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The exposure and contribution of predators and scavengers to humans

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Abstract

Humans are exerting unparalleled pressures on terrestrial vertebrates through overexploitation and development. The patterns of human destruction on the natural environment are especially prevalent within carnivore distributions because they are subject to not only habitat fragmentation and loss, but they are also perceived as a threat to human societies leading to direct conflict. Although the perceived negative impacts of predators and scavengers dominate policy and individual action towards carnivores, there is a growing body of literature pointing to the potential benefits that predators and scavengers provide within shared landscapes. **The overall aim of this thesis** is to address key gaps in our knowledge on the exposure and contribution of predators and scavengers to humans and how this information can be used to enhance conservation initiatives.

Human pressures cause species extinction. These pressures range from over-hunting and urbanization to other forms of habitat loss such as agricultural development. While human pressures and their threatening processes have been increasingly documented across a range of species and ecosystems, we do not know the extent of intense cumulative human pressures within species' geographic ranges globally. In **Chapter 2**, I aim to quantify the exposure of terrestrial vertebrates to intense human pressure, including carnivores. I use the most up-to-date spatial dataset on cumulative human pressure, which takes into account eight pressures known to cause species decline. I find that 85% of the terrestrial vertebrates assessed have more than half of their range exposed to these cumulative pressures, with carnivores having similar exposure. Specifically, carnivores have on average 75% of their ranges overlapping with intense human pressures. This work provides a useful starting point for assessing species at risk of decline, especially for species with limited information on threats.

Carnivore declines impact ecosystem stability that can result in negative impacts on human well-being. In **Chapter 3**, I aim to provide the first review of the benefits provided by predators and scavengers in shared landscapes with humans. I find that predators and scavengers have been shown to reduce zoonotic disease risk, increase agricultural output, and limit species known to cause injury and death to humans. Through the review process, I found considerable gaps in knowledge regarding the potential benefits of predators and

scavengers in shared landscapes, and I discuss future avenues of research, its caveats, and opportunities.

An important knowledge gap identified during the review was the ecological and human well-being implications of losing apex scavengers. Although there is a great deal of information about the ecological repercussions of losing apex predators, we know relatively little about the role of apex scavengers at regulating lower trophic levels and how this can impact ecosystem health and human well-being. In **Chapter 4**, I describe the mesoscavenger release hypothesis, the competitive release of mesoscavengers in the absence of apex scavengers. This work sets the foundation for future studies investigating the consequences of apex scavenger decline on ecosystems and human health and provides a springboard for conservation action on imperiled apex scavengers.

Another key question asked during the review was the potential role of large carnivores at benefitting humans. **Chapters 5-7** focus on addressing this gap. **Chapter 5** provides a case study of one of the most widespread large carnivores, leopards (*Panthera pardus*), at reducing bites and rabies risk from feral dogs in Mumbai, India. I discuss the implications of large carnivores at providing similar services around the world, especially where feral dogs are a considerable human health hazard in peri-urban environments. In **Chapter 6** I quantify the predation value of two large carnivore species on an overabundant invasive species, wild pigs (*Sus scrofa*), known to cause substantial damage to agricultural lands. This chapter offers important information for assessing the benefits of large carnivore conservation on agricultural productivity while accounting for livestock loss. In **Chapter 7** I assess the global ramifications of expanding wild pig populations, utilizing information on predicted wild pig densities and data on soil organic carbon (SOC) storage to quantify their relative impacts on SOC vulnerability. I discuss that wild pig control could be promoted through human-induced management and conservation of native predators. These case studies provide a foundation for future work investigating links between natural predation and human well-being through mitigating health hazards and increasing agricultural productivity in shared landscapes. These studies will also deliver conservation practitioners additional information on the consequences of large carnivore recovery.

This thesis highlights the state of carnivores in shared landscapes with humans and the potential crucial services they provide. I address key gaps in our knowledge on the

exposure and contribution of predators and scavengers to humans and how this information can be used to enhance conservation initiatives.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

Peer-reviewed papers

O’Bryan, C.J., Allan, J., Holden, M., Sanderson, C., Venter, O., Di Marco, M., McDonald-Madden, E., Watson, J.E.M. (2020). Intense human pressure is widespread across terrestrial vertebrate ranges. Global Ecological and Conservation 21:e00882

Braczkowski, A., Ruzo, A., Sanchez, F., Castagnino, R., Brown, C., Guynup, S., Winter, S., Gandy, D. and **O'Bryan, C.J.** (2019). The ayahuasca tourism boom: An undervalued demand driver for jaguar body parts? Conservation Science and Practice, e126: 1-4.

O’Bryan, C.J., Holden, M., Watson, J.E.M. (2019). The mesoscavenger release hypothesis and implications for ecosystem and human well-being. Ecology Letters, 22: 1340-1348.

Allan J.R., Watson J.E.M., Di Marco M., **O’Bryan C.J.**, Possingham H.P., Atkinson, S., Venter, O. (2019). Hotspots of human impact on threatened terrestrial vertebrates. PLoS Biology, 17(3): e3000158.

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Contributions by others to the thesis

Chapters 2-7 are based on manuscripts prepared for publication in collaboration with other authors. **Chapter 2** is published in Global Ecology and Conservation, **Chapter 3** is published in Nature Ecology & Evolution, **Chapter 4** is published in Ecology Letters**,** **Chapter 5** is published in Frontiers in Ecology and the Environment, **Chapter 6** is in preparation for submission for publication, and **Chapter 7** is in preparation for submission to Nature Sustainability. I have retained the text in these chapters consistent with their published or manuscript forms, including the use of the plural first-person pronoun "we"; however, I include minor edits appropriate for thesis flow. In **Chapters 1 and 8**, I use the first-person pronoun "I" to introduce and synthesise **Chapters 2-6**. I refer to my own published work as per the standard citation format (e.g. O'Bryan et al. 2018) and all other work by chapter number (e.g. Chapter 1).

Chapter 1: This chapter was written by the Candidate, with editorial input from Eve McDonald-Madden, James Watson, and Matthew Holden.

Chapter 2: James Watson and the Candidate conceived the idea for the manuscript. James Allan and the Candidate brainstormed analytical tools. The Candidate performed the analysis and wrote the manuscript. All authors contributed to revising and improving the manuscript.

Chapter 3: The Candidate conceived the general concept of the manuscript. The Candidate conducted the literature search, synthesis, and wrote the manuscript. The Candidate, Alex Braczkowski, and Hawthorne Beyer further developed the structure of the paper. All authors contributed to revising and improving the manuscript.

Chapter 4: James Watson and the Candidate conceived the idea for the manuscript. Matthew Holden and the Candidate constructed the models and analyses. The Candidate ran the models with input from Matthew Holden. The Candidate wrote the manuscript with input from all authors.

Chapter 5: Alexander Braczkowski and the Candidate conceived the idea for the manuscript. The Candidate identified methodologies to conduct the analyses, with input from Alexander Braczkowski, Martin Stringer, and Hawthorne Beyer. The Candidate, Alexander Braczkowski, Martin Stringer, and Hawthorne Beyer conducted the analyses. Alexander Braczkowski and the Candidate wrote the manuscript. All authors contributed to revising and improving the manuscript.

Chapter 6: The Candidate conceived the general concept of the manuscript. The Candidate and Matthew Holden brainstormed the analytical approach with input from Eve McDonald-Madden. Further input was provided by Mike Runge. The Candidate conducted the analyses and wrote the manuscript. All authors contributed to revising and improving the manuscript.

Chapter 7: The Candidate conceived the idea for the manuscript with initial input from Nicholas Patton. Jim Hone provided feedback for the model. Matthew Holden and the Candidate streamlined the model. The Candidate conducted the analyses, with help from Violeta Berdejo-Espinola. Eve McDonald-Madden assisted with framing and editing of the manuscript. The Candidate wrote the manuscript with additional input from all authors.

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Research Involving Human or Animal Subjects

No animal or human subjects were involved in this research.

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sub-criterion B2 of the IUCN (IUCN 2016), a 500 km^2 threshold denoted by the vertical dashed line). (B) For species considered ‘least concern’ by the IUCN, 2,478 (17.5%) could be considered for listing as threatened (using sub-criterion B2 of the IUCN (IUCN 2016), a 2,000 km^2 threshold denoted by the vertical dashed line). The first column for both (A) and (B) represents the number of species that have their entire range exposed to intense human pressure.

Figure 3.1. (a), Ranges of some species known to contribute to agricultural production. (b), Ranges of some species that may reduce disease risk. (c), Ranges of some animals known to reduce species that cause human injury and death. (d), Ranges of some species known to remove dangerous organic waste.

Figure 4.1. (A) Apex scavengers are more effective at detecting and consuming carrion than mesoscavengers (large solid arrow), resulting in less carrion available to mesoscavengers (small dotted arrow), and thus resulting in fewer mesoscavengers (small solid and dotted arrows). This may result in indirect effects such as less disease risk, pest prevalence, and invasion potential that can negatively impact humans and ecosystem structure (small dotted arrows). (B) The loss of apex scavengers can result in mesoscavenger release, which is primarily caused by increased carrion availability due to a reduction in competition (large solid arrow). Mesoscavenger release can result in indirect effects such as increased disease risk, pest prevalence, and invasion potential that can negatively impact humans and ecosystem structure (large dotted arrows).

Figure 4.2. Graphical illustration of our dynamic model to test theoretical support of the mesoscavenger release hypothesis. In the model, carcasses enter the system via animal death and leave the system through decay or by scavenging. Both apex scavengers and mesoscavengers consume carcasses with respective efficiencies and handling times. In the dynamic model, mesoscavenger and apex facultative scavenger populations have a logistic growth rate (combination of births and deaths) in the absence of carcasses (apex facultative scavenger logistic growth is denoted by the blue coloring and dashed arrows), whereas apex obligate scavengers have a mortality rate in the absence of carcasses.

Figure 4.3. Equilibrium population densities of carcasses (green dotted line), mesoscavengers (red dashed line) and apex obligate scavengers (black solid line) from the dynamic model (eqn 1) as a function of apex scavenger search efficiency. The curves

for each plot start at mesoscavengers search efficiency. The black open circle for each plot denotes the search efficiency of an apex scavenger, the griffon vulture (*Gyps fulvus*), which is 18 times more efficient than a mesoscavenger assemblage. The red and green open circles on the equilibrium axis denote the equilibrium densities of mesoscavengers and carcasses, respectively, when the apex scavengers are absent. Generally, the more efficient (i.e. functionally dominant) the apex scavenger, the more they suppress mesoscavenger populations and carcass densities. The first column of plots is for the baseline mesoscavenger search efficiency, $e_m = 1$. The second column of plots is for the case where mesoscavenger search efficiency is doubled when apex obligate scavengers are present, potentially aiding mesoscavengers in finding carcasses - as documented in some vulture systems (Kane & Kendall 2017).

Figure 4.4. Equilibrium population density of carcasses (green dotted line), mesoscavengers (red dashed line) and apex facultative scavengers (black solid line) from the dynamic model (eqn 2) as a function of apex scavenger carrying capacity in the absence of carcasses. Values on the x-axis range from 1/100th of the mesoscavenger carrying capacity value to the mesoscavenger carrying capacity value. The top model is parameterized for a known facultative scavenger, the Tasmanian devil (Cunningham et al. 2018). The bottom is parameterized for vulture systems (Morales-Reyes et al. 2017). The key difference between the two parameterisations is different mesoscavenger and apex scavenger search efficiencies, which are displayed in the top right of each plot. An imaginary effect of vultures surviving off of alternative food sources is displayed for comparison with Figure 3. As apex scavengers are able to sustain higher populations in the absence of scavenging (increasing k_a), the more they suppress mesoscavenger populations and carcass densities; however, apex facultative scavengers with higher search efficiencies relative to mesoscavengers tend to have greater impact at lower carrying capacities compared to apex scavengers with smaller search efficiencies relative to mesoscavengers.

Figure 5.1. Leopards in Mumbai’s Sanjay Gandhi National Park (SGNP) regularly leave the confines of the park to hunt stray dogs. (a) An adult female near an apartment block bordering the park’s eastern edge; (b) a female at a Muslim sacred site overlooking the city of Mumbai; (c) a young leopard walking through a village in the Aarey Milk Colony; and (d) a young leopard at a construction site in an informal settlement.

dingo expansion throughout NSW and VIC, for example, there is a 6.1% decrease in damaged agricultural land. This decrease in damaged agricultural land results in nearly $3.1 million USD potential savings across all agricultural lands assessed if dingoes achieve full expansion; whereas if they are fully excluded there will be a potential loss of $7 million USD (Panel B).

Figure 7.1. Invasive wild pigs (*Sus scrofa*) cause soil disturbance via digging for belowground plant parts, fungi, and invertebrates. Wild pigs are the most widespread and abundant human-spread mammal globally. Photo credit: Ben Teton (top left), Jesse Lewis (bottom left), and Derek Risch (right).

Figure 7.2. Global hotspots of vulnerable soil organic carbon (SOC) from invasive wild pig (*Sus scrofa*) soil disturbance across their current (hatched) and potential (colored, unhatched) non-native distribution (Panel A). Panel B shows the vulnerable SOC across their current and potential distributions, with estimates of vulnerable SOC under global wild pig reduction of 50% and targeted reduction of 75% within SOC hotspots (nearly one-fifth the area of current wild pig distribution at 10.8 million km^2 vs. 50.4 million km^2). Panel C shows potential CO_2e emissions from wild pig soil disturbance (assuming 30% loss; range 20-40%(Davidson & Ackerman 1993; Lal 2019)) across their current and potential distributions. As a comparison, the blue horizontal dashed lines represent the global CO_2e emissions from road travel (top line) and airline travel (bottom line) for the year 2010 (Sims et al. 2014), and the average yearly CO_2e emissions from the cultivation of organic soil from agriculture (FAO 2019) (middle line) for the years 1990-2017.

Figure 7.3. Methodological framework for determining the relative amount of SOC vulnerable to emissions by invasive wild pig (*Sus scrofa*) soil disturbance. We determine soil disturbance from wild pigs by employing an equation(Hone 2006) that uses the predicted wild pig density data for each 1 km^2 pixel (A) to estimate the proportion of soil disturbed as a function of wild pig density within that pixel (B). We then multiply that proportion by the amount of SOC stock within that pixel (C) to produce the relative amount of SOC stock vulnerable to wild pig soil disturbance (D).

Table 3.1. Featured case studies of predators and scavengers contributing to human well-being, their potential limitations and suggestions for furthering the case of human benefit.

Table 4.1. Studies showing the impacts of apex scavengers on mesoscavenger abundance, presence at carrion, and species richness.

List of Abbreviations

IUCN – International Union for the Conservation of Nature

NGO – Non-Governmental Organisation

SGNP – Sanjay Gandhi National Park

USD – United States Dollars

FWC – Florida Wildlife Corridor

MCP – Minimum Convex Polygon

FDEP – Florida Department of Environmental Protection

SOC – Soil Organic Carbon

UN – United Nations

SDGs – United Nation’s Sustainable Development Goals

CHAPTER 1 Introduction

The plight of biodiversity in the Anthropocene

Biodiversity includes the amalgamation of biological variability across all scales, from genetics, to plant and animal species, ecosystems, and landscapes (Walker 1992). Since the evolution of *Homo sapiens* approximately 200,000 years before present, we have exploited land and water for food production, shelter, medicine, recreation, and energy (Harari 2011). In the advent of the steam engine and the concomitant rise of the industrial revolution in the 18th Century, the extent and intensity of human exploitation of biodiversity skyrocketed, resulting in an impact on Earth so prodigious that scientists believe we have entered into a new geological epoch coined the "Anthropocene" (Crutzen 2006; Steffen et al. 2011).

The Anthropocene is manifested by artificial, human-made substances, infrastructure, and land-clearing that is steadily altering the biophysical composition of the natural world, tantamount to some of Earth's most striking natural disasters (Crutzen 2006). Such alterations to Earth's biophysical structure include the release of carbon dioxide by the excessive use of fossil fuels by humans, which has been linked to changes in global climatic patterns and processes (Sims et al. 2014). Furthermore, large-scale land-cover change and utilisation is altering nitrogen, phosphorous, and sulphur, and is changing water flow and vapour patterns, which are all fundamental to life on Earth (IPBES 2019).

The human impacts on habitats and ecosystems ranging from changes in land and sea use, to pollution and invasive species, has resulted in detrimental outcomes for native species. The effects on species span from large-scale habitat destruction and fragmentation to small-scale hunting, trapping, and persecution, with combinations of these impacts having a compounding effect on their extinction risk (Maxwell et al. 2016). While species have gone extinct across Earth's history, the rate at which they go extinct has increased by over 100 times the fossil record background rate in modern time (Pimm et al. 2014). In a recent review mandated by the United Nations, nearly 1 million plant and animal species are at risk of extinction, with over three-quarters of all land having been significantly altered by humans (IPBES 2019). Although some recent efforts have attempted to quantify species population-density as a function of land-use change within species' ranges (Santini et al. 2019), we know surprisingly little regarding the extent of cumulative human pressures within species' geographic ranges, how much human pressure has changed within species' ranges over time, and what this means for their extinction risk (Di Marco et al. 2018; Allan et al. 2019). To address this knowledge gap, I quantify the extent of intense human pressure, starting from pastureland, within terrestrial vertebrate species' geographic ranges using the most up-to-date dataset on cumulative human pressures at a global scale (as **Chapter 2** and Appendix 1 of this thesis). This work highlights not only the potential vulnerability of many terrestrial vertebrate species to human pressures, but also the troubling state of the world's carnivores.

The plight of predators and scavengers

Predators and scavengers, those species that consume live prey and/or carrion, respectively, are among some of the most imperilled terrestrial vertebrate guilds on Earth (Ripple et al. 2014; Buechley & Şekercioğlu 2016a). In the advent of the 21st Century, following suit with patterns of decline across much of biodiversity, carnivores have experienced accelerated extinction risk (Di Marco et al. 2014a). Indeed, carnivores have lost large swaths of their historic geographic distributions and are under a great deal of threat from human pressure. For example, the leopard (*Panthera pardus*), a predator, has lost nearly 70% of its historic distribution throughout Africa and Asia, with only 17% of its range currently protected (Jacobson et al. 2016). Likewise, African Lions (*Panthera leo*) occupy only 17% of their historic distribution due to continued habitat loss and indiscriminate killings by humans (Ripple et al. 2014). Even small predators such as the northern quoll (*Dasyurus hallucatus*) in Australia (Braithwaite & Griffiths 1994) and the swift fox (*Vulpes velox*) in North America are under increased threat from habitat loss and have already lost more than 75% and 60% of their historic ranges, respectively (Braithwaite & Griffiths 1994; Laliberte & Ripple 2004).

Contractions in range size are often linked with species declines (Laliberte & Ripple 2004). For example, nearly 80% of obligate scavengers, species that consume only carrion (i.e. New- and Old-World vultures), are decreasing across their remaining distributions (Buechley & Şekercioğlu 2016a). Similar effects are occurring across persisting predator and scavenger guilds, with many facultative species (species that partly consume carrion, but also prey on live animals) being at risk of decline (Laliberte & Ripple 2004). As such, conservation practitioners have recently called for emergency action to recover and abate declines of predators and scavengers (Ogada et al. 2012a; Sebastián-González et al. 2016; Ogada et al. 2016; Santangeli et al. 2019); an example stemming from Bird Life

International, which has declared a state of emergency for the World's vultures, pointing to impending extinctions within the next decade ("Vultures need you | BirdLife Magazine").

The sources of carnivore decline largely depend on the species, their life history, and their sensitivity to anthropogenic threats. Shared landscapes, areas where humans and species coexist, are the primary source of direct threats for carnivores (Ripple et al. 2014; Carter & Linnell 2016). For many native apex predators in shared landscapes, their declines are driven by conflict with human societies, stemming from consuming livestock when natural prey sources are at low densities (Wolf & Ripple 2016) and/or when carnivore ranges are forced in and around human settlements (Prasad & Tiwari 2009; Di Minin et al. 2016). When an apex predator consumes livestock or is perceived as a threat, retaliatory killings often ensue (Inskip & Zimmermann 2009). For example, carnivores in southern Africa have been targeted with poisons for their perceived threats to humans and livestock (Ogada 2014), and in the Grand Chaco of Paraguay, jaguars *(Panthera onca*) are often shot illegally in pursuit of 'eradication' for preying on calves (Altrichter et al. 2006). Furthermore, in Appendix 2 of this thesis I assisted in documenting evidence that a considerable number of jaguar body parts are being sold in tourist markets of Peru, suggestion a potential further demand for their death beyond retaliatory killings (Braczkowski et al. 2019). Similar points of conflict and decline occur for scavengers, particularly when vultures scavenge on newly-born sheep, goats, and cattle due to changing farming practices and reduced carcass availability (Ogada 2014; Buechley & Şekercioğlu 2016a; Santangeli et al. 2016). For instance, farmers in Victoria, Australia, have been reported to poison hundreds of wedge-tailed eagles in retaliation for preying and scavenging on livestock ("14 days' jail for killing 406 wedge-tailed eagles 'inadequate', animal groups say | Australia news | The Guardian").

Although many predators and scavengers are under threat due to conflict with humans that result in retaliatory killings, many are victim to indirect human pressures. Indirect pressures range from habitat loss, urban development, roadways, night lights, and invasive species spread, which can all influence vital rates of predators and scavengers (Di Marco et al. 2015; Wolf & Ripple 2016; Ripple et al. 2017). For example, vultures are thought to be declining due to collisions with power lines and accidental poisoning from veterinary pharmaceuticals (Buechley & Şekercioğlu 2016a; Ogada et al. 2016) in Africa and Asia, and the Florida panther (*Puma concolor coryii*), an endangered species, continues to lose approximately 5-10% of the meta-population per year from vehicle collisions alone (Taylor et al. 2002; Schwab & Zandbergen 2011). Indeed, pumas in the southeastern United States have nearly gone extinct as a result of range contractions and continued pressure from urbanization (Fergus & Chuck 1991). Furthermore, indirect human pressures have impacted carnivores in various ways, such as the spread of invasive species, which can modify ecosystem structure and thus species persistence (Didham et al. 2005; Dorcas et al. 2012; Bankovich et al. 2016; Bellard et al. 2016; Walsh et al. 2016).

While the pressures affecting carnivores have been thoroughly discussed and quantified across a multitude of species, there has yet to be a comprehensive evaluation of the cumulative human pressures, including direct and indirect pressures, within carnivore ranges globally and how intense human pressure within carnivore distributions compares to other terrestrial vertebrate taxa. Therefore, as part of **Chapter 2** (Box 1) I report on the extent of intense human pressures, again starting from pastureland, within the ranges of carnivores.

Implications for ecosystem health and human well-being

The loss of carnivores can have a cascading effect on ecosystems (Ripple et al. 2016b). Apex predators are species that have no natural predator in the system, and thus are functionally dominant compared to mesopredators, species that occupy mid trophic levels (Prugh et al. 2009). For environments losing apex predators, mesopredators can increase in richness and abundance (the mesopredator release hypothesis; Crooks and Soule 1999). Such trophic cascades as a result of apex predator loss have been shown to impact ecosystem stability at local and landscape scales (Ritchie & Johnson 2009b). For example, in areas of Australia where dingoes have declined or have been restricted there has been a stark increase in feral cats and foxes, non-native mesopredators, resulting in sharp declines in native birds and mammals, which are susceptible to increased predation (Johnson et al. 2007; Glen et al. 2007). Similarly, in Yellowstone National Park in the United States, declines of the native grey wolf (*Canis lupus*) metapopulation resulted in a spike in herbivore populations such as the elk (*Cervus elaphus*), which has altered vegetation richness and density, changing the dynamics of stream systems and even wildfire risk (Fortin et al. 2005; Ripple & Beschta 2012a). Not only can the decline of apex predators implicate richness and abundance of herbivores and mesospredators, but behavioural shifts of apex predators can also result in trophic cascades. For example, Suraci and colleagues (2019) recently showed that the presence of human vocalization resulted in considerable movement shifts in mountain lions (*Puma concolor*) of California, which resulted in near disappearance of medium-sized mammals such as bobcats (*Lynx rufus*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), and a sharp increase in small mammals such as deer mice (*Peromyscus maniculatus*) (Suraci et al. 2016, 2019). As such, the loss of apex predators can result in perverse outcomes for many species and ecosystems.

Perverse outcomes on ecosystems because of the loss of carnivores may result in negative impacts on human well-being. For example, we know that the loss of gray wolves in Yellowstone National Park is correlated with changes in landscape and herbivore structure and composition (Fortin et al. 2005; Ripple & Beschta 2012a), but we are unsure of how the loss of wolves impacts the surrounding human population in detail. Perhaps the loss of wolves results in increased risk of vehicle collisions near and within the National Park borders due to increases in large herbivores. Or perhaps the loss of wolves results in increased destruction of agricultural crops due to overabundant herbivores; therefore damaging local economies. Questions regarding the range of benefits provided by predators and scavengers to humans requires interdisciplinary investigation. For example, Gilbert and colleagues (2016) provide one of the first attempts at quantifying the potential direct services of large carnivores to human lives. They postulate that recolonizing North American cougars to the eastern United States could save upwards of 2 billion USD and over 150 human lives from reduced deer-vehicle collisions as a result of cougar predation on deer within 30 years of establishment (Gilbert et al. 2016). Although Gilbert and colleagues are the first to quantify the potential life-saving benefits provided by restoring an apex predator, many studies have investigated the role of carnivores at reducing disease risk and economic expenditure through predation and scavenging. However, there has been no comprehensive review of the current literature on the contribution of predators and scavengers to human health and well-being (see review of these benefits in **Chapter 3** of this thesis).

Although there is a growing body of literature on the benefits of predators to ecosystem health and human well-being, there is minimal knowledge on the mechanism driving how scavengers affect ecosystems and human health. For example, the loss of apex scavengers may result in competitive release of mesoscavengers, which can alter ecosystem structure and implicate human health (e.g. disease risk and waste removal costs; Buechley & Şekercioğlu 2016a; Hill *et al.* 2018). Mesoscavengers are those scavenger species that are functionally less dominant than apex scavengers (i.e. they are less effective at finding and consuming carcasses, and tend to be pest species). Some studies have touched on the concept of trophic cascades in scavenger communities (Sebastián-González et al. 2013; Buechley & Şekercioğlu 2016a; Şekercioğlu et al. 2016; Sebastián-González et al. 2016; Morales-Reyes et al. 2017; Hill et al. 2018), with a suite of empirical studies showing an increase in mesoscavengers in the absence of more dominant apex scavengers. For example, in areas of Spain without vultures, the apex scavenger in the system, mesoscavengers such as red foxes (*Vulpes vulpes*) have increased in abundance (Morales-Reyes et al. 2017), and the interaction dynamics between mesoscavengers has changed (Sebastián-González et al. 2016). Similarly, in Tasmania, Australia, the Tasmanian devil (*Sarcophilus harrisii*) has declined due to facial tumour disease, which has resulted in an associated increase in mesoscavengers such as forest ravens (*Corvus tasmanicus*), feral cats, and quolls (Cunningham et al. 2018). This corollary relationship between apex scavengers and mesoscavengers, although shown empirically in the scientific literature, has not been defined in a structured way as it has with predator systems (i.e. mesopredator release). While the concept of trophic cascades in carnivore communities has been discussed for decades, knowledge gaps remain on the extent and applicability of trophic cascades across systems, including the parallels in qualitative outcomes between mesopredator release and mesoscavenger release. I address this crucial gap in scavenger ecology (in **Chapter 4** of this thesis) by describing the mesoscavenger release hypothesis, summarizing the current empirical evidence to date, and presenting two dynamic models as theoretical evidence of scavenger trophic cascades due to competitive release. I then discuss the potential impacts of mesoscavenger release on human health and well-being.

Through predation and scavenging, carnivores can reduce disease risk to humans by decreasing host and vector densities through local competitive exclusion or directly through feeding on infected hosts. For example, the loss of wolves in the eastern United States has been linked to the rise in Lyme disease outbreaks due to increases in smaller mammals that act has hosts (Brisson et al. 2008; Levi et al. 2012), although the actual mechanism leading to increased Lyme risk is unclear (Mysterud et al. 2016). Likewise, the decrease in vulture populations due to the use of veterinary pharmaceuticals in India has resulted in a spike in rats and feral dogs, which has been linked to an increase in rabies incidents (Markandya et al. 2008). With more than 20,000 people dying from rabies in India per year (Menezes 2008), concern has resulted in active calls for the banning of veterinary medicines known to kill vultures (Ogada et al. 2012a; Galligan et al. 2014; Buechley & Şekercioğlu 2016b). Similar effects of carnivores on disease risk have been observed in owls, with the Tengmolm's owl (*Aegolius funereus*) being shown to selectively prey on voles infected with hantavirus, suggesting an active reduction in hosts for the disease via owl predation (Khalil et al. 2016). However, it is unclear if this predation by owls on diseased voles causes an active reduction in related diseases in nearby human populations. Although there have been case studies investigating the role of predators and scavengers on reducing disease risk, they are currently limited by species and taxonomic groups (highlighted in review **Chapter 3**). Indeed, no studies have investigated the potential services of large carnivores such as big cats, on the active reduction of disease hosts. As such, I touch on the potential services provided by one the world's most densely populated large felines, the leopards of Mumbai, India, in this thesis. Using a simple predator-prey model I investigate if the predation of leopards in Mumbai reduces feral dog populations and then discuss the potential impacts of leopard predation on dog bites associated rabies risk on the local human population (**Chapter 5** of this thesis).

Not only can carnivores potentially reduce disease risk in humans through predation and scavenging behaviour, they can also increase agricultural production by reducing pest densities that consume valuable crops. For example, predatory bats and birds consume crop-eating insects that drastically reduce pest management costs and harvest depredation in crops like coffee, alfalfa, grapes, and corn (Kross et al. 2012; Maas et al. 2015; Maine & Boyles 2015; Kross et al. 2016b). In another example Kross and colleagues (2012) show that by reintroducing New Zealand falcon (*Falco novaeseelandiae*) populations in New Zealand that there would be a parallel benefit to local wineries through the predation of passerine birds that consume grapes (Kross et al. 2012). Similarly, dingoes (*Canis lupus dingo*) have been shown to increase cattle productivity by reducing kangaroo densities in parts of Australia, even when accounting for the occasional depredation of calves by dingoes (Prowse et al. 2015). While the evidence for some carnivores providing services to agricultural areas is growing for some species and taxa (such as for birds and bats), critical gaps remain, such as for species of critical conservation importance and those that are at elevated risk of decline. For instance, large carnivores are rarely associated with providing beneficial services to agricultural communities as they are often associated with negative impacts such as livestock depredations and perceived risk of attacks on humans and pets (Inskip & Zimmermann 2009). As such, I investigate the potential positive benefits of large carnivore conservation on agricultural production (**Chapter 6** of this thesis). Specifically, I explore the possible contribution predators to agricultural lands through their consumption of invasive wild pigs (*Sus scrofa*).

Wild pigs are becoming the most widespread non-native mammal in the world, and this is due to human introductions through accidental release or intentional release for hunting (Barrios-Garcia & Ballari 2012). Invasive pigs are ecosystem engineers that excavate soil for feeding on belowground plant parts, fungi, and invertebrates (Ballari & Barrios-García 2014). Through the creation of bare soil, they can also facilitate plant invasions that can have long-term consequences beyond the presence of invasive pigs (Barrios-Garcia & Ballari 2012). Consequently, agricultural commodities such as crops and pastureland are subject to loss, and the successful conservation of native large carnivores that prey on wild pigs may provide benefits to agricultural systems. I investigate the role of the Florida panther (*Puma concolor coryi*), an endangered mountain lion sub-species (listed by the US Fish and Wildlife Service) that occupies a fragmented matrix of natural, agricultural, and residential lands in south Florida, USA; and the dingo (*Canus lupus dingo*), a widespread but non-listed large wild canid subspecies found across much of the Australian mainland, at reducing wild pig densities and concomitant agricultural damage (both case studies are incorporated in **Chapter 6**).

A reduction in wild pig densities may not only result in savings to agricultural commodities, but it may also result in co-benefits to human health through a reduction in greenhouse gas emissions. This is because the disturbance of soil affects its physical, chemical, and biological properties (Doran 1980; Lal 2004), releasing considerably higher rates of carbon compared to undisturbed soils (Reicosky 1997; Welander 2000; Haddaway et al. 2017). Since wild pigs are presently expanding their non-native range, there is not only a current large potential for soil damage (Mohr et al. 2005; Risch et al. 2010; Macci et al. 2012; Bueno et al. 2013a; Bueno & Jiménez 2014), but a looming unrecognized source of global soil carbon emissions (Mohr et al. 2005; Risch et al. 2010; Macci et al. 2012). Although the consequences of invasive pigs are well documented (Barrios-Garcia & Ballari 2012), we know relatively little about the enormity of predicted pig densities on soil disturbance globally, and what this means for ecosystem and human well-being. In **Chapter 7**, I quantify the potential implications of wild pig soil disturbance globally using a spatially explicit model of predicted pig densities and soil organic carbon storage. I focus the results on vulnerable soil organic carbon to emissions, which is a key biophysical element for healthy soils (Paustian 2000; Xu et al. 2016; Patton et al. 2019) and is an important element to manage climate change (Lal 2004). I quantify the total land surface vulnerable to invasive pigs in the absence of management and in the presence of current large carnivore distributions. The results of this chapter point to the need for enhanced control of wild pigs, which could include the conservation of native predators.

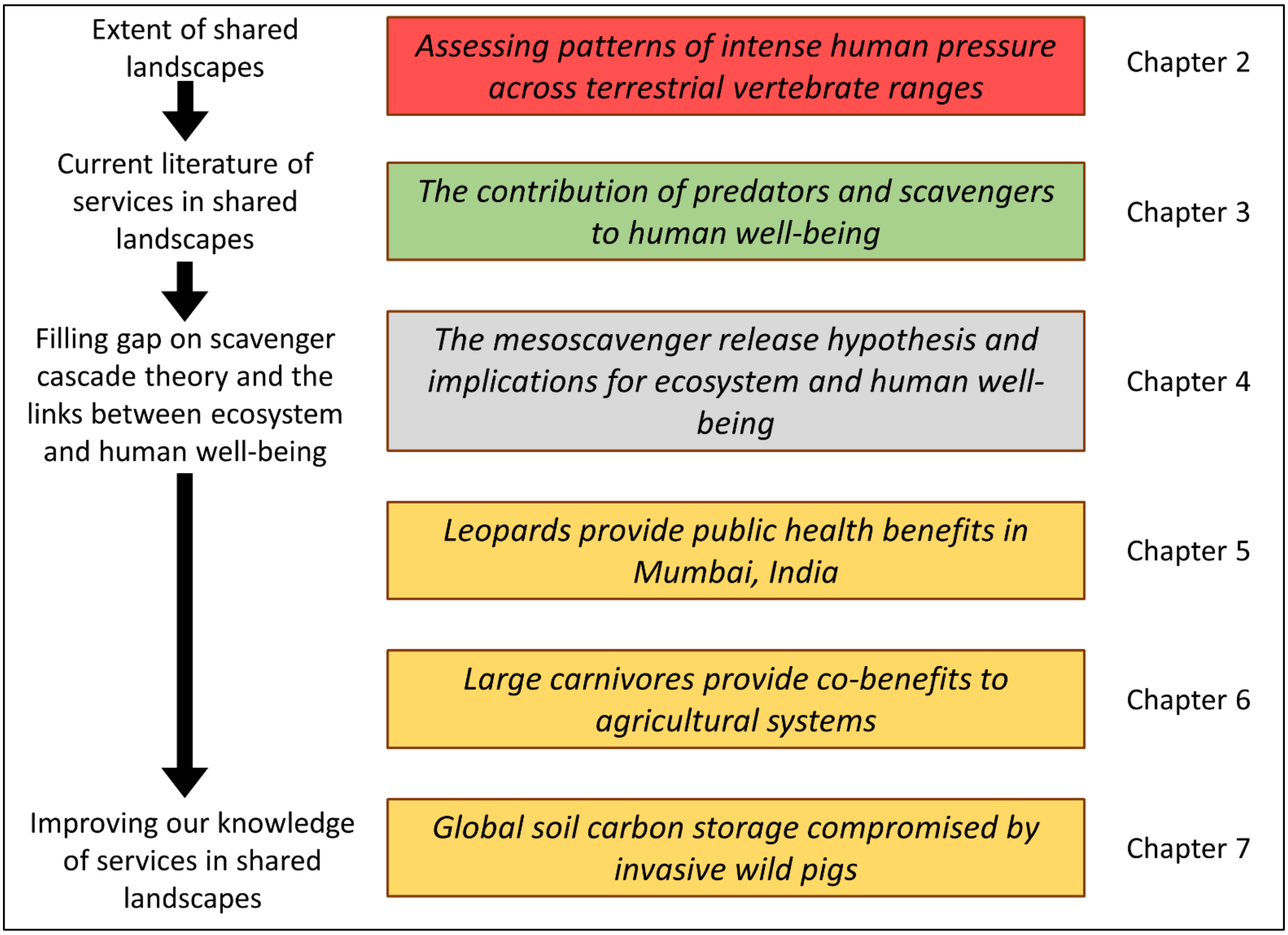
Thesis structure

There is an urgent need for information regarding the exposure and contribution of species to shared landscapes, areas where humans and species coexist, to support current conservation efforts. One method for determining the exposure of species to human-dominated landscapes is to understand the spatial patterns of intense human pressure within their geographic ranges. In **Chapter 2**, I present a global analysis of cumulative intense human pressures within terrestrial vertebrate ranges. I use the most up-to-date temporally inter-comparable, and validated spatial dataset of terrestrial human pressures for the years 1993 and 2009 (Venter et al. 2016a; McGowan 2016). These maps are comprised of a cumulative spatial index of eight key human pressures on natural ecosystems ranging from built environments and population density to agricultural lands and navigable waterways. These pressures were quantified through both remotely sensed and survey data, which overcomes drawbacks of stand-alone remotely sensed data, incorporating insidious threats such as overexploitation that are difficult to approximate from satellite imagery alone (Peres et al. 2006). **Chapter 2** underpins the analysis for intense human pressures within carnivore distributions, which I present in Box 1 of **Chapter 2**, and lays the stage for the rest of the thesis, discussing the dynamics of predators and scavengers in these human-dominated landscapes. This information is also important for informing potential threats within carnivore ranges for species lacking information on pressures known to cause their decline. For example, the human footprint has been used to assess species-specific threats within species' ranges, but this is limited to species that have information on pressures known to cause their extinction (e.g. Allan *et al.* 2019).

While there is some knowledge of the ecological consequences of losing carnivores, there is great opportunity for developing our understanding on their effects to ecosystems and human well-being. In **Chapter 3**, I provide a review of benefits of predators and scavengers in human-dominated landscapes. Through the review process, I found that predators and scavengers can benefit human health and well-being through the reduction of species that spread zoonotic diseases, through the reduction in pests that consume agricultural commodities, and through the reduction in species known to cause human death. This review is the first to summarize the contribution of predators and scavengers to human health and well-being. However, through conducting the review, I found considerable gaps in knowledge for species of significant conservation concern. For example, we know little about the trophic cascades that occur in scavenger systems and how this might affect human well-being. In **Chapter 4**, I provide the first description and justification for the mesoscavenger release hypothesis. This hypothesis states that with the loss of apex scavengers there is an associated increase in mesoscavenger and carrion biomass, which can affect human well-being through an increase in pest species and waste removal costs. Apex scavengers are functionally dominant at finding and consuming carrion relative to mesoscavengers; therefore, mesoscavenger release occurs through the reduction in exploitative competition and thus competitive release. The results of mesoscavenger release are qualitatively similar to the mesopredator release hypothesis, which has received substantial empirical and theoretical support. Another gap identified in the review is that of the contribution of large carnivores to human health and well-being (but see Gilbert *et al.* 2016) and how the consequences of restoring and conserving large predators may provide unique and previously unrecognized benefits to human societies. As such, I explore three case studies where large carnivore conservation may provide benefits in the form of lowering disease risk, increasing agricultural output, and decreasing greenhouse gas emissions. In **Chapter 5**, I study the effect of leopards in Mumbai, India on feral dog populations and what this means for bite risk and rabies potential in local communities. Specifically, I use local newspaper reports on dog bites, dog density studies, and leopard diet analyses to quantify the potential value of leopards at reducing dog densities around the periphery of the Sanjay Gandhi National Park in the centre of Mumbai. In **Chapter 6**, I investigate the role of the Florida panther in the United States, a critically endangered subspecies of mountain lion, and the dingo in Australia, at affecting feral pig populations in a matrix of intact and agricultural land. I show that by promoting their conservation in Florida and Australia that panthers and dingoes may provide unique benefits to agricultural systems by reducing the presence and abundance of invasive wild pigs, and in turn decreasing damage caused by wild pigs to valuable crops and pastureland. In **Chapter 7**, I show that unmitigated increases in wild pigs can cause considerable damage to soil globally, resulting in emissions of soil organic carbon that are critical for abating climate change. I discuss the potential benefits of wild pig control and the value of restoring native apex predators at alleviating wild pig damage. The results of these case studies will provide information for decision makers and conservation practitioners on the potential benefits that large carnivores can provide in human-dominated landscapes.

The overall aim of this thesis is to address key gaps in our knowledge on the exposure and contribution of predators and scavengers to humans and how this information can be used to enhance conservation initiatives. The overarching structure of this thesis and the links between chapters is presented in Figure 1.

Figure 1.1 Thesis structure



CHAPTER 2 Authorship Statement

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James Watson and the Candidate conceived the idea for the manuscript. The Candidate developed and refined the analytical approach for the analysis, with input from James Allan during troubleshooting. The Candidate performed the analysis and wrote the manuscript, providing a completed draft to James Watson for initial feedback. All authors contributed to revising and improving the manuscript up to submission.

CHAPTER 2 Assessing patterns of intense human pressure across terrestrial vertebrate ranges

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Abstract

The United Nation's Strategic Plan for Biodiversity 2011-2020 calls for reducing species extinctions, as it is increasingly clear that human activities threaten to drive thousands of species to decline. Yet many species lack information on their exposure to threats. Using the most comprehensive global dataset on cumulative human pressures, we assess the extent of intense human pressures, pressures starting at pastureland (a Human Footprint index score of ≥ 3) across 20,529 terrestrial vertebrate species ranges. We show that 85% (17,517) of the terrestrial vertebrate species assessed have > half of their range exposed to intense human pressure, with 16% (3,328) of the species assessed being entirely exposed to this degree of pressure. Threatened terrestrial vertebrates and species with small ranges are disproportionately exposed to intense human pressure. Our analysis suggests that there are at least 2,478 species considered 'least concern' that have considerable portions of their range overlapping with intense human pressures, which may indicate their risk of decline. These results indicate it is possible to incorporate cumulative human pressure data across species ranges, which may be a useful first step for assessing species extinction risk, especially for species with little or no existing data on their threat exposure.

Introduction

A fundamental goal of the United Nation’s Strategic Plan for Biodiversity 2011-2020 is to reduce species extinctions, as there is growing evidence that direct anthropogenic land use change such as pastureland, agriculture, and urbanization, and human activities like overharvesting threaten to drive thousands of species to decline (Newbold et al. 2015a; Tilman et al. 2017; Di Marco et al. 2018). Previous efforts to study species habitat availability have primarily focused on land cover (Andrén & Andren 1994; Betts et al. 2007; Maron et al. 2012); however, this does not capture ancillary threats that can impact species even when their habitat appears to be free of human pressure (Barlow et al. 2016; Betts et al. 2017). By taking advantage of recently available cumulative human pressure data, we capture cumulative pressures (Di Marco et al. 2018; Allan et al. 2019), not only providing a more robust understanding of how much pressure-free geographic range is available for species, but also delivering necessary results that can inform the urgency and specificity of conservation actions needed to avert species’ declines.

We use the updated human footprint (Venter et al. 2016a), a cumulative human pressure assessment that includes data on roads, built environments, human population density, railways, navigable waterways, pasturelands, and croplands, at a 1-km^2 resolution globally (Venter et al. 2016a, 2016b). The human footprint is the most comprehensive global human pressure dataset available (McGowan 2016), and given the nature of the input data, captures the greatest number of drivers of species declines (Maxwell et al. 2016), and has been shown to explain extinction risk in globally threatened vertebrates (Safi & Pettorelli 2010; Yackulic et al. 2011; Beans et al. 2012; Seiferling et al. 2014; Hand et al. 2014; Di Marco et al. 2018). We identify intense human pressure as areas on the human footprint index that are composed of pressures at or above a value of three, which is the equivalent of pastureland (Venter et al. 2016a), a land use where habitat is considered functionally unavailable for many terrestrial vertebrate species that have been assessed (Fleischner 1994; Newbold et al. 2015a). Recently, Di Marco and colleagues found that a value greater than or equal to three on the index was correlated with extinction risk in terrestrial mammals globally, and similar values held true across regions, even when compared to other factors such as species’ traits, environmental conditions, and individual pressure layers (Di Marco et al. 2018).

We first quantify the proportion of species ranges facing intense human pressure across 10,745 birds (Birdlife International and Handbook of the Birds of the World 2017), 4,592 mammals, 5,000 amphibians, and 192 reptiles, with 4,610 of the total being threatened (IUCN 2016). We focus on these taxa, as they are the only major terrestrial taxonomic groups that have been comprehensively assessed for their distribution and extinction risk (with the exception of reptiles, see Methods). We then investigate the extent of intense human pressure across taxonomic classes, species level of endangerment, and species range size. Lastly, we quantify changes in the extent of intense human pressure within species ranges between 1993 and 2009.

Methods

Species distribution data

We focused our analysis on terrestrial vertebrate classes (mammals, birds, reptiles, and amphibians). Spatial data on mammal, amphibian, and reptile distributions were obtained from the IUCN Red List of Threatened Species (IUCN 2016), and bird distributions from BirdLife International (Birdlife International and Handbook of the Birds of the World 2017). We excluded species that were considered data deficient ("DD") on the Red List, extinct, thought to be extinct, or presence uncertain. We only included the remaining extant species whose distributions overlapped with the extent of the terrestrial Human Footprint datasets (Venter et al. 2016b). We analyzed 20,529 terrestrial vertebrates, including 4,592 mammal species, 10,745 bird species, 5,000 amphibian species, and 192 reptile species. We note that for reptiles, only chameleons, crocodilians, and sea snakes had been assessed comprehensively by the IUCN at the time of our analysis; as such, we only included reptiles when reporting on all species or on all threatened species, and do not report on reptiles for class-specific metrics.

Spatial data on human pressure

Recent advances in remote sensing coupled with bottom-up survey data have facilitated the development of a spatially explicit, high-resolution global dataset on human pressures across time steps (Allan et al. 2017a), which enables the quantification of the extent of human pressures on individual species (Di Marco & Santini 2015; Allan et al. 2019). We obtained data on the distribution of terrestrial human pressure for 1993 and 2009 from the global Human Footprint maps (Venter et al. 2016b, 2016a), the most up-to-date, comprehensive, and validated global human pressure data available (McGowan 2016). These maps are comprised of a cumulative spatial index of eight key human pressures on natural ecosystems at a 1-km^2 resolution. These pressures were quantified through both remotely sensed and survey data, which overcomes drawbacks of stand-alone remotely sensed data, incorporating insidious threats such as overexploitation that are difficult to approximate from satellite imagery alone (Peres et al. 2006). The eight human pressures in the human footprint included: 1) built environments, 2) population density, 3) electric infrastructure, 4) crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. These eight individual pressures are scaled between 0 and 10 based on their estimated environmental impact and summed in 1km grid cells. Some pressures can co-occur whilst others are mutually exclusive; resulting in a combined global scale between zero and fifty where zero is wilderness and fifty is extreme urban conglomerates.

Analyzing human pressure on species distributions

We intersected individual species ranges with both the 1993 and 2009 Human Footprint (Venter *et al.* 2016) maps under a World Mollweide projection in a geographic information system using the tabulate area tool in model builder of ArcGIS (ESRI), and outputs were managed in R statistical software. This intersection resulted in a dataset with each species having the area of their range composed of each Human Footprint value (index values of 0-50 as mentioned above). We then calculated the proportion of the species' range that is composed of each of the Human Footprint index values. We adopted a threshold of the Human Footprint cumulative index where landscapes shift from relatively unmodified, low Human Footprint landscapes to modified, high Human Footprint landscapes. This threshold (a summed Human Footprint value at or above three on the index) was used to assess whether a species' distribution overlapped with areas of intense human pressure. This threshold has been used in previous studies as a standard for evaluating human pressure in ecosystems (Watson et al. 2016; Jones et al. 2018). Additionally, Di Marco and colleagues (Di Marco et al. 2018) recently found that a human footprint index value of three and above was a strong indicator of extinction risk in mammals globally, even when compared to other factors such as species' traits, environmental conditions, and individual pressure layers, and similar values held true across regions. We also assessed the proportion of a species' range containing Human Footprint index values of seven and above, which are considered to be areas that have intense industrial agriculture and urbanization (Venter et al. 2016a).

