993/022/usfws-%E2%80%93-list-the-seven-endangered-pangolin-species-not-protected-under-esa/; https://www.regulations.gov/docket?D=FWS-HQ-ES-2016-0012 **[N]**
4,000 kg of pangolin scales seized in Central Danang's Tien Sa port, Vietnam	25th Aug 2015	S	EIA database[11]
Ollie the pangolin facebook page created	9th Oct 2015	M	www.facebook.com/pg/olliethepangolin/about/?ref=page_internal
1st International APWG conference	12th – 15th Oct 2015	NG	www.paxtag.org/international-pangolin-conference-12-15-oct-2015-south-africa/
Jiangmen seizure of 2,674 whole pangolins, China	3rd Nov 2015	S	EIA database[11] **[associated with a monthly GT peak, see Fig. 2a]**
YouTube 'Guardians of the Pangolin: the fight to save the world's most trafficked animal' video published (17K views)	17th Nov 2015	M	www.youtube.com (uploaded by Coconuts TV)
WildAid video infographic (The Fight to Save Pangolins)	18th Feb 2016	NG	www.vimeo.com/155919419
World Pangolin Day 2016	20th Feb 2016	NG/M	**[N, FB]**
USFWS announce (substantial) 90-day findings for the petition to list all pangolins under the ESA[8]	15th Mar 2016	G/IG	www.eei.org/Lists/Articles/DispForm.aspx?ID=7970; www.gpo.gov/fdsys/pkg/FR-2016-03-16/pdf/2016-05699.pdf
Pangolin character in 'The Wild Life' (Robinson Crusoe movie) (trailer released)	15th Mar 2016	M	www.youtube.com/watch?v=3dyAWBMF6bE
Pangolin in Disney movie The Jungle Book	15th Apr 2016	M	www.romper.com/p/theres-a-pangolin-in-the-jungle-book-everyone-is-freaking-out-9020; www.huffingtonpost.com/jeffrey-flocken/ifaw-qa-with-the-jungle-b_b_10109890.html
WildAid and the Nature Conservancy China feature Angelababy in media campaign (say no to pangolin products)	20th May 2016	M	www.wildaid.org/news **[FB]**
4 tonnes of pangolin scales seized at Kwai Chung Customhouse Cargo Examination Compound, China	23rd Jun 2016	S	EIA database[11]
Seizure of 7,300 kg of pangolin scales, Hong Kong	19th Jul 2016	S	EIA database[11] **[FB]**
Celebrities and leaders in WildAid campaign in Vietnam	29th Jul 2016	M	www.wildaid.org/news

Event	Date/Year	Type	Source [media/interest peak, shown for 2015–2016]
IUCN Resolution supporting pangolin conservation[9]	31st Aug 2016	G/IG	www.ifaw.org/united-kingdom; portals.iucn.org/library
Jane Goodall hosts reception at IUCN World Conservation Congress supporting pangolin conservation	2nd Sept 2016	M	www.facebook.com/janegoodall/videos/10154509286492171/
Episode of Black Market: Dispatches on US TV investigates pangolin poaching	13th Sept 2016	M	www.vice.com; a YouTube clip of this episode 'The most trafficked mammal on the planet' also published online on the same day (34K views)
WildAid report (Pangolins on the Brink) released	21st Sept 2016	NG	www.wildaid.org/news/pangolins-brink
'Baba' dies at San Diego Zoo	28th Sept 2016	O	www.sandiegouniontribune.com/news
CITES Appendix I listing for all pangolin species	28th Sept 2016	G/IG	newsroom.wcs.org/News-Releases/articleType/ArticleView/articleId/9303/CITES-CoP17-Victory-Today-for-Pangolins.aspx; www.cites.org/eng/app/appendices.php **[N, FB, wGT]**
YouTube Wildest Animal Rescues video 'Saving Vietnam's Critically Endangered Pangolin' published (50K views)	5th Oct 2016	M	www.youtube.com (uploaded by Barcroft Animals)
Pangolin trade photo wins the Wildlife Photographer of the Year Photojournalist (single image) award	18th Oct 2016	M	www.nhm.ac.uk/visit/wpy/gallery/2016/images; **[FB, wGT]**
National Geographic short film (The Tragic Tale of a pangolin)	13th Nov 2016	M	www.video.nationalgeographic.com/video/short-film-showcase/the-tragic-tale-of-a-pangolin-the-worlds-most-trafficked-animal
3.1 tonnes of pangolin scales seized in Shanghai, China[10]	10th Dec 2016	S	EIA database[11] **[possibly associated with peaks in news and weekly GT on 28th Dec, see text]**

[1] Baba, an African while-bellied tree pangolin, was brought to the zoo after being intercepted by Fish and Wildlife officials in an illegal shipment, he was kept in the Children's Zoo as an ambassador for the species.

[2] Jointly organised by Wildlife Reserves Singapore and TRAFFIC SE Asia.

[3] CITES secretariat issued Alert No. 37 on fraudulent and illegal trade in pangolins.

[4] Countries across Southeast Asia took part in the largest coordinated operation against the illegal poaching and trade in pangolins. Operation Libra, coordinated by INTERPOL's Environmental Crime Programme, involved investigations and enforcement actions across Indonesia, Laos, Malaysia, Thailand and Vietnam. Supported by the Freeland Foundation through a grant from USAID, the operation led to the arrest of more than 40 individuals, with some 200 additional cases under investigation across the region.

[5] Free, week-long tournament 'Roll with the pangolins' featured in the online game Angry Birds Friends, endorsed by Prince William in his role as President of United for Wildlife.

[6] Commissioned by the environmental NGO Nature for Education Vietnam.

[7] Organised by a local NGO (1StopBruneiWildlife) and a member of the PSG.

[8] This means that it is acknowledged that legal protection may be warranted based on the evidence presented in the petition, a status review is then initiated to determine whether petition actions are warranted.

[9] Resolution/recommendation number WCC-2016-Res-015, original motion number 011: Greater protection needed for all pangolin species.

[10] Widely reported as the largest pangolin seizure in China at that time (e.g. www.phys.org/news/2016-12-china-biggest-ever-pangolin-scale-seizure.html) although there were two larger seizures in Hong Kong earlier in the Year (see Table).

[11] Pangolin Crime Dataset 2000-2017 (a dataset of poaching and seizure incidents derived from publically available sources primarily in Chinese and English languages) held by the Environmental Investigation Agency UK, (eia-international.org/illegal-trade-seizures-pangolins).

* Note that World Pangolin Day was initiated by NGOs, and, as such is categorised as an NGO event, but could now be considered to be a media event.

The EIA database contained records of a total of 712 pangolin seizures between 2005 and 2016, of which sixteen seizures fitted our definition of a major seizure event. The first major seizure occurred in 2005, followed, in 2008, by two and, from 2010, one or two per year (except 2014 when there was none documented) and three in both 2015 and 2016 (see Table 1 for details). Major seizures occurred in China (7), Vietnam (3), Indonesia (3), Malaysia (1) and the Philippines (1, with one regional event across Southeast Asia coordinated by INTERPOL's Environmental Crime Programme, Table 1).

