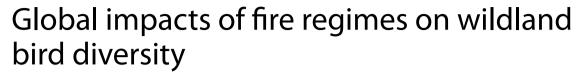


ORIGINAL RESEARCH

Open Access





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Abstract

Background Fire is a natural disturbance that significantly impacts ecosystems and plays a crucial role in the distribution and preservation of biota worldwide. The effects of fires on bird diversity can be both positive, as they can create new habitats, and negative, as they can reduce nesting success. To fully understand the ecological implications of wildfires, we need to understand the spatial distribution of wildland bird diversity and fire regimes and how fire regimes affect wildland bird diversity ecosystems. Using data collected at a global scale, we examined effects of time-averaged fire regimes on the spatial diversity of wildland bird species. Initially, we used the MaxEnt algorithm to model the potential distribution of 1,115 wildland bird species over a 20-year period. We also processed satellite observations of burned areas (FIRECCI51) during the same period to estimate fire regime characteristics, including the average proportion of burnt vegetation, interannual variability in the burnt area, and fire intensity. Finally, the association between wild bird diversity and fire variables in each biome was determined through Spearman, Bonferroni, and Kruskal-Wallis statistics.

Results Our findings revealed that (I) the most affected wildland bird communities are those found in tropical ecosystems, where the majority of fires occur; (II) high fire intensity values and a substantial proportion of burned vegetation have a positive impact on maintaining a diverse population of wildland birds in biomes characterized by savannah or grassland covers, as seen in temperate or tropical zones. Conversely, low fire intensity values and a smaller proportion of burned vegetation also promote greater diversity of wildland birds in boreal or temperate zones, and (III) in Mediterranean ecosystems, a clear association between wildland bird diversity and wildfires could not be established.

Conclusions This research could help identify areas that are ecologically vulnerable to wildfires. It could also be useful in guiding regional studies aligned with developing sustainable landscape management practices and conserving priority ecological zones in tropical ecosystems.

Keywords Wildfires, Fire regimes, Wildland bird diversity, Global scale, Biomes

Resumen

Antecedentes El fuego es una perturbación natural que impacta significativamente en los ecosistemas y juega un rol crucial en la distribución y preservación de la biota en todo el mundo. Los efectos de los incendios en la diversidad de aves pueden ser tanto positivos, dado que crean nuevos hábitats, como negativos, dado que pueden reducir el éxito de nidificación. Para entender completamente las implicaciones ecológicas del fuego, necesitamos entender la distribución espacial de la diversidad de aves silvestres en los diversos ecosistemas, así como de los regímenes de

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fuego, y cómo estos regímenes de fuego impactan en la diversidad de aves silvestres. A través de diferentes bases de datos a escala global, examinamos los efectos espaciales de los diferentes regímenes de fuego sobre la distribución espacial de la diversidad de aves silvestres. Inicialmente usamos el algoritmo MaxEnt para modelar la distribución potencial de 1.115 especies de aves silvestres durante un período de 20 años. Procesamos asimismo observaciones satelitales de áreas quemadas (FIRECCI51) durante el mismo período para estimar las características de los regímenes de fuegos, incluyendo la proporción de la vegetación quemada, la variabilidad interanual en el área quemada y la intensidad delfuego. Finalmente, la asociación entre la diversidad de las especies de aves silvestres y las variables del fuego para cada bioma fue determinada mediante los estadísticos de Spearman, Bonferroni y Kruskal -Wallis.

Resultados Nuestros resultados revelaron (I) las comunidades de aves silvestres más afectadas fueron aquellas encontradas en ecosistemas tropicales, donde ocurren la mayoría de los incendios; (II) Una alta intensidad de los fuegos y una proporción sustancial de la vegetación quemada tiene un impacto positivo en el mantenimiento de lapoblación de aves silvestres en biomas caracterizados por cobertura de sabanas y pastizales, como se ven en zonas subtropicales o templadas. Por otro lado, una baja intensidad de los fuegos y una menor proporción de vegetación quemada promueve una mayor diversidad de aves silvestres en zonas boreales o templadas, y (III) en ecosistemas mediterráneos, no pudo establecerse una clara asociación entre la diversidad de aves y el fuego.

