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A review of the effects of wildfire smoke on the health and behavior of wildlife

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^{*} Author to whom any correspondence should be addressed.E-mail: oliviavs@uw.edu**Keywords:** wildfires, smoke, air pollution, wildlife, monitoring, conservation, climate change

Abstract

Climate change is intensifying global wildfire activity, and people and wildlife are increasingly exposed to hazardous air pollution during large-scale smoke events. Although wildfire smoke is considered a growing risk to public health, few studies have investigated the impacts of wildfire smoke on wildlife, particularly among species that are vulnerable to smoke inhalation. In this review, we synthesized research to date on how wildfire smoke affects the health and behavior of wildlife. After executing a systematic search using Web of Science, we found only 41 relevant studies. We synthesized findings from this literature and incorporated knowledge gained from fields outside wildlife science, specifically veterinary medicine and air pollution toxicology. Although studies that directly investigated effects of smoke on wildlife were few in number, they show that wildfire smoke contributes to adverse acute and chronic health outcomes in wildlife and influences animal behavior. Our review demonstrates that smoke inhalation can lead to carbon monoxide poisoning, respiratory distress, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression in wildlife, including terrestrial and aquatic species, and these health effects can contribute to changes in movement and vocalization. Some species also use smoke as a cue to engage in fire-avoidance behaviors or to conserve energy. However, our review also highlights significant gaps in our understanding of the impacts of wildfire smoke on wildlife. Most notably, the lack of robust air pollution measurements in existing studies limits meta-analyses and hinders construction of dose-response relationships, thereby precluding predictions of health outcomes and behaviors under different air quality conditions, especially during extreme smoke events. We recommend that future studies leverage existing data sets, infrastructure, and tools to rapidly advance research on this important conservation topic and highlight the potential value of interdisciplinary collaborations between ecologists and atmospheric chemists.

1. Introduction

As climate change intensifies the frequency and severity of wildfires, communities around the world are increasingly vulnerable to smoke pollution (Jacob and Winner 2009). Increased wildfire activity has been linked to declines in average regional air quality and greater incidence of extreme air pollution episodes. For example, wildfires contributed to a recent increase in annual concentrations of fine particulate matter (PM_{2.5}, particles smaller than 2.5 µm in aerodynamic diameter) in the United States (McClure and Jaffe 2018, Clay and Muller 2019), and smoke

events in the Pacific Northwest, United States in 2018 and 2020 caused PM_{2.5} to spike to concentrations well above the National Ambient Air Quality Standards (Washington State Academy of Sciences 2019, Liu *et al* 2021a). Wildfire smoke directly contributes to adverse respiratory and cardiovascular health outcomes and mortality in humans (Cascio 2018, Chen *et al* 2021); in fact, studies have shown that the chemical composition of PM_{2.5} in wildfire smoke is more toxic than that of urban ambient PM_{2.5} (Franzi *et al* 2011, Aguilera *et al* 2021).

Wildfire smoke also sickens non-human animals, as illustrated by numerous case studies in veterinary

medicine that document morbidity and mortality in domestic animals exposed to smoke, including pets and livestock (Fitzgerald and Flood 2006, Marsh 2007). These case studies demonstrate that, like people, animals can suffer from carbon monoxide poisoning, thermal and chemical damage to lung tissue, and greater susceptibility to respiratory disease as a result of smoke inhalation (Wohlsein *et al* 2016). In fact, animal models, including mice, rats, rabbits, sheep, and monkeys, are often used to study the onset and progression of human disease following exposure to the toxic gases and aerosols found in smoke (David *et al* 2009). Although many animals in fire-prone habitats are able to detect and avoid wildfires, fires still pose direct threats to wildlife (Engstrom 2010, Nimmo *et al* 2021), including exposure to extreme heat and smoke. Yet, the impacts of wildfire smoke on the health and behavior of wildlife are largely unknown (Hovick *et al* 2017, Lee *et al* 2017, Erb *et al* 2018, Geiser *et al* 2018).

This paucity of research on how wildfire smoke affects the health and behavior of wild animals hinders full consideration of the direct and indirect effects of wildfires when conducting risk assessments for wildlife and developing conservation plans. In addition, research on the impacts of wildfire smoke on wildlife is published in disparate journals spanning numerous disciplines (e.g. ecology, physiology, animal behavior, veterinary medicine, etc); as such, ecologists, wildlife managers, and other stakeholders may be challenged to identify relevant studies. To date, review papers have synthesized findings on first-order effects of fire on animals, including injury, morbidity, and mortality (Engstrom 2010), considered behavioral responses of mammals to fire, specifically torpor (Geiser *et al* 2018), and discussed fire as an evolutionary force driving animal behavior and survival (Nimmo *et al* 2021), but none have focused specifically on the effects of smoke from wildfires on the health and behavior of wildlife.

Wildfires are an important type of natural disturbance (Turner 2010) in forests, grasslands, and deserts around the world, and many wildlife species benefit from resources available in post-fire landscapes (Smith 2000). However, just as people now grapple with health risks posed by routine smoke events, even in airsheds where smoke pollution was previously uncommon (Wilmot *et al* 2021), wildlife must also contend with greater—perhaps even novel—exposure to wildfire smoke with more intense wildfire activity. The magnitude of smoke events in the 21st century further underscores the urgent need to study the impacts of wildfire smoke on wildlife. Wildfire smoke persists in the atmosphere even after flames have subsided and can travel hundreds of miles, creating hazardous air quality conditions and degrading visibility across large geographic areas (figure 1). As a result, smoke from a single wildfire could impact the health and behavior of wildlife

at a much larger spatial scale than the area burned. Direct effects of wildfire smoke on individuals could scale to influence the demography of wildlife populations, with cascading community- and ecosystem-level impacts (figure 2).

In this review, we synthesized research to date on the effects of wildfire smoke on the health and behavior of wildlife. We focused specifically on the impacts of wildfire smoke rather than describing all immediate effects of wildfires on wildlife in order to more deeply investigate physiological and behavioral responses of wildlife to the large-scale smoke events that are becoming increasingly common around the world. Below, we (1) identify relevant literature on the effects of wildfire smoke on the health and behavior of wildlife, (2) highlight knowledge gaps, and (3) present opportunities for rapidly advancing research on this important topic, all of which should serve as a useful resource for guiding ecological studies and conservation actions.

2. Methods

In January 2021, we conducted two keyword searches using Web of Science (figure 3). Search terms included (1) ‘wildfire* AND smoke*’ and (2) ‘fire* AND smoke*’. We performed a basic search and entered search terms into the topic field. We excluded ‘news items’ and ‘meeting abstracts’ as document types to focus on peer-reviewed literature, then further refined our search results to include only articles from categories relevant to our review (e.g. environmental science, ecology, biology, physiology, toxicology, health sciences, veterinary sciences, etc) A complete list of topic areas is provided in the [appendix](#).

We reviewed the titles of articles in both sets of search results ($n = 4314$) (figure 3). We earmarked articles with titles that included any of the following for further review: (1) the name of a specific domestic animal, wildlife species, or taxa (e.g. mammals, birds); (2) a general reference to animals or wildlife; (3) an example of an animal behavior (e.g. migration); or (4) an example of a health effect (e.g. mortality). We did not further review papers with titles suggestive of inquiry into ecosystem-level impacts of wildfires or the effects of fire or smoke on vegetation. We also excluded titles with clear references to human demographic groups (e.g. children) or epidemiological study (e.g. hospitals, emergency rooms). Next, we reviewed abstracts of articles earmarked in the review of titles ($n = 295$) to assess their eligibility for a full-text review (figure 3). We assessed whether or not these papers presented research on the responses of animals to smoke from fires—regardless of the specific type of exposure investigated. Those that met these criteria were included in the list of papers that were read for this review ($n = 72$; figure 3).

We sorted papers into three categories: (1) experiments using animal models; (2) case studies from

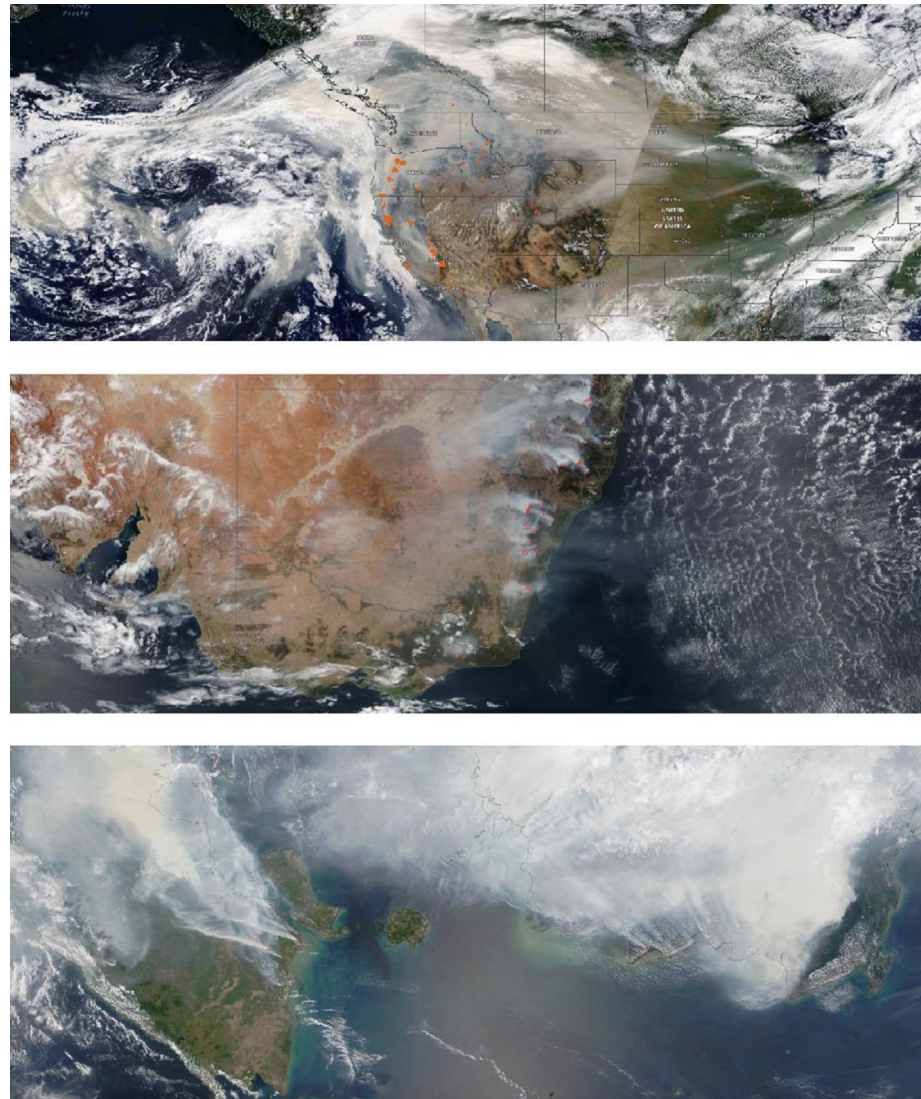


Figure 1. Satellite images of large-scale wildfire smoke events around the world. Orange points indicate locations of fires or thermal anomalies. Top: smoke blows across the Western United States on 13 September 2020. Middle: wildfires in southeast Australia send up smoke plumes on 17 December 2020. Bottom: smoke blankets much of Indonesia on 24 September 2015. We acknowledge the use of imagery from the NASA Worldview application (<https://worldview.earthdata.nasa.gov>), part of the NASA Earth Observing System Data and Information System (EOSDIS).