Trends in social and editorial media, 2005–2016

Our search revealed 6,244 FB posts on 'pangolin wildlife trade' and 1,445 news articles on pangolins, between 2005 and 2016. FB posts were posted by 3,768 unique posters that, together, elicited 22,698 comments, 89,077 'shares' and 371,785 'likes'. There was a clear and dramatic increase in both posting and response to posts over time, with fewer than 10 posts per year (and < 30 comments, < 20 likes) in 2008 and 2009 (there was none prior to 2008), increasing to over 200 (with over 1,000 comments and over 2,000 likes) in 2012 and reaching more than 4,000 (with 11,329 comments and 246,556 likes) in 2016 (Fig. 1, Suppl. material S1). Accounting for the increase in FB users over this time period, this amounted to an almost 100-fold increase in FB activity between 2009 and 2016 and a relative 55-fold increase in the number of 'new' posters posting about pangolin trade (see S1). The number of news articles showed similar, but less dramatic increases, with an overall nine-fold increase from 30–50 articles per year between 2005 and 2010, to > 100 articles in 2012 and > 400 articles in 2016 (Fig. 1, Suppl. material S2).

Peaks in public interest and co-occurrence with events, 2005–2016

Monthly google searches for 'pangolins' increased (albeit at a relatively minor rate: slope = 0.18, $p < 0.001$) between 2005 and 2016, with the first apparent increase (change in slope) occurring in February 2012 (Fig. 2a), corresponding with the reformation of the IUCN PSG and the first World Pangolin Day. Variability increased over time but one peak in the data, occurring in April 2015, was almost twice that of any others (Fig. 2a). Eight additional monthly peaks were identified at: May and November 2007, May 2012, April 2013, April 2014, November 2015, August 2016 and October 2016 (Fig. 2a). The pattern in monthly Wikipedia page views, in 2016 and the latter half of 2015, broadly matched that shown by GT (Fig. 2a). During this time period, the number of views of the Wikipedia pangolin page ranged between 1,075 and 52,869 per day with the highest volume of searches occurring on the 26th and 27th August 2016 (52,869 and 44,595, respectively, compared with a daily average of 3,222).

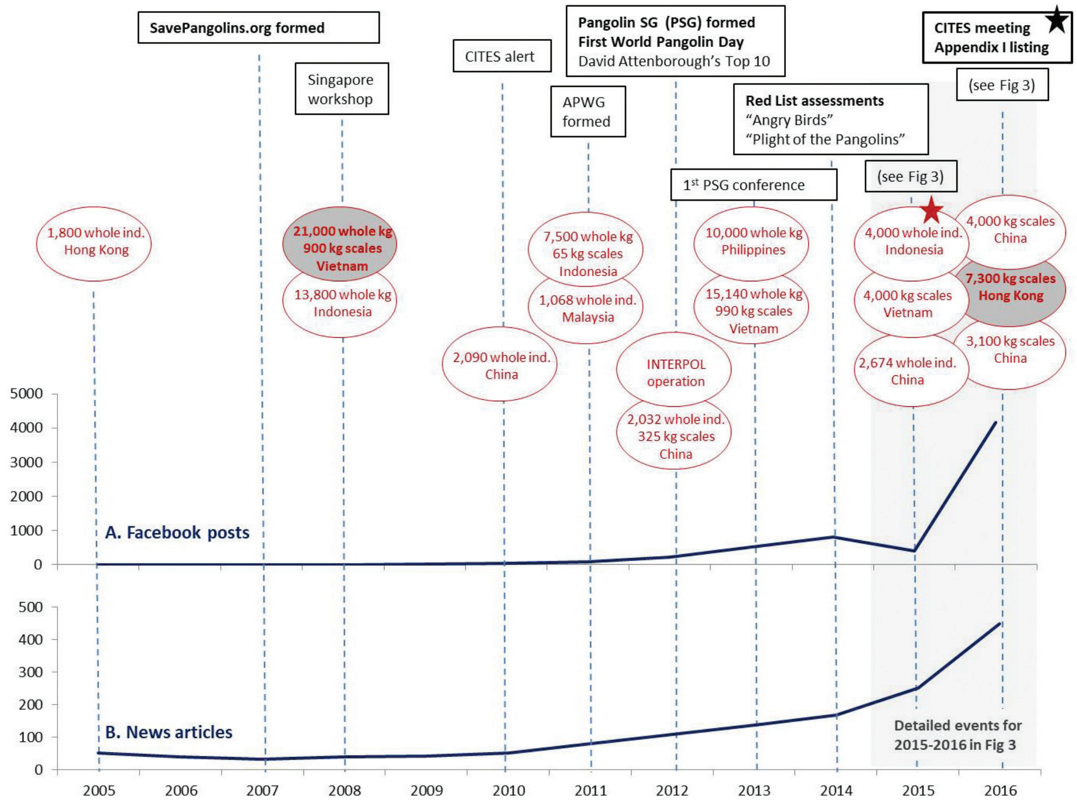

Figure 1. Annual trends in the number of **A** Facebook (FB) posts (n = 6,244) and **B** news articles (n = 1,445), related to pangolin trade (FB) and pangolins (news), respectively, between 2005 and 2016, shown against events (top), including 'major seizures' (defined as in text, where 'ind.' refers to the number of pangolins recorded, otherwise the weight of pangolins recorded). The shaded circles mark the largest seizures of whole pangolins and pangolin scales, respectively, recorded in the EIA database for the period of the study. The red star marks the Medan seizure in Indonesia in April 2015, referred to in the text; the black star marks the Appendix I listing of all pangolin species at the CITES CoP 17 meeting in September 2016.