Conclusiones Esta investigación puede ayudar a identificar áreas que son ecológicamente vulnerables a incendios. Puede también ser útil en guiar estudios regionales alineados con el desarrollo de prácticas de manejo sostenible de paisajes y de conservación de zonas prioritarias a nivel ecológicoen ecosistemas tropicales.

Background

Fire disturbance affects global ecosystems and plays an important role in the distribution and maintenance of biota over time and space (Bowman et al. 2009). Fires can have devastating consequences on bird species distribution, modifying the structure and composition of natural assemblages, decreasing nesting success (Cahill and Walker 2000), reducing species abundance (Kinnaird and O'Brien 1998), and changing species composition (Adeney et al. 2006; Barlow and Peres 2004; Blair 2005; Cochrane and Laurance 2002; Kirkman et al. 2001; Midgley and Bond 2015). However, fires can also have beneficial effects on ecosystems, allowing originally absent species to migrate to new habitats (Brotons et al. 2005; Buddle et al. 2000; Pons and Clavero 2010), and opening up the vegetation, so creating simpler plant covers and structures that can be colonized by birds that prefer open habitats, which coexist with pre-fire species with strong links to that particular place (Barlow et al. 2002; Herrando et al. 2002; Moreira et al. 2001; Puig-Giron, Brotons, and Pons 2022). Thus, habitat structure variables such as canopy openness, land use, biomass, temperature, and habitat fragmentation, among others, have an important impact on bird diversity and abundance in burnt wildlands (Barlow and Peres 2004a).

Using threatened species as bioindicators in studies investigating the global impact of disturbances on animal communities unveils crucial insights into ecological vulnerability (Borges et al. 2019). Many threatened species might be more sensitive than other species to common threats like habitat loss and overharvest, making them a non-random sample of all available species. However, the

unfortunately large number of species that are threatened today ensures that these species are increasingly representative of all avian taxa, including both specialists and those with generalist behaviors (Mace and Lande 1991). Thus, studying the worldwide spatial distribution of wild birds through the lens of threatened species underscores the importance of preserving global biodiversity and provides a comprehensive perspective on how wild-fires impact avian communities in various environments (Connell et al. 2017; Lee et al. 2022; Lindenmayer et al. 2023).

The positive and negative effects of fire depend on the particular characteristics of the fire regime. Recent trends indicate that wildfires are becoming larger and more intense, with severe environmental consequences. Extreme fires create large patches of burnt ecosystem, sometimes in excess of 100,000 ha (Cochrane and Bowman 2021; Duane et al. 2021; García et al. 2022; Kelly et al. 2020), affecting significant proportions of the ecosystem. For example, around 30% of the wildland area in southwest Australia was burned in the extreme fire season of 2019-20 (Bowman et al. 2020; Clarke et al. 2022; Jones et al. 2022).

For ecosystems that are adapted to a specific fire regime, there is growing concern about the impacts of a changing fire regime on the distribution and maintenance of wildland bird diversity (Jones et al. 2016; Lindenmayer et al. 2012; Padoa-Schioppa et al. 2006). Within this field, relatively little research has been done on the spatial dependence between fire characteristics such as extension, intensity and frequency and the diversity of wildland bird species around the world. A better

understanding of the interactions between wildfires and wildland bird diversity would be very useful in the design and implementation of effective management policies for the conservation and promotion of the ecosystem that hosts this biological diversity (Elith and Leathwick 2009; Guisan et al. 2013; Guisan and Thuiller 2005; Latif et al. 2018). Research in this field is complicated due to the wide array of variables that influence the dynamism of fire regimes. These variables include interrelated and interacting climate, social, and ecological factors, which make this multidisciplinary area of study particularly challenging. Even though several regional or local studies have explored the relationship between fire variables and bird diversity, they do not normally explore both temporal and spatial aspects of this issue (Barlow et al. 2002; Brotons et al. 2005; Buddle et al. 2000; Herrando et al. 2002; Moreira et al. 2001; Pons and Clavero 2010; Puig-Giron et al. 2022). Therefore, they do not provide a full picture of the dependencies between fire regimes and the diversity of wildland bird species nor do they address the impact of wildfires on the spatial distribution of wildland bird diversity.

