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Hazardous wildfire smoke events can alter dawn soundscapes in dry forests of central and eastern Washington, United States

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A B S T R A C T

As global wildfire activity increases, wildlife are facing greater exposure to hazardous smoke pollution – with unknown consequences for biodiversity. Research on the effects of smoke on wild animals is extremely limited, in part due to the inherent logistical challenges of observing how animals respond to smoke in real time. Passive acoustic monitoring may be a powerful tool to safely and effectively monitor biodiversity before, during, and after major smoke events. In this study, we used data collected from a large-scale network of bioacoustic recorders at 92 sites in central and eastern Washington state during August–September, 2019–2020 to investigate the effect of wildfire smoke on dawn soundscapes and, by extension, acoustically active wildlife. We used acoustic indices to document and characterize changes in soundscapes related to smoke exposure, including the Acoustic Complexity Index (ACI), Bioacoustic Index (BI), and Normalized Difference Soundscape Index (NDSI). Higher values of these indices likely indicate higher levels of biodiversity in our study area. We hypothesized that wildfire smoke would reduce bird vocalizations, leading to declines in ACI, BI, and NDSI at dawn, when birds are most active. We used linear and quantile regression models to test for an effect of daily exposure to fine particulate matter ($PM_{2.5}$), a marker of wildfire smoke, on the mean daily values and the upper 90th percentile of each index at dawn. We also conducted a before-during-after analysis of a particularly hazardous smoke event that impacted our study area on September 12–14, 2020. We did not observe linear effects of daily $PM_{2.5}$ on average or peak daily values of acoustic indices; however, we did observe a significant reduction in ACI and BI during the three-day smoke event in 2020 and in the two weeks following this air pollution episode. Our results indicate that, on average, ACI and BI were reduced by 2.7 % and 15.9 % during and 1.5 % and 11.0 % afterward, respectively. These findings add further evidence that wildfire smoke alters soundscapes, likely due to changes in the presence, abundance, or behavior of acoustically active animals. Furthermore, our study demonstrates that wildfire smoke may have delayed and/or cumulative effects on acoustically active wildlife. Our study highlights the potential for passive acoustic monitoring to

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document wildlife responses to smoke pollution and identify potentially relevant exposure periods.

1. Introduction

As climate change intensifies wildfire activity (Ellis et al., 2022; Mueller et al., 2020; Turco et al., 2023), fire emissions are contributing to rapidly deteriorating air quality in the western United States (Burke et al., 2023; O'Dell et al., 2019; Wilmot et al., 2021) and globally (Xu et al., 2023). Exposure to wildfire smoke is considered a growing risk to public health (Burke et al., 2021; Chen et al., 2021; Neumann et al., 2021; O'Dell et al., 2021) and animal welfare (Anderson et al., 2022; Black et al., 2017; Erb et al., 2018), yet consequences of smoke exposure for wildlife have rarely been considered in ecology and conservation (Sanderfoot et al., 2021). Smoke inhalation undoubtedly causes acute physiological stress in animals (Fitzgerald & Flood 2006, Wohlsein et al., 2016), which may contribute to changes in behavior (Erb et al., 2018; Overton et al., 2022). Both physiological and behavioral responses to smoke may impair overall fitness of wildlife populations. Therefore, smoke events could act as major ecological disturbances by altering demography (Dornelas, 2010) or distributions (Sheil, 2016), both in ecosystems prone to fire and in places only rarely impacted by smoke (Sanderfoot et al., 2021).

However, monitoring the effects of wildfire smoke on wildlife is inherently challenging. Fire weather forecasts are uncertain, and with humans responsible for 84 % of wildfire ignitions (Balch et al., 2017), it is difficult to anticipate where and when fires will occur. After a fire ignites, the extent and intensity of smoke is dependent on fuel source, fire characteristics (Hargrove et al., 2019; Kim et al., 2019), weather (Aguilera et al., 2020), and topography (Nakata et al., 2022), and may vary substantially day to day (Vargo, 2020). Fire emissions are also subject to long-distance transport, contributing to declines in air quality hundreds to thousands of kilometers away (Burke et al., 2021; Rogers et al., 2020). Furthermore, hazardous smoke poses direct risks to research teams; to protect the health and safety of field crews, it is often necessary to pause data collection when air pollution is dangerous. Given these limitations, existing knowledge of smoke impacts on the health and behavior of wildlife is, understandably, largely based on opportunistic and retrospective studies (Sanderfoot et al., 2021).

Passive acoustic monitoring could facilitate studies of biodiversity before, during, and after smoke events (Erb et al., 2023; Lee et al., 2017). Passive acoustic monitoring is increasingly used by ecologists to study and monitor wildlife (Browning et al., 2017), including birds (Kirschel et al., 2009; Medina and Francis, 2012), amphibians (Hsu et al., 2006; Xie et al., 2017), and insects (Gasc et al., 2018). Availability of low-cost bioacoustic recorders have made passive acoustic monitoring more affordable, allowing researchers to document soundscapes (i.e., acoustic environments – the sounds that occur at a specific place and time) at large spatial and temporal scales (Browning et al., 2017; Gibb et al., 2019). Soundscapes provide a rich source of information about ecological communities, including the presence, abundance, and behavior of wildlife (Ozga, 2017).

Wildfire smoke may alter soundscapes via changes in the health and behavior of acoustically active animals. For example, research suggests that wildfire smoke impacts vocalizations of apes: Bornean white-bearded gibbons (*Hylobates albibarbis*) sing less when it is smoky (Cheyne, 2008), and exposure to hazardous smoke reduces daily call rates of Bornean orangutans (*Pongo pygmaeus wurmbii*) and diminishes the vocal quality of their long calls (Erb et al., 2023). While no studies have specifically examined effects of smoke on avian vocalization, previous research has linked environmental pollution to smaller repertoires in passerines (Gorissen et al., 2005). Wildfire smoke has also been linked to changes in the detectability of birds (Sanderfoot and Gardner, 2021). Studies suggest that a wide range of taxa likely change their behavior during smoke events, possibly due to underlying health effects (Sanderfoot et al., 2021). If wildfire smoke exposure impacts the occurrence, frequency, duration, timing, or quality of animal vocalizations – or disrupts other acoustic signals of wildlife activity due to shifts in animal behavior – we would expect to observe subsequent changes in soundscapes.