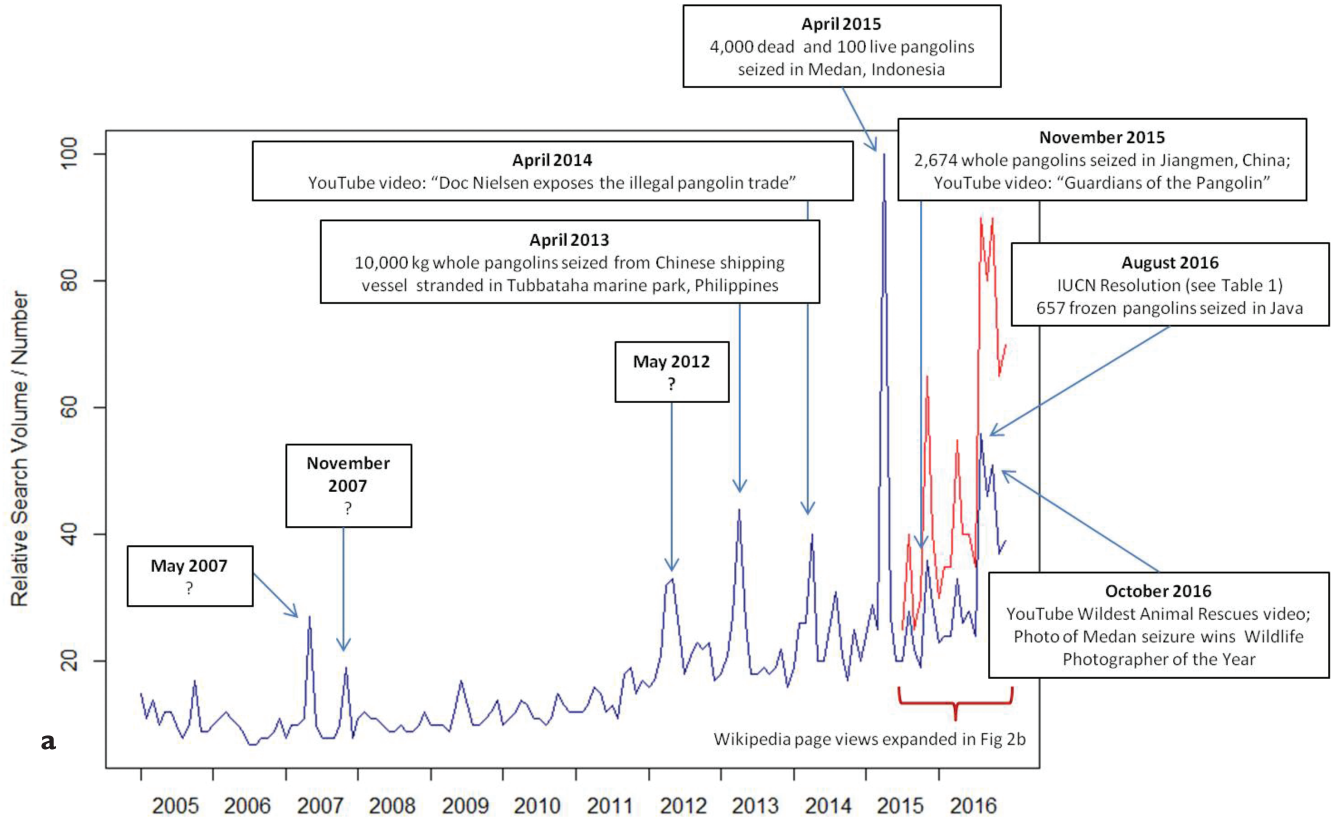

Figure 2a. Monthly Google Trends (GT) search volume (blue) shown against number of Wikipedia page views (red), 2005–2016. Note that GT shows relative search volume, where 100 represents the peak and all other values are relative to the peak; two breakpoints in the data were identified (at February 2012 and March 2015). Text boxes show events that co-occurred with peaks in GT search volume (see Table 1 and text for details); peaks that did not appear to correspond with an event are marked with a '?'. GT peaks were identified as statistical outliers in time series data (see text)

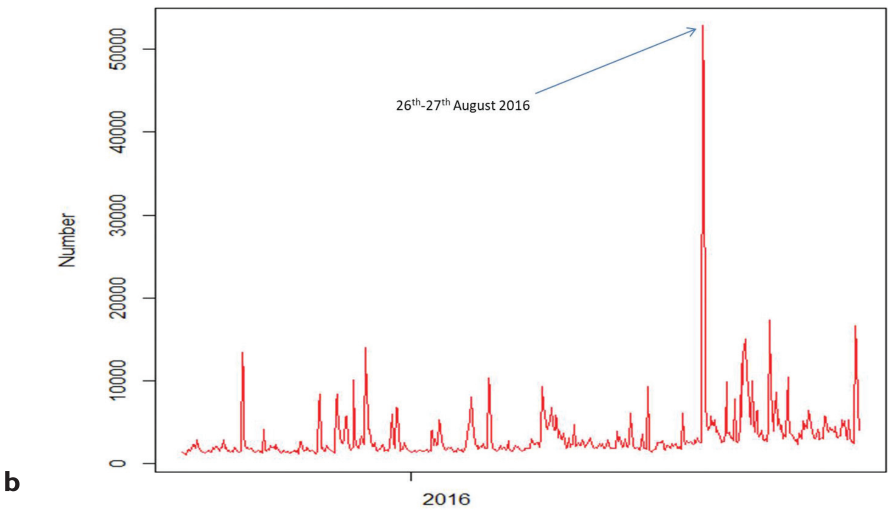

Figure 2b. Daily Wikipedia page views for July 2015 – December 2016 illustrate occurrence of the single two day peak in August 2016 that co-occurred with the seizure of 657 frozen pangolins in Java (see text).

The April 2015 GT peak may have been associated with the Medan warehouse seizure in Indonesia (where 100 live and an estimated 4,000 dead pangolins were found, Table 1) that occurred in the same month. With the exception of the August 2016 peak, all other GT peaks occurring from and including 2013, occurred in the same month as either a major seizure or the release of a YouTube video identified as an event (see Fig. 2a, Table 1). The August 2016 GT peak coincided with various pre-CITES CoP 17 meeting activities but the Wikipedia page views peak suggests that the peak in public interest at this time actually occurred on the 26th August (2016)(Fig. 2b) coinciding with news reports of a seizure of 657 whole frozen pangolins in a freezer in Java by Indonesian authorities (Pangolin Crime Dataset 2000–2017; see Methods). The Javan seizure was not identified as a major seizure but both the Javan and the Medan seizure were associated with graphic images (a large pit full of thousands of dead pangolins and pangolins wrapped in freezer bags, respectively) published in the Guardian newspaper (The Guardian 2015, 2016). The Medan photograph won the Natural History Museum Wildlife Photographer of the Year (www.nhm.ac.uk/visit/wpy.html) photojournalist award in October 2016 (see Table 1), which was announced on the 18th October 2016 and perhaps linked with the October 2016 GT peak (Fig. 2a) and the minor peak in Wikipedia page views seen on the 19th October 2016 (Fig. 2b). The three monthly GT peaks prior to 2013 did not appear to correspond with identified events.

Correlations and associations amongst peaks in editorial and social media, public interest and events, 2015–2016

We identified 29 individual daily peaks in FB posts, 16 in news articles and five weekly peaks in GT (Fig. 3; for comparison with monthly peaks shown in Fig. 2a, weekly GT