veterinary medicine; and (3) research on the effects of smoke on wildlife species (figure 3). For the last category, we considered ‘wildlife’ to include all non-domesticated fauna in terrestrial environments, including insects, as well as aquatic animals that breathe air, such as marine mammals. This allowed us to focus on the direct effects of smoke on wildlife, rather than explore all possible indirect effects that could arise from atmospheric deposition of airborne toxins found in wildfire smoke. At least one of the co-authors of this review read and documented findings from studies of animal models ($n = 36$) and case studies from veterinary medicine ($n = 18$). However, we focused our review on studies of the impacts of smoke on wildlife ($n = 18$). At least two co-authors of this review read and documented findings from each of these papers. In addition, we used Web of Science to conduct forwards searches, noting

any citations of these studies that referenced all of the following in the title: (1) smoke, or more generally air pollution associated with fires; (2) animals, wildlife, or the name of a particular species or taxa; and (3) an animal behavior or health effect. We also conducted backwards searches using two different approaches: (1) we noted citations that may be relevant to our review while reading a paper, and (2) we conducted a backwards search of all works cited in the paper using the same criteria described for the forwards search. All additional studies on the effects of smoke on wildlife species identified in forwards and backwards searches were also reviewed ($n = 16$) (figure 3). In addition to noting major findings from these papers, we pulled out several key pieces of information to characterize the research and compare results across studies, including publication year, field of study, location, type of exposure,

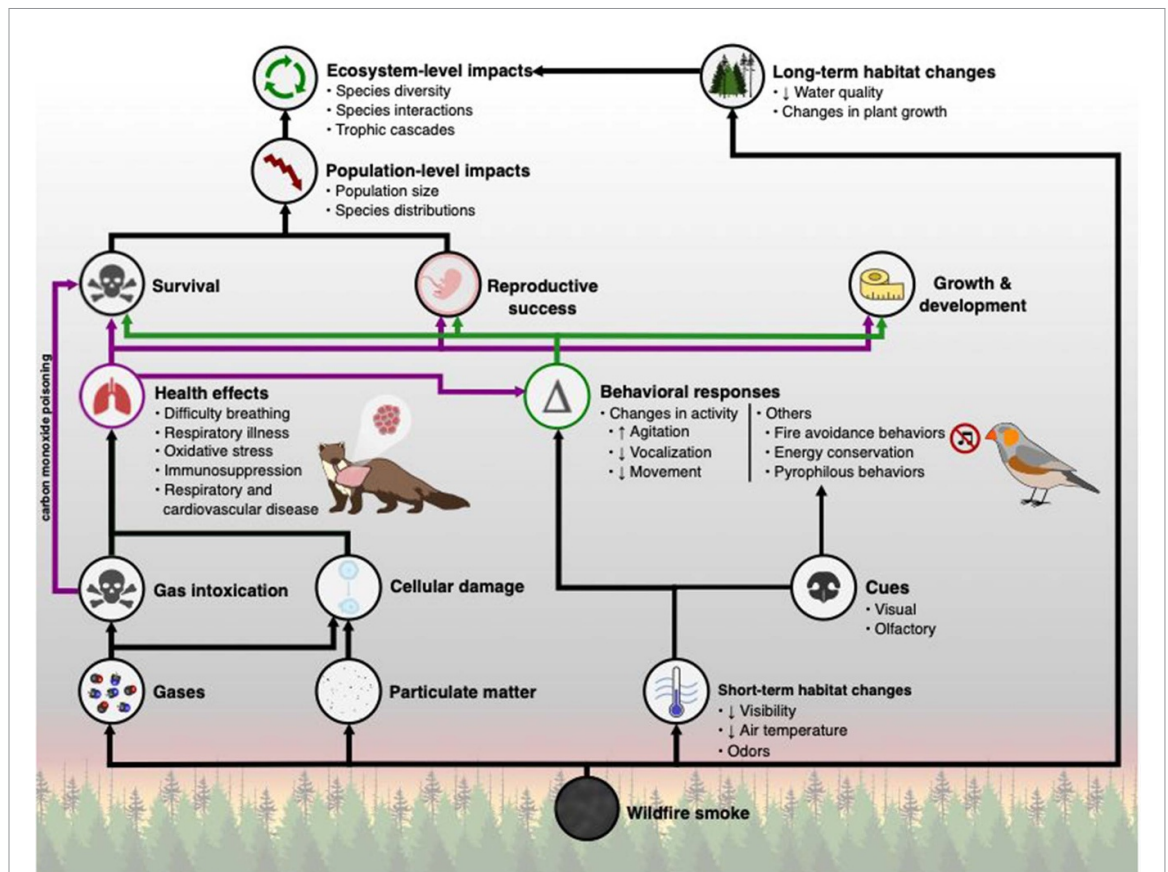


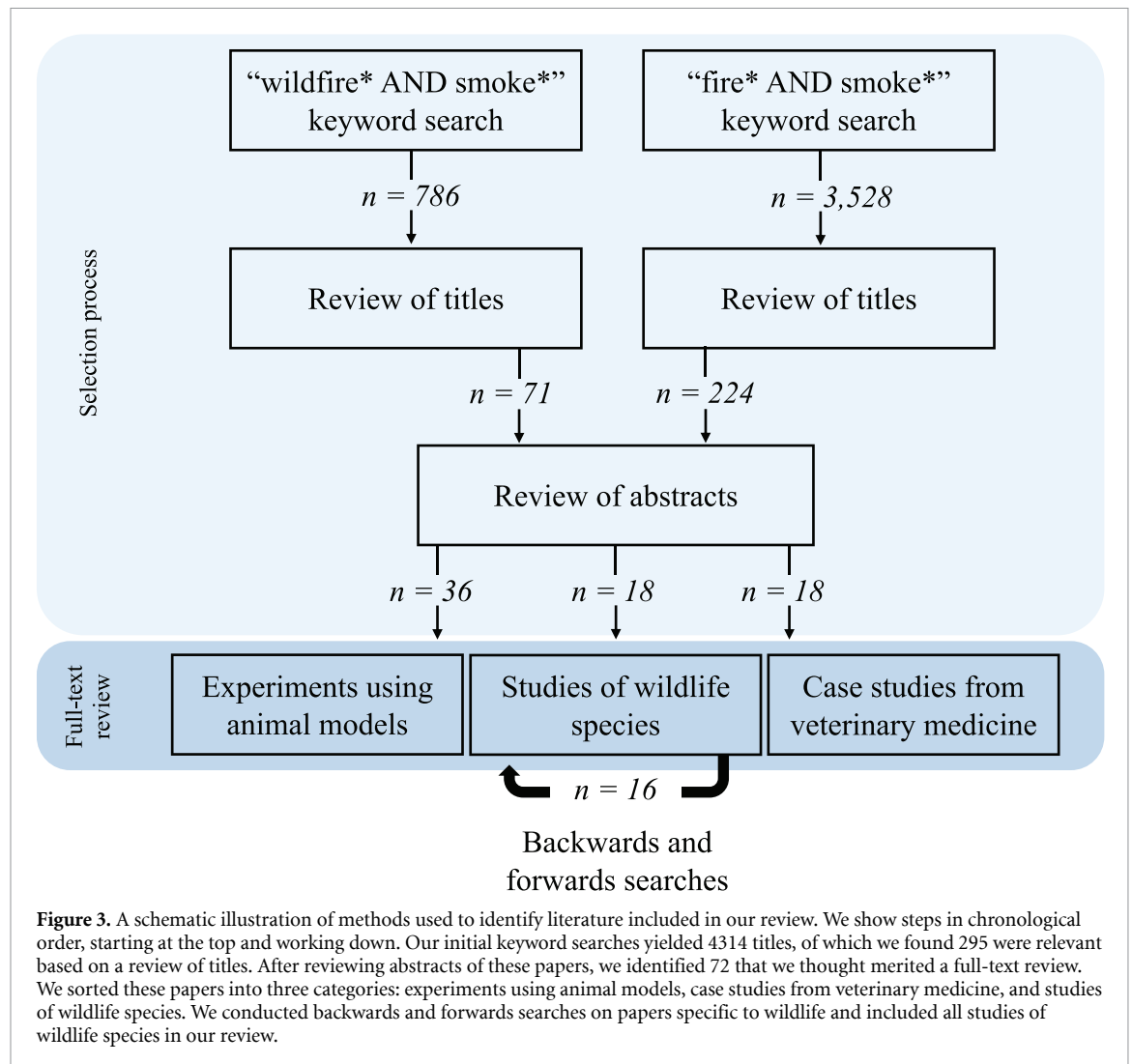
Figure 2. A conceptual model illustrating the various pathways by which wildfire smoke could influence wildlife populations and ecosystems. We hypothesize how effects of smoke on individual health and behavior could contribute to shifts in demographic rates, including growth and development, survival, and reproductive success. These parameters determine population growth, ultimately leading to community- and ecosystem-level impacts.

concentrations of air pollutants (if provided), and taxa and species of animals studied, as well as whether the animals were captive (i.e. kept in a laboratory or outdoor enclosure), or free-living (i.e. in the wild). Finally, we noted whether the ultimate goal of the study was to investigate effects of smoke in people or non-human animals. While preparing this manuscript, we learned of seven additional studies that considered the impacts of wildfire smoke on wildlife, which we also included in our review. Although we did not restrict our initial keyword searches in Web of Science by language, each subsequent step of our review was limited to text available in English. In addition, we were only able to review articles available through the University of Washington library system. All together, we reviewed 41 studies that considered the effects of wildfire smoke on wildlife (figure 3, table 1).