Results

Of the 20,529 terrestrial vertebrate species assessed, we found that 85.3% (17,517) have >50% of their range exposed to intense human pressures and that 16.2% (3,328) have no portion of their range free from intense human pressure (Appendix 3 Table 1). We also found that all taxonomic classes are experiencing intense human pressure across the majority of their range, with 39.6% (1,980) of amphibians having no portion of their range free from intense human pressure (Figure 2.1A), compared to mammals (15.2% [698]; Figure 2.1B) and birds (11.6% [1,250]; Figure 2.1C). For carnivores, see Box 1.

Threatened species (those classified as vulnerable, endangered, and critically endangered on the IUCN Red List) are disproportionately exposed to intense human pressure compared to non-threatened species, even when comparing across range sizes (Figure 2.2). Threatened species have, on average, less than 12 percent of their range free from intense human pressure (Appendix 3 Table 2), with only 0.87% (40) of threatened species having their entire range free from intense human pressure (Appendix 3 Table 1). Of the 4,610 threatened species assessed, 90.8% (4,185) have more than half of their range under intense human pressures, with 53.3% (2,457) having no portion of their range free from intense human pressure (Figure 2.1D). We found that 70.9% (1,453) of threatened amphibians have no portion of their range free from intense human pressure (Appendix 3 Table 1), with 39.4% (441) of threatened mammals and 37.5% (510) of threatened birds having no portion of their range free from intense human pressure (Appendix 3 Table 1). For threatened carnivores, see Box 1.

When adjusting the lower bounds of what is considered intense human pressure for many vertebrates (i.e. pastureland, an index value of 3) to start at industrial-level agriculture (pressures at or above a value of seven; Venter et al. 2016a) 40.5% (8,308) of all species assessed and 50.7% (3,230) of threatened species have more than half of their range under this level of intense human pressure (Appendix 3 Table 4).

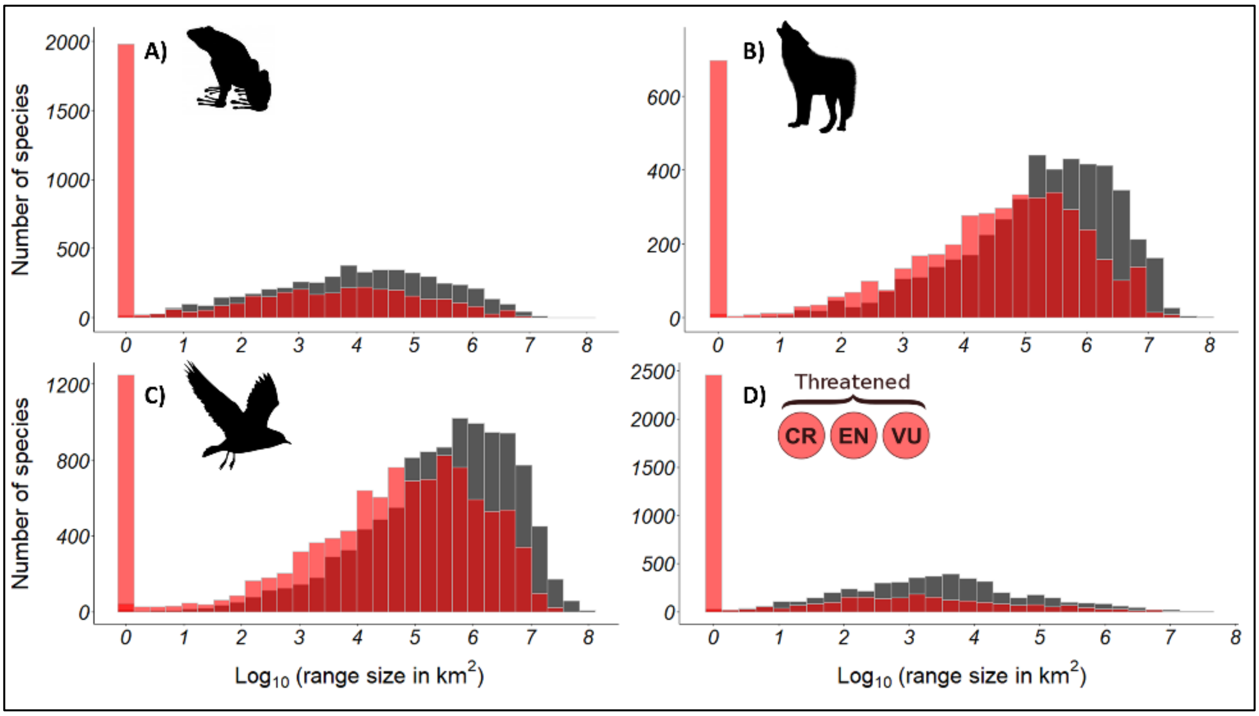
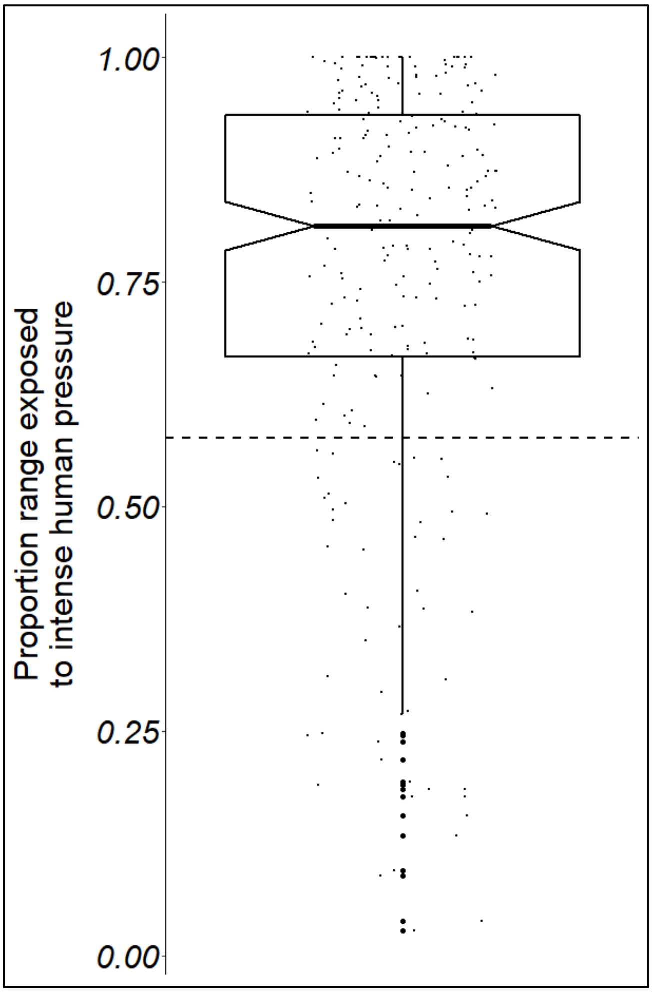


Figure 2.1. Hypothetical range change after removing areas with intense human pressure (human footprint value of ≥ 3) for all species assessed. Range size frequencies for the entire known geographic range of species (dark grey bars) and range size frequencies of the same species after excluding areas of intense human pressure (red bars) for (A) amphibians, (B) mammals, (C) birds, and (D) threatened species (including vulnerable, endangered, and critically endangered species). The first column for each plot represents the number of species that have their entire range exposed to intense human pressure.

Box 1 The exposure of carnivores to intense human pressures. We assess the proportion of carnivores exposed to intense human pressure by analysing a subset of species that are within the order Carnivora (251 species). We find that 85.3% (214) of the species assessed have >50% of their range within areas containing intense human pressures, which mirrors the results of all terrestrial vertebrates assessed. For threatened carnivores, we find that 84.6% (55 out of 65 species) have more than half of their range in these pressures, which is slightly lower than the remaining terrestrial vertebrates assessed; however, amphibians likely drive this discrepancy. Overall, carnivores have an average of 75.3% overlap (median of 81.2%; Box Figure) and threatened carnivores 77.4% (89.5% median) with intense human pressures.



Box Figure: Proportion of carnivore ranges exposed to intense human pressure. The boxplot denotes the first quartile, median, and third quartile of the data, with each dot representing an individual species' proportion of range exposed. The dashed horizontal line represents the proportion of global terrestrial surface exposed to intense human pressure (50.4%).

We found that species with small ranges have more of their distribution overlapping with intense human pressure compared to species with large ranges (Figure 2.2). This pattern is expected by random chance, since species with small ranges are the most likely ones to be fully covered by spatially aggregated regions of human pressure. However, we found that species with a median range size less than 100,000 km^2 have their entire distribution under intense human pressure (Figure 2.2). That is, 100% of range with intense human pressure for a species with range size less than or equal to the area of South Korea (larger than the area of 45% of countries). Therefore, intense human pressure is widespread even for species with moderately large range sizes.

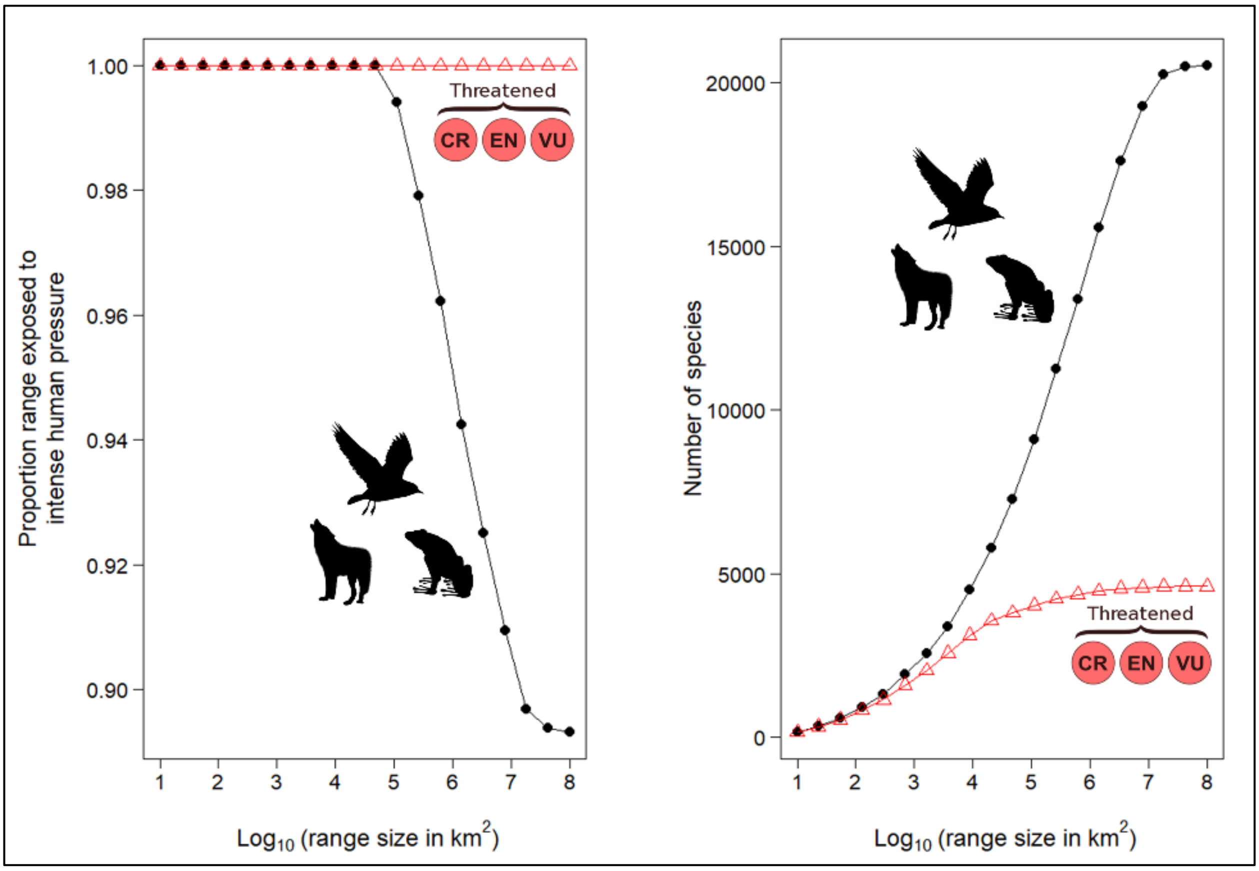


Figure 2.2. Relationship between range size and proportion overlapping with intense human pressure for both threatened (red triangles) and non-threatened (black dots) terrestrial vertebrate species assessed. The plot on the left shows the median proportion of a species' range under intense human pressure for all species assessed with the specified range size on the x-axis or smaller. For example, this shows that species with range sizes around or below 100,000 km^2 ($10^{5.0}$ km^2) have a median 100% of their range exposed to intense human pressure, and that threatened species have a median 100% exposed regardless of range size. The plot on the right shows the total number of species

in the dataset with the specified range size or smaller for both threatened and non-threatened species.

Over the last two decades, intense human pressure has increased in extent by 4.5% across Earth's terrestrial surface (Venter et al. 2016a) (Appendix 3 Table 3). For the terrestrial vertebrates assessed however, we found that intense human pressure has increased within their ranges by 6.1% on average (Appendix 3 Table 2). This may indicate that the global increase in human pressure is occurring in species-rich areas (likely containing species with already restricted ranges, as shown above), with the number of species entirely exposed to intense human pressure in 2009 being 44.1% higher than it was in 1993, and the number of species entirely free from intense human pressure 37.6% lower (Appendix 3 Table 1). Additionally, threatened species have experienced a 3.9% average increase in the proportion of their range exposed to intense human pressure over the two decade study period (Appendix 3 Table 2).

Discussion

The extent and condition of species ranges are some of the most important components of species' conservation status (Boakes et al. 2018), and are key elements for determining extinction risk (IUCN 2016). Our results suggest that 85% of all terrestrial vertebrates assessed have more than half of their range exposed to intense human pressure (Appendix 3 Table 1), and that this pressure has increased since 1993. We note that although the presence of intense human pressure is detrimental to almost all species (Di Marco et al. 2018), some species can still persist in these areas (for example in agricultural and managed forestry lands Phalan et al. 2011; Homyack et al. 2014; O'Bryan et al. 2016) and urban areas (Braczkowski et al. 2018; O'Bryan et al. 2018). As a further exploration of the intensity of human pressure on species, we adjusted the lower bounds of what is considered intense human pressure for many vertebrates (i.e. pastureland) to start at industrial-level agriculture (pressures at or above a value of seven; Venter et al. 2016a). We found that, even when shifting the lower limit to a more intense human pressure score, 40.5% (8,308) of all species assessed and 50.7% (3,230) of threatened species have more than half of their range under intense human pressure (Appendix 3 Table 4). This means that species able to persist in areas with some level of intense human pressure, such as pastureland, but not in areas where land is almost completely cleared for industrial agriculture and urbanization, may be at risk of decline. We recommend future research delve into the 'winners' and 'losers' at different levels of human footprint, perhaps by assessing whether habitat specialists are impacted more than habitat generalists by intense human pressure.

An important caveat to our work is that the human footprint data do not directly incorporate all pressures affecting biodiversity, such as anthropogenic climate change (e.g. Pecl et al. 2017), pollution (e.g. Oita et al. 2016), infectious diseases (Stuart et al. 2004; O'Bryan et al. 2012; Bower et al. 2017), and invasive species (Dorcas et al. 2012; Walsh et al. 2016; Doherty et al. 2016), making it a conservative estimate of pressure (Jones et al. 2018). However, some pressures such as invasive species are closely associated with pressures represented in the human footprint dataset (Spear et al. 2013). As such, while our results are robust across well-established pressures that are driving the global extinction crisis (Maxwell et al. 2016), additional refinement will be necessary to insure all ancillary pressures are included, as this is particularly important for taxonomic groups that are known to be sensitive to pressures that are not easily quantified. Furthermore, although human pressures may occur within species' ranges, these pressures may not evenly affect species, partially because individuals are not always evenly distributed throughout their geographic ranges and intense human pressure may not affect the majority of individuals and species in an assemblage. Future work should incorporate species-specific responses to threats (e.g. Allan et al. 2019) as well as habitat and population-density models for higher resolution analyses (e.g. Santini et al. 2019).

Range size and range reduction are two of the main values used to assess species extinction risk in the IUCN Red List, representing restricted population size and population decline over time (Visconti et al. 2016; Tracewski et al. 2016; IUCN Standards and Petitions Subcommittee 2017; Santini et al. 2019). Overestimating range size fundamentally undermines the assessment of species extinction risk and efficacy of conservation planning and action (Jetz et al. 2008). Our results, by considering cumulative human pressure within species ranges, show that some species might be facing a higher risk of extinction than previously assessed, assuming areas exposed to intense human pressure are functionally unavailable. For example, 832 (42.9%) vulnerable species would have a potential Area of Occupancy (AOO) smaller than the 500 km^2 threshold that classifies endangered species under Red List sub-criterion B2 (Mace et al. 2008), if AOO is inferred from the extent of range free from intense pressure (Figure 2.3A). Thus, if these 832 species already show evidence of population decline, fragmentation, or extreme fluctuations (at least two of these attributes must verify in order for criterion B to be applicable), then they could be deemed as endangered (Mace et al. 2008). The same logic might apply to species that are not currently acknowledged as threatened on the IUCN Red List (Bland et al. 2015a). For example, 2,478 (17.5%) least concern species could be considered threatened under the range-loss criteria B2 of the IUCN (2,000 km^2) if incorporating intense human pressure (Figure 2.3B). This has implications for how we view species' risk, and also for efforts aimed at prioritizing funding and conservation action for currently acknowledged threatened species (Di Marco et al. 2018).

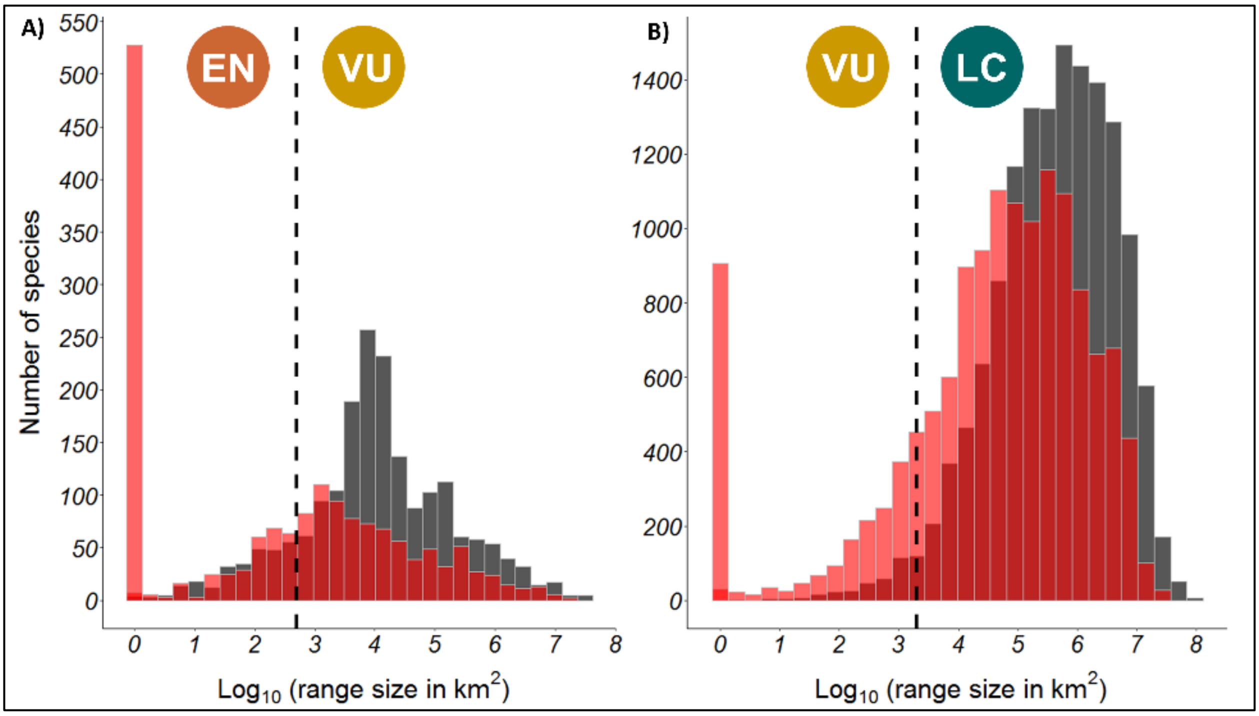


Figure 2.3. Hypothetical range change after removing areas with intense human pressure for species listed as 'vulnerable' and 'least concern'. (A) Range size frequency for species considered 'vulnerable' by the IUCN (IUCN 2016) (dark grey bars) against the range size frequency for the same species after removing areas with intense human pressure (red bars). We find that 832 (42.9%) vulnerable species could be considered for being listed as endangered if areas with intense human pressure were removed from the range (using sub-criterion B2 of the IUCN (IUCN 2016), a 500 km^2 threshold denoted by the vertical dashed line). (B) For species considered 'least concern' by the IUCN, 2,478 (17.5%) could be considered for listing as threatened (using sub-criterion B2 of the IUCN (IUCN 2016), a 2,000 km^2 threshold denoted by the vertical dashed line). The first column for both (A) and (B) represents the number of species that have their entire range exposed to intense human pressure.

We show that considering cumulative human pressures has the potential to improve how we assess threats within species' ranges, with subsequent benefits for many other areas of conservation. For example, our approach could be used as an initial examination of threats within known species geographic ranges, especially when resources are limited. This information could also inform necessary species and ecosystem-specific habitat retention and restoration targets (Maron et al. 2018). It can highlight areas where species are substantially impacted by intense human pressure (thus prioritizing habitat restoration and threat abatement in order to reopen viable space for species persistence Allan et al. 2017, 2019a; Newmark et al. 2017) and areas where species still have large swaths of their range free from intense human pressure (thus prioritizing the protection of existing quality habitat, but could also be under threat from future human actions; Noss et al. 2012; Venter et al. 2014; Watson et al. 2014). This information can aid current assessments of progress against the 2020 Aichi Targets (especially Target 12, which deals with preventing extinctions and Target 5, which deals with preventing the loss of natural habitats), and for conversations around post-2020 targets.

As intense human activities spread, habitat becomes lost to many species, and their populations will likely decline (Di Marco et al. 2014b; Di Marco & Santini 2015). Our work suggests that intense human pressure is widespread within the ranges of the terrestrial vertebrates assessed, and we are potentially overestimating how much range they have free from intense human activities. For a clearer picture on the status of species, we advocate for utilizing cumulative human pressure data, alongside other measures such as species habitat preferences and abundance (e.g. Santini et al. 2019), to identify areas within their ranges that are at a higher risk from anthropogenic threats, and where conservation action is imminently needed to ensure they have enough range to persist. Given the growing human influence on the planet, time and space are running out for biodiversity, and we need to prioritize actions against these intense human pressures.

CHAPTER 3 Authorship Statement

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The Candidate conceived the general concept of the manuscript. The Candidate conducted the literature search, synthesis, and wrote the manuscript. The Candidate, Alex Braczkowski, and Hawthorne Beyer further developed the structure of the paper. All authors contributed to revising and improving the manuscript.

CHAPTER 3 The contribution of predators and scavengers to human well-being

Christopher J. O'Bryan, Alexander R. Braczkowski, Hawthorne L. Beyer, Neil H. Carter, James E. M. Watson, Eve McDonald-Madden

Abstract

Predators and scavengers are frequently persecuted for their negative effects on property, livestock, and human life. Research has shown that these species play important regulatory roles in intact ecosystems including regulating herbivore and mesopredator populations that in turn affect floral, soil, and hydrological systems. Yet predators and scavengers receive surprisingly little recognition for their benefits to humans in the landscapes they share. We review these benefits, highlighting the most recent studies that have documented their positive effects across a range of environments. Indeed, the benefits of predators and scavengers can be far reaching, affecting human health and well-being through disease mitigation, agricultural production, and waste-disposal services. As many predators and scavengers are in a state of rapid decline, we argue that researchers must work in concert with the media, managers, and policy makers to highlight benefits of these species and the need to ensure their long-term conservation. Furthermore, instead of only assessing the costs of predators and scavengers in economic terms, it is critical to recognize their beneficial contributions to human health and well-being. Given the ever-expanding human footprint, it is essential that we construct conservation solutions that allow a wide variety of species to persist in shared landscapes. Identifying, evaluating, and communicating the benefits provided by species that are often considered problem animals is an important step for establishing tolerance in these shared spaces.

Introduction

Coadaptation, the ability of humans and predators and scavengers to modify their behavior based on benefit trade-offs, is recognized as key for their coexistence in the 21st century (Carter & Linnell 2016; Chapron & López-Bao 2016). However, coadaptation relies on human tolerance and the recognition of the wide range of benefits that predators and scavengers provide humanity (Carter et al. 2012; Treves & Bruskotter 2014). It is well established in the ecological literature that predators play regulatory roles in intact ecosystems as they exert top-down pressures on prey communities, thereby reducing herbivory of plant species important to humans (Ripple & Beschta 2012a) and scavengers consume large amounts of carcasses and organic waste (Dupont et al. 2012; Ćirović et al. 2016). It is accepted that the disappearance of predators and scavengers from ecosystems can cause a suite of deleterious effects including the loss of plant species diversity, biomass, and productivity that in turn affect disease dynamics, carbon sequestration, and wildfire risk (Ripple et al. 2014). As a result, predators and scavengers are considered flagship and keystone species (Macdonald et al. 2015) and are sometimes treated as surrogates for the health of entire ecosystems (Thornton et al. 2016).

Despite their ecological value, predators and scavengers often have a poor public reputation because of their real and perceived negative impacts on humans (Ogada et al. 2012a; Bhatia et al. 2013; Penteriani et al. 2016). These negative impacts include livestock depredations (Suryawanshi et al. 2013), killing of pets (Vickers et al. 2015), attacks on humans (Penteriani et al. 2016), and harboring of diseases and parasites (Han et al. 2016). The human culture of fear associated with predators hinders many local and regional species recovery efforts (Barua et al. 2013). Populations of many predator and scavenger species are already declining (Ripple et al. 2014; Jacobson et al. 2016) and are projected to continue to dramatically decline over the next 25 years in response to increasing human populations, political uncertainty, and climate change (Ripple et al. 2014; Chapron et al. 2014; Di Minin et al. 2016).

An understanding of the benefits of predators and scavengers on human well-being is important in strengthening conservation efforts in shared landscapes (Soulsbury & White 2015; Blackburn et al. 2016; Chapron & López-Bao 2016). For example, Egyptian vultures (*Neophron percnopterus*), which are declining globally, thrive in the towns and villages of Socotra, Yemen where they are valued for their service of removing livestock and human waste (Gangoso et al. 2013) that would otherwise cause water contamination and are expensive to remove (Markandya et al. 2008; Yirga et al. 2015; Ćirović et al. 2016). Similarly, the Tigray region of northern Ethiopia harbours high populations of spotted hyenas (*Crocuta crocuta*) that are tolerated by human societies, as they consume cattle and donkey carcasses as well as human corpses in urban settlements, reducing disease risk (Yirga et al. 2015). Yet, these examples of human communities cohabitating and actively conserving scavengers and predators are few and far between.

Here, we highlight several key, yet often overlooked, benefits provided by native predators and scavengers in shared landscapes with humans (Figure 3.1). These potential benefits include disease regulation through host density reduction and competitive exclusion, increasing agricultural output through competition reduction and consumption of problem species that destroy crops, waste disposal services, and regulating populations of species that threaten humans. Although there are a growing number of examples of benefits provided by predators and scavengers, it is often unclear how widespread these benefits may be. While some benefits, such as carcass disposal, may be common and general, other benefits, such as protection from zoonotic disease, may be highly context-dependent effects that are localized in both space and time (Table 3.1). Management of predators and scavengers must also, therefore, be context-dependent and try to appropriately balance detrimental and beneficial effects. We focus primarily on economic and health aspects of human well-being, but we recognize that well-being can encompass other material, social, and subjective components of the human experience that are not covered in this paper (Milner-Gulland et al. 2014).

Predators and scavengers regulate zoonotic diseases

Zoonoses, diseases that are maintained in animal populations but can be transmitted to humans, pose direct threats to human health as exemplified by recent outbreaks of the Zika virus (Rodriguez-Morales et al. 2016), Ebola virus (Olivero et al. 2016), and H5N1 avian influenza (Chen et al. 2005). Accounting for over 60% of known human diseases (Taylor et al. 2001), zoonotic disease outbreaks can decimate human societies and economies. For example, not only did the Ebola virus cause loss of life (>12,000 lives) (Narasimhan 2016), but it virtually halted all tourism to West Africa leading to dramatic economic suffering due to both local perception of disease risk and continent-wide economic concerns (Mizrachi & Fuchs 2016). Because of these human health and economic impacts, control of zoonoses and their vectors is important and while they may be hosts themselves in some cases (e.g. carnivores sustaining rabies cycles in some

African ecosystems (Lembo et al. 2008)), predators and scavengers may play a role in disease regulation (Harris & Dunn 2013). Indeed, some case studies have shown that they can control diseases by reducing host and vector densities (Moore et al. 2009), through local competitive exclusion (Markandya et al. 2008), or directly through feeding on infected hosts (Khalil et al. 2016) (see Figure 3.1).

Reduction of host species densities by predators can reduce the risk of disease transmission to humans by limiting the prevalence of disease in host populations when within-host transmission is density-dependent (McCallum 2001). Predators can also reduce absolute host numbers, thereby limiting the opportunity of spillover to humans when within-host transmission is either density- or frequency-dependent (McCallum 2001). For example, reduction in dog densities by leopards (*Panthera pardus*) greatly reduces the frequency of dog bites and hence human exposure to rabies near the Sanjay Gandhi National Park in Mumbai, India (Braczkowski et al. 2018). Similarly, generalist predators such as foxes may reduce Lyme disease risk in humans by controlling mice populations (*Peromyscus sp.*), the main reservoir for infected nymphal tick vectors (*Ixodes scapularis*) via dilution (Ostfeld & Holt 2004; Brisson et al. 2008; Levi et al. 2012), and frog tadpoles may play a global role in reducing dengue fever by feeding on mosquito eggs (Bowatte et al. 2013) (see Figure 3.1 for global distribution of these species).

Predators and scavengers can also reduce disease risk in humans through competitive exclusion, the action of outcompeting disease hosts for resources or space. For example, vultures have been shown to outcompete stray dogs in finding and consuming carrion (Markandya et al. 2008). Markandya and colleagues (2008) linked the severe decline in vulture populations in India (92% loss from 1990-2000) to the widespread use of diclofenac and the striking increase in stray dog populations (Markandya et al. 2008). They suggest in the absence of vultures consuming carrion, stray dog populations will continue to rise, resulting in an increase in human dog bites and exposure to rabies. Furthermore, other facultative scavengers can replace vultures, including gulls, rats, and invasive foxes (Buechley & Şekercioğlu 2016a), all of which can pose risks to humans and can themselves be disease hosts. However, no study has synthesized empirical and theoretical evidence of scavenger trophic cascades and how they might influence human health and well-being.

Predators can indirectly increase agricultural output

Species that consume crops account for 10-20% of agricultural financial losses globally and current control measures are estimated to be only 40% effective on average (Oerke & Dehne 2004). Conventional pest-control methods, particularly chemical control, can be detrimental to human health (Alavanja et al. 2013) and costly. Biological control provides an alternative to unhealthy chemical control methods (Barzman et al. 2015), and some case studies have shown that natural predators can reduce financial burden and crop loss by consuming problem species.

Airborne predators can play an important role in agricultural management (Labuschagne et al. 2016), a reason why some bat and bird species are often considered the most economically important non-domesticated group of animals (Kunz et al. 2011; Maine & Boyles 2015). For example, field experiments show that some bat communities in the USA suppress pest larval densities of the detrimental corn earworm moth (*Helicoverpa zea*) and cucumber beetle (*Diabrotica undecimipunctata howardi*) by nearly 60% and significantly reduce associated pest fungal growth in large-scale corn productions (Maine & Boyles 2015). Based on these experiments, the authors estimate that bat control of crop pests may save farmers more than US$1 billion globally per year, thereby providing a substantial service to farmer livelihoods (Maine & Boyles 2015). Similarly, birds and bats in the tropical cacao plantations of Indonesia's central Sulawesi have been shown to save over 30% of crop output (~US$730 ha^{-1}) by hunting pest populations of Lepidoptera and Heteroptera species (Maas et al. 2013). Additionally, insectivorous birds can reduce weevil density by over 33% in alfalfa fields of central California, USA (Kross et al. 2016b).

Large avian predators can also have marked impacts on problem species that cause agricultural damage (Figure 3.1). For example, the barn owl (*Tyto alba*) has a diet made up of ~99% agricultural pest species in fields of California, USA (Kross et al. 2016a). Similarly, barn owls reduce man-hours worked and baiting costs for rat (*Rattus sp.*) control in oil palm plantations of Malaysia (Wood & Fee 2003). Likewise, New Zealand falcons (*Falco novaeseelandiae*) have increased winery output in six New Zealand wineries by preying on four crop-raiding bird species (Kross et al. 2012).

Livestock depredation by carnivores can be costly for pastoralists (Suryawanshi et al. 2013), resulting in retaliatory killings of predators (Treves & Bruskotter 2014). However, in pasture environments where livestock and wild herbivores are present, predators may increase livestock productivity by reducing competition with other herbivores (Sundararaj et al. 2012). For instance, the dingo (*Canis lupus dingo*) (Figure 3.1) has been shown to increase agricultural output by controlling populations of red kangaroo (*Macropus rufus*), Australia's largest native herbivore and a major competitor with livestock on commercial grazing land (Prowse et al. 2015). Cattle farmers often kill dingoes due to their reputation for killing valuable livestock but dingoes are estimated to increase pasture biomass by 53 kg ha^{-1} and improve profit margins by US$0.83 ha$^{-1,}$(Prowse et al. 2015).

The value of other predatory species as pest regulators requires further investigation. For example, pest insects form over 50% of the diet of a suite of frog species in the Nepalese rice plantations of Chitwan (Khatiwada et al. 2016) and in southeast China, frog species depredate rice leaf rollers (*Cnaphalocrocis medinalis*), a problematic species that causes blight. By consuming leaf rollers, frogs increase the number of seedlings and stem width of rice plants (Teng et al. 2016) that may ultimately increase health and crop size for rice farmers. Similarly, skunks (*Miphitis spp.*) in North America have been shown to reduce pests in family gardens, potentially reducing the need for pest management (Rosatte et al. 2010).

Predators and scavengers provide benefits in urbanizing environments

Negative human-wildlife interactions are a longstanding and growing problem (Barua et al. 2013) that is often exacerbated in areas with high human density and an abrupt 'wilderness' interface (Soulsbury & White 2015). Many species are attracted to the high calorie food items, shelter, and breeding resources common to urban areas, and they may form permanent populations in shared areas irrespective of wilderness proximit (Samia et al. 2015). For instance, bobcat and puma densities in Colorado, USA, are the same across semi-urban areas and wildland habitats provided that prey densities are similar (Lewis et al. 2015). As a result, predators and scavengers will utilize urban areas, and some case studies have shown that they may provide benefits to humans above and beyond the disease benefits discussed above, including waste regulation and reduction of species abundances that cause direct human injury and death (Ćirović et al. 2016; Gilbert et al. 2016; Braczkowski et al. 2017).

Scavengers provide organic waste regulatory services by feeding on carcasses or decaying food matter (Figure 3.1). For example, golden jackals (*Canis aureus*) reduce >3,700 tons of domestic animal waste in Serbia per year, including road-killed animals and waste dumps (Ćirović et al. 2016). One estimate indicates that jackals remove >13,000 tons of organic waste across urban landscapes in Europe amounting to >US$0.5 million in saved waste-control (Ćirović et al. 2016) that would otherwise cause groundwater contamination and other health risks (Markandya et al. 2008). Vultures can also provide long-term carcass removal services for the livestock industry, leading to savings in man-hours and reduced disease risk in valuable herds (Dupont et al. 2012). This service has been observed in many developing regions, particularly in Africa and Asia where waste-disposal infrastructure is lacking (Markandya et al. 2008; Olea & Mateo-Tomás 2009; Gangoso et al. 2013).

Large terrestrial predators can provide services in urban landscapes by reducing abundances of species that cause human death and injury (Figure 3.1). For example, leopards reduce the density of stray dogs in Mumbai, India, thereby reducing bites and injury accrued on residents and save the municipality nearly 10% of their annual dog management budget (Braczkowski et al. 2017). Stray dogs are responsible for thousands of bites on Mumbai's citizens annually that result in hundreds of work days lost and subsequent financial burden (Gogtay et al. 2014). As stray dog populations currently exceed well over 1 billion globally and are expected to continue to grow as the human population increases (Treves & Bonacic 2016), large wild predators in these urban landscapes should be considered a valuable asset in reducing the ongoing and potential damage accrued from urban stray dogs on human health and well-being.

Predators can also reduce the abundance of species that are responsible for costly wildlife-vehicle collisions (Figure 3.1). Where large carnivores have declined or been extirpated, herbivore populations have often increased (Ripple & Beschta 2012b). This trophic response not only impacts ecological structure, but can directly influence human well-being. Gilbert et al. (2016) found that the potential recolonization of cougars over a 30-year period in the eastern United States would reduce deer populations and thereby curtail deer-vehicle collisions by 22% (Gilbert et al. 2016). They estimated that this reduction in collisions would result in 155 less human deaths, 21,400 less human injuries, and US$2.13 billion saved in costs. This study illustrates how the ecological effects of large predators can potentially save human lives and decrease government spending.

Predator and scavenger conservation in the 21st century

Only 12.5 percent of the earth's terrestrial surface is protected for conservation (Watson et al. 2014), and as the human population grows, and our global footprint expands, 'shared' landscapes will prevail across Earth's terrestrial surface (Di Minin et al. 2016; Venter et al. 2016a). Currently, predators and scavengers receive relatively high attention in protected landscapes (Verissimo et al. 2011), but receive relatively little conservation attention in shared landscapes (Dobrovolski et al. 2013; Di Minin et al. 2016) considering large portions of many species ranges occur in these areas (Di Minin et al. 2016). For example, leopards have disappeared across 78% of their historic range (Jacobson et al. 2016), African lions (*Panthera leo*) are predicted to continue to decline by half outside of protected areas (Bauer et al. 2015), and 17 out of the 22 vulture species are declining due to human activities (Buechley & Şekercioğlu 2016a). Shared landscapes must be managed to achieve effective conservation for all species and improving our understanding of the services provided by predators and scavengers may facilitate their conservation (Frank & Schlenker 2016).

One obstacle to effective conservation of predators and scavengers in shared landscapes is bias in media, government, and public perception. Skewed viewpoints can sensationalize the negative effects of predators and scavengers (Bhatia et al. 2013; McCagh et al. 2015) that can have long-lasting repercussions on human perception, behavior, and policy (Kissui 2008; McCagh et al. 2015). For example, much of the media framed leopards as the perpetrators when attacks occurred in the city of Mumbai, India (Bhatia et al. 2013), and the main local newspaper in Bangladesh pointed to the tiger (*Panthera tigris*) as being the cause of conflict with a 2x higher frequency when compared to the international "The Guardian" newspaper (Sadath et al. 2013). In Florida, USA, instead of taking a neutral stance, local newspapers asserted risks that Florida panthers (*Puma concolor coryi*) might harm people and domestic animals (Jacobson et al. 2012). Likewise, most media coverage in the USA and Australia emphasized the risks sharks pose to people despite the threatened status of many shark species (Muter et al. 2013). An emphasis on wildlife-related risks from the media can lead to risk-averse policy such as when the Western Australia Government deployed drum lines to catch and kill sharks thought to be a threat to the public (McCagh et al. 2015). These "signals" the public receives from governments can influence human behavior directed toward wildlife. For example, Chapron and Treves (2016) suggest that the repeated policy signal to allow state culling of wolves in Wisconsin and Michigan, USA, may have sent a negative message about the value of wolves or acceptability of poaching to the public (Chapron & Treves 2016). The authors contend that these policy signals contributed to poaching of wolves and slowed their population growth (Chapron & Treves 2016).

Another issue is the asymmetry between stakeholders that incur the costs from wildlife, such as the local communities living near them (Howe et al. 2014), and those that benefit from wildlife, such as specific industries (e.g. tourism) or society as a whole. For example, the international community values orangutans for their conservation and intrinsic value in Indonesia, yet local people incur the cost of crop raiding and personal injuries from orangutan attacks (Davis et al. 2013). Consequently, local people kill orangutans to reduce those costs (Davis et al. 2013; Carter et al. 2014). Likewise, although ecotourism companies benefit from predator-viewing activities in Bhutan's Jigme Singye Wangchuk National Park, low income agropastoralists suffer from depredated livestock by tigers and leopards. These losses amount to more than two-thirds of average annual household income (Wang & Macdonald 2006).

Initiatives that have directly provided local stakeholders with benefits from large predators and scavengers have achieved substantial and sustained reductions in conflict. Two seminal examples include profit-sharing and compensation schemes in Kenya's Kuku group ranch and Mbirikani ranch, which provide local stakeholders with a proportion of tourist industry revenue. This has led to reductions in the incidence of lion deaths resulting from poisoning (Hazzah et al. 2014; Bauer et al. 2015). Such schemes may help balance the economic benefits between private stakeholders and the local public who accrue most of the costs of predators and scavengers. Similar incentive schemes have been used successfully by conservation NGO's and governments to promote changes in human behavior, such as reducing carnivore killings (Nyhus et al. 2003). However, the success of these schemes can be jeopardised if they lack sufficient logistic and financial support, they do not award adequate compensation to offset losses, or if compensation is awarded inequitably (Dickman et al. 2011). Such schemes may also have limited effectiveness in reducing killings motivated by cultural, political or historical reasons (Goldman et al. 2013). Hence, profit-sharing and compensation schemes must be implemented in conjunction with broader management programs that attempt to identify and address the wide range of factors that contribute to killing of wildlife, and that encourage the participation of all stakeholders in an inclusive decision-making process that recognizes multiple systems of knowledge and values (Pascual et al. 2014).

In addition to improving equity in various forms associated with predators and scavengers, there is also an urgent need to promote human tolerance to these species through education about benefits (Steinmetz et al. 2014; Reid 2016; Skupien et al. 2016; Marley et al. 2017). Dedicating outreach teams to communicate the benefits of endemic predators and scavengers to local communities could be an effective conservation strategy. Demonstrations of the effectiveness of education programs include: an improvement in the belief in potential for co-existence with alligators (*Alligator mississippiensis*) following education (Skupien et al. 2016), greater tolerance of black bears (*Ursus americanus*) following education of benefits provided by bears (Slagle et al. 2013), and greater tolerance of bats among Costa Rican men following education regarding ecosystem service provision (Reid 2016). Although more research is required to understand how long the benefits of education programs may last and how best to deliver them to people from a variety of cultural, educational and religious backgrounds, education can be an effective tool for conservation of predators and scavengers in shared landscapes.

In addition to the benefits predators and scavengers provide to the public as a whole, they may also benefit a wide range of business, agricultural, and tourism interests. Much can be done to bolster the services of predators and scavengers in these sectors through local government and individual action. For example, Italian city councils are encouraging residents to purchase bat nesting boxes in response to increasing mosquitos that cause chikungunya fever (Day 2010), although it is unclear the extent of impact that bats have on disease-carrying mosquitoes in this region. Similarly, the city of Dubai in the United Arab Emirates invests in consultancies that work with peregrine falcons to reduce feral pigeon populations that cause severe damage to infrastructure (Choksi 2015). Ecotourism revenue can be substantial, though it is often difficult to estimate how much particular species contribute to overall economic value (O’Mahony et al. 2017). The presence of jaguars (*Panthera onca*) in Brazil, for example, may contribute greatly to Pantanal ecolodges. One study estimates that the large felids bring nearly US$7 million in annual land-use revenue, which is 52 times higher than other industries in the region (Tortato et al. 2017).

Predators may also benefit vehicle drivers by reducing insurance premiums in areas where predators have been effective in reducing the abundance of large prey like deer, which can be a leading source of vehicle collision damage (Gilbert et al. 2016). Similarly, obligate scavengers have been shown to save ca. $50 million in insurance payments by farmers and national administrations in Spain by supplanting transportation of livestock carcasses to processing facilities (Morales-Reyes et al. 2005). Scavengers may also provide savings by reducing costs associated with meat contamination (Whelan et al. 2015). There may be additional benefits from predators by reducing densities of invasive ecosystem engineers such as wild pigs (*Sus scrofa*) that disturb soil and disrupt soil organic carbon, thus reducing greenhouse gas emissions. More work is needed to document the financial and health benefits of predators and scavengers to different sectors of society.

Managing the trade-offs between the costs and benefits of accommodating predators and scavengers in shared landscapes is a difficult and unresolved problem due to the complexity of human and ecological systems (Table 3.1). Risk-averse management may tend to place undue importance on eliminating the detrimental impacts of predators and scavengers over maintaining the benefits, particularly if the impacts include direct hazard to human life. In some cases, however, this may be a short-sighted and poorly justified perspective that could lead to a net increase in risk to humans if these animals also provide benefits that reduce exposure of risk to humans. Important unanswered questions include: how do the benefits from predators and scavengers change as the density of those species varies over time (Courchamp et al. 2006)? How does the composition of the predator guild alter human perception of the costs associated with those predators (Dickman et al. 2014)? Integrating the natural and social sciences can help answer these questions by evaluating the full range of both costs and benefits. Doing so will enable conservationists to determine if and when there is a net-benefit in shared landscapes and develop strategies to encourage net benefits (Carter et al. 2014). Moreover, as the extent of shared landscapes increases globally, it is imperative that we identify new approaches to management that allow wildlife and humans to coexist. Failing to do so is likely to result in the extinction of many species.

Human societies depend greatly on the living components of the natural world (Pecl et al. 2017), and these natural services are being altered by human dominance of landscapes (Worm & Paine 2016) and climate change (Scheffer et al. 2015). While, predators and scavengers currently face great threats in shared landscapes (Buechley & Şekercioğlu 2016a; Ripple et al. 2017), they can coexist in areas where local communities accept and tolerate these species (Gangoso et al. 2013; Treves & Bruskotter 2014; Skupien et al. 2016). Traditional conservation approaches such as safeguarding land may not lead to comprehensive protection of species in human-dominated areas (Di Minin et al. 2016), leading to a requirement for alternative approaches for saving species in these shared landscapes. An important alternative is using services that predators and scavengers provide for human well-being to enhance protection (Frank & Schlenker 2016). By adopting an approach that communicates and educates these benefits to communities that live with predators and scavengers while accounting for cultural values and equitable conservation decision-making, we may be able to stem the decline of these persecuted guilds and make progress toward more expansive protection and increased instances of a net-gain in shared landscapes.

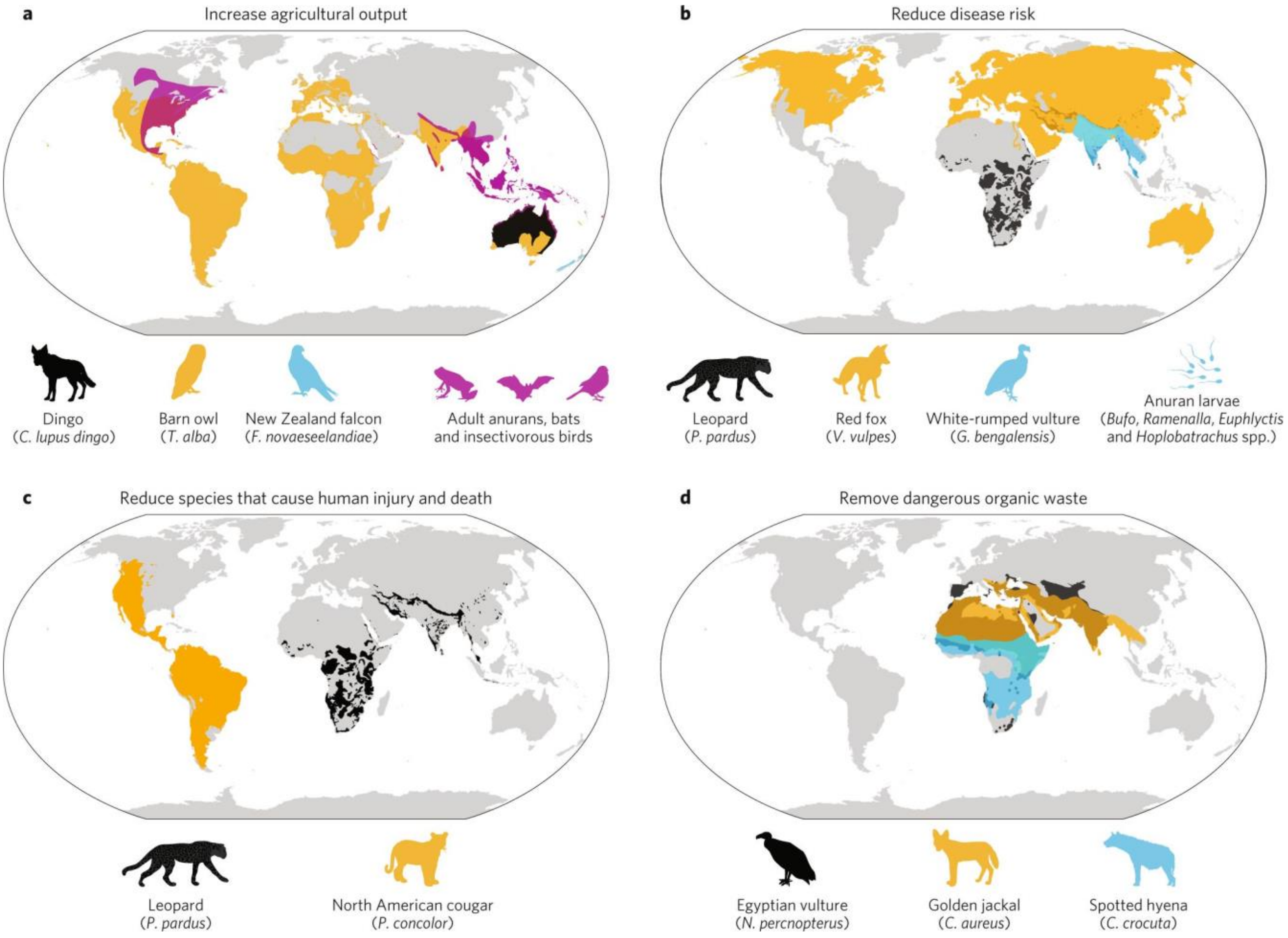

Figure 3.1. (a), Ranges of some species known to contribute to agricultural production. (b), Ranges of some species that may reduce disease risk. (c), Ranges of some animals known to reduce species that cause human injury and death. (d), Ranges of some species known to remove dangerous organic waste.

