

Global patterns of reported human-wildlife interactions in areas of land-use change

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Abstract

Emerging infectious diseases are one of the greatest and most pertinent threats to human health and security. Land-use changes, which are increasing globally, are a key driver of emerging infectious disease outbreaks; they increase contact between wildlife and humans and create opportunities for transmission of pathogens between them. While there is great emphasis to characterize the circumstances underlying disease outbreaks in search of mitigation strategies, a global synthesis of documented human-wildlife interactions in the context of land-use change has not been previously done. We conducted a scoping literature review to identify the geographic, taxonomic, and land-use change focus of reported interactions between wildlife, humans, and domestic animals, and discuss the implications of our results in the context of understanding high-risk settings for pathogen exposure. From 529 included articles, we show that human-wildlife interactions are most often reported in Asia and Africa and are most associated with agriculturalization on a global scale except in North America and Oceania, where urbanization was more commonly associated with interactions. Humans and domestic animals interacted with 1021 species of wildlife, including various amphibians, birds, mammals, and reptiles. Interactions with mammals were reported most often, mostly with species in the orders Artiodactyla, Carnivora, Primates, and Rodentia. The type of interactions, and thus potential for cross-species pathogen transmission, varied significantly among continent and wildlife taxa. Our review highlights increased human risks for wildlife pathogen exposure in areas of Africa and Asia with high rates of agriculturalization, and from even-toed ungulates, carnivores, primates, and rodents on a global scale. Further, we identified important gaps in knowledge, such as a lack of documented human interactions with wildlife in central and southwestern Asia and northern Africa and a surprising lack of documented human interactions with bats globally, despite their high number of synanthropic species and role as hosts of zoonoses.

Keywords: agriculturalization, human-wildlife contact, land restoration, pathogen surveillance, spillover, urbanization, zoonoses

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Introduction

Emerging infectious diseases (EIDs) are an increasing threat to global human health and security, as evidenced by the current monkeypox virus outbreak and COVID-19 pandemic (Daszak et al. 2000, Morens and Fauci 2013, Wang et al. 2022, Zumla et al. 2022). Most EIDs are zoonotic in origin, reaching human populations via transmission from wildlife and domestic animal host species (spillover), with the majority initiating in wildlife hosts (Jones et al. 2008). Once in human populations, zoonotic diseases have the potential to spread efficiently due to high population densities and connectedness in contemporary globalized societies, hindering the ease and potential efficacy of downstream mitigation efforts (Coltart et al. 2017).

A major research priority is to understand the circumstances by which wildlife pathogens are transmitted to humans (Plowright and Hudson 2021). Exposure to pathogens at the human-wildlife interface is the obligatory first step in zoonotic spillover and is driven by multiple ecological mechanisms, including the distribution and abundance of reservoir host species, the prevalence and intensity of infection within reservoir hosts, and the persistence of pathogens once outside the host (Plowright et al. 2017, Wilkinson et al. 2018). Human exposure to wildlife pathogens can occur via direct (e.g., contact with wildlife through butchering and consumption) and indirect (e.g., contact with excreted pathogens in environments where human and wildlife activities overlap) mechanisms (Wolfe et al. 2005, Magouras et al. 2020). Additionally, domestic animals, including pets and livestock, can serve as intermediate (bridging) hosts between wildlife and humans, as occurred with several recent high profile disease outbreaks (e.g., pigs and horses for Nipah and Hendra viruses, respectively; Chua et al. 2000, Playford et al. 2010).

One of the principal drivers of human exposure to wildlife pathogens is land-use change (LUC), or anthropogenically induced environmental changes (Foley et al. 2005, Woolhouse and Gowtage-Sequeria 2005, Jones et al. 2008, Gottdenker et al. 2014). Land-use change can impact the abundance and distribution of wildlife and shape wildlife-pathogen interactions, collectively increasing pathogen shedding by reservoir hosts and creating new contact opportunities that facilitate intra- and interspecies pathogen spread (Patz et al. 2004, Keesing et al. 2010, Jones et al. 2013, Faust et al. 2018, Mendoza et al. 2019, Carlson et al. 2022). For example, Nipah virus emergence in Malaysia is believed to have occurred due to *Pteropus* bats moving to roost and feed in orchards surrounding pig farms following deforestation and El Niño-induced drought in their habitat (Chua et al. 2002); Nipah virus was shed in bat saliva and excreta, infecting pigs below, which in turn transmitted the virus to humans. Land-use change has also been associated with spillover of *Borrelia burgdorferi* (the causative agent of Lyme disease), hantaviruses, ebolaviruses, and Hendra virus through effects on pathogen exposure (Allan et al. 2003, Wolfe et al. 2007, Plowright et al. 2011, Prist et al. 2017, Rulli et al. 2017).