This study uses data from around the world to assess which fire regimes promote or reduce avian diversity. First, geographic information systems and machine learning were applied to model the diversity of wild-land bird species, using the biodiversity data provided by Global Biodiversity Information Facilities (GBIF) for the 2001–2020 period. Fire regime variables were computed from a dataset of satellite observations of burnt areas for the 2001–2020 period. Indices measuring fire intensity, interannual variability, and the proportion of burnt vegetation were included in a statistical model to analyze the relationship between these fire variables and the distribution of wildland bird diversity by biome.

Materials and methods

The methodology is outlined in Fig. 1. The aim of the first step was to obtain a spatial distribution of wildland bird species diversity (BSD), using a well-known statistical approach. The aim of step 2 was to estimate fire regime variables from a dataset derived from long-term satellite observations of burnt areas. Finally, the two datasets were linked using various statistical methods to identify which fire regime variables were more significantly associated with wildland bird diversity. Both databases were reprojected at a resolution of 0.25 ° to achieve a reasonable balance between computational efficiency and the need to capture regional patterns (Arrogante-Funes et al. 2021; García et al. 2022).

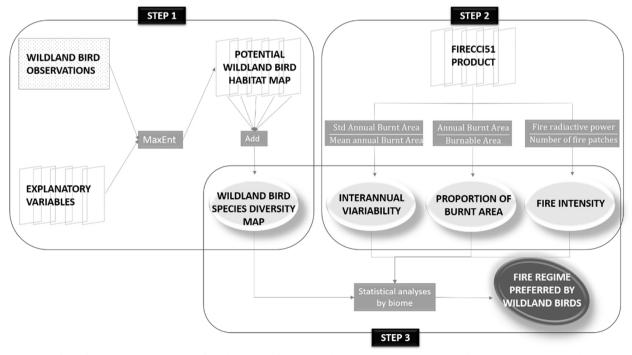


Fig. 1 Workflow of the methodology to identify and assess the fire regimes that either promote or harm wildland bird diversity within their respective ecosystems

Potential bird diversity map Bird data

The wildland bird diversity dataset for the period 2000 to 2020 was obtained from the platform of the Global Biodiversity Information Facility (GBIF) (https://www.gbif. org/es/ last access: 30 November 2022), an international organization that aims to provide free, open access to biodiversity data on a global scale. The GBIF operates as a network of member countries and organizations that contribute to a shared infrastructure and data portal. Its mission is to facilitate the mobilization, access, discovery, and use of biodiversity data to support scientific research, conservation, and sustainable development. The GBIF provides access to a wide range of biodiversity data, including species occurrence records, taxonomic classifications, and ecological data. The data come from a variety of sources, including natural history collections, research institutions, and citizen science projects.

Based on the Red List of Threatened Species, we selected 1115 forest, savannah, and grassland bird species that are categorized as Critically Endangered, Endangered, and Vulnerable (https://www.iucnredlist.org/fr/search?query=birds&searchType=species last access: 30 November 2022). These categories were chosen because they are commonly used in habitat conservation (Hilton-Taylor 2000). The areas inhabited by endangered species are also of particular interest for researchers as they often

have a rich biodiversity because they are also inhabited by other less specific, more common types of bird (Mace and Lande 1991). Out of the total number of species on the list (10,569), only 1115 were selected as they were the only ones for which there was a sufficient amount of observations in the GBIF database, approximately 5.5 million observations. We analyzed the data from the GBIF as to the different places in which the presence or habitat of these 1115 species had been detected (these were often detections of single individuals). After repeated entries and entries with missing coordinates had been filtered out, a total of 3,224,856 geographic points were obtained.

In order to analyze the possible association between wildland bird diversity and fire regimes at spatial scale, the point observations available in the GBIF were converted into a continuous spatial layer with a resolution of 0.25° using the Maxent (Phillips 1997) probabilistic algorithm.