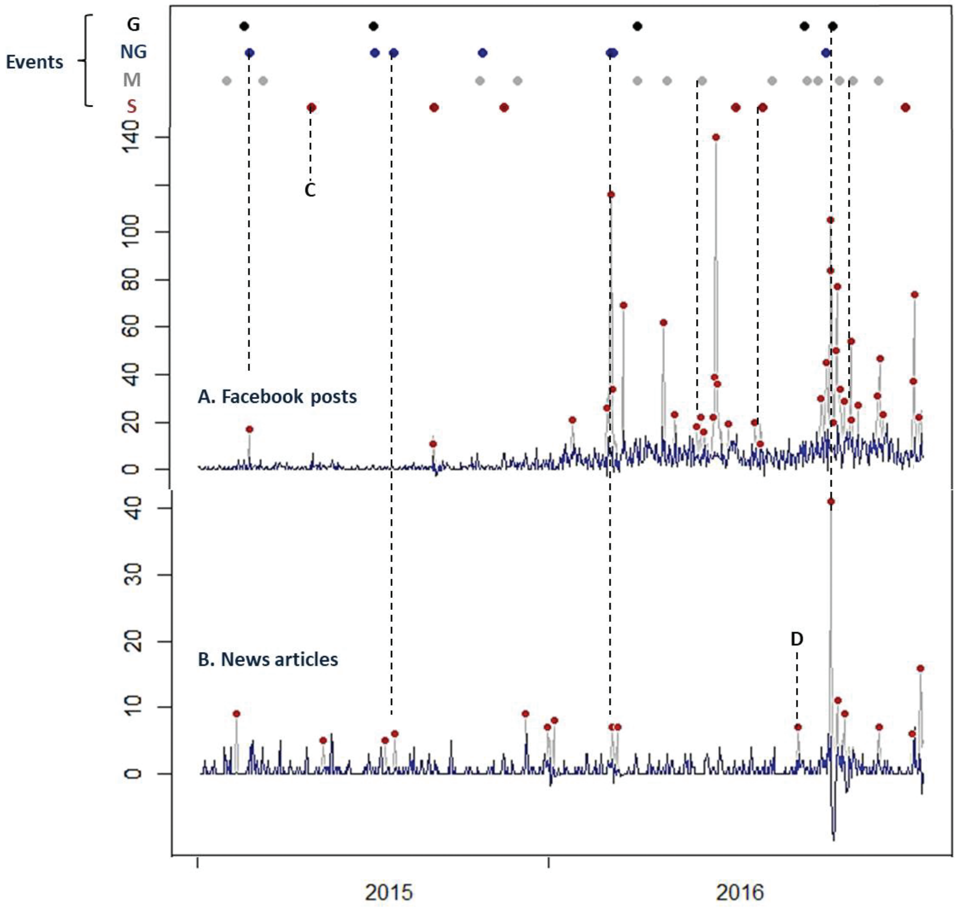

Figure 3. Daily trends in **A** the number of Faceook (FB) posts and **B** the number of news articles, showing peaks in activity (red circles) against the occurrence of events (top), 2015–2016. G=governmental event, NG=non-governmental event, M=media event or 'other', S='major seizure'; for details of events see Table 1. Peaks in FB posts/news articles were identified as statistical outliers in time series data (see text; note that all positive outliers are shown in A but only 29 of these occurred on non-consecutive days and were thus counted as peaks in activity). C marks the Medan seizure associated with a peak in weekly GT (not shown); D marks the Javan seizure that was not identified as an event but corresponded with a peak in news articles (shown) and weekly GT (not shown) (both seizures are referred to in the text).

peaks occurred in April 2015 and August, September, October and December 2016). There were statistically significant but very weak cross correlations between news article peaks and FB post peaks at zero time lag (CCF=0.139), -7 days (CCF=0.141) and +4 days (CCF=0.139): peaks in news articles and FB posts coincided (on the same day) on four occasions, there were six occasions on which peaks in FB posts were preceded by a peak in news (by between one and seven days) and five on which the opposite was true (by between one and four days). Approximately half of all peaks in both news articles and FB posts (n= 8 and n=15, respectively) occurred in the absence of the other (within a seven day period, Fig. 3). Direct (same day) correspondence of peaks in media interest with events was similarly rare, but equally (un)likely for editorial and social media (Fisher's exact test, p=1.0) occurring on only four occasions for news peaks (25% of news peaks) and six for FB peaks (21%) (including three occasions on which both peaked simultaneously). Eight (50%) news peaks and 13 (45%) FB peaks occurred within seven days of an event. It was not possible to test formally for cross correlations between GT and either FB posts or news articles or between GT and events, because they were measured at different time scales but comparing dates, identified as peaks, revealed that correspondence between GT and media peaks was similarly inconsistent: GT peaks encompassed daily peaks in news articles once, FB posts once, both twice and neither once. Three of the five weekly GT peaks overlapped with events; another weekly GT peak overlapped with the (non-major) Javan seizure as identified in Fig. 2a (which also corresponded directly with a peak in news) and the fifth may have been associated with a seizure but with a 19-day time lag (see below).

There were statistically significant but weak, or very weak, cross correlations between news article peaks and events (at zero time lag [CCF=0.161] and – 7 days [CCF=0.209]) and between FB post peaks and events (at zero time lag [CCF=0.148]). Overall, only eight of the 32 events occurring in 2015–2016 corresponded directly with peaks in either social or editorial media or public interest (see Table 1, Fig. 3). These eight peak-associated events included all event types (one inter-governmental event [the CITES meeting], one official non-governmental event [the USFWS/ESA petition], two that could be considered as non-governmental-media events [the two World Pangolin Days], two media events [a celebrity-supported 'say no to pangolin products' campaign in China and a pangolin trade photo winning an award in the Wildlife Photographer of the Year competition] and two major seizures of pangolin scales, see Table 1 for details). Combining social and editorial media and public interest, there was no significant association between type of event (categorised as governmental/inter-governmental [G/IG], non-governmental/media [NG/M] combined and major seizures [S]) and the occurrence of a peak response (χ^2 = 0.305, df=2, p=0.859). Sample size was too small to test for differences in co-occurrence with event type amongst media type and public interest, but post hoc checks of collated news articles and FB posts for the week during which an event occurred (for all events listed in Table 1, 2015–2016), suggested that coverage rather than activity peaks (i.e. whether or not an event was mentioned that week) differed between editorial and social media with news articles most likely to cover governmental events and least likely to cover media events ($\chi 2$ = 13.93, p=0.001), while FB posts were equally likely to cover events of all types ($\chi 2$ = 4.44, p=0.218).

We identified four dates at which level shifts occurred in the number of FB posts and two at which level shifts occurred in the number of news articles (Fig. 3; no level shift outliers were detected for GT data). Whilst not necessarily causative, level shifts marked a point in the time series at which there was an overall increase in baseline media activity (number of news articles or of FB posts). Predictably, two of the dates identified (in the FB time series) corresponded with the 2016 World Pangolin Day and the CITES meeting on 28 September 2016. For the news time series, a level shift on 26 September 2016 corresponded with a peak in news articles two days later and appeared to be due to articles covering the lead up to the CITES meeting (on the 28th). The two additional level shifts in the FB time series occurred on the 21st December 2016 (associated with an open letter to the Chinese ambassador in Namibia raising the issue of Chinese nationals involved in commercial wildlife crime in Namibia that was widely shared through social media, Brown 2016) and the 5th June 2016 (World Environment Day, with the theme 'Zero tolerance for illegal wildlife trade'). The second level shift in news articles occurred on 28 December 2016, associated with what was widely reported (at the time) to be the 'biggest ever scale seizure", in China on the 10th December (18 days earlier) in Shanghai, China (and co-occurring with a weekly peak in GT, see Fig. 3, Table 1).

Discussion

Between 2005 and 2016, alongside intensified efforts by NGOs, governments and scientists, interest in pangolins and in the threats posed by the international trade in their meat and scales, has undergone a significant increase in the editorial and social media and amongst global western audiences. In addition to underlying increasing trends, time series describing editorial and social media activity and GT were characterised by considerable fluctuations and clear peaks in activity. Whilst it was difficult to detect generalisable patterns for peaks in activity amongst datasets or between datasets and external events and bearing in mind that co-occurrence does not necessarily imply causation, our exploratory analysis revealed a number of potentially insightful observations.

First, although only a quarter of events were associated with a peak in either social or editorial media or public interest, there was no evidence that any particular type of event was more likely to generate a significant response than any other. This suggests that all types of events may have a role to play in increasing the public profile of conservation issues. Certainly, there are reasons for combining different types of events – for example, whilst conservation-themed 'big screen' animations can trigger considerable interest across a broad viewership, Yong et al. (2011) suggested that they are more effective when combined with supporting educational materials and campaigns.