Existing review articles have evaluated links between LUC and pathogen spillover and emergence (Jones et al. 2013, Gottdenker et al. 2014, Johnson et al. 2015). These reviews focus on zoonotic disease outbreaks as a measure of spillover risk but do not evaluate exposure risk specifically. This nuance is crucial because documented disease outbreaks only capture a small fraction of total disease outbreaks (e.g., Glennon et al. 2019), and miss the many exposure opportunities that could have – but did not – lead to disease outbreaks (Plowright et al. 2017). Given that LUC primarily increase pathogen spillover and disease emergence in humans through effects on exposure risk, mechanistic insights into how LUC has influenced zoonotic spillover can be gained through evaluation of studies that link LUC with exposure. To this end, we conducted a scoping, quantitative literature review that characterizes the global breadth of studies that document human exposure to wildlife in the context of LUC to: 1) identify the geographic, taxonomic, and LUC focus of reported interactions; and 2) discuss and compare our results with previously identified geographic and taxonomic hotspots for spillover and emergence risk to highlight the most at risk settings and identify research needs.

Methods

We conducted a scoping literature search in Web of Science in May 2022 to identify empirical articles that report on wildlife interactions with humans and domestic animals in areas of LUC (Figure 1; a full description of the search strategy is available in the Supplementary Materials). To ensure that articles contained relevant information, we applied the following criteria. First, studies had to report human-wildlife interactions within the context of human-induced LUC that is occurring or has occurred in the study area and describe the type of modification. Second, studies had to identify the type of wildlife involved to at least order level. Third, studies had to report the type of human-wildlife interaction (direct, indirect, or domestic animal contact, see below). Fourth, studies must have been based on empirical data. We limited our scope to terrestrial and arboreal vertebrates since they are the overwhelming reservoir source of zoonotic disease outbreaks (Han et al. 2016, Olival et al. 2017).

For each included article, we extracted the following information: the country where the interaction occurred, type of LUC, wildlife taxa involved, domestic animals involved, type of interaction, and standard journal article details (publication date, publishing journal). Land-use change was categorized into five types (Foley et al. 2005): (1) agriculturalization, (2) energy development, (3) land restoration, (4) resource extraction, and (5) urbanization (full definitions of each category are provided in the Supplementary Materials). Interactions between humans and wildlife were categorized into three types: (1) direct physical contact, such as humans touching or consuming wildlife and their effluent, (2) indirect contact, such as when humans and wildlife occupy the same areas but not necessarily simultaneously (e.g., humans observing wildlife on their property), or (3) domestic animal-mediated contact, as a way of quantifying the potential for exposure via intermediate host species that also have contact with humans (Table S1). Lastly, we collected information on the type of study (before-after comparison, cross-sectional, experimental, and longitudinal) and on techniques of data collection to understand methods applied within included studies.

To investigate how the total number of publications reporting human-wildlife interactions varied by continent, taxa, interaction type, and LUC type, we used chi-square analyses. Post-hoc testing was done to understand interactions between every two categorical variable combination (package “chisq.posthoc.test”; Ebbert 2022). Due to a lack of studies on energy development and resource extraction, and given their similar characteristics with urbanization, these three LUC types were combined to permit more robust analyses. Due to lack of studies reporting human interactions with amphibians, we removed these records from analyses. For studies mentioning multiple continents, wildlife taxa, levels of interaction intensity, or LUC types, we counted the study for multiple categories (Gottdenker et al. 2014). Lastly, because of the differing zoonotic potential amongst wildlife orders, we used a chi-square analysis to compare publication count among orders within each class. Due to the large number of orders involved in interactions, we only included orders documented in 10 or more publications in this set of analyses.