The analysis of this database was based on the biomes proposed by Olson et al. (2001) and uploded by Dinerstein et al. (2017) (Fig. 2), which are homogeneous pieces of land in terms of communities, dynamic processes, and environmental conditions and are particularly appropriate for global-scale studies (Pausas and Ribeiro 2017). From these original biomes, the following were retained for further analyses as places where fire activity has been

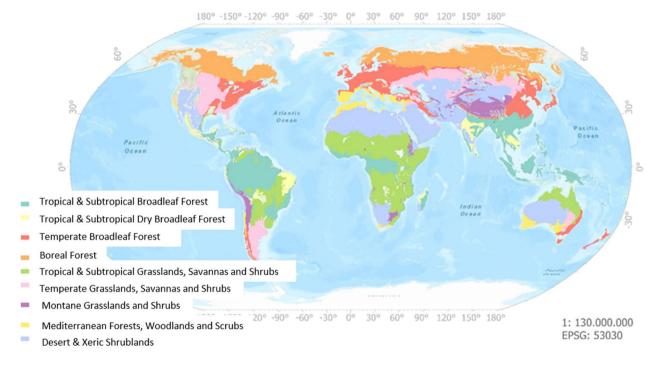


Fig. 2 Terrestrial biomes used in this study (Source: Dinerstein et al. 2017)

Esri, HERE, FAO, NOAA

recorded: tropical and subtropical moist broadleaf forests; dry broadleaf forests and grasslands; tropical and subtropical savannas and shrubs; temperate broadleaf and mixed forests; temperate grasslands, savannas, and shrubs; Mediterranean forests, woodlands, and scrubs; montane grasslands and shrubs; boreal forests; and deserts and xeric Shrubs.

Explanatory wildland bird diversity variables

Based on previous studies (Keast 1990; Petty and Avery 1990), a set of 23 explanatory variables (Table 1) were chosen to model the spatial distribution of bird diversity. Climatic, environmental, geological, topographic, anthropic, and dynamic factors were included in the analysis (Bradie and Leung 2017). All the explanatory variables were discretized at a scale of 0.25° using the average values for each cell. The numerical variables were normalized using a linear function from 1 to 100, with

the exception of the population density variable, which was normalized using a logarithmic function because it does not have a normal distribution (Arrogante-Funes et al. 2021).

Climatic factors were obtained from the Terra Climate database (Abatzoglou et al. 2018), covering global monthly variables with a 1/24° (~4 km) spatial resolution from 1958. This product uses WorldClim, CRU Ts4.0, and the Japanese 55-year Reanalysis. The Palmer Drought Severity Index is a dimensionless numerical variable that expresses the relationship between real evapotranspiration (ET) and potential evapotranspiration (ET0) of the Earth's surface. The value of the index decreases as drought conditions increase. Thermal amplitude is a numerical variable that indicates the difference between the maximum and minimum temperature of the Earth's surface in degrees Celsius. Higher values are therefore observed in more extreme climates with large differences

 Table 1
 Summary of the explanatory wildland bird diversity variables

Factor	Variable	Pre-processed	Source		
Climatic	Palmer Drought Severity Index	Normalized mean data per pixel for a 20-year	Abatzoglou et al. 2018		
	Thermal amplitude	time series			
	Mean temperature				
	Precipitation accumulation				
	Evapotranspiration				
	Land cover	Mask: remove water bodies, ice areas, among others	https://lpdaac.usgs.gov/data/, last access: 20 June 2021		
	Distance to water bodies	Euclidean distance to water bodies and normalized data for each pixel			
	Net photosynthesis	Normalized mean data per pixel for a 20-year			
	Normalized difference vegetation index	time series			
	Biomass	Normalized mean data per pixel			
	Vegetation continuous field	Normalized mean data per pixel for the period of 2014–2020			
Geological	Soil map	Grouping into the 26 main soil categories	Nachtergaele et al. 2010		
3	<i>X</i> coordinate	Estimation of the centroid of each pixel	https://lpdaac.usgs.gov/data/, last access: 20		
	Y coordinate		June 2021		
	Slope	Normalized data for each pixel			
	Digital elevation model				
	Aspect	Estimation from digital elevation model, normalized data for each pixel			
Anthropic	Road density	Normalized data for each pixel	https://www.globio.info/resources, last access 20 June 2021		
	Population density	Normalized mean data per pixel for a 20-year time series	Dobson et al. 2000		
	Distance to human infrastructures	Euclidean distance to human infrastructures and normalized data for each pixel	https://lpdaac.usgs.gov/data/, last access: 20 June 2021 https://www.globio.info/resources, last access 20 June 2021		
Dynamic	Tree canopy cover change	Normalized mean data per pixel	https://glad.umd.edu/dataset/, last access: 25		
,	Short vegetation cover change	for the period 1982–2016	June 2021		
	Bare coil cover change				

between maximum and minimum temperatures. Precipitation accumulation is a numerical variable measuring the average rainfall accumulated annually in millimeters. Lastly, evapotranspiration is quantified in a numerical variable measuring mean annual evapotranspiration in millimeters.

