The impact of wildfire smoke on local avian biodiversity*

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Abstract

Land use alternations and climate change are shifting natural fire regimes, leading to prolonged and intensified fire seasons accompanied by widespread air pollution, with potentially important consequences for local wildlife. Combining data from the North American Breeding Bird Survey with high-resolution satellite imagery, we estimate the impact of wildfire-specific smoke pollution (PM2.5) on avian biodiversity in the contiguous United States (US) from 2008 to 2022. The panel fixed effects instrumental variable estimation results indicate a short-term adverse effect of PM2.5 on taxonomic and phylogenetic diversity metrics. More specifically, a standard deviation (sd) increase in wildfire-specific PM2.5 pollution reduces species richness, abundance, and phylogenetic diversity by about 0.1 sd, largely driven by observations in the Western US. For the most polluted transects the effect is up to 2-3 standard deviations. The adverse effects on biodiversity metrics vary markedly across ecosystems. While the decrease in phylogenetic diversity is most pronounced in the Western US, for the taxonomic metrics it is the Eastern Temperate Forests, the Northern Forests, and the North American Deserts, which are driving the adverse effect of wildfire smoke. These findings underscore the need for targeted fire management and conservation strategies to mitigate biodiversity loss, especially in the face of increasing wildfire intensity and smoke exposure projected for many regions worldwide.

Keywords: biodiversity, ecosystem services, forest disturbance, land use, natural capital, phylogeny, pollution, smoke, wildfire

JEL classification codes: Q54, Q57, Q58, R14

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1 Introduction

Biodiversity, a key component of natural capital, is declining at rates unprecedented in human history (Pimm et al., 2014), with profound implications for economic stability and human well-being (Dasgupta, 2021). Reflecting its economic importance, the World Economic Forum ranks biodiversity loss and ecosystem collapse as the second largest global risk over the next decade (WEF Report, 2025). Among the various drivers of biodiversity loss, the shift of natural fire regimes has emerged as an urgent and complex challenge (Kelly et al., 2020; Doherty et al., 2024).[1] While fire has played a critical role in shaping global biodiversity by influencing ecosystem processes and species distribution for millions of years (He et al., 2019), human activities – particularly land-use alterations, fire management policies, and climate change – are reshaping fire regimes, leading to prolonged and intensified fire seasons accompanied by increased smoke pollution (Richardson et al., 2022; UNEP, 2022; Brown et al., 2023; Cunningham et al., 2024). With the observed and projected surge in wildfires due to climate change across many regions of the world (UNEP, 2022; Cunningham et al., 2024), conservation of global biodiversity is deemed unlikely to be achieved without incorporating the critical role of wildfires (Kelly et al., 2020; Doherty et al., 2024).

With a focus on burned area, Kelly et al. (2020) find that globally altered fire regimes threaten 15% of terrestrial and freshwater species listed on the International Union for Conservation of Nature's (IUCN) Red List. Notably, with 18.6% of species under threat, IUCN-listed birds are the most affected among faunal biodiversity. Building on this concern, avian biodiversity, with its widespread geographical distribution (Lees et al., 2022), ubiquity, and essential role in ecosystems, including seed dispersal, pollination, and pest control (Şekercioğlu et al., 2004; Whelan et al., 2008, 2015), has been the focus of numerous case studies. Moreover, birds are widely recognised as indicator species due to their sensitivity to environmental changes, including habitat loss and ecosystem disturbances such as fire, making them valuable proxies for assessing the broader impacts of environmental disturbances (Bibby, 1999). From an economics perspective, this sensitivity is consequential because changes in avian

[1]The term "fire regime" refers to the recurring pattern of fire activity within a particular area, characterised by elements such as fire type, frequency, intensity, seasonal timing, and spatial extent.

biodiversity can signal welfare-relevant losses through degraded ecosystem services, reduced non-market values, and diminished ecological resilience.[2]

While research has highlighted varied impacts of wildfire on birds – ranging from reduced habitat for the greater sage-grouse (Riginos et al., 2019) to shifts in community composition depending on fire severity and ecosystem type (Tingley et al., 2016; Regos et al., 2018; Arrogante-Funes et al., 2024) – emerging evidence points to wildfire smoke as an additional threat to avian species. For example, Nihei et al. (2024) find that wildfire smoke negatively impacts bird health and behaviour, with acute PM2.5 exposure reducing capture rates and chronic exposure impairing body condition (i.e., loss of body mass) in passerine species in California. Although not exclusively focused on wildfire-specific pollution, Sanderfoot and Holloway (2017) highlight broader avian vulnerabilities to air pollution, including wildfire smoke, and document adverse effects, such as respiratory distress, immunosuppression, and reduced reproductive success. Yet, neither Nihei et al. (2024) nor Sanderfoot and Holloway (2017) explicitly disentangle wildfire-specific PM2.5 pollution from other potential sources, such as urban and industrial pollution, leaving room for ambiguity in terms of being able to attribute the observed impacts to wildfire emissions.

The current study investigates the impact of wildfire-specific smoke pollution on avian biodiversity in the contiguous United States (US), where wildfire activity has markedly increased in recent decades and is projected to rise further under climate change (Abatzoglou and Williams, 2016; Iglesias et al., 2022; Jones et al., 2022). Data from the North American Breeding Bird Survey (BBS), which provides systematic annual observations conducted each summer (June–August) across over 2,800 road transects, is leveraged to construct a number

[2]Empirical work in environmental economics shows that changes in bird populations can translate into large welfare losses when they disrupt ecosystem functioning. For example, Frank et al. (2025) document how the eradication of sparrows in China reduced pest control services, lowered agricultural productivity, and contributed to excess human mortality. More generally, Paul et al. (2020) emphasise that biodiversity-value relationships are context-dependent and often non-linear, implying that biodiversity losses can reduce welfare through ecosystem services, non-market values, and resilience even when such effects are difficult to monetise.

of diversity indices.[3] More specifically, we construct biodiversity metrics that alternatively capture species richness, their relative abundance (evenness) in terms of taxonomic diversity, and evolutionary distinctiveness reflecting phylogenetic diversity. These metrics are integrated with high-resolution wildfire-specific PM2.5 pollution, burned area, land cover, food crop diversity, fire danger indices, and climatological variables to create a 15-year panel dataset. We employ an instrumental variable strategy that uses the fire weather index (FWI) as an exogenous predictor of wildfire activity to address endogeneity concerns arising from the correlation of wildfires and smoke exposure with human land-use patterns. Our identification strategy relies on the FWI, which captures the non-linear interaction of temperature, humidity, wind, and precipitation that drives fire potential, while controlling for general climatological conditions. This isolates the meteorological component of wildfire risk, allowing us to identify the causal effects of wildfire-specific smoke on taxonomic and phylogenetic diversity and to assess ecosystem-specific biodiversity resilience.

Our results indicate a short-term negative effect of wildfire-specific smoke pollution on all biodiversity metrics. Biodiversity in a given survey year declines in response to cumulative wildfire smoke exposure during the preceding calendar year, reflecting an impact observable within the following breeding season. On average, a standard deviation (sd) increase in mean annual PM2.5 leads to a ≈ 0.1 sd decrease in biodiversity outcomes, with the most polluted observations showing decreases of 2-3 standard deviations. At the level of four broad geographical regions, we find that the Western US is driving the negative effect on phylogenetic diversity, with a 0.2 sd decline per sd increase in PM2.5. Disaggregating the results by ecoregions reveals substantial spatial heterogeneity in biodiversity responses. The strongest declines in species richness occur in the Eastern Temperate Forests (≈ 0.4 sd per 1-sd increase in PM2.5) and the North American Deserts (≈ 0.2 sd). For relative abundance and evenness (Shannon index), the largest effects are likewise found in the Eastern Temperate Forests (≈ 0.3 sd) and the Northern Forests (≈ 0.2 sd). In contrast, no ecoregion shows a statistically detectable effect on *phylogenetic diversity*, underscoring that conclusions depend on the biodiversity metric examined. These spatial patterns are consistent with increasing

[3]Although not a complete bird census, as argued by Taylor and Weder (2024) this data provides a robust foundation for analysis through systematic, repeated sampling.

wildfire-sourced smoke pollution in parts of the Western US (Childs et al., 2022), suggesting limited adaptation to shifting fire regimes. However, the adverse effects are not confined to regions with rising smoke trends, as the Eastern Temperate and Northern Forests also exhibit declines in species richness and relative abundance. Although the observed effects represent a short-term shock, they may still undermine ecological resilience, as the temporary displacement of a key species can push ecosystems past critical thresholds and lead to collapse, especially in systems already under stress (Giglio et al., 2024). These findings provide valuable information for policy making, by, for instance, informing targeted fire suppression efforts to protect vulnerable populations or keystone species as suggested in Woinarski et al. (2023).

Our study contributes to the emerging literature of pollution and biodiversity in several ways. First, we provide causal estimates of the effect of wildfire-specific smoke pollution on biodiversity using an instrumental variable approach to address endogeneity concerns related to wildfire (smoke) occurrence – representing, to the best of our knowledge, the first such estimates. More specifically, our econometric strategy incorporates panel-fixed effects (controlling for unobserved confounding factors such as geography and landscape management practices), while also controlling for a rich set of time varying bird survey, crop diversity, land use, and climatic controls. In addition, we include a measure of the burnt area and are therefore able to disentangle the effect of wildfire smoke from direct habitat destruction. Second, while most studies focus on a single species (e.g., Rae et al. (2023)) or on species composition and richness (Mestre et al., 2013; Loyn and McNabb, 2015), we evaluate a range of biodiversity metrics. Beyond the commonly used taxonomic metrics including species richness, and the Shannon-Wiener biodiversity index (incorporating richness and relative abundance), we use the phylogenetic trees by Jetz et al. (2012) to assess phylogenetic diversity (evolutionary distinctiveness), which is broadly recognised as a critical factor in maintaining ecosystem function and resilience (Metrick and Weitzman, 1998) and is increasingly emphasized in conservation priority setting (Weitzman, 1992; Crozier, 1997; Weitzman, 1998; Isaac et al., 2007). Third, unlike existing case studies that are limited in geographic or temporal scope, our analysis covers over a decade of wildfire smoke exposure across the contiguous US. This broad coverage accounts for smoke transported from outside the study region and enables us to differentiate its effects on biodiversity across time and diverse ecosystems.

The remainder of this paper is organised as follows. Section 2 explains the biodiversity metrics studied, and Section 3 provides an overview of the data along with descriptive statistics. Section 4 outlines the empirical framework, and the findings are presented and discussed in Section 5. Last, Section 6 offers concluding remarks.

2 Biodiversity Metrics

Traditionally, biodiversity metrics have been based on taxonomic classifications of species (Magurran and McGill, 2010). Taxonomic metrics, such as species richness, are straightforward to construct and widely used to evaluate the diversity of species within a particular community or region. However, these metrics often fail to account for functional or evolutionary differences between species, which are crucial for understanding local ecosystem functions and stability (Srivastava et al., 2012; Cadotte and Tucker, 2018). For instance, the loss of species with unique ecological roles may disproportionately affect ecosystem functioning compared to the loss of closely related species with overlapping functions.

To address these limitations, researchers have developed biodiversity indices based on functional traits – morphological, physiological, and phenological characteristics that influence species' growth, reproduction, and survival (Cadotte et al., 2012; Gravel et al., 2012; Staab et al., 2021). However, gathering and quantifying these traits across species is often challenging. An increasingly popular alternative is the use of *phylogenetic* measures of diversity, which leverage molecular data to capture evolutionary relationships among species (Magurran and McGill, 2010). These measures are particularly valuable because they capture differences in functional traits among species (Gravel et al., 2012; Cadotte and Tucker, 2018) and serve as reasonable predictors of local ecosystem stability and functionality (Cadotte et al., 2009; Srivastava et al., 2012).

A key feature of this literature is the recognition that the loss of an evolutionarily distinct species may represent a greater loss of biodiversity than the loss of many closely related species (Albright et al., 2010). This argument is exemplified by Weitzman (1998)'s discussion of the "Noah's Ark problem," which emphasises the challenge of prioritising species conservation when resources are limited. It proposes that species distinctiveness, combined with utility

and survival probabilities, should guide conservation priorities. Similarly, Solow et al. (1993) emphasise distinctiveness as a key determinant of a species' option value, while Weitzman (1993) highlights the importance of "diversity theory" based on species dissimilarities to inform conservation strategies. With these principles in mind, the evolutionary distinctiveness of species is now commonly regarded as a critical consideration in conservation priority setting (Crozier, 1997; Isaac et al., 2007).

To capture biodiversity comprehensively, this study employs three complementary metrics: species richness, the Shannon-Wiener Index (both measuring taxonomic diversity), and the phylogenetic diversity entropy measure. These metrics are described below.

Species richness R is the simplest measure of biodiversity, representing the total number of species present in a community:

$$R = \text{total number of species in the community.} \tag{1}$$

While species richness provides a straightforward measure of biodiversity, it does not account for the relative abundances (evenness) of species within a community. To address this limitation, the Shannon-Wiener Index incorporates both species richness and evenness, offering a more comprehensive measure of taxonomic diversity. It is defined as:

$$SHANNON = -\sum_{i=1}^{R} p_i \ln(p_i), \tag{2}$$

where p_i is the proportion of individuals in the community belonging to species i, and R is the total number of species. Higher values of the Shannon index indicate greater biodiversity, reflecting a more even distribution of individuals across species.

Last, to incorporate phylogenetic diversity, we follow the approach implemented in Cole et al. (2021) and Strobl (2022), utilising the Abundance-Weighted Evolutionary Distinctiveness (AED) metric, which accounts for evolutionary history by integrating species abundances and their evolutionary relationships. This metric requires genetic tree and species abundance data for a specific area, obtained from Jetz et al. (2012). For species i in community j, AED

is calculated as:

$$AED_{ijT} = \sum_{b \in B(i,T)} \lambda_b \frac{n_{ijT}}{N_{jT}}, \tag{3}$$

where $B(i,T)$ represents the set of branches connecting species i to the root of the phylogenetic tree T, while λ_b denotes the length of branch b in evolutionary years. The term n_{ijT} refers to the abundance of species i in community j, and N_{jT} represents the total abundance of all species in community j that share the same set of branches $B(i,T)$.

Building on AED, the Phylogenetic Diversity Entropy Measure ($HAED$) integrates genetic richness and evenness to capture community-level phylogenetic diversity. $HAED$ is defined as:

$$HAED_{jT} = -\sum_{i=1}^{R_j} \frac{AED_{ijT}}{\sum_{i=1}^{R_j} AED_{ijT}} \ln \left(\frac{AED_{ijT}}{\sum_{i=1}^{R_j} AED_{ijT}} \right), \tag{4}$$

where R_j is the total number of species in community j, and AED_{ijT} is the abundance-weighted evolutionary distinctiveness of species i in community j. In essence, compared to AED_{ijT}, $HAED_{jT}$ also takes into account whether a few species may be driving the measured genetic diversity.

Integrating these three metrics provides a robust framework for comprehensively assessing biodiversity. Species richness and the Shannon index reveal taxonomic patterns, while $HAED$ captures evolutionary distinctiveness, hereafter referred to as "phylogenetic diversity." Together, they enable a nuanced evaluation of how environmental stressors, such as wildfire smoke, impact avian biodiversity.