Results

A total of 529 articles were identified that met our inclusion criteria (Figure 1; a full list of included articles and their citations are provided in the Supplementary Materials). Articles were published from 1994-2022 in 173 different journals and two pre-print servers. Over 85% of included articles were published since 2012 ($n = 462$), demonstrating a strong recent increase in relevant literature. Almost 70% of included articles included cross-sectional data ($n = 357$), followed by longitudinal ($n = 231$), experimental ($n = 15$), and before-after comparisons ($n = 8$). There were 13 main types of data collection techniques, with the most common methods including human interviews ($n = 298$), structured observation ($n = 137$), and analysis of government, non-governmental organization, or public records ($n = 121$; Table S2).

We identified differences in reporting of human-wildlife interactions within all four categories. Human-wildlife interactions were reported in 96 countries, including all continents except Antarctica, with most reported in Asia and Africa and the least reported in Europe and Oceania ($\chi^2 = 246.27$, $df = 5$, $P < 0.001$; Figure 2). Agriculturalization was the most common LUC type reported ($n = 407$), followed by urbanization ($n = 285$), and restoration ($\chi^2 = 37.805$, $df = 2$, $P < 0.001$; $n = 263$). Human and domestic animals interacted with

wildlife belonging to 50 distinct orders and 1,021 species, all of which fall into amphibians, birds, mammals, and reptiles (Classes: Amphibia, Aves, Mammalia, and Reptilia, respectively). Human interactions with mammals were reported most often ($n = 493$), followed by birds ($n = 74$) and reptiles ($\chi^2 = 616.19$, $df = 2$, $P < 0.001$; $n = 45$). Wildlife was documented to interact with 21 different species of domestic animal, with cows ($n = 99$), goats ($n = 71$), and sheep ($n = 63$) most reported. Indirect contacts (i.e., human spatial proximity to wildlife without physical contact) were the most common type of human-wildlife interaction ($n = 400$), followed by domestic animal-mediated contact (i.e., interactions between wildlife and domestic animals; $n = 223$), and direct contact (i.e., physical contact between a human and wildlife or their effluent; $\chi^2 = 76.14$, $df = 2$, $P < 0.001$; $n = 219$).

We identified interactions in four of the six possible pair-wise variable combinations. We detected an interactive effect between wildlife taxa and interaction type ($\chi^2 = 11.281$, $df = 4$, $P = 0.023$). Interaction type did not vary within birds or mammals; however, within reptiles, direct and domestic animal-mediated interactions were significantly more common than indirect interactions ($P = 0.029$). There was an interactive effect between LUC type and continent ($\chi^2 = 34.672$, $df = 10$, $P < 0.001$), with reported interactions in areas of urbanization in Oceania and North America more common than in other LUC types on these continents ($P \leq 0.001$; Figures 3 and 4). We detected an interactive effect between wildlife taxa and continent ($\chi^2 = 18.456$, $df = 10$, $P = 0.047$), with reported interactions with mammals in Asia more common than reports of interactions with other taxa ($P = 0.028$). Lastly, there was an interactive effect between continent and interaction type ($\chi^2 = 19.504$, $df = 10$, $P = 0.034$), with reports of direct interactions in Europe less common than other interaction types ($P = 0.038$; Figure 5). There were no interactive effects between LUC type and wildlife taxa ($\chi^2 = 3.4819$, $df = 4$, $P = 0.481$) or LUC type and interaction type ($\chi^2 = 6.733$, $df = 4$, $P = 0.151$).

Order diversity within taxa varied considerably. Humans and domestic animals interacted with one amphibian, 27 avian, 19 mammalian, and three reptilian orders (Figure 6). Our analysis of the number of publications reporting interactions with different taxa varied among avian ($\chi^2 = 14.44$, $df = 6$, $P = 0.025$), mammalian ($\chi^2 = 829.45$, $df = 10$, $P < 0.001$) and reptilian ($\chi^2 = 17.10$, $df = 2$, $P < 0.001$) orders. Across avian orders, only Galliformes were reported more often than expected, with all other orders (Accipitriformes, Anseriformes, Charadriiformes, Columbiformes, Passeriformes, and Psittaciformes) reported as often as expected ($P = 0.025$). Within Mammalia, the orders Artiodactyla, Carnivora, Primates, and Rodentia were reported more often in the literature than expected; the orders Chiroptera, Cingulata, Didelphimorphia, Lagomorpha, Perissodactyla, and Pholidota were reported less often than expected; and the order Proboscidea was reported as often as expected ($P < 0.001$). Within Reptilia, the order Crocodilia was reported more often than expected, the order Testudines was reported less often than expected, and the order Squamata was reported as expected ($P = 0.002$).