Environmental data were obtained from different datasets from the National Aeronautics and Space Administration (NASA). The Land Cover map was obtained from the MCD12Q1 product, generated by the Moderate Resolution Imaging Spectroradiometer (MODIS) (https://lpdaac.usgs.gov/data/, last access: 20 October 2022). Distance to water bodies is a numerical variable captured in a raster image measuring the distance from each pixel to the center of the closest water mass (from the LC variable). Net photosynthesis (PsnNet) data from the MOD17A2H product is a numerical variable based on the radiation-use efficiency concept that expresses the gross primary productivity minus the maintenance respiration, measured in kg C/m² at a spatial resolution of 500 m. The normalized difference vegetation index (NDVI) from the MOD13A2 is a dimensionless numerical variable that highlights the plant cover and bare soils over large areas. Places with dense, healthy vegetation obtain high values, while areas with poor or scattered vegetation, or with no vegetation at all, have low values which indicate the scarcity or absence of photosynthetic activity. The biomass value obtained from the GFCC30SR product is a numerical variable that expresses the percentage of ground covered by woody vegetation (over 5 m), based on Landsat images at 30 m. Finally, vegetation continuous field data from MOD44B is a numerical variable indicating the percentage of ground covered by vegetation at 250 m. With the set of variables described above, we can get some idea of the condition of the ecosystems.

Geological variables were obtained from the Food and Agriculture Organization of the United Nations (FAO) in association with the International Institute for Applied Systems Analysis (IIASA), the International Soil Reference and Information Centre (ISRIC), the Institute of Soil Science – Chinese Academy of Sciences (ISSCAS), and the Joint Research Centre of the European Commission (JRC) (Nachtergaele et al. 2010). The Soil Map from the Harmonized World Soil Database is a categorical variable expressing the 28 major soil groupings based on existing regional and national updates of soil information worldwide at a spatial resolution of ~ 1 km.

Topographic factors were derived from NASA data (https://lpdaac.usgs.gov/data/, last access: 10 October 2022). The *X* and *Y* coordinates are numerical variables identifying the centroid of the reference pixel. The digital elevation model from the NASA DEM product obtained by the Shuttle Radar Topography Mission (SRTM) is a

numerical variable that expresses elevation data at one arc-second spacing. For more accurate geolocation, the information was combined with Geoscience Laser Altimeter System (GLAS) data obtained from observations from on board the Icesat satellite. Other reprocessing improvements include interpolation for gap filling based on the Advanced Land Observing Satellite Panchromatic Remote-sensing instrument for Stereo Mapping (PRISM) AW3D30 DEM, among others. With this product, we generated the slope and aspect. The slope is a numerical variable measuring the slope of the terrain in percentage terms based on the NASA DEM. Finally, aspect is a categorical variable resulting from the reclassification of the aspect terrain raster layer into eight classes of 45° (Table 2), from northeast to northwest in a clockwise direction.

The anthropic factor was assessed in four ways: firstly, using data from the Oak Ridge National Laboratory (ORNL) (Dobson et al. 2000), the Global Biodiversity Model for Policy Support (GLOBIO) (https://www.globio.info/, last access: 20 June 2022), and NASA (https:// lpdaac.usgs.gov/data/, last entry: 20 June 2021), and secondly, using population density data from the LandScan Global produced by ORNL, a numerical variable expressing the number of people per hectare yearly around the world at 30 arc seconds (~1 km) from 2000 m; the Land-Scan product uses geospatial science, remote sensing data, and machine learning algorithms, so as to capture people's full potential activity during both day and night rather than just their residential location; and thirdly, using road density data obtained from the Global Roads Inventory Projects (GRIP) (https://datacatalog.world bank.org/search/dataset/0040289, last access: 20 June 2021), a numerical variable that measures the meters of road per km² at a five arcminutes resolution ($\sim 8 \times 8$ km). GRIP contains five levels of roads worldwide and is based on different sources, such as Open Street Map. Lastly, distance to human infrastructures from LC is a numerical variable that expresses the Euclidean distance between