3. Results

We found that although research to date on the impacts of wildfire smoke on wildlife is limited, existing evidence suggests that smoke pollution has wide-ranging direct and indirect effects on both terrestrial and aquatic wildlife. Studies have linked smoke

inhalation to acute and chronic health outcomes in animals and sought to characterize how smoke influences animal behavior. Whereas the designs of these studies are highly variable, two general approaches have emerged in the literature: (1) experiments in which animals were intentionally exposed to smoke or constituents of smoke in a controlled environment (i.e. ‘controlled exposure’) and (2) opportunistic monitoring of free-living animals or animals in captivity during wildfire smoke events (i.e. ‘*in situ* exposure’). The studies we reviewed were conducted on five continents, including North America, Australia, Europe, Asia, and Africa (figure 4), and published between 1968 and 2021. They explored responses in a wide variety of taxa, including mammals, birds, reptiles, and insects, in both controlled and *in situ* settings (figure 5). A complete list of studies reviewed is provided in table 1. In sections 4 through 6, we detail findings from this literature while also incorporating knowledge gained from fields outside wildlife science, specifically veterinary medicine and air pollution toxicology. Finally, in section 7, we briefly summarize studies of indirect effects of smoke on wildlife and consider how a species’ life-history strategy mediates its exposure to smoke pollution.



4. Acute and chronic health outcomes

Few studies have explicitly considered the impact of wildfire smoke on the health of wildlife (table 1); however, research from veterinary medicine and air pollution toxicology clearly demonstrates that smoke inhalation contributes to acute and chronic health outcomes in animals. Case studies detailing the symptoms, treatment, and recovery of pets and livestock following structural fires establish that animals are vulnerable to negative health outcomes from smoke inhalation (e.g. Drobatz *et al* 1999a, 1999b, Marsh 2007). In addition, there are numerous examples of laboratory experiments designed to investigate the effects of inhalation exposure to wildfire smoke in humans using animal models (e.g. Hargrove *et al* 2019, Martin *et al* 2020) including mice, rats, rabbits, and sheep. Although the objective of these studies is to characterize the underlying physiological mechanisms that contribute to respiratory and cardiovascular disease in humans, their findings allude to health effects we could observe in other mammalian species.

These experiments have incorporated *in vivo*, *ex vivo*, and/or *in vitro* approaches. Some studies have also used animal models to study possible treatment interventions to improve health outcomes in humans following smoke inhalation (e.g. Janssens *et al* 1994, Wang *et al* 1999, Wong *et al* 2004, Syrkinia *et al* 2007, Hamahata *et al* 2008, Dunn *et al* 2018).

Research has largely focused on mammals, but all animals that breathe air—whether terrestrial or aquatic—are vulnerable to inhalation exposure to airborne toxins, including the reactive gases and aerosols that make up smoke (e.g. carbon monoxide (CO), hydrogen cyanide (HCN), and coarse and fine particulate matter (PM)). Many animals are susceptible to CO poisoning during smoke inhalation (Chaturvedi *et al* 1995, Fitzgerald and Flood 2006, Kent *et al* 2010, Ashbaugh *et al* 2012, Dörfelt *et al* 2014, Stern *et al* 2014), which can be fatal (Wohlsein *et al* 2016). CO binds to hemoglobin, a protein molecule containing iron that nearly all vertebrates (Ruud 1954) and many invertebrates depend on to carry oxygen through the bloodstream. This limits oxygen transport, resulting

Table 1. Summary of studies of wildlife species included in our review. For each paper, we provided the in-text citation, broad taxonomic category and specific species studied, and type of exposure (i.e. *in situ* or controlled) investigated. We also indicated whether a study assessed impacts in captive or free-living animals. In addition, we included the location and continent where each study took place. If locations for studies of captive animals were not provided, we noted the location of the research institution of the first author. We also provided a description of smoke exposure. Finally, we indicated if a health outcome and/or a behavioral response was observed. Citations are listed in alphabetical order.

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Álvarez <i>et al</i> (2015)	Insects	Pine sawyer (<i>Monochamus galloprovincialis</i>)	Controlled (excised antennae)	Insects captured in Valencia, Spain. Experiment conducted in Palencia, Spain	Europe	Excised antennae exposed to six smoke volatiles	No	Yes
Álvarez-Ruiz <i>et al</i> (2021)	Reptiles	Large psammodromus (<i>Psammodromus algirus</i>)	Controlled (captive)	Lizards captured on the eastern Iberian Peninsula in Spain. Study conducted in Valencia, Spain	Europe	Smoke generated from burning pine	No	Yes
Bova <i>et al</i> (2011)	Birds	Red-cockaded woodpecker (<i>Dryobates borealis</i>)	Controlled	Ohio, United States	North America	Smoke generated by burning maple twigs, branches, and leaf litter	No (only effects on habitat studied)	
Braun De Torres <i>et al</i> (2018)	Mammals	Florida bonneted bat (<i>Eumops floridanus</i>)	<i>In situ</i> (free-living)	Fred C. Babcock-Cecil M. Webb Wildlife Management Area and Florida Panther National Wildlife Refuge, Florida, United States	North America	Smoke from prescribed burns	No	Yes
Cahill and Walker (2000)	Birds	Red-knobbed Hornbill (<i>Aceros cassidix</i>)	<i>In situ</i> (free-living)	Tangkoko-Dua Saudara Nature Reserve, Sulawesi, Indonesia	Asia	Smoke from 1997 wildfire	Yes	Yes
Cheyne (2008)	Mammals	Bornean white-bearded gibbon (<i>Hyllobates albibarb</i>)	<i>In situ</i> (free-living)	Natural Laboratory of Peat-swamp Forest, Indonesia	Asia	Smoke from 2006 wildfire. Months were categorized as 'smoky' if the Indeks Standar Pencemar Udara (ISPU), an air quality index, exceeded Category 3—indicative of unhealthy air quality ($PM_{10} > 100 \mu g m^{-3}$)—on more than 75% of days	No	Yes
Dickinson <i>et al</i> (2009)	Mammals	Indiana bat (<i>Myotis sodalis</i>) and Northern long-eared bat (<i>Myotis septentrionalis</i>)	<i>In situ</i> (free-living)	Daniel Boone National Forest, Kentucky, United States	North America	Smoke from prescribed burns. CO peaked at ≥ 400 parts per million	No	Yes

(Continued.)

Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Dickinson <i>et al</i> (2010)	Mammals	Indiana bat (<i>Myotis sodalis</i>)	N/A (modeling exercise; data on air pollution from prescribed burns in Tar Hollow State Forest and Daniel Boone National Forest, United States)	United States	Australia	No (no animals or specimens observed)	No	No
Doty <i>et al</i> (2018)	Mammals	Gould's long-eared bat (<i>Nyctophilus gouldi</i>)	Controlled (captive)	Armidale, New South Wales, Australia		Smoke generated by burning eucalyptus leaves. Air quality measured using a smoke meter. Smoke level was measured at 6 (on a scale of 0–6), indicative of thick smoke	No	Yes
Engstrom (2010)	Multiple	Multiple	N/A (review, focused on first-order effects of fire in animals)				Yes	Yes
Erb <i>et al</i> (2018)	Mammals	Bornean orangutans (<i>Pongo pygmaeus wurmbii</i>)	<i>In situ</i> (free-living)	Tuanan Research Station, Central Kalimantan, Indonesia	Asia	Smoke from 2015 wildfire During wildfire season, daily mean concentrations of PM ₁₀ exceeded unhealthy levels (i.e. 150 $\mu\text{g m}^{-3}$) most days (79%). PM ₁₀ peaked at 1829 $\mu\text{g m}^{-3}$	Yes	Yes
Geiser <i>et al</i> (2018)	Mammals	Multiple (focus on small mammals)	N/A (review, focused on data from the southern hemisphere)				Yes	Yes
Hinz <i>et al</i> (2018)	Insects	Australian 'firebeetle' (<i>Merimna atrata</i>)	Controlled (captive)	Insects collected in Perth, Western Australia. Experiment carried out in Bonn, Germany	Europe	Insects exposed only to visual cues of smoke (e.g. projected image of a smoke plume)	No	Yes
Höcherl and Tautz (2015)	Insects	European paper wasp (<i>Polistes dominula</i>)	Controlled (free-living)	Wüzberg, Germany	Europe	Smoke generated by burning poplar wood	No	Yes

(Continued.)

Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Hovick <i>et al</i> (2017)	Birds	Multiple (raptors)	<i>In situ</i> (free-living)	The Nature Conservancy Tallgrass Prairie Preserve and Oklahoma State University Cross Timbers Experimental Range, Oklahoma, United States	North America	Smoke from prescribed burns	No	Yes
Jordaan <i>et al</i> (2020)	Reptiles	Multiple (6 lizard and 8 snake species)	<i>In situ</i> (free-living)	Tembe Elephant Park, South Africa	Africa	Smoke from prescribed burns	Yes	Yes
Klocke <i>et al</i> (2011)	Insects	<i>Microsania australis</i> , <i>Hypocertides nearticus</i> , and <i>Anabarhynchus hyalipennis</i>	<i>In situ</i> (free-living)	Perth, Western Australia, Australia	Australia	Smoke from wildfires in 2006–2009	No	Yes
Layne (2009)	Mammals	Eastern red bat (<i>Lasiurus borealis</i>)	Controlled (captive)	Animals captured within and studied in outdoor enclosures at the Peck Ranch Conservation Area, Missouri, United States	North America	Smoke generated by burning leaf litter. CO peaked at 40 ppm	No	Yes
Lee <i>et al</i> (2017)	Multiple (ecoacoustics study, soundscape likely dominated by birds and insects)		<i>In situ</i> (free-living)	'EcoLink' wildlife overpass connecting Bukit Timah Nature Reserve and Central Catchment Nature Reserve, Singapore	Asia	Smoke from 2015 wildfire. During smoke event, the Pollutant Standards Index (PSI) ranged from 97 to 267, indicative of moderate to very unhealthy air quality	No	Yes
Liu <i>et al</i> (2021b)	Insects	Painted lady butterfly (<i>Vanessa cardui</i> L.)	Controlled (captive)	London, England, United Kingdom	Europe	Smoke generated by burning incense. Concentrations of PM _{2.5} during experiments ranged from 0.15 mg m ⁻³ to 1.28 mg m ⁻³	No	Yes
Mendyk <i>et al</i> (2020)	Reptiles	Pinecone lizards (<i>Tiliqua rugosa</i>)	<i>In situ</i> (captive)	Audubon Zoo, New Orleans, Louisiana, United States	North America	Smoke not generated intentionally. Animals exposed to smoke when a pastry burned in a nearby toaster	No	Yes
Milberg <i>et al</i> (2015)	Insects	Multiple	Controlled (free-living)	Ostergotland County, Sweden	Europe	Smoke generated by burning birch wood	No	Yes
Nimmo <i>et al</i> (2021)	Multiple	Multiple	N/A (review, focused on behavioral responses to fire)				No	Yes