Discussion

This study is the first to characterize publication trends documenting human and domestic animal exposure to wildlife in the context of LUC. We show that human-wildlife interactions are most often reported in Asia and Africa and are most commonly associated with agriculturalization on a global scale but with urbanization in North America and Oceania, specifically. Humans and domestic animals interacted with over 1000 species of wildlife, but interactions with mammals were documented most often, particularly with members of the Artiodactyla (even-toed ungulates), Carnivora, Primate, and Rodentia orders. Interaction type varied among continent and wildlife taxa, which has important implications for the risk of zoonotic pathogen spillover following wildlife exposure. We further focus on understanding how these geographic and taxonomic hotspots of human-wildlife interactions relate to known zoonotic disease emergence and identify areas for future research that will facilitate a comprehensive picture of zoonotic disease risk.

Hotspots of interactions

Emerging infectious disease outbreaks have been documented globally, with hotspots identified in eastern North America, western Europe, Japan, and Oceania (Jones et al. 2008). Numerous but more sparse

outbreaks have also been detected in South America outside of Amazonia, sub-Saharan Africa, and southern Asia, many of which continue to pose high risk for future outbreaks (Jones et al. 2008, Han et al. 2016, Allen et al. 2017). Our results partially mirror these trends, with our study identifying high numbers of reported human-wildlife interactions in Brazil, China, India, Nepal, Uganda, and the United States. While publication reports from these countries may be inflated due to reporting bias, several of these countries have regions of growing population densities where remaining natural lands continue to be developed for agriculture (Deng et al. 2009), making them high-risk areas for human-wildlife interactions. This overlap in patterns suggests that our data can be used to identify regions with opportunities for exposure to zoonotic pathogens, ultimately informing efforts to predict future EID outbreaks.

Our results further indicate common reports of human-wildlife interactions in agricultural portions of Africa and Asia akin to previous studies on zoonotic disease emergence. Areas of southern and eastern Asia and western and eastern Central Africa have previously been identified as regions with high potential for zoonotic disease emergence due to a combination of factors including high mammalian diversity, large tracts of remaining forest threatened by increasing rates of agriculturalization, and growing human populations (Grace et al. 2012, Allen et al. 2017, Jagadesh et al. 2022). Human populations in these regions of Africa and Asia with high rates of LUC may be exposed to an exceptional diversity of wildlife, providing ample opportunities for human interactions with novel wildlife pathogens (Allen et al. 2017). For example, LUC via agriculturalization destroys forested areas, leading to an increase in deforestation and creation of forest edges. While human-wildlife interactions occur across all land cover types, they are especially high in areas of intermediate LUC, where the increase of edge facilitates high levels of contact among humans, domestic animals, and wildlife (Kretser et al. 2008, Merkle et al. 2011, Faust et al. 2018). The abundance of human-wildlife interactions, and thereby potential for pathogen exposure, necessitates disease risk surveillance in these regions.

Urban regions in parts of Europe and North America have also been identified as high-risk areas for zoonotic pathogen transmission (Allen et al. 2017) and our results show that the urbanizing areas on these continents, and Oceania, are similarly hotspots for reports of human-wildlife interactions. While some of this weight may be from reporting bias, urbanizing areas in these continents are facing growing human populations due to myriad reasons, including better healthcare for resident populations, the increasing rate of rural to urban migration, and movement from the global south to the global north (de Haas et al. 2019). This increase in human population often leads to local environmental degradation, which can negatively affect the health of local wildlife species and create new opportunities for human-wildlife interactions that can lead to zoonotic pathogen transmission (Soulsbury and White 2015, Plowright et al. 2017, Weber and Sciubbbba 2019). Subsequent reductions in environmental quality and local biodiversity have ramifications for zoonotic disease emergence, as generalist wildlife species able to cope with urbanization proliferate, increasing pathogen prevalence as they move into areas left vacant by more specialized species (Schmidt and Ostfeld 2001, Reusken and Heymann 2013, Hough 2014, Hassell et al. 2017).