For major seizures specifically, co-occurrence with peaks in media activity was low but 'different' seizures (see below) were associated with peaks in public interest and there was some evidence of time delays in media response. The only major seizure (of six recorded from 2015–2016) that co-occurred directly with a media peak (FB posts) was the largest scale seizure (7.3 tonnes) recorded in the EIA database at the time of this study; another, that appeared to be associated with a news peak with an 18-day time lag, involved 3.1 tonnes of pangolin scales but was widely reported in the news to be 'China's biggest ever pangolin scale seizure' (see Table 1, 19 July and 10 December 2016, respectively). Between 2010 and 2015, there was a global increase in the weight of pangolin scale seizures and an increase in the proportion of large-quantity shipments of scales (Heinrich et al. 2017) and it is intuitive that successively larger seizures would continue to attract media attention, as each is reported to be 'the largest ever' (see e.g. AFP 2016). There has been no such increase in the size of seizures of whole pangolins (Heinrich et al. 2017), but peaks in public interest (at either weekly or monthly resolution) appeared to be associated with seizures of whole pangolins (alive or dead) and sometimes with seizures of whole pangolins that did not meet our *a priori* definition of a major seizure (see Table 1, Figs 2, 3). Although sample size was small, this suggests that seizures of whole pangolins attract attention amongst the general public (regardless of the numbers involved) and/or that there are other features of whole pangolin seizures that attract attention. With respect to the latter, we suspect that accompanying 'shocking' images (such as in the Medan warehouse raid; The Guardian 2015) may be key (see also Pinholster and Ham 2013; Papworth et al. 2015; Wu et al. 2018).

Second, only a quarter of the peaks in either social or editorial media activity clearly corresponded with an event. News articles and FB posts partly reflect public interest (e.g. Phillis et al. 2013), but news can also be agenda-driven (Papworth et al. 2015) and repeat-posters on FB, in this study, were predominantly professional or semi-professional organisations rather than individuals (see Suppl. material S1). Social and editorial media activity, thus, reflect the combined extent of scientific communication and advocacy, in addition to public response and are presumably driven by several factors, which may include, for example, organisational planning and schedules not necessarily related to external events. In contrast and notwithstanding differences in resolution, there was some evidence of slightly higher correspondence with events for GT. GT does not provide information on the opinion or motives of the interested public (Proulx et al. 2014), but it is considered a 'valid tracker of public curiosity [sic]' (Mccallum and Bury 2013). In this case, the relatively high correspondence between GT peaks and events (at least five of nine monthly GT peaks and at least three of five weekly GT peaks, see Fig. 2 and Table 1), together with an apparent association with seizures, highlights the importance of the news coverage of these types of incidents in raising awareness (see also Bolsen 2011, who found that news itself was driven more by real-world events than by messages supplied by advocacy groups or governments seeking to influence public discourse).

Third, whilst peaks in FB activity and news articles sometimes co-occurred, most often they did not. Co-occurrence between peaks in social and editorial media was sometimes, but not always, associated with a time lag of between one and seven days – but, whilst peaks in news articles sometimes appeared to lead peaks in social media, social media peaks preceded news peaks on an almost equal number of occasions. These apparently inconsistent observations presumably reflect the dual function of social media in both relaying news in the traditional editorial media (with some time lag) and creating news (Copeland 2011), as well as underlying differences in the types of events covered by editorial versus social media. Timing of peaks in public interest, similarly, differed from that of peaks in either news or social media activity, but overlapped (within the week in which GT data were collated) on different occasions with both. Social media is widely used as a news source (a recent YouGov survey found that over half of

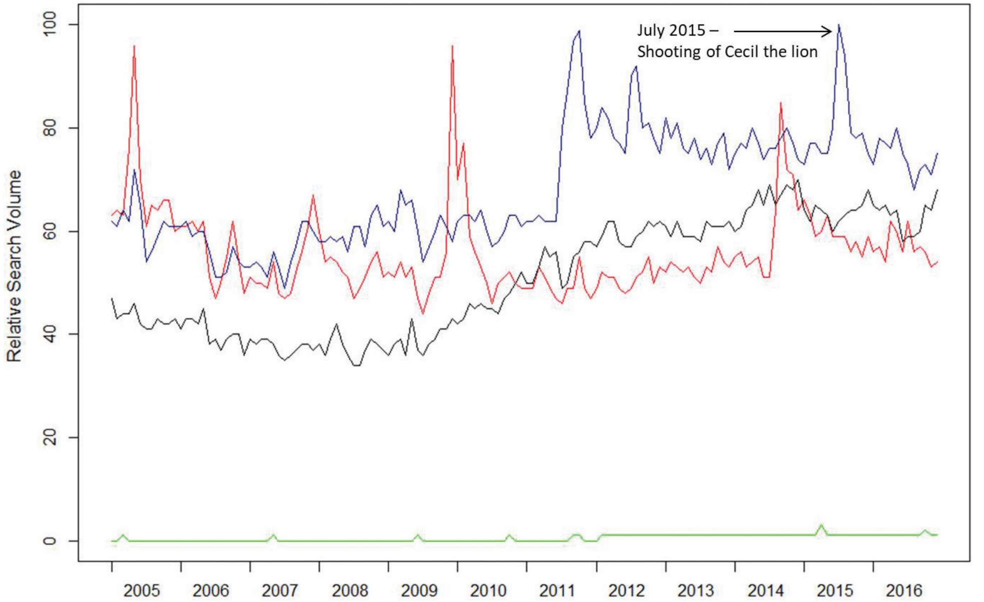

Figure 4. Google Trends (GT) for pangolins (green) compared with three large, well-known, 'charismatic' species – tigers (red), elephants (black) and lions (blue), 2005–2016. Data shown are relative search volume, where 100 represents the peak and all other values, for all species, are relative to the peak. Note the very low search volume for pangolins, relative to the other species; the highest relative search volume occurs in July 2015, coinciding with the shooting of Cecil the lion (Macdonald et al. 2016, see text).

respondents from 36 countries get their news from social media sites; YouGov 2017), but editorial media still clearly has a role, independently of, and as a driver of, social media. Further, whilst social media peaks through 2016 were ten times in magnitude that of editorial media peaks over the same period, these extreme peaks in social media activity were not seen until 2016; whereas smaller, more frequent peaks in editorial media were seen throughout 2015 (Fig. 3), suggesting that social media activity, more generally, may, at least in part, have been a response to persistent news coverage. That public interest peaks independently of peaks in the media (but responds to events covered in the media) suggests that media content is more influential than the number of articles or posts produced (this is probably also true of FB posts posted in response to news articles).

In accordance with other studies of media attention surrounding high-profile events (e.g. the 'climategate' media event, Anderegg and Goldsmith 2014; and the shooting of Cecil the lion, Macdonald et al. 2016), the vast majority of peaks identified in media activity and were transient and, in this study, in most cases, had returned to former levels within a few days (GT could not be assessed at time scales less than a week). This short-lived nature observed in public interest is common (Downs 2018) and unsurprising since media coverage of events tends to be ephemeral (e.g. Sampei and Aoyagi-Usui 2009). There was some evidence of sustained higher levels of media activity following World Pangolin Day 2016 and the CITES CoP 17 meeting (also in 2016), but the gradual increase in public interest (as evidenced by GT) was not clearly related to any particular event.

Finally, it is noteworthy that, relative to other species, public interest in pangolins was still relatively low. GT for pangolins, relative to for example tigers, elephants or lions, were small (Fig. 4) and there was no evidence that any of the FB posts or YouTube videos described in key events, went viral (the precise definition of 'viral' is complex but usually involves > 1 million 'likes', comments and 'shares' or views, Rayson 2017). Maximum 'likes' and 'shares' recorded in this study for any one FB post were 36,000 and 3,500 (Suppl. material S1), respectively and the maximum views of any one YouTube video 34,000 (see Table 1).