Benefit	Predator/scavenger species & location of case study	Key finding(s)	Potential limitations of case study	Additional research needed to further demonstrate human well-being benefits
Regulating zoonoses	Leopard (*Panthera pardus*) (Braczkowski et al. 2017) Mumbai, India 	Leopards consume nearly 1,500 feral dogs per year, reducing injury rates and potentially saving approximately 90 human lives.	Human benefit inferred from leopards consuming feral dogs that bite and infect humans, yet lacks direct measure of benefit, or controls for comparisons in similar dog-infested areas without leopards. Small spatial scale.	Conduct similar analyses in locations without leopard presence. Estimate prevalence of dog rabies rates in Mumbai and analysis of trade-offs between dog and leopard attacks on humans. Are these results in line with similar systems globally?
Regulating zoonoses	Red fox (*Vulpes vulpes*) (Levi et al. 2012) USA 	The decline of red foxes is spatially correlated with Lyme disease outbreaks.	Potential benefit inferred from correlation (cause and effect not established).	Better mechanistic understanding of system required to evaluate effect of multiple predators on prey (host) populations, and explicitly link this to host-pathogen dynamics.

Regulating zoonoses	Amphibian larvae (*Polypedates cruicger, Bufo melanostictus, Ramanella obscura, Euphlyctyis cyanophlyctis*) (Bowatte et al. 2013) Sri Lanka; Lab experiment 	Amphibian larvae feed aggressively on dengue mosquito (*Aedes aegypti*) eggs.	Lab-based experiment that does not account for alternative food availability that can dilute predatory effects. No direct quantification of human well-being. For example, lack of analyses on cost savings associated with vector control or reduced infection rates in humans as a result of amphibian predation of mosquito eggs.	Conduct field studies on amphibian larvae gut content across a variety of geographic areas subject to mosquito-borne diseases. Investigate whether predation of larvae by amphibians results in lower densities of adult mosquitos. Quantify how many human lives amphibian communities could affect.
Regulating zoonoses	Old world vultures (*Gyps spp.*) (Markandya et al. 2008) India 	Vulture declines are linked to increased feral dogs that cause rabies.	Potential benefit inferred from correlation (cause and effect not established).	Must identify other potential factors implicated in vulture declines and rule them out. Compare with vulture population trends in areas in which feral dogs have not increased.
Increasing agricultural output	Barn owl (*Tyto alba*) (Kross et al. 2016a)	Barn owls consume >99% rodent pests in	No demonstration of increased crop yield. No calculation of cost	A controlled replicated experiment may be feasible to demonstrate a causal link

	California, USA 	row crops of California, USA.	savings from pest species consumption.	between barn owls and increased crop yield. Calculate cost savings through work-hours, chemical control, and trap costs saved from pest predation by owls.
Increasing agricultural output	New Zealand falcon (*Falco novaeseelandiae*) (Kross et al. 2012) New Zealand 	New Zealand falcons reduce the presence of four crop-raiding bird species, increasing profit margins in wineries from US$234-326/ha.	Geographically- limited case study.	Replication in other areas and other systems required to better establish generality. Include calculations on work-hours saved by having falcons present on wineries.
Increasing agricultural output	Dingo (*Canis lupus dingo*) (Prowse et al. 2015) New South Wales, Australia 	Dingoes increase gross profit margins by reducing the density of kangaroos, which compete with cattle.	Geographically-limited case study based on a metamodel.	Fieldwork needed to show that forage availability is proportional to kangaroo density. Must account for both forage quantity and quality effects. Include calculations on work-hours saved. Conduct exclusion experiments. Are the

				results similar to the metamodel?
Increasing agricultural output	Thirteen frog species (*Bufonidae, Microhylidaae, Ranidae, Rhacopphoridae*) (Khatiwada et al. 2016) Chitwan, Nepal 	Frogs increase the number of rice seedlings and stem width of rice plants by consuming leaf rollers (*Cnaphalocrocis medinalis*)	No calculation of increased crop yield or cost savings from pest species consumption.	Demonstrate crop yield increases when frogs are present, ideally using field experiments. Calculate cost savings through work-hours, chemical control, and trap costs saved from pest predation by frogs.
Waste removal	Egyptian vulture (*Neophron percnopterus*) (Gangoso et al. 2013) Socotra, Yemen 	Vultures dispose of >22% of organic waste.	Clearer link to human well-being needed, such as disease implications and cost savings of waste scavenging. Small spatial scale.	Test water sources near waste dumps with and without vulture access. Additionally, assess costs of waste removal. Quantify how organic waste has negative impacts on humans.

Waste removal	Spotted hyena (*Crocuta crocuta*) (Yirga et al. 2015) Tigray, Ethiopia 	Nearly 90% of studied hyenas were located at waste dumps.	Human benefit inferred from hyena abundance at waste dumps. Clearer link to human well-being needed, such as estimation of waste removal, disease implications, and cost savings. Small spatial scale.	Conduct diet analysis similar to Gangoso and colleagues (Gangoso et al. 2013), but take additional steps to address costs of waste removal and/or human disease implications.
Reducing species abundance that cause human injury/death	North American cougar (*Puma concolor*) (Gilbert et al. 2016) Eastern USA 	Potential recolonization of cougars over 30 years would curtail deer-vehicle collisions by 22%, saving 155 human lives, 21,400 injuries, and US$2.13 billion.	Human benefit based on a projected recolonization scenario for the eastern USA.	Account for the costs of cougar recolonization, such as increased incidences of livestock predation. Do the benefits on human well-being outweigh the costs?

Table 3.1. Featured case studies of predators and scavengers contributing to human well-being, their potential limitations and suggestions for furthering the case of human benefit.

CHAPTER 4 Authorship Statement

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James Watson and the Candidate conceived the idea for the manuscript. Matthew Holden and the Candidate constructed the models, with the Candidate conducting the analyses. The Candidate ran the models with input from Matthew Holden. The Candidate conducted the literature review, synthesized model results, and wrote the manuscript with input from all authors.

CHAPTER 4 The mesoscavenger release hypothesis and implications for ecosystem and human well-being

Christopher J. O’Bryan, Matthew H. Holden, James E.M. Watson

Abstract

Many apex scavenger species, including nearly all obligate scavengers, are in a state of rapid decline and there is growing evidence these declines can drastically alter ecological food webs. Our understanding of how apex scavengers regulate populations of mesoscavengers, those less-efficient scavengers occupying mid-trophic levels, is improving; yet, there has been no comprehensive evaluation of the evidence around the competitive release of these species by the loss of apex scavengers. Here we present current evidence that supports the mesoscavenger release hypothesis, the increase in mesoscavengers and increase in carrion in the face of declining apex scavengers. We provide two models of scavenger dynamics to demonstrate that the mesoscavenger release hypothesis is consistent with ecological theory. We further examine the ecological and human well-being implications of apex scavenger decline, including carrion removal and disease regulation services.

Introduction

Apex scavengers are functionally dominant at scavenging, meaning they can find and consume carcasses more efficiently than other scavengers (Sebastián-González et al. 2016), and can be either obligate or facultative scavengers. Obligate scavengers (i.e. Old and New World vultures) are dependent entirely on carrion, but facultative scavengers rely partly on carrion (Ogada et al. 2012a). Apex scavengers (i.e. vultures and functionally dominant facultative scavengers) are facing unprecedented declines due to direct persecution, human disturbance, collision with infrastructures and electrocution, poisons and other dietary toxins, human disturbance, habitat loss and degradation, food shortage caused by sanitary regulations, or abandonment of traditional farming practices (Ripple et al. 2014; Buechley & Şekercioğlu 2016b). As such, it is imperative to understand the ecological and human well-being impacts of apex scavenger declines (Buechley & Şekercioğlu 2016b). There is growing evidence of scavenger competitive release across Earth, where mid-sized, less efficient scavengers (i.e., mesoscavengers) can increase in abundance in the absence of competition from more efficient apex scavengers (the mesoscavenger release hypothesis; Figure 4.1) (Butler & du Toit 2002; Sekercioğlu et al. 2004; Markandya et al. 2008; Ogada et al. 2012b; Buechley & Şekercioğlu 2016b; Morales-Reyes et al. 2017). The population effects of mesoscavenger release from apex scavengers can be qualitatively similar to well documented patterns observed in predatory systems, where the absence of apex predators releases mesopredators (Crooks & Soulé 1999; Ritchie & Johnson 2009a; Ripple et al. 2014; Newsome et al. 2017). However, the mechanism behind mesoscavenger release is different; it is caused by reduced competition over a shared resource, not the loss of top-down control. Here, we present evidence pointing to the release of mesoscavengers by the loss of apex scavengers, and we discuss potential ecosystem and human well-being implications of mesoscavenger release.

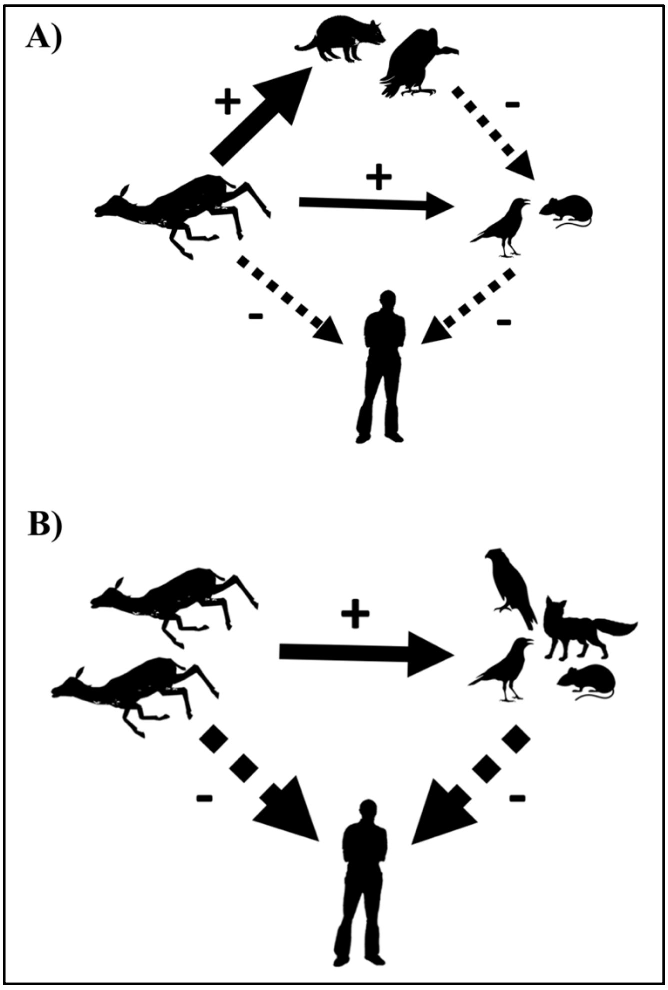

Figure 4.1. (A) Apex scavengers are more effective at detecting and consuming carrion than mesoscavengers (large solid arrow), resulting in less carrion available to mesoscavengers (small dotted arrow), and thus resulting in fewer mesoscavengers (small solid and dotted arrows). This may result in indirect effects such as less disease risk, pest prevalence, and invasion potential that can negatively impact humans and ecosystem structure (small dotted arrows). (B) The loss of apex scavengers can result in mesoscavenger release, which is primarily caused by increased carrion availability due to a reduction in competition (large solid arrow). Mesoscavenger release can result in indirect effects such as increased disease risk, pest prevalence, and invasion potential that can negatively impact humans and ecosystem structure (large dotted arrows).

Empirical support for the mesoscavenger release hypothesis

Mesoscavengers have been shown to be more abundant and diverse in areas that are absent of apex scavengers (Table 4.1), which can affect ecosystem structure. For example, red foxes (*Vulpes vulpes*), which are facultative mesoscavengers, were significantly more abundant in areas of south-eastern Spain that lack vultures (*Gyps spp.*)

compared to areas with vultures (Morales-Reyes et al. 2017). Morales-Reyes and colleagues contend that mesoscavengers had increased scavenging opportunities and thus consumed more carrion in the absence of vultures, therefore resulting in increased abundance of foxes. An increase in mesoscavengers has also been observed in India, where growing feral dog (*Canis lupus*) and rodent populations have been linked to the widespread decline of vultures caused by ingestion of veterinary pharmaceuticals (i.e. diclofenac) (Markandya et al. 2008). The authors suggest that the concomitant rise of carrion without vultures resulted in a spike in mesoscavenger populations (Markandya et al. 2008). In Tasmania, Australia, areas where Tasmanian devils (*Sarcophilus harrisii*) have declined due to facial tumour disease have resulted in an increased abundance of feral cats (*Felis catus*) and forest ravens (*Corvus tasmanicus*) (Cunningham et al. 2018). The authors show that forest ravens have increased across all of Tasmania during the period of Tasmanian devil decline. In areas of Spain and South Africa where apex scavengers were lacking, species richness and composition drove the consumption of carrion; however, context-dependent effects (i.e. species abundance) had a greater effect where apex scavengers were common (Mateo-Tomás et al. 2017). These apex scavengers not only included globally widespread species such as wild boar (*Sus scrofa*), but also imperilled species like gyps vultures (*Gyps spp.*) and African lions (*Panthera leo*) (Mateo-Tomás et al. 2017). Likewise, in the Mendocino National Forest of California, foxes, corvids, and rodents had significantly higher species richness at deer carcasses in the absence of black bears and puma – the apex facultative scavenger and apex predator, respectively (Allen et al. 2014). The authors argue that the nestedness, or structure of the scavenger community, increased at carcasses where large carnivores were present (Allen et al. 2014).

In the absence of apex scavengers, mesoscavengers are thought to be less effective at locating carrion, resulting in a longer carcass decomposition time. For instance, when turkey vultures (*Cathartes aura*) and black vultures (*Coragyps atratus*) were experimentally excluded from carrion in South Carolina, USA, 80 percent of carcasses were not scavenged by mesoscavengers, resulting in a ten-fold increase in carrion that were not fully scavenged compared to controls (Hill et al. 2018). A similar pattern was observed in Australia where nearly 70 percent of carrion were not scavenged by mesoscavengers (rats, dogs, foxes, and corvids) in the absence of apex facultative scavenging species such as kites (*Haliastur spp.*) and white-bellied sea eagles (*Haliaeetus leucogaster*) (Huijbers et al. 2015). Similarly, carrion persisted 2.6 times longer in areas where

Tasmanian devils declined due to a facial tumor disease (Cunningham et al. 2018). Carcasses were scavenged three times slower in the absence of vultures in the Laikipia District of central Kenya (Ogada et al. 2012b) and thirteen times slower in areas without vultures in south-eastern Spain (Morales-Reyes et al. 2017). Not only are vultures more efficient at locating and consuming carrion in the Masai Mara National Reserve in Kenya, they have also been shown to aid mesoscavengers in locating carrion (Kane & Kendall 2017). As such, the loss of apex scavengers can result in increased available carrion biomass and slower decomposition time likely due to a lower scavenging efficiency by mesoscavengers.

Apex scavenger(s) (obligate and/or facultative)	**Mesoscavenger(s) (obligate and/or facultative)**	**Impacts on mesoscavenger(s)**	**Location**	**Source**
Griffon vulture (*Gyps fulvus*)	Red fox (*Vulpes vulpes*)	Abundance of foxes increased with vulture absence	South-eastern Spain	(Morales-Reyes et al. 2017)
Black bear (*Ursus americanus*)	Bobcat (*Lynx rufus*), gray fox (*Urocyon cinereoargenteus*), western spotted skunk (*Spirogale gracilis*), ringtail (*Bassariscus astutus*), common raven (*Corvus corax*)	Total feeding time and presence of mesoscavengers on carrion decreased with bear presence	Mendocino National Forest, California	(Allen et al. 2014); (Allen et al. 2015)
Long-billed vulture (*Gyps indicu*), slender-billed vulture (*Gyps tenuirostris*), oriental white-backed vulture (*Gyps bengalensis*)	Feral dogs (*Canis familiaris*)	Numbers of dogs significantly increased with vulture declines	India	(Markandya et al. 2008)
Wild boar (*Sus scrofa*), griffon vulture (*Gyps fulvus*), white-back vulture (*Gyps africanus*), African lion (*Panthera leo*)	Marten (*Martes spp*), red fox (*Vulpes vulpes*), feral dog (*Canis familiaris*), Eurasian jay (*Garrulus glandarius*), azure-winged magpie (*Cyanopica cyanus*), Eurasian magpie (*Pica pica*), crows (*Corvus spp*)	Species richness and composition drove carcass consumption in ecosystems where apex scavengers were rare, but context dependent factors (e.g. species abundance) drove carcass consumption where apex scavengers were common.	Mediterranean Spain and subtropical South Africa	(Mateo-Tomás et al. 2017)
Palm-nut vulture (*Gypohierax angolensis*), hooded vulture (*Necrosyrtes monachus*), white-backed vulture (*Gyps africanus*), Rüppell's vulture (*G. rueppellii*), lappet-faced vulture (*Torgos tracheliotus*)	Hyenas (*Crocuta & Haena spp*), black-backed jackal (*Canis mesomelas*), Egyptian mongoose (*Herpestes ichneumon*)	Increase in contacts between mesoscavengers and number of species at carcasses without vultures	Laikipia District, Kenya	(Ogada et al. 2012b)
Griffon vulture (*Gyps fulvus*)	Red kite (*Milvus milvus*), black kite (*Milvus migrans*), common raven (*Corvus corax*), marsh harrier (*Circus aeruginosus*), golden eagle (*Aquila chrysaetos*)	Vultures dominated carcasses in predictable locations, reducing species abundance of mesoscavengers	Northern Spain	(Cortés-Avizanda et al. 2012)
Tasmanian devil (*Sarcophilus harrisii*)	Feral cat (*Felis catus*), forest raven (*Corvus tasmanicus*), spotted-tailed quoll (*Dasyurus maculatus*)	Mesoscavengers increased carrion consumption in areas where Tasmanian devils have declined. Raven populations increased 2.2 fold following devil declines.	Tasmania, Australia	(Cunningham et al. 2018)

Table 4.1. Studies showing the impacts of apex scavengers on mesoscavenger abundance, presence at carrion, and species richness.

Theoretical support for the mesoscavenger release hypothesis

Unlike the mesoscavenger release hypothesis, the mesopredator release hypothesis has been shown to be consistent with the outputs of classic predator-prey models (Crooks & Soulé 1999). To determine if the mesoscavenger release hypothesis is also consistent with ecological theory, we built two simple dynamic models, one of apex obligate scavengers and mesoscavengers competing over carcasses for food, and the second model where the apex scavenger is facultative.

Apex obligate scavenger model

Consider an obligate scavenger model (see Figure 4.2 for a graphic description of the model),

(1)

$$\frac{dA}{dt} = -\mu A + \frac{g_a e_a C A}{1 + h_a e_a C} \ ,$$

$$\frac{dM}{dt} = rM\left(1 - \frac{M}{k}\right) + \frac{g_m e_m C M}{1 + h_m e_m C} \ ,$$

$$\frac{dC}{dt} = p - \delta C - \frac{e_a C A}{1 + h_a e_a C} - \frac{e_m C M}{1 + h_m e_m C} \ ,$$

where A, M, and C are apex scavenger, mesoscavenger, and carrion biomasses, respectively. For the sake of the model above, we consider all apex scavengers to be obligate scavengers that die in the absence of carrion at rate μ. Mesoscavengers are assumed to have alternate food sources, and therefore in the absence of carrion grow logistically at rate r, with carrying capacity k. Apex scavengers and mesoscavengers convert food into increased reproduction at rates g_a and g_m, respectively. The efficiency at which they find carrion is e_a and e_m, and scavenger handling time is h_a and h_m. Note that e_a will always be greater than e_m under mesoscavenger release due to apex scavengers being functionally dominant at scavenging relative to mesoscavengers. Carrion increase due to animal death at a constant rate p and decay at rate δ. The model assumes that carrion are from non-modelled species and are therefore mathematically similar in structure to chemostat models of resource dynamics where resources enter and exit a system at constant rates (Smith & Waltman 1995). While mesoscavenger and apex scavenger carcasses can contribute to scavenged carrion, this contribution is generally inconsequential compared to the carcasses of other species, and are often avoided due to the coevolutionary relation between carnivores and their parasites (Moleón et al. 2017).

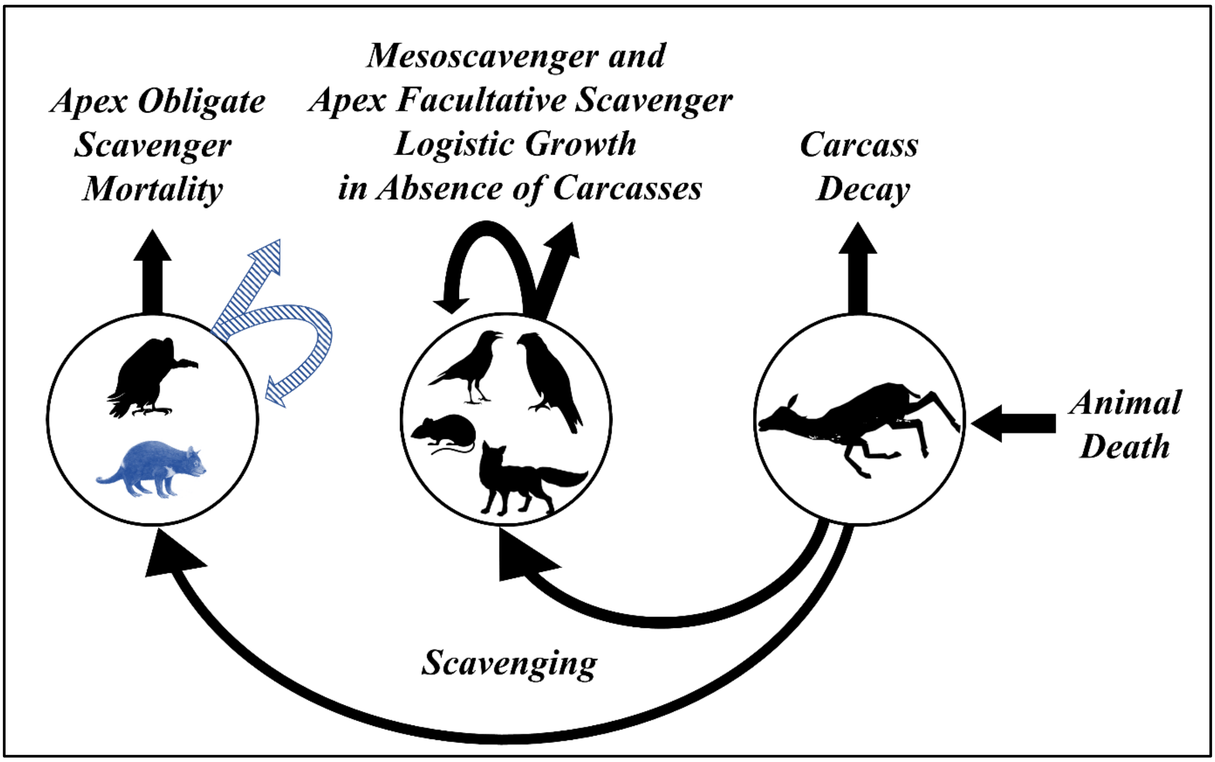

Figure 4.2. Graphical illustration of our dynamic model to test theoretical support of the mesoscavenger release hypothesis. In the model, carcasses enter the system via animal death and leave the system through decay or by scavenging. Both apex scavengers and mesoscavengers consume carcasses with respective efficiencies and handling times. In the dynamic model, mesoscavenger and apex facultative scavenger populations have a logistic growth rate (combination of births and deaths) in the absence of carcasses (apex facultative scavenger logistic growth is denoted by the blue coloring and dashed arrows), whereas apex obligate scavengers have a mortality rate in the absence of carcasses.

We parameterize our model using known mortality, efficiency, decay, and carrion availability rates and scavenger handling times (Appendix 5 Table 1). Known parameters on apex obligate scavengers are obtained from studies on cape vultures (*Gyps coprotheres*) (Komen 1992), griffon vultures (*Gyps fulvus*) (Houston 1974), and multi-scavenger systems with vultures present (Morales-Reyes et al. 2017). Known parameters on mesoscavengers are obtained from a study on scavenger systems with vultures absent (Morales-Reyes et al. 2017), with information on carrion availability and decay rates from field experiments in Africa and the USA, respectively (Houston 1985; Carter et al. 2006). Population growth rate of the mesoscavenger in the absence of carrion, and the food conversion rates for both scavengers are arbitrarily set equal to the mortality rate of apex scavengers in the absence of food. We vary the carrying capacity of the mesoscavengers in the absence of carcasses from 0.5 – 2.0, to capture differing dependence and/or preference for non-carrion food sources. We also consider the case where scavenging efficiency of the mesoscavenger is doubled in the presence of an apex obligate scavenger due to evidence of following behaviour by mesoscavengers on vultures (Kane & Kendall 2017). We note that this model could be non-dimentionalised to reduce the number of parameters, but we present the model here in its most biologically interpretable form, for clarity.

We define mesoscavenger release as the increase in functionally less dominant mesoscavengers in the absence of more functionally dominant apex scavengers, where functional dominance is determined by a scavenger's relative ability to efficiently locate and consume carrion (Mateo-Tomás et al. 2017). Under the assumed conditions (i.e. that apex scavengers are stronger competitors than mesoscavengers) a reduction of apex scavengers leads to an increase in mesoscavengers and carrion in our model, which is consistent with the mesoscavenger release hypothesis. These results therefore suggest that a decrease in apex obligate scavengers may lead to increases in mesoscavengers and carrion, which is also consistent with observational data (e.g. Morales-Reyes *et al.* 2017). When apex obligate scavengers are removed from the system, mesoscavenger equilibrium densities increase along with carrion density. For example, in the baseline parameterisation, with an apex obligate scavenger 18 times more efficient (e.g. *Gyps fulvus*) than the typical mesoscavenger assemblage, removing the apex scavenger causes a 13-fold increase in equilibrium carrion density (Figure 4.3). The effect is strongest when apex scavengers are substantially more efficient than the mesoscavengers, and when mesoscavenger carrying capacity is low (although mesoscavenger release occurs across a range of carrying capacities; Figure 4.3 & Appendix 5 Figure 1). For example, removing an apex scavenger that is only three times as efficient as the typical mesoscavenger increases carrion density two-fold. Furthermore, when mesoscavengers have a high carrying capacity in the absence of carrion, apex obligate scavengers still reduce carrion density by over half, due to their relatively high search efficiency (Figure 4.3).

When doubling mesoscavenger search efficiency in the presence of apex scavengers, the mesoscavenger release response is qualitatively similar to the baseline case (Figure 4.3). The only differences are that mesoscavenger density slightly increases (4.7% increase) and carrion density drops by 5.3% when apex scavengers improve mesoscavenger search efficiency (measured at the baseline apex scavenger search efficiency). A full local sensitivity analysis of the model parameterisation is presented in the Supplementary Material (Appendix 4 Figure 1).

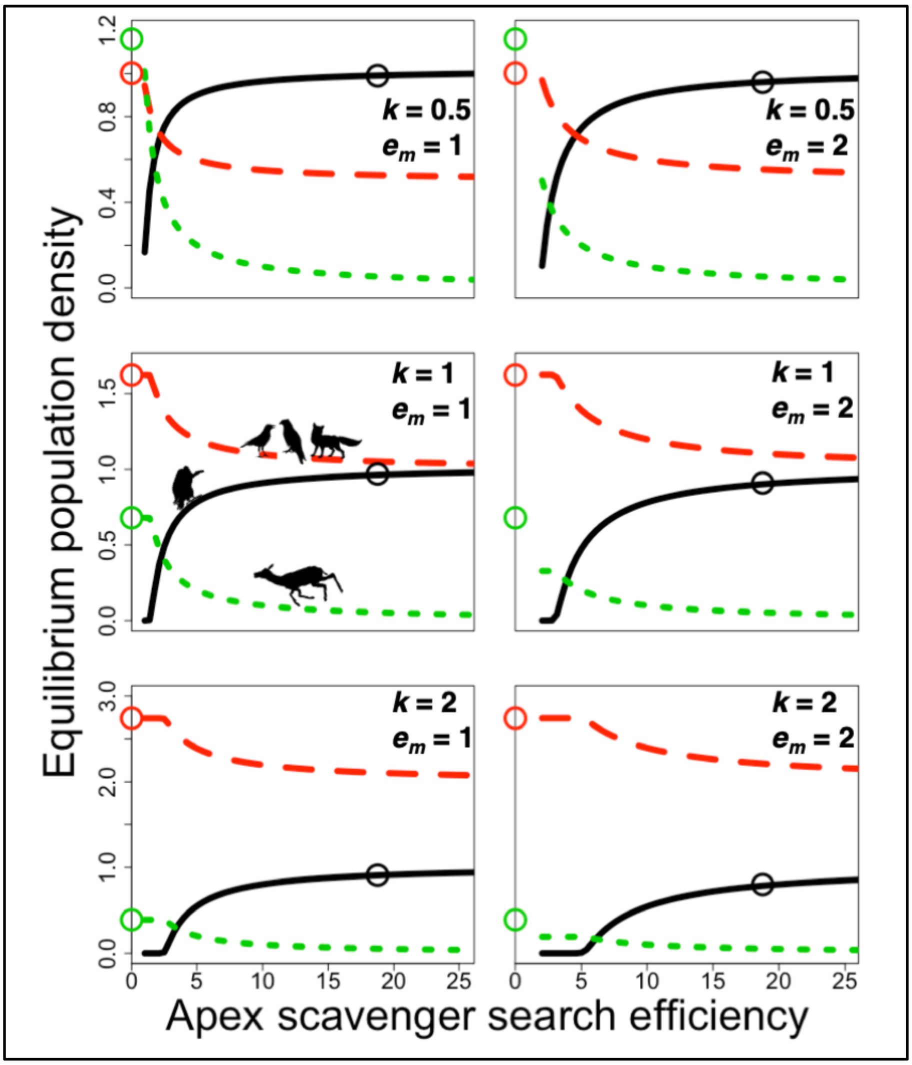

Figure 4.3. Equilibrium population densities of carcasses (green dotted line), mesoscavengers (red dashed line) and apex obligate scavengers (black solid line) from the dynamic model (eqn 1) as a function of apex scavenger search efficiency. The curves for each plot start at mesoscavengers search efficiency. The black open circle for each plot denotes the search efficiency of an apex scavenger, the griffon vulture (*Gyps fulvus*), which is 18 times more efficient than a mesoscavenger assemblage. The red and green open circles on the equilibrium axis denote the equilibrium densities of mesoscavengers and carcasses, respectively, when the apex scavengers are absent. Generally, the more efficient (i.e. functionally dominant) the apex scavenger, the more they suppress mesoscavenger populations and carcass densities. The first column of plots is for the baseline mesoscavenger search efficiency, $e_m = 1$. The second column of plots is for the case where mesoscavenger search efficiency is doubled when apex obligate scavengers are present, potentially

aiding mesoscavengers in finding carcasses - as documented in some vulture systems (Kane & Kendall 2017).

Our models do not consider interactive effects of other carnivore species at modulating the ability of vultures to exploit carrion. For example, apex predators may have differing effects on scavenging behavior and consumption patterns of both apex scavengers and/or mesoscavengers at and around carcasses (Selva & Fortuna 2007; Olson et al. 2012; Barton et al. 2013; Allen et al. 2014; Moleón et al. 2014; Sivy et al. 2018; Cunningham et al. 2018). More research is needed to investigate the role of other carnivore species at regulating scavenger behavior and population dynamics.

Apex facultative scavenger model

As apex scavengers can also be facultative, consider a similar dynamic model, but with apex scavengers capable of alternate feeding strategies. Apex scavengers now grow logistically at rate r_a, with carrying capacity k_a in the absence of carrion,

(2)

$$\frac{dA}{dt} = r_a A\left(1 - \frac{A}{k_a}\right) + \frac{g_a e_a C A}{1 + h_a e_a C} \quad .$$

We parameterize our model using known efficiency and handling times from a study on Tasmanian devils (Cunningham et al. 2018). Other parameters, describing carrion decay and carrion availability, are set to the baselines in the previous model (Appendix 5 Table 1). We explore the parameter space for this system by varying handling times, search efficiencies, growth rates, and carrying capacities against equilibrium population densities for the Tasmanian system (Appendix 5 Figure 2 & 3). We also consider a hypothetical system using the vulture parameterisation. The vulture parameterisation allows us to see how the mesoscavenger release generated from the obligate scavenger model would be affected by allowing an apex facultative scavenger with considerably high search efficiency to consume non-carrion food sources. Here, all parameters are set to match the vulture parameterisation in the obligate apex scavenger model. We vary carrying capacity of the apex facultative scavenger in the absence of carrion to range between 1/100th of mesoscavenger carrying capacity to mesoscavenger carrying capacity, as we do not expect apex facultative scavengers to have higher densities than mesoscavengers in the absence of carrion.

We find that mesoscavenger release occurs in facultative systems. For example, in the vulture-parameterized model in Figure 4.4, mesoscavenger and carrion densities drop 3-fold when the apex facultative scavenger's carrying capacity in the absence of carrion reaches 1/10th of the mesoscavengers' carrying capacity (Figure 4.4). However, in the Tasmanian devil-parameterized model, mesoscavenger densities are only slightly impacted, likely due to the relatively close search efficiencies between the apex scavengers and mesoscavengers (Figure 4.4). This suggests that apex facultative scavengers with higher search efficiencies (i.e. more functionally dominant) relative to mesoscavengers tend to have greatest impact on mesoscavenger and carrion densities, especially at lower apex scavenger carrying capacities in the absence of carrion (Figure 4.4). A full local sensitivity analysis of the model parameterisation is presented in the Supplementary Material (Appendix 4 Figures 2 and 3).

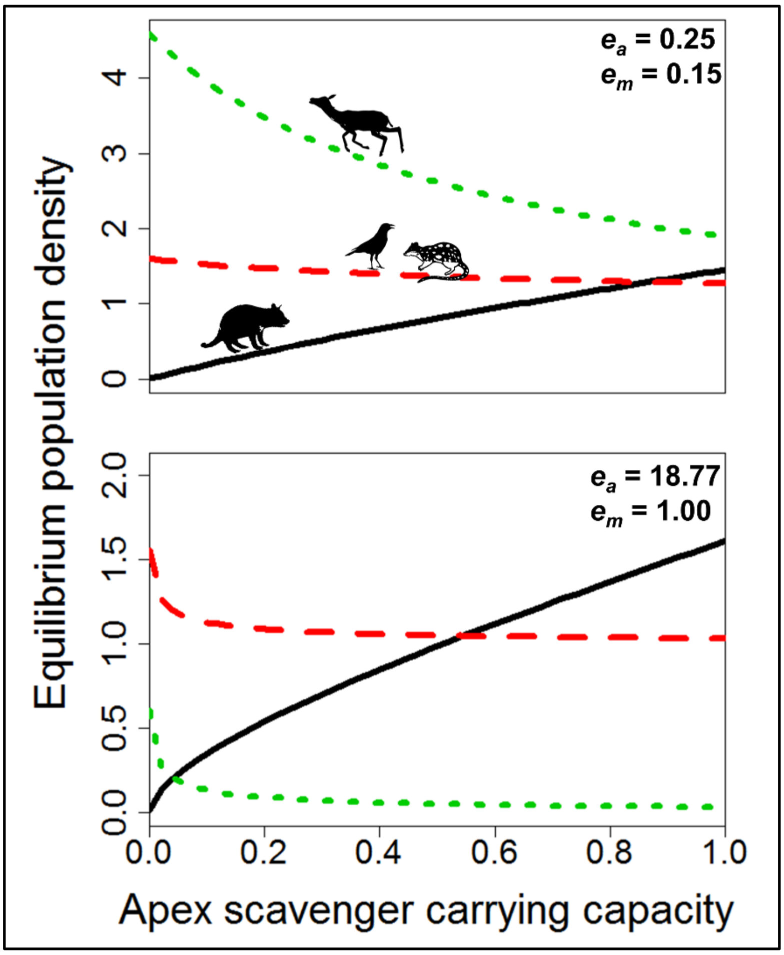

Figure 4.4. Equilibrium population density of carcasses (green dotted line), mesoscavengers (red dashed line) and apex facultative scavengers (black solid line) from the dynamic model (eqn 2) as a function of apex scavenger carrying capacity in the absence of carcasses. Values on the x-axis range from 1/100th of the mesoscavenger carrying capacity value to the mesoscavenger carrying capacity value. The top model is parameterized for a known facultative scavenger, the Tasmanian devil (Cunningham et al. 2018). The bottom is parameterized for vulture systems (Morales-Reyes et al. 2017). The key difference between the two parameterisations is different mesoscavenger and apex scavenger search efficiencies, which are displayed in the top right of each plot. An imaginary effect of vultures surviving off of alternative food sources is displayed for comparison with Figure 4.3. As apex scavengers are able to sustain higher populations in the absence of scavenging (increasing k_a), the more they suppress mesoscavenger populations and carcass densities; however, apex facultative scavengers with higher search efficiencies relative to mesoscavengers tend to have greater impact at lower

carrying capacities compared to apex scavengers with smaller search efficiencies relative to mesoscavengers.

We assume that facultative scavengers do not decrease their search effort on carrion when the carrion are at low densities. It may be true that facultative scavengers reduce their search efficiency for carrion when carrion densities are low, and alternatively increasingly target live prey if more available, which is consistent with optimal foraging theory (Kane et al. 2017; Margalida et al. 2017). However, it is empirically unclear how facultative scavenger search efficiency fluctuates depending on food availability. Food switching could be modelled as a discontinuous functional response, or even approximated by a Holling's Type III sigmoidal functional response, which is an approach taken in food-source-switching models of predation (van Baalen et al. 2001). More research on facultative scavenger behaviour is needed to realistically explore the effect of food switching on the mesoscavenger release hypothesis.

Known consequences of losing apex scavengers

The literature we review in this paper, along with our dynamic models, suggest that without apex scavengers, organic waste may be left unscavenged for longer periods and at higher biomass, and this can increase mesoscavenger abundance (biomass in our models) due to the increase in carrion biomass. Such increases in mesoscavengers and waste can change ecosystem structure (Sebastián-González et al. 2016) and impact human well-being (Markandya et al. 2008; Braczkowski et al. 2018; O'Bryan et al. 2018). Mesoscavengers are often pest species. Their population increases can lead to a loss of species at lower trophic levels (Ackerman et al. 2006), increased invasive species (Brown et al. 2015), increased associated pest control costs (Buechley & Şekercioğlu 2016b), and disease risk (Markandya et al. 2008). There is evidence that some facultative mesoscavengers have faster reproductive rates and can therefore increase in population size with more available resources compared to apex obligate scavengers, assuming that increased carrion will result in increased fecundity (Buechley & Şekercioğlu 2016b). Research in the Canary Archipelago showed that increased scavenging opportunities at "vulture restaurants" resulted in increased predation of native ground-nesting birds by facultative scavengers (Cortés-Avizanda et al. 2009). Similarly, the California gull

(*Larus californicus*) depredated 61 percent of American avocet chicks (*Recurvirostra americana*) and 23 percent of black-necked stilt chicks (*Himantopus mexicanus*) in San Francisco Bay as a result of an increase in available refuse (Ackerman et al. 2006). Furthermore, with the loss of apex scavengers and the increased availability of carcasses under a mesoscavenger release scenario, it is likely that invertebrate scavengers will have higher importance in reducing carcass biomass. Future investigations on the relationship between mesoscavengers and invertebrate scavenger resource exploitative competition would be informative. For example, it is plausible that invertebrate scavenger release may occur with the loss of apex scavengers, but these dynamics are poorly understood (but see DeVault et al. 2004). As a result, examination of the mesoscavenger release hypothesis and the impacts across multiple taxonomic and functional groups would be an important future research agenda.

Burgeoning mesoscavenger populations may affect human well-being (Braczkowski et al. 2018; O'Bryan et al. 2018), such as the spread of bubonic plagued rats of the 1300's (Keeling & Gilligan 2000). More recently, rabies risk has increased dramatically following the rapid decline of India's apex obligate scavengers, vultures (Markandya et al. 2008) and more than 20,000 Indian citizens have died from rabies each year since 1985 (Menezes 2008). There have been numerous recent calls for vulture conservation and feral dog sterilization (Markandya et al. 2008). Not only does increased carrion result in increased mesoscavengers, but it can also result in amplified carcass-borne diseases, such as spongiform encephalopathies found in unconsumed livestock remains in the European Union (Gwyther et al. 2011). Additionally, in Kenya, carcasses without vultures had a three-fold increase in interactions between facultative mesoscavengers (Ogada et al. 2012b), and the authors contend a potential change in patterns of disease transmission between mesoscavengers as a result. Thus, the loss of apex scavengers can alter scavenging assemblages that can cause risk to ecosystem structure and human health either by increasing disease hosts or by increasing carcass decay time. However, empirical evidence that apex scavengers alter mesoscavenger dynamics at carcasses and thus disease dynamics on its own does not indicate that similar patterns hold at the population-level. As such, the mesoscavenger release hypothesis should be vigorously tested, especially around the effect of removing apex scavengers on mesoscavengers at the population-level.

Apex scavenger conservation in the 21st century

Vultures and many apex facultative scavengers are among the most threatened functional groups worldwide (Estes et al. 2011; Buechley & Şekercioğlu 2016b; Ogada et al. 2016). A better understanding of the effects of apex scavengers on mesoscavenger communities is important to illuminate where and when to undertake conservation action. This has been clearly demonstrated for apex predators and mesopredator release, with significant efforts now underway to rewild and re-introduce populations of apex predators in North America and Europe (Svenning et al. 2016). These efforts could be expanded to include the protection of apex scavengers, particularly in places where mesoscavenger release could have negative consequences for humans or ecosystems. Areas such as southern and eastern Africa, South Asia, and the Iberian Peninsula appear to be of high priority for Old World vulture conservation given current threats and lack of protection (Santangeli et al. 2019). Additionally, developing nations may be particularly susceptible to the consequences of apex scavenger loss due to a lack of waste disposal infrastructure and increased disease risk from harmful mesoscavengers.

Since scavengers feed on organic waste, they are often found in human-dominated areas where anthropogenic waste is prevalent. Indeed, avian scavengers in the Middle East and Africa strongly select for habitats associated with humans, such as highways, power distribution lines, and towns (Buechley et al. 2018). Apex scavenger persistence in shared landscapes will therefore require tolerance from local people who live alongside these species. However, apex scavengers are frequently persecuted and viewed as nuisance animals as they can be found around these human dwellings (Buechley & Şekercioğlu 2016b). An improved understanding of the importance of apex scavengers and the benefits they provide could help raise their profile and make their conservation a global priority. For example, there is evidence of a variety of human communities that tolerate apex scavengers. In the Tigray region of Ethiopia, for instance, spotted hyenas (*Crocuta crocuta*), facultative scavengers, are tolerated because of the traditional belief that they eat evil spirits as they remove livestock remains and other garbage in and around waste dumps (Baynes-Rock 2015; Yirga et al. 2015). Similarly, Egyptian vultures (*Neophron percnopterus*) are thriving in urban areas of Socotra, Yemen where they dispose of 22.4 percent organic waste produced in towns annually (Gangoso et al. 2013). Nevertheless, when apex scavenger species are no longer tolerated, facultative mesoscavengers may increase in abundance and richness, which is likely to result in increased human-wildlife conflict. For example, the loss vultures in India resulted in an increase in feral dog bites on humans (Markandya et al. 2008).As such, it is imperative that future research focus on the relationship between scavenger trophic interactions and human tolerance (Morales-Reyes et al. 2018).

Conclusion

While there is both empirical and theoretical evidence for apex scavengers releasing mesoscavengers (the mesoscavenger release hypothesis), there is still much to learn about the impacts of different apex scavengers on mesoscavenger assemblages. We find in our simple dynamic models that the relationship between apex facultative scavengers and mesoscavengers vary depending on their handling times, search efficiencies, and carrying capacities (Figures 4.4, Appendix 4 Figures 1 & 2). We recommend that future work explore the dynamics of these parameters as they pertain to different feeding strategies. Further to this, there is much debate on how scavenger assemblages are arranged in time and space, such as the influence of carcass species and type (Olson et al. 2016; Moleón et al. 2017), carcass size (Moleón et al. 2015), season (Pereira et al. 2014), or location (Smith et al. 2017) among others on community dynamics. There may be variable effects of apex scavenger removal on obligate versus facultative mesoscavengers. Additionally, most of the apex scavenger and mesoscavenger examples illustrated in this manuscript, and the ones used in our models, pertain to terrestrial scavengers, with vulture systems dominating the literature. As such, our models do not consider the contribution of invertebrate scavengers relative to vertebrate scavengers (DeVault et al. 2003; Griffiths et al. 2018), and we recommend future research incorporate invertebrates in models investigating the mesoscavenger release hypothesis. Thus, our simple models are useful as a starting point for future studies exploring the effects of apex scavengers on mesoscavengers across a multitude of systems.

Apex scavenger conservation is especially important given the potential negative impacts of released mesoscavengers on ecosystem and human health. Based on a global meta-analysis, there is already skewed dominance towards mesopredators and mesoscavengers that is likely due to altered top-down control mechanisms from declining apex scavenger and predator populations (Mateo-Tomás et al. 2015). Considering nearly 80 percent of obligate scavenger species are currently in a rapid state of decline (Buechley & Şekercioğlu 2016b), and widespread evidence that human pressures alter apex scavenger distributions and population viability (Ogada et al. 2012a; Huijbers et al. 2015; Di Marco & Santini 2015; Buechley & Şekercioğlu 2016b; Șekercioğlu et al. 2016), we urge proactive management tailored to apex scavengers similar to approaches applied as a result of mesopredator release. By building the research base associated with the mesoscavenger release hypothesis, we will likely better understand the vulnerability of critical ecosystem and human well-being services that apex scavengers provide and can therefore administer more effective conservation action.

CHAPTER 5 Authorship Statement

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Alexander Braczkowski and the Candidate conceived the idea for the manuscript. The Candidate identified methodologies to conduct the analyses, with input from Alexander Braczkowski, Martin Stringer, and Hawthorne Beyer. The Candidate wrote the initial manuscript with substantial input from Alexander Braczkowski. The Candidate, Alexander Braczkowski, Martin Stringer, and Hawthorne Beyer conducted the analyses. Alexander Braczkowski and the Candidate revised the manuscript following co-author feedback. The Candidate edited the manuscript heavily and refined the analyses after journal feedback. All authors contributed to revising and improving the manuscript.

CHAPTER 5 Leopards provide public health benefits in Mumbai, India

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Abstract

Populations of large carnivores are often suppressed in human-dominated landscapes because they can kill or injure people and domestic animals. However, carnivores can also provide beneficial services to human societies, even in urban environments. We examined the services provided by leopards (*Panthera pardus*) to the residents of Mumbai, India, one of the world’s largest cities. We suggest that by preying on stray dogs, leopards reduce the number of people bitten by dogs, the risk of rabies transmission, and the costs associated with dog sterilization and management. Under one set of assumptions, the presence of leopards in this highly urbanized area could save up to 90 human lives per year. A further indirect benefit of leopard presence may be an increase in local abundance of other wildlife species that would otherwise be predated by dogs. The effective conservation of carnivores in human-dominated landscapes involves difficult trade-offs between human safety and conservation concerns. Quantitative assessments of how large carnivores negatively and positively affect urban ecosystems are critical, along with improved education of local communities about large carnivores and their impacts.