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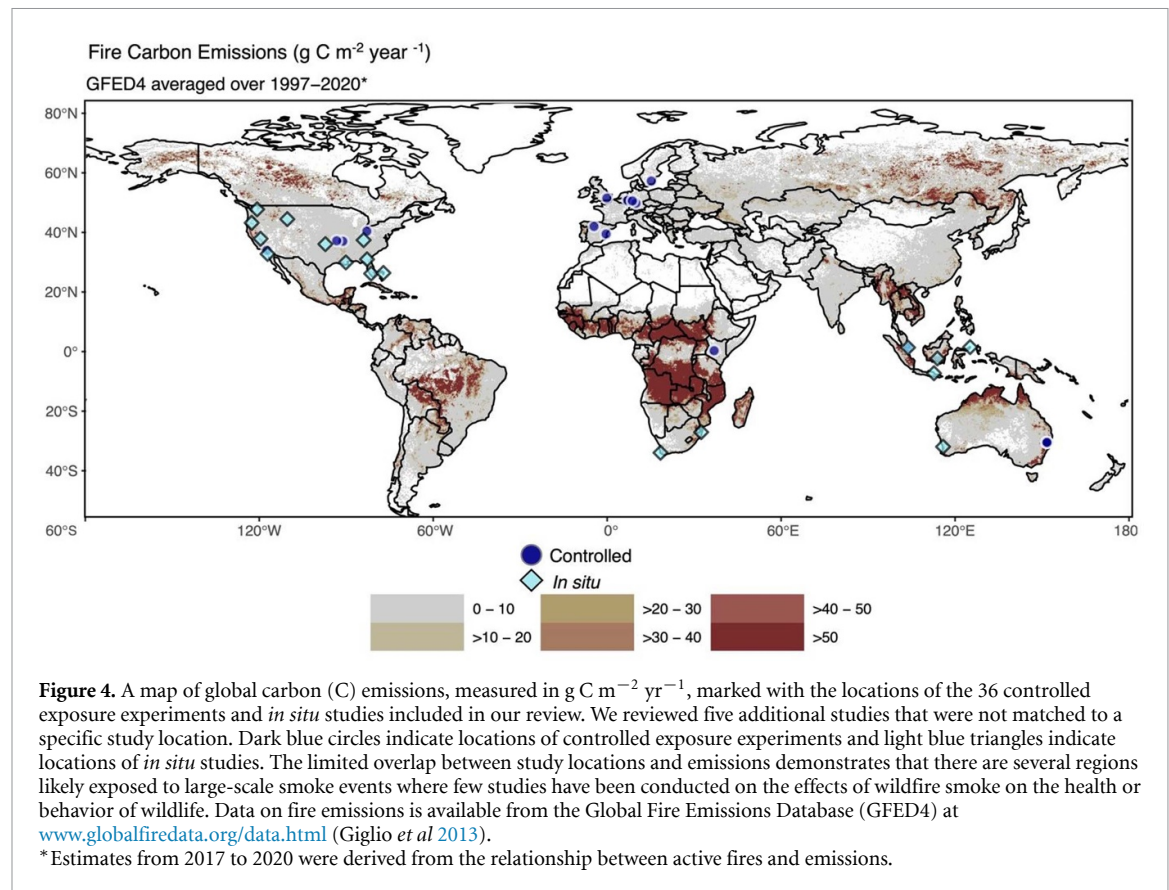
Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Nowack <i>et al</i> (2016)	Mammals	Eastern pygmy possum (<i>Cercartetus nanus</i>)	Controlled (captive)	Animals captured in Dorrig, New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia	Australia	Possums exposed only to olfactory cues of smoke, specifically the scent of wood smoke	No	Yes
Nowack <i>et al</i> (2018)	Mammals	Sugar gliders (<i>Petaurus breviceps</i>)	Controlled (captive)	Animals captured in the Dorrig and Imbota Nature Reserves in New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia	Australia	Smoke generated by burning branches, sawdust, and leaves. Air quality measured using a smoke meter. Smoke level was measured between 3.2 and 4.1 (on a scale of 0 = clean air to 6 = thick smoke)	No	Yes
O'Brien <i>et al</i> (2006)	Birds	Cuban parrot (<i>Amazona leucocephala</i>)	<i>In situ</i>	Great Abaco, Bahamas	North America	Smoke from a prescribed burn. The maximum CO ₂ concentration in the surrogate nesting cavity was 2092 ppm	No (only effects on habitat)	
Sanderfoot and Gardner (2021)	Birds	71 common bird species	<i>In situ</i> (free-living)	Washington, United States	North America	Smoke from wildfires in 2015–2018. Daily mean concentration of PM _{2.5} ranged from 0 to 295.8 $\mu\text{g m}^{-3}$, with an average value of 8.6 $\mu\text{g m}^{-3}$	No (only effects on detection studied)	
Sanderfoot and Holloway (2017)	Birds	Multiple	N/A (review, focused on effects of air pollution on birds)				Yes	Yes
Scesny (2006)	Mammals	Eastern red bat (<i>Lasiurus borealis</i>)	Controlled (captive)	Animals captured in the Peck Ranch Conservation Area in Missouri, United States. Study conducted in Springfield, Missouri, United States	North America	Smoke generated by burning leaf litter	No	Yes
Schütz <i>et al</i> (1999)	Insects	Black fire beetle (<i>Melanophila acuminata</i>)	Controlled (excised antennae)	Giessen, Germany	Europe	Excised antennae exposed to volatiles generated from burning pine	No	Yes
Sensenig <i>et al</i> (2017)	Insects	<i>Crematogaster sjostedii</i> , <i>C. mimosae</i> , <i>C. nigricaps</i> , and <i>Tetraponera penzigi</i>	Controlled (free-living)	Mpala Research Centre, Kenya	Africa	Smoke generated by burning elephant dung	No	Yes

(Continued.)

Table 1. (Continued.)

Citation	Taxa	Species	Type of exposure	Location	Continent	Description of smoke exposure	Health outcome	Behavioral response
Singer <i>et al</i> (1989)	Mammals	Elk (<i>Cervus elaphus</i>)	<i>In situ</i> (free-living)	Yellowstone National Park, United States	North America	Smoke from the 1988 wildfires	Yes	Yes
Snoddy and Tippins (1968)	Insects	<i>Microsania imperfecta</i>	<i>In situ</i> (free-living)	Clinch County, Georgia, United States	North America	Smoke from an incinerator	No	Yes
Stawski <i>et al</i> (2015)	Mammals	Fat-tailed dunnart (<i>Sminthopsis crassicaudata</i>)	Controlled (captive)	Armidale, New South Wales, Australia	Australia	Smoke generated by burning eucalyptus	No	Yes
Stawski <i>et al</i> (2017)	Mammals	Yellow-footed antechinus (<i>Antechinus flavipes</i>)	Controlled (captive)	Animals captured in the Aberlady Nature Reserve, New South Wales, Australia. Study conducted in Armidale, New South Wales, Australia	Australia	Air quality measured using a smoke spot tester. Smoke level was measured at 5 (on a scale of 0–6), indicative of thick smoke	No	Yes
Tan <i>et al</i> (2018)	Insects	Squinty bush brown (<i>Bicyclus anynana</i>)	Controlled (captive)	National University of Singapore, Singapore	Asia	Smoke generated from burning incense. Average concentration of PM _{2.5} was 117 $\mu\text{g m}^{-3}$	Yes	No
Thompson and Purcell (2016)	Mammals	Fisher (<i>Pekania pennanti</i>)	<i>In situ</i>	Yosemite National Park and Sierra National Forest, United States	North America	Smoke from prescribed burns. The maximum CO concentration in dens ranged from 5.5 to 563.5 ppm, with a mean value of 170.8 ppm	No (only effects on habitat studied)	
Tribe <i>et al</i> (2017)	Insects	Cape honeybee (<i>Apis mellifera capensis</i>)	<i>In situ</i> (free-living)	Table Mountain National Park, South Africa	Africa	Smoke from 2015 wildfire	No	Yes
Venn-Watson <i>et al</i> (2013)	Mammals	Bottlenose dolphin (<i>Tursiops truncatus</i>)	<i>In situ</i> (free-living)	San Diego, California, United States	North America	Smoke from wildfires in 2003 and 2007. Maximum daily mean concentrations of PM _{2.5} reported for study years: 170 mg m^{-3} (2003) and 70 mg m^{-3} (2007)	Yes	No
Visser <i>et al</i> (1995)	Insects	Honey bee (<i>Apis mellifera</i>)	Controlled (excised antennae)	Riverside, California, United States	North America	Smoke generated by burning burlap	No	Yes
Yang <i>et al</i> (2021)	Birds	Multiple species	<i>In situ</i> (free-living)	Western United States	North America	Smoke from 2020 wildfires	Yes	No