3 Data and descriptive statistics

3.1 North American breeding bird survey

The North American Breeding Bird Survey (BBS) serves as the primary source of information for estimating bird population trends and modelling the effects of various potential

stressors in the United States.[4] The BBS was first conducted for the entire US in 1968 and is carried out annually along randomly selected secondary roads deemed to be representative of the broader region.[5] It is conducted in the summer months and each transect is about 40 km long. Notably, the survey methodology has remained consistent since its inception: a voluntary observer selects a morning, and starting 30 minutes before sunrise, stops at 50 pre-determined locations spaced 800 meters apart. At each stop, the observer exits their vehicle and conducts a 3-minute count, recording the bird species seen or heard within a 400-meter radius. To ensure consistency in data collection, the same stops are surveyed each year.

Although the BBS currently includes more than 3,000 active transects, the availability of volunteers determines the number of those actually covered annually. For the 2008–2022 sample period, 2,883 routes were surveyed, with each route having data for an average of 10 out of 14 possible years (2020 was not observed due to the COVID-19 pandemic). Birds recorded in the BBS are classified based on the American Ornithologists' Union taxonomy. Of the 914 bird species naturally occurring in the US, this analysis focuses on 700 native species after excluding non-native species. Limiting the analysis to native species eliminates the potential for observed increases in avian diversity to be attributed to the introduction or spread of non-native species, an outcome often viewed negatively from a conservation standpoint.

The BBS also collects various survey-specific variables. Each observer is assigned a unique identification number, facilitating the measurement of observer experience and recording whether an assistant was present during the survey. Additional information includes the number of cars observed, the number of stops with noise disturbances, and meteorological conditions such as temperature, sky clarity (measured using the Weather Bureau scale), and wind speed (recorded according to the Beaufort scale) at the start and end of the survey morning. Finally we include the start and end time of the survey as well as an indicator variable for the survey month. These variables are incorporated as transect-level controls in

[4]Further information can be accessed under https://www.usgs.gov/centers/eesc/science/north-american-breeding-bird-survey.

[5]Multiple studies show that BBS trends are reliable at broad spatial scales, with population trends closely matching those derived from eBird and other community science data (Horns et al., 2018; Feng and Che-Castaldo, 2021; Robinson et al., 2025).

the analysis and shown in Table 1. Note, that these survey specific weather variables capture only the meteorological and observational conditions on the morning of the survey and are therefore distinct from the climatological controls described below, which summarise average weather conditions over a calendar year.

3.2 Wildfire smoke

We use the daily wildfire smoke product provided by the Environmental Change and Human Outcome (ECHO) lab at the University of Stanford introduced in Childs et al. (2022) with a 10km resolution. Specifically, we rely on the extended Version 2.0 through 2023 outlined in Childs et al. (2024). For each transect, the average annual PM2.5 exposure is calculated from the daily values which fall within the defined landscape around the transects.

This dataset is generated using a parsimonious machine learning model designed to estimate daily wildfire-driven PM2.5 concentrations across the contiguous US. The model combines data from ground monitoring stations, satellite-based smoke plume identification, and reanalysis datasets to capture local and temporal variations in smoke PM2.5 concentrations starting from 2006. The approach involves identifying "smoke days" based on satellite-derived smoke plume boundaries and air trajectory simulations, attributing PM2.5 anomalies at ground monitoring stations to wildfire smoke, and using a gradient-boosted tree model to predict smoke PM2.5 for locations without monitors. Unlike process-based chemical transport models (CTMs), this statistical methodology directly derives ground-based measures of wildfire smoke and predicts them from input variables, bypassing the need to parametrise physical processes such as emissions inventories and plume injection heights, which are often difficult to empirically constrain. These statistical approaches have demonstrated better agreement with surface observations compared to CTM-based methods (Ye et al., 2021; Li et al., 2023).

To construct transect-level measures, we extract the daily smoke PM2.5 values for all grid cells whose centroids fall within the 5km landscape around each transect. These daily values are averaged to obtain the annual mean smoke PM2.5 exposure used in the main analysis. In robustness checks, we additionally employ two frequency-based measures: the number of *smoke days* per year (days with wildfire-sourced PM2.5 above 0 $\mu g/m^3$) and the number of

high smoke days, defined as days exceeding 35 $\mu g/m^3$.[6]

In an additional analysis we proxy wildfire smoke using data on aerosol optical depth (AOD) from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction (MAIAC) land product.[7] The main advantage over the Childs et al. (2022) product is that it is available at a very high resolution of 1km, which makes it particularly suitable for local analysis. The data product quantifies the extent to which sunlight is attenuated through scattering or absorption by atmospheric particles. In essence, it provides a measure of the optical thickness of aerosol layers, including those composed of dust, smoke, and pollutants. We utilise the 0.55 μm wavelength (green band), a standard choice in AOD products, as it is considered particularly effective for observations over vegetated or bright land surfaces.[8] Even though the transect fixed effects arguably capture much of the background pollution, and the instrument is still exogenous, the AOD would potential capture a different channel (than wildfire smoke) if, for instance, wildfires smoke causes less car traffic and, hence, less pollution.

Similar to the PM2.5 implementation, the monthly average AOD values are extracted for all AOD gridcells that fall within the defined landscape of 5km around each transect. The final outcome variable denotes the average monthly AOD value for each year. While the measure is unitless, an optical thickness of less than 0.1 indicates a clear sky.[9]

3.3 Burned area

The data source for the burned area perimeters is the Moderate Resolution Imaging Spectraradiometer (MODIS) MCD64A1.061 global monthly burned area product at 500 meter

[6]The 35 $\mu g/m^3$ threshold corresponds to the US Environmental Protection Agency 24-hour PM2.5 standard (EPA, 2024).

[7]The data set was accessed on Google Earth Engine under: https://developers.google.com/earth-engine/datasets/catalog/MODIS_061_MCD19A2_GRANULES.

[8]The full user guide is available here: https://lpdaac.usgs.gov/documents/1500/MCD19_User_Guide_V61.pdf.

[9]The NASA Earth observatory provides information on guiding threshold values under https://earthobservatory.nasa.gov/global-maps/MODAL2_M_AER_OD.

spatial resolution provided by the NASA Distributed Active Archive Centres.[10] This product employs a burn-sensitive Vegetation Index derived from MODIS surface reflectance bands and active fire observations to determine the Julian day of burn (i.e., the day of the year, ranging from 1 to 365) for each 500-meter grid cell, offering detailed and dynamic burned-area information. We extract the monthly burned area within each landscape around the transects in hectares and subsequently calculate the percentage burnt of each landscape around a transect per year.

3.4 Land cover and cropland

The National Agricultural Statistics Service (NASS) Cropland Data Layer by the US Department of Agriculture is an annual crop-specific data product at a spatial resolution of 30m outlined in Boryan et al. (2011), and is used to create control variables at the landscape level (i.e., 5km buffer around transects).[11] It is derived combining satellite imagery and extensive ground truth data and is available for the contiguous US since 2008, which determines the starting year of this analysis. Using this data, a metric for food crop phylogenetic diversity is created following Strobl (2022). Furthermore, the percentage of food crops, pasture, fallow crop, shrubland, barren land, forest, wetland, water, and a range of urban density variables are calculated for each landscape.

3.5 Fire danger metrics

The fire weather index (FWI) is a key component of the Canadian Forest fire weather index System, first introduced by Van Wagner and Pickett (1985). It is a composite metic designed to summarise the interaction of weather and soil conditions relevant for wildfire ignition, spread, and intensity. Figure 1 provides an overview of the FWI structure. The FWI is widely used to assess relative fire potential and serves as an important reference index for producing fire danger maps. In its construction, the FWI combines two fire behaviour indices: (1) the Initial Spread Index (ISI) and (2) the Buildup Index (BUI). The ISI estimates the potential

[10] For further information, see https://lpdaac.usgs.gov/products/mcd64a1v061/.

[11] The data product is available under this link: https://www.nass.usda.gov/Research_and_Science/Cropland/SARS1a.php.

rate of fire spread by integrating the Fine Fuel Moisture Code (FFMC), which represents moisture conditions in fine, surface-level litter fuels sheltered under the forest canopy, along with surface wind speed. The BUI provides insight into the potential heat output of a fire by incorporating moisture levels in deeper fuel layers. Specifically, it combines the Duff Moisture Code (DMC), which accounts for moisture in decomposed organic materials below the surface litter, and the Drought Code (DC), which evaluates the moisture content of compacted deep layers, reflecting the effects of long-term drought on heavier fuels. Both the DMC and DC are evolve with antecedent weather conditions and are adjusted for seasonal variation in day length, reflecting differences in drying rates and potential evapotranspiration across the year.

As illustrated in Figure 1, the meteorological variables underlying the FWI include temperature, relative humidity, wind speed, and precipitation, all measured at solar noon local standard time, with precipitation accumulated over a 24-hour period. These variables are combined through a sequence of non-linear and threshold-based functions to construct the fuel moisture codes operating at different temporal horizons and, subsequently fire behaviour indices. While the reader is referred to Van Wagner and Pickett (1985) for the full derivation of all intermediate components of the Canadian FWI system, Appendix B details how the FWI is constructed from the fire behaviour indices, namely the ISI and BUI.

For this study, we utilise the average monthly FWI values derived from the reanalysis product provided by Natural Resources Canada, as described in McElhinny et al. (2020). The underlying meteorological inputs are sourced from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 HRES reanalysis product. This dataset offers a spatial resolution of $0.25°$, corresponding to $\approx$ 25–28km for the contiguous US. Note, that the version of the FWI, which integrates the overwintered DC accounting for precipitation during the winter months, is used. This approach improves accuracy compared to the default initialisation values by capturing inter-seasonal drought effects more precisely.

In a robustness check shown in Section 5.5, we utilise an alternative measure of fire danger, namely the Energy Release Component (ERC). The ERC is a key output of the National Fire Danger Rating System (NFDRS), which is widely used in fire management applications across the US. This metric quantifies the potential energy available to be released during combustion, serving as an indicator of the dryness of fuels and, consequently, the intensity of a potential

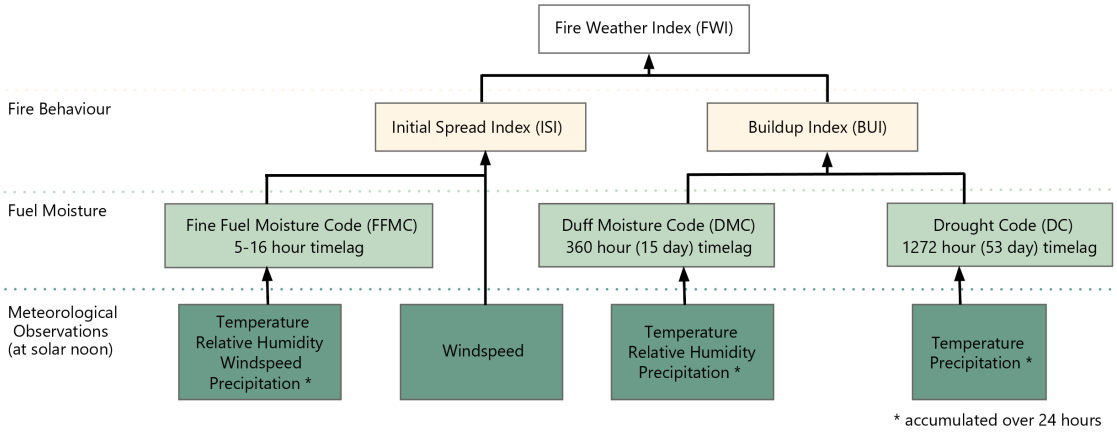


Figure 1: Structure of the Canadian fire weather index System based on Van Wagner and Pickett (1985) adopted from Meier et al. (2023).

wildfire. The ERC is derived from daily meteorological variables such as temperature, relative humidity, and precipitation, combined with information on fuel moisture content. Unlike some other fire danger indices, the ERC does not directly incorporate wind speed but reflects the cumulative energy available for combustion, based on the dryness of live and dead fuels.

The ERC data we use is sourced from the University of Idaho Gridded Surface Meteorological Dataset (GRIDMET), which is provided by the University of California Merced.[12] The GRIDMET product offers ERC estimates at a high spatial resolution of ≈4km, making it well-suited for local analyses of fire danger. However, despite its finer resolution, our analysis reveals that the ERC performs less effectively than the fire weather index in predicting wildfire-specific PM2.5, which is our variable of interest. This limitation is likely due to differences in the construction of the indices and their underlying assumptions, with the FWI arguably being more robust for applications involving fire-related emissions. Given the ERC's inferior predictive performance compared to the FWI based on the first stage F-Statistic, we do not include it in our baseline estimations. Nevertheless, its use as a robustness check provides valuable supplementary insights and validates the use of fire danger as in instrumental variable to assess smoke emissions.

[12]The data is publicly available under https://www.climatologylab.org/gridmet.html.

3.6 Climate

For monthly precipitation and temperature we use the Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate data by the Northwest Alliance for Computational Science and Engineering at ≈4km spatial resolution.[13] Data on the relative humidity and the palmer severity drought index (pdsi) is obtained from GRIDMET.[14] Similar to the PRISM data, it is provided at approximately 4km spatial resolution and is outlined in Abatzoglou (2013). Specifically, we use the minimum and maximum monthly relative humidity. Last, we obtain the monthly wind velocity values of the u-component (windspeed in zonal direction) and v-component (windspeed in meridional direction) from the European Centre for Medium-Range Weather Forecasts (ECMWF) Climate Reanalysis available from the Copernicus Climate Data Store at a resolution of ≈ 23km.[15]

We calculate the annual average values of all these climate variables within the landscape around each transect. Wind speed is calculated using the wind velocity components as $wind\ speed = \sqrt{u^2 + v^2}$ denoting the total windspeed independent of direction.

3.7 Descriptive statistics

A map of the contiguous US showing the transects and average daily wildfire smoke sourced PM2.5 pollution from 2008 to 2022 is provided in Figure 2. The BBS transects are geographically relatively evenly distributed, suggesting they are broadly representative of the US. After excluding observations with missing values for any transect specific variable, the sample consists of an unbalanced panel of 2,883 transects, encompassing a total of 23,923 observations.

Table 1 presents the descriptive statistics for all variables used in the estimations. The average number of species observed on a transect is 55 with a minimum of 6 and a maximum of 267 species. The Shannon Index ranges from 0.6 to 4.88 with an average value of 3.23 and

[13]The data can be accessed here: https://www.prism.oregonstate.edu/.

[14]All datasets are described and publicly available here: https://www.climatologylab.org/gridmet.html.

[15]The ECMWF reanalysis data is available here: https://cds.climate.copernicus.eu/datasets/reanalysis-era5-land-monthly-means?tab=overview.