In a nutshell

Predation of stray dogs by leopards (*Panthera pardus*) in areas within Mumbai, India, likely benefits humans by reducing dog bite incidents, and thereby potentially preventing 90 people from dying of rabies

The presence of leopards also saves US$18,000 per year in dog management costs

The indirect beneficial impacts of large carnivores on human well-being may be substantial and are underestimated, especially in urban environments

Management of the world's large carnivores is a polarizing issue (Ripple et al. 2014). In many areas, carnivores are vilified for attacks on livestock, charismatic wildlife species, and humans (Packer et al. 2005; Dickman 2015), which often leads to the retaliatory killing of carnivores (McManus et al. 2015). Yet large carnivores are often flagship species for many of the world's ecosystems (Ripple et al. 2014), and play essential roles in regulating numerous ecosystem processes, from controlling prey populations (Ripple et al. 2014) and suppressing smaller carnivores (Berger et al. 2008), to reducing parasite loads in humans (Harris & Dunn 2010) and promoting seed dispersal (Sarasola et al. 2016).

The contribution of large carnivores to human well-being in shared landscapes has received little attention. Along with the growth of human populations in many developing nations, there have been concomitant increases in the populations of "pests", such as stray dogs, in both urban and agricultural landscapes (Hughes & Macdonald 2013). We estimated the ecosystem service value of a small population of ~35 leopards (*Panthera pardus*; Surve et al. 2015) that feed on stray dogs. This population of leopards lives in and around the 104-km^2 Sanjay Gandhi National Park (SGNP), which borders the city of Mumbai, India, currently ranked as the sixth largest urban agglomeration in the world (UN 2015a). Mumbai is home to an estimated 96,000 stray dogs (Hiby 2014), which regularly attack people (Harris 2012) and whose primary predator is the leopard (Hayward et al. 2006). The leopards of Mumbai are a striking example of humans and large carnivores living in close proximity, and of how a large carnivore may benefit humans through their regulation of stray dog populations.

Leopards living on an urban edge

Approximately 35 mature leopards live in SGNP and the adjoining Aarey Milk Colony, a suburb of Mumbai (Figure 5.1; Surve et al. 2015). Sanjay Gandhi National Park is a nationally designated protected area characterized by moist deciduous forest, whereas Aarey, a former dairy colony connected to the southwest corner of SGNP, consists of a 16-km^2 matrix of pastures, forest patches, and human settlements (Figure 5.2). The park is slowly being encroached upon by some of the largest slums in Mumbai, and at present approximately 250,000 people are estimated to live within just 500 m of the park's borders (K Tiwari pers comm; Prasad & Tiwari 2009), with an additional 100,000 people living in and around Aarey (P Variyar pers comm; Appendix 5).

Figure 5.1. Leopards in Mumbai's Sanjay Gandhi National Park (SGNP) regularly leave the confines of the park to hunt stray dogs. (a) An adult female near an apartment block bordering the park's eastern edge; (b) a female at a Muslim sacred site overlooking the city of Mumbai; (c) a young leopard walking through a village in the Aarey Milk Colony; and (d) a young leopard at a construction site in an informal settlement.

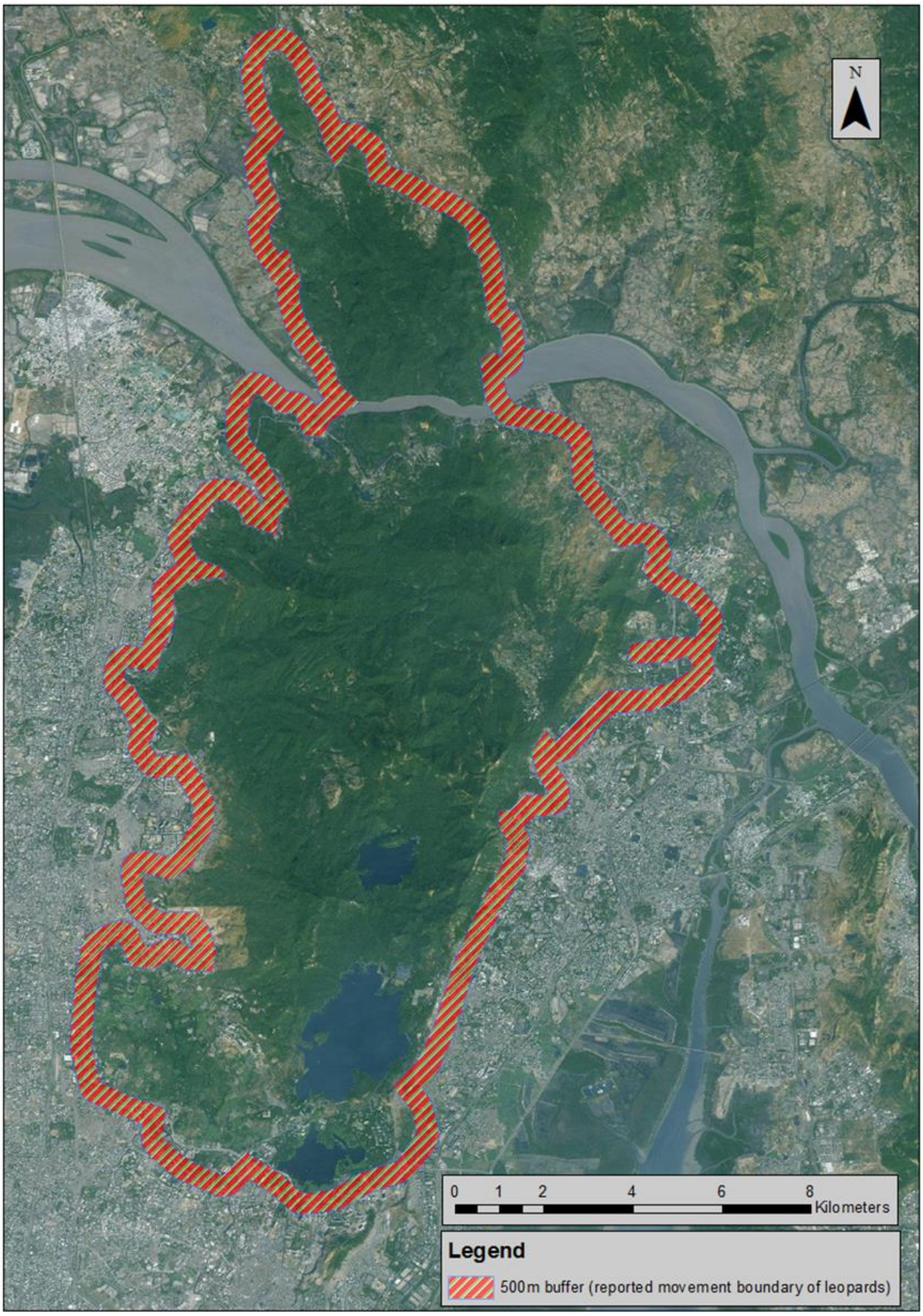

Figure 5.2. Map of the 104-km^2 SGNP and 16-km^2 Aarey Milk Colony on the southwest side of the park. The hatched area represents a 500-m buffer zone from the forest edge (buffer area = 43 km^2) where leopards predate on stray dogs and where an estimated 350,000 people live, mostly in informal settlements.

Mumbai is home to one of the largest populations of stray dogs in the world (an estimated 96,000 animals), which roam freely throughout both urban and rural slums (Hiby 2014). This abundance of stray dogs arises as a result of human tolerance and the hundreds of tons of uncollected refuse and carrion that accumulate within slums (Prasad & Tiwari 2009), exacerbated by the catastrophic decline in carrion-eating vulture populations over the past 20 years due to the widespread use of diclofenac, an anti-inflammatory drug, to treat cattle (Markandya et al. 2008).

Leopard impacts on stray dog populations

Dogs have been the primary prey source for leopards in SGNP over the past 15 years (Edgaonkar & Chellam 2002; Prasad & Tiwari 2009; Surve et al. 2015). Dog biomass represents approximately 42% (range 25–58%; Edgaonkar & Chellam 2002; Surve et al. 2015) of the diet of leopards inhabiting this area. Assuming a leopard daily food intake of 4.7 kg (Odden & Wegge 2009), and given that 17.1 kg of an average dog can be consumed (assuming 95% of the carcass is eaten; Stander et al. 1997; Athreya et al. 2016), a population of 35 leopards will kill about 1500 dogs per year (range 878–2036, depending on diet range) in and around SGNP (see Appendix 5 for a detailed explanation).

Few dogs, if any, live within the interior of SGNP itself (Surve et al. 2015), which may suggest behaviorally mediated distribution effects by leopards or a paucity of resources for the dogs (Butler et al. 2004). We assumed that leopard activity in urban areas is concentrated within 500 m of the forest edge, based on expert opinion and 10 sightings of leopards outside the park (see Appendix 5 for details). This 500-m strip around the park covers an area of 43 km^2 and, given a mean dog population density of 17.3 ± 0.3 dogs km^{-2} (Surve et al. 2015), we infer that this region could contain 730–760 dogs, or about half the number of dogs the leopards consume. This difference between the number of dogs on the periphery of the park and the number of dogs consumed by leopards in the same area suggests that dogs disperse into this low-density area from surrounding neighborhoods and are subsequently preyed upon.

The value of leopard predation in combating the stray dog problem can be assessed in comparison with the local government's ongoing dog sterilization program, which is conducted at a cost of US$11.90 per dog (www.wsdindia.org). If the total number of dogs that leopards consume in this system (ie ~1500 individuals) is multiplied by the cost of sterilizing each dog (US$11.90), then predation by leopards is arguably worth about US$18,000 in saved sterilization costs, equivalent to ~8% of Mumbai's existing annual sterilization budget (US$208,000; Correspondent 2015).

Dog impacts on human populations

Although rabies transmitted by stray dogs are responsible for the deaths of over 20,000 people in India per year (Biswas 2016), it is illegal to kill stray dogs (Section 428 of the Indian Penal Code, 1860, and The Prevention of the Cruelty of Animals Act, 1960), so Mumbai citizens often carry rocks and bamboo rods to fend them off (Harris 2012). Stray dogs are the primary source of rabies transmission to humans (Knobel et al. 2005), and an average of 74,603 bite cases have been reported per year among a human population of 21 million people in Mumbai (2011–2015 5-year mean; Table 1 of Appendix 5). For Mumbai's 96,000 stray dogs, this corresponds to 0.78 bites per dog per year, or 3.6 bites per 1000 people per year. This is likely a conservative estimate, however, as disease incidents are greatly underreported in developing areas; for example, Singh et al. (2006) estimated that leishmaniasis was underreported by a factor of 8.13 in Bihar, India, and even in the US state of Pennsylvania, dog bites were greatly underreported in 1980 (Beck & Jones 1985).

As stray dogs gravitate toward the resources available in and around slums, their populations often overlap with those of humans, and thus dog bites and rabies transmission disproportionately affect the poorest members of society (Acosta-Jamett et al. 2010; Gogtay et al. 2014). Although rabies vaccinations and post-exposure treatments are subsidized by some hospitals (Gogtay et al. 2014), they cost on average US$33.75 (range US$26–42; Table 2 of Appendix 5), which represents a substantial expenditure for the majority of bite victims, who typically live below the poverty line. On average, people living on the periphery of SGNP earn just US$0.75–1.50 per day (CPDR 2000).

Leopards may benefit human health and dog management

The statistics noted above can be used to estimate the reduction in exposure to dog bites for the 350,000 people living within leopards range (ie the 500-m buffer), as compared to typical exposure for those living elsewhere in the city. The estimated dog density in the park periphery (17.3 km^{-2}) is 40 times lower than densities in four urban slums located deeper within the city (a dog density of 688 dogs km^{-2} is found 2.5–13.6 km [mean = 7.4 km] from the park boundary; Hiby 2014) and nearly 10 times lower than the citywide average (96,000 dogs in 603 km^2 = ~160 dogs km^{-2}). Assuming that bite rates will be roughly proportional to both dog density and human population, we estimated that people living immediately adjacent to the park experience about 10 times fewer dog-bite incidents than is typical for the city. At an average bite rate of about 3.6 bites per 1000 citizens for the city as a whole (approximately 74,603 bitten out of a total population of 21 million), a region of 350,000 people would expect to see around 1200 bite incidents per year. However, because the dog density near the park is just 11% of the average density for the city, people living immediately alongside SGNP may experience just 11% of the number of bites, or perhaps fewer than 140 bites in total annually. In other words, leopard predation may prevent over 1000 bites per year in this region.

If leopards were absent from the park, then the surrounding dog population would increase not merely to the average value but to match the many hundreds of dogs per square kilometer that are found in other slums, suggesting that the benefit derived from the presence of these large carnivores is even greater than it would initially appear. We used a simple Lotka-Volterra predator–prey model to explore the potential increase in stray dog numbers and subsequent attacks on humans per year around the park in the absence of leopards (Figure 5.3). We assumed that the stray dog carrying capacity is equivalent to the highest documented dog density in the region (688 dogs km^{-2}), and that if leopards were removed from the system, then dog densities would increase to carrying capacity. We estimated the dog population growth rate (r) – based on the assumption that leopards are holding the dog population around the park at its current density – using the equation $r = (p/N_0)/(1 - N_0/K)$, where p is the number of dogs predated by leopards per year, N_0 is the current number of dogs within the leopards' range, and K is the carrying capacity.

Under this scenario, the increase in dog numbers resulting from the absence of leopards could lead to increases in dog bites of humans from under 140 to over 5000 per year (Figure 5.3a). Given that >78% of dog bites in Mumbai require medical treatment and 2.14% require treatment with immunoglobulin (ie bites that pose a risk of rabies exposure; Gogtay et al. 2014), it follows that nearly 4000 medical treatments and 90 lives may be saved each year by leopards limiting the expansion of the dog population in this region. Under the worst-case scenario, medical treatment costs in this area could reach as high as ~US$200,000 per year (Figure 5.3b). This estimate is based on an average treatment cost of US$33.75 per person, 350,000 people, and a bite rate of 3.6 bites per 1000 people that increases to 15.5 bites per 1000 people as a result of the dog density rising from 160 to 688 dogs km^{-2}, and assuming that every bite victim requires post-exposure treatment.

With both human and dog populations likely to increase over the coming decades, the value of retaining the leopards in SGNP may become even greater than these estimates indicate. Mumbai's human population is projected to double by 2050 (to 42.4 million people; Hoornweg & Pope 2014), and if accompanied by a doubling of the dog population, epidemiological theory would predict that the number of dog bites to humans, along with the associated costs to human health and livelihoods, would increase a further fourfold (Figure 5.3b).

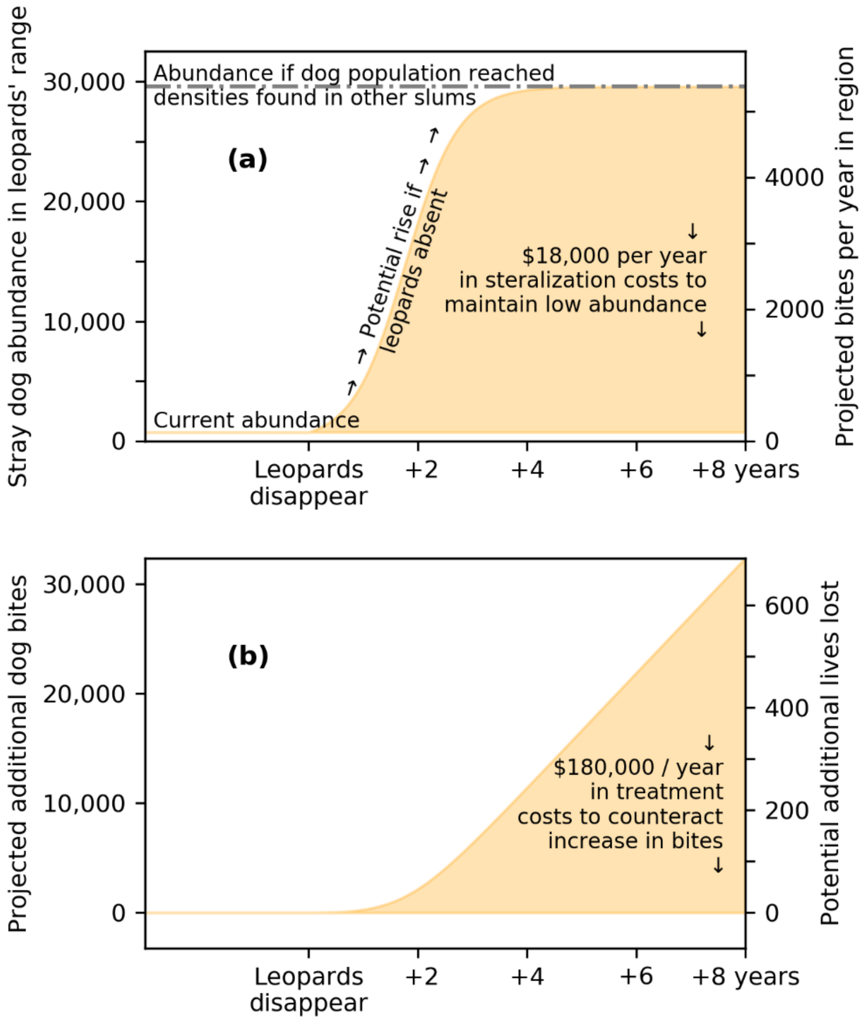

Figure 5.3. (a) Projected dog bites per year and dog sterilization costs, along with (b) bite treatment costs and potential additional human lives lost if leopards were removed from SGNP.

Although our estimates are based on known leopard diet and dog densities within and around SGNP, there remains substantial uncertainty about the valuation of this ecosystem service. For example, we assumed that dogs continue to predominate in the leopards’ diet; however, large carnivore diets are variable across space and time (Johnson et al. 1993). Moreover, only approximate estimates of dog bite rates on humans (Sharma et al. 2016) and the human population size for the area around the park are available. Recent research on bite rates from stray dogs in Delhi, India, revealed an annual per capita bite rate of 0.025, which is considerably higher than our estimate of 0.0034 bites person^{-1} year^{-1} (Sharma et al. 2016). We also assumed that dog bite rates were consistent across the region, reflecting the findings of

Sharma et al. (2016), who determined that bite rates were similar across urban areas.

Regarding leopard spatial dynamics, local knowledge and newspaper reports led us to conclude that leopards frequently roam in and around a 500-m buffer zone bordering SGNP, but there are no published data detailing leopard movements in this area. Overall, it is unclear whether our work over- or underestimates the value of services provided by leopards in this system. Further research on the interactions among leopards, dogs, and people will improve the accuracy of these estimates and the areal extent over which they occur, but our analysis indicates the value of these services to be substantial. However, linking leopard predation of dogs to human well-being also requires careful assessment of the costs of leopards as well, including mental health effects (such as the stress and fear associated with living in such close proximity to an apex predator) that could offset any indirect benefits of leopard presence.

Human–wildlife conflict and the future of leopards in Mumbai

The negative impacts of leopards on humans around SGNP have been managed and largely mitigated, with leopard attacks in Mumbai dropping substantially (to one or two cases per year) following the abandonment of leopard translocation programs in 2003, and the development and implementation of dedicated environmental awareness and “best practice” campaigns directed toward people entering the forest. As of 2015, there had not been a single human death from leopards in Mumbai since October 2013 (Surve et al. 2015). By comparison, attacks on humans by leopards peaked at 25 incidents in 2002 (Athreya et al. 2011). Previous attacks were largely attributed to intraspecific conflict caused by translocations of foreign “problem leopards” to the park by local Forest Department personnel (Athreya et al. 2011; Bhatia et al. 2013). In March 2017, however, a leopard attacked a child in the Aarey Milk Colony near SGNP (Alok 2017). This attack, in combination with other reports of attacks on humans by neighboring leopard populations, will likely increase fear and stress levels among the local residents. The negative impacts of leopards also reach far beyond direct human injury and death, and include depredating both livestock and domestic pets in areas around the park, and reducing the abundance of bushmeat species that are valued by local people (Inskip & Zimmermann 2009).

Conservation of leopards in Mumbai will therefore be a challenge in the future. With urban Mumbai expected to grow 26% by 2020 (Moghadam & Helbich 2013), the slums will likely further encroach upon forested areas and the leopard habitat they provide (Figure 5.2). Furthermore, SGNP and the adjoining Aarey Milk Colony are under constant threat from development, and the recent approval of the Metro III train car shed project in the Aarey colony is likely to lead to the clearing of large swaths of leopard habitat.

Global impacts of large carnivores in urban environments

Nineteen other studies across Africa and Asia have shown that leopards prey on stray dogs (Butler et al. 2013), suggesting that our results are not isolated and that leopards may benefit humans more broadly across their range. More generally, these benefits may be realized in shared landscapes where wildlife frequently prey upon stray dogs. This may be limited to areas where stray dogs and felids (eg. Jaguars *Panthera onca*) still occur. Dog attacks on humans have a wide range of consequences above and beyond direct injury, including time off work or even job loss, lost wages, medical expenses, and reduced ability to care for dependents (Knobel et al. 2005; Gogtay et al. 2014). In many countries, dogs are infected with rabies, which can be fatal to humans and livestock if post-exposure treatment is not administered quickly (Gogtay et al. 2014). Unfortunately, high densities of people and stray dogs often occur in the poorest communities, such as slums, where dog attacks can have the most severe impacts (Gogtay et al. 2014). As populations of large felids are threatened and declining in many areas (Ripple et al. 2014, 2017; Jacobson et al. 2016), there is a risk that the benefits of their regulatory effects on dog populations will be reduced or lost, further exacerbating the impacts of stray dogs on local human populations (Treves & Bonacic 2016).

Large carnivores are valued for their ecological roles in regulating trophic levels and habitat structure in protected areas (Fortin et al. 2005; Ripple & Beschta 2012b). However, less is understood about the role of carnivores as ecosystem service providers in shared landscapes. Previous research has established that European jackals (*Canis aureus moreoticus*), a subspecies of the golden jackal (*Canis aureus*), and spotted hyenas (*Crocuta crocuta*) reduce organic waste by scavenging in urban areas of Serbia and Ethiopia, respectively (Yirga et al. 2015; Ćirović et al. 2016). In addition, Gilbert et al*.* (2016) postulated that indirect benefits to humans (eg reduced loss of life and injury, lower rates of property damage) would result from the re-colonization of North America by cougars (*Puma concolor*) via reductions in vehicle collisions with prey species as a result of lower prey densities. Further research is needed to better quantify the full range of social, economic, and ecological impacts of carnivores in shared landscapes.

Wildlife attacks on humans, which are often featured in and sensationalized by the media (Bhatia et al. 2013), may result in risk-averse management strategies at local scales; for example, the Government of Western Australia initiated a shark-culling program as a direct result of media coverage of shark attacks (McCagh et al. 2015). It is critical that such attacks from carnivores, though tragic, do not prompt ill-considered and reactionary management responses, such as local eradication programs, because there is little or no evidence that such programs are effective and in fact they may even be counterproductive (McCagh et al. 2015). It is essential that the reduction in attacks on humans achieved through carnivore eradication be weighed against the potentially much greater number of lives saved, among other benefits, by the presence of these carnivores.

The long-term survival of carnivores in shared landscapes requires the effective management of human–carnivore conflict. Whereas the negative effects of carnivores have been well documented in the scientific literature (Inskip and Zimmerman 2009) and in the popular media (Bhatia et al. 2013; McCagh et al. 2015), the benefits provided by carnivores to human well-being and ecosystem services have not (eg Jacobson et al. 2012). Tolerance of large carnivores and their acceptance by humans (Bruskotter & Fulton 2012) are more likely to occur if the benefits of the species are understood (Bruskotter & Wilson 2014). Experimental studies have shown that the perceived benefit of the presence of large predators and scavengers by local societies is a predictor of tolerance levels (Bruskotter & Fulton

2012; Bruskotter & Wilson 2014). For example, Egyptian vultures (*Neophron percnopterus*), populations of which are declining globally, thrive in the towns and villages of Socotra, Yemen, an archipelago of four islands, because of local recognition of the valuable livestock and human waste processing services they provide. These services are otherwise lacking in this area (Gangoso et al. 2013). Tolerance of large carnivores is also highly dependent on social factors, such as whether or not a neighbor tolerates the species (Treves and Bruskotter 2014).

Education and communication initiatives are important components of programs geared toward improving tolerance. For example, Slagle et al. (2013) found that people were more tolerant of black bears (*Ursus americanus*) when given information describing the benefits of the presence of bears. In this regard, the popular media may be an important avenue for communicating carnivore benefits. For instance, Bhatia et al. (2013) found that mass media focused on human–carnivore conflicts in India, were willing to correct erroneous perceptions, and in some areas even helped to facilitate proper management and mitigation. Research into the ecosystem services associated with wildlife must be actively communicated in order to establish a more balanced perspective on the value of wildlife to the general public. The continued persistence of carnivores in shared landscapes is contingent upon identifying ways to mitigate detrimental impacts while simultaneously recognizing and facilitating the benefits provided by these species.

CHAPTER 6 Large carnivores provide co-benefits to agricultural systems

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Abstract

Large carnivores are often perceived as a purveyor of misfortune in shared landscapes. Yet the loss of large carnivores has a deleterious impact on ecosystems that can in turn affect human societies. Here we provide two case studies on the beneficial consequences of restoring large carnivores using a predictive model. We show that through their successful expansion, large carnivores can reduce damage to agricultural lands by decreasing invasive wild pig densities. We find that restoration of the Florida panther (*Puma concolor coryi*) could save 20% of agricultural land from pig destruction (at least \$10.5 million USD in equivalent yield value of crops and beef production after accounting for livestock loss to predation). Contrastingly, we find that panther extinction would result in \$3.2 million USD loss in equivalent market value. Similarly, the restoration of dingo (*Canis lupus dingo*) in New South Wales and Victoria, Australia could save 6% of agricultural land amounting to \$3.1 million USD in otherwise lost crops and beef production. If dingoes are fully excluded in these states, then \$7 million USD market value could be lost to wild pig damage. While our analysis provides an initial assessment of the ecosystem services of large carnivore restoration to agricultural systems, there is much opportunity to explore the many socioeconomic services that carnivores can provide in shared landscapes, providing crucial tools for conservation practitioners, decision scientists, and policy makers.

Introduction

The global decline of large carnivores has resulted in a suite of deleterious effects on ecosystems (Estes et al. 2011; Ripple & Beschta 2012b; Ripple et al. 2014). Their loss can result in increased mesopredator and prey abundances that can alter ecosystem structure. This is because large carnivores have a top-down effect on species through direct predation, changes in habitat use, and decreased foraging time (Laundré et al. 2001; Sinclair et al. 2003; Winnie & Creel 2017). Not only can the loss of large carnivores result in ecosystem change, but the increase in certain prey species has been shown to impact human well-being, ranging from increased vehicle collisions (Côté et al. 2004) and disease risk (Levi et al. 2016), to amplified competition with livestock (Prowse et al. 2015) and destruction of agricultural lands (Barrios-Garcia & Ballari 2012). The destruction of agricultural lands by overabundant prey species has led to significant costs to farmers through the reduction in crops or destruction of soil in areas where large carnivores have declined (Schley & Roper 2003; Barrios-Garcia & Ballari 2012; Bankovich et al. 2016; Gren et al. 2019). The recovery and expansion of large carnivores may reduce overabundant prey species known to cause damage in agricultural lands – providing a crucial ecosystem service. However, little work has explored the potential of large carnivores at mitigating this damage and the ensuing savings to agricultural lands.

One of the most widespread non-native prey species, invasive wild pigs (*Sus scrofa*) (hereafter wild pig; Keiter et al*.* 2016), has been shown to cause significant damage to agricultural productivity, indeed in the United States over $1.5 billion USD annually is lost (Pimental 2007) from the destruction of crops and reduction of forage grasses for cattle (Barrios-Garcia & Ballari 2012). In one state in the United States alone, Florida, millions of dollars in damage to agriculture is caused by wild pigs (Bankovich et al. 2016). In Australia, wild pigs were deemed a pest as early as 1795 due to their destruction of agricultural lands (Bengsen et al. 2014). Such destruction still occurs today, with estimates that wild pigs can consume greater than 60% of their dietary biomass from agricultural products, as highlight by a study in northern Queensland (Gentle et al. 2015). Such consumption has amounted to greater than 9 million AUD in damages to lamb, wool, and grain production throughout Australia (Gong et al. 2009) with some estimates of damage and mitigation costs at greater than 106 million AUD per year (McLeod 2004). Wild pig populations are predicted to rise globally (Lewis et al. 2019). In Florida the population could potentially grow to upwards of 1 million individuals if all quality habitat is utilized by wild pigs (Lewis et al. 2019). It is recognised in Australia that a similar broadening of the wild pig distribution across the continent is likely without control (Long 2003; Bengsen et al. 2014). Unfettered increases in wild pig populations are likely to bring with them important economic implications for agriculture. To avert this, management actions are likely to be required (Lewis et al. 2017, 2019), and may be actively informed through an understanding of the impacts of native predators on invasive wild pig populations.

Here we provide two case studies of the benefits and costs of recovery and expansion of large carnivores at reducing wild pig abundance, and the potential ecosystem services this has on agricultural lands while accounting for potential depredations of livestock. We assess two iconic large carnivore species, with contrasting conservation status, the Florida panther (*Puma concolor coryi*) and the dingo (*Canus lupus dingo*) in Australia.

Case study introduction: The role of Florida panthers (*Puma concolor*) at reducing agricultural damage

The Florida panther (also referred to as panther and puma) is the only native predator of invasive wild pigs within the state, comprising nearly half of their diet (Maehr et al. 1990; Caudill et al. 2019). Panthers are a federally endangered species, and the last remaining puma species in the eastern United States (Johnson et al. 2010). Having lost 95% of their historic range, panthers are restricted to South Florida (Figure 6.1), with a total population estimated to be under 150 individuals (Gross 2005; McClintock et al. 2015). The initial cause of the decline of panthers stems from the early 1900’s when panthers were still hunted (Fergus & Chuck 1991). Hunting pressure (outlawed in 1967), compounded with severe habitat loss and fragmentation due to land conversion for agriculture and urban development, spelled the demise for the species, and panthers nearly went extinct by the end of the 20th Century (Fergus & Chuck 1991). As a result of the isolation of the population in south Florida, the population has experienced severe threats ranging from genetic malformations (Johnson *et al.* 2010), vehicle collisions due to increasing road development (McClintock et al. 2015), and increasing deaths from intraspecific aggression due to shrinking territories (Maehr et al. 1991).

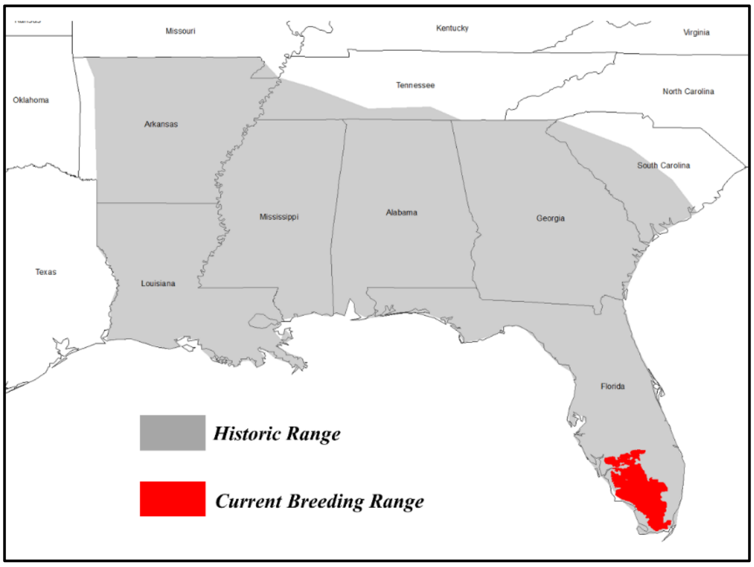

Figure 6.1. Florida panthers (*Puma concolor coryii*) have lost 95% of their historic distribution, and their core breeding population is restricted to South Florida (USFWS 2008).

Recovery of the Florida panther requires the protection and expansion of large swaths of habitat (Saremi et al. 2019) in the central and northern part of the state, where the population can expand through natural dispersal or through reintroduction schemes (USFWS 2008; Frakes et al. 2015). Current habitat connectivity initiatives are underway that address multi-species objectives, such as the Florida Wildlife Corridor (hereafter referred to as 'FWC'; Figure 6.2A; see: http://floridawildlifecorridor.org). However, over 41% of the corridor is unprotected land (Figure 6.2B; see Appendix 6) and as such is susceptible to numerous threats, for example, impending road development (Main 2019), suggesting unparalleled importance of private lands for the expansion of the species (Kreye & Pienaar 2015; Frakes et al. 2015). Indeed, Florida panthers have been utilizing habitats (including private lands) north of the core breeding range (albeit a limited number of dispersing males), into existing and proposed Florida Fish and Wildlife Conservation Commission areas (FWC ; Figure 6.2A). This indicates the importance of retaining existing habitat within the FWC, and safeguarding lands that are critical links between intact habitats (Figure 6.2B; Fergus & Chuck 1991; Team 2008; Johnson et al. 2010; Onorato et al. 2011; Frakes et al. 2015; Kreye & Pienaar 2015; Criffield et al. 2018).

Due to the current and potential expansion of Florida panthers within private and public lands north of their core breeding range, there is a growing concern from landowners, particularly the agricultural community, including concerns around increased risks of attacks on humans, pets, and livestock (Jacobson et al. 2012; Langin & Jacobson 2012; Kreye et al. 2017; Rodgers & Pienaar 2018). Such concerns on the perceived consequences of panther expansion can inhibit land connectivity and habitat recovery schemes that require community support (Madden 2008). However, the potential positive consequences of Florida panther conservation and subsequent expansion have not been quantified, including their effects on invasive wild pig densities and ensuing agricultural savings.

We assess the current agricultural benefits (land area and subsequent yield savings) of Florida panther predation on wild pigs, and examine their additional benefits if the population undergoes an expansion, assuming the successful expansion of the species through the FWC, which would connect the core panther breeding range in South Florida with that of habitats throughout the state (Figure 6.2A). We assess the relative impacts of the Florida panther on wild pigs and agricultural land savings for the current distribution of panthers, the distribution of the species under population expansion assuming protection and restoration of the FWC and its critical links (see gaps in Figure 6.2B), and a scenario where panthers go extinct. We hypothesize that invasive wild pig density is reduced as a function of Florida panther presence in the landscape with an associated savings in agricultural land from invasive wild pig damage. Our results will provide information on the potential consequences of Florida panther expansion on invasive wild pig and agricultural lands, and will represent a framework for future studies investigating the consequences of large carnivore recovery and expansion.

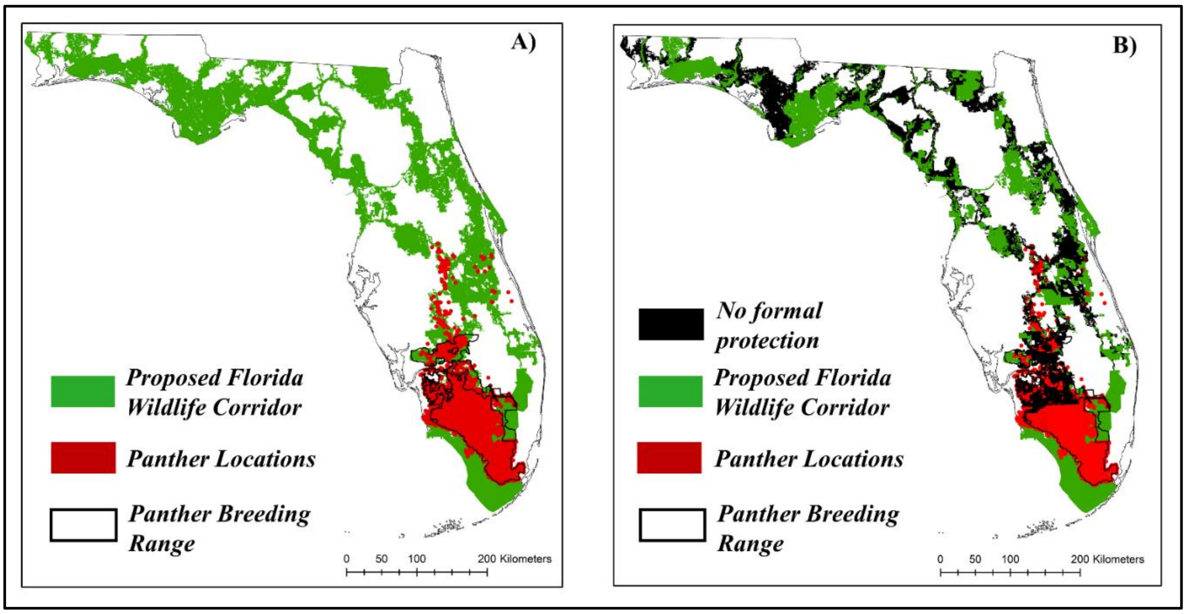

Figure 6.2. Panel A) shows Florida panther telemetry locations (red dots; for the years 1981-2018; Florida Fish and Wildlife Conservation Commission) on lands north of the core breeding range of the species (black outline), and this expansion is within the extent of the proposed Florida Wildlife Corridor (green polygon). However, panel B) shows the extensive gaps of formal protection (black polygons) within the proposed Florida Wildlife Corridor (green polygon), and a large portion of the panther's core breeding range (red polygon) is in unprotected land.

Case study introduction: The role of dingoes (*Canis lupus dingo*) at reducing agricultural damage

The dingo (also referred to as wild dog depending on the region and genetic purity; Stephens et al. 2015) is the only non-human mammalian predator of wild pigs remaining in Australia, with pigs comprising 3-29% frequency occurrence in their diet (Newsome et al. 1983; Corbett 1995; Forsyth et al. 2019). Dingoes have variable effects on wild pig populations (Forsyth et al. 2019). Some studies suggest that the dingo has minimal influence on pig numbers (Corbett 1995), while others propose that dingoes play a regulatory role (Woodall 1983; Saunders 1993) through the consumption of young pigs (less than 6 months-old) (Corbett 1995) and potentially through their behavioural modification (e.g. creating a 'landscape of fear'; Ritchie & Johnson 2009). Nevertheless, the highest recorded densities of wild pigs in Australia have been in areas absent of dingoes (Bryant et al. 1984; Saunders & Bryant 1988 as cited in Forsyth et al. 2019), suggesting a need for further research on the effects of dingoes on pig density and abundance.

The dingo was likely introduced to Australia around 3,500-4,000 years ago (Milham & Thompson 1976) and is controversially considered a native Australian mammal today (Fleming et al. 2001). Dingoes are widespread throughout most of Australia (Figure 6.3) that is to the north and west of the barrier fence (Fleming et al. 2001). The barrier fence (also referred to as dog fence or dog-proof fence) was built during the 1880's and runs for about 5,600 km from Fowlers Bay in South Australia to south-eastern Queensland to keep dingoes out of sheep and cattle rangelands (Fleming et al. 2001). Indeed, dingoes prey on cattle, sheep, and other livestock, which has resulted in retaliatory lethal control (Fleming & Korn 1989) and exclusion (Fleming et al. 2001; West 2008). However, a growing number of studies suggest that dingoes have a suppressive effect on native kangaroo and other herbivore populations that compete with livestock (see review of studies in Letnic et al. 2012). This reduction in native herbivores by dingoes can benefit livestock productivity (even when accounting for depredations) (Prowse et al. 2015) as long as dingoes have a healthy pack structure (Glen et al. 2007; Johnson & Wallach 2016). As such, there is considerable dialogue on the value of restoring dingo populations where they have declined (Dickman et al. 2009; Ritchie et al. 2012; Newsome et al. 2015). However, no studies have investigated how restoring dingoes in areas where they are absent south of the barrier fence will affect the predicted densities of wild pigs and how the reduction of pig densities by dingoes will affect agricultural lands.

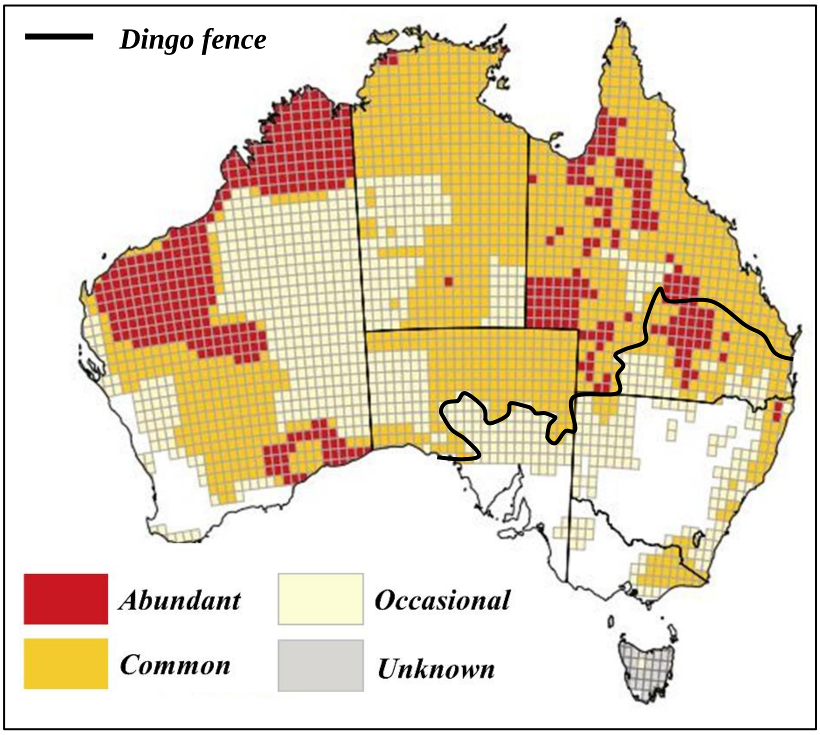

Figure 6.3. Distribution of the dingo (*Canis lupus dingo*) throughout Australia. Map adapted from West (2008). Note the dingo fence is an approximation as there is not an accessible geospatial layer.

We investigate the benefits of dingo to agricultural lands through their predation of wild pigs, and we assess their additional benefits if the population is restored in areas south of the barrier fence in New South Wales and Victoria, Australia (Appendix 6 Figure 2). As such, we examine the impacts of dingoes within their current distribution in these states, their distribution under expansion (assuming the barrier fence is removed and/or dingo lethal control is halted), and a scenario where dingoes are excluded or culled from the region. This work will aid current and future dialogue associated with expanding dingo populations and will provide additional data surrounding the effects that dingoes may have on wild pig populations and agricultural commodities at a regional scale.

Methods

Identifying large carnivore distribution and expansion areas

We identify existing extent of occurrence for both the Florida panther and the dingo using published data on individual locations (in the case of panthers) and estimates of distributions (in the case of dingoes). We then determine the potential expansion/recovery areas based on species habitat preferences (for both species) and proposed corridor conservation (in the case of panthers).

We determine the Florida panther's existing extent of occurrence as the minimum convex polygon (MCP) of known panther locations from 1981-2018 (Florida Fish and Wildlife Conservation Commission 2019; Figure 6.2A), a common approach used by the IUCN (Joppa et al. 2016b). We identify the panther core breeding range as the MCP of all telemetry locations south of the Caloosahatchee River following previous work (Fergus & Chuck 1991; Onorato et al. 2011; Frakes et al. 2015). We consider the area north of the breeding range as the primary expansion zone (Appendix 6 Figure 1), which is where dispersing males and a single gravid female have expanded their range. Areas north of the primary expansion zone are considered the secondary and panhandle expansion zones (Appendix 6 Figure 1), which have no known panthers, and are within the proposed Florida Wildlife Corridor (Figure 6.2A; see: *http://floridawildlifecorridor.org*). All expansion zones north of the breeding range represent key opportunity areas for continued population expansion of the species (Maehr et al. 2002; USFWS 2008). We assume panthers use all forest patches and habitat within 1 km distance of a given forest patch, as Florida panthers have been shown to utilize these habitats for dispersal and hunting (see Onorato et al. 2011). We identify this 1km distance from forest patches as the predation buffer, as panthers are known to prefer hunting along forest edges (Onorato et al. 2011). We delineate forest patches using known upland forests from the Florida Department of Environment Protection's state-wide land use and land cover dataset (FDEP 2019). We use the resultant predation buffer for quantifying the effects of puma on invasive wild pigs.

Since the dingo/wild dog distribution covers the majority of the Australian continent, we only assess areas south of the barrier fence where dingoes (and wild dog/dingo hybrids; Cairns et al. 2019) are of occasional occurrence or are absent, particularly within the states of New South Wales, Victoria, and South Australia (Fleming et al. 2001; West 2008; Figure 6.3), and delineate their existing extent of occurrence based on West (2008). Unlike the Florida panther distribution, we assume dingoes utilize all habitat types within the study region given they have been shown to not use habitat types disproportionate to their availability (Edwards et al. 2002; but see Newsome et al. 2013).

Quantifying invasive wild pig densities

We model predicted pig densities in the absence of human management based on biotic and abiotic variables known to explain wild pig densities globally, including large carnivore presence (Lewis et al. 2017; see Appendix 6 Table 1 for a list of variables, sources, and parameter estimates). We adopt the parameter estimates from Lewis and colleagues' (2017) based on their multiple linear regression analysis to predict pig densities at a 1km^2 resolution; however, we use state-level data on agricultural lands (FDEP 2019 for Florida and Geoscience Australia's dynamic land cover dataset for Australia; Lymburner et al. 2011). For Florida, USA and New South Wales and Victory, Australia, wild pigs are estimated to be widespread (Hernández et al. 2018; see Appendix 6 Figure 2 for known distribution of wild pigs in Australia vs. the study region).

We assess the impacts of panthers and dingoes on wild pig densities using the wild pig density model above (i.e. as the variable for large carnivores in the model; see Appendix 6). We modify the large carnivore variable depending on the conservation scenario per pixel (e.g. the pixels where large carnivores are present get a "1" vs. not present a "0"). We also provide an estimate of the number of individual pigs likely killed by panthers per year in Appendix 6 as supplementary information.

Quantifying invasive wild pig damage on agricultural lands

To identify agricultural areas susceptible to wild pig damage, we mask wild pig densities to agriculture-buffered forest patches. This is because the presence and probability of invasive wild pig damage to agricultural lands has been found to be highest near woody edges where they have significant cover (Meriggi & Sacchi

2001; Calenge et al. 2004; Thurfjell et al. 2009; Amici et al. 2012; Morelle & Lejeune 2015). We identify all upland wooded patches that are adjoining agricultural lands using state-wide land cover data (FDEP 2019 for Florida and Geoscience Australia's dynamic land cover dataset for Australia; Lymburner et al. 2011). We only include agricultural lands adjoining forest patches that are within 1 km from a forest edge to determine the relative area of agricultural land susceptible to invasive wild pig damage (Calenge et al. 2004; Thurfjell et al. 2009), which matches the resolution of the predicted densities. We then calculate the proportion of that agricultural land area vulnerable to predicted wild pig densities, assuming that the relationship between wild pig density and soil damage is a positively curved relationship as described by Hone (2006, 2012). See Appendix 6 for a detailed description of the pig density-disturbance relationship.

Quantifying the economic value of invasive wild pig damage to agricultural lands

We determine the value of wild pig damage to croplands using average yearly market rates per unit area. For Florida, we use the average yearly market rates (for 2018) per acre for three agricultural land cover classes: row crops, field crops, and hay crops from the USDA National Agricultural Statistics Service (USDA 2018). For Australia, we obtained data on the average yearly market rate (for 2017) for irrigated and rainfed crops from the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES 2017). We convert the values of each crop type to km^2.

To estimate the economic loss from wild pig destruction of livestock pasture, we modified a simple economic model from Bankovich et al. (2016; originally modified from Ferrell et al. 2006), which assesses calf weight, produced under stocking densities per unit area. We assumed that the amount of pasture is directly related to the ability of a unit area to produce beef and that any loss in pasture area would result in similar loss to beef production (Bankovich et al. 2016). We also modify the model by incorporating loss of calves from predation. We define the model as:

$$C = \frac{W * CW * k}{R}$$

Where C is calf kilograms produced per hectare (ha) per year, W is the weaning proportion of cows (we used 0.75 to reflect the Florida average [Bankovich et al. 2016] and 0.76 to reflect the Australia average [ABS 2013]). CW is the average calf weight (249.5 kg; Bankovich et al. 2016); k is the proportion of unit area not rooted and R is the stocking rate (one cow-calf pair per 1.2 ha for Florida [Bankovich et al. 2016] and one cow-calf pair 1.6 ha for Australia [Blackwood et al. 2006]). The value of calf weight was determined at current market rates (~3.84 USD/kg for Australia and ~5.68 USD/kg for Florida).