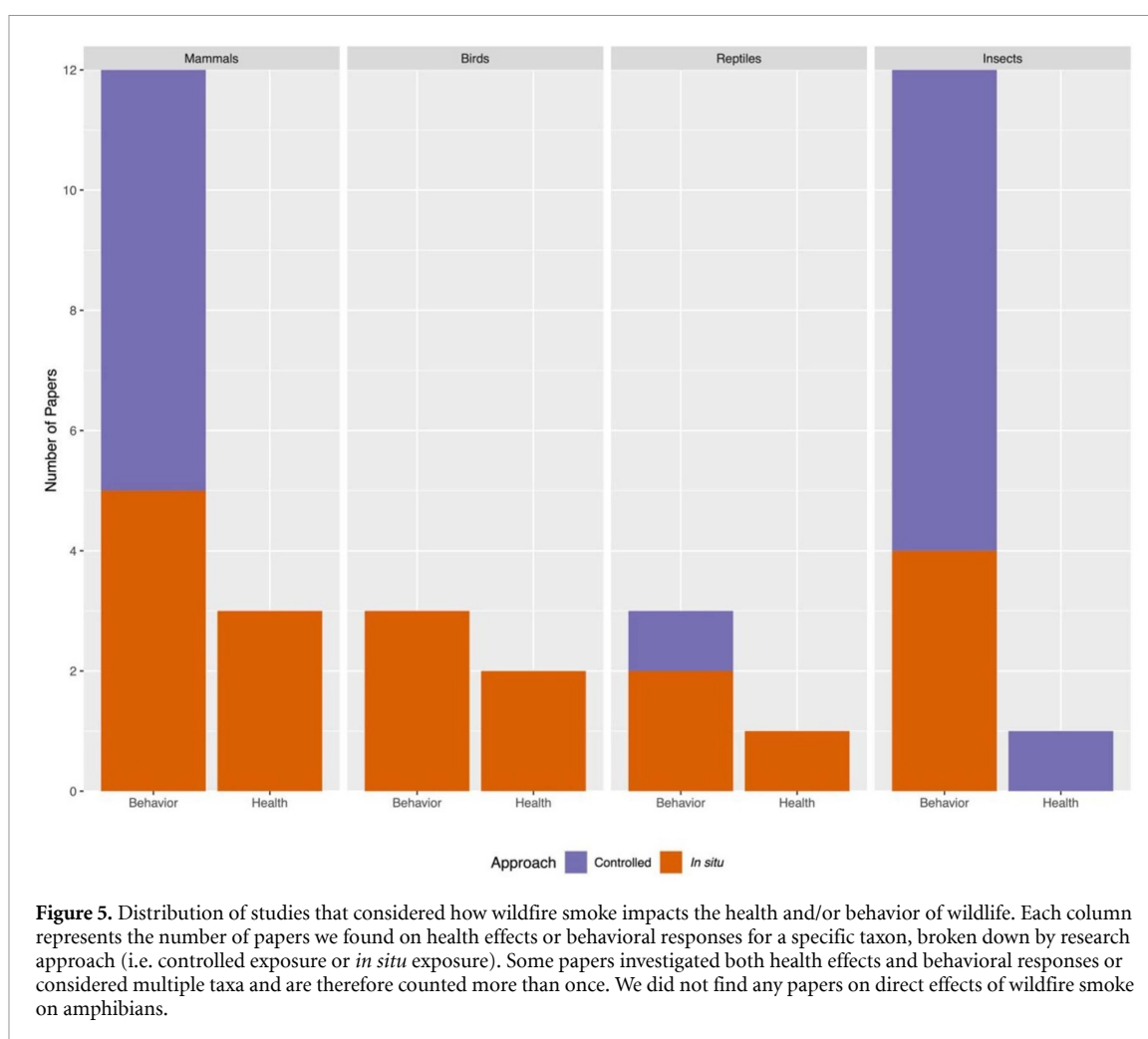


in low blood oxygen levels (i.e. hypoxemia) and insufficient supply of oxygen to tissues and organs (i.e. hypoxia) (Wohlsein *et al* 2016). Neurological symptoms of hypoxic brain damage could include confusion and stupor (Drobatz *et al* 1999a, 1999b, Mariani 2003, Kent *et al* 2010, Weiss *et al* 2011, Guillaumin and Hopper 2013). Hypoxia could also make animals more vulnerable to predation as they attempt to flee wildfires (Braithwaite and Estbergs 1987).

Smoke inhalation also causes both thermal and chemical damage to lung tissue in terrestrial and aquatic vertebrates (Fitzgerald and Flood 2006, Marsh 2007, Wohlsein *et al* 2016). As a result of this injury, fluid can accumulate in the lungs, a condition known as pulmonary edema (Bidani *et al* 1998, Jordaan *et al* 2020), which has been documented in pets and livestock exposed to smoke during structural fires (Verstappen and Dorrestein 2005, Fitzgerald and Flood 2006, Marsh 2007). Symptoms of smoke inhalation injury can be immediate or delayed and include labored breathing (i.e. dyspnea) (Verstappen and Dorrestein 2005, Fitzgerald and Flood 2006), rapid breathing (i.e. tachypnea) (Mariani 2003, Fitzgerald and Flood 2006), wheezing (Kemper *et al* 1993), panting (i.e. polypnea) (Dörfelt *et al* 2014), coughing (Kemper *et al* 1993, Fitzgerald and Flood 2006, Dörfelt *et al* 2014), foaming at the nostrils (McPherson 1993, Wohlsein *et al* 2016), and rapid heart rate (i.e. tachycardia) (Dörfelt *et al* 2014), which are consistent with acute respiratory distress syndrome (Guillaumin and Hopper 2013). If untreated, smoke

inhalation injury can quickly impair gas exchange, resulting in hypoxemia (Wohlsein *et al* 2016) and elevated levels of acid in the blood (i.e. acidosis) (Bidani *et al* 1998). For example, in a retrospective analysis of health records of captive bottlenose dolphins (*Tursiops truncatus*), researchers found that blood carbon dioxide (CO_2) levels were elevated in the month following a wildfire smoke event in 2003, possibly due to respiratory acidosis (Venn-Watson *et al* 2013). Air-breathing invertebrates might also be vulnerable to smoke inhalation. Tan *et al* (2018) investigated effects of smoke exposure in captive squinty bush brown butterflies (*Bicyclus anynana*) and found that particles accumulated in the entryway of spiracles—external openings in the exoskeleton that vent the insect respiratory system—but did not enter the trachea.

Wildfire smoke contributes to chronic respiratory and cardiovascular health outcomes in animals. Smoke inhalation can jeopardize an animal's immune system, which is designed to protect the body from foreign matter, such as bacteria, viruses, and toxins. In mammals, smoke inhalation immediately triggers production of immune cells, including lymphocytes (e.g. T cells) and macrophages (Bidani *et al* 1998, Barrett *et al* 2006, Syrkinina *et al* 2007, Hamahata *et al* 2008, Hargrove *et al* 2019)—a type of white blood cell that engulfs and digests (i.e. phagocytizes) foreign particles. However, exposure to wildfire smoke can alter (Venn-Watson *et al* 2013) or weaken (Black *et al* 2017) the immune response in animals. For example, whereas macrophages are able to sequester



toxic particles in wildfire smoke, they are unable to destroy them; this precludes macrophages from helping to prevent infection (Wohlsein *et al* 2016). Furthermore, toxins in smoke also destroy antioxidants, substances that neutralize free radicals—highly reactive, oxygen-containing compounds that damage tissue (Shalini *et al* 1994, Hamahata *et al* 2008, Wegesser *et al* 2010). Oxidative stress can ultimately contribute to compromised immune function by destroying macrophages or other types of immune cells (Franzi *et al* 2011, Williams *et al* 2013). Lung injury and a weakened immune response can leave animals more vulnerable to respiratory infection and illness, such as pneumonia (Attwood *et al* 1996a, 1996b, Marsh 2007, Simone-Freilicher 2008, Lange *et al* 2010, Guillaumin and Hopper 2013, Wohlsein *et al* 2016) or laryngotracheitis (Morris *et al* 1986). For example, captive bottlenose dolphins were three times more likely to have bacterial pneumonia at time of death after exposure to smoke during a wildfire in 2003 (Venn-Watson *et al* 2013). However, age also influenced the incidence of pneumonia, and after controlling for age, the effect of fires was no longer statistically significant (Venn-Watson *et al* 2013). A study of rhesus macaque monkeys (*Macaca mulatta*) housed in outdoor enclosures found that newborn monkeys

exposed to wildfire smoke exhibited reduced lung capacity and weakened immune responses in adolescence compared to those born in a subsequent year with good air quality (Black *et al* 2017). Whereas this study was designed to investigate pediatric health outcomes in humans associated with wildfire smoke, these results suggest that wildlife could experience long-term, adverse health outcomes from a single smoke event. Smoke inhalation can also impair cardiovascular function in vertebrates (Kim *et al* 2014, Wohlsein *et al* 2016, Thompson *et al* 2018, Sharpe *et al* 2020) and repeated or prolonged exposure to smoke can lead to chronic heart disease (Thompson *et al* 2018, Martin *et al* 2020).

Health outcomes associated with inhalation of wildfire smoke vary as a function of its toxicity. Research from air pollution toxicology demonstrates that toxicity of biomass smoke is dependent on its chemical and biological composition (Franzi *et al* 2011, Kim *et al* 2019), which is determined by the substrate burned (e.g. peat, oak, eucalyptus, etc) and combustion conditions (e.g. flaming, smoldering) (Hargrove *et al* 2019, Kim *et al* 2019). Smoke is also subject to chemical transformation during long-range transport (Jalava *et al* 2006). This suggests that the specific types of vegetation burned during

wildfires, the stage and severity of the fires, and the distance smoke travels ultimately affect respiratory and cardiovascular health outcomes associated with smoke inhalation in wildlife.

5. Impacts on demography

Negative health outcomes associated with inhalation exposure to wildfire smoke could ultimately influence demographic rates in wildlife populations, including survival, growth, and reproductive success (figure 2). *In vivo* studies of animal models (e.g. Bidani *et al* 1998, Dubick *et al* 2002, Lee *et al* 2005, Syrkin *et al* 2007, Lange *et al* 2010) and case studies from veterinary medicine (e.g. Morris *et al* 1986, Drobatz *et al* 1999b, Kent *et al* 2010, Dörfelt *et al* 2014, Stern *et al* 2014) provide clear evidence that animals can die from smoke inhalation. For example, Anderson *et al* (2020) linked elevated concentrations of PM_{2.5} during a large-scale smoke event to increased mortality in dairy cows, specifically calves. Yet, we found only four studies that considered the effect of smoke on survival of wildlife species. A study of captive butterflies reared in smoky conditions found that caterpillars exposed to smoke exhibited a higher mortality rate than those in the control group, likely due to gas intoxication (Tan *et al* 2018). Gas intoxication was also hypothesized as a contributing factor to the death of lizards and snakes that did not survive prescribed burns in Tembe Elephant Park, South Africa (Jordaan *et al* 2020). Few specimens exhibited signs of burn injury, yet Jordaan *et al* found that 61% of specimens collected at the site of one fire exhibited pulmonary edema and noted particles accumulated in the lungs of two of these specimens. These findings suggest that reptiles that did not survive the fire died from asphyxiation, CO or HCN poisoning, or heat-induced cardiac arrest. Large mammals are also vulnerable to smoke inhalation—Singer *et al* (1989) reported that smoke inhalation injury or gas intoxication likely killed 246 elk (*Cervus elaphus*) that perished in the 1988 wildfires in Yellowstone National Park. Finally, Yang *et al* (2021) found that smoke from extensive wildfires in the Western United States contributed to a mass avian mortality event in 2020.

Wildfire smoke could also reduce growth rates and reproductive success. Tan *et al* (2018) reported that captive squinty bush browns exposed to smoke developed more slowly and weighed less as pupae. Cahill and Walker (2000) reported that the nesting success of Red-knobbed Hornbills (*Aceros cassidix*) declined at the Tangkoko Nature Reserve in Indonesia following extensive wildfires in 1997, possibly due to exposure to extreme heat and smoke. Although the Red-knobbed Hornbill example was the only study we found that considered the impacts of wildfire smoke on reproductive success in wild animals, a case study of domestic chickens exposed to smoke during a structural fire suggests that smoke inhalation

could reduce egg production (Morris *et al* 1986). Previous research has linked other types of air pollution to reduced hatching success and lower clutch size in birds (e.g. Eeva and Lehikoinen 1995), which suggests that wildfire smoke could also impair avian reproductive success. In addition, PM—a major component of wildfire smoke—dirty bird feathers, which can render them less attractive to potential mates (Griggio *et al* 2011) and interfere with other color-based signaling or camouflage.

6. Behavioral responses

Wildfire smoke can also trigger shifts in animal behavior, including movement and vocalization. Such behavioral changes could be due to underlying health effects (Erb *et al* 2018) or serve to limit exposure to airborne toxins (Singer *et al* 1989, Dickinson *et al* 2009, Liu *et al* 2021b). Some species rely on smoke as an early-warning signal that helps them to avoid wildfires (Engstrom 2010, Höcherl and Tautz 2015, Álvarez-Ruiz *et al* 2021) or prepare to conserve energy in a post-fire landscape (Geiser *et al* 2018), whereas others use smoke as a cue to navigate toward newly available resources in burned habitats (Schütz *et al* 1999, Klocke *et al* 2011, Milberg *et al* 2015). Animals could also change their behavior in response to alterations in the physical environment that result from smoke pollution (Cheyne 2008, Lee *et al* 2017), such as reduced visibility (Haider *et al* 2019) or cooler air temperatures (Robock 1991). Emerging evidence suggests that behavioral responses to wildfire smoke could ultimately influence the short- and long-term fitness of wildlife (Cheyne 2008, Erb *et al* 2018).