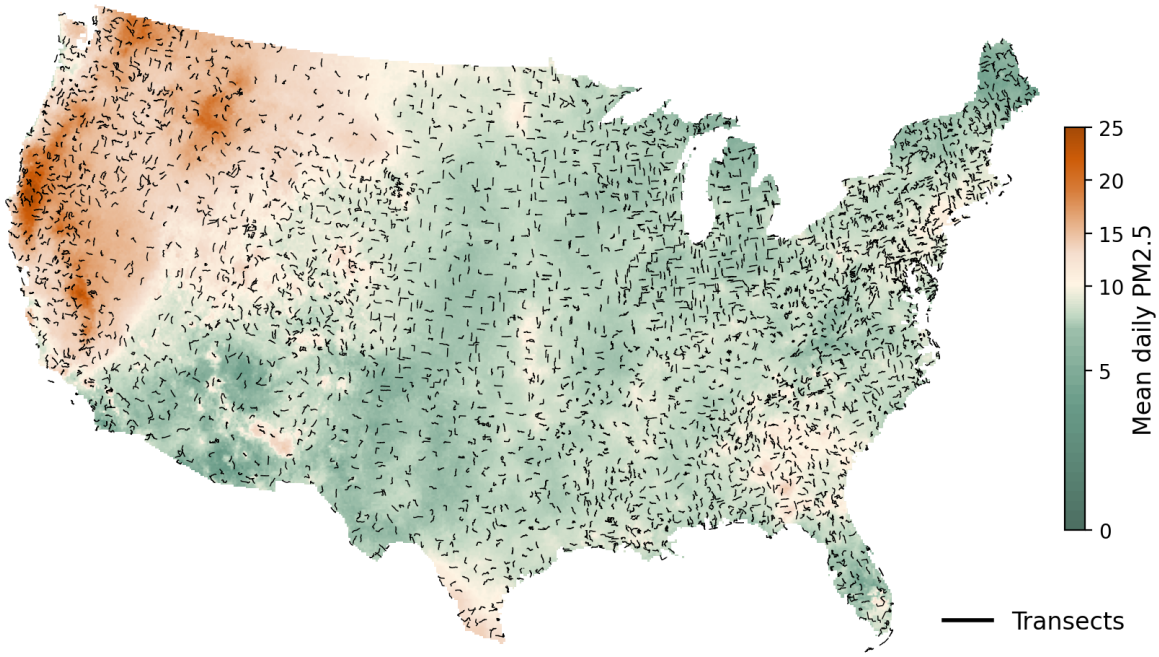


Figure 2: North American Breeding Bird Survey (BBS) transects and average daily wildfire-specific PM2.5 pollution from 2008 to 2022. *Notes:* (i) the transects are from the BBS and wildfire PM2.5 data is from the Environmental Change and Human Outcomes (ECHO) lab (Childs et al., 2022) Version 2.0 at a spatial resolution of 10km; (ii) the colour scale is calibrated based on the EPA's average annual PM2.5 concentration standard threshold of 9 μg/m^3.

the metric capturing phylogenetic diversity ranges from 1.67 to 4.04 with an average value of 3.17. The average annual wildfire-specific PM2.5 pollution value (derived from daily data) is 4.48 with a range from no wildfire smoke pollution to a value of 83 for the most polluted observation. As of March 2024, the Environmental Protection Agency (EPA) has lowered the average annual PM2.5 concentration standard from 12 μg/m^3 to 9 μg/m^3 – and thus, any value above that threshold does not meet the health-based criteria for air quality under the revised National Ambient Air Quality Standards (NAAQS) (EPA, 2024). Figure A1 in Appendix A shows the spatial variation in wildfire-specific PM2.5 pollution by year. As an alternative exposure metric, we calculate the number of smoke days per year, which we use in a robustness check. Transects experienced an average of 35 smoke days annually, with a range from 0 to 139. The mean and median values of aerosol optical depth (AOD) are approximately 0.1, which is commonly regarded as the threshold distinguishing a "clean" atmosphere from a

polluted one. Furthermore, the maximum AOD value observed is approximately 0.3, indicative of moderate pollution levels. Note, that these values reflect annual averages, and as such, large peaks are not expected in the dataset. The average annual aerosol optical depth values for each year from 2008-2022 in the US are visualised in Figure A2 in Appendix A.

In regard to the fraction of burned area within each landscape (defined as the 5km buffer around a transect), the average is 0.3% with a maximum value of 50% being burnt annually. A map of the transects and the burned area for 2008 to 2022 is provided in Figure A3 in Appendix A. The annual mean fire weather index is "low" on average (9.6). However, there is considerable variation with a minimum value of 0.5 indicating "very low" fire danger to 59 which denotes "extreme" fire danger. Similarly, the range of the climatological variables is broad. Average annual rainfall ranges from roughly 2 mm to 317 mm, and temperature from freezing point to 26°C. Average annual minimum relative humidity is 41% and the maximum relative humidity is about 86%. The palmer drought severity index (pdsi) ranges from -7 (extreme drought) to 8 (extremely wet) with a "normal" average.

In terms of land cover and cropland variables within the 5km landscape around the transects, it is apparent that the food crop phylogenic diversity with a value of 1.6 is on average much lower than the avian phylogenetic diversity. Moreover, the decomposition of land use shows that, on average, 49% of the landscapes are food crops. The second largest average land cover share is forest (30%) followed by open urban (8%), and pasture (4%). Examining the survey variables, it is notable that observation experience ranges from volunteers with an experience in surveying 1 to 195 transects. The majority of transects are observed by only one person and for about a third of observations they had an assistant. The average number of cars per transects is 58. However, there are observations with no cars at all, as well as some with more than 3,000 cars. On 50% of the transects noise was reported at only one out of the roughly 50 stops. On average, the survey started at around 5am and the observed wind speed according to the Beaufort scale was 0.7 corresponding to "calm" conditions, the temperature was 16°F, and the clarity of the sky in terms of the Weather Bureau scale was 0.9.[16] The survey usually ended around 10am with slightly stronger winds (1.6), a temperature of about

[16]A sky value of 0 corresponds to a clear sky and the value of 1 indicates a partly cloudy sky. The maximum value of the Weather Bureau scale is 8 denoting showers.

23°F and slightly cloudier skies (0.8).

Table 1: Summary table of all variables.

	Mean	Median	SD	Min	Max
Biodiveristy metrics					
# Species	55	56	15	6	267
log # Species	3.97	4.03	0.29	1.79	5.59
Shannon index	3.23	3.32	0.42	0.60	4.88
Phylogenetic diversity	3.17	3.24	0.36	1.67	4.04
Smoke pollution					
Mean daily PM2.5	4.48	3.75	3.44	0.00	83.39
# smoke days (PM2.5 $> 0\mu g/m^3$)	34.8	28.2	25.2	0.0	139.1
# high smoke days (PM2.5 $> 35\mu g/m^3$)	0.4	0.0	2.5	0.0	46.6
Mean daily aerosol optical depth	0.11	0.11	0.02	0.04	0.31
Burnt area and fire danger					
% landscape burnt	0.003	0.000	0.02	0	0.60
Mean daily fire weather index	9.64	6.56	8.53	0.54	59.33
Mean daily energy release component	29.0	25.3	11.8	4.8	87.4
Climate variables					
Monthly rainfall (mm)	83.13	85.96	38.16	1.45	317.50
Monthly temperature (° C)	11.86	11.17	5.00	0.13	25.92
Monthly minimum relative humidity (%)	41.38	43.67	8.85	12.33	69.03
Monthly maximum relative humidity (%)	85.78	88.08	8.23	38.20	99.88
Monthly mean wind speed (m/s)	0.79	0.72	0.6	0	4.40
Monthly pdsi (scale)	0.06	0.05	2.2	-7	8
Land cover and cropland variables					
Food crop phylogenetic diversity	1.60	1.72	0.6	0	3
Food crop (%)	0.49	0.52	0.4	0	1
Pasture (%)	0.04	0.00	0.1	0	1
Fallow crop (%)	0.0001	0.0000	0.0	0	0.5
Shrubland (%)	0.01	0.00	0.1	0	1
Barren (%)	0.02	0.00	0.1	0	1
Forest (%)	0.30	0.07	0.4	0	1
Wetland (%)	0.002	0.000	0.0	0	1
Water (%)	0.003	0.000	0.0	0	1
Open urban (%)	0.08	0.03	0.1	0	1
Low urban (%)	0.02	0.01	0.1	0	1
Medium urban (%)	0.01	0.00	0.0	0	1
High urban (%)	0.003	0.000	0.1	0	1
Survey variables					
Obs. experience (# transects)	13.65	9.00	15.7	1	195
Assistant	0.27	0.00	0.4	0	1
Cars (#)	58.06	30.00	93.5	0	3556
Noise (# stops noise)	2.46	1.00	4.0	0	50
Start wind (scale)	0.73	0.00	1.0	0	5
End wind (scale)	1.62	2.00	1.1	0	6
Start temperature (°F)	15.60	16.11	5.7	-7.8	37.0
End temperature (°F)	22.79	22.78	5.6	-1.1	73.0
Start sky (scale)	0.9	1.0	1.2	0	8
End sky (scale)	0.8	1.0	1.0	0	8
Start time (hrmin)	0508	0514	0046	0401	1300
End time (hrmin)	0987	0959	0077	0456	1730

Notes: (i) Biodiversity and survey variables data are from the North American Breeding Bird Survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0, and aerosol optical depth is obtained from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product; (ii) Burnt area is from the MODIS MCD64A1.061 monthly burned area product and the FWI is provided by McElhinny et al. (2020); (iii) Climate variables and the energy release component are obtained from PRISM and GRIDMET, and land cover and cropland variables are from the National Agricultural Statistic Service Cropland Data Layer by the US Department of Agriculture; (iv) the landscape around a transect is defined as 5km.

4 Empirical framework

4.1 Identification strategy

Wildfire occurrence, and thus resulting fire-sourced smoke pollution, is strongly linked to human activities such as land management policies, land-use changes, infrastructure, intentional fire for legal or illegal purposes (Balch et al., 2017; Grala et al., 2017; Cattau et al., 2020). However, many of these factors may also be correlated with biodiversity outcomes. Therefore, fire-sourced smoke pollution can not be treated as truly exogenous events. To address this concern, we estimate a fixed effects two-stage least squares linear panel model instrumenting wildfire smoke with the fire weather index controlling for the general weather conditions including temperature, precipitation, relative humidity, windspeed, and the palmer drought severity index following a approach akin to Meier et al. (2023).

Although the FWI is constructed from meteorological inputs, it is not a linear function of these variables. Instead, it aggregates them through non-linear and threshold-based transformations and through fuel moisture codes that depend on antecedent weather conditions and cumulative drying with up to a 2-month time lag. As a result, conditional on the included climate controls, identification exploits the residual variation in FWI that arises from the complex construction using specific threshold values and non-linear interactions of the underlying meteorological inputs, as well as from their differing temporal aggregation. Importantly, while weather systems are determined at much broader spatial scales, wildfire occurrence and resulting smoke exposure are highly location-specific, reflecting local fuel conditions and ignition probabilities. The FWI is explicitly designed to map broad-scale meteorological conditions into a measure of local fire danger, and it is this residual, fire-specific variation that we use for identification. To further separate smoke exposure from direct local fire effects, we control for the percentage of area within the landscape that burns.

Our main specification uses wildfire-sourced PM2.5 averaged over the previous calendar year because the ecological pathways through which smoke affects bird populations extend beyond immediate, acute responses. Although extreme smoke events can cause short-term physiological stress and, in rare documented cases, direct mortality, the empirical literature indicates that population-level impacts more commonly arise from sublethal and cumulative

processes. Banding data show that repeated exposure to high-smoke days leads to progressive losses of body mass and birds entering subsequent seasons in poorer physiological condition (Nihei et al., 2024).[17] Controlled and field studies further document that air pollutants can reduce hatchability (the proportion of fertilised eggs that successfully hatch), offspring viability, and chick growth, including through direct toxic effects on embryos such as carbon monoxide penetration of the eggshell (Sanderfoot and Holloway, 2017; Sanderfoot et al., 2021). These mechanisms, together with smoke-induced respiratory damage, immune disruption, and oxidative stress, affect survival and reproductive success over the months following exposure. Because BBS surveys are conducted in summer, they precede much of the same year's fire season. Using prior-year exposure therefore captures the complete fire season and allows us to assess the demographic impacts that persist into the next breeding period, while maintaining consistency with the annual land-cover and cropland controls. We also examine smoke exposure from January to June of year t to evaluate whether any immediate impacts are detectable from the months directly preceding the survey, while noting that this window necessarily omits much of the fire season, which typically peaks in late summer and autumn.

4.2 Econometric specification

We estimate a fixed-effects two-stage least squares (2SLS) linear panel model. The corresponding first stage and second stage equations are shown in Equation (5) and Equation (6), respectively. The unit i denotes the transect, and t represents the year of the summer bird survey, covering the period 2008–2022. The term $t-1$ refers to variables summarising wildfire smoke and other annual conditions over the preceding calendar year (January–December of year $t-1$).

$$PM2.5_{i,t-1} = \beta_1 FWI_{i,t-1} + \boldsymbol{C}_{i,t-1}\boldsymbol{\gamma}_1 + \boldsymbol{LC}_{i,t-1}\boldsymbol{\delta}_1 + \boldsymbol{S}_{i,t}\boldsymbol{\eta}_1 + \theta_1 BA_{i,t-1} + \pi_t + \mu_i + \varepsilon_{i,t}, \quad (5)$$

$$BIODIV_{i,t} = \beta_2 \widehat{PM2.5}_{i,t-1} + \boldsymbol{C}_{i,t-1}\boldsymbol{\gamma}_2 + \boldsymbol{LC}_{i,t-1}\boldsymbol{\delta}_2 + \boldsymbol{S}_{i,t}\boldsymbol{\eta}_2 + \theta_2 BA_{i,t-1} + \pi_t + \mu_i + \varepsilon_{i,t}. \quad (6)$$

[17] Banding data are collected by capturing, marking, and releasing individual birds so that, when they are captured again, changes in their body condition can be measured over time.

Thereby, $\text{PM2.5}_{i,t-1}$ denotes the average daily wildfire smoke sourced PM2.5 pollution within the relevant landscape of each transect i and $\text{FWI}_{i,t-1}$ is the average value of the fire weather index. Furthermore, the vectors $\mathbf{C}_{i,t-1}$ represent the climatological controls (including temperature, precipitation, relative humidity, wind speed, and the palmer drought severity index), $\mathbf{LC}_{i,t-1}$ land cover and crop land (e.g., crops, crop diversity, pasture), and $\mathbf{S}_{i,t}$ the BBS survey controls (e.g., date of the survey, observer experience, presence of assistant, start- and end time, weather conditions, survey month). Furthermore, $BA_{i,t-1}$ denotes the percentage of area burned within the landscape around the transect, and π_t and μ_i account for unobserved year and transect fixed effects, respectively. $\epsilon_{i,t}$ are idiosyncratic errors. In Equation (6), $\text{BIODIV}_{i,t}$ is replaced by each of the three biodiversity metrics and $\widehat{\text{PM2.5}}_{i,t-1}$ is the predicted value of wildfire smoke PM2.5 in Equation (5).

Given that the unit of analysis is on a local level (i.e., landscape around a transect), concerns about spatial correlation across transects may arise. Specifically, ecological integration between transects is likely to intensify with geographical proximity, and thus, shocks to biodiversity may be correlated. To address this issue, the regression models are estimated using methods that are not only robust to heteroskedasticity but also account for spatial correlation up to 100km. This choice is motivated by the fact that, within this range, each transect has at least one neighbouring transect. However, given this threshold selection is somewhat arbitrary, we assess how sensitive our estimates are up to a distance cutoff of 500km. In addition, the regressions are specified to account for serial correlation up to a lag of two years.[18] Thereby, we follow the implementation of spatial and serial correlation adjustment for regressions with high dimensional fixed effect with instrumental variables building on Hsiang (2010) and implemented in Baum-Snow and Han (2024).[19]

In addition to examining the impacts of wildfire smoke from the prior year, we investigate whether wildfire-specific air pollution has a more sustained effect on the biodiversity metrics by incorporating lagged values of the PM2.5 variable up to $t-1-z$ in Equation (6). When

[18] The maximum number of temporal lags for the Bartlett window, where serial correlation is assumed to vanish, follows Greene (2000)'s rule of thumb of $T^{0.25}$, where T is the number of time periods. For $T = 14$ this suggests a lag cutoff of $\approx$2 periods.