Many of geographic hotspots for zoonotic disease emergence have been designated as such because of their high mammalian biodiversity (Allen et al. 2017, Wilkinson et al. 2018). Previous work has demonstrated that mammals represent a high risk for zoonotic pathogen transmission because of their phylogenetic relatedness to humans and the wide breadth of their ranges, which often facilitates close contact with humans (Streicker et al. 2010, Han et al. 2016, Olival et al. 2017). While all mammalian orders most often involved in human-wildlife interactions are known to harbor zoonotic pathogens, disease risk varies widely among these orders, mostly due to variations in within-order diversity (Mollentze and Streicker 2020). Groups like rodents (order: Rodentia) and primates (order: Primates) have been thoroughly investigated for their zoonotic pathogen potential due to their high species diversity and human relatedness, compared to elephants for example (order: Proboscidea), which have received comparatively less zoonotic pathogen surveillance attention (Johnson et al. 2015, Han et al. 2016, Olival et al. 2017). Our results show that disease surveillance efforts of these mammalian orders are particularly warranted given their repeated interactions with human and domestic animals stemming from growing rates of LUC (Johnson et al. 2015, Han et al. 2016, Olival et al. 2017).

Future research needs

Although our results align with many of the recognized geographic hotspots and taxonomic risks, our study shows that reports on human-wildlife interactions are lacking for certain geographic regions and taxonomic groups that are important for zoonotic disease risk. Our search found minimal publications reporting human-wildlife interactions in northern Africa, northern South America, central Asia, and southwestern Asia. While some of these may be due to few human-wildlife interactions, such as northern Africa where the Sahara Desert predominates, other areas have been implicated in disease emergence events (Han et al. 2016). For example, the bubonic plague-causing bacterium, *Yersinia pestis*, most likely emerged from the steppes of central Asia in modern-day Kyrgyzstan several hundred years ago (Spyrou et al. 2022). More recently, Middle Eastern Respiratory Syndrome (MERS-CoV) emerged simultaneously in several countries within southwestern Asia (Raj et al. 2014). While less commonly reported than other parts of the world, EID outbreaks are known to occur in these regions, and our results show that these areas may suffer from research bias and warrant targeted investigation of human-wildlife interactions (Jones et al. 2008). Additionally, the concentrated effects of LUC, human population growth, and climate change are altering the landscapes of these regions, and likely increase opportunities for human-wildlife interactions in rapidly changing environments (Naboureh et al. 2020, Zittis et al. 2022).

While further research on better-known mammalian orders will continue to be beneficial, increased pathogen surveillance efforts on underrepresented orders that commonly interact with humans in areas of LUC, such as carnivores and even-toed ungulates, are particularly warranted. In contrast, of the many wildlife orders reported to have interactions with humans and domesticated animals that are focal taxa for zoonotic disease research (Olival et al. 2017), bats (order: Chiroptera), which carry numerous zoonotic pathogens, are infrequently reported in the literature compared to other mammalian orders. This trend likely demonstrates a reporting bias and highlights the need for hypothesis-driven research to understand the nuances of interactions between bats, humans, and domestic animals, especially within a disease transmission framework. Understanding the frequency, types of interactions, and location of these interactions is integral to developing zoonotic disease transmission models for numerous bat-borne zoonotic pathogens, as well as mitigating human-bat conflict and cross species pathogen transmission (Plowright et al. 2017, Plowright and Hudson 2021).