To assess the costs of large carnivores, we consider the potential proportion of calf production lost to predation, and assume that the calf mortality is directly proportional to the loss in equivalent calf weight per unit area. We assume that 5.3% of calf production is lost to panther depredations in Florida based on panther calf loss from two commercial cattle farms in southwest Florida (Jacobs et al. 2015). This offtake percentage is reflected in recent diet estimates from panther necropsy and scat contents (Caudill et al. 2019). Calf depredations from dingoes are less clear, some studies suggest that the variation in dingo depredation vs. natural mortality is negligible, while others estimate calf losses from dingoes reach 30% (Glen et al. 2007). We set our estimate of calf production loss due to dingoes at 30%, but we recognize the suite of diet studies that suggest consumption of livestock is lower (Newsome et al. 1983; Thomson 1992; Glen et al. 2007; Allen et al. 2012). For both case studies, we provide estimates of damage saved to pastureland in both the presence and absence of large carnivore livestock predation.

Results: Florida panther case study

Considering predicted wild pig numbers in Florida if panthers go extinct, we find they would be 0.3% higher overall than current numbers (5.9% higher within the FWC, from 200,861 to 212,711 individuals), with density estimates remaining the same on average (at 2.9 pigs km^{-2}). This increase in pig numbers corresponds to a 6.9% increase (10.7 km^2) in damaged agricultural land within the FWC (Figure 6.4A; 144.1 km^2 vs. 154.8 km^2), according to our pig density-soil disturbance model (Appendix 6 Table 3). This increase in damage to agricultural land translates to nearly $700,000 USD loss in market value for crops (about $10.5 million USD damage under status quo vs. \$11.2 million USD damage under panther extinction; Appendix 6 Table 4). For pastureland, this amounts to nearly \$2.5 million USD loss in equivalent beef production after accounting for depredations (Appendix 6 Table 5), which amounts to \$3.2 million USD lost across all assessed agricultural types (Figure 6.4B).

When assessing the predicted number of wild pigs under successful panther expansion (i.e. panther extent of occurrence encompassing the FWC in addition to their core breeding range; Figure 6.4A), we find that predicted wild pig numbers drop by 22.5% throughout Florida relative to the current numbers (42% reduction within the FWC, from 200,861 to 116,439 individuals). The concomitant density estimates slightly drop from 2.9 to 2.2 pigs km^{-2} on average throughout the state. Considering this change in pig density in terms of reduced soil disturbance throughout Florida, we find that 216 km^2 of equivalent land could be saved from wild pig rooting. Regarding destruction of agricultural lands within the FWC, this decrease in pig densities means a 19.8% reduction (28.5 km^2; Appendix 6 Table 3) in damaged land (115.6 km^2) from pig rooting, which translates to about \$2.2 million USD in equivalent market value savings for a subset of crops (approx. \$8.3 million vs. \$10.5 million USD in damage; Appendix 6 Table 4) and \$8.2 million USD for beef production (Appendix 6 Table 5). This amounts to a total market value savings of \$10.4 million USD for the assessed agricultural types (Figure 6.4B). Under a situation where panthers do not kill any calves, then the total market value savings across all agricultural would be \$10.5 million USD.

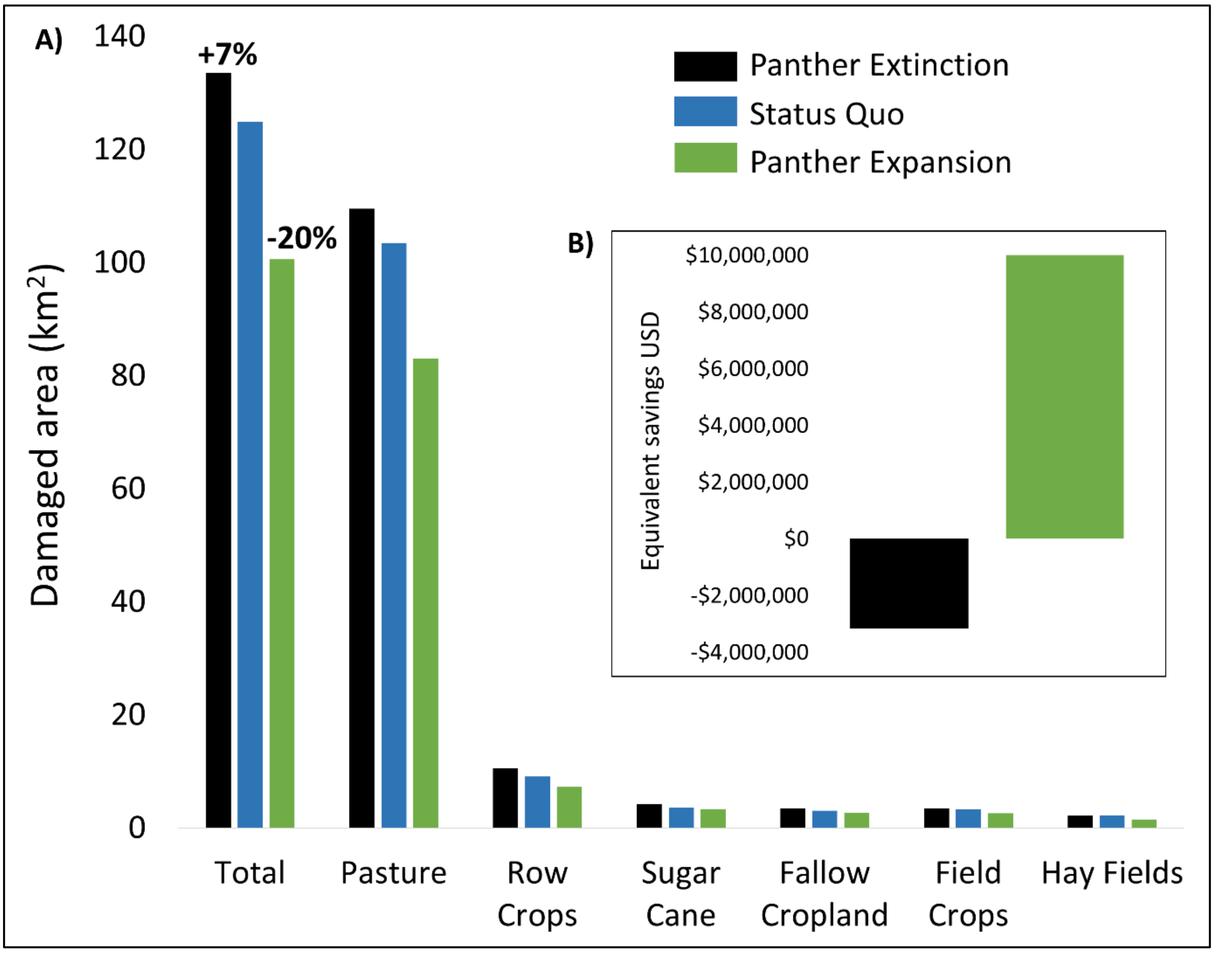

Figure 6.4. Damaged area from invasive wild pigs for the top six agricultural land cover types as a function of Florida panther conservation scenarios (Panel A). As conservation intensity increases, there is a concomitant decline in wild pig damage to agricultural lands. With full panther expansion, for example, there is a 19.8% decrease in damaged agricultural land. This decrease in damaged agricultural land could result in $10.5 million USD potential savings to crops and beef production if panthers achieve full expansion; whereas if they go extinct, there will be a loss of $3.2 million USD (Panel B).

Results: Dingo case study

Regarding predicted wild pig numbers in agricultural lands of NSW and Victoria, Australia under full dingo exclusion, we find that wild pigs would be 19.7% higher (from 572,962 to 713,053 individuals), according to our predicted pig density model. The predicted pig density estimates would increase from 2.3 pigs km^{-2} under the status quo to 2.9 pigs km^{-2} under full exclusion. This increase in pig densities corresponds to a 9.7% increase (62.9 km^{2}) in damaged agricultural land (Figure

6.5A; 587.7 km^2 vs 650.5 km^2; Appendix 6 Table 6) according to our pig density-soil disturbance model. This increase in pig disturbance translates to over $5 million USD in market value loss for crops (about $47.3 million USD damage under status quo vs. $52.4 million USD damage under dingo exclusion; Appendix 6 Table 7). For pastureland, this amounts to nearly $2 million USD loss in equivalent beef production after accounting for dingo offtake (Appendix 6 Table 8), which totals greater than $7 million USD in losses across all assessed agricultural lands (Figure 6.1B).

Considering the predicted number of wild pigs under successful dingo restoration (i.e. the dingo distribution encompassing all NSW and VIC), we find that their numbers drop by 10.9% compared to the dingo exclusion scenario (from nearly 572,962 to 510,301 individuals). The corresponding density estimates drop from 2.3 to 2.1 pigs km^{-2} on average. This reduction in pig densities results in 6.1% less damage to agricultural land (Figure 6.5A) from pig disturbance (35.7 km^2 saved; Appendix 6 Table 6), which translates to around $2.9 million USD in equivalent market value savings for crops (approx. $44.5 million USD damage under dingo expansion vs. $47.3 million USD damage under status quo; Appendix 6 Table 7). This also means a savings in beef calf production of $0.2 million USD, with a total savings across all agricultural lands assessed being $3.1 million USD (Figure 6.5B). If dingoes do not kill any calves, then the total savings would be about $4.1 million USD.

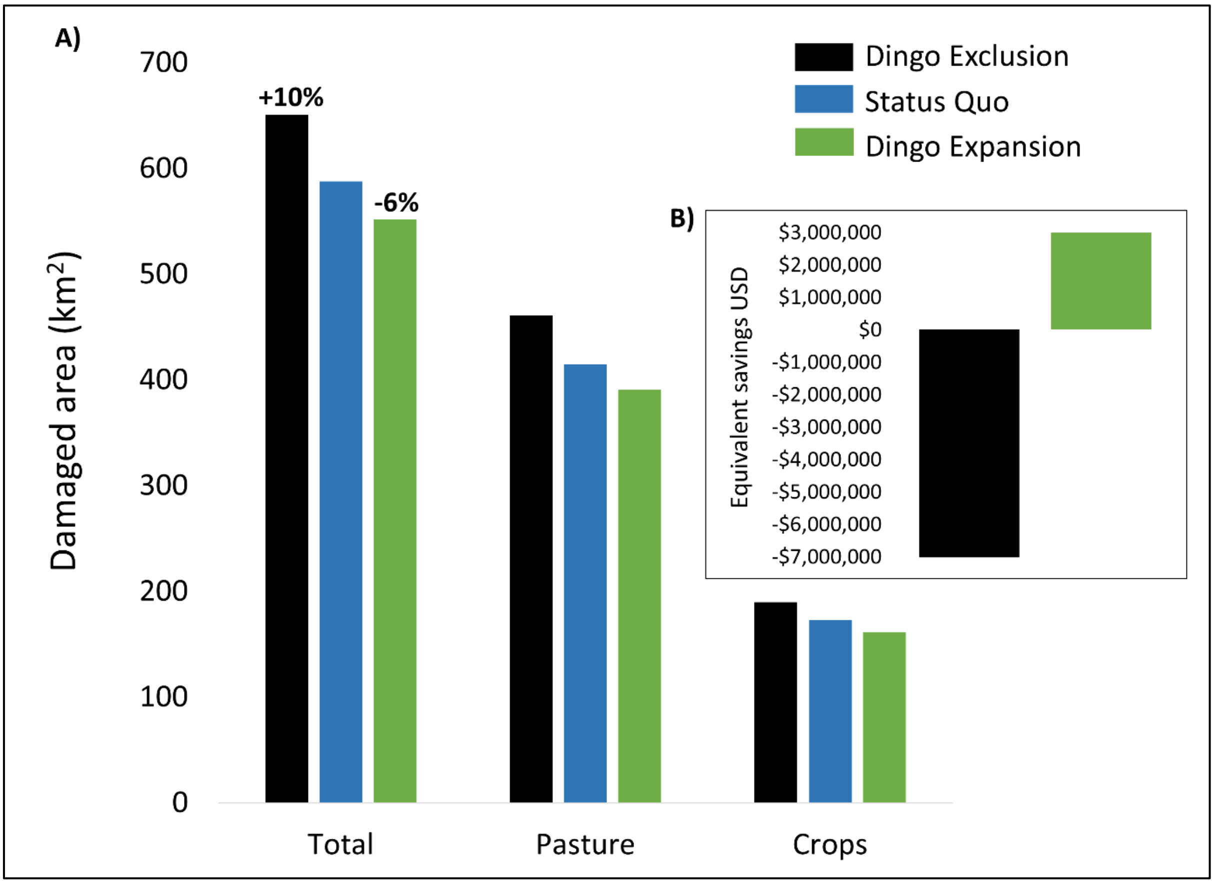

Figure 6.5. Damaged area from invasive wild pigs for the top agricultural land cover types as a function of dingo conservation scenarios (Panel A). As conservation intensity increases, there is a concomitant decline in wild pig damage to agricultural lands. With full dingo expansion throughout NSW and VIC, for example, there is a 6.1% decrease in damaged agricultural land. This decrease in damaged agricultural land results in nearly $3.1 million USD potential savings across all agricultural lands assessed if dingoes achieve full expansion; whereas if they are fully excluded there will be a potential loss of $7 million USD (Panel B).

Discussion

We show that the successful conservation of two large carnivore species can have substantial net economic benefit by reducing wild pig densities in and around agricultural lands. We find that large carnivore restoration could potentially save $10.5 million USD (in Florida) and $3.1 million USD (in Australia) in crops and beef production that would otherwise be lost from unmitigated wild pig soil disturbance. Given the widespread distribution of invasive ungulates, other large carnivores are likely providing similar ecosystem services to agricultural systems around the world.

Estimation of such socio-ecological cascades may provide an opportunity for presenting additional consequences and predictions of large carnivore recovery to stakeholders and engage communities in their conservation.

The socio-economic benefits and costs of large carnivore restoration extend well beyond their value to crops. Similar benefits may be seen in the reduction of disease transmission and risk of predation by pigs on livestock (e.g. lambs; Barrios-Garcia & Ballari 2012). The reduction of pigs may also reduce vehicle damage and human deaths related to collisions (Beasley et al. 2013). There may also be co-benefits to ecosystems as wild pigs have been linked to greater than 30% of assessed IUCN species' declines (Gurevitch & Padilla 2004), and may present additional risk to already threatened species (McClure et al. 2018). While our paper focuses on one ecosystem service provided by large carnivores, there may be many co-benefits that have otherwise not been realized, and we urge future research to consider ancillary benefits when assessing the consequences of large carnivore recovery.

While this work builds our understanding of the impacts of large carnivores on agricultural output it is subject to a number of caveats related to system complexity. Predators often have numerous prey species beyond wild pigs many of which are known to damage agricultural commodities (e.g. deer in Florida [Garrison & Gedir 2006] and kangaroos in Australia [Prowse *et al.* 2015]). In this study we focus on wild pigs as a widespread, highly abundant prey species, however the inclusion of more prey species (e.g. deer and kangaroos) would be important to reflect further cascading implications of predator population increases. This would also help inform how natural prey-density affects livestock killing. To assess the potential impacts of pigs in the future it was essential to use the best available information on predicted pig densities. In Florida these predictions are based on the assumption that pigs will utilize all available habitat within the study area; while this may not be the case there is some evidence that near full expansion via human-assisted translocation is possible (Hernández et al. 2018). In addition, our predicted pig density model does not take into account species-specific predation pressures of panthers and dingoes on pigs, or of other protector species (e.g. guardian dogs). It is likely that panthers consume more pigs on average than dingoes based on published diet estimates

(Newsome et al. 1983; Maehr et al. 1990; Corbett 1995; Caudill et al. 2019); however, dingoes exhibit pack-style predation tactics similar to wolves, which may result in pigs being excluded from areas where dingoes are present (Fleming et al. 2001; West 2008). As such, future work should incorporate population and predator-prey dynamics.

To calculate the economic impacts of wild pigs and net benefits of predators a number of assumptions were required. For example, our calculation of savings on agricultural commodities assumes that all pasturelands are being used by cattle at the specified stocking rate, but the stocking rate may fluctuate depending on whether the pasture is improved versus unimproved, and depending on the breed of cattle. Further there may be other livestock species using the pastureland, such as sheep and goats, which we do not account for in our study. While we considered damage across all agricultural land, accurate crop data for market valuation are limited to a subset of irrigated and/or rainfed crops in both case studies, suggesting a potential underestimate of savings. To ensure we captured the net economic outcomes it was essential to measure the depredation of livestock by both predator species, a factor also of key concern to landholders. For simplicity we assumed fixed depredations in both case studies, however in reality these values are likely to change depending on a number of factors, for example pack dynamics for dingoes (Forsyth et al. 2019) and the proximity of cattle from forest edges for panthers (Jacobs et al. 2015). There is also opportunity for implementing additional costs and benefits ranging from tourism and hunting (of wild pigs) value to wild fire risk, hydrological impacts, and restoration costs associated with large carnivore recovery. Based on the above there is great potential for improvement in future work to not only account for the potential benefits in more detail, such as quantifying the economic savings across all agricultural types, but also accounting for the variability of potential loss (in the case of livestock), or the perceived fear of having an apex predator in the landscape (Lucherini & Merino 2008).

Large carnivores are declining due to human conflict (Ripple et al. 2014) driven by a strong public perception that they are detrimental to humans (Treves & Karanth 2003; Hazzah 2006; Inskip & Zimmermann 2009). Our work could be harnessed to enhance the plight of carnivores by articulating their services to society from an economic and human well-being perspective. As such, the recovery and expansion of large carnivores will require a balance of perceived costs and benefits to human communities, both in losses to their livelihoods (e.g. livestock predation; Inskip & Zimmermann 2009) and threat to human life (Hunter et al. 2007; McCagh et al. 2015), and benefits such as the reduction of negative impacts of overabundant non-native prey.

CHAPTER 7 Authorship Statement

In preparation for submission to Nature Sustainability as of February 2020.

The Candidate conceived the idea for the manuscript with initial input from Nicholas Patton. Jim Hone provided feedback for the model. Matthew Holden and the Candidate streamlined the model, with the Candidate testing the model. The Candidate conducted the analyses, with help from Violeta Berdejo-Espinola. Eve McDonald-Madden assisted with framing and editing of the manuscript. The Candidate wrote the manuscript with additional input from all authors.

CHAPTER 7 Global soil carbon storage compromised by a widespread invasive species

Christopher J. O'Bryan, Violeta M. Berdejo-Espinola, Jim Hone, Jesse S. Lewis, Nicholas R. Patton, Derek R. Risch, Matthew H. Holden, Eve McDonald-Madden

Abstract

Global climate commitments require member nations to account for carbon loss (UNFCCC 2019). Carbon loss can occur through the disruption of soil, the largest pool of stored carbon (Carvalhais et al. 2014). Invasive wild pigs (*Sus scrofa*), one of the most widespread non-native vertebrates, excavate soil for feeding (Ballari & Barrios-García 2014); however, the global extent of wild pig damage on soil and resultant carbon vulnerability are unknown. Here we show that over one metric gigatonne of soil organic carbon storage is vulnerable to wild pig densities in their current distribution, which is 40% higher than the world's yearly airline travel, with a potential of nearly four gigatonnes if they continue to expand. Our work suggests that managing wild pig densities can reduce vulnerability of soil carbon to emissions. For countries committed to global climate agreements, unmanaged wild pig densities can compromise a substantial portion of their carbon pledges. Our work provides a first assessment of global soil organic carbon storage at risk from a widespread invasive vertebrate and provides information on the consequences of invasive species management on global climate commitments.

Main

A reduction of human-induced carbon emissions is critical for mitigating the negative effects of climate change (UNFCCC 2019). The importance of this reduction is recognized through binding international regulations and agreements (Savaresi 2016; UNFCCC 2019). One of the factors contributing to carbon emissions is the disruption of soil, the largest pool of carbon on land (Lal 2004; Carvalhais et al. 2014). The most recognized human activity leading to soil disruption is agricultural production (Amundson et al. 2015) where the tillage of soil affects its physical, chemical, and biological properties (Doran 1980; Lal 2004), releasing considerably higher rates of carbon compared to untilled soils (Reicosky 1997; Welander 2000; Haddaway et al. 2017). Soil disruption associated with agriculture and other human development activities (e.g. urbanization Amundson et al. 2015) has dominated the focus of the soil carbon literature; however, there may be unexplored avenues to reduce impacts on soil organic carbon stocks.

Invasive wild pigs (*Sus scrofa*)(hereafter referred to as wild pigs) are the most widespread and abundant human-spread mammal globally and are ecosystem engineers, causing soil disturbance via digging for belowground plant parts, fungi, and invertebrates (Barrios-Garcia & Ballari 2012) (Figure 7.1). Wild pigs are also currently expanding their non-native range, leading to not only a current large potential for soil damage (Mohr et al. 2005; Risch et al. 2010; Macci et al. 2012; Bueno et al. 2013a; Bueno & Jiménez 2014), but a looming unrecognized source of global soil carbon emissions (Mohr et al. 2005; Risch et al. 2010; Macci et al. 2012). In this paper, we present the first attempt to assess and quantify the potential implications of wild pigs on global soil carbon using a spatially explicit model capturing the most current data on predicted global pig distributions (Lewis et al. 2017) and soil carbon storage (Hengl et al. 2017) (see Methods). The outcomes of our model provide an estimation of soil organic carbon (SOC) storage that is vulnerable to emissions from wild pig soil disturbance (i.e. the proportion of SOC storage that has the potential to be emitted from soil disturbance) in their current and potential distributions (Figure 7.2A).

Figure 7.1. Invasive wild pigs (*Sus scrofa*) cause soil disturbance via digging for belowground plant parts, fungi, and invertebrates. Wild pigs are the most widespread and abundant human-spread mammal globally. Photo credit: Ben Teton (top left), Jesse Lewis (bottom left), and Derek Risch (right).

We find that wild pigs are jeopardizing 1.07 (SE 0.37-3.42) metric gigatonnes (gt) of SOC across their current non-native distribution (Figure 7.2B) (mean 121.16, SE 40.13-397.54 t SOC km^{-2}). Assuming 30% of SOC is released in the form of CO_2 (similar to agriculture tillage) (Davidson & Ackerman 1993; Lal 2019), then that would result in 1.18 gt CO_2 equivalent (CO_2e), which is about 40% greater than the annual CO_2 loss from all aviation travel globally (Sims et al. 2014) (Figure 7.2C). If we could reduce wild pigs worldwide by half, then we could save a concomitant third SOC (to 0.80 gt CO_2e). However, a targeted reduction of wild pig densities by three-quarters solely within the global hotspots of soil carbon vulnerability (i.e. areas greater than the global mean SOC) would save over 38% gt SOC (to 0.74 gt CO_2e), which is nearly one-fifth the area of current wild pig distribution (10.8 million km^2 vs. 50.4 million km^2). Reductions of wild pig density of such magnitude have been previously reported (Hone 2012), which suggests that aggressive management within existing wild pig areas, especially areas of high vulnerability, is feasible and could have a significant impact on SOC storage similar to that of widespread reduction efforts (Figure 7.2B).

Without concerted management there is significant likelihood that wild pigs could expand beyond their current distribution, a highlight in recent predictions of wild pig densities globally (Snow et al. 2017; Lewis et al. 2019). The impact on SOC storage that could result is likely substantial (Figure 7.2). For example, we find that when considering predicted wild pig densities outside of their current non-native distribution, vulnerable SOC goes up by 2.5 fold (to 3.81 gt, SE 1.40-11.35 gt) (mean 94.44, SE 33.87-288.67 t SOC km^{-2}; Figure 7.2B) with potential loss of CO$_2$e at 4.20 gt, which is nearly four times the average yearly emissions from soil cultivation in agricultural lands (Figure 7.2C) (FAO 2019).

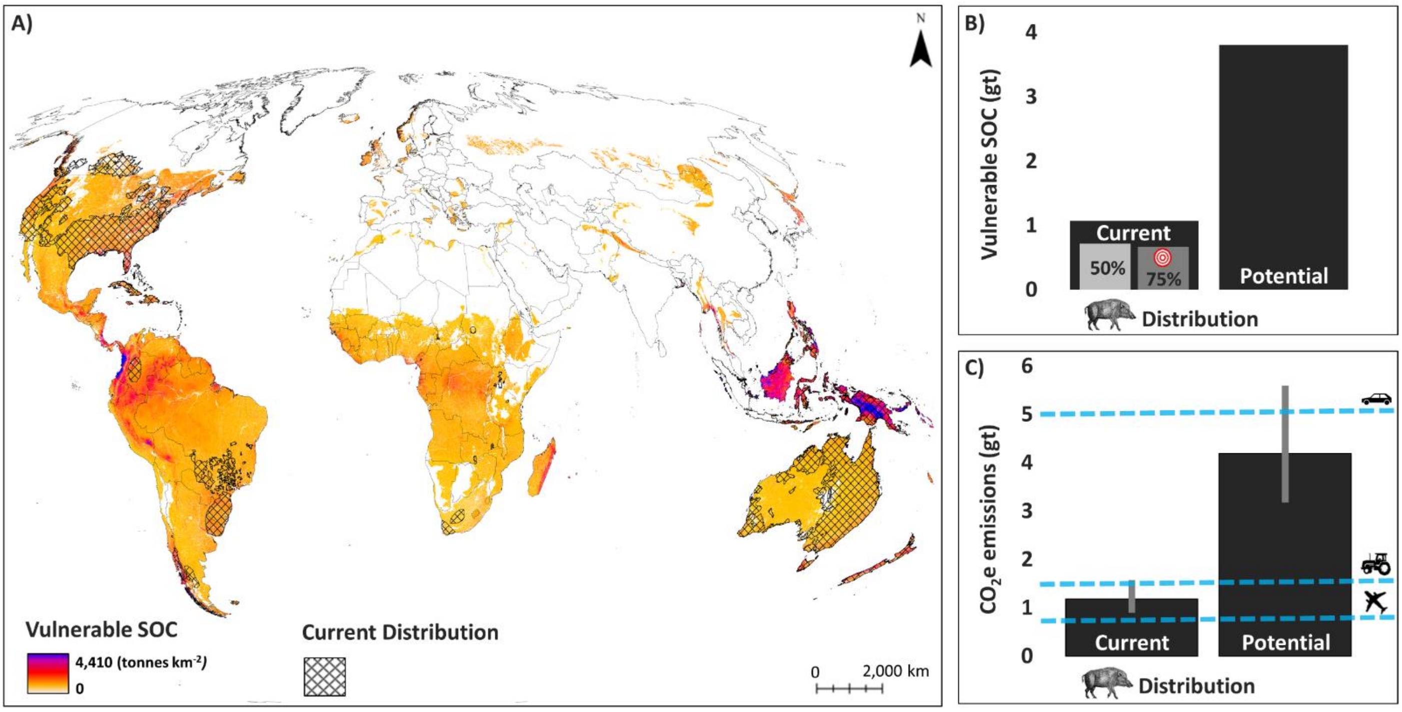

Figure 7.2. Global hotspots of vulnerable soil organic carbon (SOC) from invasive wild pig (*Sus scrofa*) soil disturbance across their current non-native distribution (hatched) and potential (colored, unhatched) non-native distribution (Panel A). Panel B shows the vulnerable SOC across their current and potential distributions, with estimates of vulnerable SOC under global wild pig reduction of 50% and targeted reduction of 75% within SOC hotspots (nearly one-fifth the area of current wild pig

distribution at 10.8 million km^2 vs. 50.4 million km^2). Panel C shows potential CO_2e emissions from wild pig soil disturbance (assuming 30% loss; range 20-40%(Davidson & Ackerman 1993; Lal 2019)) across their current and potential distributions. As a comparison, the blue horizontal dashed lines represent the global CO_2e emissions from road travel (top line) and airline travel (bottom line) for the year 2010 (Sims et al. 2014), and the average yearly CO_2e emissions from the cultivation of soil from agriculture (FAO 2019) (middle line) for the years 1990-2017.

Management and reduction of wild pigs could not only lead to a potential reduction in carbon emissions, but it may also result in co-benefits to sustainable development goals such as food security, economic development, and biodiversity protection (UN 2015b). Wild pigs have been shown to damage important food crops and have indeed been shown to reduce agricultural yields (Barrios-Garcia & Ballari 2012; Gentle et al. 2015). For example, wild pig destruction of pasture forage causes a loss of 2 million USD in Florida (Bankovich et al. 2016) and at least $1.5 billion USD annually in damages and control costs alone (Pimental 2007). Such reductions are not only damaging from an economic perspective, but they may reduce our productive capacity for food consumption. Beyond agriculture, wild pigs have been shown to have dramatic impacts on terrestrial ecosystems. For instance, wild pigs are thought to have played a role in nearly 30% of assessed species being threatened (Gurevitch & Padilla 2004) and may pose additional threat to species already imperiled (McClure et al. 2018). More specifically, wild pigs have been shown to reduce populations of plants through their rooting behavior (Bankovich et al. 2016), consume eggs of and prey on endangered species, facilitate invasive plant spread, and spread emerging infectious diseases (Barrios-Garcia & Ballari 2012). Through their rooting behaviour, wild pigs can also cause erosion (Bruland et al. 2010) that may exacerbate threats to food production (Pimentel & Burgess 2013) and biodiversity. While the aim of this paper is to capture the potential benefits of wild pig control on SOC and its release in the form of CO_2, the impacts of wild pigs on human well-being and biodiversity show potential collateral benefits of their control that are relevant to the United Nations' Sustainable Development Goals.

The results we present are subject to caveats. To explore the global perspective of the potential role of wild pigs in disturbing soil carbon storage we used a model of predicted wild pig density because global wild pig density data are unavailable. For the broad scale results presented here, this is unlikely to cause a major issue; however, such an approach should be used with caution to present results at a local scale. Further, we assume that soil disturbance results in carbon vulnerability. Soil disturbance by wild pigs may result in varying levels of carbon emissions, and our wild pig-soil disturbance model is parameterized from a long-term study in Australia (Hone 2002a, 2006, 2012) that does not necessarily reflect variation in ecosystems and climates that are present at a global scale. However, according to a global meta-analysis on the effects of agricultural tillage on SOC storage, soil type and climate zone did not influence the effects of soil turnover on SOC at 0-15cm depth (Haddaway et al. 2017). We also do not consider potential emissions caused by managing wild pigs, such as the use of vehicles and other resources that emit carbon. As such, we urge future research to incorporate wild pig disturbance and revegetation parameters at more local scales in addition to the costs of wild pig management to prioritize actions for achieving lower carbon emissions.

A fundamental goal of the United Nation’s Paris Agreement is for member countries to combat climate change through the reduction of carbon emissions (UNFCCC 2019). Our results indicate that substantial amounts of SOC are vulnerable to wild pig soil disturbance across Earth, and this may result in loss of carbon storage that can compromise global climate commitments if not addressed. We hope this paper stimulates discussion on the potential role of controlling wild pigs at not only abating potential carbon emissions, but also spurring further research that looks at the local benefits to countries at tackling growing wild pig populations to reach their climate obligations – a research direction that could bring both reduced emissions and benefits to biodiversity and food security.

Methods

Analysis

We determine the estimated relative proportion of soil that is vulnerable to wild pig disturbance based on the predicted density of wild pigs per 1 km^2 pixel in the absence of management. We calculate the area that is vulnerable to wild pig disturbance per pixel by assuming that the rate of change of undisturbed to disturbed soil is related to wild pig density and the area of undisturbed soil (Hone 2002a, 2006, 2012) (Appendix 7 Figure 1). The calculation and subsequent wild pig-soil disturbance model can be found in the Supplementary Material. We parameterize our model from a long-term study of ground disturbance by wild pigs in Namadgi National Park, south-eastern Australia (Appendix 7 Table 1), the only known study that provides parameters suitable for our global analysis (Hone 2002a). We present results using these parameter estimates with their standard errors given in Appendix 7. For this initial calculation, we assume that every 1 km^2 pixel is available for wild pig disturbance (i.e. nothing impedes invasive wild pigs from rooting soil). We then multiply the subsequent proportion of soil disturbance per 1 km^2 pixel with that of the SOC stock in the upper 15cm of soil depth for that pixel (see *SOC data* below), which results in the relative amount of SOC that is vulnerable to wild pig soil disturbance, reported in metric tonnes per pixel (1 km^2) (Figure 7.3). For the SOC that is vulnerable to wild pig soil disturbance, we assume that the depth of disturbance is consistent across pixels. We then calculate a range of CO_2 equivalent (CO_2e) that could be emitted from the aforementioned soil disturbance based on previously reported estimates of carbon release from arable agriculture practices, a 30% loss (range 20-40%) mostly occurring <1 year to 5 years since disturbance (Davidson & Ackerman 1993).

We remove pixels that overlap with human built-up areas, including roadways, railways, paved areas, buildings, and urban parks, as these are areas where we assume invasive wild pigs cannot access soil. Water bodies were also excluded as a function of the soil carbon data. We then calculate the relative amount of SOC and carbon dioxide equivalent (see Appendix 7) that is vulnerable to wild pig soil disturbance across continents (excluding Antarctica) and countries using publicly available data on administrative areas (https://gadm.org/), which is presented in Appendix 7. Our methodological framework is illustrated in Figure 7.3.

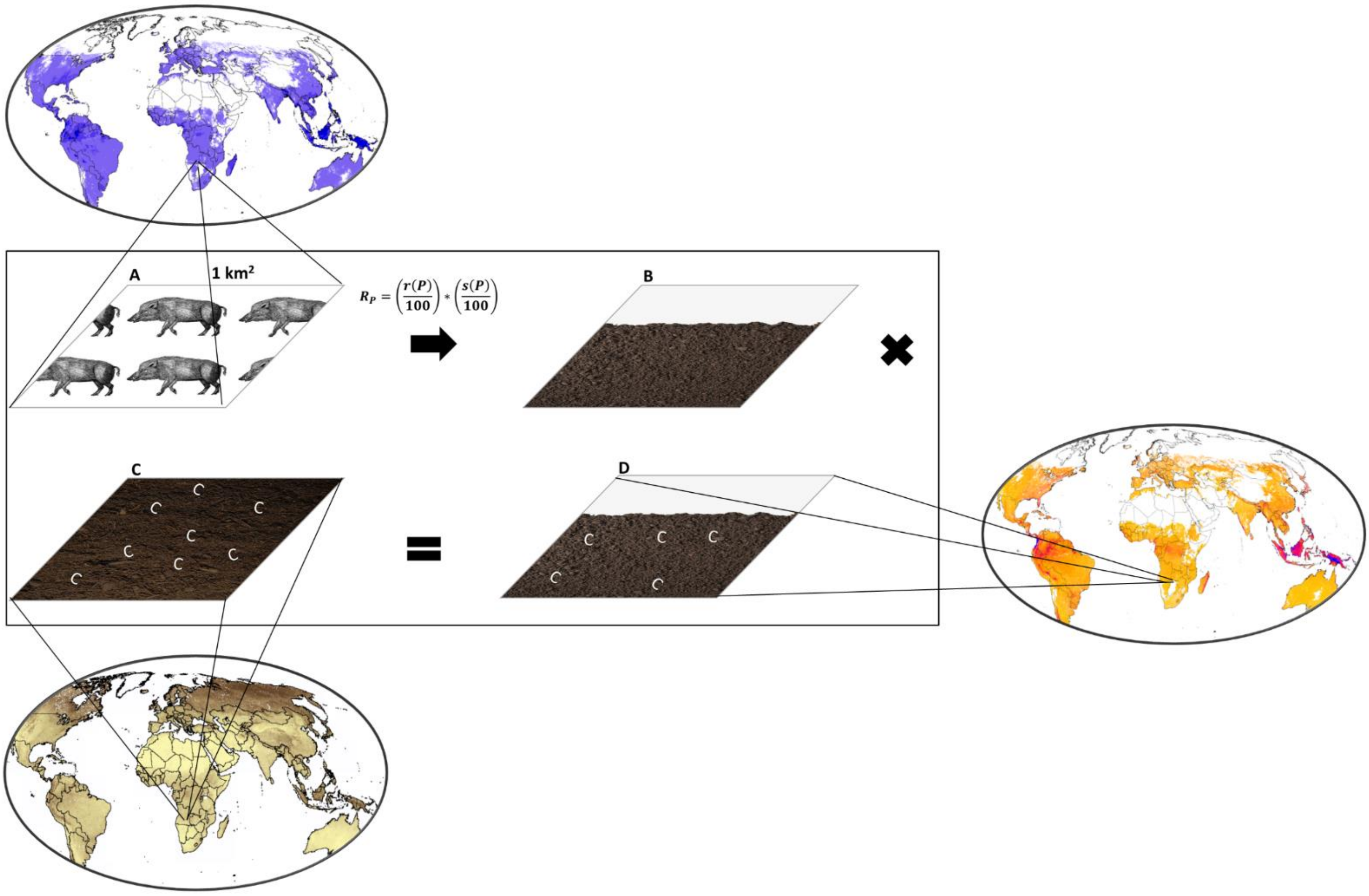

Figure 7.3. Methodological framework for determining the relative amount of SOC vulnerable to emissions by invasive wild pig (*Sus scrofa*) soil disturbance. We determine soil disturbance from wild pigs by employing an equation(Hone 2006) that uses the predicted wild pig density data for each 1 km^2 pixel (A) to estimate the proportion of soil disturbed as a function of wild pig density within that pixel (B). We then multiply that proportion by the amount of SOC stock within that pixel (C) to produce the relative amount of SOC stock vulnerable to wild pig soil disturbance (D).

Predicted wild pig density data

Wild pigs are currently absent from broad extents where there is high quality wild pig habitat, yet there is great potential for their expansion (Snow et al. 2017; Lewis et al. 2017, 2019). We use the most comprehensive spatial dataset on predicted wild pig densities (in the absence of pig management). Lewis and colleagues use known records of 129 wild pig densities across five continents to evaluate seven biotic and abiotic factors in predicting population density of wild pigs using generalized linear models and model selection techniques (see Lewis *et al.* 2017 Supplementary

Information). Specifically, they assess biotic factors such as large carnivore richness (predation risk) and vegetation structure, and abiotic factors such as potential evapotranspiration and precipitation at explaining wild pig density (Lewis et al. 2017). Because the predicted wild pig densities includes areas where they do not currently occur but have potential to occur at a global scale (Lewis et al. 2017) (Appendix 7 Figure 2), we mask their native geographic range, which is derived from the IUCN (IUCN 2016). We resample (bilinear method) the predicted wild pig density data to reveal density at a 1 km^2 resolution (World Mollweide projection), and we only consider predicted wild pig densities >0.5 pigs km^{-2} to eliminate unlikely pig locations (e.g. Siberia, the Australian outback, and the Sahara Desert; Appendix 7 Figure 2). For a portion of our analysis, we assess wild pig densities in currently known non-native distributions that are derived from Lewis and colleagues (Lewis et al. 2017).

Soil organic carbon data

We use a global dataset on SOC stock at 0-15 cm depth reported in metric tonnes per hectare at a 250 m resolution (Hengl et al. 2017) (Appendix 7 Figure 3). We choose a depth of 0-15 cm as wild pigs have been shown to disturb soil at depths of 10.7 cm on average (+/- 0.3 cm) (Bueno et al. 2013b; Bueno & Jiménez 2014) and have been suggested to disturb at depths ranging from 5-15 cm deep (Kotanen 1995; Groot Bruinderink & Hazebroek 1996; Cushman et al. 2004). Hengl and colleagues (Hengl et al. 2017) predict global SOC based on approximately 150,000 soil profiles and 158 remote sensing-based soil covariates using machine learning methods such as random forest, gradient boosting, and/or multinomial logistic regression (Hengl et al. 2017). We resample (bilinear method in a World Mollweide projection) the predicted SOC data to reveal SOC stock at a 1 km^2 resolution and snap to the predicted wild pig density pixels, which allows for analyses on predicted SOC stock that is vulnerable to wild pig soil disturbance. We then multiply the resultant carbon value by 100 to get the amount of carbon in metric tonnes for each pixel.

Built-up areas data

We use data on built-up areas from Venter and colleagues' updated human footprint dataset (Venter et al. 2016a) (Appendix 7 Figure 4), which is at a 1 km^2 resolution and represents 13.1 million km^2 of Earth's terrestrial surface. These built-up areas correspond to human infrastructure, including buildings, paved land, urban parks, roadways, and railways for the year 2009 (Venter et al. 2016a).

CHAPTER 8 Conclusion

Overview

The overall aim of this thesis was to address key knowledge gaps relevant to the exposure and contribution of predators and scavengers to humans (**Chapter 1**), including the ecological and human well-being consequences of predators and scavengers. I present a global analysis on the exposure of terrestrial vertebrates to cumulative intense human pressures (**Chapter 2**) with a focus on carnivores (**Chapter 2**, Box 1). These shared landscapes are the focal areas for questions regarding the role of carnivores at contributing to key ecological and human well-being processes and outcomes. I produced a global review on the contribution of predators and scavengers to human health and well-being (**Chapter 3**). From the review, I identified key gaps in our knowledge on scavenger ecology. I provided a formal description of the mesoscavenger release hypothesis including two simple models to illustrate the dynamic effects of declining apex scavengers on carrion and mesoscavenger biomass (**Chapter 4**). By doing so, I filled a critical gap in our knowledge on scavenger trophic dynamics by presenting both empirical and theoretical evidence on the subject. This work also helped connect the dots between ecological and human health and well-being outcomes from losing apex scavengers. Another key gap identified in the review was that of services provided by large carnivores in human-dominated landscapes. One such service is that of their potential to reduce injury and disease risk, which became the impetus for a case study investigating the potential of leopards in Mumbai, India to reduce bites and rabies risk to humans by feral dogs (**Chapter 5**). The reduction of pest species by large carnivores can have far-reaching benefits beyond injury and disease risk – from an economic perspective they can support agricultural productivity. In **Chapter 6**, I provided two case studies on the implications of conserving and restoring large carnivores in areas where they have declined, specifically investigating the net benefits they can provide to agriculture. I examine the role of Florida panther conservation in the United States, a critically endangered subspecies of mountain lion, and the dingo in Australia, at affecting invasive wild pig populations in a matrix of intact and agricultural land. I show that restoring these species in Florida and Australia may provide unique benefits to agricultural systems by reducing the presence and abundance of wild pigs, and in turn reducing damage to agricultural lands where wild pigs are prevalent. In **Chapter 7**, I show that expanding wild pig populations can cause considerable damage beyond agriculture, to soil globally, resulting in emissions of soil organic carbon that are critical for abating climate change. I discuss the potential benefits of invasive wild pig control and the value of restoring native apex predators at mitigating pig damage. The results of these case studies provide crucial information for decision makers and conservation practitioners on the potential benefits that large carnivores have in human-dominated landscapes and thus are a novel tool to encourage landholder and community engagement in and support of their protection.

Scientific advancements and conservation implications

Faced with increasing evidence that human activities and land uses such as pastureland, urbanization, and over-exploitation threaten to drive thousands of species to decline, it is imperative to report these pressures within their geographic ranges globally. Previous efforts have been limited to a small number of species that have species-specific threat data (e.g. Allan et al. 2019; Appendix 1), which begs the question about how exposed are the 20,000+ terrestrial vertebrates that have limited data on pressures within their distributions? Recent work has attempted to address this question by assessing population trends as a function of land-use change (e.g. Santini et al. 2019) or by focusing on the extinction risk across changes in human footprint for a single taxonomic group (e.g. Di Marco et al. 2018); however these approaches require extensive analytical effort. To overcome this, I provided a simple methodological framework in **Chapter 2** that can be used as an initial assessment for species exposure to threatening pressures at a fine resolution, which can be particularly helpful when resources are limited (Bland et al. 2015a, 2015b). I presented a global analysis of cumulative human pressure (at a 1 km^2 resolution) across the ranges of 20,529 terrestrial vertebrate species. I use a threshold of the human footprint index that is linked to extinction risk (a value of 3; pressures roughly starting at pastureland) recently published by Di Marco and colleagues (2018). I found that over 85% (17,517) of assessed species are exposed to intense human pressures across >half of their range, and 3,328 species across their entire range. For carnivores, I found that they are exposed across 66% of their ranges on average

(**Chapter 2**, Box 1). As such, this chapter provides an easily replicable method for initial assessments of intense human pressures within species' geographic ranges, and will guide future work on mapping species-specific threats.

With these threatening processes comes a great potential for further range contractions and population declines of carnivores (Laliberte & Ripple 2004; Ripple et al. 2014; Di Minin et al. 2016; Jacobson et al. 2016; Tucker et al. 2018). Such declines can affect human health and well-being. While the concept of 'ecosystem services' (the aspects of ecosystems utilized [actively or passively] to produce human well-being; Fisher & Kerry Turner 2008; Fisher et al. 2009) has been around for decades (Daily 1997), there has been minimal effort to summarize the contemporary literature around the benefits provided by predators and scavengers. Reviews on the topic of predator and scavenger services to humans have primarily focused on one service by a single taxonomic group. For example, reviews have been limited to the benefits provided by insectivorous bats due to their consumption of pest insects that damage agricultural systems (thus saving pest control costs and increasing agricultural yield; Kunz et al. 2011) and the role of birds at consuming disease-carrying rodents and the potential human health implications (Donázar et al. 2016). Similar syntheses have been done on vultures, assessing their human health effects by their reduction of carcasses and organic waste (Buechley & Şekercioğlu 2016a; Şekercioğlu et al. 2016). In **Chapter 3**, I ameliorated this gap by publishing a review on the known benefits provided by both predators and scavengers in shared landscapes (O'Bryan et al. 2018). I demonstrated that some predators and scavengers are providing services in the form of zoonotic disease regulation, agricultural productivity, and reduction of species known to cause human injury and death. I postulated in my review that these services can be used as a springboard for conservation in areas where humans and carnivores cohabitate (Carter & Linnell 2016). I suggest that through an inclusive process, decision makers can use this information to inform and elaborate conservation in contentious areas where predators and scavengers may have been originally persecuted for their perceived negative impacts.

During the review process presented in this thesis, I identified a number of gaps in our knowledge regarding the effects of losing apex scavengers. Although there is strong empirical and theoretical evidence surrounding the effects of losing apex predators on pest species and even food web structure, there is considerably less information on the role of apex scavengers. Buechley and Şekercioğlu (2016) touch on the concept of how vultures influence trophic structure in their global review. They discuss the consequences of losing these apex scavengers and the competitive release of smaller scavenger species, postulating that the phenomenon of mesopredator release can occur in similar function following vulture declines (Buechley & Şekercioğlu 2016b). There are a number of studies pointing to the rise of mesoscavengers, those scavengers that are less efficient at finding and consuming carrion compared to apex scavengers, when apex scavengers have declined or are absent from the system (Sebastián-González et al. 2013, 2016; Buechley & Şekercioğlu 2016a; Şekercioğlu et al. 2016; Morales-Reyes et al. 2017; Hill et al. 2018). However, no studies have thoroughly quantified and described trophic cascade theory in scavenger communities as has been done with predators (e.g. the mesopredator release hypothesis; Crooks & Soulé 1999). In **Chapter 4**, I described the mesoscavenger release hypothesis using both empirical and theoretical evidence (O'Bryan et al. 2019). I summarized our current knowledge base on apex scavengers competitively excluding mesoscavengers and provided two dynamic models of scavenger systems parameterized by studies on apex scavengers such as vultures in Spain and Tasmanian devils in Australia that are obligate and facultative apex scavenger species, respectively. This work will aid conservation efforts by providing a better understanding of the ecological impacts of losing apex scavengers. For example, as knowledge grew on the relative impacts of apex predators on mesopredators and ecosystem structure, efforts to 'rewild' parts of Europe and North America ensued, which has had substantial success (Ritchie et al. 2012; Svenning et al. 2016; Lindsey et al. 2017). I argued that similar efforts could take place for scavengers in areas where apex scavengers are declining rapidly or have disappeared altogether.

One of the gaps identified in the review was a lack of information on the role of large carnivores at mitigating direct human injury or death by consuming 'problem' species. The only analytical study that has been recently published on the subject was by Gilbert and colleagues (2016), who posited that by re-establishing North American cougars in their native range in the eastern United States that there would be a concomitant decrease in the number of deer-vehicle collisions (through their reduction in deer densities). In an attempt to build the literature base on the subject, I presented a perspective and quantification of the potential role of leopards at saving human injury and death by reducing densities of feral dogs in Mumbai, India (**Chapter 5**; Braczkowski & O'Bryan et al. 2018). This project was unique in that it focused on a species and location associated with high human-carnivore conflict as dozens of leopard attacks are reported throughout India per year (Athreya et al. 2011; Surve et al. 2015), presenting great opportunity for utilizing information on their services to reduce conflict and retaliatory killings (e.g. Carter & Linnell 2016; Skupien et al. 2016).