Acoustic indices may be useful in efficiently documenting changes in soundscapes during or after periods of hazardous smoke, thereby providing insight into the effects of smoke on acoustically active wildlife. Ecologists have developed dozens of acoustic indices to summarize information contained within soundscapes; each considers specific features of audio recordings that may relate to characteristics of an ecological community (Alcocer et al., 2022; Farina, 2018). Four commonly used acoustic indices are the Acoustic Complexity Index (Pieretti et al., 2011), Bioacoustic Index (Boelman et al., 2007), Acoustic Diversity Index (Villanueva-Rivera et al., 2011), and Normalized Difference Soundscape Index (Kasten et al., 2012). The Acoustic Complexity Index (ACI) is based on differences in the intensity of sound within frequency bands across very short time steps and, by design, is relatively robust to continuous background noise (Alcocer et al., 2022; Bradfer-Lawrence et al., 2019; Pieretti et al., 2011). ACI was originally envisioned as an assessment of bird singing activity (Pieretti et al., 2011) and has been linked to avian diversity in many ecosystems (e.g., Raynor et al., 2017, Beason et al., 2023), including mountainous forests of the western United States (McGrann et al., 2022). The Bioacoustic Index is calculated as the area under the "bioacoustic spectra" – a curve that depicts how sound intensity (in decibels) varies by frequency (in hertz) – and intentionally excludes low-frequency sounds typical of anthropogenic activity (Boelman et al., 2007). Higher values of BI arise from larger differences in the volume of sound between the loudest and quietest frequencies (Bradfer-Lawrence et al., 2019). BI was designed to monitor the relative abundance of birds (Boelman et al., 2007) and has been correlated with avian species richness in a wide range of habitats, including temperate forests (e.g., Budka et al., 2023; Eldridge et al., 2018). The Acoustic Diversity Index (ADI) considers how sound is distributed across frequency bands and is analogous to the Shannon diversity index, a metric used to evaluate both species richness and species evenness. The Normalized Difference Soundscape Index is the ratio of biophony (i.e., the sounds produced by non-human animals) to anthrophony (i.e., the sounds produced by humans and their technology). Acoustic indices such as ACI, BI, ADI, and NDSI have been used to monitor wildlife and investigate effects of disturbance on ecological communities (Doser et al., 2020; Linke and Deretic, 2020), including fires (Duarte et al., 2021; Meyer et al., 2022) and smoke events (Lee et al., 2017).

Recent research suggests that acoustic indices are not always reliable proxies of biodiversity across ecosystems (Alcocer et al., 2022; Llusia, (2024); Sethi et al., (2023). For example, ACI has been shown to correspond well with species richness in North American grasslands (Raynor et al., 2017) and forests (McGrann et al., 2022), but not in subtropical forests in China (Mammides et al., 2017). The performance of acoustic indices in biodiversity assessments may also vary daily or seasonally (Budka et al., 2023). Furthermore, acoustic indices can be difficult to interpret. For instance, higher values of ADI indicate an even distribution of sound, which could mean that a soundscape is rich in biophony of many frequencies, but could also suggest that a soundscape is completely silent (Bradfer-Lawrence et al., 2019). However, a recent meta-analysis did find a moderate, positive correlation between acoustic indices and biodiversity, with ACI and NDSI performing particularly well (Alcocer et al., 2022). Acoustic indices may also be valuable in monitoring biodiversity in places where a relationship between specific acoustic indices and diversity metrics has already been established. For example, McGrann et al. (2022) found that ACI is moderately correlated with species richness of birds (determined from point counts and interpreted recordings) along the Pacific Crest Trail in California, a recreational hiking trail that crisscrosses several types of habitats. They concluded that ACI would be a “useful, albeit coarse, surrogate of alpha diversity [of birds] across large regions” in temperate climates.

Although recent critiques of acoustic indices urge caution in their use as universal indicators of biodiversity, these metrics can help identify the occurrence, extent, and duration of smoke impacts on soundscapes and, by extension, acoustically active wildlife. For example, Lee et al. (2017) used acoustic indices to document changes in local biodiversity on a wildlife overpass in Singapore during an extreme smoke event in 2015. They found that ACI, BI, ADI, and NDSI all decreased as air pollution intensified, which suggests that smoke impacted the presence, abundance, and/or behavior of animals, most likely birds and insects (Lee et al., 2017). Furthermore, Lee et al. found that these declines persisted for at least four months, providing the first evidence of long-lasting effects of smoke

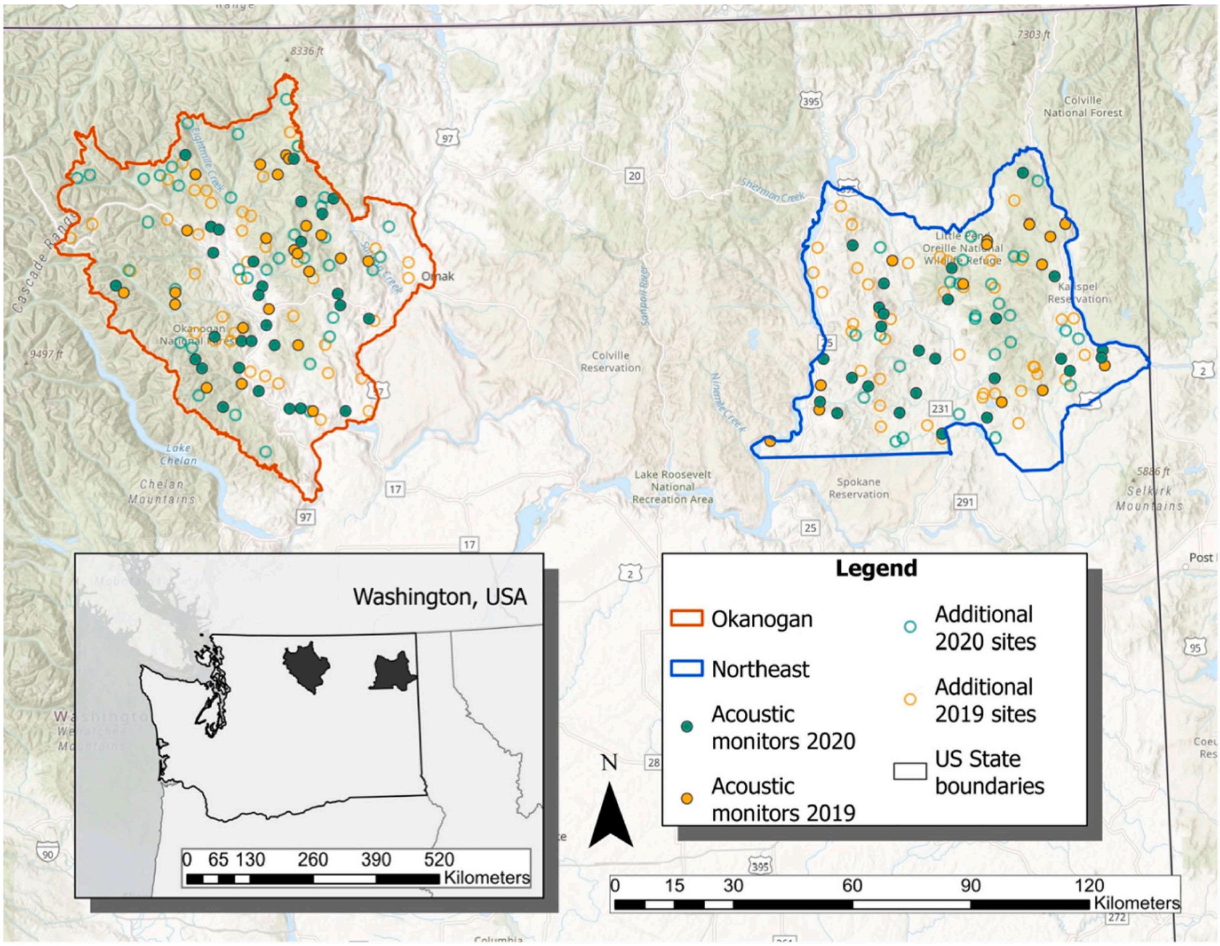

Fig. 1. Map of study areas and monitoring sites. We collected bioacoustic data during July 1–October 30, 2019–2020 in two study areas in central and eastern Washington: the Okanogan (outlined in red) and the Northeast (outlined in blue). Both study areas represent dry, coniferous forests prone to frequent, low-intensity fire and routinely experience smoke impacts. Circles mark the locations of all 240 monitoring sites included our passive acoustic monitoring network and are color coded by year (orange – 2019; green – 2020). Our analysis included observations from a subset of 92 sites, noted as shaded circles.

exposure on wildlife acoustic activity. While Lee et al. could not isolate the mechanisms driving the declines in biophony, their seminal work provided proof of concept that acoustic indices can provide an initial snapshot of the effects of wildfire smoke on acoustically active fauna and help determine relevant exposure periods. However, more research is needed to validate this approach and consider how wildfire smoke might alter soundscapes across larger monitoring networks and in different biomes.