Limitations

As many of the seizure records in the EIA database were originally sourced from news articles, news articles and seizures were not entirely independent. Social media activity was based only on FB and on English language search terms. It is likely that a proportion of global social media activity was carried out in different languages and on alternative platforms, particularly WeChat or Weibo (prominent social media platforms in China). Data resolution may also have been too coarse to disentangle the order of events insofar as news reports, available first thing in the morning, may generate social media reaction throughout the day (but on a daily basis appear to be simultaneous). These limitations require some caution in interpretation of our findings; nevertheless, our data explorations offer some useful insights into the apparent response of the media and the general public to different events and the differences and similarities amongst them.

Conclusions

The CITES Appendix I listing for pangolins and the trade ban were an important legal step. That there has been considerable global activity and attention directed at pangolins both proceeding and in response to this event is clear. However, seizures of ever increasing size continue to be reported – during the writing of this paper, 11.9 tonnes of pangolin scales were seized in Shenzhen, Hong Kong, on the 29th November 2017 (IFAW 2017; this is larger than any of the seizures included in this analysis and represents the largest seizure yet reported). Efforts are now needed to translate the ban and associated enforcement into effective action and behaviour change on the ground (Challender and MacMillen 2014; Challender et al. 2015).

Insofar as public awareness can help drive these efforts, social media clearly can have considerable reach, but traditional editorial media is also needed and the two are not necessarily directly linked. Continued widespread coverage and reporting of pangolin seizures is probably paramount. The unpredictable nature of events (in terms of generating attention, remembering that not all events were specifically designed to raise awareness) raises a number of questions that warrant further study. For example, what is it about a conservation- or trade-related social media post that makes readers want, or feel the need to, share it? In the case that news leads social media, what influences journalists? How (via what media and what networks?) should the public be informed of inter-governmental and governmental actions? How influential (positive or negative) are celebrities (e.g. Duthie et al. 2017)? How important are powerful images (e.g. Wu et al. 2018)? These types of questions have relevance beyond pangolins (see e.g. Pearson et al. 2016; Wu et al. 2018), but high profile issues that have evolved over time (in terms of media and public interest), such as pangolin trade, will likely offer useful case studies.

Online science communication is complex. Propagation of messages, for example, depends on the susceptibility (as well as the influence) of individual members of social networks (Aral and Walker 2012) and comments (and the dynamics of online communication) can have a greater influence on a persons' perception of a post or article than the content itself (Brossard and Scheufele 2013). We found (Suppl. material S1) that most (> 90%) social media posts actually attracted little attention (< 100 'likes', < 10 comments) and that over 80% were unlikely to be 'shared'; it may be that message spread is determined almost entirely by the poster (and the size of their social network) rather than by the actual content of the post (the 'Kardashian effect', see e.g. Hall 2014). Many of these ideas could be explored experimentally in a wildlife protection context and, in the current emerging field of conservation marketing (Wright et al. 2015; Verissimo and McKinley 2016), these types of studies will be increasingly relevant.

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References

Anderegg WRL, Goldsmith GR (2014) Public interest in climate change over the past decade and the effects of the 'climategate' media event. Environmental Research Letters 9(5): 054005. https://doi.org/10.1088/1748-9326/9/5/054005

AFP [Agence France-Presse] (2016) China in biggest-ever pangolin scale seizure: reports. Mail Online, 28 December 2016. http://www.dailymail.co.uk/wires/afp/article-4069908/China-biggest-pangolin-scale-seizure-reports.html

Aral S, Walker D (2012) Identifying Influential and Susceptible Members of Social Networks. Science 337(6092): 337–341. https://doi.org/10.1126/science.1215842

Baillie J, Challender D, Kaspal P, Khatiwada A, Mohapatra R, Nash H (2014) *Manis crassicaudata*. The IUCN Red List of Threatened Species 2014: e.T12761A45221874. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12761A45221874.en

BBC (2017) YouTube channels need 10,000 views for adverts. http://www.bbc.co.uk/news/technology-39527043 [Apr 2017]

Boakye MK, Pietersen DW, Kotzé A, Dalton DL, Jansen R (2015) Knowledge and Uses of African Pangolins as a Source of Traditional Medicine in Ghana. PLoS One 10(1): e0117199. https://doi.org/10.1371/journal.pone.0117199

Bolsen T (2011) The construction of news: Energy crises, advocacy messages, and frames toward conservation. The International Journal of Press/Politics 16(2): 143–162. https://doi.org/10.1177/1940161210392782

Braczkowski A, Holden MH, O'Bryan C, Choi C, Gan X, Beesley N, Gao Y, Allan J, Tyrrell P, Stiles D, Brehony P, Meney R, Brink H, Takashina N, Lin M, Lin H, Rust N, Salmo SG III, Watson JE, Kahumbu P, Maron M, Possingham HP, Biggs D (2018) Reach and messages of the world's largest ivory burn. Conservation Biology 32(4): 765–773. https://doi.org/10.1111/cobi.13097

Brossard D, Scheufele DA (2013) Science, New Media, and the Public. Science 339(6115): 40–41. https://doi.org/10.1126/science.1232329

Brown C (2016) Open letter to Ambassador Xin Shunkang of the People's Republic of China to Namibia. Namibian Chamber of Environment, Windhoek, Namibia. conservationaction.co.za/wp-content/uploads/2017/01/Open-letter-to-Chinese-ambassador-wildlife-crimes-21-December-2016.pdf

Challender DWS, Baillie JEM, Waterman C (2012) Catalysing conservation action and raising the profile of pangolins – IUCN–SSC Pangolin Specialist Group (Pangolin SC). African Journal of Conservation Biology 1: 140–141.

Challender DWS, Hywood L (2012) African pangolins under increasing pressure from poaching and intercontinental trade. Traffic Bulletin 24: 53–55. http://www.traffic.org/bulletin/

Challender DWS, Waterman C, Baillie J (2014a) Scaling up pangolin conservation. IUCN SSC Pangolin Specialist Group Conservation Action Plan. Zoological Society of London, London.

Challender D, Nguyen Van T, Shepherd C, Krishnasamy K, Wang A, Lee B, Panjang E, Fletcher L, Heng S, Seah Han Ming J, Olsson A, Nguyen The Truong A, Nguyen Van Q, Chung Y (2014b) *Manis javanica*. The IUCN Red List of Threatened Species 2014: e.T12763A45222303. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12763A45222303.en

Challender D, Baillie J, Ades G, Kaspal P, Chan B, Khatiwada A, Xu L, Chin S, KC R, Nash H, Hsieh H (2014c) *Manis pentadactyla*. The IUCN Red List of Threatened Species 2014: e.T12764A45222544. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12764A45222544.en

Challender DWS, Harrop SR, MacMillan DC (2015) Understanding markets to conserve trade-threatened species in CITES. Biological Conservation 187: 249–259. https://doi.org/10.1016/j.biocon.2015.04.015

Challender DWS, Baillie JEM, Waterman C, Pietersen D, Nash H, Wicker L, Parker K, Thomson P, Nguyen TV, Hywood L, Shepherd CR (2016) On scaling up pangolin conservation. Traffic Bulletin 28: 19–21.

Challender DWS, MacMillen DC (2014) Poaching is more than an enforcement problem. Conservation Letters 7(5): 484–494. https://doi.org/10.1111/conl.12082

Choudhary AN, Badola S, Fernandes M, Chhabra DB (2018) Factsheet: Pangolins 2018. TRAFFIC India, New Delhi, India. www.traffic.org/site/assets/files/2647/factsheet_scale_of_pangolin_trade_in_india_2009_2017.pdf

Copeland R (2011) Tweet all about it: Social media and the news revolution. Metro: Media & Education Magazine 2011: 96–100.