Another gap identified in the review process was the lack of information on large carnivores at increasing agricultural yield through the reduction of crop pests. Indeed, there is no information on the benefits of restoring large carnivore populations in areas where they have declined or disappeared. Previous work has eluded to the role of carnivores at affecting agricultural yield, such as owls preying on rodents in California crops (Kross et al. 2016a), golden jackals consuming crop rodents in Serbia (Ćirović et al. 2016), and dingoes reducing competition between kangaroos and cattle (Prowse et al. 2015). However, these studies do not assess how multiple conservation scenarios will effect agricultural commodities. In **Chapter 6**, I quantified the relative contribution of large carnivore species at increasing agricultural output under three scenarios: status quo, full carnivore expansion, and carnivore extinction/exclusion. I presented two case studies of the prospective value of conserving large carnivore species, one on the Florida panther in Florida, USA and the other on dingoes in Australia. I provided results of large carnivore presence at reducing the densities of invasive wild pigs and the resultant savings in agricultural products that would otherwise be destroyed from wild pigs. As such, this work is valuable for decision makers when assessing consequences of actions related to large carnivore recovery within a structured decision-making framework (Conroy & Peterson 2013). This work also aids in potentially reducing negative perceptions of stakeholders (e.g. pastoralists) towards large carnivores that are thought to cause only negative effects on human societies (e.g. depredation of livestock and attacks on humans; Riley & Decker 2000; Conforti & de Azevedo 2003; Prokop & Usak 2011; Muter et al. 2013; Suryawanshi et al. 2013; Morales-Reyes et al. 2018).

The reduction in wild pig densities can also lessen greenhouse gas emissions. Although there is a strong body of literature documenting the detrimental effects of wild pigs on soil structure and its effects on ecosystems, such studies are limited to local scales (e.g. Ickes et al. 2001; Hone 2002; Mitchell et al. 2007; Risch et al. 2010; Barrios-Garcia & Ballari 2012; Macci et al. 2012; Ballari & Barrios-García 2014; Bueno & Jiménez 2014). Furthermore, few studies have quantified the role of pigs at disturbing soil carbon (Risch et al. 2010; Barrios-Garcia & Ballari 2012; Macci et al. 2012) and only one study on the direct effects of pigs on soil carbon emissions in the form of CO_2 (Risch et al. 2010). The study by Risch and colleagues (2010) focused their analysis on one forested region in Switzerland and extrapolated their results across all of Switzerland without accounting for variation in organic soil carbon storage and invasive pig densities. To fill these gaps, I provided a quantification of potential soil damage by unmitigated wild pig populations around the world (**Chapter 7**), focusing my analysis on the role of this invasive ecosystem engineer at destroying soil through rooting and grubbing behaviour, and how this behaviour affects organic soil carbon storage. This study builds our knowledge on the effects of overabundant (and non-native) species, and points to the potential adverse impacts of losing apex predators that would otherwise reduce the density and abundance of these species.

Research limitations and future research priorities

Although this thesis provides a great deal of new information crucial for the conservation of carnivores in human-dominated landscapes, there are a number of caveats and priorities for future research. Below I highlight three overarching opportunities for improvement and subsequent research endeavours.

Connecting human footprint and extinction: one threshold may not fit all taxa

In **Chapter 2** I refer to intense human pressure as starting at pastureland, with a strict threshold of three or greater on the human footprint index (Venter et al. 2016a). However, the threshold of human footprint for mammals presented by Di Marco and colleagues (2018) may not apply across all taxonomic groups presented in my analysis, suggesting a need for future studies to investigate whether the same threshold applies across all vertebrate species classes and functional groups. Although there is strong evidence to suggest that land-clearing associated with agriculture and rangelands has detrimental effects on many species (Fleischner 1994; Newbold et al. 2015a), there is also evidence that some species can survive in human-dominated landscapes and across varying levels of human pressure ranging from agricultural lands (Phalan et al. 2011; Homyack et al. 2014; O'Bryan et al. 2016) to urban areas (Morey et al. 2007). A solution for quantifying human pressures more accurately across species ranges is to map the individual species-specific threats that are known to cause their decline. In Appendix 1, I assisted in an attempt to link the individual pressure layers from Venter and colleagues' human footprint map with that of species for which those threats are known to cause their population decline (Allan et al. 2019). While this analysis was limited to threatened mammals, birds, and amphibians on the IUCN Red List (IUCN 2016), it suggests an avenue for future research that considers all species that have available data on threats (not just species listed as threatened, endangered, or critically endangered on the Red List).

The complexity of species interactions

Species interactions are incredibly complex – driven by countless biotic and abiotic factors that are difficult to capture in a modelling framework. For example, in **Chapter 4,** I modelled the effects of functional dominance by apex scavengers on mesoscavengers and carrion – I did not account for intraspecific behavioural modification of mesoscavengers on apex scavengers. Although rare, there are cases in the scavenger community where apex scavengers are excluded from carrion solely by mesoscavengers portraying physical dominance over a carcass (Butler & du Toit 2002). Similarly, in **Chapter 5**, leopards may alter the behaviour of feral dogs and thus exclude them from many areas surrounding the Sanjay Gandhi National Park without preying on them *per se*. There is a growing body of literature surrounding the concept of the "landscape of fear" as it pertains to predator-prey dynamics and the ancillary effects that predators have on their prey (Suraci et al. 2019) that I did not capture within my work. As such, there is opportunity for future work to consider additional behavioural effects such as how dominance influences feeding behaviour and how the fear of a predator affects prey resource use.

Predators and scavengers may also fluctuate their feeding behaviour depending on food availability or other extraneous factors. In **Chapters 4-6** I assume that facultative scavenger and predator diets mirror that of previous studies (Newsome et al. 1983; Maehr et al. 1990; Athreya et al. 2016; Caudill et al. 2019; Forsyth et al. 2019), but diets are likely to shift and fluctuate through time and space (van Baalen et al. 2001). Although my approach is common practice for studies on predator-prey interactions, future work could incorporate prey-switching (such as a Holling's Type III sigmoidal functional response; van Baalen et al. 2001).

Uncertainty in distribution data

The spatial information and distribution data used throughout the thesis is subject to caveats and improvements. For example, **Chapter 2** was limited to the polygons provided by the IUCN spatial data repository, and does not necessarily represent the most accurate depiction of species' distributions (e.g. some distributions are represented as area of occupancy, while others are represented as extent of occurrence depending on available locality information; Mace et al. 2008). While these data are the global standard for assessing species extinction risk their underlying limitations could affect the outcomes of the analysis of species in human-dominated landscapes presented in **Chapter 2**. In **Chapter 5**, I used local knowledge and newspaper reports to conclude that leopards frequently roam in and around a 500-m buffer zone bordering the Sanjay Gandhi National Park, however specific data on the spatial movement pattern of leopards in this area are lacking. Overall, it is unclear whether this work over-or underestimates the value of services provided by leopards in this system. In **Chapter 6**, I assume that the Florida panther and the dingo distribute their populations evenly and at the same density during expansion; however, their consumption may be different since dingoes exhibit complex pack structure in some areas, consuming larger prey, and hunt solo in other areas, consuming smaller prey (Thomson 1992). Similarly, the Florida panther population assessed may maintain their core breeding population and thus have limited expansion even if habitat connectivity were to be successful (Maehr et al. 2002). Likewise, **Chapters 6-7** are based on predicted wild pig densities/distributions that are subject to a number of assumptions. I adopt and modify the model published by Lewis and colleagues (2017) who predict pig densities using a series of biotic and abiotic variables, including large carnivore presence, at a 1km^2 resolution, but many environmental processes that influence wild pig density occur at finer scales (Hone 2002b; Thurfjell et al. 2009; Barrios-Garcia & Ballari 2012; Lopez et al. 2014). For instance, wild pigs have been shown to increase their rooting behaviour in Sweden and Australia as soil moisture increases (Welander 2000; Hone 2012) and as elevation increases (Hone 1988), but other studies have shown different patterns depending on season (e.g. Bowman & Mcdonough 1991). The uncertainty inherent the spatial data used throughout my work could be rectified with extensive studies to improve the data. However, first an assessment of the importance of variation in such data on the outcomes of my work should be implemented using sensitivity analysis. From a practical perspective improving spatial information is expensive and time consuming (McDonald-Madden et al. 2010). Future research could therefore be prioritised based on those uncertainties that if improved could inform better decision-making with regard to predator conservation and management. To achieve this a focus on the value of information as it pertains to quantifying high-resolution species distributions could be of benefit and can be guided by recent work on Expected Value of Information Theory in ecology (e.g. Runge et al. 2011; Xiao et al. 2019).

Concluding remarks

This thesis showed that predators and scavengers have large portions of their range in human-dominated areas (**Chapter 2**, Box 1) and the loss of predators and scavengers may impact ecosystems that can affect human well-being in a number of ways (**Chapter 5**), including human health through the competitive exclusion (**Chapter 4**) and predation (**Chapter 5**) of species at lower trophic levels, agricultural productivity (**Chapter 6**), and greenhouse gas emissions (**Chapter 7**). Humans have been in direct conflict with predators and scavengers since we arrived on the landscape (Lee-Thorp et al. 2000), which has led to their unprecedented decline. Credible metrics on the role predators and scavengers play in both ecosystems and human well-being are urgently needed. A shift from focusing only on mitigating negative perceptions of large carnivores to a more balanced approach of accounting for both their adverse and positive effects is a necessary step toward achieving their effective conservation in shared landscapes. While there are many examples of human societies coexisting with predators and scavengers, there is an overwhelming majority of societies that do not. I hope that this thesis provides a starting point for future research to delve deeper into the role carnivores have in shared landscapes and how conservationists and decision makers can use this information for maximizing coexistence.

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APPENDIX 1 Hotspots of human impact on threatened terrestrial vertebrates

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Abstract

Conserving threatened species requires identifying where across their range they are being impacted by threats, yet this remains unresolved across most of Earth. Here we present a global analysis of cumulative human impacts on threatened species by using a spatial framework that jointly considers the co-occurrence of eight threatening processes and the distribution of 5,457 terrestrial vertebrates. We show that impacts to species are widespread, occurring across 84% of Earth's surface, and identify hotspots of impacted species richness, and coolspots of unimpacted species richness. Almost one quarter of assessed species are impacted across > 90% of their distribution, and ~7% are impacted across their entire range. These results foreshadow localized extirpations, and potential extinctions, without conservation action. The spatial framework developed here offers a tool for defining strategies to directly mitigate the threats driving species declines, providing essential information for future national and global conservation agendas.

Introduction

Human activities and land-uses are exerting unprecedented pressure on natural environments (Newbold et al. 2015b; Venter et al. 2016a), threatening to drive tens of thousands of species to extinction (IUCN 2016). The main drivers of species declines include the conversion of natural habitats for land-uses such as crops, pasture and infrastructure, and the overexploitation of species through activities such as hunting (IUCN 2016; Maxwell et al. 2016). The distribution of these activities varies across Earth's terrestrial surface (Venter et al. 2016a), as do the distributions of the species they threaten (Jenkins et al. 2013). Understanding and quantifying spatial patterns of where human pressures overlap with sensitive species (i.e. mapping human impacts to threatened species) will improve our ability to prioritise actions to manage and mitigate human impacts on biodiversity (Wilson et al. 2006; Allan et al. 2013). Importantly, it will allow for the identification of areas across species distributions that are free from those threats which the species is sensitive to, and this information can be used to map global 'coolspots' of what we call 'threat refugia'. Both forms of information are essential for conservation planning and can guide action towards securing these impact-free refugia, which are paramount for the survival of many threatened species (Hoffmann et al. 2010; Waldron et al. 2017; Watson et al. 2018a, 2018b).

Mapping impacts to biodiversity requires linking spatial data on the distributions of threats, with the distributions of species known to be sensitive to those threats (Halpern et al. 2008). To date, no efforts undertaken at either regional (Woolmer et al. 2008; Halpern et al. 2009) or global extents (Sanderson et al. 2002; Vörösmarty et al. 2010; Geldmann et al. 2014; Venter et al. 2016a; Ramírez et al. 2017) have accounted for the distribution and sensitivity of species and their threats, and therefore do not directly map likely human impacts (Martins et al. 2012). Past efforts that simply map threats (Venter et al. 2016a) fail to account for the distribution of species that respond to those threats, and even overlapping threats with species ranges (Evans et al. 2011) does not account for the specific sensitivities of each species to co-occurring threats. Some efforts to map threats to the marine realm estimated their impacts at the coarse ecosystem scale but did not account for individual species sensitivities (Halpern et al. 2008, 2015). The few studies that do account for species have either been conducted at fine spatial resolutions (Bellard et al. 2015) or consider a limited number of taxonomic groups (Maxwell et al. 2013; Shackelford et al. 2018), and many suffer from the assumption that species are exposed to threats across their entire range, not just where the threat occurs, overestimating impacts (Schipper et al. 2008; Evans et al. 2011; Moran & Kanemoto 2017). Clearly our understanding of where individual species are being impacted by threats, or where their threat-free refugia are, remains limited at the global scale (Joppa et al. 2016a), and is a major gap in our ability to prioritize conservation actions (Tulloch et al. 2015b; Joppa et al. 2016a).

Here, we present the first global assessment of the spatial distribution of human impacts on globally threatened and near threatened terrestrial birds, mammals and amphibians. We developed a novel method for quantifying and mapping human impacts that jointly considers the distributions of 5,457 threatened and near threatened species (1,277 mammals, 2120 birds, and 2060 amphibians), and the distribution of species-specific threats, and the extent to which the distribution of each species is impacted by relevant threats (Fig. 1).

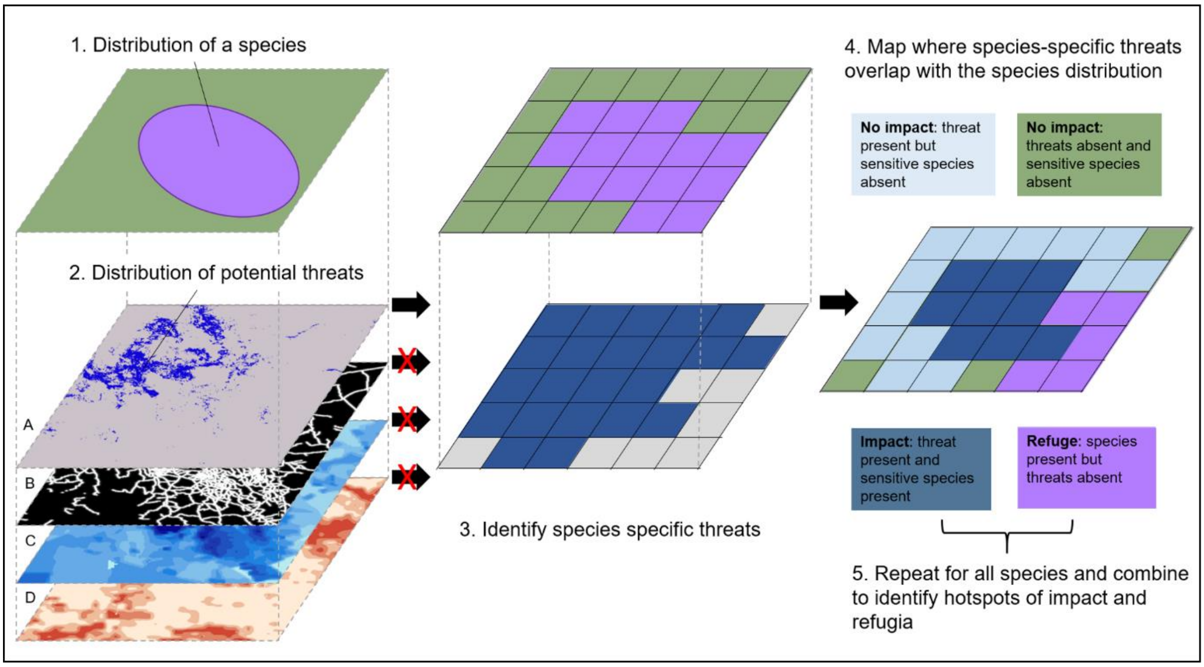

Fig. 1. Methodological framework for mapping cumulative human impacts on threatened vertebrate species.

Spatial data on threats was obtained from the recently updated Human Footprint (Venter et al. 2016a), which is unique for considering eight human pressures globally at a 1km^2 resolution, including: built environments, crop lands, pasture lands, human population density, night lights, railways, major roadways and navigable waterways. This makes the Human Footprint the most complete and highest resolution globally consistent dataset of anthropogenic threats (McGowan 2016). Each individual pressure was linked to a species if they directly or indirectly correspond to threats identified by the IUCN Red List (IUCN 2016) as driving the endangerment of that species. The Human Footprint data correspond with seven major classes, and 15 sub-classes of IUCN threats (Table 1; S1 Table). Although these do not include all threats to species, they do include all of the most prevalent drivers of global biodiversity decline (Maxwell et al. 2016). We calculated the proportion of each species range that is currently impacted by a threat, and then mapped cumulative human impacts in a 30 km x 30 km grid globally (see Methods). We also examined patterns of human impacts across individual species distributions, taxonomic groups and threat status categories. Finally, we used the inverse of our cumulative impact maps to identify threat refugia, the places where high numbers of threatened (and near threatened) species persist unimpacted by human activity.

Table 1. Major classes and sub-classes of threats to biodiversity, as classified in the IUCN Red List of Threatened Species, and the corresponding spatially explicit pressure variable from the updated Human Footprint dataset.

Major threat class (IUCN)	**Sub-class threats (IUCN)**	**Pressure (Human Footprint)**	**Species Impacted**
1. Residential & commercial development	1.1 Housing & urban areas	Electric infrastructure (nightlights) Built environments	1748
	1.2 Commercial & industrial areas	Electric infrastructure (nightlights) Built environments	349
2. Agriculture & aquaculture	2.1 Annual and perennial non-timber crops	Crop lands	4017
	2.3 Livestock farming & ranching	Pasture lands	1850
4. Transportation & service corridors	4.1 Roads & railroads	Railways Roads	563
	4.2 Utility &service lines	Roads	88
5. Biological resource use	5.1 Hunting and collecting terrestrial animals	Navigable waterways Population density Roads	1594
	5.2 Gathering terrestrial plants	Navigable waterways Population density Roads	149

6. Human intrusions & disturbance	6.1 Recreational activities*	Electric infrastructure (nightlights) Population density	373
	6.3 Work & other activities	Electric infrastructure (nightlights) Population density	196
8. Invasive & other problematic species, genes & diseases	8.1 Invasive non-native / alien species / diseases	Population density Roads	1319
9. Pollution	9.1 Domestic and urban waste water	Population density Built environments	205
	9.3 Agriculture & forestry effluents	Crop lands	805
	9.4 Garbage & solid waste	Built environments	27
	9.6 Excess energy	Electric infrastructure (nightlights) Built environments	24

*We excluded navigable waterways as these pressures are generally limited to aquatic-dwelling species by the IUCN, and our analysis focuses on terrestrial species. Additionally, we excluded roads as the pressures described by the IUCN for this category are generally limited to dirt roads, which are not represented in the human footprint.

Results

Human impacts on threatened vertebrate species

We found that on average 38% of a species' distribution range is impacted by one or more relevant threats (Table 2, S1 Data), including an average 21% of the distribution impacted by multiple co-occurring threats. Mammals are the most impacted of all taxa, with on average 52% of a species' distribution impacted by relevant threats. Concerningly, almost one quarter of all species (23%, n=1237) are impacted by threats across >90% of their distribution, with 395 (7%) impacted by at least one relevant threat across their entire distribution. Conversely, we found that one third of all species (34%, n=1863) are not exposed to the threats we mapped across any portion of their distribution; however, this result should be interpreted within the context of threats we consider. We also found that the proportion of a species distribution impacted by threats correlates with its threat status (IUCN Red List categories; Fig. 2) (Analysis of variance P <0.001, F = 7.5). Species classified as critically endangered on the IUCN Red List had almost half their distribution impacted by threats on average (46%, n=851), whilst near threatened species had one third of their distribution impacted by threats on average (31%, n=1439).

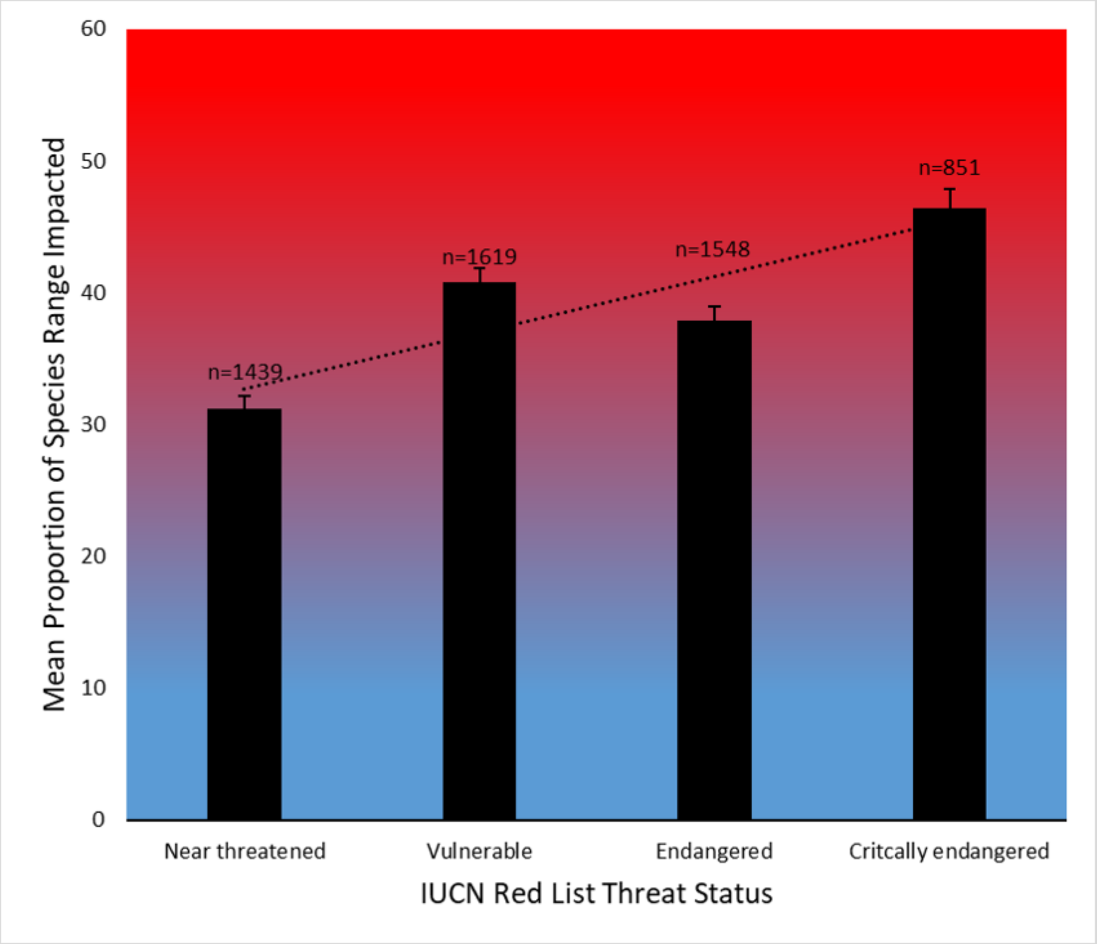

Fig. 2. Mean proportion of species distributions impacted by threats across extinction risk categories of threatened and near threatened terrestrial vertebrates. Bars represent means with standard errors. The data underlying this figure are freely available (doi:10.1594/PANGAEA.897391). Species extinction risk assessed by the International Union for Conservation of Nature (IUCN 2016).

Table 2. The number (and percentage) of species and the proportion of their distribution impacted by threats. The most common category for each taxon is shown in bold.

		Proportion of range impacted by threats					
	Total number of species	0%	1-50%	50-90%	90-99%	100%	Mean (%)
Amphibians	2060	1082 (52.5%)	293 (14.2%)	301 (14.6%)	213 (10.3%)	171 (8.3%)	31.5
Birds	2120	387 (18.3%)	911 (43%)	442 (20.8%)	292 (13.8%)	88 (4.2%)	37.2
Mammals	1277	337 (26.4%)	259 (20.3%)	216 (16.9%)	354 (27.7)	111 (8.7%)	51.5
Total	5457	1806 (33.1%)	1463 (26.8)	959 (17.6%)	859 (15.7%)	370 (6.8%)	38.4

Global hotspots of human impact

Human impacts on threatened vertebrates are widespread, extending across 84% of Earth’s terrestrial surface (S2 Table; S1 Fig; S2 Fig). There is strong spatial variation in the intensity of human impacts, with alarming peaks in Southeast Asia (Fig. 3). Hotspots of human impact differ spatially between taxa (S3 Fig), and as expected, are largely driven by patterns of threatened species richness (S4 Fig) and human pressure, although they are not congruent.

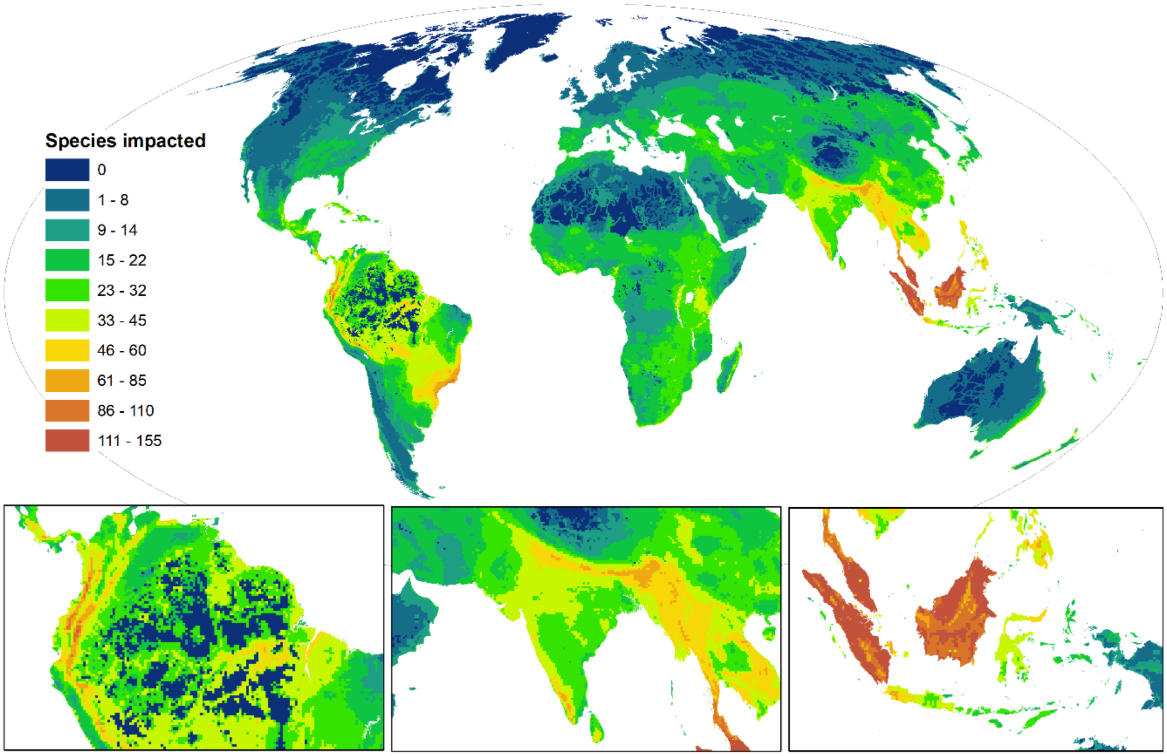

Fig. 3. Cumulative human impacts on threatened and near threatened terrestrial vertebrates (n=5457). Legend indicates the number of species in a grid cell impacted by at least one threat. Maps use a 30x30 km grid and a Mollweide equal area projection. The data underlying this figure are freely available (doi:10.1594/PANGAEA.897391).

The top five countries most impacted by anthropogenic threats to species are all found in Southeast Asia (S3 Table), which we confirm is overwhelmingly the dominant global hotspot of impacts to species (Sodhi et al. 2004). Malaysia has the highest average human impact score (125 species impacted per grid cell), followed by Brunei and Singapore (124 and 112 species respectively). These scores are substantially higher than the global average of 15.6 species impacted per grid cell. Concerningly, there are 13 grid cells (11,700km^2) in Southeast Asia where >150 species are impacted by threats.

When aggregated across biomes and ecoregions, which represent distinct biogeographic spatial units at the global scale (Olson et al. 2001) (S4 Table; S5 Table), the highest human impacts are in *Mangroves*, where on average 35 species are impacted per grid cell. Human impacts are also high throughout the tropical forests which harbour Earth's richest biota, and are critically important for biodiversity conservation (Gibson et al. 2011). The *Tropical and sub-tropical moist broadleaf forests* in Southeast Brazil, Malaysia, and Indonesia are the second most impacted biome, followed by the *tropical and subtropical dry broadleaf forests* in India, Myanmar, and Thailand (35 and 34 species impacted per 900km^2 grid cell).

Global coolspots of threat refugia

We mapped threat refugia for threatened vertebrates by combining the unimpacted parts of each species' distribution. Less than half of Earth's surface (43%) hosts at least one unimpacted threatened species, acting as a potential refugium for that species (Fig. 4); however, impacted and unimpacted species co-occur across 28% of Earth's surface, identifying places where species with divergent sensitives to threatening processes are present. There is strong spatial variation in the intensity of threat refugia for threatened species, and between coolspots for different taxa (S5 Fig). The Amazon rainforest is the overwhelmingly dominant global coolspot. Interestingly, threat refugia follow similar patterns to hotspots of impact in many places, including parts of East Africa, Southeast Asia, and the Amazon. Although counterintuitive, our results are driven by species richness and individual species different sensitivities to threats. Therefore, in species rich areas it is logical that many species will be impacted, whilst many others remain unimpacted. The highest average threat refugia score is in Liberia (23 species unimpacted per grid cell), but the highest score for an individual grid cell occurs in

Malaysia, where 87 species are unimpacted. Encouragingly, there are 12 grid cells (10,800km^2) in Southeast Asia with >60 unimpacted species, although this is primarily due to the large number of threatened species in the region.

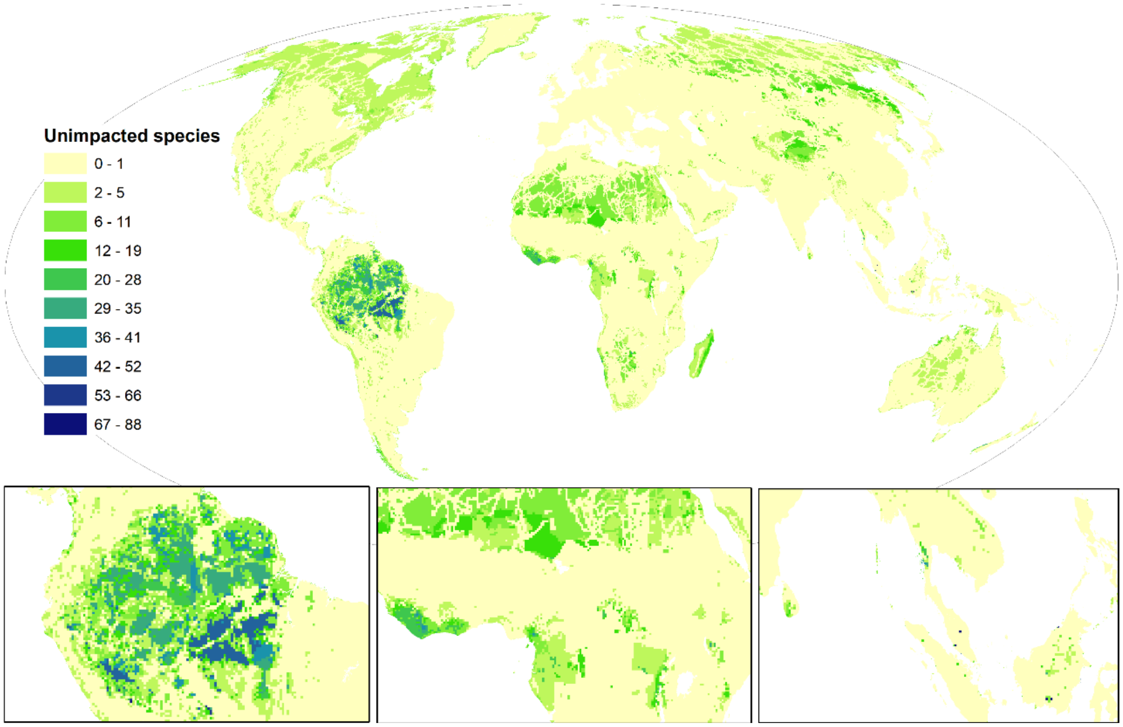

Fig. 4. Coolspots of refugia for threatened and near threatened terrestrial vertebrates (n=5457). Legend indicates the number of species that are not impacted by any threats in a grid cell. Maps use a 30x30 km grid and a Mollweide equal area projection. The data underlying this figure are freely available (doi:10.1594/PANGAEA.897391).

Other coolspots of threat refugia include Liberia in West Africa, The Albertine Rift Valley in East Africa, and Southern Myanmar. When aggregated across Biomes and ecoregions (S4 Table; S5 Table), the *Tropical and sub-tropical moist broadleaf forests*, and *Tundra* act as the greatest threat refugia supporting on average 5.2 and 2.5 unimpacted species per grid cell respectively. The *Tropical and sub-tropical moist broadleaf forests* are also one of the most impacted biomes, demonstrating that despite this, there is still considerable conservation opportunity here. The *Tundra* is the only Biome where more species are unimpacted than impacted on average.

Proportion of species impacted

Some areas of the planet contain low numbers of threatened species (e.g. the high latitudes, or arid and desert regions). Therefore, it is instructive to examine the corresponding proportions of impacted versus unimpacted species. On average there are more impacted than unimpacted species in a grid cell globally (15.6 versus 1.9; ratio 8) (Fig. 5; S6 Fig). The proportion varies for taxonomic groups, with Amphibians having the highest ratio of impacted versus unimpacted species (2.3 versus 0.2; ratio 12.2), compared to birds and mammals (birds 10.5 versus 1.3; ratio 8.1 & mammals 5.4 versus 0.7; ratio 7.8).

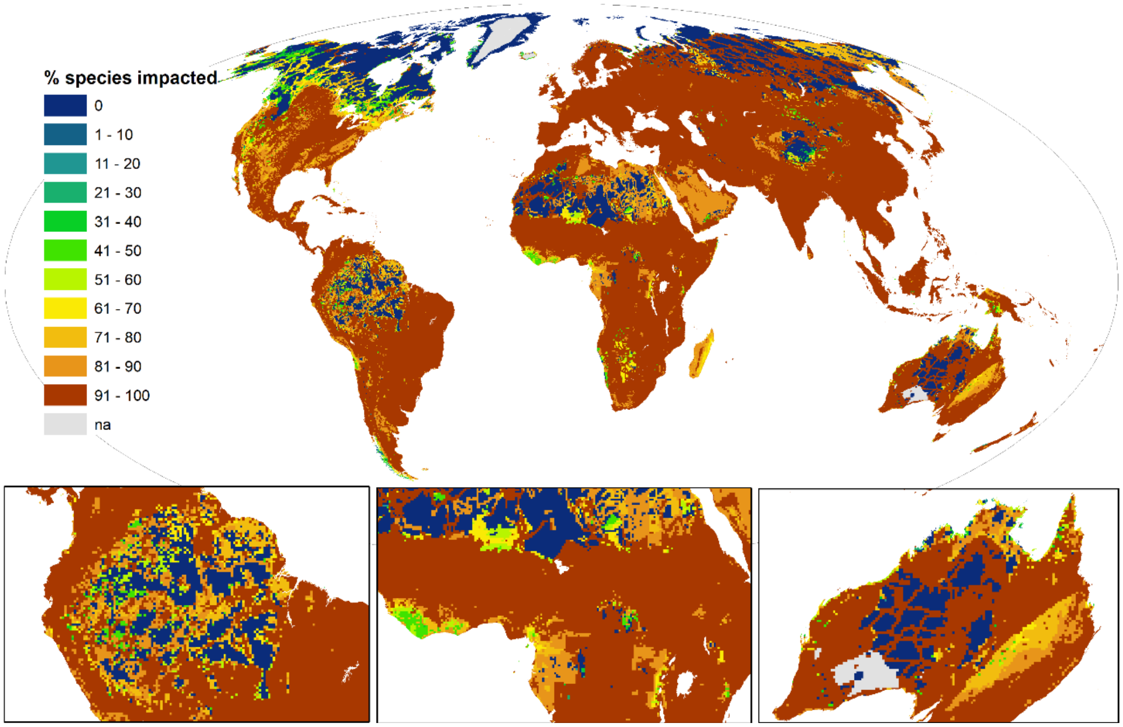

Fig. 5. The percentage of species in a grid cell impacted by a threat (and inversely the number of unimpacted species for whom it is a refuge) for all taxa (n=5457). Maps use a 30x30 km grid and a Mollweide equal area projection. The data underlying this figure are freely available (doi:10.1594/PANGAEA.897391).

In our 30 km^2 grid cells, the proportion of species impacted extends across the full range from 0 – 100%. We found that > 90% of species were impacted in 107,102 grid cells globally, amounting to a staggering 96 million km^2 (66.7% of Earth's terrestrial area). Encouragingly, species are present but none are impacted in 23,865 grid cells (21.5 million km^2; 14.8% of Earth's terrestrial area). The majority of this is wilderness where no human pressures occur. However, we found 426 grid cells (383,400 km^2; 0.27% of terrestrial area) where a species and a human pressure co-occur, but there is no impact (i.e. none of the species present are sensitive to the human activity or land use occurring in that area).

The distribution of areas with high proportions of impacted species is extensive and differs substantially from hotspots of human impact. Europe, North and Central America, and Africa now emerge as hotspots, particularly for mammals and amphibians. The proportion of birds impacted presents a more spatially homogenous pattern, with hotspots in Southeast Asia and the Southeast South America. When aggregated across biomes, *Tropical and subtropical dry broadleaf forests* have the highest mean proportion of impacted species (98.3%), followed by *Temperate grasslands savannas and shrublands* (97.8%) (S4 Table). The *Tundra* and *Boreal/taiga forests* have the lowest mean proportions of impacted species (48.6% and 60.3% respectively).

Discussion

Implications for biodiversity conservation

Our results represent the current best estimate of the spatial distribution of human impacts on terrestrial vertebrates. Continued extirpations, the precursors of extinction, will continue to occur in the impacted portions of species ranges, which our results demonstrate are substantial. Consequently, completely impacted species, or those persisting in threat refugia that are too small to support viable populations in the long term (Maron et al. 2012), likely face imminent extinction. These findings complement recent work showing that hundreds of mammals have lost considerable portions of their historic distributions (Ceballos et al. 2017), and that habitat fragmentation has greatly reduced the proportion of highly suitable habitat within species distributions, reducing their movements (Tucker et al. 2018), and increasing their extinction risk (Crooks et al. 2017).

Although our results are concerning, there is room for hope. The threats we map can be mitigated by *in situ* conservation actions, but diverse approaches are required. To ensure the survival of highly impacted species with little or no threat refugia, active threat management, restoration and rewilding efforts (Ceaușu et al. 2015) are needed to open up enough viable habitat for species to persist. Conservation action in the hotspots of human impact we identify will have high benefits since they are areas with exceptionally high threatened species richness and species-specific threats (Myers et al. 2000). Our results therefore extend previous efforts to identify biodiversity hotspots (Myers et al. 2000), which were developed following somewhat similar logic, and have helped guide conservation action and millions of dollars of funding. The hotspots of human impact we identify are priorities for actions that mitigate the specific threats (Brooks et al. 2006).

Rather than being purely reactive and focusing solely on securing a future for imperiled species in the short term, conservation efforts would also benefit from proactively securing coolspots of species refugia and avoiding any initial human impacts in these places (Betts et al. 2017). This will help ensure many species long term persistence, especially in a time of a rapid climate change, where areas free of threatening processes will be critical for species adaptation (Martin & Watson 2016; Scheffers et al. 2016). Securing refugia will be particularly effective if protection is targeted at the most species rich places that currently remain threat free but may soon be jeopardized (Margules & Pressey 2000; Venter et al. 2018). Additionally, conservation action is also likely to have a high chance of success in threat refugia and be more cost-effective (Balmford et al. 2003; Tulloch et al. 2015a). Proactive and reactive approaches to conservation have historically been pitted against each other (Kareiva & Marvier 2003), with reactive approaches deemed more urgent and taking precedence (Kareiva & Marvier 2003; Hoekstra et al. 2004; Pressey et al. 2017). However, our discovery of the spatial overlap existing between hotspots of impacted species richness and coolspots of unimpacted species richness provides opportunities for multi-faceted conservation action that is reactive for some species, while simultaneously being proactive for others.

The utility of our work extends beyond conservation, and can inform sustainable development planning. Conservation action within some the hotspots of impact we identified (especially in Southeast Asia) are likely to deliver synergistic benefits to other environmental goals, such as carbon conservation and global reduction of deforestation rates (Di Marco et al. 2016). Additionally, according to our definition, species threat refugia do not necessarily have to be off limits to human development, just free of the actions and land-uses that directly threaten species found in that area. This provides a unique framework for quantifying the trade-offs associated with the development of alternate human activities and land-uses, and for identifying locations and strategies to minimise their impacts on biodiversity. This has implications for nations striving to meet ambitious development targets such as the United Nations Sustainable Development Goals (SDGs), especially where achieving development goals involves trade-offs with biodiversity goals (Ibisch et al. 2016; Singh et al. 2018). The framework presented here could be adapted to inform conservation and development planning from local to regional scales, and could be particularly useful in South East Asia, Latin America and sub-Saharan Africa; regions that are undergoing rapid economic development, but are also hotspots of human impact and coolspots of threat refugia (Laurance et al. 2009; Wadey et al. 2018).

It is important to note that our data are not comprehensive of all threats to all species. For example, our analysis does not take into account infectious diseases, a driver of global declines in amphibians (Stuart et al. 2004), or climate change, a threat already impacting many species across all taxa (Scheffers et al. 2016). The results are therefore conservative, and many species will be more impacted than our maps indicate. Notably, one of the fundamental ways to manage global scale threats such as climate change, is to stop more easily abatable threats such as those considered in this analysis [58], to avoid antagonistic or synergistic interactions between multiple threats [59,60]. Other caveats worthy of discussion are that we assume the intensity of threats (e.g. agricultural land use or roads) are equal across their distribution, and that species are equally sensitive to each threat known to affect them. This assumption could mean we are overestimating impacts in cases where species are sensitive to several threats where only the secondary threat is present. The IUCN has collected data on the severity of threats to species, but a comprehensive database is still lacking, as this information is often unknown. The further development of these data would allow important nuances to be included in future extensions of this work.

A species and threat overlap does not necessarily mean that the threat is acting in that location. However, our analysis extends beyond a species threat overlay by incorporating three co-occurring and connected forms of data; a species distribution, a threat distribution, and that species vulnerability to that threat. To the best of our knowledge, this is the first time species-specific sensitivity to threats has been incorporated into an impact mapping exercise at this scale. By mapping species-specific threats, it is much more likely that a threat is acting in a given location and impacting a species. This approach does rely on the current knowledge of threats to species, and cannot account for the possibility that undocumented threats could be impacting a species. We sourced information on threats to species from the IUCN, who are the main authority on assessing species extinction risk, and limited our analyses to threatened terrestrial vertebrates, which include the most studied taxa globally (Di Marco et al. 2017a). Yet, it is important to note that there is still variation between species assessments due to taxonomic and geographical biases which could influence our findings (Donaldson et al. 2017). For example, our understanding of threats to mammals is greater than for amphibians, which could partly explain why our results show mammals as the most impacted taxon, whilst amphibians are generally regarded as the more threatened taxon.

This analysis provides a framework for mapping human impacts that represents a conceptual advance over cumulative pressure mapping or threatened species richness mapping that can be applied to any scale, taxa or realm. Furthermore, the framework and baseline can be continually updated and enhanced as additional data on species distributions, their sensitivity to threats, and the spatial distribution of threats become available, and our understanding of threat interactions improves. Improvements in our understanding of species sensitivity to threats will also allow this analysis to be extended to other forms of life such as plant and invertebrate species. We have shown that human impacts on species are almost ubiquitous across Earth, and that hundreds of species have no refuge from these impacts, including many of the most charismatic large mammals. The survival of these species, and many more, hinges on humanity's ability and willingness to compromise and share space.

Methods

Spatial data on threatened species ranges

We focused our analysis on terrestrial vertebrate groups (amphibians, birds, mammals) with distribution maps and assessment of identified threat available for all species. Spatial data on mammal and amphibian distributions was obtained from the IUCN Red list of threatened species (IUCN 2016), and bird distributions from Birdlife International and NatureServe (Birdlife International and Handbook of the Birds of the World 2017). We focused on species which are listed as near threatened, vulnerable, endangered or critically endangered since their major threats have been identified and comprehensively assessed for the IUCN Red List of Threatened Species (Rodrigues et al. 2006; IUCN 2016; Brooks et al. 2016; Maxwell et al. 2016). Following established practice we only considered native and reintroduced parts of each species distribution range in our analysis, which are listed as extant, possibly extant or possibly extinct within their range (Butchart et al. 2015). We excluded introduced, vagrant and extinct species as well as species whose origin or presence is uncertain. Although reintroduced species ranges may be theoretically subject to less threats, they may still be under threats not realised during the reintroduction process (Seddon et al. 2014). As such, incorporating all portions of a species range, including reintroduced areas, can provide a robust picture of the threats for a given species. Finally, we only included species whose distribution overlapped (even just partially) with the extent of the Human Footprint threat dataset, which does not include Antarctica. A total of 2060 amphibian species, 2120 bird species, and 1277 mammal species qualified for our analysis based on these criteria.

Spatial data on threats to species

Spatially explicit data on the distribution of threats to species was obtained from the recently updated Human Footprint maps (Venter et al. 2016a, 2016b). These are globally standardised maps of cumulative human pressures on the natural environment at 1km^2 resolution globally for eight of the most harmful pressures humans exert on nature including: 1) built environments, 2) population density, 3) electric infrastructure, 4) crop lands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. This makes the Human Footprint the most up-to-date and comprehensive global cumulative pressure/threat map available (McGowan 2016). The Human Footprint is also the first global scale threat dataset to have been validated for accuracy. This was done by visually confirming if human pressures were present or absent across thousands of randomly selected 1km x 1km plots globally [68]. The data were found to exhibit an excellent degree of accuracy (88.5% agreement between visual plots and human footprint data), especially at identifying threat free areas (98.9% agreement between visual plots and wilderness) (Allan et al. 2017b).

In the Human Footprint each pressure layer is scaled between 1 and 10 based on its estimated impact on the environment. These scores are then cumulated in each pixel to give a total score out of 50. We converted these scores to binary (present or absent in any 1km^2 pixel) for our analyses since there is no data on the relative severity of individual threats to species. To convert pressure layers from continuous scales to binary (present/absent) we set cutoffs where the pressure was considered absent. For example, roads have a direct pressure score of 8 up to 500 meters either side, beyond this the pressure score decays exponentially from a score of 4 out to 0 at 15km. When converting this to a binary score, we set a threshold that considered the pressure present up to 3 km either side of the road, and absent beyond this (see S6 Table for comprehensive details on how each layer was handled).

Mapping species-specific threats

We identified cases where the eight pressures in the updated Human Footprint dataset directly or indirectly correspond with threats to biodiversity as listed in the IUCN Red List

(IUCN 2016) (Table 1. S1 Table). This allowed us to globally map seven major classes, and 15 sub-classes of threats. Although this is not comprehensive of all the threats to species, it importantly includes the biggest drivers of biodiversity declines globally (Maxwell et al. 2016). For example, multiple forms of agriculture, urban development and transportation corridors are directly accounted for by our pressure data. Whilst biological resource use and over-exploitation through hunting, pollution, human disturbance, and invasive species are indirectly accounted for by human population density, roads and navigable river networks which act as proxies (Hulme 2009; Laurance et al. 2009, 2015; Meunier & Lavoie 2012; Ripple et al. 2016a).

Analysing the extent of human impacts on individual species

For a pressure to impact a species, it must spatially overlap with that species' distribution, and have been identified in the IUCN Red List as a threat to that species (Martins et al. 2012). Therefore, we calculated the extent of overlap between each species distribution, and each pressure layer which that species is sensitive to at a 1km^2 resolution globally. We accounted for the overlap between threats, identifying where multiple threats are present. All spatial data was analysed in a Mollweide equal area projection in ESRI ArcGIS and PostGIS, and statistics were calculated in R statistical software. We used a one-way analysis of variance to test for correlation between a species extinction risk category and the proportion of that species range impacted by threats.

Mapping hotspots of cumulative human impacts

We estimated cumulative human impacts on threatened species using a global 30km x 30km planning unit grid, since this has been identified as the ideal resolution for reducing the effects of commission errors (where species are thought to be present but are not) when working with species range maps (Di Marco et al. 2017b). An impact was scored in a grid cell if a species and at least one threat it is sensitive to were both present. This means that the presence of a threat and a species in the same grid cell is not considered an impact unless the species is known to be sensitive to that threat. We then calculated the sum of all impacted species in a grid cell to give a total estimate of cumulative human impact.