6.1. Effects of smoke on wildlife activity

Exposure to smoke can influence wildlife activity, including movement and vocalization. Case studies from veterinary medicine demonstrate that animals sometimes alter their behavior due to acute, adverse health effects associated with smoke inhalation; for example, pets and livestock exposed to smoke from structural fires can become agitated (Fitzgerald and Flood 2006, Marsh 2007, Weiss *et al* 2011, Guillaumin and Hopper 2013, Mendyk *et al* 2020), vocalize more (Fitzgerald and Flood 2006, Weiss *et al* 2011), reduce their activity (Simone-Freilicher 2008) or exhibit signs of neurological impairment, such as disorientation (Marsh 2007, Weiss *et al* 2011, Guillaumin and Hopper 2013). Researchers observed that pinecone lizards (*Tiliqua rugosa*) in captivity exhibited rapid tongue-flicking when exposed to smoke near their enclosure, a sign of agitation (Mendyk *et al* 2020). Animals in the wild could also alter their behavior in response to smoke pollution, possibly due to underlying health effects, as noted in one of the only studies to directly link wildfire smoke exposure to specific health outcomes for a wildlife species

(Erb *et al* 2018). In this study, researchers documented the daily activity of male Bornean orangutans (*Pongo pygmaeus wurmbii*) before, during, and after an extensive wildfire smoke event in Indonesia. They also collected urine samples opportunistically to test for ketones, a marker of fat catabolism associated with energy expenditure. The researchers found that orangutans rested more both during and after the smoke event. Furthermore, after the smoke event, orangutans traveled shorter distances and increased their caloric intake, but expended more energy (i.e. increased fat catabolism). Despite conserving energy and eating more food, orangutans still burned more calories than they consumed after an extended period of smoke exposure, which suggests that smoke inhalation negatively affected their energy budgets. The researchers postulated this could have been due to stress or a heightened immune response (Erb *et al* 2018).

In addition to movement, smoke can also influence animal vocalization. For example, a study of singing behavior in Bornean white-bearded gibbons (*Hylobates albibarbis*) in Indonesia found that gibbons sang less when it was smoky—during months when wildfire smoke led to unhealthy air quality, both the number of days gibbons sang and the length of singing bout decreased (Cheyne 2008). Changes in vocalization during wildfire smoke events may ultimately influence entire soundscapes (Lee *et al* 2017). An analysis of audio recordings collected in Singapore during a haze event brought on by wildfires showed that wildlife acoustic activity, as measured by four acoustic indices, was negatively correlated with smoke pollution. Although the mechanisms driving this response were beyond the scope of the study, its authors hypothesized that several factors could have contributed to a decrease in acoustic activity, including reduced vocalization, a shift in ecological activity outside the recording period, or mortality due to direct effects of smoke exposure or reduced foraging success. Acoustic activity was suppressed for months following the smoke event, illustrating that smoke could have long-term impacts on species and communities (Lee *et al* 2017).

6.2. Use of smoke as a cue

6.2.1. Fire avoidance behaviors

Wildlife across taxa, including insects, reptiles, and mammals, rely on smoke as a cue to engage in fire avoidance behaviors (Nimmo *et al* 2021). Insects may relocate after detecting smoke to evade fires. Researchers in Germany exposed European paper wasps (*Polistes dominula*) to biomass smoke and found that the insects increased their thorax temperature in response to this stressor (Höcherl and Tautz 2015). Many insects must warm up their thoraxes before flying; as such, the results of this experiment suggest that smoke prompts a pre-flight warm-up behavior in wasps that prepares them for a quick

escape from nearby fire (Höcherl and Tautz 2015). Researchers exposed ants in Kenya to smoke generated by burning elephant dung and found that two of the four study species evacuated in response to smoke, relocating up to 1800 m (Sensenig *et al* 2017). Of the two ant species that responded to smoke, the subordinate ant species (*Crematogaster nigriceps*) evacuated twice as quickly as the dominant competitor (*C. mimosae*). These results suggest that subordinate species may be more willing to adopt a colonist strategy following disturbance and therefore are better equipped to escape and survive wildfires (Sensenig *et al* 2017). However, some insects, such as the Cape honeybee (*Apis mellifera capensis*), may not attempt to evade fire and instead use smoke as a cue to retreat to protective nest structures, (Tribe *et al* 2017). Regardless of their fire avoidance strategy, smoke could compromise the ability of insects to escape fires by impairing flight performance (Liu *et al* 2021b). Liu *et al* (2021b) found that the duration, distance, and speed flown by painted lady butterflies (*Vanessa cardui* L.) decreased following exposure to smoke, which could adversely impact other insect behaviors as well, such as foraging and migration (Liu *et al* 2021b).

Studies of captive lizards suggest that smoke can also trigger fire avoidance behaviors in reptiles (Mendyk *et al* 2020, Álvarez-Ruiz *et al* 2021). For example, captive *Psammmodromus* lizards (*Psammmodromus algirus*) exhibited a variety of escape behaviors when exposed to smoke, including running and scratching at their terrariums (Álvarez-Ruiz *et al* 2021). Furthermore, lizards were more likely to increase their activity in response to smoke if they were captured in habitats prone to wildfires, regardless of an individual's previous experience with fire. These results indicate that in areas that experience frequent fires, selective pressure drives greater sensitivity to smoke, increasing the ability of local populations to detect and evade fires (Álvarez-Ruiz *et al* 2021).

Smoke can also prompt mammals to arouse from torpor, enabling them to escape fires (Scesny 2006, Layne 2009, Stawski *et al* 2015, Nowack *et al* 2016, Doty *et al* 2018). However, not all torpid mammals flee in response to smoke, or react quickly enough to survive; responses to fire stimuli are likely to vary by species, sex, and individual (Layne 2009, Nowack *et al* 2016, 2018). In addition, lower ambient temperatures slow torpor arousal following smoke exposure, which suggests that torpid mammals are less able to evade fires on colder days (Layne 2009, Nowack *et al* 2016, Doty *et al* 2018). Furthermore, animals that detect smoke and arouse from torpor at cooler temperatures might not return to steady-state torpor, which increases their energy expenditure (Doty *et al* 2018).

To avoid fires, small animals might seek shelter underground or in rock crevices (Engstrom 2010); however, burrowing may not always protect animals

from extreme heat and smoke. For example, Jordaan *et al* (2020) noted that fossorial species were well-represented in their samples of dead reptile specimens collected after prescribed burns in Tembe Elephant Park, South Africa. They hypothesized that cause of death was likely asphyxiation, gas intoxication, or heat-induced cardiac arrest, which suggests that even burrowing animals are susceptible to smoke inhalation during fires (Jordaan *et al* 2020).

6.2.2. Energy-saving behaviors

Some animals rely on smoke as an indicator of impending food scarcity, prompting them to engage in energy-saving strategies. Small mammals must maintain high metabolic rates, which is difficult after fires due to limited availability of food and water. Studies of captive small mammals show that smoke can increase use of torpor in some species, allowing animals to conserve energy and survive post-fire conditions (Geiser *et al* 2018). For example, exposure to smoke and a substrate of charcoal and ash increased duration of torpor in captive yellow-footed antechinuses (*Antechinus flavipes*) (Stawski *et al* 2017) and captive sugar gliders (*Petaurus breviceps*) (Nowack *et al* 2018). However, use of torpor after fires depends on food availability, and is likely to vary by species (Nowack *et al* 2018) and sex (Stawski *et al* 2017).

6.2.3. Resource availability

Pyrophilous insects (i.e. fire-associated species that benefit from resources available in post-fire landscapes) can use smoke as a cue to navigate toward fires, responding to thermal and/or olfactory signals (Schütz *et al* 1999, Klocke *et al* 2011, Álvarez *et al* 2015, Milberg *et al* 2015). Some are even known to swarm in smoke plumes, such as ‘smoke flies’ of the genera *Microsania* and *Hormopeza*, possibly to mate near burned trees where they deposit their eggs (Evans 1966, Snoddy and Tippins 1968, Sinclair and Cumming 2006). Schütz *et al* (1999) found that the antennae of fire bugs (*Melanophila acuminata*) respond to volatiles generated in the combustion of pine, suggesting that the smell of smoke helps some beetles detect and locate burned trees. Insects may also respond to visual cues of smoke plumes but results from experimental studies are ambiguous (Hinz *et al* 2018). An influx of aerial insects to burned habitats could enhance foraging opportunities for bats (Braun De Torrez *et al* 2018) and insectivorous birds; unlike small, quadrupedal mammals, bats might actually decrease their use of torpor after fires to take advantage of this increase in food availability (Geiser *et al* 2018). Raptors may also be attracted to smoke plumes, which could signal an opportunity to prey on insects and small mammals fleeing fire (Hovick *et al* 2017).

Whereas pyrophilous insects appear to rely on olfaction to locate burned areas, exposure to smoke can impair detection of other scents. Visscher *et al*

(1995) found that the antennae of honey bees (*Apis mellifera*) exposed to smoke were less responsive to both a floral odor and alarm pheromones. This suggests that detection of smoke could have short-term impacts on foraging and defensive behaviors in insects (Visscher *et al* 1995).

7. Effects on wildlife habitat

Several studies have sought to quantify potential exposure to smoke for species that use specific habitats, although they did not evaluate the impact of smoke on animal health or behavior (e.g. O’Brien *et al* 2006, Bova *et al* 2011, Thompson and Purcell 2016). O’Brien *et al* (2006) measured air quality in a hole that could be used as a nesting cavity by Cuban parrots (*Amazona leucocephala*) during a prescribed burn. They found that as flames passed the cavity entrance, smoke accumulated inside for about 20 min, and CO₂ concentrations sharply increased to 2092 parts per million (ppm). O’Brien *et al* (2006) described these conditions as ‘benign,’ but pointed to the lack of research to date on inhalation exposure to air pollution in birds. Thompson and Purcell (2016) took a similar approach to assess the vulnerability of fishers (*Pekania pennanti*) to smoke during prescribed burns, measuring the concentration of CO in tree cavities that were previously used or could be used as den sites. They found that whereas levels of CO during burns might not be harmful to adult fishers, they are hazardous to developing fetuses and newborns. Dickinson *et al* (2010) used air quality data collected during prescribed burns to determine if smoke exposure endangered Indiana bats (*Myotis sodalis*). They determined that CO concentrations during low-intensity prescribed burns were unlikely to be dangerous but suggested that bats that roost in foliage or under bark could be more vulnerable to gas intoxication during fires than bats that roost in cavities or crevices where concentrations of poisonous gases are lower (Dickinson *et al* 2010). Dickinson *et al* (2009) found that CO concentrations during a prescribed burn did not exceed the threshold at which incapacitation of bats would likely occur; however, they noted that bats that roost closer to the ground would be more at risk of exposure to elevated concentrations of toxic gases. Cave-roosting bats in particular could be in danger of smoke inhalation because caves could fill with smoke before bats have a chance to escape (Dickinson *et al* 2009, Geiser *et al* 2018). These findings illustrate that exposure to air pollution during wildfires varies widely, depending on the specific habitats used by wildlife.