In this study, we used data collected from a large-scale array of bioacoustic recorders in central and eastern Washington state in 2019 and 2020 to investigate the effect of wildfire smoke on soundscapes in the dry, coniferous forests of the Pacific Northwest. We intentionally deployed our passive acoustic monitoring network in anticipation of smoke impacts in our study area; our work represents one of the first efforts to collect data specifically for the purpose of documenting the effects of smoke on wildlife activity. We hypothesized that wildfire smoke would reduce bird vocalizations, given anecdotal reports from birders (Lacitis, 2020; Petersen, 2020) and findings from Lee et al., (2017). Thus, we expected that ACI, BI, and NDSI at dawn, when birds are most active, would decline as smoke intensified. To test if wildfire smoke has a linear effect on either the average or peak levels of wildlife acoustic activity at dawn, we used linear mixed models and quantile regression. To test for non-linear effects of wildfire smoke on wildlife acoustic activity at dawn, we conducted a before-during-after analysis of a particularly hazardous smoke event that impacted our study area in September 2020. Our study is one of a mere few to link wildfire smoke to wildlife activity at a large spatial scale (but see Sanderfoot and Gardner, 2021, Ayars et al., 2023), and the first to use acoustic data collected from a large passive acoustic monitoring network to investigate how exposure to wildfire smoke impacts signals from acoustically active wildlife.

2. Methods

2.1. Data collection

2.1.1. Study areas

We collected acoustic data in two study areas in central and eastern Washington, USA, during the 2019 and 2020 fire seasons (July 1–October 30, when peak wildfire activity is expected in the Pacific Northwest): the Northeast (4535 km^2 centered on -117.719° longitude, 48.283° latitude) and the Okanogan (5300 km^2, centered on -120.120° longitude, 48.430° latitude) (Fig. 1). Both study areas represented predominately dry, coniferous forests with frequent, low-intensity fire regimes (U.S.D.A. Forest Service, 2019). The Northeast study area was characterized by mixed conifer forests (elevation ranged 378–2079 m; Williams et al., 1995), whereas the Okanogan was characterized by mixed conifer forests at higher elevations and open grassland and shrub-steppe habitats at lower elevations (elevation ranged 225–2790 m; Williams and Lillybridge, 1983). Both study areas were mountainous, although the terrain

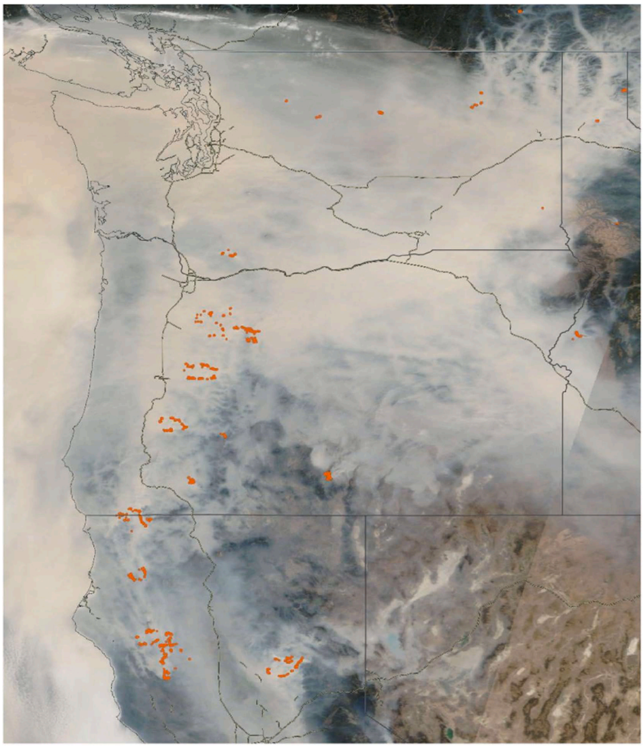

Fig. 2. Satellite image of the Pacific Northwest on September 13, 2020. Thick wildfire smoke blanketed the region, including our study areas in central and eastern Washington. Orange dots mark the locations of fires and other thermal anomalies detected by satellite instruments. *Source:* NASA Worldview.

in the Okanogan was more variable with steeper slopes and deeper valleys compared to the Northeast (Williams et al., 1995, Williams and Lillybridge, 1983). Both regions encompassed numerous towns interspersed by agricultural or undeveloped areas (Commission for Environmental Cooperation, 2023). For a more detailed description of our study areas, please see Bassing et al. (2023).

Several large wildfires burned near our study areas in 2019 and 2020, notably the Cold Spring Fire (76,859 ha) and the Pearl Hill Fire (90,540 ha) which occurred just east of the Okanogan in 2020. Our study area was also impacted by smoke from wildfires that burned elsewhere in Washington state as well as Oregon and California during the unprecedented 2020 wildfire season (Liu et al., 2021) (Fig. 2).

2.1.2. Bioacoustic sampling

We deployed low-cost bioacoustic recorders (AudioMoths, v. 1.1.0, Open Acoustic Devices) in both study areas in 2019 and 2020. Recorders were co-located with camera traps within an existing monitoring network established as part of the Washington Predator-Prey Project, a joint partnership between the Washington Department of Fish & Wildlife and the University of Washington. We sampled 120 monitoring sites (55 in the Northeast and 65 in the Okanogan) in each year (2019 and 2020) that were chosen using a random sampling design stratified by elevation, as described by Bassing et al. (2023). Bioacoustic recorders were deployed near to camera trap locations (within 5–10 m); camera traps were not baited and used infrared flash to minimize disturbance to wildlife. We focused our analysis on soundscapes at dawn, when birds are most active. To capture the dawn chorus, AudioMoths were set to record continuously for several hours each morning, beginning before sunrise. We programmed our recorders on several different schedules to account for shifts in local sunrise time. AudioMoths were configured to record at a sampling rate of 32 KHz with medium gain, which ensured that we fully captured all animal vocalizations <16 KHz (Browning et al., 2017). This includes most wildlife species that emit sounds in the frequency range audible to human ears (20–20,000 Hz).