As a sensitivity analysis, we calculated the area of each species distribution within each planning unit and the area of each pressure in each planning unit, converting both to proportions of planning unit area. To estimate how impacted each species is within each planning unit, we multiplied the proportion of the species distribution by the proportion of each pressure which threatens and then summed the scores. By using the proportion of planning unit area, we scale for the likelihood of a species and a pressure overlapping within a grid cell. Finally, we calculated the sum all the individual species impact scores within each grid cell, to give a total estimate of cumulative human impact. Spatial patterns of impact were strongly coherent between the two approaches so we report on the more intuitive binary metric in the manuscript. We also ran a multiple linear regression on 10,000 randomly selected grid cells comparing the binary impact metric reported in the paper (a species and ≥ 1 threat = 1 impact in a grid cell) (response variable), and species richness and the mean human footprint in a grid cell as predictor variables. We obtained an R squared value of 0.9, which shows that the human footprint and richness explain 90% of the variation in the model, but also suggests that including species sensitivities to threats explains the other 10% of the variation. When we incorporate cumulative impacts (1 species + 3 threats = 3 impacts in a grid cell) and re-run the multiple linear regression the R squared drops to 0.77, suggesting that in areas where multiple threats are present, including species-specific threats is particularly important.

Mapping coolspots of threatened vertebrate anthropogenic refugia

We followed similar methods to mapping human impacts, where a cell was scored as an anthropogenic refuge if a species was present in the cell, but no pressures that threaten it were present. These were then summed to give a cumulative score of the number of unimpacted species in a cell.

APPENDIX 2 The ayahuasca tourism boom: An undervalued demand driver for jaguar body parts?

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Main

The jaguar *Panthera onca* is threatened across much of its range, due to habitat loss, retaliatory killings, and poaching. Consequently, it is listed as near threatened on the IUCN Red List (Quigley et al. 2017). There is evidence of a growing trade in jaguar body parts across Latin America, particularly in Brazil, Bolivia, Suriname, Costa Rica, and Peru (Berton 2018). For example, on February 23, 2018, two Chinese citizens were apprehended in Santa Cruz de la Sierra, Bolivia for possession of 185 jaguar teeth and three skins (Berton 2018). Similarly, in Brazil at least 30 seizures of jaguar parts have occurred in the past 5 years (Berton 2018).

In Southeast Asia, jaguar claws and teeth are worn as jewellery; their skins are bought for home decor; and a glue paste (made from boiled jaguar parts) is consumed to heal various ailments. Most organized trafficking appears to be by contractors working for foreign companies hired to hunt cats to export body part (Berton 2018). With Latin America's current ayahuasca and shamanic tourist boom there are additional demands for jaguar products, which is our focus.

Each year, thousands of ayahuasca tourists travel to Peru, generating significant revenue for retreat centers that administer the brew (Fotiou 2016). For example, a 2015 study found that in Iquitos, Peru's largest Amazonian city, 10 of the 40 largest retreats generated over USD 6.5 million annually (Alvarez 2015). Ayahuasca is a traditional Amazonian medicine that has become a global phenomenon. It is a psychoactive brew made from the ayahuasca vine Banisteriopsis caapi and chakruna leaves *Psychotria viridis*. It is traditionally administered in ritualized shamanic ceremonies for both spiritual and physical healing; however, recreational users now ingest it for entheogenic experiences. It is the subject of extensive scientific research, global conferences, tourism, and even religious movements.

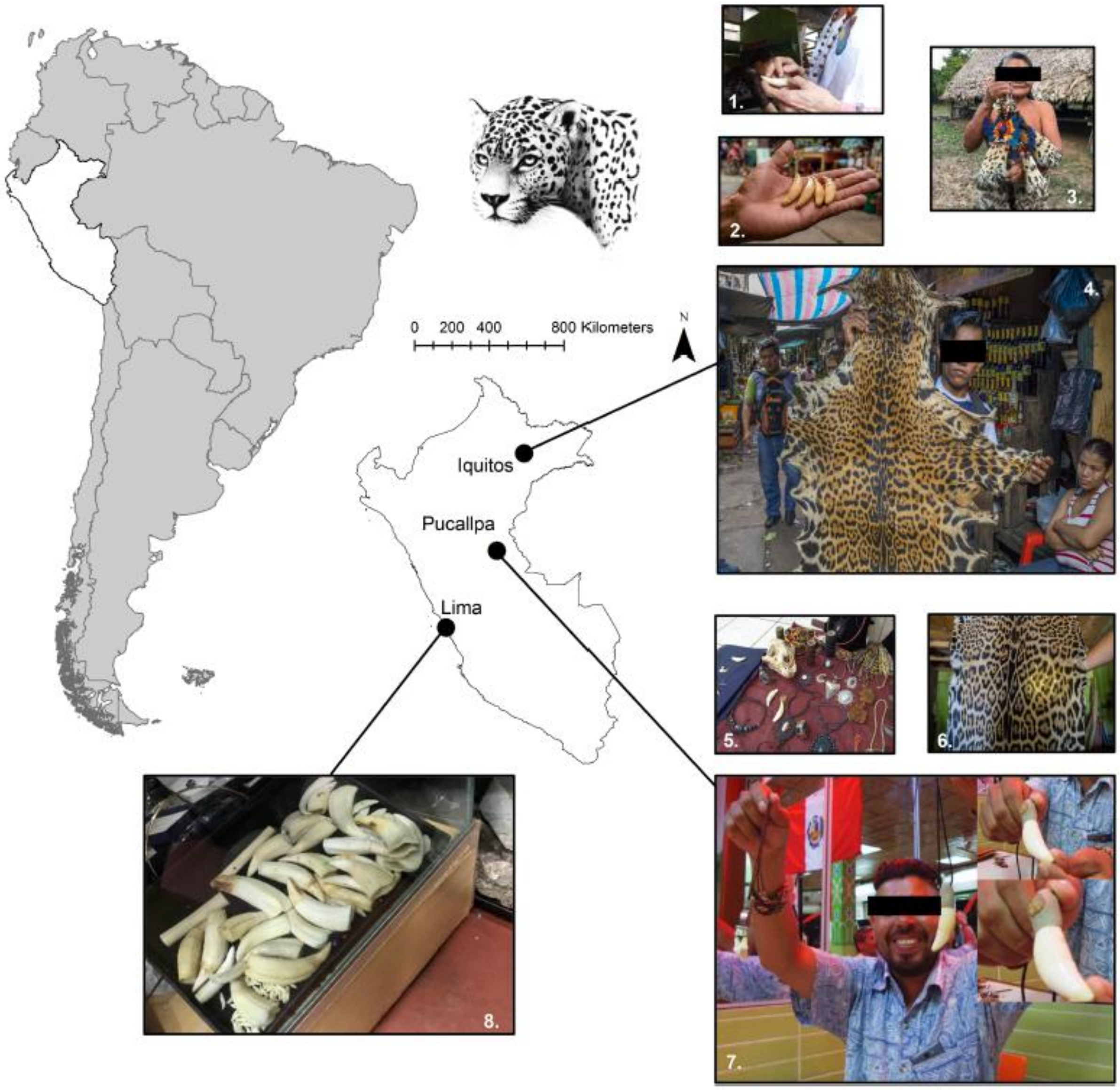

Figure 1. The three Peruvian cities where markets sold jaguar parts (8 locations total). Images 1 (an ayahuasca tourist with a newly purchased jaguar tooth), 2 (jaguar teeth held by a local trader) and 4 (a jaguar skin held by a trader) were taken in the Passage

Paquito section of Belen market, Iquitos; Image 3 (a village elder holds 3 jaguar paws) was shot in the Barrio Florido community, Punchana district, outskirts of Iquitos. Images 5 (teeth and a jaguar skull for sale in a craft market) and 7 (jaguar tooth pendants) were taken in Yarinacocha Market, Pucallpa. Image 6 (jaguar skin with shotgun pellet holes) was taken at the Clock Plaza of Pucallpa. Image 8 was shot in Lima, and shows jaguar, sea lion and caiman teeth in a small exhibit box. We also took images of two skins at the edge of the Momon River, Iquitos (Punchana district; Supplementary Information 1). Images by Steve Winter (2, 4 and 6), Alex Braczkowski (1, 3,5 and 7) and Devlin Gandy (8). Total sample sizes for discussions with vendors, shamans and individuals engaged in the tourism industry are as follows: One trip in August 2019 by the second author, one trip by the third author in April 2019; and an earlier trip in August 2017 by the first, second, third, fifth and sixth authors to a) Pucallpa – 9 shamans (Mestizo, Ahaninka, and Shipibo-Conibo), 3 airport secuirty guards tasked with searches of wildlife products, 3 local mediators, 1 veterinarian (San Juan Beer Company), five street-side shops (7 sellers), b) Lima – 2 small shops, c) Iquitos - approximately 14 sellers: 7 at Passage Paquito section of Belen market (one of them with 3 family members), 2 at Arteanal San Juan, 1 Barrio Florido community, 4 at the Boulevard. In addition there were 4 intermediaries who assisted in connecting the third author to vendors, 5 shamans, and 4 tourists interested in sessions with ayahuasca.

We present findings from investigations into the jaguar parts trade in local markets in Peru, considered a top tourist and ayahuasca tourism destination. We postulate that commercialized ayahuasca tourism may be an undervalued contributor to the trade.

Findings

Investigations were conducted between August 2016 and August 2019 in the cities of Lima, Iquitos, and Pucallpa (Figure 1). This information was collected while working on a story for National Geographic Magazine. Sales of items incorporating jaguar body parts to tourists were most prevalent in the Amazonian cities of Iquitos and Pucallpa. In Lima, a few jaguar fangs were found as “specialty items” at a curio a shop and at an open-air tourist market.

In Iquitos, jaguar skins ranged in price from S/. 150 (Peruvian soles) to S/. 500 (USD 49–152); a single paw could be purchased for S/. 30 (USD 9). Jaguar skin purses were sold for S/. 20 (USD 6); a stuffed jaguar head was priced at S/. 100 to S/. 300 (USD 30–91). Jaguar canines cost anywhere from S/. 200 to S/. 400 each (USD 61–122); two street vendors and a local trader In Pullcapa sold jaguar canine pendants for S/. 250 to S/. 330 each (USD 76–100). Prices for jaguar skins in Pucallpa and Iquitos were similar, selling at USD 80–200. Sellers were also willing to transport the skins internationally, using airport and customs agent contacts. We were approached repeatedly by local vendors to purchase jaguar body parts in touristic locations. In contrast, our team had to inquire specifically for jaguar body parts in less touristic areas, but still found them. We note that there are also decoys: South American sea lion *Otaria flavescens*, and caiman *Melanosuchus niger* teeth were being sold as jaguar fangs in both Lima and Iquitos.

Discussion with street-side vendors, shamans, and individuals working in the tourism industry (sample sizes are in Figure 1) revealed that jaguar canine pendants, jaguar skin bracelets, and other items are being sold to “enhance the ayahuasca experience” (Figure 1). This appears to be a case of rebranding, specifically using “ayahuasca marketing” for sellers to charge a premium on jaguar parts. Local indigenous shamans and healers from the Pucallpa area (Shipibo, Conibo, and Ashaninka ethnicities) denied the notion that jaguar parts enhance the ayahuasca experience for visiting tourists, and suggested that this practice is being marketed by “charlatan shamans” seeking financial gain from the ayahuasca boom.

East Asian demand for jaguar parts remains the main market (Berton 2018; Plotkin 2018) however, we suggest that the ayahuasca tourism industry is quickly becoming an important additional driver of poaching. We argue that the drivers behind all demand for these products in Peru and other ayahuasca tourism hubs must be investigated further, and recommend future research to identify the main buyers (Chinese nationals or tourists, and their countries of origin), and their motivation (memorabilia, ayahuasca ceremony or traditional Chinese medicine).

Solutions

1. Government regulations—Peru has implemented a national anti-wildlife trafficking policy, which includes jaguar trafficking (Supreme Decret N_ 011-2017-MINA GRI) that punishes wildlife traffickers with a prison sentence of 3–5 years, as established in article 308 of the 2016 Peruvian penal code.
2. Education of tourists—a formal media campaign to educate ayahuasca tourists on the plight of wild jaguars, and discouraging them from buying jaguar parts is urgently needed.
3. Regulate and sensitize shamanic tourism operations—we suggest that a concerted effort to formalize ayahuasca tourism and educate both tourists and tour operators could play an important role in discouraging the trade in this niche market. The shamans we encountered in Iquitos and Pucallpa stressed the importance of the jaguar to the Amazon ecosystem and as a powerful totem in the spiritual world. The leadership of ayahuasca retreats could be important champions for jaguar conservation in Peru, Costa Rica, Colombia, Brazil, and other regions where ayahuasca is used, and they could discourage tourists from using jaguar parts.
4. Bettered enforcement—enforcement by local police is limited and sellers in Peru, and traffickers are finding ways to hide the products in warehouses, in the back of their stalls and other locations (Supplementary information 1). Bettered support and more resources are needed for anti-trafficking police in Peru.

APPENDIX 3 Supplementary Material for Chapter 2

Table 1. Proportions of species that have varying levels of intense human pressure across years. The table column headings contain the categories of species assessed, including all species, all threatened species (IUCN classifications of Vulnerable, Endangered, and Critically Endangered), all amphibians, threatened amphibians, all mammals, threatened mammals, all birds, and threatened birds (out of the 22,752 species assessed in this study). The exact number of species assessed are in parenthesis under each column heading. We calculate the proportion of species under varying levels of intense human pressure: 0%, >50%, and 100%. As such, each entry corresponds to the proportion of species (and the absolute number of species in parentheses) within a specific category as mentioned above that have: 1) no intense human pressure within their range; 2), more than half of their range exposed to intense human pressure; or 3) all of their range exposed to intense human pressure. We calculate the proportion of species with no intense human pressure by taking the sum of proportions within a species' range that fall within the Human Footprint index of three and above (e.g. Di Marco *et al.* 2018) and reporting on the number of species that have a sum of proportions of exactly zero. We calculate the proportion of species with >50% of their range exposed to intense human pressure by taking the sum of proportions that fall within the Human Footprint index of three and above and report on the number of species that have a sum of proportions of exactly 0.5 or greater. Lastly, we calculate the proportion of species with all of their range exposed to intense human pressure by taking the sum of proportions that fall within the Human Footprint index of three and above and report on the number of species that have a sum of proportions of one (i.e. those species that have 100% of their range exposed to intense human pressure). All summed proportions were rounded to six decimal places before reporting on each

threshold (although each entry for proportion of species in the table is reported to four decimal places). We obtained the Human Footprint data from Venter *et al*. (2016).

	All species (N=20,529)	All threatened species (n=4,610)	All amphibians (n=5,000)	Threatened amphibians (n=2,050)	All mammal (n=4,592)	Threatened mammals (n=1,118)	All birds (n=10,745)	Threatened birds (n=1,360)
1993_proportion species with 0% intense human pressure (# species in parentheses)	0.0041 (85)	0.0115 (53)	0.0090 (45)	0.0047 (30)	0.0028 (13)	0.0015 (8)	0.0025 (27)	0.0014 (15)
2009_proportion species with 0% intense human pressure (# species in parentheses)	0.0058 (53)	0.0087 (40)	0.0072 (36)	0.0127 (26)	0.0011 (5)	0.0027 (3)	0.0011 (12)	0.0081 (11)
1993_proportion species with >50% intense human pressure (# species in parentheses)	0.8081 (16,589)	0.8796 (4,055)	0.8344 (4,172)	0.2909 (1,870)	0.7905 (3,630)	0.1772 (942)	0.8010 (8,606)	0.1080 (1,166)
2009_proportion species with >50% intense human	0.8533 (17,517)	0.9078 (4,185)	0.8772 (4,386)	0.9376 (1,922)	0.8380 (3,848)	0.8766 (980)	0.8466 (9,097)	0.8860 (1,205)

pressure (# species in parentheses)								
1993_proportion species with 100% intense human pressure (# species in parentheses)	0.1125 (2,310)	0.4744 (2,187)	0.3468 (1,734)	0.6522 (1,337)	0.1276 (586)	0.3345 (374)	0.0985 (1,058)	0.3250 (442)
2009_proportion species with 100% intense human pressure (# species in parentheses)	0.1621 (3,328)	0.5330 (2,457)	0.3960 (1,980)	0.7088 (1,453)	0.1520 (698)	0.3944 (441)	0.1163 (1,250)	0.3750 (510)

Table 2. Average and median proportions of intense human footprint within species' ranges across years. The table column headings contain the categories of species assessed, including all species, all threatened species (IUCN classifications of Vulnerable, Endangered, and Critically Endangered), all amphibians, threatened amphibians, all mammals, threatened mammals, all birds, and threatened birds (out of the 22,752 species assessed in this study). The exact number of species assessed are in parenthesis under each column heading. We calculate intense human pressure within species' ranges by taking the sum of proportions within species' ranges that fall within the Human Footprint index of three and above (e.g. Di Marco *et al.* 2018) and report on the average and median proportions across all species that fall within the aforementioned categories. As such, each entry in the table corresponds to the average proportion with median proportions in parentheses; however, the last row in the table corresponds to the percent change in average proportions of intense human pressure within species ranges. We obtained the Human Footprint data from Venter *et al*. (2016).

	All species (N=20,529)	All threatened species (n=4,610)	All amphibians (n=5,000)	Threatened amphibians (n=2,050)	All mammal (n=4,592)	Threatened mammals (n=1,118)	All birds (n=10,745)	Threatened birds (n=1,360)
1993_average proportion of intense human footprint within species range (median in parentheses)	0.7453 (0.8415)	0.8485 (0.9969)	0.8038 (0.9550)	0.8948 (1.000)	0.7313 (0.8260)	0.8009 (0.9392)	0.7216 (0.7974)	0.8152 (0.9465)

2009_average proportion of intense human footprint within species range (median in parentheses)	0.7897 (0.8932)	0.8812 (1.0000)	0.8413 (0.9855)	0.9193 (1.0000)	0.7749 (0.8782)	0.8410 (0.9811)	0.7693 (0.8572)	0.8527 (0.9787)
Percent change in average proportion of intense human pressure within species ranges between 1993 and 2009	5.9573%	3.8539%	4.6653%	2.7380%	5.9620%	5.0069%	6.6103%	4.6000%

Table 3. The proportions of cumulative human pressures across Earth's terrestrial surface for 1993 and 2009, showing an increase in intense human pressure by 4.5% between years. We obtained the Human Footprint data from Venter *et al*. (2016). For clarity, "No human pressure" has a Human Footprint index value of 0, "No/Low human pressure" has index values of 0-2, and "Intense human pressure" has index values of 3-50. Each entry in the table for the first two columns reports the proportion with the area in km^2. The third column of the table reports the percent change between years.

Human pressure thresholds	1993 proportion of Earth's terrestrial surface	2009 proportion of Earth's terrestrial surface	Percent increase/decrease from 1993 to 2009
No human pressure	0.2854 (38,265,091 km^2)	0.2718 (36,441,429 km^2)	-4.7652%
No/Low human pressure	0.1632 (21,878,153 km^2)	0.1521 (20,392,433 km^2)	-6.8015%
Intense human pressure	0.5514 (73,921,142 km^2)	0.5761 (77,230,524 km^2)	4.4795%

Table 4. *Post hoc* analysis of proportions and number species that are exposed to intense human pressure, but shifting the lower limits from pasture land (Human Footprint index value of 3) to industrial agricultural infrastructure (Human Footprint index value of 7) such as large-scale cropland and roadways. We obtained the Human Footprint data from Venter *et al*. (2016). The table column headings contain the categories of species assessed, including all species and all threatened species (IUCN classifications of Vulnerable, Endangered, and Critically Endangered). The exact number of species assessed are in parenthesis under each column heading. We calculate the proportion of species with >50% of their range exposed to this level of intense human pressure by taking the sum of proportions that fall within the Human Footprint index of seven and above and report on the number of species that have a sum of proportions of exactly 0.5 or greater.

	All species for 2009 human footprint data (N = 20,529)	All threatened species for 2009 human footprint data (n = 4,610)
The proportion of species with ranges >50% exposed to a Human Footprint index value of 7 and above (# species in parentheses)	0.4047 (8,308)	0.5071 (3,230)

APPENDIX 4 Supplementary Material for Chapter 4

Table 1. Parameters for two dynamic models of mesoscavenger release, including known mortality, efficiency, handling times, carcass availability, and decay rates from the literature for obligate scavengers and facultative scavengers.

Symbol	System	Notes and units	Parameter	Species	Citation
μ	Obligate: areas where vultures are present	Mortality rate of apex scavengers in the absence of carcases (1/days till death without food)	0.05 (1/20 days)	Cape vultures (*Gyps coprotheres*)	(Komen 1992)
e_a	Obligate: areas where vultures are present	Mean time to detect carcasses (efficiency) for apex scavengers (1/days till location of carcass)	18.77 (1/0.053264 days)	Griffon vultures (*Gyps fulvus*)	(Houston 1974)
h_a	Obligate: areas where vultures are present	Average consumption time (handling time) of carcasses by apex scavengers (days/kg)	0.00983 days/kg	Scavenger assemblage with vultures in the system	(Morales-Reyes *et al.* 2017)
e_a	Facultative: areas where Tasmanian devils are healthy and present	Mean time to detect carcasses (efficiency) for apex scavengers (1/days till location of carcass)	0.2534 (1/ 3.9456 days)	Tasmanian devils (*Sarcophilus harrisii*)	(Cunningham et al. 2018)
h_a	Facultative: areas where Tasmanian devils are healthy and present	Average consumption time (handling time) of carcasses by apex scavengers (days/kg)	0.0309 days/kg	Tasmanian devils (*Sarcophilus harrisii*)	(Cunningham et al. 2018)

e_m	Facultative: areas where vultures are absent	Mean time to detect carcasses (efficiency) for mesoscavengers (1/days till location of carcass)	1.0 (1/1 day) (doubles in the presence of apex obligate scavengers)	Scavenger assemblage without vultures in the system	(Morales-Reyes *et al.* 2017) (Kane & Kendall 2017)
e_m	Facultative: areas where Tasmanian devils are diseased and declining	Mean time to detect carcasses (efficiency) for mesoscavengers (1/days till location of carcass)	0.1504 (1/6.6497 days)	Forest ravens (*Corvus tasmanicu*) and spotted-tailed quolls (*Dasyurus maculatus*)	(Cunningham et al. 2018)
h_m	Facultative: areas where vultures are absent	Average consumption time (handling time) of carcasses by mesoscavengers (days/kg)	0.1344 days/kg	Scavenger assemblage without vultures in the system	(Morales-Reyes *et al.* 2017)
h_m	Facultative: areas where Tasmanian devils are diseased and declining	Average consumption time (handling time) of carcasses by mesoscavengers (days/kg)	0.0330 days/kg	Forest ravens (*Corvus tasmanicu*) and spotted-tailed quolls (*Dasyurus maculatus*)	(Cunningham et al. 2018)

p		Rate at which carcasses become available on the landscape (days/kg/km^2)	1.02 days/kg/km^2	Mammal assemblage in Kibale Forest of East Africa	(Houston 1985)
δ		Rate of decay of a carcass (1/days to dry stage of decay)	0.0125 (1/80 days)	Pig (*Sus scrofa*) carcasses	(Carter et al. 2006)

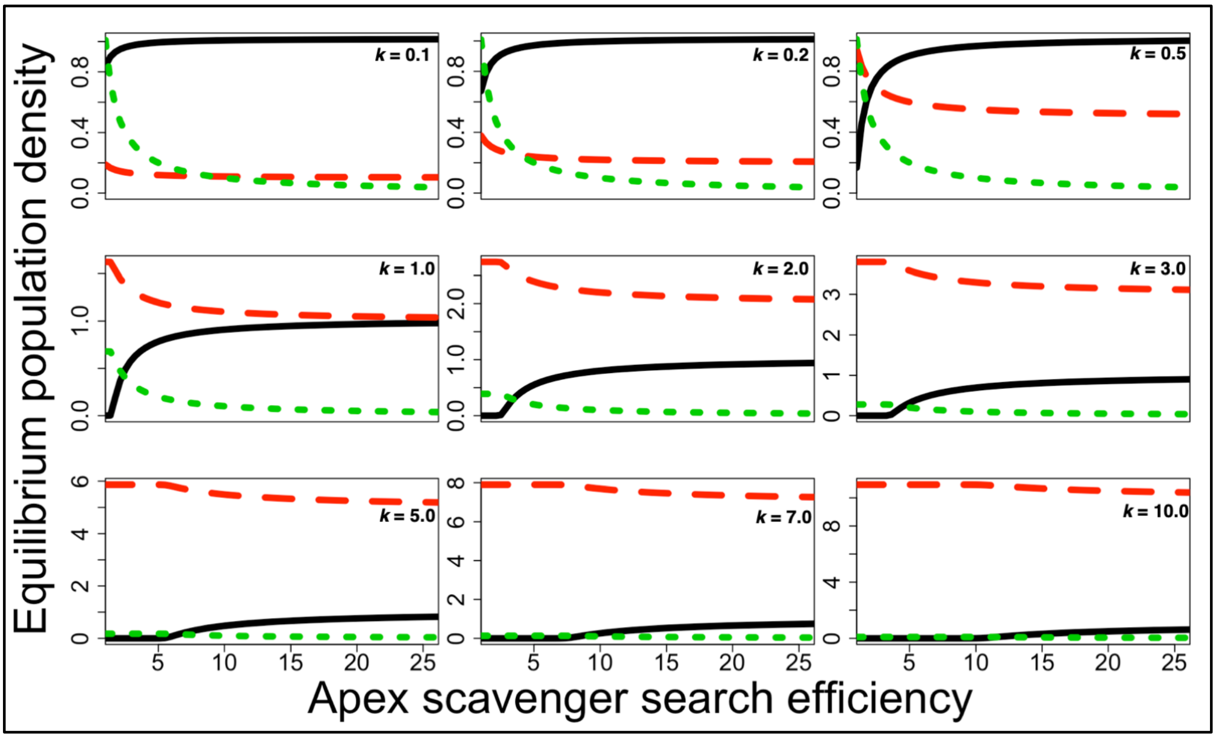

Figure 1. Exploration of equilibrium population densities of carcasses (green dotted line), mesoscavengers (red dashed line) and apex obligate scavengers (black solid line) from the dynamic model (eqn 1 in the main text) as a function of apex scavenger search efficiency, e_a, across varying mesoscavenger carrying capacities, *k*, in the absence of carcasses. The left-most value on the x-axis for each plot is equivalent to mesoscavenger search efficiency, such that apex scavengers are more efficient at locating carcasses. Generally, the more efficient (i.e. functionally dominant) the apex scavenger, the more they suppress mesoscavenger populations and carcass densities. Additionally, *k* appears to have a strong effect on carcass and apex scavenger densities.

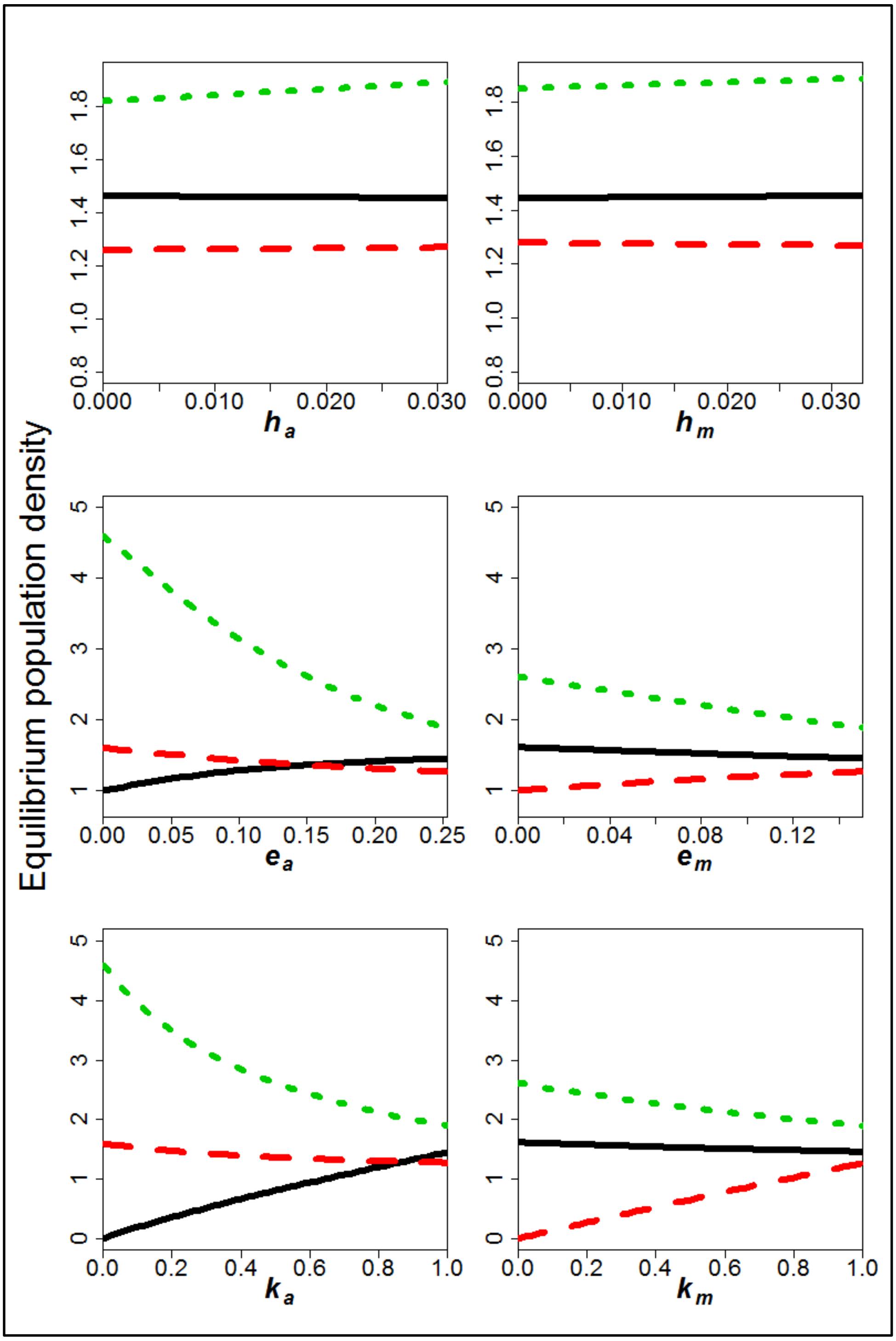

Figure 2. Exploration of equilibrium population densities of carcasses (green dotted line), mesoscavengers (red dashed line), and apex facultative scavengers (black solid line) from the dynamic model (eqn 2 in the main text) as a function of apex facultative scavenger and mesoscavenger handling times of carrion (h_a and h_m), search efficiencies for carrion (e_a and e_m), and carrying capacities in the absence of

carrion (k*a* and k*m*) from a Tasmanian devil system (Table 1). The carcass production (*p*) rate is the same as that of the apex obligate scavenger system.

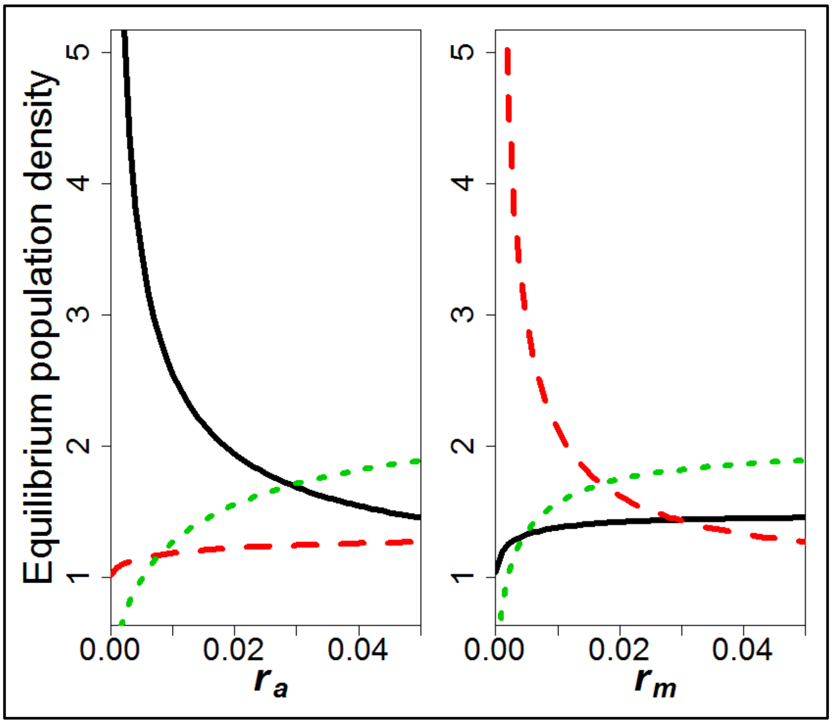

Figure 3. Exploration of equilibrium population densities of carcasses (green dotted line), mesoscavengers (red dashed line), and apex facultative scavengers (black solid line) from the dynamic model (eqn 2 in the main text) as a function of apex facultative scavenger and mesoscavenger logistic growth rate (r_a and r_m). The carcass production (*p*) rate is the same as that of the apex obligate scavenger system. We find that when r_a and r_m go to zero, density dependence is removed in our model, and therefore the population always increases in the presence of carcasses. One could consider the same model but with an alternate parameterization,

$$\frac{dA}{dt} = \beta_a A - \mu_a A^2 + \frac{g_a e_a C A}{1 + h_a e_a C} ,$$

$$\frac{dM}{dt} = \beta_m M - \mu_m M^2 + \frac{g_m e_m C M}{1 + h_m e_m C} .$$

This is equivalent to the logistic model, but with a linear birth rate, β_a and β_m, and non-linear death rate, μ_a and μ_m for apex and mesoscavengers respectively. In this formulation, mesoscavengers and apex scavengers have carrying capacities $\frac{\beta_a}{\mu_a}$ and $\frac{\beta_m}{\mu_m}$, respectively, in the absence of carcasses. When running a sensitivity analysis of growth rate at low densities, one could increase β (rather than *r* in the original models), in which case scavenger equilibrium density increases with increasing birth rate, and decreases with increasing death rate. The benefit of this alternate model is that density dependence is unaffected by the parameter that controls the growth rate at low densities. The following figure is the result of exploring this alternate model with a baseline β and μ all set to 0.5:

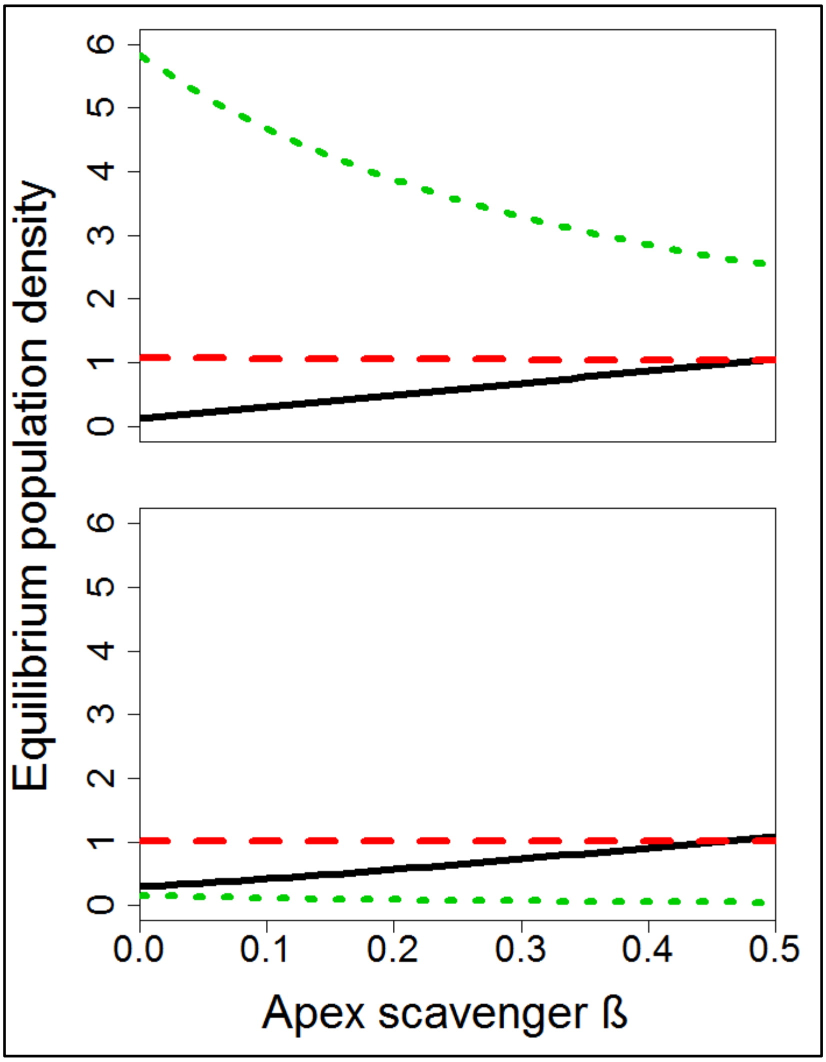

Figure 4. Equilibrium population density of carcasses (green dotted line), mesoscavengers (red dashed line) and apex facultative scavengers (black solid line) as a function of apex scavenger birth rate β in the absence of carcasses. The top model is parameterized for a known facultative scavenger, the Tasmanian devil

(Cunningham et al. 2018). The bottom is parameterized for vulture systems (Morales-Reyes *et al.* 2017). The key difference between the two parameterisations is the mesoscavenger and apex scavenger search efficiencies. An imaginary effect of vultures surviving off alternative food sources is displayed for comparison, similar to Figure 4 in the manuscript. As apex scavenger birth rate increases apex scavenger density increases and carrion density decreases.

APPENDIX 5 Supplementary Material for Chapter 5

Explanation of leopard dog consumption and occurrence around SGNP

Evidence of leopard consumption of dogs

Dogs were estimated to constitute 25% (Surve et al. 2015) and 58% (Edgaonkar & Chellam 2002) of the total leopard diet biomass in Sanjay Gandhi National Park (SGNP). Acknowledging that large carnivore diets can exhibit pronounced seasonality (eg Johnson et al. 1993), we adopted the mean of these two studies (ie 42% dog biomass in leopard diet), which was consistent with the estimate calculated by Prasad and Tiwari (2009) that dogs comprised 47% of leopard diets.

Number of dogs consumed by leopards around SGNP annually

Assuming dog biomass constituted ~42% of leopard diet, we applied the following calculation: leopard daily food consumption ([4.7 kg; Odden & Wegge 2009] × dog biomass of diet [42%]) × (365 days)/(average consumed dog weight assuming leopards eat 95% of carcass [17.1 kg; Stander et al. 1997; Athreya et al. 2016]) × (35 leopards) ≈ 1475 dogs consumed per year by the 35 leopards residing in and around SGNP. We rounded this figure up to 1500 dogs in the manuscript to avoid a false sense of accuracy. The range for this estimate was 878–2036 dogs, depending on biomass estimates of 25% (Surve et al. 2015) or 58% (Edgaonkar & Chellam 2002), respectively.

Assumption that leopard impacts are concentrated within 500 m of SGNP

Local scientist K Tiwari (Mumbaikers for SGNP, a local NGO working on leopard-human conflict and education in communities surrounding SGNP) reported that leopards rarely stray farther than 500 m from the SGNP boundaries (K Tiwara pers comm). We believe this estimate is prudent in light of several reports and photographs of leopards outside of or near to residences that straddle the park (mean distance = 282 m; range = 0–1.04 km):

(1) Leopard sighted in Hirandani, near Supreme Business Park (1.04 km from forest edge): www.mid-day.com/articles/leopard-spotted-paw-mumbai-powai-building-supreme-business-park-hiranandani/17632181.

(2) Leopard sighted and photographed in Kujapada (157 m from forest edge): www.dnaindia.com/mumbai/report-need-anymore-proof-of-leopard-in-kajupada-2245528.
(3) Leopard cub captured in Mumbai Indian Institute of Technology (2003, within forested area): www.rediff.com/news/2003/aug/05leo.htm.
(4) Leopard found in Mumbai Indian Institute of Technology (2016, within forested area): www.ndtv.com/mumbai-news/leopard-enters-iit-bombay-campus-hides-behind-a-generator-593120.
(5) Leopard crossed Mumbai's 42 State Highway, which hugs the western edge of SGNP (1 km from forest edge): http://colabradio.mit.edu/when-a-leopard-crosses-state-highway-42-in-mumbai-to-get-into-the-forest/.
(6) Leopard killed a Rottweiler in a residence near Ghodbunder Road, Thane (206 m from forest edge): www.hindustantimes.com/mumbai/mumbai-locals-live-in-fear-as-leopard-cub-kill-dog-in-thane/story-cn2CFHdidyKcttLX4AIe4L.html.
(7) Leopard photographed being chased by a stray dog near the Hill View building in Mumbai (104 m from forest edge): www.ndtv.com/mumbai-news/mumbais-chase-of-the-year-stray-dog-chases-leopard-away-552594.
(8) Leopard attempted to attack a dog at a house in Borivali (within forested area): www.ndtv.com/mumbai-news/caught-on-camera-dog-chases-away-leopard-from-house-in-mumbai-775451.
(9) Leopard repeatedly sighted on the Khatau Mill/Ekta Meadows boundary (within forested area): http://mumbaimirror.indiatimes.com/mumbai/other/Panic-as-Leopards-venture-into-Borivali-society/articleshow/19942529.cms?
(10) Leopard sighted in Poonam Nagar (314 m from forest edge): http://timesofindia.indiatimes.com/city/mumbai/Leopard-caught-napping-in-staircase-of-Andheri-building/articleshow/17472551.cms.

Evidence that leopards do not occur in districts located farther from SGNP

We found no online or newspaper reports of leopards occurring in suburbs located >2 km from our designated 500-m buffer beyond the forest edge. Leopards require the safety of forest and vegetation cover (at least intermediate levels of cover; Balme et al. 2007) in order to hunt successfully. This has been shown in a diversity of habitats, ranging from woodland savannas (Balme et al. 2007) to semi-deserts, where leopards hunt in dry riverbeds in which trees are present (eg Bothma & Le Riche 1984). The only reports of the occurrence of leopards in suburbs included in the city-wide dog census were (1) Bhandup West (a part of this suburb directly borders the SGNP), (2) Borivali (borders the park), (3) Mulund (borders the park), (4) Kandivali (borders the park), and (5) Goregaon (borders the park).

Estimate of human population within or directly adjacent to SGNP

P Variyar (Sanctuary Asia; pers comm) and K Tiwari (Mumbaikers for SGNP; www.mumbaikarsforsgnp.com; pers comm) suggested that ~350,000 people live within or directly adjacent to SGNP (this is a more recent estimate than the last human population census, which was conducted in 2011).

Table 1. Estimated annual number of dog bites on humans in Mumbai, India

Year	**# bites**	**Source**
2011	67,463	http://timesofindia.indiatimes.com/city/mumbai/2011-dog-bite-cases-67463-ampamp-counting/articleshow/11214730.cms
2012	82,247	www.hindustantimes.com/mumbai/82-247-cases-of-dog-bites-reported-in-2012/story-MNlG9XGA4JErNmF0Gd3aYP.html
2013	81,716	http://timesofindia.indiatimes.com/city/mumbai/Stray-population-at-66K-yet-dog-bites-increase-to-82K/articleshow/40310447.cms
2014	83,273	www.freepressjournal.in/mumbai/dog-bite-cases-on-the-rise-in-city/566698
2015	58,317	www.hindustantimes.com/mumbai/58-317-dog-bite-cases-in-mumbai-this-year/story-wR4lI5YiK5OWGyI8qhPBFO.html
Average	**74,603**	

Table 2. Estimated costs of post-exposure rabies treatment in humans

Post Exposure Treatment after bite and vaccine course (human)	Immunoglobin (post bite) = average US$26	http://www.drugsupdate.com/brand/generic/Vaccine,Rabies/4088 and “Treatment Costs.xlsx”
	Vaccine treatment full course=average US$41.50	http://www.drugsupdate.com/brand/generic/Vaccine,Rabies/4088 and “Treatment Costs.xlsx”
	2.14% of bite cases result in immunoglobulin treatment (Gogtay et al. 2014)	(Knobel *et al*. 2005)

APPENDIX 6 Supplementary Material for Chapter 6

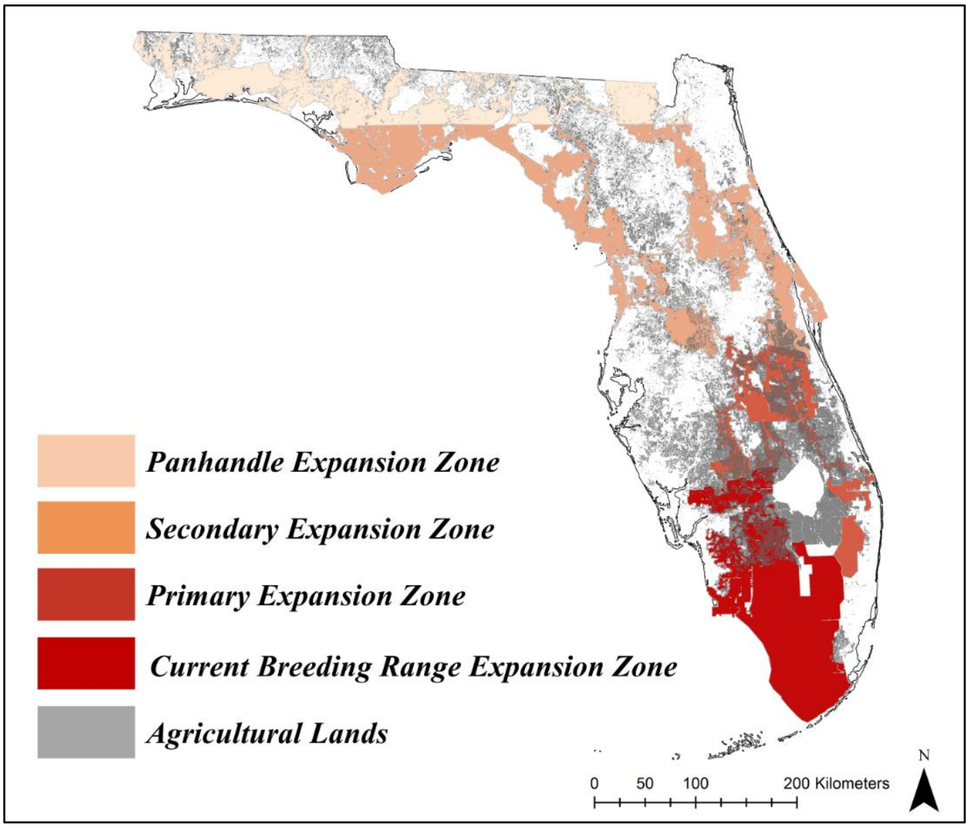

Figure 1. The current and expansion zones of the Florida panther (*Puma concolor coryi*) in Florida, USA. The breeding zone and primary expansion zone have documented panther locations; however, there are little to no known recent panther locations in the secondary and panhandle zones, which represent opportunity for panther expansion.

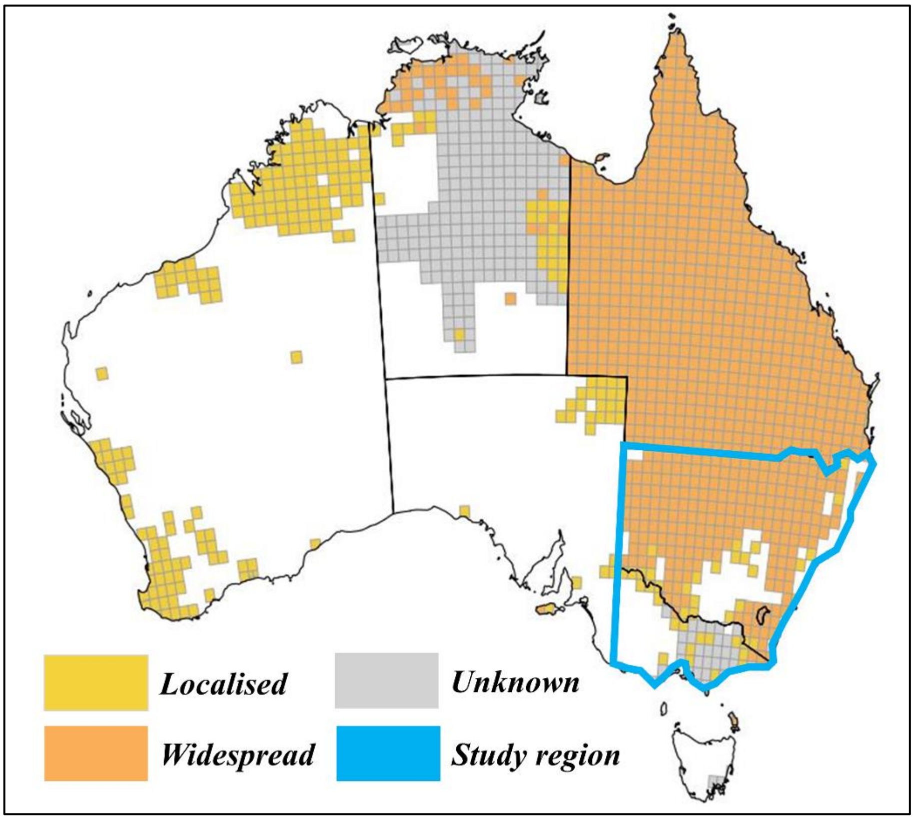

Figure 2. The distribution of invasive wild pigs (*Sus scrofa*) in Australia and the outline of study region, which includes both NSW and Victoria states. Map adopted from West (2008).