Di Minin E, Tenkanen H, Toivonen T (2015) Prospects and challenges for social media data in conservation science. Frontiers in Environmental Science 3: 63. https://doi.org/10.3389/fenvs.2015.00063

Do Y, Kim JY, Lineman M, Kim D-K, Joo G-J (2014) Using internet search behaviour to assess public awareness of protected wetlands. Conservation Biology 29(1): 271–279. https://doi.org/10.1111/cobi.12419

Downs A (2018) Up and down with ecology: the issue-attention cycle. National Affairs 37: 38–50. https://www.nationalaffairs.com/public_interest/detail/up-and-down-with-ecologythe-issue-attention-cycle

Duthie E, Veríssimo D, Keane A, Knight AT (2017) The effectiveness of celebrities in conservation marketing. PLoS One 12(7): e0180027. https://doi.org/10.1371/journal.pone.0180027

Gao Y, Clark SG (2014) Elephant ivory trade in China: Trends and drivers. Biological Conservation 180: 23–30. https://doi.org/10.1016/j.biocon.2014.09.020

Hall N (2014) The Kardashian index: A measure of discrepant social media profile for scientists. Genome Biology 15(7): 424. https://doi.org/10.1186/s13059-014-0424-0

Haas TC, Ferreira SM (2016) Combating Rhino Horn Trafficking: The Need to Disrupt Criminal Networks. PLoS One 11(11): e0167040. https://doi.org/10.1371/journal.pone.0167040

Hassanin A, Hugot J-P, Jansen van Vuuren B (2015) Comparison of mitochondrial genome sequences of pangolins (Mammalia, Pholidota). Comptes Rendus Biologies 338(4): 260–265. https://doi.org/10.1016/j.crvi.2015.02.003

Heinrich S, Wittmann TA, Prowse TAA, Ross JV, Delean S, Shepherd CR, Cassey P (2016) Where did all the pangolins go? International CITES trade in pangolin species. Global Ecology and Conservation 8: 241–253. https://doi.org/10.1016/j.gecco.2016.09.007

Heinrich S, Wittman TA, Ross JV, Shepherd CR, Challender DWS, Cassey P (2017) The Global Trafficking of Pangolins: A comprehensive summary of seizures and trafficking routes from 2010–2015. TRAFFIC, Southeast Asia Regional Office, Petaling Jaya, Selangor, Malaysia. https://www.traffic.org/publications/reports/the-global-trafficking-of-pangolins/

Hyndman RJ (2017) forecast: Forecasting functions for time series and linear models. R package version 8.2, http://pkg.robjhyndman.com/forecast/

IFAW (2017) China's largest seizure of pangolin scales, despite global ban, demonstrates need for more action to curtail demand. 1 December 2017. https://www.ifaw.org/africa/news/china%E2%80%99s-largest-seizure-pangolin-scales-despite-global-ban-demonstrates-need-more-action-curt

IUCN (2018) The IUCN Red List of Threatened Species. Version 2018-1. https://www.iucnredlist.org [Downloaded on 03 October 2018]

IUCN PSG [Pangolin Specialist Group] (2016) The conservation status, illegal trade and use of pangolins (*Manis* spp.). CITES SC66 Inf. 23. IUCN SSC Pangolin Specialist Group, 1–8. http://cites.org/sites/default/files/eng/cop/17/InfDocs/E-CoP17-Inf-59.pdf

Kämpt M, Tessenow E, Kenett DY, Kantelhardt JW (2015) The detection of emerging trends using Wikipedia traffic data and context networks. PLoS ONE 10: e0141892. https://doi.org/10.1371/journal.pone.0141892

Kim JY, Do Y, Im R, Kim G, Joo G (2014) Use of large web-based data to identify public interest and trends related to endangered species. Biodiversity and Conservation 23(12): 2961–2984. https://doi.org/10.1007/s10531-014-0757-8

Lagrada L, Schoppe S, Challender D (2014) *Manis culionensis*. The IUCN Red List of Threatened Species 2014: e.T136497A45223365. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T136497A45223365.en

Lindemann-Matthies P, Bose E (2008) How Many Species Are There? Public Understanding and Awareness of Biodiversity in Switzerland. Human Ecology 36(5): 731–742. https://doi.org/10.1007/s10745-008-9194-1

López-de-Lacalle J (2017) tsoutliers: Detection of Outliers in Time Series. R package version 0.6-6. https://cran.r-project.org/web/packages/tsoutliers/index.html

Macdonald DW, Jacobsen KS, Burnham D, Johnson PJ, Loveridge AJ (2016) Cecil: A moment or a movement? Analysis of media coverage of the death of a lion, *Panthera leo.* Animals (Basel) 6(5): 26. https://doi.org/10.3390/ani6050026

Macdonald D (2004) The new encyclopedia of mammals. Oxford University Press, Oxford.

Mahmood T, Irshad N, Hussain R, Akrim F, Hussain I, Anwar M, Rais M, Nadeem MS (2015) Breeding habits of the Indian pangolin (*Manis crassicaudata*) in Potohar Plateau, Pakistan. Mammalia 80(2): 231–234. https://doi.org/10.1515/mammalia-2014-0153

Mahmood T, Irshad N, Hussain R (2014) Habitat Preference and Population Estimates of Indian Pangolin (Manis crassicaudata) in District Chakwal of Potohar Plateau, Pakistan. Russian Journal of Ecology 45(1): 70–75. https://doi.org/10.1134/S1067413614010081

Mccallum ML, Bury GW (2013) Google search patterns suggest declining interest in the environment. Biodiversity and Conservation 22(6–7): 1355–1367. https://doi.org/10.1007/s10531-013-0476-6

Nghiem LTP, Papworth SK, Lim FKS, Carrasco LR (2016) Analysis of the Capacity of Google Trends to Measure Interest in Conservation Topics and the Role of Online News. PLoS One 11(3): e0152802. https://doi.org/10.1371/journal.pone.0152802

Pantel S, Chin SY [Eds] (2009) Proceedings of the Workshop on Trade and Conservation of Pangolins Native to South and Southeast Asia, 30 June-2 July 2008, Singapore Zoo, Singapore. TRAFFIC Southeast Asia, Petaling Jaya, Selangor, Malaysia. http://www.trafficj.org/publication/09_proceedings_pangolin.pdf

Papworth SK, Nghiem TPL, Chimalakonda D, Posa MRC, Wijedasa LS, Bickford D, Carrasco LR (2015) Quantifying the role of online news in linking conservation research to FB and Twitter. Conservation Biology 29(3): 825–833. https://doi.org/10.1111/cobi.12455

Pearson E, Tindle H, Ferguson M, Ryan J, Litchfield C (2016) Can We Tweet, Post, and Share Our Way to a More Sustainable Society? A Review of the Current Contributions and Future Potential of Social media for sustainability. Annual Review of Environment and Resources 41(1): 363–397. https://doi.org/10.1146/annurev-environ-110615-090000

Phillis CC, O'Regan SM, Green SJ, Bruce JE, Anderson SC, Linton JN, Favaro B (2013) Multiple pathways to conservation success. Conservation Letters 6(2): 98–106. https://doi.org/10.1111/j.1755-263X.2012.00294.x