[19] The module can be installed from: https://github.com/Ramin001/reg2hdfespatial.

instrumenting for these lagged values, we do not include the full set of lagged FWI variables in a joint 2SLS framework. This is because it would be inaccurate to assume that $t-1-z$ values of FWI could serve as valid predictors for $t-1-z+n$ values of PM2.5, where $n = 1, \ldots, N$. Instead, we estimate Equation (5) to generate predicted values $\widehat{\text{PM2.5}}_{i,t-1}$, which are then included, along with their lagged counterparts, in Equation (6). However, the predicted $\widehat{\text{PM2.5}}_{i,t-1}$ and their lagged values have their own unique distribution, making spatial heteroskedasticity and autocorrelation consistent (HAC) standard errors unsuitable in this context. While one could theoretically use bootstrapped standard errors if spatial correlation were not a concern, there is currently no widely accepted method for incorporating spatial correlation into standard bootstrapping techniques. As a result, we opted to use HAC bootstrapped standard errors with 500 replications in the lagged estimations, acknowledging that this method does not account for spatial correlation. Consequently, the findings regarding lagged impacts should be interpreted with caution.

5 Results and discussion

5.1 Short-term impact

Column (1) of Table 2 shows the first stage estimation results of Equation (5). We find that the fire weather index is a strong predictor of smoke pollution with a unit increase of the average annual FWI leading to an increase in average annual wildfire-specific PM2.5 of ≈0.2 μg/m^3. The first stage joint F-statistic of 78.0 indicates that a weak instrument problem can be excluded (Stock et al., 2002). Furthermore, columns (2) to (4) show the reduced form estimates regressing the biodiversity outcomes on the instrumental variable. The results indicate a negative significant relationship between fire danger and all the biodiversity metrics.

The outcomes of regressing the biodiversity metrics on average wildfire smoke pollution of the prior year as described in Equation (6) are shown in Table 3.[20] Columns (1), (3), and (5) show the results of the OLS estimations. The estimates are negative but relatively small and

[20]The full regression table is shown in Table A1 in Appendix A and the estimation of the contemporaneous year (January to June) are shown in Table A2 in Appendix A.

Table 2: First stage regression and reduced form estimates.

	(1) Mean daily PM2.5 $_{t-1}$	(2) ln (Species Richness) $_{t}$	(3) Shannon Index $_{t}$	(4) Phylogenetic Diversity $_{t}$
FWI monthly mean $_{t-1}$	0.2143***	-0.0021***	-0.0020**	-0.0020**
	(0.0243)	(0.0006)	(0.0007)	(0.0007)
1st stage F-Statistic	78.0			
Model	1st stage	RF	RF	RF
N	23,917	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) RF = Reduced form; (iii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iv) the biodiversity metrics are constructed using the North American Breeding Bird survey, daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0, and the the daily fire weather index data is provided by McElhinny et al. (2020).

Table 3: Wildfire smoke and biodiversity (2008-2022).

	ln (Species Richness) $_{t}$		Shannon Index $_{t}$		Phylogenetic Diversity $_{t}$	
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_{t-1}$	-0.0001	-0.0099***	-0.0007	-0.0094**	-0.0003	-0.0095**
	(0.0003)	(0.0028)	(0.0004)	(0.0035)	(0.0005)	(0.0032)
% of landscape burnt $_{t-1}$	-0.1098**	0.2181*	0.0443	0.3413**	-0.0977	0.2132
	(0.0392)	(0.1104)	(0.0513)	(0.1301)	(0.0530)	(0.1221)
Model	OLS	IV	OLS	IV	OLS	IV
Transect & year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	23,917	23,917	23,917	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

insignificant. Using the IV estimations in Columns (2), (4), and (6), and thus accounting for the endogeneity concerns over wildfire smoke, all three estimates are negative and significant on the 1% level. Using the descriptive statistics shown in Table 1, the beta coefficients indicate that a 1-standard deviation increase in wildfire smoke leads to a 0.12 ($-0.0099 \times 3.44/0.29 = -0.117$), 0.08 ($-0.0094 \times 3.44/0.42 = -0.076$), and 0.09 ($-0.0095 \times 3.44/0.36 = -0.091$) standard deviation decrease in species richness, in the Shannon index, and in phylogenetic

diversity, respectively.[21] While these effects may appear relatively small, they imply that for the average PM2.5 value in the sample (4.48), the estimated impact is a decrease of ≈ 0.04 in species richness ($-0.0099 \times 4.48 = -0.044$), the Shannon index ($-0.0094 \times 4.48 = -0.042$), and phylogenetic diversity ($-0.0095 \times 4.48 = -0.043$). For the most polluted observation in the sample (83.39), the corresponding impacts result in a decreases of ≈ 0.8 in the biodiversity outcomes, equivalent to ≈2-3 standard deviations in the biodiversity metrics.

Adding the controls used in Equation (6) sequentially shows a relatively stable coefficient for all three biodiversity metrics. For example, it ranges from -0.0074 using only unit and year fixed effects to -0.0098 for the full estimations with all the controls when regressing species richness on wildfire-specific smoke pollution. The full tables are available in Appendix A, where Table A3 shows the full table for species richness, Table A4 for the Shannon index, and Table A5 for phylogenetic diversity.

While our main estimation already controls for burned area to isolate the impact of wildfire smoke, further stratifying the transects by burned area occurrence within a landscape around a transect provides additional insight by disentangling the effects on transects with burned areas from those without, allowing us to fully exclude the influence of direct habitat destruction. Table 4 presents the results of stratifying transects based on burned area occurrence. The larger coefficients in Columns (1), (3), and (5) indicate that the negative overall effects of wildfire smoke on the biodiversity metrics are predominantly driven by transects where no area is burnt within the relevant landscape. These results corroborate that our findings are primarily driven by wildfire smoke originating from fires in surrounding or upwind areas, and that we are not capturing direct habitat destruction caused by the flames. Furthermore, Table 5 shows the results when the sample is stratified by the median PM2.5 value ($\approx 3.75 \mu g/m^3$). In the subsample with above median PM2.5 exposure shown in Columns (2),

[21] To contextualise magnitudes, other significant continuous controls show smaller or comparable standardised effects: assistant presence (-0.07 sd), start-of-survey wind (-0.03 sd), start temperature (+0.001 sd), number of stopis with noise (-0.0005 sd), and the PDSI (+0.004 sd) (point estimates in Table A1). Nevertheless, one should note that these coefficients are not intended to be interpreted causally, but simply illustrate relative effect sizes. Also, we do not compare land-cover shares, as their 0-1 scaling makes their coefficients not directly comparable to continuous variables.

Table 4: Wildfire smoke and biodiversity stratified by burned area within a landscape (2008-2022).

	ln (Species Richness) $_t$		Shannon Index $_t$		Phylogenetic Diversity $_t$	
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_{t-1}$	-0.0108***	-0.0058	-0.0106**	-0.0029	-0.0111**	-0.0011
	(0.0029)	(0.0060)	(0.0035)	(0.0072)	(0.0035)	(0.0067)
Model	no BA	% BA > 0	no BA	% BA > 0	no BA	% BA > 0
Transect & Year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	19,714	4,203	19,714	4,203	19,714	4,203

Notes: (i) stars indicate significance according to * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

(4), and (6), the point estimate is significant, while the below median observations do not show a statistically significant decline in biodiversity.

Table 5: Wildfire smoke and biodiversity stratified by median PM2.5 values (2008-2022).

	ln (Species Richness) $_t$		Shannon Index $_t$		Phylogenetic Diversity $_t$	
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_{t-1}$	-0.020	-0.020**	-0.012	-0.021**	-0.020	-0.016*
	(0.013)	(0.007)	(0.013)	(0.008)	(0.013)	(0.007)
Model	< median	> median	< median	> median	< median	> median
Transect & Year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	11,959	11,958	11,959	11,958	11,959	11,958

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

5.2 Heterogeneity by geographical regions and ecoregions

Wildfire smoke may have substantially different impacts on avian biodiversity across geographical areas and ecosystems due to variations in species composition, habitat types, and adaptive capacities. Certain regions may host species that are particularly vulnerable to smoke exposure due to their physiology, behaviour, or ecological roles, while others may exhibit resilience derived from long-term exposure to natural disturbances. Additionally, ecosystem characteristics, such as vegetation type, landscape connectivity, and the quality and quantity of environmental resources, can influence the severity of wildfire smoke impacts. For example, ecosystems with a dense forest cover may act as reservoirs of biodiversity but are also more prone to prolonged wildfire smoke exposure. Conversely, open grasslands may experience shorter impacts.

To capture these heterogeneous spatial effects, the analysis utilises geographical areas pro-

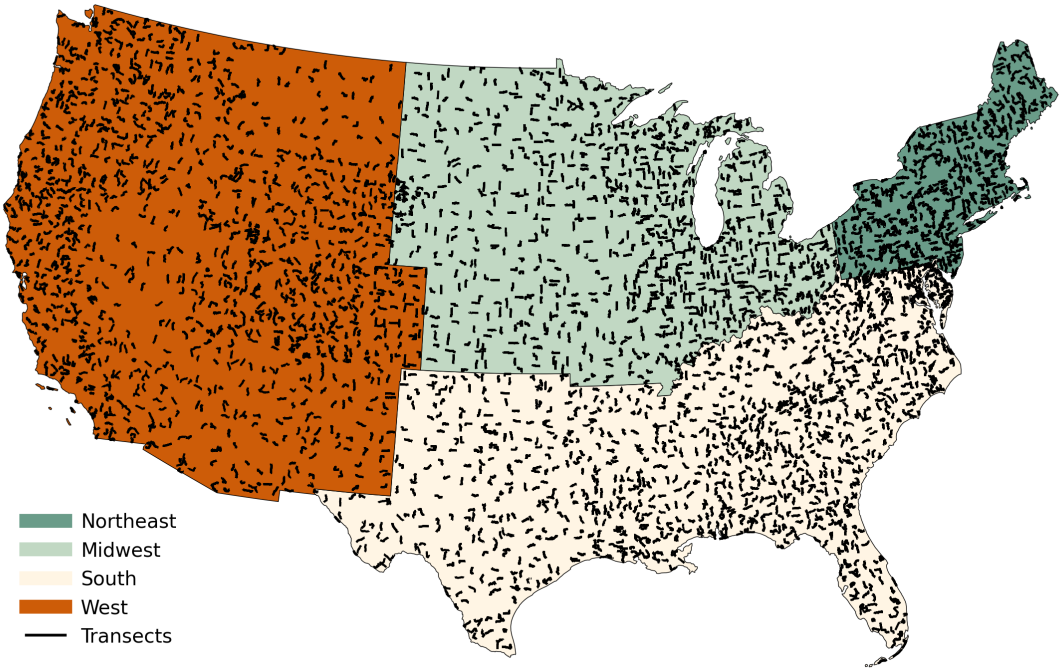


Figure 3: American Breeding Bird survey transects and broad geographical regions in the contiguous United States.

vided by the US Census Bureau[22] dividing the US in four broad geographical regions shown in Figure 3, and in terrestrial ecoregions defined by the Commission for Environmental Cooperation[23] shown in Figure 4. The terrestrial ecoregions dataset, classified at Level 1, divides North America into 15 broad ecological regions, which reflect areas of general similarity in ecosystems and environmental resources. These regions serve as an effective spatial framework for understanding ecosystem-level impacts by providing a structure for research, assessment, and management. By examining the effects of wildfire smoke within this ecological framework, the analysis accounts for variations in the type, quality, and quantity of environmental resources, offering insights into the interplay between smoke exposure and avian biodiversity

[22]The shapefile used for the four broad geographical regions in the contiguous US is available at: https://www.census.gov/geographies/mapping-files/time-series/geo/carto-boundary-file.html.

[23]Descriptions and access to the ecoregions dataset can be found at: http://www.cec.org/north-american-environmental-atlas/terrestrial-ecoregions-level-i/.

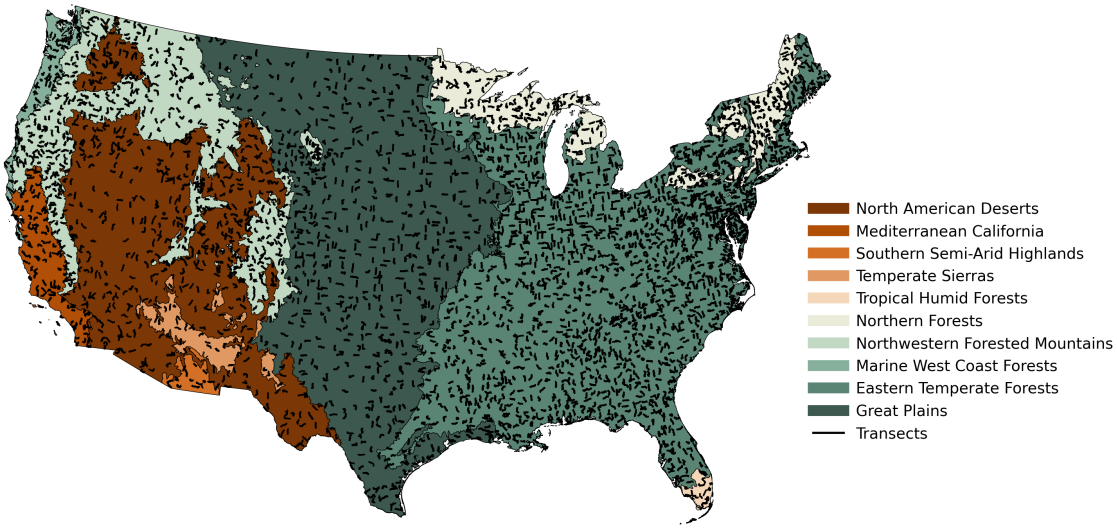


Figure 4: American Breeding Bird survey transects and North American terrestrial ecoregions level 1 in the contiguous United States.

in different ecological contexts.

For all regional estimations, Equation (6) is estimated using the methodology of Driscoll and Kraay (1998), which provides standard errors that are robust to heteroskedasticity, serial correlation (with a bandwidth parameter set to 2 lags), and cross-sectional dependence. This approach is employed because estimating spatial standard errors, as in the baseline estimation, is not feasible for all subsamples due to the small sample sizes and the challenges in adapting the spatial cutoff value. By applying the Driscoll and Kraay (1998) method, consistency is maintained across the regional estimates despite this limitation.

Examining the impact of wildfire smoke on avian biodiversity for the four broad US geographical regions, we find that the overall negative effect on phylogenetic diversity (Table 6) is driven by the West with a significant negative point estimate about 34% larger than in the baseline estimation. Using the descriptive statistics in Table A6 in Appendix A, the beta coefficient of wildfire smoke for the Western US indicates that a 1-standard deviation increase in wildfire-specific PM2.5 pollution leads to a 0.2 ($-0.0127 \times 6.09/0.41 = -0.189$) standard deviation decrease phylogenetic diversity. Note, that while the instrument is strong for the estimations in the West (as well as for the Midwest), it is weak for the Northeast and the

Table 6: Wildfire smoke and biodiversity by geographical regions (2008-2022).