Birds and reptiles were commonly documented interacting with humans and domestic animals, most often through indirect and direct contact, respectively. Such interactions are opportunities for zoonotic pathogen spillover and warrant efforts to understand the zoonotic disease potential of these taxa. Zoonotic pathogen exposure potential from birds is high given their proximity to humans and poultry livestock and their heavy use of human-dominated landscapes, which is reflected in our results and previous literature (Webster et al. 1992, Marzluff 2001, Gilbert et al. 2008, Phillippon et al. 2020). Reptiles, on the other hand, often host bacteria and parasites with zoonotic potential, requiring ingestion to be transmitted to humans (Harris et al. 2009, Patrick et al. 2013, Cantlay et al. 2017). Therefore, reptiles most likely pose disease risks through direct interactions, like human consumption, which was the most common type of human-reptile interaction found in our study (Wang et al. 2011, Cantlay et al. 2017, Perez-Flores et al. 2017, Yudhana et al. 2019). With human population growth a key driver of LUC, it seems likely that pressure on reptiles as a food source will continue to grow, facilitating increased reptile-borne food illnesses (Broglia and Kapel 2011, Martin et al. 2021). Further scrutiny of zoonotic pathogens hosted by reptiles is needed to understand the dangers of these increased interactions.

Ultimately, our study provides a unique summary of human-wildlife interactions occurring in areas of LUC and evaluates their potential for zoonotic disease spillover. The information from this scoping review provides evidence that interactions with multiple orders of wildlife in areas of agriculturalization, especially in Africa and Asia, are commonly reported across the literature and warrant efforts to mitigate exposure. Further, wildlife species within Artiodactyla, Carnivora, Primates, and Rodentia are frequently reported interacting with humans and domestic animals and require additional and continued scrutiny as hosts for zoonotic pathogens. There are also noticeable gaps in reported human-wildlife interactions, largely in areas of northern

Africa, northern South America, central Asia, and southwestern Asia. The history of zoonotic disease emergence, increasing human populations, and rates of LUC in these regions necessitates further research. Lastly, taxa known to pose risks for zoonotic disease transmission, like bats, require more research focus to understand the nature of their interactions with humans. Information provided by closing these gaps will inevitably benefit efforts to predict and mitigate the emergence of zoonotic diseases in human populations.

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Author Contributions

RTJ, TJL, and KMF formulated the review idea. RTJ, MRM, and KMF developed the search strategy. RTJ performed the literature search and data extraction. RTJ, TLJ, and NM performed data analysis. RTJ wrote the original draft. All co-authors contributed to editing, approved the final version, and agree to be held accountable for the work.

Data Accessibility

All data will be made accessible on Dryad pending acceptance for publication.

Conflicts of Interest

The authors report no conflicts of interest.

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Figure legends:

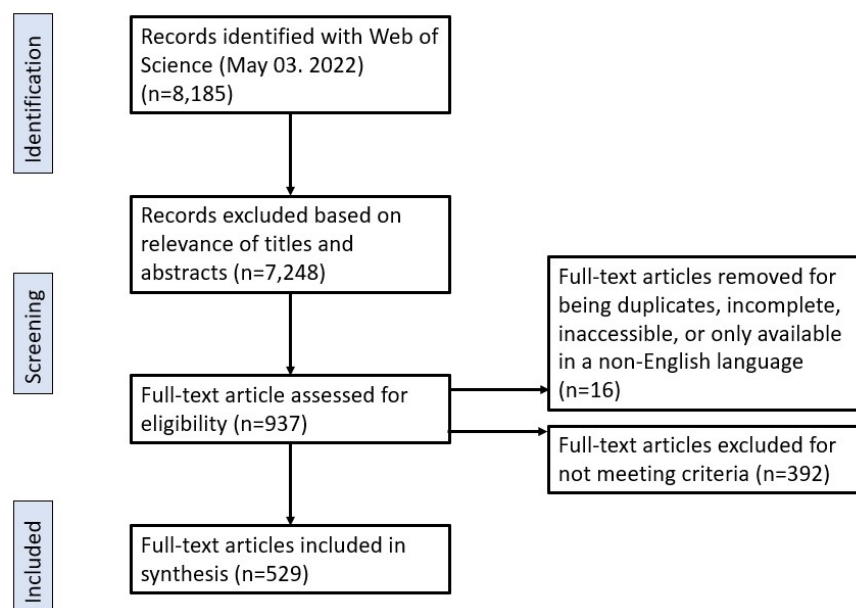


Figure 1: Figure 1. PRISMA style workflow of the scoping literature search and article inclusion process. We performed a Boolean search in Web of Science on May 3, 2022, for articles published since 1970.