Pietersen DW, McKechnie AE, Jansen R (2014a) Home range, habitat selection and activity patterns of an arid-zone population of Temminck's ground pangolin *Smutsia temminckii*. African Zoology 49(2): 265–276. https://doi.org/10.3377/004.049.0215

Pietersen D, Waterman C, Hywood L, Rankin P, Soewu D (2014b) *Smutsia temminckii*. The IUCN Red List of Threatened Species 2014: e.T12765A45222717. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12765A45222717.en

Pinholster G, Ham B (2013) Science communication requires time, trust and twitter. Science 342: 1464. https://doi.org/10.1126/science.342.6165.1464

Proulx R, Massicote P, Pépino M (2014) Googling Trends in Conservation Biology. Conservation Biology 28(1): 44–51. https://doi.org/10.1111/cobi.12131

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/

Rayson S (2017) The most shared FB content 2017. The top viral posts, articles and videos. http://buzzsumo.com/blog/the-most-shared-facebook-content-posts-videos/

Sampei Y, Aoyagi-Usui M (2009) Mass-media coverage, its influence on public awareness of climate-change issues, and implications for Japan's national campaign to reduce greenhouse gas emissions. Global Environmental Change 19(2): 203–212. https://doi.org/10.1016/j.gloenvcha.2008.10.005

Sodhi NS, Brook BW, Bradshaw CJA (2009) Causes and consequences of species extinctions. In: Levin SA (Ed.) The Princeton Guide to Ecology. Princeton University Press, Princeton, 514–20.

Soriano-Redondo A, Bearhop S, Lock L, Votier SC, Hilton GM (2016) Internet-based monitoring of public perception of conservation. Biological Conservation 206: 304–309. https://doi.org/10.1016/j.biocon.2016.11.031

Statista (2017) Most famous social network sites worldwide as of September 2017, ranked by number of active users (in millions). http://www.statista.com/statistics/272014/global-social-networks-ranked-by-number-of-users/

Styles R (2014) William teams up with Angry Birds in a bid to save the scaly anteater which is in danger of being 'eaten to death' in its native China. http://www.dailymail.co.uk/femail/article-2837620/William-teams-Angry-Birds-bid-save-scaly-anteater-danger-eaten-death-native-China.html [Mail Online 17 November 2014]

Sutter JD (2014) The most trafficked mammal you've never heard of. Change the list, CCN.com edition.cnn.com/interactive/2014/04/opinion/sutter-change-the-list-pangolin-trafficking/

The Guardian (2015) The big picture: illegal wildlife trade. Thousands of frozen pangolins lie in a pit in Indonesia. http://www.theguardian.com/environment/picture/2015/apr/30/thousands-of-frozen-pangolins-lie-in-a-pit-in-indonesia [30 Apr 2015]

The Guardian (2016) Illegal wildlife trade. Indonesia seizes hundreds of frozen pangolins. http://www.theguardian.com/environment/2016/aug/26/indonesia-seizes-hundreds-of-frozen-pangolins [26 Aug 2016]

Tisdell C (2006) Knowledge about a species' conservation status and funding for its preservation: Analysis. Ecological Modelling 198(3–4): 515–519. https://doi.org/10.1016/j.ecolmodel.2006.04.021

UNODC [United Nations Office on Drugs and Crime] (2016) World Wildlife Crime Report. Trafficking in protected species. United Nations, New York. http://www.unodc.org/documents/data-and-analysis/wildlife/World_Wildlife_Crime_Report_2016_final.pdf

Verissimo D, McKinley E (2016) Introducing conservation marketing: Why should the devil have all the best tunes? Oryx 50(01): 14–14. https://doi.org/10.1017/S0030605315001180

Waterman C, Pietersen D, Soewu D, Hywood L, Rankin P (2014a) *Phataginus tetradactyla*. The IUCN Red List of Threatened Species 2014: e.T12766A45222929. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12766A45222929.en

Waterman C, Pietersen D, Soewu D, Hywood L, Rankin P (2014b) *Phataginus tricuspis*. The IUCN Red List of Threatened Species 2014: e.T12767A45223135. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12767A45223135.en

Waterman C, Pietersen D, Hywood L, Rankin P, Soewu D (2014c) *Smutsia gigantea*. The IUCN Red List of Threatened Species 2014: e.T12762A45222061. https://doi.org/10.2305/IUCN.UK.2014-2.RLTS.T12762A45222061.en

Wright AJ, Veríssimo D, Pilfold K, Parsons ECM, Ventre K, Cousins J, Jefferson R, Koldewey H, Llewellyn F, McKinley E (2015) Competitive outreach in the 21st century: Why we need conservation marketing. Ocean and Coastal Management 115: 41–48. https://doi.org/10.1016/j.ocecoaman.2015.06.029

Wu Y, Xie L, Huang S-L, Li P, Yuan Z, Liu W (2018) Using social media to strengthen public awareness of wildlife conservation. Ocean and Coastal Management 153: 76–83. https://doi.org/10.1016/j.ocecoaman.2017.12.010

Yong DL, Fam SD, Lum S (2011) Reel conservation: Can big screen animations save tropical biodiversity. Tropical Conservation Science 4(3): 244–253. https://doi.org/10.1177/194008291100400302

YouGov (2017) Half use social media as a source of news – but many remain sceptical. https://yougov.co.uk/news/2017/07/17/half-use-social-media-source-news-many-remain-scep/

Zeileis A, Leisch F, Hornik K, Kleiber C (2002) strucchange: An R Package for Testing for Structural Change in Linear Regression Models. Journal of Statistical Software 7(2): 1–38. www.jstatsoft.org/v07/i02/. https://doi.org/10.18637/jss.v007.i02

Zhang F, Wu S, Zou C, Wang Q, Li S, Sun R (2016) A note on captive breeding and reproductive parameters of the Chinese pangolin, *Manis pentadactyla* Linnaeus, 1758. ZooKeys 618: 129–144. https://doi.org/10.3897/zookeys.618.8886

Zhou Z-M, Zhou Y, Newman C, Macdonald DW (2014) Scaling up pangolin protection in China. Frontiers in Ecology and the Environment 12(2): 97–98. https://doi.org/10.1890/14.WB.001

Supplementary material 1

Facebook posts

Authors: Lauren A. Harrington, Neil D'Cruze, David W. Macdonald

Data type: social media data

Explanation note: Posters, date and number of comments, likes and shares, for all Facebook posts, 2005–2016, under the search term 'pangolin wildlife trade' (note that the first post on 'pangolin wildlife trade' was posted in 2008).

Link: https://doi.org/10.3897/natureconservation.30.28651.suppl1

Supplementary material 2

News articles. Complete text of all news articles retrieved from Nexis UK under the search term 'pangolin', January 2005 – December 2016

Authors: Lauren A. Harrington, Neil D'Cruze, David W. Macdonald

Data type: social media data

Link: https://doi.org/10.3897/natureconservation.30.28651.suppl2

Supplementary material 3

Collated datasets

Authors: Lauren A. Harrington, Neil D'Cruze, David W. Macdonald

Data type: measurement

Explanation note: Annual Facebook posts and news articles, 2005–2016; monthly Google Trends, 2005–2016 (including daily Wikipedia July 2015 – December 2016); weekly Google Trends, 2015–2016; daily Facebook posts and news articles, 2015–2016.

Link: https://doi.org/10.3897/natureconservation.30.28651.suppl3