	Phylogenetic Diversity $_{t}$			
	(1) Northeast	(2) Midwest	(3) South	(4) West
Mean daily PM 2.5 $_{t-1}$	-0.0077	-0.0063	0.3086	-0.0127*
	(0.0348)	(0.0093)	(1.4709)	(0.0050)
1st stage F-Statistic	8.6	290.0	0.4	51.8
Transect & year FE	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓	✓
N	3,102	6,619	8,369	5,826

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are computed using the methodology by Driscoll and Kraay (1998) and are robust to heteroskedasticity, serial correlation, and cross-sectional dependence. The bandwidth parameter is set to 2 lags; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

South. Furthermore, we find no clear driver for the decline in species richness (see Table A7 in Appendix A) or the Shannon index shown in Table A8 in Appendix A.

With regard to the analysis by ecoregions, we focus on the five terrestrial ecoregions with more than 500 observations in our sample out of the 10 ecoregions present in our study area.[24] These are the Eastern Temperate Forests (1,356 transects with 11,699 observations), the Great Plains (575 transects with 4,859 observations), the Northwestern Forested Mountains (307 transects with 2,299 observations), the Northern Forests (259 transects with 2,260 observations), and the North American Deserts (250 transects with 1,820 observations). Our analysis shows that the overall negative effect on species richness is driven by the Eastern Temperate Forests and the North American Deserts. Compared to the baseline estimation, the magnitude of the adverse effect is particularly large for the Eastern Temperate Forests,

[24]The excluded ecoregions lack a sufficient number of transects for meaningful analysis, with counts ranging from 9 to 62.

Table 7: Wildfire smoke and species richness by ecoregion (2008-2022).

	ln(Species Richness) $_t$				
	(1) East. Temp. For.	(2) Gr. Plains	(3) Northw. For. Mount.	(4) North. For.	(5) North Americ. Des.
Mean daily PM 2.5 $_{t-1}$	-0.0593*	0.0061	-0.0045	-0.0115	-0.0203*
	(0.0241)	(0.0098)	(0.0029)	(0.0073)	(0.0089)
1st stage F-Statistic	21.0	97.4	58.6	114.5	38.1
Transect & year FE	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓	✓	✓
N	11,699	4,859	2,299	2,260	1,820

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are computed using the methodology by Driscoll and Kraay (1998) and are robust to heteroskedasticity, serial correlation, and cross-sectional dependence. The bandwidth parameter is set to 2 lags; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

where a 1-standard deviation increase in wildfire-specific PM2.5 pollution leads to a -0.5 ($-0.0593 \times 1.62/0.21 = -0.46$) standard deviation decrease in species richness shown in Table 7.[25] In the North American Deserts a 1-standard deviation increase in PM2.5 decreases species richness by -0.2 ($-0.0203 \times 4.13/0.37 = -0.23$) standard deviation.

Similar to species richness, the Eastern Temperate Forests and the North American Deserts are drivers of the adverse effects of wildfire smoke on the Shannon index (Table 8 Column (1)). In addition, the Northern Forests are also experience a significant decline in biodiversity (Table 8 Column (4)). In terms of magnitude, a 1 standard deviation increase in wildfire-specific PM2.5 is associated with a reduction of 0.3 standard deviations in the Shannon index in the Eastern Temperate Forests ($-0.0618 \times 1.62/0.32 = -0.34$), 0.2 standard deviations in the North American Deserts ($-0.0276 \times 4.13/0.48 = -0.24$), and 0.2 standard deviations in the Northern Forests ($-0.0208 \times 1.63/0.22 = -0.16$). Turning to phylogenetic diversity, the ecoregion-specific estimates do not reveal any statistically detectable effects. As shown in Table A10 in Appendix A, no single region is driving the overall pattern.

The driving effects in the West for phylogenetic diversity, and more specifically in the

[25]The standard deviations to calculate the beta coefficients for the ecoregion estimates are shown in Table A9 in A.

Table 8: Wildfire smoke and the Shannon index by ecoregion (2008-2022).

	Shannon Index $_t$				
	(1) East. Temp. For.	(2) Gr. Plains	(3) Northw. For. Mount.	(4) North. For.	(5) North Americ. Des.
Mean daily PM 2.5 $_{t-1}$	-0.0618*	0.0138	-0.0034	-0.0208*	-0.0276*
	(0.0312)	(0.0126)	(0.0037)	(0.0093)	(0.0128)
1st stage F-Statistic	21.0	97.4	58.6	114.5	38.1
Transect & year FE	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓	✓	✓
N	11,699	4,859	2,299	2,260	1,820

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are computed using the methodology by Driscoll and Kraay (1998) and are robust to heteroskedasticity, serial correlation, and cross-sectional dependence. The bandwidth parameter is set to 2 lags; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

North American Deserts (species richness, Shannon index) align with research showing that these areas have experienced an increase in wildfire smoke exposure over the last few decades (Liu and Peng, 2019; Burke et al., 2021; Childs et al., 2022). This suggests that species may not be adapting effectively to increasing levels of smoke pollution, which are closely linked to shifting wildfire regimes. However, in the ecosystem-specific analysis, our results also show the Eastern Temperate Forests (species richness, Shannon index) and the Northern Forests (Shannon index) to be a driver of the adverse impact of PM2.5, a pattern that cannot be attributed to the same underlying reasoning. In conclusion, wildfire-specific PM2.5 pollution appears to have a detrimental impact on avian biodiversity, irrespective of whether pollution levels have been increasing or remained stable over the studied period.

5.3 Persistence of impact

Wildfire smoke exposure may have effects on biodiversity that extend beyond a single breeding season. To examine the persistence of these impacts, we re-estimate Equation (6) including up to five annual lags of wildfire-specific PM2.5 exposure, assessing whether species richness, the Shannon index, and phylogenetic diversity continue to respond to past smoke

events over multiple years. As highlighted in Section 4.2 the reported standard errors of all lagged estimations are not robust to spatial correlation, and thus must be interpreted cautiously. Columns (1) to (5) in Table 9 show that species richness is negatively impacted by PM2.5 predominantly for the prior year for up to five lags. Yet, there may be a small positive effect from the second prior year when adding lag 4 and 5, and thus some weak evidence that species richness is "bouncing back" after two years. However, the magnitude of the coefficient is much smaller, so this effect would not fully compensate the adverse effect. Moreover, as the number of lags increases, the sample size decreases substantially. To check whether our baseline result hinges on the larger sample size, Column (6) replicates the baseline estimation (lag 1) using the reduced sample size from lag 5 in Column (5). The coefficient remains highly significant and slightly larger, reinforcing that our baseline estimate is not an artifact of a larger sample size.

Table 9: Wildfire smoke and species richness with lags (2008-2022).

	ln (Species Richness) $_t$					
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_{t-1}$	-0.0099***	-0.0100***	-0.0081**	-0.0086**	-0.0079*	-0.0111**
	(0.0026)	(0.0028)	(0.0028)	(0.0030)	(0.0034)	(0.0034)
Mean daily PM2.5 $_{t-2}$		0.0003	0.0007	0.0011**	0.0011*	
		(0.0004)	(0.0004)	(0.0004)	(0.0005)	
Mean daily PM2.5 $_{t-3}$			0.0012*	0.0010	0.0009	
			(0.0005)	(0.0006)	(0.0006)	
Mean daily PM2.5 $_{t-4}$				-0.0008	-0.0012	
				(0.0006)	(0.0007)	
Mean daily PM2.5 $_{t-5}$					0.0003	
					(0.0006)	
N	23,917	18,171	14,858	12,125	9,815	9,815

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are bootstrapped (500 replications) and robust to heteroskedasticity and autocorrelation; (iii) the regression includes transect and year fixed effects, climate controls (average monthly rainfall, temperature, minimum and maximum relative humidity, palmer drought severity index), land cover & cropland controls (percentage of food crop, pasture, and land cover types), and survey-level controls (observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month); (iv) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Exploring the lagged estimations for the Shannon index shown in Table 10, the results indicate that the coefficient of lag 1 becomes insignificant when adding lag 3 (Column 3). Furthermore, when reducing the sample size to the lag 5 size (Column 5) the baseline estimate

is insignificant. This indicates that we are somewhat less confident in the negative effect of wildfire-specific PM2.5 pollution on the Shannon index. In contrast, the lagged impacts of wildfire smoke on phylogenetic diversity shown in Table 11 strongly suggest that there is a stable effect of the prior year adding additional lags similar to the findings reported for species richness. For phylogenetic diversity, running Equation (6) with the substantially smaller sample size used for the lag 5 estimations (Column 5) shows a larger effect size of -0.0128 displayed in Table 11 in Column (6).

Table 10: Wildfire smoke and the Shannon index with lags (2008-2022).

	Shannon Index $_{t}$					
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_{t-1}$	-0.0094**	-0.0091*	-0.0053	-0.0023	-0.0002	-0.0055
	(0.0033)	(0.0036)	(0.0038)	(0.0043)	(0.0051)	(0.0049)
Mean daily PM2.5 $_{t-2}$		-0.0002	0.0001	0.0009	0.0007	
		(0.0006)	(0.0007)	(0.0007)	(0.0008)	
Mean daily PM2.5 $_{t-3}$			0.0006	0.0005	0.0005	
			(0.0007)	(0.0007)	(0.0008)	
Mean daily PM2.5 $_{t-4}$				0.0003	0.0005	
				(0.0008)	(0.0010)	
Mean daily PM2.5 $_{t-5}$					0.0002	
					(0.0010)	
N	23,917	18,171	14,858	12,125	9,815	9,815

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are bootstrapped (500 replications) and robust to heteroskedasticity and autocorrelation; (iii) the regression includes transect and year fixed effects, climate controls (average monthly rainfall, temperature, minimum and maximum relative humidity, palmer drought severity index), land cover & cropland controls (percentage of food crop, pasture, and land cover types), and survey-level controls (observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month); (iv) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table 11: Wildfire smoke and phylogenetic diversity with lags (2008-2022).

	Phylogenetic Diversity $_{t}$					
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_{t-1}$	-0.0095**	-0.0114***	-0.0096**	-0.0096*	-0.0095*	-0.0128**
	(0.0031)	(0.0034)	(0.0037)	(0.0040)	(0.0047)	(0.0045)
Mean daily PM2.5 $_{t-2}$		0.0005	0.0005	0.0015*	0.0014*	
		(0.0005)	(0.0006)	(0.0006)	(0.0007)	
Mean daily PM2.5 $_{t-3}$			0.0011	0.0012	0.0007	
			(0.0007)	(0.0008)	(0.0009)	
Mean daily PM2.5 $_{t-4}$				-0.0007	-0.0011	
				(0.0008)	(0.0010)	
Mean daily PM2.5 $_{t-5}$					0.0002	
					(0.0009)	
N	23,917	18,171	14,858	12,125	9,815	9,815

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are bootstrapped (500 replications) and robust to heteroskedasticity and autocorrelation; (iii) the regression includes transect and year fixed effects, climate controls (average monthly rainfall, temperature, minimum and maximum relative humidity, palmer drought severity index), land cover & cropland controls (percentage of food crop, pasture, and land cover types), and survey-level controls (observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month); (iv) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

5.4 Aerosol Optical Depth as wildfire smoke proxy

In addition to using wildfire-specific PM2.5 data, we study biodiversity effects proxying wildfire smoke pollution with aerosol optical depth (AOD) since this data product is available at a higher resolution of 1km. The first stage F-Statistic is 58.9 and, similar to the wildfire-specific PM2.5 data, all the reduced form estimates are negative and significant at the 1% level (see Table A11 in Appendix A). The outcomes of regressing the biodiversity metrics on average aerosol optical depth from the prior year as described in Equation (6) are shown in Table 12. Columns (1), (3), and (5) present the results of the OLS estimations. The estimates are negative but relatively small and insignificant for species richness and phylogenetic diversity. However, the coefficient of the Shannon index is negative and significant. Using the IV estimations in Columns (2), (4), and (6), and thus accounting for the endogeneity concerns over wildfire smoke, all three estimates are negative and significant.

Using the descriptive statistics shown in Table 1, the beta coefficients indicate that a 1-standard deviation increase in aerosol optical depth leads to a 0.17 ($-2.47 \times 0.02/0.29 = -0.17$), 0.11 $-2.36 \times (0.02/0.42 = -0.11)$, and 0.13 $-2.39 \times (0.02/0.36 = -0.13)$ standard

Table 12: Aerosol optical depth and biodiversity (2008-2022).

	ln (Species Richness) $_t$		Shannon Index $_t$		Phylogenetic Diversity $_t$	
	(1)	(2)	(3)	(4)	(5)	(6)
AOD monthly mean $_{t-1}$	-0.05	-2.47***	-0.28**	-2.36**	-0.14	-2.39**
	(0.06)	(0.72)	(0.09)	(0.88)	(0.09)	(0.82)
% of landscape burnt $_{t-1}$	-0.11**	0.03	0.04	0.17*	-0.10	0.03
	(0.04)	(0.06)	(0.05)	(0.07)	(0.05)	(0.07)
Model	OLS	IV	OLS	IV	OLS	IV
Transect & year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	23,917	23,917	23,917	23,917	23,917	23,917

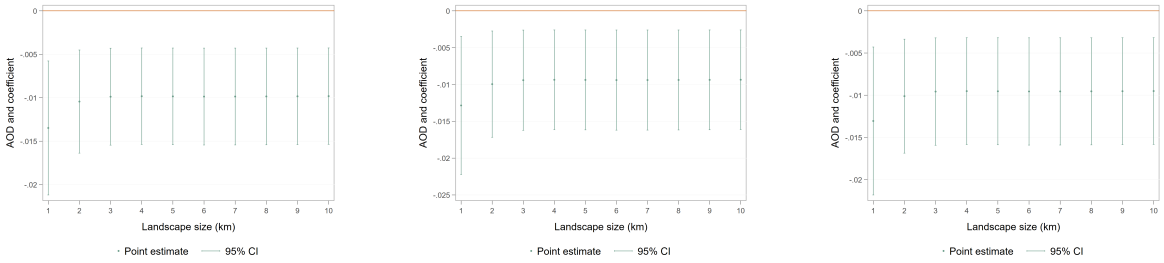
Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and aerosol optical depth is obtained from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product.

deviation decrease in species richness, in the Shannon index, and in phylogenetic diversity, respectively. Although these effects may seem modest, for the average AOD value in the sample of ≈0.1, the coefficients translate to a reduction of 0.27 in species richness ($-2.47 \times 0.111 = -0.278$), 0.26 in the Shannon index ($-2.36 \times 0.111 = -0.266$), and 0.27 in phylogenetic diversity ($-2.39 \times 0.111 = -0.269$). For the highest observed AOD exposure in the sample (0.308), the estimated impacts become more pronounced, with declines of 0.77 in species richness, 0.74 in the Shannon index, and 0.75 in phylogenetic diversity. Similar to the PM2.5 results, this translates into a decrease of 2-3 standard deviations. These findings corroborate the general adverse effects observed on biodiversity metrics when using the wildfire smoke-specific product. However, the slightly larger average AOD results may be attributed to the higher spatial resolution of 10km in the PM2.5 data, which could introduce measurement error, potentially biasing the estimates toward zero.