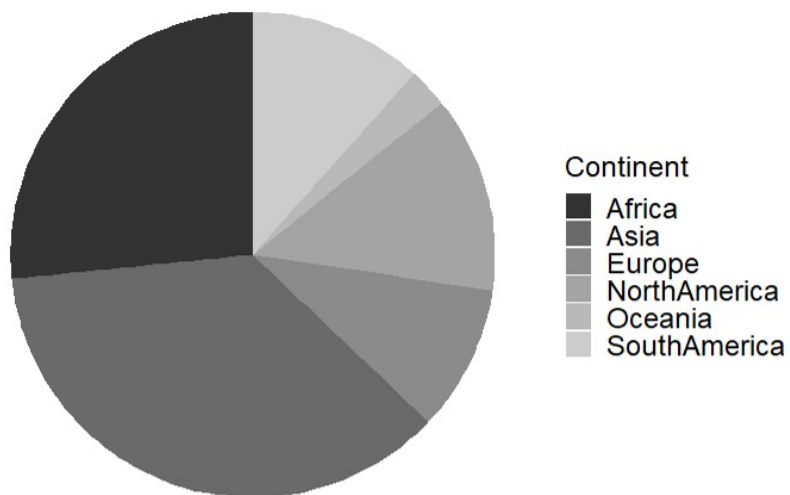


Figure 2: Figure 2. Total number of studies that reported human-wildlife interactions within each included continent.

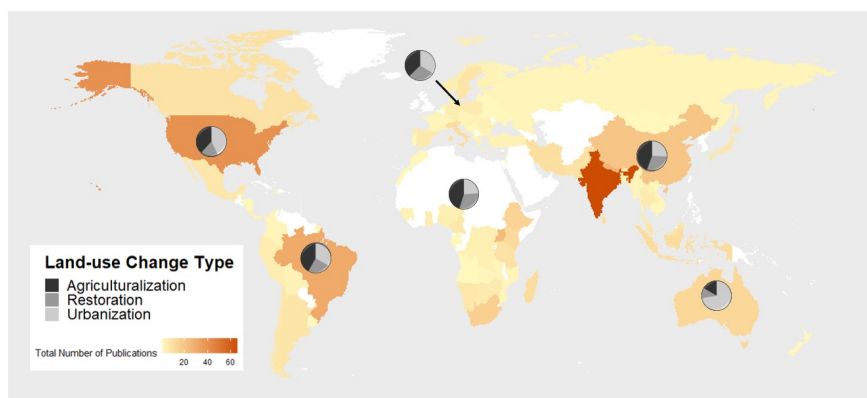


Figure 3: Figure 3. Geographic distribution of reported human-wildlife interactions and the type of land-use changes (LUC) involved. Map lines delineate assumed country boundaries and do not necessarily depict accepted national boundaries.

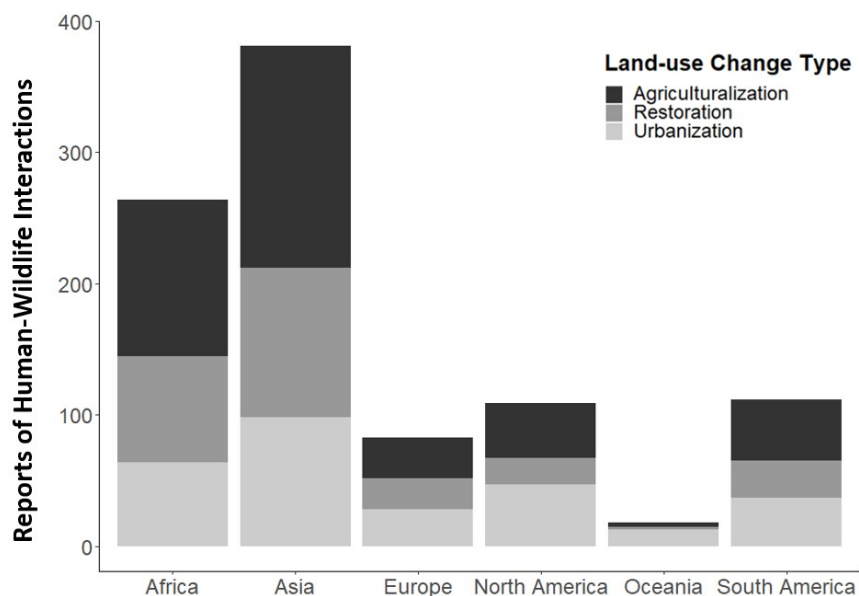


Figure 4: Figure 4. Reported human-wildlife interactions based on continent and land-use change type.