AudioMoths collected data until they ran out of battery (lasting approximately one month). To extend sampling, we replaced units at monitoring sites throughout the summer and fall as our field crew's time and resources allowed. Our goal was to maintain a passive acoustic monitoring network that would collect daily recordings of the dawn chorus at each site throughout the fire season; however, due to resource limitations, equipment failures, and the occasional removal of our recorders by suspected wildlife, there are gaps in our sampling. To limit any impact our field crew may have had on soundscapes included in our analysis, we excluded recordings collected on days when we conducted fieldwork.

Although we collected bioacoustic data in July–October, we limited our analysis to the months of August and September. We expected wildlife acoustic activity would be more stable during this limited time frame and less likely to be impacted by seasonal changes in bird and insect activity. Further, these are the only months for which smoke impacted air quality in our study areas in 2019 and 2020.

2.1.3. Acoustic indices

We used the *soundecology* package (Villanueva-Rivera and Pijanowski, 2018) in R (R Core Team, 2021) to calculate ACI, BI, ADI, and NDSI for each 10-minute subsample in all morning recordings collected by our network of AudioMoths (Bradfer-Lawrence et al., 2019),. For each day in our study period (August 1–September 30, 2019–2020), we used the *suncalc* package (Thieuremel and Elmarhraoui 2022) to determine the exact sunrise time at each monitoring site and defined the dawn chorus as a window that started one hour before and ended one hour after sunrise. Then, we computed the daily average ACI, BI, ADI, and NDSI for each day at each site, using only subsamples that fell within the dawn chorus. We limited our analysis to observations with a minimum of six, 10-minute subsamples (i.e., a minimum of one hour of acoustic data) during the two-hour dawn chorus.

2.1.4. Environmental covariates

Some wildlife species adjust their behavior in response to changes in weather (e.g., wind or rain), which could impact soundscapes. To better isolate the effects of wildfire smoke on soundscapes, we focused our analysis on otherwise fair weather days by excluding observations from rainy and/or windy days. Filtering out these observations also helped to limit the influence of geophonic noise that can affect acoustic indices (Müller et al., 2022; Sánchez-Giraldo et al., 2020). First, we used data from the North American Regional Reanalysis (NARR) to determine the accumulated precipitation and average wind speed for each day at each monitoring site. NARR is run by the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Prediction (NCEP); data were provided by the NOAA Physical Sciences Laboratory (PSL) in Boulder, Colorado, USA from their website at https://psl.noaa.gov/data/gridded/data.narr.html. Next, we excluded observations from days with more than one millimeter of precipitation and above 12.9 kilometers per hour wind speeds, the lower threshold for a "gentle breeze" according to the Beaufort Wind Scale (National Weather Service, 2023). We acknowledge that use of modeled variables to retrospectively consider weather conditions does not guarantee that we did not include observations from rainy and/or windy days, or that soundscapes included in our analysis were free of geophonic noise; however, in lieu of site-specific, ground-based measurements, this approach allowed us to limit the overall impact of changing weather conditions on our inference.

We considered fine particulate matter ($PM_{2.5}$; all suspended solid and liquid particles <2.5 microns in aerodynamic diameter) to be a reliable marker of wildfire smoke at our monitoring sites. We used estimates of $PM_{2.5}$ from AIRPACT (Air Indicator Report for Public Awareness and Community Tracking), a regional air quality model run by the Laboratory for Atmospheric Research at Washington State University. Although ground-based measurements of air pollution are considered the "gold standard" for measuring air quality, atmospheric models are a valuable tool for exposure assessment in remote areas far from local monitors, such as our study areas (Diao et al., 2019). AIRPACT is an integrated meteorological-emissions model that predicts the daily mean concentration of $PM_{2.5}$ at a 4-kilometer resolution based on the transformation and transport of emissions from point sources, including wildfires (O'Neill et al., 2023).

We used the AIRPACT Kalman Filter bias-corrected 24-hr average $PM_{2.5}$ developed by June et al. (2021). In this product, a Kalman Filter is used to estimate the bias of the model, which is then removed from the AIRPACT $PM_{2.5}$, resulting in post-processed $PM_{2.5}$ estimates that better represent observations of $PM_{2.5}$ than the raw AIRPACT $PM_{2.5}$ forecast (June et al., 2021). Estimates of total $PM_{2.5}$ from AIRPACT are not specific to smoke; however, wildfires are by far the largest source of $PM_{2.5}$ in our study areas during the summer and fall, and spikes in $PM_{2.5}$ during the fire season are indicative of smoke events. More details on the AIRPACT Kalman Filter bias-correction are provided in June et al., 2021. Daily mean $PM_{2.5}$ values were extracted from the AIRPACT Kalman Filter bias-corrected product for each day at each site using the model's 4-kilometer grid.

2.2. Statistical analysis

2.2.1. Final data set

We limited our data set to sites with a minimum of 14 valid daily observations (i.e., those based on a minimum of six 10-minute subsamples during the dawn chorus, defined as one hour before to one hour after sunrise) on fair weather days (i.e., for which daily accumulated precipitation did not exceed 1 millimeter and daily average wind speeds were not faster than a gentle breeze). Our final data set included 1790 observations of daily acoustic activity from 92 monitoring sites across two regions of Washington state (Fig. 1). The number of 10-minute subsamples used to calculate daily mean acoustic indices ranged from 6 to 11, with a median value of 10; in total, our analysis includes data from 2777 hours of audio recordings.

Daily mean concentrations of $PM_{2.5}$ associated with these observations of soundscapes ranged from 0.0 to 410.2 μg/m^3 (mean = 20.7 μg/m^3). The National Ambient Air Quality Standard for $PM_{2.5}$ is just 35 μg/m^3; $PM_{2.5}$ concentrations above 55.5 μg/m^3 are