5.5 Robustness and sensitivity

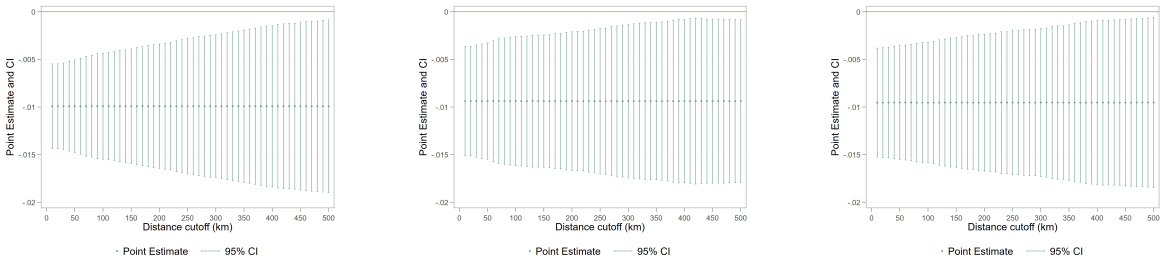
First, we check how sensitive our main results are to the choice of the "relevant" landscape around each transect. This defines the buffer area around each BBS transect for which we calculate the impact of wildfire smoke and for the baseline estimation is chosen at 5km.

Figure 5 shows that the coefficients for all three biodiversity metrics are remarkably robust to the landscape choice varying from 1 to 10km with a slightly higher estimate for the 1km landscape but then stabilising after 3km. Furthermore, we also explore how sensitive our point estimates of Table 3 are to the choice of the cutoff value for the spatial standard errors. Our default choice is 100 km, for which each transect has at least one neighbouring transect. Figure 6 shows that the three main coefficients are significant at the 95% level up to a spatial distance cutoff of 500km.



(a) Species Richness **(b)** Shannon Index **(c)** Phylogenetic diversity

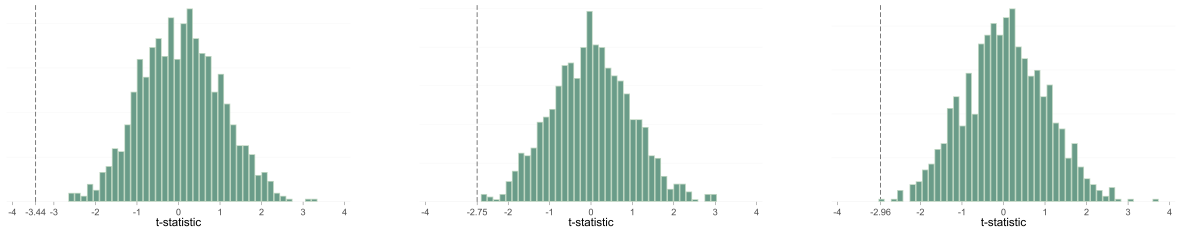
Figure 5: Sensitivity of main coefficients to the relevant landscape around the transects spanning from 1 to 10 kilometres.



(a) Species Richness **(b)** Shannon Index **(c)** Phylogenetic diversity

Figure 6: Sensitivity of main coefficients to the spatial standard errors' distance cutoff.

To assess the robustness of the baseline point estimates to random chance, we perform the Fisher randomisation test, originally introduced by Fisher (1937). This method involves randomly reshuffling the PM2.5 values across time and space, while keeping the instrumental variable and control variables fixed, and re-estimating Equation (6) in 1,000 iterations with replacement. The results, visualised in Figure 7, demonstrate a very high level of statistical



(a) Species Richness **(b)** Shannon Index **(c)** Phylogenetic diversity

Figure 7: Fisher randomisation test of biodiversity estimates with 1,000 iterations. *Note:* the vertical dashed line indicates the t-statistic of our actual estimate.

significance for species richness, the Shannon index, and phylogenetic diversity. The t-statistic of the actual estimate, represented by the vertical dashed line, lies far in the left-hand tail of the distribution, corresponding to a p-value below 0.001 for species richness and the Shannon index, and of 0.01 for phylogenetic diversity. These findings provide strong evidence that the observed results are not driven by chance but rather reflect a genuine relationship. In a similar vein, we conduct a placebo test by regressing the biodiversity metrics on wildfire-specific air pollution in the subsequent year. As expected, the results confirm that we are capturing a genuine lagged effect, with no significant effects observed for events in the future, as presented in Table A12 in Appendix A. This reinforces the validity of our baseline results by demonstrating that the observed effects are not driven by spurious or unrelated temporal dynamics.

One may be concerned that the estimated negative impact of wildfire smoke on bird diversity is driven by movements of birds between neighbouring transects, possibly resulting in biodiversity losses in affected areas merely reflecting displacement to nearby sites, a potential violation of the Stable Unit Treatment Value Assumption (SUTVA). To address this, we create 500 subsamples in which no two transects are closer than 30 km, using a random greedy thinning algorithm that iteratively retains one transect and excludes its neighbours within the distance threshold. The 30 km cutoff corresponds to the median natal dispersal distance of North American bird species as derived from data taken from Chu and Claramunt (2023), ensuring that transects are sufficiently far apart to preclude spillovers through typical bird movements. Imposing this minimum-distance criterion retains roughly 60% of the original sample, providing a large number of independent transects for inference. We rerun

our instrumental-variable estimations across all 500 subsamples and summarise the resulting distribution of coefficients, treating the variation across draws analogously to a bootstrap. As shown in Table 13, the effects of wildfire smoke are negative and statistically significant at the 0.1% level for all three biodiversity metrics. The magnitude of the coefficient for species richness is about 3% smaller than in the baseline specification, whereas the estimates for the Shannon Index (+19%) and phylogenetic diversity (+10.5%) are larger. These estimates demonstrate that our previous findings are not an artefact of birds redistributing into adjacent transects but instead capture genuine declines in biodiversity at the affected locations.

Table 13: Wildfire smoke and bird diversity under transect minimum-distance (30km) sampling.

	ln (Species Richness) $_t$	Shannon Index $_t$	Phylogenetic Diversity $_t$
	(1)	(2)	(3)
Mean daily PM2.5 $_{t-1}$	-0.0095***	-0.0112***	-0.0105***
	(0.0013)	(0.0017)	(0.0017)
Transect & year FE	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓
Survey Ctrl.	✓	✓	✓
Climate Ctrl.	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓
N	14,706	14,706	14,706

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are derived from the variation of the estimated coefficients across 500 random minimum-distance (30 km) subsamples, analogous to a bootstrap procedure; (iii) N reports the average number of observations across the draws; (iv) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (v) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (vi) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vii) the biodiversity metrics are constructed using the North American Breeding Bird survey and aerosol optical depth is obtained from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product.

As an alternative to annual mean smoke exposure, we also examine the frequency of smoke pollution events, measured as the number of days with wildfire-specific $PM_{2.5}$ above $0\,\mu g/m^3$ ("smoke days") and the number of days above $35\,\mu g/m^3$ ("high smoke days"). This responds directly to concerns that biodiversity may be particularly sensitive to acute, short-run smoke episodes rather than annual averages. The first stage results in Table A13 in Appendix A show that the fire weather index provides a strong predictor for both measures (F-statistics of 62.6 and 28.4) and that a unit increase in the FWI is associated with approximately 1 additional smoke day. Similar to the baseline results, the second stage estimates reported in

Table 14 indicate that the OLS coefficients are small and (with the exception of the Shannon index for smoke days) statistically insignificant, whereas the IV estimates are negative and statistically significant at the 1% level for all three biodiversity metrics. Using the descriptive statistics in Table 1, a 1-standard deviation increase in the number of smoke days implies decreases of 0.17 ($-0.0020 \times 25.2/0.29 = -0.174$), 0.11 ($-0.0019 \times 25.2/0.42 = -0.114$), and 0.13 ($-0.0019 \times 25.2/0.36 = -0.133$) standard deviations in species richness, the Shannon index, and phylogenetic diversity, respectively. When using high smoke days (results shown in Table A14 in Appendix A), the corresponding effects are slightly larger but estimated less precisely, consistent with the substantially lower frequency of extreme smoke days. Taken together, these analyses demonstrate that our findings are not an artefact of relying on annual averages. Rather both event-based measures and mean exposure indicate that wildfire smoke reduces local avian biodiversity.

Table 14: Wildfire smoke days and biodiversity (2008-2022).

	ln (Species Richness) $_t$		Shannon Index $_t$		Phylogenetic Diversity $_t$	
	(1)	(2)	(3)	(4)	(5)	(6)
Days with PM_2.5 $> 0\,\mu g/m^3$ $_{t-1}$	-0.0001	-0.0020***	-0.0003**	-0.0019**	-0.0002	-0.0019**
	(0.0001)	(0.0006)	(0.0001)	(0.0007)	(0.0001)	(0.0006)
% of landscape burnt $_{t-1}$	-0.1120**	-0.0686	0.0284	0.0678	-0.1052*	-0.0641
	(0.0381)	(0.0373)	(0.0492)	(0.0496)	(0.0527)	(0.0483)
Model	OLS	IV	OLS	IV	OLS	IV
Transect & year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	23,917	23,917	23,917	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

A further concern is that transect-level survey participation may respond systematically to wildfire activity in the preceding year, thereby generating non-random attrition. To examine this, we construct a transect-year dropout indicator equal to one if a route is surveyed in year $t-1$ but not in year t. We then regress this indicator on prior-year burnt area (binary) using two complementary specifications: (i) a fixed-effects linear probability model with transect

and year fixed effects, and (ii) a probit model in which we report the marginal effect of prior-year burning on the probability of dropout. Both models include the full baseline set of climate and land cover controls. The results, presented in Table A15 in Appendix A, show that the coefficient on prior-year burning is precisely estimated and statistically indistinguishable from zero in both specifications. This indicates that wildfire exposure does not induce systematic attrition of transects and therefore does not bias our main estimates through selective non-observation. A related concern is that wildfire exposure could mechanically affect detectability rather than true abundance e.g., if burning reduces vegetation density and increases visibility. To assess this possibility, we regress the year-to-year changes in the number of birds observed an an indicator for prior-year fire exposure, conditional on the full set of baseline controls. As shown in A16 in Appendix A, the estimates show no evidence of systematic changes in detection.

Finally, we employ an alternative fire danger index, namely the Energy Release Component (ERC), which is a product of the National Fire Danger Rating System and offers a higher spatial resolution ($\approx 4km$) compared to the fire weather index. As shown in Table 15, while the ERC remains a strong instrument, the F-statistic for Equation (5) is lower than that of the FWI. The point estimates are similar for the Shannon Index and slightly lower for species richness and phylogenetic diversity compared to using the fire weather index.

Table 15: Wildfire smoke and biodiversity using the energy release component as the instrumental variable (2008-2022).

	Mean daily PM 2.5 $_{t-1}$	ln (Species Richness) $_t$	Shannon Index $_t$	Phylogenetic Diversity $_t$
ERC monthly mean $_{t-1}$	0.3956***			
	(0.0550)			
Mean daily PM 2.5 $_{t-1}$		-0.0082**	-0.0094**	-0.0074*
		(0.0026)	(0.0034)	(0.0030)
F-Statistic	51.7			
Model	1st stage	IV	IV	IV
N	23,917	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and aerosol optical depth is obtained from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product, and the energy release component is extracted from the Idaho Gridded Surface Meteorological Dataset (GRIDMET).

6 Conclusion

This study provides the first comprehensive evidence quantifying the impact of wildfire-specific smoke pollution on avian biodiversity across the contiguous United States, a key component of natural capital with direct and indirect relevance for human well-being. By assembling a 15-year panel-data set combining the North American Breeding Bird Survey with high-resolution data products on wildfire-specific PM2.5 pollution, burned area, fire danger, land cover, and climate variables, we find significant adverse effects of smoke pollution on both taxonomic and phylogenetic diversity. Furthermore, our findings highlight that the impact of wildfire smoke on avian biodiversity varies across different ecosystems, underscoring the nuanced relationship between ecosystem characteristics and biodiversity responses. More specifically, the Eastern Temperate Forests and North American Deserts are particularly affected by wildfire smoke-driven biodiversity decline. In contrast to the country-level analysis, where all metrics indicate clear biodiversity losses, the ecoregion-specific results reveal that the magnitude and detectability of smoke-driven impacts vary by both ecosystem and metric. Certain metrics capture declines in particular regions while others do not, highlighting the inherent complexity of biodiversity measurement and the importance of metric choice when assessing ecological responses.

While our results show only short-term biodiversity loss following wildfire smoke exposure, this does not imply that such disturbances are harmless. Much like a Jenga tower, a game where players take turns removing blocks from a stacked structure, ecosystems seem to be able absorb the temporary removal or relocation of individual components without immediate collapse. Often, these changes appear harmless, but occasionally, one critical piece (or species) triggers a cascading system failure – and we rarely know in advance which block that will be. Giglio et al. (2024) model this dynamic explicitly, showing that biodiversity loss has highly non-linear effects: even small, temporary shocks can erode functional redundancy, reducing ecosystem resilience and amplifying the impact of future disturbances. In this light, transient disruptions to avian populations may still contribute to long-run ecological fragility, with downstream implications for ecosystem services and economic stability, particularly in already stressed systems.

Finally, it is important to interpret our estimates in light of the distinction between short-run exposure to individual smoke events and long-run adaptation to changing fire regimes. Our empirical strategy exploits year-to-year variation in wildfire-specific PM2.5, analogous to using extreme weather events to study climate impacts. As in the climate literature, such variation is informative about near-term responses but may not fully capture the consequences of persistent shifts in underlying regimes. Long-run increases in smoke frequency or duration could induce changes in species composition, migration patterns, or ecosystem structure that are not well proxied by annual fluctuations in mean exposure. To the extent that repeated smoke exposure erodes ecological resilience or interacts with other stressors, estimates based on short-run variation may therefore understate the long-run biodiversity costs of a warming, fire-prone climate. Understanding these regime-level effects remains an important direction for future research.

Combined, our findings underscore the ecosystem-specific vulnerabilities of avian communities to increasing wildfire-specific PM2.5, offering critical insights into how smoke pollution independently drives biodiversity loss. By disentangling the impacts of wildfire-specific PM2.5 pollution from direct habitat destruction, this research significantly advances our understanding of wildfire-biodiversity dynamics and addresses a crucial gap in the literature. The results of this study carry important implications for economic stability through biodiversity conservation policies. While wildfire management is necessarily prioritised around protecting human health, lives, and property, our findings indicate that wildfire smoke also imposes additional, largely unpriced costs through biodiversity loss. In this context, our findings can guide targeted fire suppression efforts aimed at protecting vulnerable species and ecosystems downwind, as suggested by Woinarski et al. (2023). Proactive strategies, such as managing vegetation to reduce smoke emissions and integrating smoke pollution metrics into conservation planning, are essential for enhancing ecosystem resilience to climate-driven fire regime shifts. Even though quantification of direct economic impacts is challenging (Giglio et al., 2024), it is well-established that intact ecosystems are essential for economic prosperity (Dasgupta, 2021). Future research on the effect of wildfires on biodiversity could build on this foundation by developing methods to monetise the disappearance of specific species, an area where important early contributions are emerging, such as the work by Frank and Sudarshan

(2024), which links biodiversity loss to direct economic costs. More generally, integrating biodiversity impacts with health and property damages in unified evaluation frameworks could help refine conservation and fire management strategies under increasing budget constraints and escalating wildfire risk.