Although we primarily focused our review on the direct effects of wildfire smoke on the health and behavior of wildlife, it is worth considering how smoke pollution indirectly affects wildlife by driving short-term changes in habitat. Smoke limits visibility

(Haider *et al* 2019) and cools air temperatures (Robcock 1991)—changes in the physical environment that could influence the health and behavior of wild animals. While vegetative succession following wildfires generates habitat for a wide variety of fauna (Smith 2000, Jones and Tingley 2021, Stillman *et al* 2021), smoke from wildfires also has immediate impacts on plant growth. For example, wildfire smoke triggers seed germination in plants that grow in fire-prone habitats (Van Staden *et al* 2000). Smoke can also positively or negatively influence plant productivity, depending on the extent to which aerosols absorb or scatter sunlight, as well as ambient concentrations of co-pollutants that damage plants (Hemes *et al* 2020). Furthermore, pollutants in smoke can deposit on soils or vegetation, which can indirectly affect wildlife (Phaneuf *et al* 1995). Plants can absorb toxins in smoke that, if consumed, could compromise the health of herbivorous animals (Tan *et al* 2018). Wildfire smoke also affects aquatic habitats (Jaafar and Loh 2014). Smoke limits how far light penetrates underwater, which can influence the vertical distribution of microorganisms (Urmy *et al* 2016) or primary productivity of coral reefs (Risk *et al* 2003). Atmospheric deposition of aerosols in smoke can also degrade water quality (Phaneuf *et al* 1995, Earl and Blinn 2003, Corbin 2012), which can in turn alter the composition of macroinvertebrate communities (Earl and Blinn 2003) and negatively affect the health of fish or other water-breathing animals (Gresswell 1999, Gonino *et al* 2019).

8. Discussion

We found that the available literature clearly demonstrates that wildfire smoke has direct and indirect effects on wildlife, including terrestrial and aquatic species (figure 2, table 1). Smoke inhalation contributes to adverse acute and chronic health outcomes in animals (Venn-Watson *et al* 2013, Black *et al* 2017), including CO poisoning, respiratory distress, neurological impairment, respiratory and cardiovascular disease, oxidative stress, and immunosuppression. These health effects could contribute to changes in wildlife activity, including movement (Erb *et al* 2018) and vocalization (Cheyne 2008). Animal behavior could also be influenced by changes in the physical environment that co-occur with smoke pollution, such as reduced sunlight or cooler air and water temperatures. Finally, many species that depend on fire-prone habitats have evolved to use smoke as a cue to engage in fire avoidance (Nimmo *et al* 2021) or energy-conserving behaviors (Geiser *et al* 2018) or perceive smoke as a signal of resource availability (Schütz *et al* 1999). Both the immediate, direct effects of wildfire smoke on the health and behavior of animals and the long-term impacts of smoke on wildlife habitat could ultimately influence the demography of wildlife populations (figure 2).

However, our review also demonstrates that a limited number of studies have investigated—or even considered—the impacts of wildfire smoke on wildlife (table 1). For decades, naturalists have observed how wildlife respond to smoke from wildfires (e.g. Komarek 1969, Braithwaite and Estbergs 1987) and noted the vulnerability of animals exposed to smoke during wildfires or prescribed burns (e.g. Geluso *et al* 1986). Yet, we found few peer-reviewed studies that directly investigated health outcomes or behavioral responses in wildlife associated with inhalation or detection of biomass smoke. After conducting a comprehensive search, we only identified 41 relevant studies, several of which did not explicitly test for an effect of smoke on animals and, instead, only considered how the presence of smoke could explain the responses observed (e.g. Cahill and Walker 2000, Jordaan *et al* 2020). Furthermore, research to date is unequally distributed across taxa (figure 5) and world regions (figure 4), with most studies conducted on mammals (39%) or insects (29%) in North America (37%), followed by Europe (17%) and Australia (15%) (figure 4). Our keyword searches were conducted in English, which could have influenced the geographic distribution of the studies we reviewed.

Researchers have used a variety of methods to investigate the impacts of smoke on wildlife, which makes it challenging to compare findings across existing studies. Monitoring animals before, during, and after wildfires or prescribed burns (e.g. Dickinson *et al* 2009, Jordaan *et al* 2020) allows researchers to study how free-living animals respond to the onset and progression of a smoke event and enables direct inference about the impacts of biomass smoke on wildlife. However, such studies are difficult to plan, tend to be logistically complicated, and can jeopardize the health and safety of the research team (Erb *et al* 2018). Alternatively, researchers have studied how animals respond to smoke generated in a controlled environment, such as a laboratory or outdoor enclosure (e.g. Nowack *et al* 2018, Tan *et al* 2018). This approach may be easier to implement because it does not require coordination with a fire management team or planning fieldwork around unpredictable wildfires. Controlled conditions also allow researchers to investigate specific health outcomes and behaviors in animals that would be difficult to assess in the wild. However, despite attempts to simulate biomass smoke that is representative of what animals would be exposed to during a wildfire smoke event in their natural habitat (e.g. Layne 2009), controlled exposure experiments cannot reproduce the exact air quality and visibility conditions animals are likely to encounter in the wild. In addition, controlled studies are often limited to smaller species that are relatively easy to capture (e.g. insects, small mammals), and captive animals could exhibit behavioral changes during experiments that arise from confinement and should not be attributed to air pollution

exposure (Sterner 1993a, 1993b). In sum, the experience of smoke exposure for animals is likely to be vastly different between *in situ* and controlled studies, which makes it difficult to compare their findings.

Another limiting factor in connecting findings from existing research is the lack of robust air pollution measurements during field studies and experiments. Primary components of wildfire smoke include water vapor, CO₂, CO, PM, volatile organic compounds, nitrogen oxides, and hazardous air pollutants, such as acrolein, benzene, and formaldehyde (De Vos *et al* 2009). However, the exact biological (Kobziar and Thompson 2020) and chemical composition of smoke—and therefore its toxicity (Franzi *et al* 2011, Kim *et al* 2019)—is determined by fuel source (e.g. peat, oak, eucalyptus, etc), combustion conditions (e.g. flaming, smoldering) (Hargrove *et al* 2019, Kim *et al* 2019), weather, topography, and long-range transport (Jalava *et al* 2006). Without measuring the concentrations of reactive gases and aerosols animals are exposed to, it is impossible to construct dose-response relationships for specific health outcomes (Jaafar and Loh 2014, Sanderfoot and Holloway 2017). Furthermore, the composition of smoke could affect the visual and olfactory cues that elicit behavioral responses in wildlife. For example, Komarek observed that the behavior of Carolina grasshoppers (*Dissotera carolina*) varied depending on smoke conditions—when exposed to dense, white smoke, the grasshoppers ceased all activity, yet when exposed to black smoke, grasshoppers exhibited fire avoidance behaviors. To facilitate comparisons and meta-analyses of findings across studies, it is critical that future investigations move beyond qualitative descriptions of smoke and actually quantify exposure by measuring concentrations of specific gases and aerosols (Engstrom 2010, Sanderfoot and Holloway 2017).

More research is needed to identify which taxa and species are most threatened by wildfire smoke and determine how their vulnerability is influenced by physiology, behavior, and life-history strategy. It is well-established that birds are more sensitive to air pollution than other taxa (Brown *et al* 1997) and therefore more likely to be susceptible than other animals to direct health effects associated with smoke inhalation. Cetaceans, like birds, exchange most of the air in their lungs with each breath, which might put them at greater risk than other mammals of experiencing adverse health outcomes during smoke events (Venn-Watson *et al* 2013). Animal behavior and habitat use within and across species can also influence smoke exposure, thereby mediating risks. For example, bats that roost at higher heights are more protected from toxic gases during prescribed burns, and bats in torpor are less exposed to airborne toxins than they would be if they were active (Dickinson *et al* 2009). Furthermore, overlap between the timing of smoke pollution episodes and life-history events

likely contributes to species-specific vulnerability to wildfire smoke. For instance, birds attending to chicks (Cahill and Walker 2000) or bats caring for pups (Dickinson *et al* 2009) are likely more threatened by heat and smoke during fires than adults not tending to offspring, and fossorial reptiles are in greater danger when they come to the surface to feed or seek a mate (Jordaan *et al* 2020). Comparing species distributions with spatial and temporal trends in air pollution could help wildlife managers determine if smoke should be considered alongside other threats, such as habitat degradation, when developing wildlife conservation plans.

Animals have evolved alongside wildfires for thousands of years, but megafires driven by climate change are generating novel disturbance stressors, such as large-scale smoke events, that could exert selective pressure on wildlife (Nimmo *et al* 2021). The fire regimes species are adapted to are changing, and the traits that allow them to co-exist with fire and smoke may not be sufficient in the age of megafires (Nimmo *et al* 2021). For example, typical fire avoidance behaviors might not be sufficient to protect wildlife from injury or morbidity during more severe, fast-moving fires (Engstrom 2010, Nimmo *et al* 2021), and even animals that are not in the direct path of fires can still be exposed to dangerous levels of wildfire smoke (Erb *et al* 2018) (figure 1). As climate change intensifies smoke pollution, more animals are at risk of acute and chronic health outcomes associated with smoke inhalation, which could lower survival and reproductive success (figure 2). Over time, animals may adapt behavioral responses to detect hazardous air quality and limit their exposure to toxic gases and aerosols; however it is also possible that during large-scale smoke events, even well-adapted species may not find any refuge. Fire-adapted species might respond to visual and olfactory cues during large-scale smoke events even when fires are far away, which could have cascading impacts on wildlife communities. Pyrophilous species that rely on smoke as a cue to navigate toward burned areas may become disoriented during large-scale smoke events that occur hundreds of miles from fires, which could lead to reduced fitness and increased vulnerability to predation. Other species that use visual and olfactory cues from smoke to initiate fire-avoidance behaviors may do so at the expense of unnecessary energy expenditure when a fire is not an immediate threat (Dickinson *et al* 2009). Animals that exhibit escape behaviors when it is smoky could also be more vulnerable to predation; natural history observations suggest that raptors hunt insects and small mammals at the edge of fires (Braithwaite and Estbergs 1987) and may be attracted to smoke plumes as a signal of prey availability (Hovick *et al* 2017). Additionally, prey species often use scent cues to detect and avoid predators (Blumstein *et al* 2002); large-scale smoke events may mask olfactory signals and affect the ability of

prey to detect predators, further increasing their predation risk. Shifts in predator-prey interactions during smoke events could ultimately influence wildlife populations and community dynamics (figure 2).