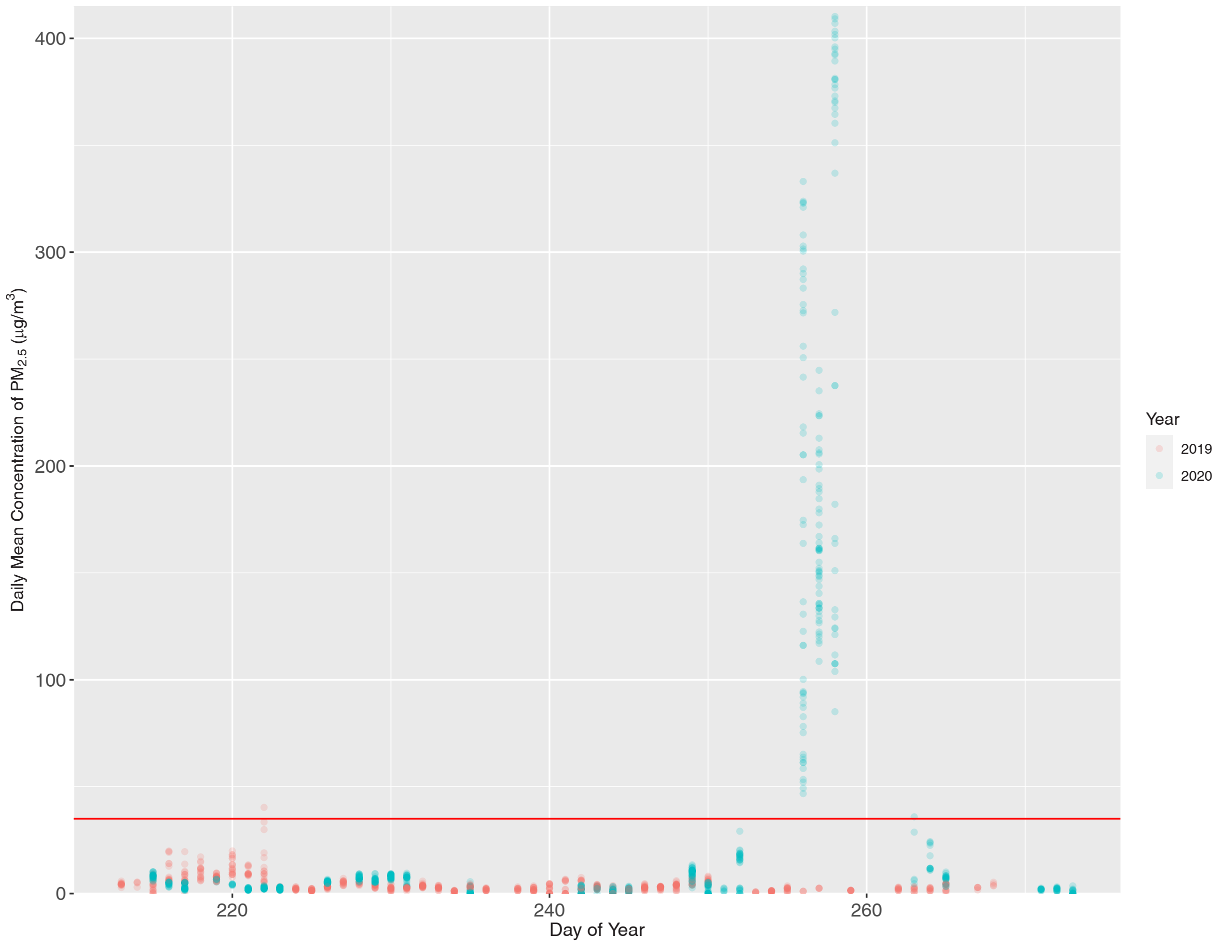

Fig. 3. Our analysis includes 1790 observations of dawn soundscapes on fair weather days in August–September, 2019–2020 at 92 monitoring sites in two study areas in central and eastern Washington state (Fig. 1). This plot shows the daily mean concentration of $PM_{2.5}$, a marker of wildfire smoke, associated with each observation. Observations from 2019 are shown in orange, and observations from 2020 are shown in teal. The horizontal red line marks 35.5 μg/m^3, the threshold above which air quality is considered unhealthy for sensitive groups by the U.S. Environmental Protection Agency. While our study areas generally experienced good air quality in 2019, the unprecedented 2020 fire season contributed to a particularly hazardous smoke pollution episode that impacted our passive acoustic monitoring network on September 12–14.

considered unhealthy by the U.S. Environmental Protection Agency, and concentrations above 250.5 μg/m^3 are considered hazardous. Forty-three observations of dawn soundscapes included in our analysis occurred during conditions with $PM_{2.5}$ exceeding 250.5 μg/m^3. All of these observations occurred during a particularly extreme smoke event that impacted our study area in September 2020 (Fig. 2, Fig. 3).

2.2.2. *Regression models*

We used linear mixed regression models to explore acute, immediate effects of wildfire smoke on dawn soundscapes. First, we evaluated the relationship between the daily mean concentration of $PM_{2.5}$ and daily mean ACI, BI, ADI, and NDSI. Second, we estimated the effect of $PM_{2.5}$ on the upper 90th percentile of the daily acoustic indices. This approach allowed us to consider how wildfire smoke impacts both average and peak levels of wildlife acoustic activity.

To examine the effect of smoke on average levels of wildlife acoustic activity, we built linear mixed models using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2024). Although these acoustic indices are not truly normally distributed variables – ACI, ADI, and BI are nonnegative and NDSI varies between −1 and +1 – it is common practice to use a normal distribution to model these indices, on the condition that the data either roughly follow a normal distribution (Khanaposhtani et al., 2019; Mammides et al., 2017; Myers et al., 2019; Pekin et al., 2012) or have been transformed to better meet this assumption (Gasc et al., 2018; Myers et al., 2019; Raynor et al., 2017). After inspecting model residuals, we decided to log transform ACI, BI, and ADI. For NDSI, we used the following transformation, as described by Doser et al. (2020):

$$\log\left(\frac{(NDSI+1)}{(1-NDSI)}\right)$$

We modeled the log of the daily mean of each index for day *i* and site *j* as:

$$log.INDEX_{i,j} = \alpha_{0,j} + \alpha_1 * \log\left(PM_{2.5_{i,j}} + 0.001\right) + \alpha_2 * day\ of\ year_{i,j} + \alpha_3 * day\ of\ year_{i,j}{}^2$$

We included a fixed effect of log daily mean concentration of $PM_{2.5}$ to directly evaluate the relationship between smoke and acoustic indices; we used a log transformation to minimize the influence of more extreme $PM_{2.5}$ values. We also included linear and quadratic effects of day of year to account for potentially non-linear seasonal changes in wildlife behavior (e.g., migration) that may impact wildlife acoustic activity. We allowed the intercept α_0 to vary by site *j* as a random effect to account for differences in habitat across monitoring sites. All continuous covariates were standardized to a mean of 0 and standard deviation of 1 prior to analysis. To assess model fit, we used the *performance* package (Lüdecke et al., 2019) to calculate marginal and conditional R^2 values. We used 95 % confidence intervals to evaluate effects of $PM_{2.5}$ on acoustic indices.

To examine the effect of smoke on peak levels of wildlife acoustic activity, we built quantile models using the *lqmm* package (Geraci, 2014) in R (R Core Team, 2023). As in our linear mixed models of the mean, response variables were log transformed. Predictors included fixed effects of $PM_{2.5}$ (logged), day of year, and day of year squared, with the intercept varying by site as a random effect. All continuous covariates were standardized to a mean of 0 and standard deviation of 1 prior to analysis. Due to high variance in parameter estimates, we conducted additional bootstrap resampling (20,000 iterations) and based our inference on output from this procedure. We used 95 % confidence intervals, determined from the quantiles of the bootstrapped output, to evaluate effects of $PM_{2.5}$ on response variables.

Finally, we conducted a before-during-after analysis to explore delayed and cumulative effects of wildfire smoke on dawn soundscapes, focusing on a particularly hazardous smoke event that impacted our study area on September 12–14, 2020 (Fig. 2, Fig. 3). We limited this analysis to the subset of 17 sites for which we had at least three valid observations on fair weather days before (August 1–September 11, 2020), during (September 12–14, 2020), and after (September 15–September 30, 2020). We built linear mixed models using the *lme4* package (Bates et al., 2015) in R (R Core Team, 2024) to model the log of the daily mean of each index for day *i* and site *j* as:

$$log.INDEX_{i,j} = \alpha_{0,j} + \alpha_1 * Period_{i,j}$$

where period is a factor variable that indicated if an observation occurred before, during, or after the smoke event. As with our regression models above, we allowed the intercept α_0 to vary by site *j* as a random effect to account for differences in habitat across monitoring sites. We also conducted an identical before-during-after analysis for the same dates in 2019, when smoke did not impact our monitoring network. This analysis was limited to the subset of 7 sites for which we had at least two valid observations on fair weather days before (August 1–September 11, 2019), during (September 12–14, 2019), and after (September 15–September 30, 2019). We used 95 % confidence intervals to evaluate effects of exposure periods on acoustic indices.