Predicting feral pig densities with and without the presence of an apex predator

We predict feral pig densities using multiple linear regression coefficients and intercept values derived from Lewis and colleagues (2017). They assessed predicted wild pig densities at a global scale using seven abiotic and biotic variables (Table 1). We use higher-resolution data on agricultural lands and the presence of large carnivores by identifying their current likely distributions and their potential distributions assuming all quality habitat is utilized (see methods).

Variable	Potential Evapo-transpiration (mean)	Large Carnivore (mean number)	Precipitation Wet Season (mean)	Unvegetated area (proportion area)	Agriculture (proportion area)	Precipitation Dry Season (mean)	Forest canopy cover (mean)
Parameter Estimate (Standard Error)	m: 0.443 (0.056) q: −0.226 (0.046)	−0.243 (0.043)	0.233 (0.055)	−0.203 (0.061)	m: 0.236 (0.076) q: −0.118 (0.038)	0.100 (0.050)	−0.001 (0.029)
Original data source that was used in Lewis et al. (2017)?	Yes	No	Yes	Yes	No	Yes	Yes

Data source used for case study	Trabucco, Antonio; Zomer, Robert (2019): Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2. figshare. Dataset.	See methods.	Bioclim WorldClim World Climate Data – Bio 16 Precipitation of Wettest Quarter (mm); 1950–2000	https://globalmaps.github.io/glcnmo.html#reference	FDEP 2019 (Florida) GA (Australia)	Bioclim WorldClim World Climate Data – Bio 17 Precipitation of Driest Quarter (mm); 1950–2000	https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.0.html

Table 1. Description, values, and source of landscape variables considered in Lewis and colleagues (2017) analyses for predicting wild pig densities across their global distribution.

Calculating the area of land within the proposed Florida Wildlife Corridor that is not currently formally protected

We calculated the area of land that is not formally protected within the proposed Florida Wildlife Corridor by intersecting the Florida Wildlife Corridor (Florida Environmental Greenways Network 2016) shapefile with that of the Florida Natural Areas Inventory shapefile of Florida Conservation Lands (http://www.fnai.org/gis_data.cfm; last updated June 2019; accessed August 2019), which is the most up-to-date data layer for Florida public (and some private) protected lands. This intersection resulted in 41.4% (28,003.29 km^2) of the total area of the proposed Florida Wildlife Corridor (67,714.46 km^2) being unprotected. We conducted the intersection in a geographic information system (Albers projection).

Calculating the relationship between feral pigs and soil disturbance

We determine the relative proportion of an area that is rooted (also referred to as 'disturbed') as a function of wild pig density as,

$$R_P = \left(\frac{r(P)}{100}\right) * \left(\frac{s(P)}{100}\right) \qquad eqn. 1$$

based on a long-term study of wild pig disturbance in Namadgi National Park, Australia (Hone 2002b), where *r* is the percentage of sampling plots that have rooting as a function of wild pig density (*P*) in pigs per km^2, and *s* is the percentage of wild pig rooting within a given sampling plot, assuming some prior disturbance, as a function of pig density (*P*). Specifically,

$$r = \frac{c(a + b\,P)^g}{100} \qquad eqn. 2$$

and

$$s = \frac{h(a + b\,P)^j}{100} \qquad eqn. 3$$

where *a, b, c, g, h, and j* are parameters whose values have been fit to data from Namadgi National Park in the peer-reviewed literature (Table 2). With these values *eqn. 1* produces the following relationship between wild pig density and proportion of area disturbed (Figure 3). See more detail in the description below.

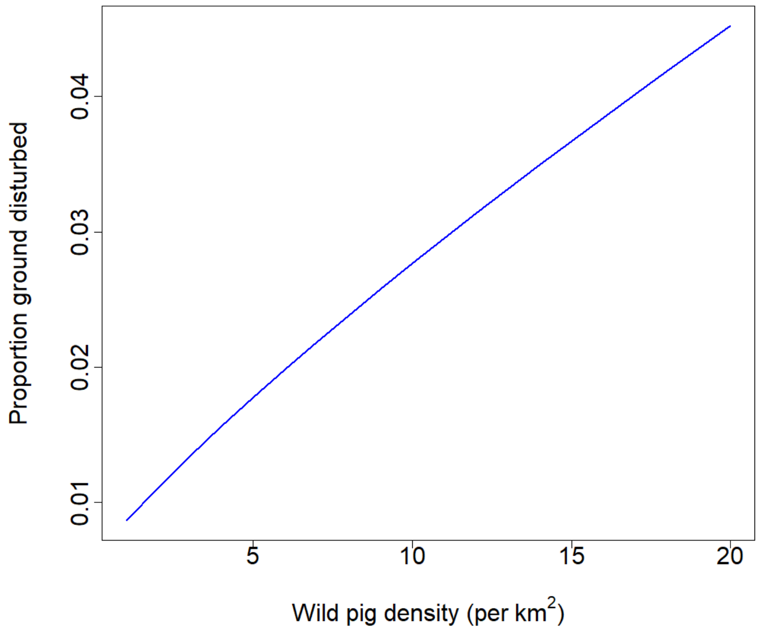

Figure 3. The proportion of ground rooted (or disturbed) as a function of wild pig density per km^2.

Details of quantifying the relative proportion of ground rooting (or disturbance) as a function of wild pig density

We determine the relative proportion of ground rooted as a function of wild pig density from a long-term study in Namadgi National Park in south-eastern Australia (Hone 2002b, 2012). The study was conducted from 1985 to 2000, with a sampling design comprised of 700 sampling plots, with seven sites (1 km^2 each) containing 100 plots randomly allocated across a range of vegetation types and elevations (for more information refer to Hone 2002). The original study terms are not in the spatial extent of ground rooting or pig density as is necessary for this manuscript, they are rather in terms of the percentage of sampling plots with pig dung as a function of the percentage of sampling plots with ground rooting by wild pigs. Nevertheless, the percentage of pig dung is related to wild pig density as described below. Note that all fitted parameters are given in Table 2.

The percent of plots with pig dung (*d*) is related to pig density (*P*) as,

$$d = a + bP \qquad eqn. 4$$

The percentage of sampling plots with ground rooting by pigs (*r*) is related to the percentage of sampling plots with pig dung (*d*) as,

$$r = c * d^g \qquad eqn. 5$$

This can be related as the proportion of sampling plots with ground rooting (*R*) from equation 5 as a function of pig density (*P*) from equation 4 such that,

$$R = \frac{c(a + bP)^g}{100} \qquad eqn. 6$$

However, just because rooting occurred in a sampling plot does not mean that the whole plot was rooted. As such, the percentage of a given sampling plot that has ground rooting (*s*) is related to the percentage of sampling plots with pig dung (*d*) as,

$$s = h * d^j \qquad eqn. 7$$

This can be related to pig density (*P*) from equation 4 as a proportion of a sampling plot that is uprooted (*s*) based on equation 4 such that,

$$S = \frac{h(a + bP)^j}{100} \qquad eqn. 8$$

Our objective is to determine the relative proportion of rooted area (R_P) based on a given pig density (*P*) by multiplying equations 6 and 8, and simplifying, such that,

$$R_P = \frac{ch(a + b\ P)^{g+j}}{10000} \qquad eqn. 9$$

All parameter estimates are provided in Table 2 below.

Parameter	**Estimate**	**Lower SE**	**Upper SE**	**Source**
a	5.149	3.113	7.185	(Figure 4.3; Hone 2012)
b	2.970	2.301	3.639	(Figure 4.3; Hone 2012)
c	13.490	12.257	14.723	(Figure 5.10; Hone 2012)
g	0.389	0.274	0.504	(Figure 5.10; Hone 2012)
h	1.21	N/A	N/A	(Hone 2002b)
j	0.408	0.284	0.532	(Hone 2002b)

Table 2. Parameter estimates and standard errors derived from a long-term study on wild pig damage (Hone 2002; Hone 2006; Hone 2012) in Australia used to assess the relationship between wild pig density and proportion of area disturbed from rooting behavior by wild pigs.

It should be noted that *s* is actually the linear proportion of a given sampling plot (the plots were 10m x 2m in size, but rooting was measured as a linear proportion along the 10m length of the plot) (Hone 2002b). Because the measurements were taken along the middle of a given sampling plot, and the fact that the area of a single pig rooting event is rather large (e.g. Bankovich *et al.* 2016), we assume this proportion can be thought of as percent area. We verified this logic with the author of the original study (Jim Hone, Personal Communication).

Application of the pig density-disturbance equation

We apply the pig density-disturbance equation above within a geographic information system raster calculator using the expressions below for the baseline estimate of damage.

```
((13.49 * (5.149 + 2.970 * "Pig_density_raster.tif")**0.389)/100) * ((1.21 * (5.149 + 2.970 * "Pig_density_raster.tif")**0.408)/100)
```

Table 3. The agricultural land cover codes and types assessed for the Florida case study (FDEP 2019) and the corresponding savings in land surface due to a reduction in pig densities under three scenarios: Florida panther extinction, status quo (panthers are restricted to their current breeding range), or a scenario where panthers fully expand throughout the Florida Wildlife Corridor. The values in the table were derived from a spatially-explicit wild pig density-soil disturbance model as described in the section above titled, “Calculating the relationship between feral pigs and soil disturbance”.

Agricultural land cover type	Extinction scenario (land damage from pigs in km^2)	Status quo scenario (land damage from pigs in km^2)	Full expansion scenario (land damage from pigs in km^2)
2110: Improved Pastures	79.57	75.74	60.67
2120: Unimproved Pastures	16.65	15.62	12.47
2130: Woodland Pastures	13.32	12.10	9.88
2210: Citrus Groves	11.51	9.65	8.18
2140: Row Crops	10.55	9.16	7.29
2156: Sugar Cane	4.26	3.64	3.39
2610: Fallow Cropland	3.50	3.08	2.72
2150: Field Crops	3.49	3.27	2.60
2153: Hay Fields	2.20	2.26	1.54
2100: Cropland and Pastureland	2.04	1.98	1.37

2600: Other Open Lands (Rural)	1.57	1.56	1.05
2510: Horse Farms	0.94	0.97	0.65
2240: Abandoned Groves	0.89	0.82	0.63
2520: Dairies	0.73	0.75	0.64
2420: Sod Farms	0.60	0.61	0.46
2410: Tree Nurseries	0.47	0.47	0.31
2143: Potatoes and Cabbage	0.40	0.41	0.27
2190: Wildlife Strip Crops	0.38	0.39	0.28
2431: Shade Ferns	0.28	0.29	0.19
2230: Other Groves (Pecan, Avocado, Coconut, Mango, etc)	0.26	0.25	0.21
2432: Hammock Ferns	0.24	0.24	0.16
2200: Tree Crops	0.23	0.18	0.14
2430: Ornamentals	0.21	0.19	0.14
2310: Cattle Feeding Operations	0.17	0.17	0.13
2300: Feeding Operations	0.09	0.09	0.06
2540: Aquaculture	0.08	0.08	0.06

2400: Nurseries and Vineyards	0.07	0.07	0.05
2240: Abandoned Tree Crops	0.03	0.03	0.02
2320: Poultry Feeding Operations	0.03	0.03	0.02
2160: Mixed Crops	0.03	0.03	0.02
Total	154.80	144.14	115.60

Table 4. The agricultural land cover codes and types assessed for the Florida case study (FDEP 2019) and the equivalent market value cost in USD from wild pig rooting on agricultural lands under three scenarios: Florida panther extinction, status quo (panthers are restricted to their current breeding range), or a scenario where panthers fully expand throughout the Florida Wildlife Corridor. The values in the table were derived from 2018 agriculture yield data from the USDA National Agricultural Statistics Service for the state of Florida (USDA, 2018).

Agricultural land cover type	Extinction scenario (market value cost in USD)	Status quo scenario (market value cost in USD)	Full expansion scenario (market value cost in USD)
2140: Row Crops*	10,489,693.04	9,819,965.06	7,818,311.37
2150: Field Crops**	466,756.86	436,956.17	347,889.16
2153: Hay Fields	258,054.21	265,279.11	180,029.22
Total	11,214,504.11	10,522,200.34	8,346,229.74

*based on average 2018 market value of beans, blueberries, cabbage, cucumbers, melons, peanuts, peppers, potatoes, strawberries, sweet corn, sweet potatoes, and tomatoes in Florida (USDA 2018).

**based on average 2018 market value of wheat and cotton crops in Florida (USDA 2018).

Table 5. Estimates of beef calf production and the equivalent market value savings in USD from reduced wild pig rooting on agricultural lands under three scenarios: Florida panther extinction, status quo (panthers are restricted to their current breeding range), or a scenario where panthers fully expand throughout the Florida Wildlife Corridor. We assume that Florida panthers reduce total production savings by 5.3% (Jacobs et al. 2015).

Scenario	Calf production (kg km^{-2})	Total calf production (kg)	Total production savings (kg)	Calf value USD km^{-2}	Gross savings USD km^{-2}	Total Gross savings	Panther offtake from total production (kg)	Panther cost USD	Total net savings
Extinction	15352.79	108,835,954.38	0.00	$87,203.87	0.00	$0.00	0.00	$0.00	$0.00
Status quo	15366.17	108,930,764.38	94,810.00	$87,279.83	75.97	$2,469,188.90	2,022.52	$11,487.91	$2,467,166.38
Full expansion	15411.11	109,249,344.69	413,390.31	$87,535.09	331.23	$10,766,150.93	21,909.69	$124,447.02	$10,744,241.24

Table 6. The agricultural land cover codes and types assessed for the Australia case study (Lymburner et al. 2011) and the corresponding savings in land surface due to a reduction in pig densities under three scenarios: dingo extinction, status quo (dingoes are restricted to their current range), or a scenario where dingoes fully expand throughout the NSW and VIC. The values in the table were derived from a spatially-explicit wild pig density-soil disturbance model as described in the section above titled, "Calculating the relationship between feral pigs and soil disturbance".

Agricultural land cover type	Extinction scenario (land damage from pigs in km^2)	Status quo scenario (land damage from pigs in km^2)	Full expansion scenario (land damage from pigs in km^2)
9 Rainfed pasture	459.52	413.65	389.59
8 Rainfed cropping	186.03	169.59	158.12
5 Irrigated cropping	3.74	3.37	3.19
6 Irrigated pasture	1.21	1.05	1.02
7 Irrigated sugar	0.01	0.01	0.01
Total area	650.51	587.67	551.94

Table 7. The agricultural land cover codes and types assessed for the Australia case study (Lymburner et al. 2011) and the equivalent market value cost in USD from wild pig rooting on agricultural lands under three scenarios: dingo extinction, status quo (dingoes are restricted to their current range), or a scenario where dingoes fully expand throughout the NSW and VIC. The values in the table were derived from 2017 estimates of yield from the Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES 2017)

Agricultural land cover type	Extinction scenario (market value cost in USD)	Status quo scenario (market value cost in USD)	Full expansion scenario (market value cost in USD)
Irrigated and rainfed cropping (codes 5 & 8)	52,393,696.00	47,332,007.69	44,454,239.27

Table 8. Estimates of beef calf production and the equivalent market value savings in USD from reduced wild pig rooting on agricultural lands under three scenarios: Dingo exclusion, status quo (dingoes are restricted to their current distribution), or a scenario where dingoes fully expand throughout NSW and VIC, Australia. We assume that dingoes reduce total production savings by 30% (Glen et al. 2007). This analysis assumes that all pastureland is used for cattle production.

Scenario	Calf production (kg km^{-2})	Total calf production (kg)	Total production savings (kg)	Calf value USD km^{-2}	Gross savings USD km^{-2}	Total Gross savings	Dingo offtake from total production (kg)	Dingo cost USD	Total net savings
Exclusion	11,398.31	370,490,572.59	0.00	43,797.42	$0.00	$0.00	0.00	$0.00	$0.00
Status quo	11,414.68	371,022,781.40	532,208.81	43,860.34	$62.91	$2,044,985.74	20,912.73	$80,356.11	$1,964,629.64
Full expansion	11,423.25	371,301,232.56	810,659.97	43,893.26	$95.83	$3,114,920.41	243,197.99	$934,476.12	$2,180,444.29

Calculating the contribution of feral pigs (*Sus scrofa*) to the diet of Florida panthers (*Puma concolor coryi*)

Summary

We replicate previously published techniques that lead to the quantification of the number of individual prey items killed per year by an apex predator (Braczkowski et al. 2018; Barry et al. 2019). We then determine the relative number of individual invasive wild pigs killed by a single adult puma per year by multiplying the mean relative biomass contribution of invasive wild pigs by their mean body size distribution from published estimates.

Methods and results

We identify two studies that explicitly report on the food habits of Florida panthers (Maehr et al. 1990; Caudill et al. 2019). These studies report on the percent occurrence of prey items found in scat contents (in the case of both studies) or stomach contents (in the case of Caudill and colleagues). While Maehr and colleagues (Maehr et al. 1990) report on the percent biomass consumption by Florida panthers, a more accurate representation of diet, Caudill and colleagues (Caudill et al. 2019) do not. Therefore, we calculate the relative biomass consumed using a correction factor for prey that are highly variable in size (Ackerman et al. 1984) and assumptions of live prey weight. We use Caudill and colleagues estimates of occurrence to calculate relative biomass consumed. We treat Caudill and colleagues' percent occurrence estimates of feral pigs in scat contents as corrected frequencies due to the fact that only 6.1% (19 of 312) of scats contained more than one prey item (Henschel et al. 2005). As such, we calculate relative biomass consumed by taking the ingested biomass per deposited scat (Y) (from Caudill *et al.* 2019), and the mean live weight (Table 7 and 8) of the prey species (X). The resulting linear relationship, $Y = 1.98 + 0.035X$, can then be applied in the form of a correction factor (Table 9), to convert frequency of occurrence to relative biomass consumed (by multiplying the corrected frequency of occurrence for one species by the correction factor for that species and then dividing that product by the sum of the products for all species in the diet; Table 59; phrasing and methodology taken from Henschel *et al.* 2005, calculation originally from Ackerman *et al.* 1984). We then take the average relative biomass between that calculated from Caudill et al. (2019) with that of estimates from Maehr and colleagues (Maehr et al. 1990) as our final estimates for mean relative biomass consumed by Florida panthers, which is reflected in Table 9. To calculate relative weight (kg) of species killed by Florida panthers per day, we used the mean kill rate of pumas from Elbroch and colleagues (2014), which held consistent across field sites (in North America and South America) and seasons (10.10 kg/day; Elbroch *et al.* 2014) multiplied by the mean relative biomass estimate in Table 9. To calculate relative numbers of individual animals by species, we took the estimated weight of species killed per day divided by the mean live weight of that species (Table 9). Similar methods have been used to calculated relative numbers of individuals killed (e.g. Henschel *et al.* 2005; Braczkowski *et al.* 2018). We calculate that a single adult non-gravid Florida panther removes approximately 34.40 (range 27.96 – 52.53 pigs) individual invasive wild pigs per year, assuming kill rate and relative biomass consumed remain static.

Table 7. Estimates of mean live body weight of prey species analysed in scat samples reported by Caudill and colleagues diet study (Caudill et al. 2019). Note that some prey item average weight estimates have no literature source as they lack specific information on the species from Caudill and colleagues; therefore, we estimated a reasonable mean body size of such prey items (specifically 'Rodentia' and 'Other').

Prey species	Mean Body Weight (kg)	Source
Wild pig (*Sus scrofa*)	44.9	Table 2
White-tailed deer (Odocoileus virginianus)	56.7	(Garrison & Gedir 2006)
Racoon (*Procyon lotor*)	4.41	(Mugaas et al. 1993)
Nine-banded armadillo (*Dasypus novemcinctus*)	5.0	(McBee & Baker 1982)
Rodentia	0.11*	(Joule & Cameron 1974)**
Viginia opossum (*Didelphis virginiana*)	2.4*	(McManus 1974)
Domestic cat (*Felis catus*)	4.0*	(Brothers et al. 1985)
Rabbit (*Sylvilagus* spp.)	1.2	(Elder & Sowls 1942)
Other	0.1***	NA***
Livestock (goats)	20.0	(Field & Taylor 2008)

*averaged between males and females

**assuming majority of rodentia diet is similar to that of bobcats (*Lynx rufus*), which primarily consists of *Sigmodon hispidus* in Florida (Maehr & Brady 1986).

***Caudill and colleagues (Caudill et al. 2019) do not indicate animal type, so we assume the size of this category to be similar to that of the 'rodentia' category (i.e. small species that are difficult to identify).

Table 8. Body mass estimates of feral pigs (*Sus scrofa*). Note that mean body mass was calculated as the average between the mean male and mean female body mass from the Saunders and McLeod study (Saunders & McLeod 1999).

Location	Mean body mass (kg)	Citation
Santa Catalina Island, California	27.5	(Baber & Coblentz 1986 as reported in Saunders & McLeod 1999)
Galapagos	40.0	(Coblentz & Baber 1987 as reported in Saunders & McLeod 1999)
Hawaii	50.5	(Diong 1982 as reported in Saunders & McLeod 1999)
South Carolina	49.0	(Wood & Brenneman 1980 as reported in Saunders & McLeod 1999)
South Carolina	57.5	(Kurz & Marchinton 1972 as reported in Saunders & McLeod 1999)

Table 9. Calculation of mean relative biomass consumed across two known diet studies on the Florida panther (*Puma concolor coryi*) in southwest Florida, USA. The resulting mean biomass estimate is used throughout the manuscript. Frequency occurrence of diet consumed by Florida panther (*Puma concolor coryi*) taken from Caudill and colleagues (Caudill et al. 2019) and converted to relative biomass consumed based on assumed average weight of prey from Table 7. Note that the two frequency occurrence and biomass estimates are from pre- and post-genetic restoration era samples of panther scats (Caudill et al. 2019). We then calculated the relative number of individuals consumed following methodology by Henschel and colleagues (Henschel et al. 2005).

Prey item	% occurrence in panther diet (pre*)	% occurrence in panther diet (post*)	Body weight (kg) from Table 1	Correction factor (kg/scat) **	Biomass in panther diet (pre*)	Biomass in panther diet (post*)	Biomass in panther diet from Maehr et al. 1990***	Mean biomass in panther diet (all studies)	Kg killed day^{-1}****	Individuals killed day^{-1}	Individuals killed year^{-1}
Feral pig (*Sus scrofa*)	55.93	21.97	44.9	3.5515	0.582267575	0.264597714	0.41	0.418955096	4.231446475	0.09424157	34.3981729
White-tailed deer (*Odocoileus virginianus*)	27.12	28.03	56.7	3.9645	0.315169422	0.376838904	0.35	0.347336109	3.508094698	0.061871159	22.58297292

Racoon (*Procyon lotor*)	5.08	21.97	4.41	2.13435	0.031783032	0.159015664	NA	0.063599565	0.642355609	0.145658868	53.1654869
Nine-banded armadillo (*Dasypus novemcinctus*)	3.39	6.82	5	2.155	0.021414747	0.049839751	0.11	0.060418166	0.610223474	0.122044695	44.54631363
Rodentia	1.69	2.27	0.11	1.98385	0.009827918	0.015271402	0.07	0.031699773	0.320167708	2.910615529	1062.374668
Viginia opossum (*Didelphis virginiana*)	0	3.79	2.4	2.064	0	0.026527304	0.026	0.017509101	0.176841924	0.073684135	26.89470922
Domestic cat (*Felis catus*)	0	3.79	4	2.12	0	0.027247037	NA	0.009082346	0.091731692	0.022932923	8.370516857
Rabbit (*Sylvilagus* spp.)	0	4.55	1.2	2.022	0	0.031198719	NA	0.010399573	0.105035687	0.087529739	31.94835471
Other	6.8	5.3	0.1	1.9835	0.039537307	0.035649405	0.026	0.033728904	0.340661931	3.406619308	1243.416047

Livestock (goats)	0	1.52	20	2.68	0	0.0138141	0.049	0.020938033	0.211474137	0.010573707	3.859402992

*based on Caudill et al. 2019

**based on Ackerman et al. 1984

***We took the average estimates of relative biomass consumed from Maehr and colleagues (1990) as they provide estimates for both ‘North’ and ‘South’ in southwest Florida.

****based on Elbroch et al. 2014 estimate of 10.10 kg/day kill rate multiplied by mean biomass

APPENDIX 7 Supplementary Material for Chapter 7

Overview of quantifying the relative proportion of ground rooting (or disturbance) as a function of wild pig density

We determine the relative proportion of an area that is rooted (also referred to as ‘disturbed’) as a function of wild pig density as,

$$R_P = \left(\frac{r(P)}{100}\right) * \left(\frac{s(P)}{100}\right) \qquad eqn. 1$$

based on a long-term study of wild pig disturbance in Namadgi National Park, Australia (Hone 2002b), where *r* is the percentage of sampling plots that have rooting as a function of wild pig density (*P*) in pigs per km^2, and *s* is the percentage of wild pig rooting within a given sampling plot, assuming some prior disturbance, as a function of pig density (*P*). Specifically,

$$r = \frac{c(a + b\,P)^g}{100} \qquad eqn. 2$$

and

$$s = \frac{h(a + b\,P)^j}{100} \qquad eqn. 3$$

where *a, b, c, g, h, and j* are parameters whose values have been fit to data from Namadgi National Park in the peer-reviewed literature (Table 1). With these values *eqn. 1* produces the following relationship between wild pig density and proportion of area disturbed (Figure 1). See more detail in the description below.

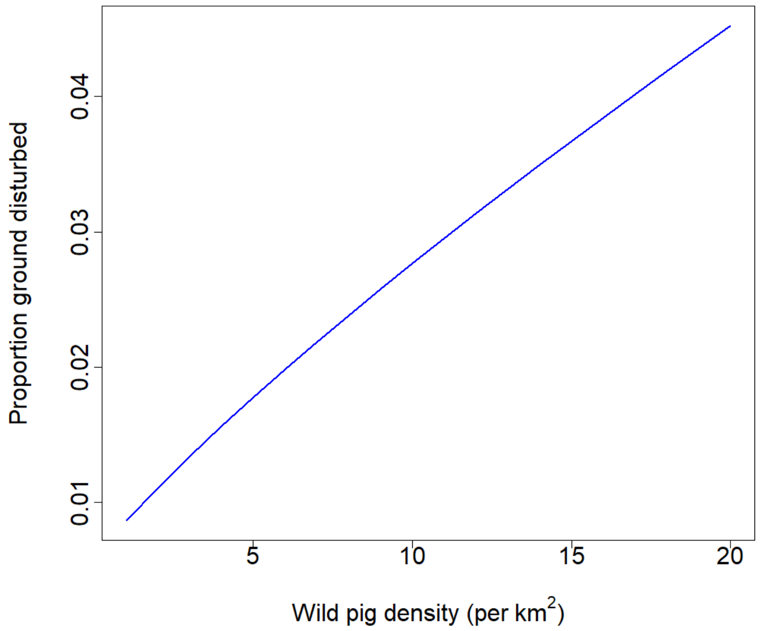

Figure 1. The proportion of ground rooted (or disturbed) as a function of wild pig density per km^2.

Details of quantifying the relative proportion of ground rooting (or disturbance) as a function of wild pig density

We determine the relative proportion of ground rooted as a function of wild pig density from a long-term study in Namadgi National Park in south-eastern Australia (Hone 2002b, 2012). The study was conducted from 1985 to 2000, with a sampling design comprised of 700 sampling plots, with seven sites (1 km^2 each) containing 100 plots randomly allocated across a range of vegetation types and elevations (for more information refer to Hone 2002). The original study terms are not in the spatial extent of ground rooting or pig density as is necessary for this manuscript, they are rather in terms of the percentage of sampling plots with pig dung as a function of the percentage of sampling plots with ground rooting by wild pigs. Nevertheless, the percentage of pig dung is related to wild pig density as described below. Note that all fitted parameters are given in Table 1.

The percent of plots with pig dung (*d*) is related to pig density (*P*) as,

$$d = a + bP \qquad eqn. 4$$

The percentage of sampling plots with ground rooting by pigs (*r*) is related to the percentage of sampling plots with pig dung (*d*) as,

$$r = c * d^{g} \qquad eqn. 5$$

This can be related as the proportion of sampling plots with ground rooting (*R*) from equation 5 as a function of pig density (*P*) from equation 4 such that,

$$R = \frac{c(a + bP)^{g}}{100} \qquad eqn. 6$$

However, just because rooting occurred in a sampling plot does not mean that the whole plot was rooted. As such, the percentage of a given sampling plot that has ground rooting (*s*) is related to the percentage of sampling plots with pig dung (*d*) as,

$$s = h * d^{j} \qquad eqn. 7$$

This can be related to pig density (*P*) from equation 4 as a proportion of a sampling plot that is uprooted (*s*) based on equation 4 such that,

$$S = \frac{h(a + bP)^{j}}{100} \qquad eqn. 8$$

Our objective is to determine the relative proportion of rooted area (R_P) based on a given pig density (*P*) by multiplying equations 6 and 8, and simplifying, such that,

$$R_P = \frac{ch(a + b\ P)^{g+j}}{10000} \qquad eqn. 9$$

All parameter estimates are provided in Table 1 below.

Parameter	Estimate	Lower SE	Upper SE	Source
a	5.149	3.113	7.185	(Figure 4.3; Hone 2012)
b	2.970	2.301	3.639	(Figure 4.3; Hone 2012)
c	13.490	12.257	14.723	(Figure 5.10; Hone 2012)
g	0.389	0.274	0.504	(Figure 5.10; Hone 2012)
h	1.21	N/A	N/A	(Hone 2002b)
j	0.408	0.284	0.532	(Hone 2002b)

Table 1. Parameter estimates and standard errors derived from a long-term study on wild pig damage (Hone 2002; Hone 2006; Hone 2012) in Australia used to assess the relationship between wild pig density and proportion of area disturbed from rooting behavior by wild pigs.

It should be noted that s is actually the linear proportion of a given sampling plot (the plots were 10m x 2m in size, but rooting was measured as a linear proportion along the 10m length of the plot) (Hone 2002b). Because the measurements were taken along the middle of a given sampling plot, and the fact that the area of a single pig rooting event is rather large (e.g. Bankovich et al. 2016), we assume this proportion can be thought of as percent area. We verified this logic with the author of the original study (Jim Hone, Personal Communication).

Application of the pig density-disturbance equation

We apply the pig density-disturbance equation above within a geographic information system raster calculator using the expressions below for the baseline estimate of damage and the lower and upper standard error estimates across all parameters (the standard error estimates are expressed as a range of values).

<u>Baseline estimate of damage:</u>

((13.49 * (5.149 + 2.970 * "Pig_density_raster.tif")**0.389)/100) * ((1.21 * (5.149 + 2.970 * "Pig_density_raster.tif")**0.408)/100)

<u>Lower SE estimate of damage:</u>

((12.257 * (3.113 + 2.301 * " Pig_density_raster.tif “)**0.274)/100) * ((1.21 * (3.113 + 2.301 * " Pig_density_raster.tif ")**0.284)/100)

<u>Upper SE estimate of damage:</u>

((14.723 * (7.185 + 3.639 * " Pig_density_raster.tif ")**0.504)/100) * ((1.21 * (7.185 + 3.639 * " Pig_density_raster.tif ")**0.532)/100)

Quantifying carbon dioxide equivalent (CO_2e)

We convert our estimate of carbon into carbon dioxide (at one-tonne stock) by taking the molecular weight of carbon dioxide (44 amu) and dividing by the atomic weight of carbon (12 amu), which equals 3.67 metric tonnes of carbon dioxide equivalent. By multiplying the carbon dioxide equivalent by our estimates of carbon we report on the equivalent carbon dioxide that is vulnerable to wild pig soil disturbance (in metric tonnes per km^2) using a geographic information system raster calculator. We then determine the proportion of soil organic carbon storage that is emitted in the form of CO_2e based on estimates of SOC lost in the form of CO_2 from arable agricultural practices (30%, range of 20-40%; Davidson & Ackerman 1993).

Global maps of data used to assess the amount of vulnerable organic soil carbon stock from predicted wild pig soil disturbance

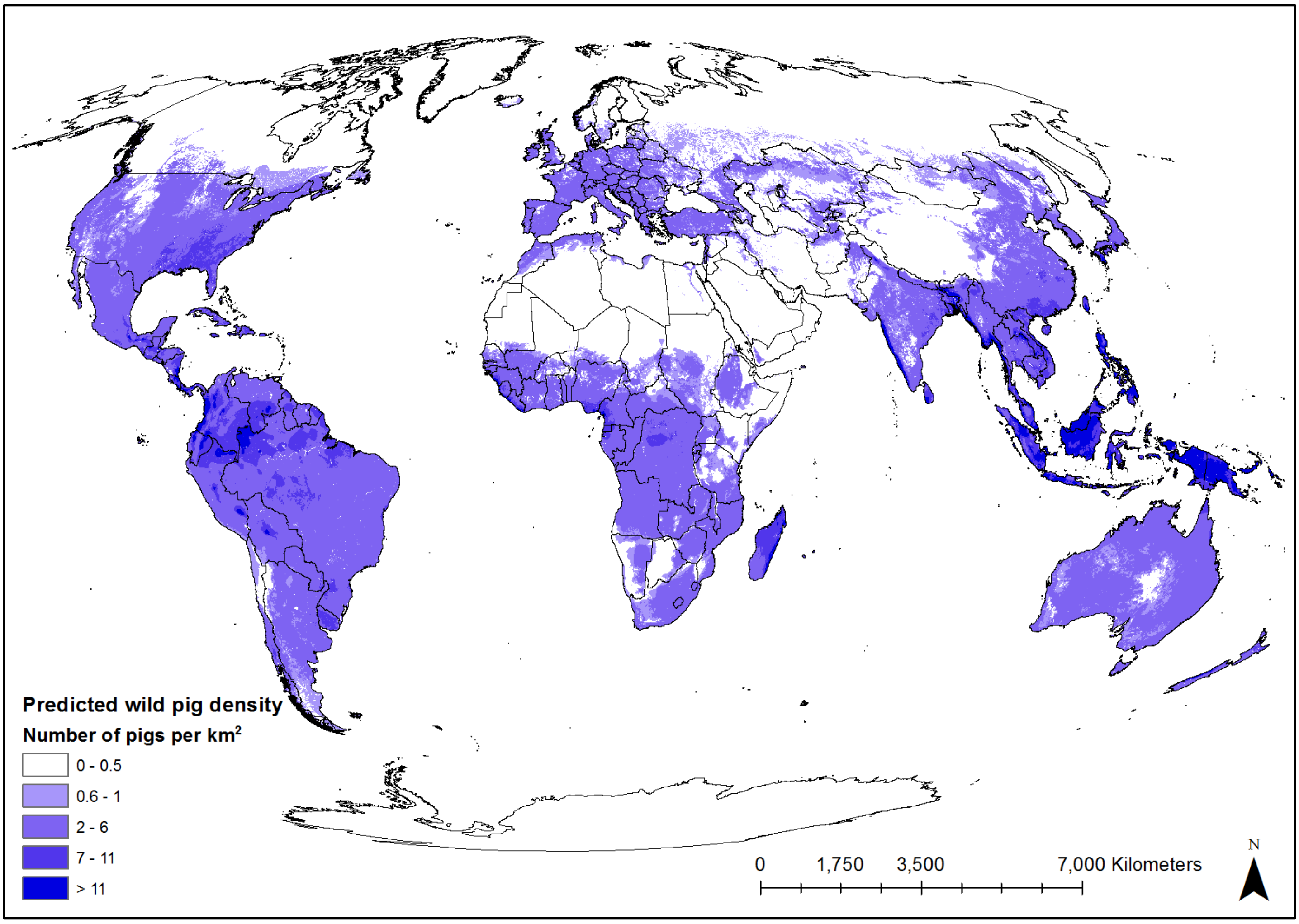

Figure 2. Global map on predicted wild pig density (per km^2) in the absence of pig management used in this study. The data are originally reported in Lewis *et al.* (2017).

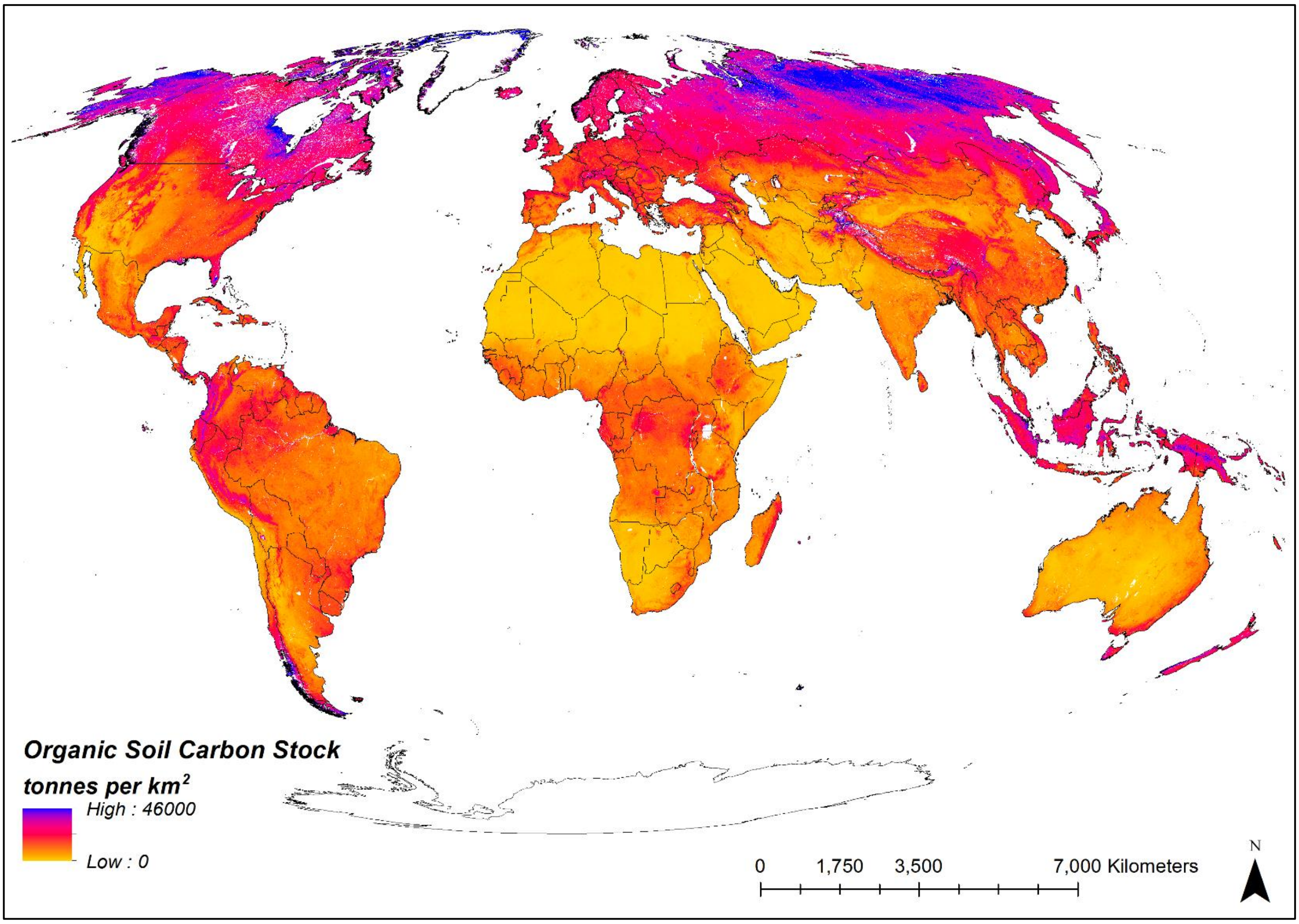

Figure 3. Global map of predicted organic soil carbon storage (in tonnes per km^2) at a depth of 0-15cm, obtained from the Soil Grid database (Hengl et al. 2017)**.**

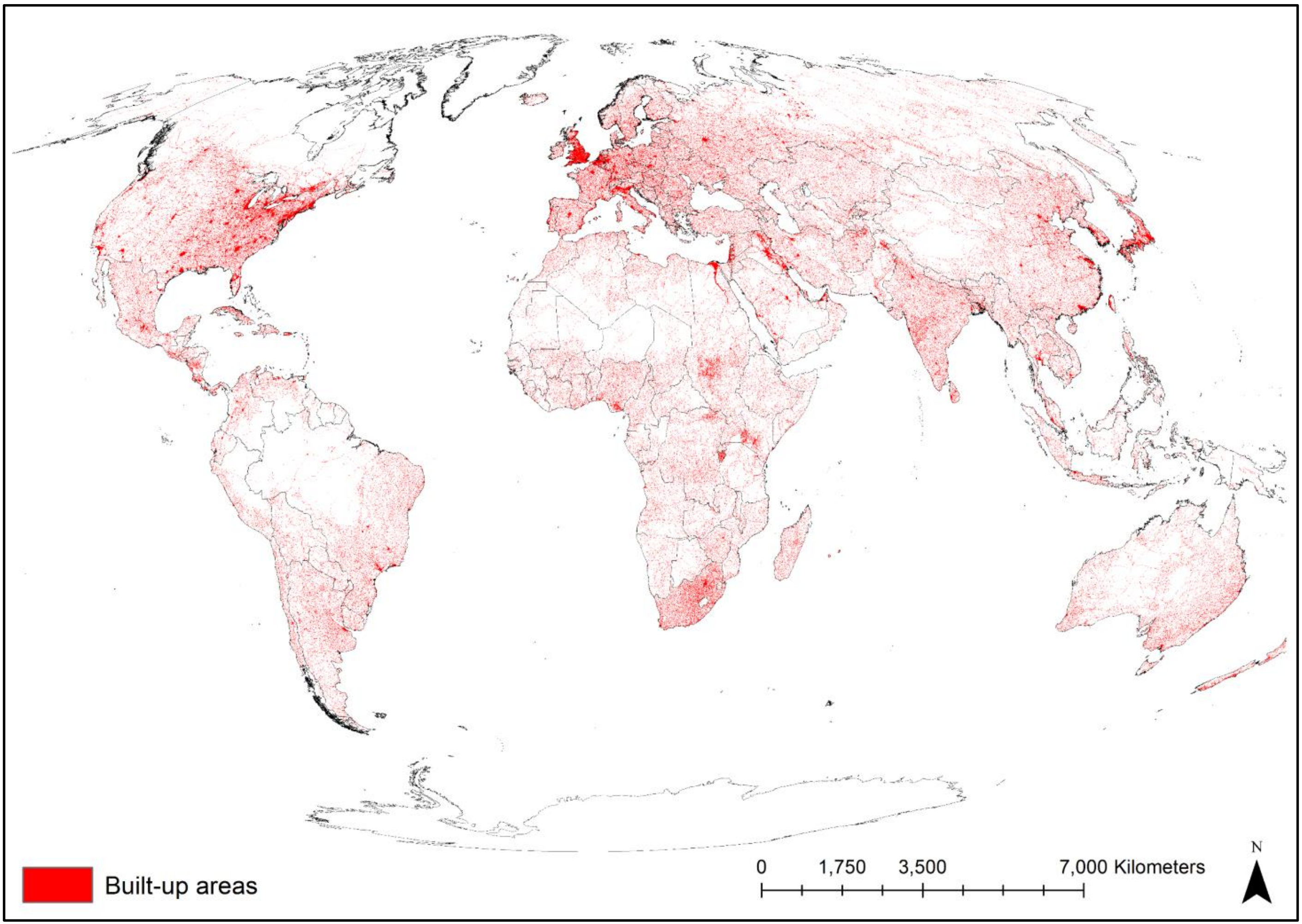

Figure 4. Global map of the World's built-up areas at a 1 km^2 resolution during the year 2009 from Venter and colleagues (Venter et al. 2016a). These built-up areas correspond to human infrastructure, including buildings, paved land, urban parks, roadways, and railways.

Continent	**Total vulnerable organic soil carbon stock (in millions of t)**	**Lower SE (in millions of t)**	**Upper SE (in millions of t)**	**Mean vulnerable organic soil carbon stock (t km^{-2})**	**Lower SE (t km^{-2})**	**Upper SE (t km^{-2})**
Oceania	371.69	124.64	1223.93	77.71	26.06	255.90
Asia	313.73	94.94	1114.06	344.30	104.19	1222.65
North America	273.97	105.35	763.54	79.80	30.69	222.41
South America	111.32	42.30	313.44	83.04	31.55	233.82
Africa	3.91	1.65	9.88	20.94	8.14	52.90

Table 2. The total (in millions of tonnes) and mean (in tonnes per km^2) vulnerable organic soil carbon stock from wild pig (*Sus scrofa*) soil disturbance across their known non-native distribution organized by continent. The standard errors are derived from the model parameters' standard errors as reported in Table 1.

Continent	**Total vulnerable organic soil carbon stock (in millions of t)**	**Lower SE (in millions of t)**	**Upper SE (in millions of t)**	**Mean vulnerable organic soil carbon stock (t km^{-2})**	**Lower SE (t km^{-2})**	**Upper SE (t km^{-2})**
South America	1354.40	494.73	195.73	85.77	31.33	195.16
North America	671.35	266.14	2245.39	73.28	29.05	778.56
Asia	654.97	206.65	1712.47	227.10	71.65	121.25
Africa	632.25	250.74	1360.71	44.77	17.75	184.09
Oceania	419.29	142.82	1819.35	56.73	19.32	198.59
Europe	79.22	34.23	4017.16	78.99	34.13	254.39

Table 3. The total (in millions of tonnes) and mean (in tonnes per km^2) vulnerable organic soil carbon stock from wild pig (*Sus scrofa*) soil disturbance across their predicted expansion distribution organized by continent. The standard errors are derived from the model parameters' standard errors as reported in Table 1.

Rank	**Country**	**Total current vulnerable organic soil carbon stock (in millions of t)**	**Lower SE (in millions of t)**	**Upper SE (in millions of t)**	**Total predicted vulnerable organic soil carbon stock (in millions of t)**	**Lower SE (in millions of t)**	**Upper SE (in millions of t)**
1	Indonesia	259.16	78.34	921.95	434.64	133.16	1521.28
2	United States	237.55	91.11	663.19	399.36	158.38	1079.52
3	Papua New Guinea	199.24	56.96	752.97	199.28	56.97	753.08
4	Australia	133.00	53.36	354.50	162.71	66.05	428.68
5	Brazil	59.95	23.26	165.09	569.07	212.30	1633.12
6	New Zealand	39.44	14.33	116.46	39.46	14.33	116.50
7	Philippines	30.61	9.47	105.96	64.05	19.33	227.61
8	Malaysia	23.96	7.13	86.15	68.30	20.37	244.71
9	Colombia	22.12	7.99	65.40	215.92	67.89	759.69
10	Uruguay	16.03	5.80	47.24	16.09	5.82	47.42
11	Canada	15.63	6.80	38.35	103.00	44.95	251.70
12	Cuba	9.64	3.49	28.40	9.65	3.49	28.41
13	Chile	9.33	3.60	25.91	55.66	21.55	155.24

14	Dominican Republic	4.75	1.70	14.17	4.75	1.70	14.17
15	Argentina	3.85	1.64	9.71	92.71	38.37	239.44
16	Haiti	2.53	0.89	7.64	2.53	0.89	7.64
17	South Africa	2.17	0.92	5.43	19.09	7.96	48.88
18	Jamaica	1.42	0.48	4.49	1.42	0.48	4.49
19	Bahamas	1.24	0.47	3.49	1.25	0.47	3.50
20	Uganda	0.72	0.31	1.81	9.19	3.87	23.32
21	Zambia	0.49	0.20	1.24	25.28	10.64	64.09
22	Puerto Rico	0.47	0.16	1.49	0.47	0.16	1.49
23	Cameroon	0.27	0.10	0.76	29.73	11.25	84.35
24	Guadeloupe	0.20	0.07	0.62	0.20	0.07	0.63
25	Dominica	0.17	0.05	0.54	0.17	0.05	0.54
26	Sudan	0.15	0.06	0.35	19.08	8.36	46.39
27	Tanzania	0.11	0.05	0.27	21.56	9.15	54.24
28	Martinique	0.10	0.03	0.31	0.10	0.03	0.31
29	Saint Lucia	0.08	0.03	0.25	0.08	0.03	0.25
30	Saint Vincent and the Grenadines	0.06	0.02	0.19	0.06	0.02	0.19

Table 3. The estimated organic soil carbon stock that is vulnerable to wild pig (*Sus scrofa*) soil disturbance in their current and predicted distributions for the top 30 countries. The total organic soil carbon is reported in millions of metric tonnes. The lower and upper standard errors are based on model outputs from the fitted parameter estimates' lower and upper standard errors as reported in Table 1.