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A Supplementary Information

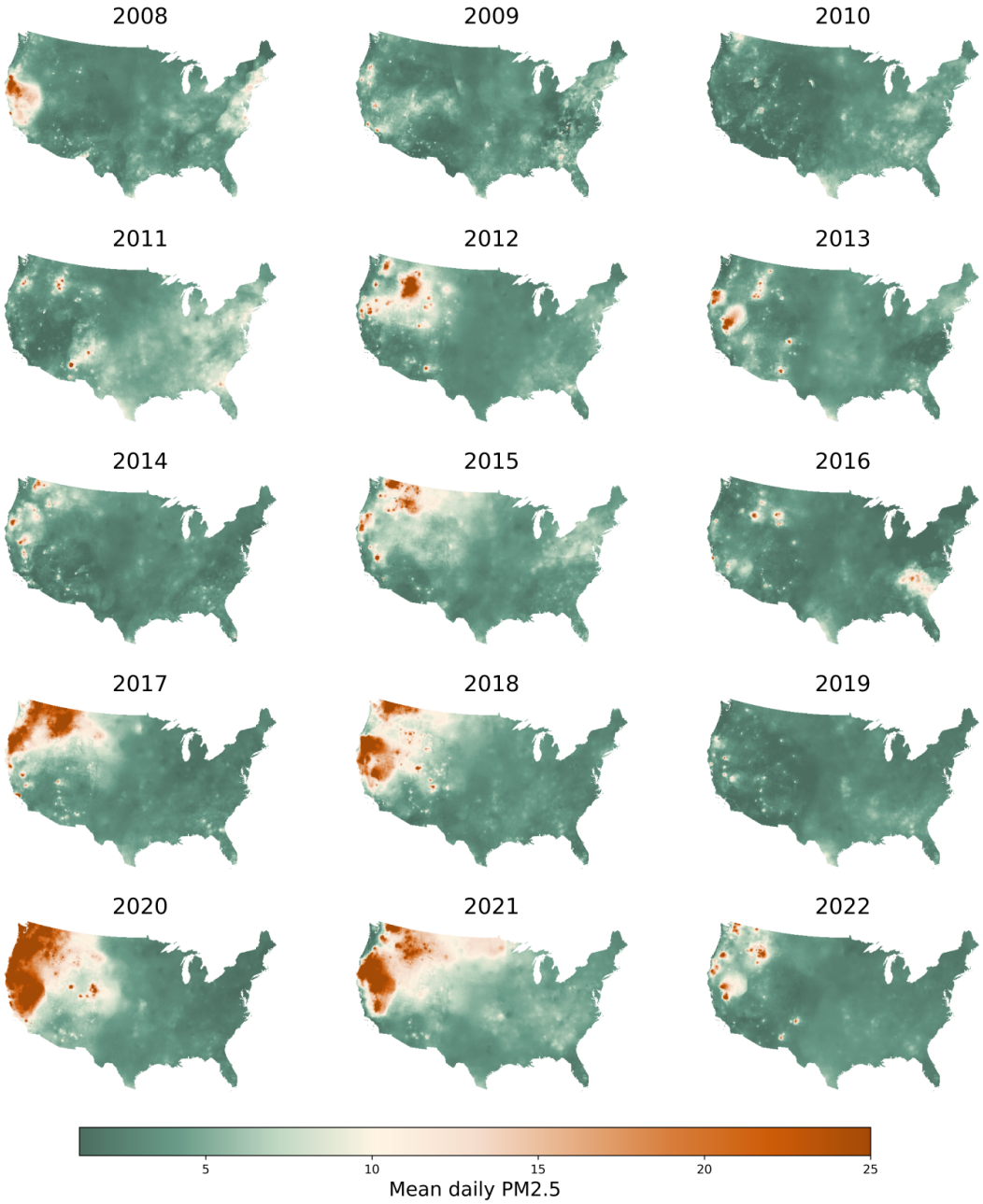


Figure A1: Annual average daily wildfire-specific PM2.5 pollution from 2008 to 2022 by year. *Note:* the daily wildfire PM2.5 data is from the Environmental Change and Human Outcomes (ECHO) lab (Childs et al., 2022) Version 2.0 at a spatial resolution of 10km.

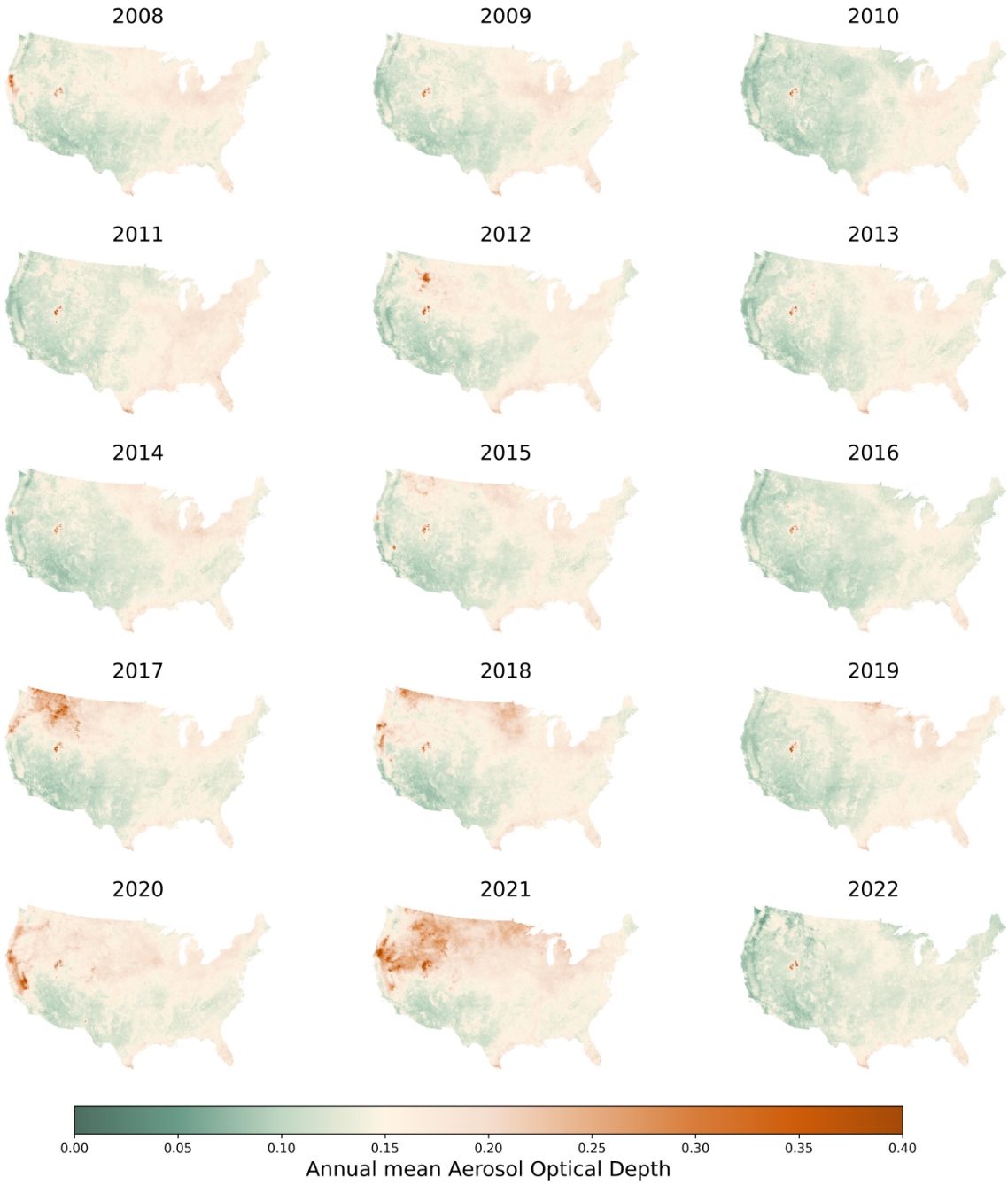


Figure A2: Annual mean aerosol optical depth from 2008 to 2022 by year. *Note:* the data source is the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product.

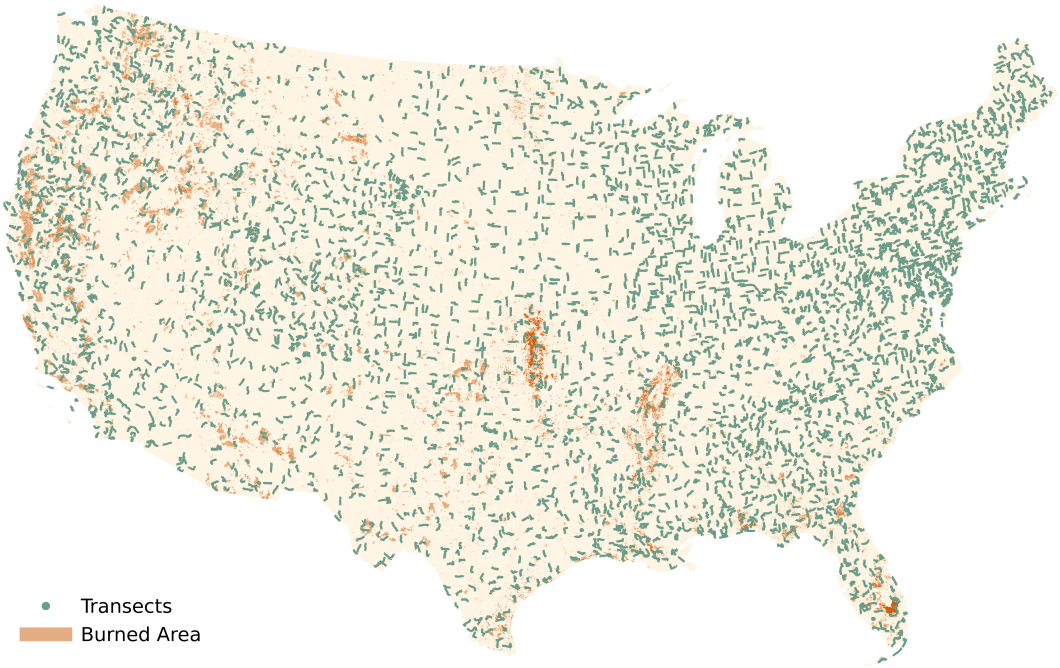


Figure A3: North American Breeding Bird Survey (BBS) transects and 2008-2022 burned area. *Note:* the transects are from the BBS and the burned area from the MODIS MCD64A1.061 monthly burned are product.

Table A1: Wildfire smoke and phylogenetic diversity showing all point estimates (2008-2022).

	(1) Phylogenetic Diversity $_{t}$	
Mean daily PM2.5 $_{t-1}$	-0.0095**	(0.0032)
% of landscape burnt $_{t-1}$	0.2132	(0.1221)
Obs. experience (# transects)	-0.0002	(0.0001)
Assistant	0.0084*	(0.0042)
Cars (#)	-0.0000	(0.0000)
Noise (# stops noise)	-0.0009*	(0.0004)
Start wind (scale)	-0.0079***	(0.0014)
End wind (scale)	-0.0023*	(0.0011)
Start temperature (°F)	-0.0021***	(0.0004)
End temperature (°F)	0.0003	(0.0004)
Start sky (scale)	-0.0034**	(0.0010)
End sky (scale)	-0.0057***	(0.0013)
Start time (hrmin)	-0.0004**	(0.0001)
End time (hrmin)	0.0002***	(0.0000)
Food crop phylogenetic diversity	0.0038	(0.0037)
Food crop (%)	-0.0479	(0.0262)
Pasture (%)	-0.0102	(0.0385)
Fallow crop (%)	0.0331	(0.1409)
Shrubland (%)	-0.0341	(0.0286)
Barren (%)	-0.0640*	(0.0298)
Forest (%)	-0.0374	(0.0268)
Open urban (%)	-0.0370	(0.0287)
Low urban (%)	-0.1603***	(0.0431)
Medium urban (%)	-0.0436	(0.0394)
High urban (%)	-0.0390	(0.0340)
Wetland (%)	0.0174	(0.0494)
Water (%)	-0.0652	(0.0387)
Rainfall (mm)	0.0000	(0.0001)
Temperature (°C)	-0.0028	(0.0024)
Windspeed (m/s)	-0.0154*	(0.0077)
Minimum relative humidity (%)	-0.0039***	(0.0011)
Maximum relative humidity (%)	0.0017**	(0.0006)
Palmer drought severity index (scale)	0.0028***	(0.0008)
N	23,917	

Notes: (i) stars indicate significance according to * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A2: Wildfire smoke and biodiversity January to June in survey year (2008-2022).

	ln (Species Richness) $_t$		Shannon Index $_t$		Phylogenetic Diversity $_t$	
	(1)	(2)	(3)	(4)	(5)	(6)
Mean daily PM2.5 $_t$	-0.0008	-0.0149***	-0.0007	-0.0030	-0.0003	-0.0073
	(0.0005)	(0.0044)	(0.0007)	(0.0054)	(0.0007)	(0.0051)
% of landscape burnt $_t$		0.1789	-0.0328	-0.0036	0.1195	0.1962
		(0.1017)	(0.0868)	(0.1163)	(0.1020)	(0.1265)
Model	OLS	IV	OLS	IV	OLS	IV
Transect & year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	23,862	23,862	23,862	23,862	23,862	23,862

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A3: Wildfire smoke and species richness adding controls sequentially (2008-2022).

	ln (Species Richness) $_t$				
	(1)	(2)	(3)	(4)	(5)
Mean daily PM2.5 $_{t-1}$	-0.0074***	-0.0078***	-0.0078***	-0.0095***	-0.0099***
	(0.0017)	(0.0018)	(0.0017)	(0.0027)	(0.0028)
Transect & year FE	✓	✓	✓	✓	✓
Land cover & crop Ctrl.		✓	✓	✓	✓
Survey Ctrl.			✓	✓	✓
Climate Ctrl.				✓	✓
Burnt area Ctrl.					✓
N	23,922	23,922	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A4: Wildfire smoke and the Shannon index adding controls sequentially (2008-2022).

	Shannon Index $_{t}$				
	(1)	(2)	(3)	(4)	(5)
Mean daily PM2.5 $_{t-1}$	-0.0075***	-0.0080***	-0.0081***	-0.0089**	-0.0094**
	(0.0022)	(0.0022)	(0.0022)	(0.0033)	(0.0035)
Transect & year FE	✓	✓	✓	✓	✓
Land cover & crop Ctrl.		✓	✓	✓	✓
Survey Ctrl.			✓	✓	✓
Climate Ctrl.				✓	✓
Burnt area Ctrl.					✓
N	23,922	23,922	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A5: Wildfire smoke and phylogenetic biodiversity adding controls sequentially (2008-2022).

	Phylogenetic Diversity $_{t}$				
	(1)	(2)	(3)	(4)	(5)
Daily PM2.5 $_{t-1}$	-0.0087***	-0.0091***	-0.0090***	-0.0092**	-0.0095**
	(0.0020)	(0.0021)	(0.0020)	(0.0031)	(0.0032)
Transect & year FE	✓	✓	✓	✓	✓
Land cover & crop Ctrl.		✓	✓	✓	✓
Survey Ctrl.			✓	✓	✓
Climate Ctrl.				✓	✓
Burnt area Ctrl.					✓
N	23,922	23,922	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A6: Summary table of main variables by geographical region.