To evaluate compliance with assumptions of linear models, we carefully examined plots of fitted versus residual values. Diagnostic plots showed evidence of non-constant variance in models of ADI, even after using a log transformation; as such, we do not report or further consider results of these models in our study.

3. Results

Contrary to our expectations, we did not find a statistically significant effect of $PM_{2.5}$ on average (i.e., mean) daily values of ACI or BI (Fig. 4, Table 1), nor did we find a statistically significant effect of $PM_{2.5}$ on peak (i.e, upper 90th percentile) daily values of ACI, BI, or NDSI (Fig. 4, Table 2). We did observe a small, positive effect of $PM_{2.5}$ on average daily values of NDSI (Fig. 4, Table 2); however, R^2

values suggest that fixed effects only explained 0.3 % of the variation in mean NDSI, suggesting that the impact of $PM_{2.5}$ on this measure of soundscapes was minor.

However, we found that ACI and BI were significantly reduced during and after the 2020 smoke event (Fig. 5, Table 3). We did not find any effects of the periods “during” and “after” in our 2019 counterfactual example (Table 3).

4. Discussion

In our study, we leveraged a large passive acoustic monitoring network to evaluate the effect of wildfire smoke on dawn soundscapes captured during the 2019 and 2020 fire seasons in dry, coniferous forests of central and eastern Washington state. We found evidence that dawn soundscapes changed during and after a hazardous smoke event in 2020. However, we did not observe a linear relationship between daily mean concentrations of $PM_{2.5}$, a reliable marker of smoke pollution, and daily values of acoustic indices calculated from recordings of the dawn chorus. Together, our results suggest that smoke may have delayed or cumulative effects on biophony in dawn soundscapes on otherwise fair weather days. Although the effect sizes we report are small, our results nevertheless suggest that soundscapes are different during and after wildfire smoke events and provide further evidence that smoke may act as a disturbance in ecological communities (Erb et al., 2023, 2018; Lee et al., 2017; Overton et al., 2022) by altering the presence, abundance, and/or behavior of acoustically active animals (Cheyne, 2008; Erb et al., 2023; Lee et al., 2017; Sanderfoot et al., 2021).

We expected to observe a negative relationship between daily mean concentrations of $PM_{2.5}$ and daily values of ACI, BI, and NDSI of dawn soundscapes. We focus our analysis on the dawn chorus because birds are most active just before and after sunrise, and we were primarily interested in considering how smoke may impact avian acoustic activity. ACI has already been established as a coarse

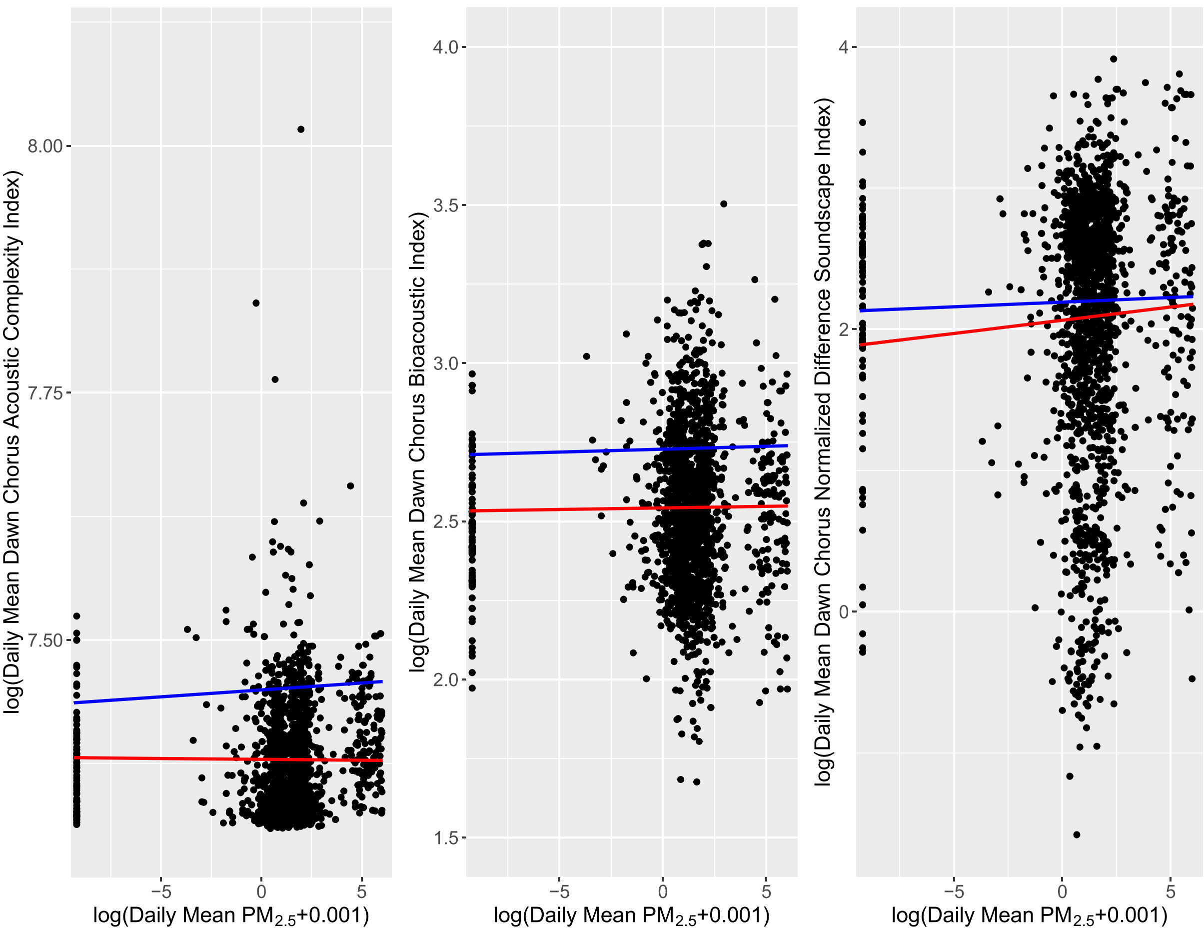

Fig. 4. Scatterplots illustrating the relationship between acoustic activity during the dawn chorus and daily mean concentration of $PM_{2.5}$, a marker of wildfire smoke. We considered three measures of acoustic activity: A) the Acoustic Complexity Index (ACI), B) the Bioacoustic Index (BI), and C) the Normalized Difference Soundscape Index (NDSI). Higher values of ACI and BI may suggest higher levels of bird activity in our study area, whereas higher values of NDSI indicate a higher ratio of biophonic to anthrophonic sound. Red lines show the predicted mean value of each index and blue lines show the predicted 90th percentile of each index at daily mean concentrations of $PM_{2.5}$ ranging from 0 to 450 μg/m^3, assuming average levels of all other predictors.