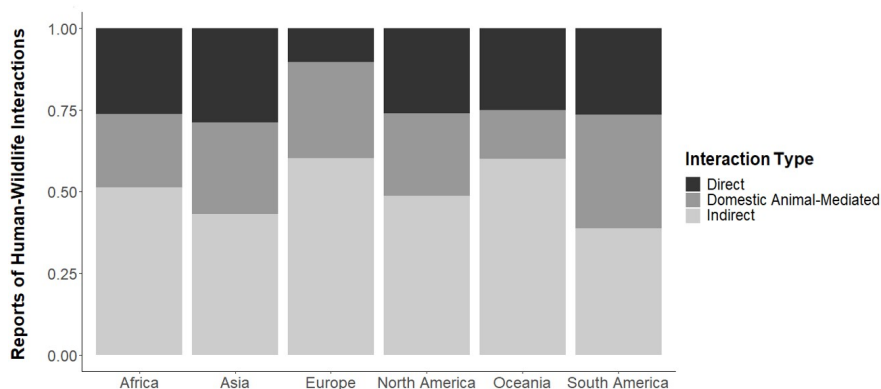


Figure 5: Figure 5. Proportions of human-wildlife interactions based on continent and interaction type.

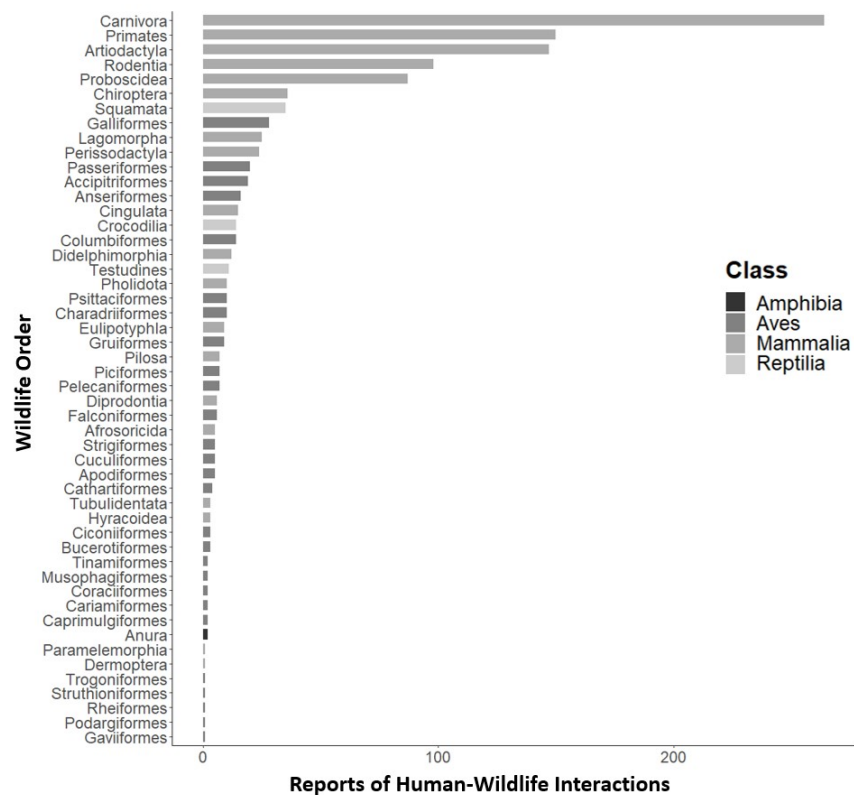


Figure 6: Figure 6. Total number of studies that reported human-wildlife interactions involving an identifiable order of wildlife. Interactions with mammals were most documented (19 orders, 493 unique studies), followed by birds (27 orders; 74 unique studies), reptiles (3 orders, 45 unique studies), and amphibians (1 order, 2 unique studies).