Earlier and more prolonged wildfire seasons might pose novel threats to species that now encounter wildfire smoke during a critical stage of their life cycle, such as reproduction or migration. For example, the breeding phenology of songbirds may increasingly overlap with the smoke season, which could adversely impact songbirds in a reproductive state. Individuals that breed earlier, thereby avoiding reproductive activities during peak smoke season, could have higher reproductive success. This could lead to the evolution of traits, such as more synchronous or asynchronous breeding (Iwasa and Levin 1995), depending on the risks and benefits associated with the timing of breeding in relation to the threats posed by smoke events. Similarly, climate change is thought to be driving earlier breeding periods in many songbirds (Hällfors *et al* 2020), a trend that could be reinforced as smoke pollution worsens air quality during the summer months. Although wildfire smoke could function as an ecological disturbance that forces some species to adapt their life-history strategies, it is unlikely that all species threatened by smoke pollution will be able to adapt their phenology to match changing environmental conditions (Both and Visser 2001). More research is needed to assess how the frequency and timing of massive smoke events affects species adaptations to fire across different fire regimes.

We did not find any studies that explicitly linked wildfire smoke to demographic rates in wildlife populations (figure 2); however, emerging evidence suggests that the impact of large-scale smoke events on survival of wildlife species could be substantial. Yang *et al* (2021) found that air quality contributed to the spatial distribution of bird deaths in a mass avian mortality event in the Western United States in late summer 2020 (Yang *et al* 2021). This was not the first study to suggest that air pollution has negative demographic consequences for bird populations—a recent study also found that reductions in ozone (O_3) pollution in the United States prevented the loss of more than one billion birds (Liang *et al* 2020). Although O_3 is not a component of wildfire smoke, concentrations of O_3 can be higher on smoky days (Brey and Fischer 2016). Smoke inhalation has also been implicated in the death of insects (Tan *et al* 2018), reptiles (Jordaan *et al* 2020), and mammals (Singer *et al* 1989). Taken together, these findings emphasize the need to consider if and how wildfire smoke affects demographic rates in wildlife populations (figure 2).

Shifts in animal behavior during wildfire smoke events might ultimately affect the probability of observing wildlife, which has important implications for wildlife research and monitoring. For example,

animals that use smoke as cue to engage in fire-avoidance (e.g. burrowing) or energy-conserving behaviors (e.g. torpor) could be more difficult to observe during wildfire smoke events (Geiser *et al* 2018). Sanderfoot and Gardner (2021) investigated how wildfire smoke affected detection of 71 common bird species in Washington, United States and found that particle pollution during the wildfire season influenced the probability of observing 37% of study species—as $PM_{2.5}$ increased, 16 species were less likely to be observed and 10 species were more likely to be observed. These results suggest that species-specific behavioral responses to wildfire smoke ultimately influence researchers' ability to detect wildlife. Failing to account for how smoke affects observations of wildlife could bias inference about wildlife activity and population demographics (Sanderfoot and Gardner 2021).

To develop effective policy for wildlife conservation, we must rapidly expand our understanding of the effects of wildfire smoke on wildlife. We believe that ecologists and wildlife managers are well-positioned to tackle this challenge by leveraging pre-existing resources and infrastructure to address critical knowledge gaps. For example, camera traps, GPS tags, and acoustic recorders are often deployed in fire-prone areas as part of long-term monitoring projects, many of which are likely to overlap with the wildfire season (figure 6). Data collected by these instruments could be paired with long-term air quality monitoring data to investigate how wildfire smoke drives shifts in observations of wildlife (e.g. Lee *et al* 2017) or explore specific behavioral responses to smoke pollution, such as movement and vocalization. This equipment could also be deployed to monitor wildlife before, during, and after prescribed burns. Studies of marked individuals pre- and post-fire could also provide insight into the direct effects of fires on demographic rates (Engstrom 2010). In addition, retrospective analyses of health records of captive animals housed in outdoor enclosures at zoos and aquariums could be used to assess how sudden, extreme smoke events influence the health of wildlife across a wide variety of taxa (Venn-Watson *et al* 2013, Black *et al* 2017). Finally, data from existing large-scale databases, such as the North American Breeding Bird Survey, eBird, eMammal, iNaturalist, Movebank, and Map of Life, could be used in correlative studies to link smoke exposure to observations of wildlife.

To facilitate comparison of future studies, we recommend that researchers at minimum (1) identify the primary type of vegetation burned during prescribed burns or wildfires, or alternatively the substrate burned to generate smoke in controlled experiments and (2) incorporate measurements of $PM_{2.5}$ during exposure. $PM_{2.5}$ is often the focus of epidemiological investigations into the impacts of wildfire smoke on public health (McClure and Jaffe 2018,



Figure 6. Photo captures of wildlife in eastern Washington during the 2018 and 2020 wildfire seasons. (A) Smoke settles in the valley behind a male white-tailed deer (*Odocoileus virginianus*). (B) A group of mule deer (*Odocoileus hemionus*) navigate through thick smoke. (C) Smoke obscures the view over a ridge as a coyote (*Canis latrans*) carries its prey. (D) A wild turkey (*Meleagris gallopavo*) forages through haze. All photos were taken by camera traps deployed as part of the Washington Predator-Prey Project, a collaboration between the Washington Department of Fish & Wildlife and the University of Washington.

Aguilera *et al* 2021, Liu *et al* 2021a); as such, there is a multitude of resources available to characterize particle pollution during smoke events or controlled experiments, including data from ground-based air pollution sensors, air quality models, and satellite instruments (Diao *et al* 2019). Data from ground-based air quality monitors are considered the ‘gold standard’ for estimating exposure to air pollution (Diao *et al* 2019) and are often available to the public—for example, the U.S. Environmental Protection Agency provides data on air pollution across the United States, Puerto Rico, and the U.S. Virgin Islands on the web at www.epa.gov/outdoor-air-quality-data. If data from ground-based monitors is not available at relevant spatial and temporal scales, atmospheric scientists might rely on statistical interpolation or Land-Use Regression (LUR) models to build $PM_{2.5}$ exposure estimates (Jerrett *et al* 2005, Zou *et al* 2009). Alternatively, output from chemical transport models (CTMs) can be used in retrospective analyses and forecasting (Zou *et al* 2009). CTMs simulate air pollution by modeling transformation and transport of emissions (Jerrett *et al* 2005); examples of CTMs include the Community Model for Air Quality (CMAQ) and the Weather Research and Forecasting Model—Chemistry (WRF-Chem). Satellite data are also increasingly used to build $PM_{2.5}$ exposure estimates, although measurements from instruments on polar-orbiting satellites are only available once or

twice a day (West *et al* 2016, Diao *et al* 2019). Some of these approaches could be readily implemented with minimal training (Diao *et al* 2019), but others require technical knowledge. Regardless, careful consideration of the location and behavior of the target population is essential in determining exposure to specific pollutants. We recommend that ecologists studying the impacts of wildfire smoke on wildlife collaborate with atmospheric scientists to build $PM_{2.5}$ exposure estimates using the best available tools.

9. Conclusion

The frequency and severity of large-scale smoke events are increasing as climate change intensifies global wildfire activity (Westerling *et al* 2011, Abatzoglou and Williams 2016), posing new risks to wildlife (Nimmo *et al* 2021). Despite substantial research linking wildfire smoke to adverse health outcomes in humans, few studies have investigated the physiological and behavioral responses to wildfire smoke in animals (figure 4, table 1) (Erb *et al* 2018, Geiser *et al* 2018). However, research to date suggests that smoke inhalation contributes to negative acute and chronic health outcomes in a diversity of air-breathing animals, including mammals, birds, reptiles, and insects (figure 2, table 1). Detection of smoke triggers fire-avoidance and/or energy-conserving behaviors in some wildlife species, and

some species use smoke as a cue to navigate toward fires to take advantage of resources available in burned habitats (figure 2). However, even species that are adapted to fire-prone habitats are at risk of health outcomes linked to smoke inhalation, and it is unclear how they will cope with more extreme smoke pollution episodes. To inform the study and conservation of wildlife in a rapidly warming world, it is imperative that we expand our knowledge of wildfire smoke impacts on wildlife. Bridging the divide between the disciplines of ecology and atmospheric science will be essential in meeting this goal. We strongly recommend that scientists and managers build interdisciplinary partnerships and leverage existing data sets, infrastructure, and tools to quickly and efficiently address knowledge gaps and tackle research questions of global importance.

Data availability statement

No new data were created or analysed in this study.

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Author contributions

O V S: conceptualization, methodology, investigation, writing—original draft, writing—review & editing, visualization, project administration, funding acquisition; S B B, J L B, R L E, S J G, and K S: methodology, investigation, writing—review & editing, visualization; B G: methodology, investigation, writing—review & editing, visualization, funding acquisition.

Conflict of interest

We have no conflicts of interest to declare.

Appendix

We refined results from our initial keyword search in Web of Science to include only articles from categories deemed relevant to our literature review. We considered the top 100 Web of Science categories for each keyword search. Articles from the following categories were included from each keyword search.

fire* AND smoke*

Environmental Sciences, Public Environmental Occupational Health, Forestry, Plant Sciences, Ecology, Geosciences Multidisciplinary, Toxicology, Medicine General Internal, Multidisciplinary Sciences, Remote Sensing, Respiratory System, Environmental Studies, Oceanography, Water Resources, Biodiversity Conservation, Cardiac Cardiovascular Systems, Mathematics Interdisciplinary Applications, Biochemistry Molecular Biology, Computer Science Interdisciplinary Applications, Agriculture Multidisciplinary, Oncology, Biotechnology Applied Microbiology, Veterinary Sciences, Agronomy, Physiology, Biology, Infectious Diseases, Allergy, Genetics Heredity, Immunology

wildfire* AND smoke*

Environmental Sciences, Public Environmental Occupational Health, Forestry, Geosciences Multidisciplinary, Remote Sensing, Toxicology, Ecology, Multidisciplinary Sciences, Environmental Studies, Respiratory System, Plant Sciences, Water Resources, Oceanography, Medicine General Internal, Biodiversity Conservation, Biochemistry Molecular Biology, Geography, Agriculture Multidisciplinary, Allergy, Biology, Cardiac Cardiovascular Systems, Immunology, Marine Freshwater Biology, Agronomy, Cell Biology, Communication, Computer Science Interdisciplinary Applications, Development Studies, Genetics Heredity, Mathematics Interdisciplinary Applications, Physiology, Statistics Probability, Area Studies, Behavioral Sciences, Biotechnology Applied Microbiology, Developmental Biology, Entomology, Evolutionary Biology, Horticulture, Limnology, Mathematical Computational Biology

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