	Min	Mean	SD	Median	Max	N
Northeast						
# Species	26	60.5	11.3	60.0	144	3,102
log # Species	3.26	4.09	0.18	4.09	4.97	3,102
Shannon index	1.72	3.42	0.25	3.45	4.33	3,102
Phylogenetic diversity	2.20	3.30	0.26	3.34	3.84	3,102
Mean daily PM2.5	0.45	4.25	1.86	4.28	13.86	3,102
% landscape burnt	0	0.00005	0.00	0.00000	0.08	3,102
Mean daily fire weather index	0.7	3.5	1.5	3.2	8.6	3,102
Midwest						
# Species	6	57.8	12.6	58.0	133	6,620
log # Species	1.79	4.03	0.24	4.06	4.89	6,620
Shannon index	1.06	3.21	0.38	3.26	4.25	6,620
Phylogenetic diversity	1.67	3.24	0.33	3.31	4.04	6,620
Mean daily PM2.5	0.74	3.69	1.42	3.44	14.63	6,620
% landscape burnt	0	0.00202	0.02	0.00000	0.60	6,620
Mean daily fire weather index	0.5	6.2	4.2	4.9	35.6	6,620
South						
# Species	16	56.2	15.7	56.0	267	8,373
log # Species	2.77	4.00	0.25	4.03	5.59	8,373
Shannon index	0.80	3.33	0.35	3.39	4.88	8,373
Phylogenetic diversity	2.08	3.19	0.33	3.25	3.95	8,373
Mean daily PM2.5	0.00	4.01	1.58	3.75	17.21	8,373
% landscape burnt	0	0.00493	0.02	0.00000	0.45	8,373
Mean daily fire weather index	1.0	9.3	7.1	7.2	52.9	8,373
West						
# Species	7	47.5	15.3	48.0	115	5,827
log # Species	1.95	3.80	0.36	3.87	4.74	5,827
Shannon index	0.60	3.02	0.51	3.12	4.03	5,827
Phylogenetic diversity	1.83	2.97	0.41	3.01	4.04	5,827
Mean daily PM2.5	0.00	6.15	6.09	4.21	83.39	5,827
% landscape burnt	0	0.00363	0.02	0.00000	0.53	5,827
Mean daily fire weather index	0.6	17.3	10.6	15.4	59.3	5,827

Notes: the biodiversity metrics are derived from the North American Breeding Bird survey and the geographical regions are obtained from the US Census Bureau.

Table A7: Wildfire smoke and species richness by geographical region (2008-2022).

	ln(Species Richness) $_{t}$			
	(1) Northeast	(2) Midwest	(3) South	(4) West
Mean daily PM 2.5 $_{t-1}$	-0.0063	-0.0068	0.4242	-0.0123
	(0.0232)	(0.0062)	(2.0333)	(0.0065)
1st stage F-Statistic	8.6	290.0	0.4	51.8
Transect & year FE	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓	✓
N	3,102	6,619	8,369	5,826

Notes: (i) stars indicate significance according to * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; (ii) standard errors in parentheses are computed using the methodology by Driscoll and Kraay (1998) and are robust to heteroskedasticity, serial correlation, and cross-sectional dependence. The bandwidth parameter is set to 2 lags; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A8: Wildfire smoke and the Shannon index by geographical region (2008-2022).

	Shannon Index $_{t}$			
	(1) Northeast	(2) Midwest	(3) South	(4) West
Mean daily PM 2.5 $_{t-1}$	0.0193	-0.0053	0.2899	-0.0129
	(0.0463)	(0.0090)	(1.4710)	(0.0081)
1st stage F-Statistic	8.6	290.0	0.4	51.8
Transect & year FE	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓	✓
N	3,102	6,619	8,369	5,826

Notes: (i) stars indicate significance according to * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; (ii) standard errors in parentheses are computed using the methodology by Driscoll and Kraay (1998) and are robust to heteroskedasticity, serial correlation, and cross-sectional dependence. The bandwidth parameter is set to 2 lags; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A9: Summary table of main variables by North American level 1 terrestrial ecoregions.

	Min	Mean	SD	Median	Max	N
East. Temp. For.						
# Species	21	58.9	13.1	59.0	263	11,699
log # Species	3.04	4.05	0.21	4.08	5.57	11,699
Shannon index	0.80	3.36	0.32	3.41	4.88	11,699
Phylogenetic diversity	2.08	3.27	0.28	3.32	3.94	11,699
Mean daily PM2.5	0.00	4.00	1.62	3.77	17.21	11,699
% landscape burnt	0	0.00257	0.01	0.00000	0.45	11,699
Mean daily fire weather index	0.5	5.8	2.9	5.2	32.3	11,699
Gr. Plains						
# Species	6	48.9	16.4	49.0	267	4,859
log # Species	1.79	3.84	0.31	3.89	5.59	4,859
Shannon index	1.06	2.95	0.44	3.02	4.68	4,859
Phylogenetic diversity	1.67	2.99	0.40	3.05	4.04	4,859
Mean daily PM2.5	0.60	3.89	1.81	3.44	34.78	4,859
% landscape burnt	0	0.00468	0.03	0.00000	0.60	4,859
Mean daily fire weather index	2.2	14.4	9.3	12.0	54.2	4,859
Nortw. For. Mount.						
# Species	15	54.6	13.6	54.0	115	2,299
log # Species	2.71	3.97	0.26	3.99	4.74	2,299
Shannon index	0.60	3.30	0.34	3.33	4.03	2,299
Phylogenetic diversity	1.98	3.15	0.35	3.21	4.04	2,299
Mean daily PM2.5	1.03	7.79	8.01	5.08	83.39	2,299
% landscape burnt	0	0.00438	0.03	0.00000	0.50	2,299
Mean daily fire weather index	0.8	10.6	5.3	9.5	36.3	2,299
North. For.						
# Species	26	61.7	10.4	62.0	99	2,260
log # Species	3.26	4.11	0.18	4.13	4.60	2,260
Shannon index	1.82	3.47	0.22	3.49	4.08	2,260
Phylogenetic diversity	2.21	3.31	0.26	3.35	3.98	2,260
Mean daily PM2.5	0.55	3.85	1.63	3.69	14.63	2,260
% landscape burnt	0	0.00023	0.00	0.00000	0.09	2,260
Mean daily fire weather index	0.7	3.3	1.3	3.1	8.3	2,260
North Americ. Des.						
# Species	7	39.8	13.3	40.0	90	1,820
log # Species	1.95	3.62	0.37	3.69	4.50	1,820
Shannon index	0.77	2.79	0.48	2.86	4.01	1,820
Phylogenetic diversity	1.83	2.78	0.37	2.78	3.81	1,820
Mean daily PM2.5	0.00	5.40	4.13	4.04	39.90	1,820
% landscape burnt	0	0.00396	0.02	0.00000	0.44	1,820
Mean daily fire weather index	1.6	24.2	10.8	21.4	59.3	1,820

Notes: the biodiversity metrics are derived from the North American Breeding Bird survey and the terrestrial ecoregions are obtained from the Commission for Environmental Cooperation.

Table A10: Wildfire smoke and phylogenetic diversity by ecoregion (2008-2022).

	Phylogenetic Diversity $_{t}$				
	(1) East. Temp. For.	(2) Gr. Plains	(3) Northw. For. Mount.	(4) North. For.	(5) North Americ. Des.
mean annual PM 2.5 $_{t-1}$	-0.0545	0.0166	-0.0083	-0.0191	-0.0178
	(0.0279)	(0.0129)	(0.0044)	(0.0112)	(0.0115)
1st stage F-Statistic	21.0	97.4	58.6	114.5	38.1
Transect & year FE	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓
Burnt area Ctrl.	✓	✓	✓	✓	✓
N	11,699	4,859	2,299	2,260	1,820

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are computed using the methodology by Driscoll and Kraay (1998) and are robust to heteroskedasticity, serial correlation, and cross-sectional dependence. The bandwidth parameter is set to 2 lags; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A11: First stage regression and reduced form estimates of aerosol optical depth and the biodiversity metrics.

	(1) AOD monthly mean $_{t-1}$	(2) ln (Species Richness) $_{t}$	(3) Shannon Index $_{t}$	(4) Phylogenetic Diversity $_{t}$
FWI monthly mean $_{t-1}$	0.0009***	-0.0021***	-0.0020**	-0.0020**
	(0.0001)	(0.0006)	(0.0007)	(0.0007)
1st stage F-Statistic	58.9			
Model	1st stage	RF	RF	RF
N	23,917	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) RF = Reduced form; (iii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iv) the biodiversity metrics are constructed using the North American Breeding Bird survey, daily aerosol optical depth values are derived from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product., and the the daily fire weather index data is provided by McElhinny et al. (2020).

Table A12: Regressing biodiversity metrics on lead wildfire smoke.

	ln (Species Richness) $_{t}$	Shannon Index $_{t}$	Phylogenetic Diversity $_{t}$
	(1)	(2)	(3)
Mean daily PM2.5 $_{t+1}$	0.006	0.002	0.000
	(0.004)	(0.005)	(0.004)
Transect and Year FE	✓	✓	✓
Climate Ctrl.	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓
Survey Ctrl.	✓	✓	✓
N	18,156	18,156	18,156

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and aerosol optical depth is obtained from the MCD19A2.061 Terra & Aqua Multi-angle Implementation of Atmospheric Correction land product.

Table A13: First stage regression using smoke days as the impact variable.

	(1)	(2)
	# of smoke days $_{t-1}$	# of high smoke days $_{t-1}$
FWI monthly mean $_{t-1}$	1.069***	0.091***
	(0.135)	(0.017)
1st stage F-Statistic	62.6	28.4
N	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) Smoke days are defined as days with wildfire-specific PM2.5 $> 0\mu g/m^3$ and high smoke days are defined as days exceeding $35\mu g/m^3$; (iii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iv) the biodiversity metrics are constructed using the North American Breeding Bird survey, daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0, and the the daily fire weather index data is provided by McElhinny et al. (2020).

Table A14: Wildfire smoke **days** above 35 $\mu g/m^3$ and biodiversity (2008-2022).

	ln (Species Richness) $_t$		Shannon Index $_t$		Phylogenetic Diversity $_t$	
	(1)	(2)	(3)	(4)	(5)	(6)
Days with PM_2.5 $> 35\,\mu$g/m^3 $_{t-1}$	-0.0006	-0.0232**	-0.0010	-0.0221*	-0.0008	-0.0224**
	(0.0005)	(0.0076)	(0.0006)	(0.0088)	(0.0007)	(0.0083)
% of landscape burnt $_{t-1}$	-0.0995*	0.5023*	0.0482	0.6124*	-0.0883	0.4882*
	(0.0395)	(0.2349)	(0.0517)	(0.2555)	(0.0528)	(0.2474)
Model	OLS	IV	OLS	IV	OLS	IV
Transect & year FE	✓	✓	✓	✓	✓	✓
Climate Ctrl.	✓	✓	✓	✓	✓	✓
Land cover & crop Ctrl.	✓	✓	✓	✓	✓	✓
Survey Ctrl.	✓	✓	✓	✓	✓	✓
N	23,917	23,917	23,917	23,917	23,917	23,917

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are robust to heteroskedasticity, serial correlation up to 2 years, and to spatial correlation within a distance of 100km; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index; (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) survey controls include observer experience, presence of an assistant, number of cars, noise, start and end measures of wind, temperature, cloud coverage, time, and the survey month; the full set of variables is shown in Table 1; (vi) the biodiversity metrics are constructed using the North American Breeding Bird survey and daily wildfire smoke pollution (PM2.5) is obtained from Childs et al. (2022) Version 2.0.

Table A15: Transect dropout regressed on burnt area in the prior year: fixed-effects and probit models.

	(1) Dropout $_t$	(2) Dropout $_t$
Fire exposed $_{t-1}$	-0.0025	0.0088
	(0.0067)	(0.0058)
Model	FE	Probit
Transect FE	✓	
Year FE	✓	✓
Land cover & crop Ctrl.	✓	✓
Climate Ctrl.	✓	✓
N	27,545	27,545

Notes: (i) stars indicate significance according to * p < 0.05, ** p < 0.01, *** p < 0.001; (ii) standard errors in parentheses are clustered at the route level and are robust to heteroskedasticity and arbitrary serial correlation within routes and include route fixed effects and year fixed effects; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index: (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) the dependent variable is an indicator for dropout, equal to one if a route was surveyed in year $t-1$ but not in year t; (vi) note, that survey information can not be controlled for given the dependent variable are survey dropouts.

Table A16: Detectability check: year-to-year change in observed birds and fire exposure.

	(1) Δ in bird number (t vs. t-1)
Fire exposed $_{t-1}$	-7.81
	(11.53)
Transect & year FE	✓
Climate Ctrl.	✓
Land cover & crop Ctrl.	✓
Survey Ctrl.	✓
N	18,178

Notes: (i) stars indicate significance according to * p $<$ 0.05, ** p $<$ 0.01, *** p $<$ 0.001; (ii) standard errors in parentheses are clustered at the route level and are robust to heteroskedasticity and arbitrary serial correlation within routes and include route fixed effects and year fixed effects; (iii) climate controls include average monthly rainfall, temperature, minimum and maximum relative humidity, and the palmer drought severity index: (iv) the land cover and cropland controls consist of food crop phylogenic diversity, percentage of food crop, pasture, and land cover types; (v) the dependent variable is the year-to-year change in the number of birds observed on a surveyed route; (vi) the sample is restricted to route–years with a survey in both $t-1$ and t, such that the specification tests for detectability-related changes in observed counts rather than survey participation.

B Fire Weather Index (FWI) construction

This appendix documents the final steps of the Canadian Forest Fire Weather Index System that derive the Fire Weather Index (FWI) from the fire behaviour indices, namely the Initial Spread Index (ISI) and the Buildup Index (BUI). The recursive updating equations for the fuel moisture codes (FFMC, DMC, DC), together with the wind and fuel moisture response functions used to construct the ISI and BUI, are detailed in Van Wagner and Pickett (1985).

The Initial Spread Index shown in Equation (7) captures the potential rate of fire spread at the fire front and is defined as

$$\text{ISI} = 0.208 \times f(W) \times f(F), \tag{7}$$

where $f(W)$ denotes a non-linear wind function and $f(F)$ denotes the fine fuel moisture function derived from the Fine Fuel Moisture Code.

The Buildup Index presented in Equation (8) represents total fuel available for combustion, conditional on moisture content in the duff and deep organic fuel layers and is constructed as a function of the Duff Moisture Code, denoted by P, and the Drought Code, denoted by D:

$$\text{BUI} = \begin{cases} \dfrac{0.8\,P\,D}{P + 0.4\,D}, & \text{if } P \leq 0.4D, \\ P - \left[1 - \dfrac{0.8\,D}{P + 0.4\,D}\right]\left[0.92 + (0.0114\,P)^{1.7}\right], & \text{if } P > 0.4D. \end{cases} \tag{8}$$

This piecewise formulation introduces threshold behaviour that shifts the relative influence of the two moisture codes depending on their relative dryness.

The Buildup Index is used to calculate the duff moisture function, $f(D)$, which applies a non-linear transformation to the Buildup Index to express fuel moisture conditions in terms of their contribution to fire intensity, as an intermediate step, in Equation (9):

$$f(D) = \begin{cases} 0.626 \times \text{BUI}^{0.809} + 2, & \text{if BUI} \leq 80, \\ 1000\left(25 + 108.64 e^{-0.023 \times \text{BUI}}\right), & \text{if BUI} > 80. \end{cases} \tag{9}$$

The non-linear scaling and threshold at BUI = 80 reflect a change in the relationship between fuel moisture and fire intensity under very dry conditions.

Subsequently, the duff moisture function is combined with the ISI to derive B in Equation (10), an intermediate form of the FWI representing potential fire intensity prior to final scaling.

$$B = 0.1 \times \text{ISI} \times f(D). \tag{10}$$

Finally, the Fire Weather Index is defined as a non-linear transformation of B shown in Equation (11):

$$\text{FWI} = \begin{cases} B, & \text{if } B \leq 1, \\ 2.72\,(0.434\ln(B))^{0.647}, & \text{if } B > 1. \end{cases} \tag{11}$$

This final transformation ensures that the index exhibits increasing sensitivity to extreme fire weather conditions while remaining comparable across a wide range of fire danger levels.