Table 1
Summary of results of the linear mixed models used to evaluate the effect of wildfire smoke on average levels of wildlife acoustic activity in dry, coniferous forests of central and eastern Washington, USA in August–September, 2019–2020. We used three acoustic indices to characterize changes in soundscapes, including the Acoustic Complexity Index (ACI), Bioacoustic Index (BI), and Normalized Difference Soundscape Index (NDSI). Columns 1–3 show parameter estimates and 95 % confidence intervals for fixed effects of day of year, day of year squared, and log of the daily mean concentration of $PM_{2.5}$. Columns 4–5 show conditional and marginal R^2 values. Acoustic indices were log transformed prior to analysis as described in Section 2.2.2. Statistically significant fixed effects ($p < 0.05$) are **bolded.**

Acoustic Index	Day of Year	Day of Year^2	$\log(PM_{2.5_{ij}})$	Conditional R^2	Marginal R^2
ACI	**0.004 (0.002, 0.006)**	**-0.004 (-0.005, −0.002)**	0.000 (-0.002, 0.001)	0.610	0.007
BI	0.004 (-0.006, 0.014)	**-0.011 (-0.020, −0.002)**	0.003 (-0.006, 0.011)	0.449	0.002
NDSI	-0.003 (-0.037, 0.031)	-0.018 (-0.049, 0.013)	**0.049 (0.019, 0.079)**	**0**.546	0.003

Table 2
Summary of results of the quantile regression models used to evaluate the effect of wildfire smoke on peak (i.e., upper 90th percentile) levels of wildlife acoustic activity in dry, coniferous forests of central and eastern Washington, USA in August–September, 2019–2020. We used three acoustic indices to characterize changes in soundscapes, including the Acoustic Complexity Index (ACI), Bioacoustic Index (BI), and Normalized Difference Soundscape Index (NDSI). Columns 1–3 show parameter estimates and 95 % confidence intervals for fixed effects of day of year, day of year squared, and log of the daily mean concentration of $PM_{2.5}$. Acoustic indices were log transformed prior to analysis as described in Section 2.2.2. We did not find any statistically significant fixed effects ($p < 0.05$) in our quantile regression.

Acoustic Index	Day of Year	Day of Year^2	$\log(PM_{2.5_{ij}})$
ACI	0.010 (-0.001, 0.021)	-0.006 (-0.014, 0.002)	0.004 (-0.003, 0.010)
BI	-0.017 (-0.059, 0.034)	0.006 (-0.021, 0.036)	0.005 (-0.012, 0.022)
NDSI	0.028 (-0.032, 0.093)	-0.003 (-0.044, 0.036)	0.017 (-0.014, 0.043)

indicator of alpha diversity of avifauna in the ecoregion that encompasses our study areas (McGrann et al., 2022), and BI has been found to be a reliable marker of avian diversity in temperate forests (e.g., Budka et al., 2023; Eldridge et al., 2018). We considered both the effect of daily $PM_{2.5}$ on average (i.e., mean) and peak (i.e., the upper 90th percentile) daily values of ACI, BI, and NDSI. Contrary to our expectations, we did not observe a statistically significant effect of $PM_{2.5}$ on average or peak ACI or BI (Fig. 4, Table 1, Table 2). In addition, we observed a small, statistically significant, positive effect of $PM_{2.5}$ on average NDSI (Fig. 4, Table 1), suggesting that the proportion of biophony in dawn soundscapes on otherwise fair weather days in our study areas may actually increase very slightly as smoke intensifies. We suspect this may be due to changes in human behavior on smoky days, with fewer people engaging in outdoor recreation (e.g., hiking, birding). Although our monitoring sites were located in highly rural areas, most were established near trails (i. e., hiking paths) and roads (e.g., U.S. Forest Service roads). Analyses of data collected from co-located camera traps suggested that some of our monitoring sites were used by outdoor recreationists. If people were less likely to spend time outdoors when air quality was poor, we could have observed a decrease in anthrophonic noise and a subsequent increase in NDSI. However, the effect of $PM_{2.5}$ on mean daily values of NDSI was small, and fixed effects explained very little variance in this metric. As such, any impact of smoke on the proportion of dawn soundscapes dominated by biophony was minimal. Indeed, the mean value of NDSI across all observations included in our analysis was 0.71, indicating that soundscapes typically included more biophony than anthrophony, regardless of atmospheric conditions.

However, we did find that ACI and BI were significantly reduced during and after a hazardous smoke event that impacted our study areas on September 12–14, 2020 (Fig. 5, Table 3). Our results indicate that, on average, ACI and BI were reduced by 2.7 % and 15.9 % during and 1.5 % and 11.0 % afterward, respectively. Our counterfactual before-during-after analysis of the same exposure periods in 2019 showed no statistically significant differences in daily values of acoustic indices (Table 3). Our findings suggest that hazardous wildfire smoke decreased biophony in dawn soundscapes in the dry, coniferous forests of central and eastern Washington, possibly due to reduced acoustic activity of birds, as ACI has been found to be a reasonable proxy for alpha diversity of avifauna in similar habitats (McGrann et al., 2022). This could substantiate claims from birders that skies are quieter on smoky days (Lacitis, 2020; Petersen, 2020). However, without ground truthing the relationship between these indices and the presence and/or abundance of birds or other acoustically active taxa, we cannot be sure that the shifts in soundscapes we report here are due to changes in bird activity. The results of our before-during-after analysis generally support findings of Lee et al., (2017), the only other study to examine impacts of wildfire smoke on acoustic indices. Lee et al. (2017) found significant reductions in ACI, BI, and NDSI during and after a hazardous smoke event in southeast Asia. While we did observe reductions in ACI and BI during and after the 2020 smoke event in Washington state, we did not observe a relationship between NDSI and exposure periods. This discrepancy could arise from differences in baseline anthropogenic activity in our study areas – whereas Lee et al. observed soundscapes on a wildlife corridor near a busy overpass, we observed soundscapes in a largely rural area. Furthermore, the smoke impacts documented by Lee et al. occurred during one of the worst air pollution episodes on record (Wooster et al., 2018). Although some of our monitoring sites were exposed to hazardous levels of $PM_{2.5}$, smoke exposure in our study areas was not as extreme as that observed by Lee et al. (2017). The intensity of smoke examined in these two studies may have been sufficiently different as to constitute unique stressors, with different impacts on biophony.

Our study demonstrates that wildfire smoke may have delayed and/or cumulative effects on acoustically active wildlife. Whereas we did not observe linear effects of daily $PM_{2.5}$ on average or peak daily values of acoustic indices, we did observe a significant

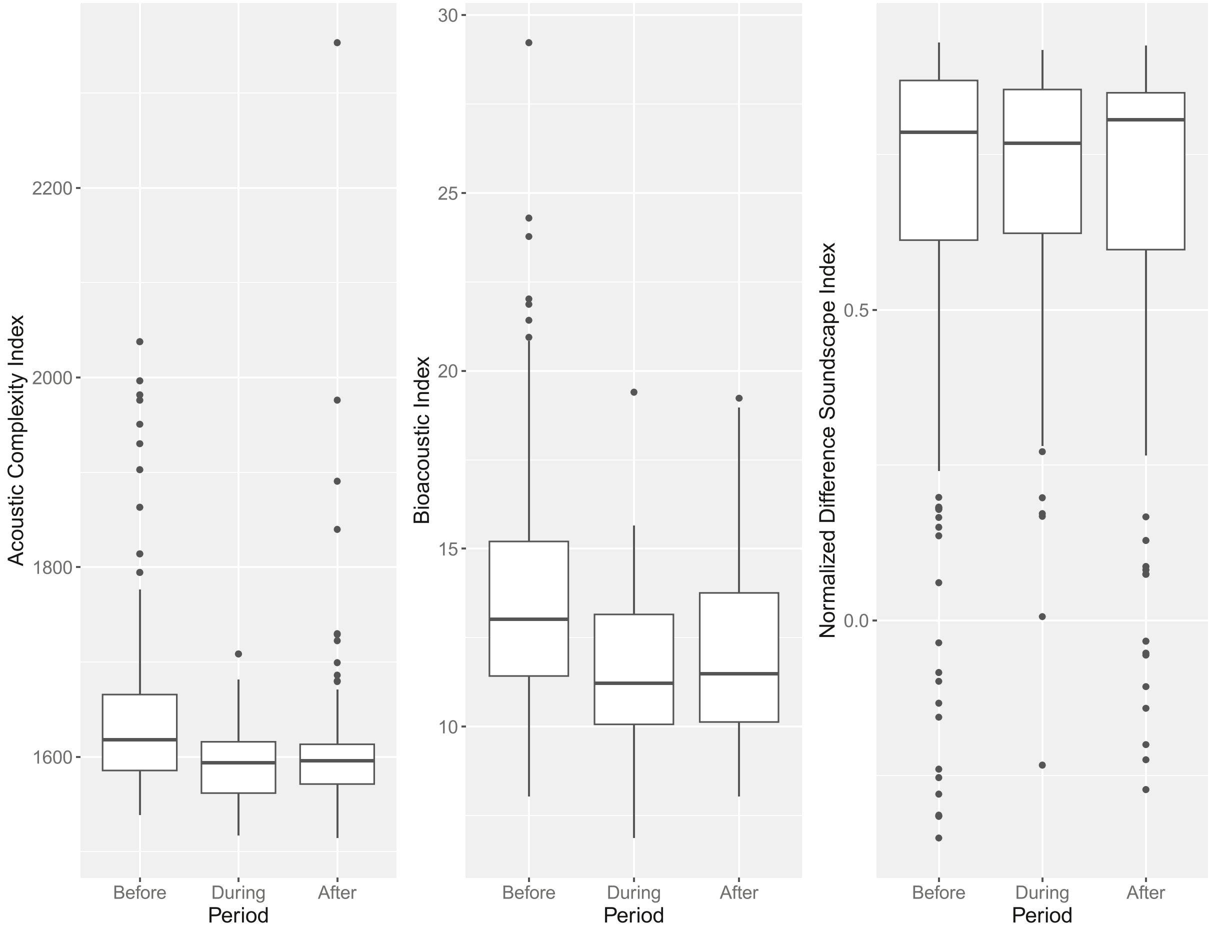

Fig. 5. Boxplots showing the distribution of daily values of the Acoustic Complexity Index, Bioacoustic Index, and Normalized Difference Soundscape Index before, during, and after the wildfire smoke event that occurred on September 12–14, 2020.

Table 3
Summary of results, including parameter estimates and 95% confidence intervals, of the before-during-after analyses used to compare daily values of three acoustic indices (Acoustic Complexity Index (ACI), Bioacoustic Index (BI), and Normalized Difference Soundscape Index (NDSI)) before (August 1–September 11, 2020), during (September 12–14, 2020), and after (September 15–September 30, 2020) a large smoke event and between the same date ranges in 2019 when smoke did not affect our study area. Acoustic indices were log transformed prior to analysis as described in Section 2.2.2. Statistically significant effects ($p < 0.05$) are **bolded**.

	2020			2019		
Acoustic Index	**Intercept**	**During**	**After**	**Intercept**	**During**	**After**
ACI	7.40 (7.38, 7.42)	**-0.027 (-0.037, -0.017)**	**-0.015 (-0.024, -0.006)**	7.33 (7.33, 7.34)	-0.001 (-0.015, 0.013)	0.002 (-0.007, 0.011)
BI	2.59 (2.52, 2.66)	**-0.173 (-0.222, -0.124)**	**-0.117 (-0.158, -0.076)**	2.59 (2.49, 2.69)	-0.037 (-0.131, 0.058)	0.029 (-0.033, 0.090)
NDSI	1.94 (1.56, 2.32)	-0.043 (-0.229, 0.143)	-0.100 (-0.257, 0.057)	2.21 (1.32, 3.09)	-0.121 (-0.387, 0.146)	-0.106 (-0.280, 0.067)

reduction in ACI and BI during the three-day smoke event in 2020 and in the two weeks following this smoke pollution episode. This suggests that while acoustically active wildlife may not respond immediately to smoke or do not exhibit behavioral changes that are linearly dependent on the intensity of smoke, prolonged or repeated exposure to smoke does affect species contributing to biophony in ways that ultimately influence characteristics of soundscapes. Our finding contributes to emerging consensus that to understand the impact of wildfire smoke on ecological communities, it will be critical to consider both acute and chronic exposure to toxic air (Nihei et al., 2024).

Our inference is limited to the effects of smoke on dawn soundscapes on fair weather days in the dry, coniferous forests of the Pacific Northwest. To further explore effects of smoke on acoustically active wildlife, we encourage researchers to leverage existing archives of bioacoustic data to investigate changes in soundscapes during and after smoke events in other biomes. It would be particularly valuable to consider impacts of smoke on nighttime soundscapes to further knowledge of effects of smoke on nocturnal wildlife. While acoustic indices would offer a snapshot of smoke impacts on ecological communities, use of existing automated classifiers (e.g., BirdNet) would support testing of mechanistic hypotheses relating smoke exposure to changes in the calling rates of specific species or taxa. However, recent research suggests that smoke may adversely impact the quality of animal vocalizations (Erb et al., 2023), possibly impairing the ability of these algorithms to identify species. It may be necessary to train classifiers on recordings collected both during good air quality conditions and on smoky days.

5. Conclusion

Our study demonstrates that passive acoustic monitoring is a valuable tool to investigate how wildlife respond to wildfire smoke – an increasing stressor in ecosystems around the world. Our results add to emerging evidence of widespread impacts of smoke on wildlife (Sanderfoot et al., 2021) and suggest that the effects of smoke on ecological communities are non-linear and that wildlife may respond to smoke in unexpected ways. We recommend that future studies leverage existing archives of bioacoustic data to further explore the relationship between smoke and wildlife acoustic activity. Bioacoustic data collected in studies designed to ground-truth acoustic indices would be particularly useful, as relationships between soundscape characteristics and biodiversity metrics have already been established.

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CRediT authorship contribution statement

Olivia Sanderfoot: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Morgan W. Tingley:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis. **Sarah B. Bassing:** Writing – review & editing, Visualization, Project administration, Investigation, Data curation. **Joseph K. Vaughan:** Writing – review & editing, Investigation. **Nicole A. June:** Writing – review & editing, Investigation. **Beth Gardner:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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