Table 2 Aspect classes and abbreviations used

Aspect intervals	Name	Abbreviation
0°-45°	North-East	NE
45°-90°	East-North	EN
90°-135°	East-South	ES
135°-180°	South-East	SE
180°-225°	South-West	SW
225°-270°	West-South	WS
270°-315°	West-North	WN
315°-360°	North-West	NW

the center of each pixel and the nearest urban area at a resolution of 1 km.

The dynamic factor was provided by Global Land Discovery and Analyses (GLAD) through the Long-Term Global Land Change 1982–2016 dataset at a spatial resolution of 0.05 ° (https://glad.umd.edu/dataset/, last access: 25 June 2021). This product was developed from Advanced Very High-Resolution Radiometer (AVHRR) remote sensing data to obtain the net annual land use changes (taking into account both gains and losses) in categories such as vegetation continuous field (VCF), tree canopy (TC) cover, short vegetation (SV) cover, and bare ground (BG) cover. The range of values is between 1 and 100. Tree canopy cover change, short vegetation cover change, and bare ground cover change are numerical variables that measure the net changes over the world over the last 35 years.

Wildland bird species distribution modeling: MaxEnt

The presence-only MaxEnt algorithm (Phillips 1997), which has proved very robust in similar studies (Bradie and Leung 2017), was used for modeling the potential distribution of each wildland bird species. MaxEnt works by identifying patterns in the data, given the constraints imposed on the system, and then choosing the most likely option for the system based on Shannon's entropy maximization principle.

This algorithm calculates a logistic output (mean, maximum, minimum, mode) that can be interpreted as an estimate of the relative probability of species distribution in a certain geographic area (Elith et al. 2011). Values range from 0 (lowest probability) to 1 (highest probability).

MaxEnt can handle continuous numerical and categorical variables and automatically includes the interactions between them. To optimize the model, the regularization multiplier was set to 2.0, and its characteristics were based on variations in Akaike's information criterion and the mean area under the curve (AUC: Elith et al. 2011). Furthermore, to maximize the sensitivity of the model (Freeman and Moisen 2008), various thresholds were tested: threshold=0.5, sensitivity=specificity, maximization (sensitivity+specificity)/2, and minimization of the distance between the ROC plot and (0, 1). In the end, we selected the last of these, i.e., minimization of the distance between the ROC plot and (0, 1).

The MaxEnt model was executed for each species at the biome level. Within each biome, we selected those species which, according to the GBIF, had been observed in that biome. The models were run at a cell resolution of 0.25° by selecting the median value of the 3×3 neighborhood cells. A total of 7928 runs of MaxEnt were executed. In all cases, the input explanatory variables were the same, and

the models were built with 80% of the sample for training and the remaining 20% for validation. Internal calibration of the models was based on 10-fold cross-validation before the final model in each run was selected. Model accuracies were based on AUC values and the Kappa agreement index. To mitigate the border effect between the different biomes, the Maxent models were run after extending the modeling area three cells beyond the edge of each biome and then computing the average probability value within the cells that appeared in the intersection between two adjacent biomes. All the probability maps of presence and absence for each bird species were combined to obtain the map of wildland bird species diversity (BSD) diversity at biome level (a probability value of between 0 and 1 of having that species). Apart from that, moreover, we produce another map with three BSD categories (low, medium, and high), using Jenks Natural, in line with similar studies (Arrogante-Funes et al. 2021; Martínez Vega et al. 2007) in order to subsequently apply different statistics.

Fire regime data

Fire occurrence data was obtained from the FireCCI51 global burnt area product, which was generated as part of the Fire Disturbance project of the European Space Agency's Climate Change Initiative program (https:// climate.esa.int/es/projects/fire/, latest access: October 2022). This product is based on satellite observation data, using Terra-MODIS 250 m near infrared reflectance data. These data are complemented and endorsed by active fire data from the same sensor at a resolution of 1 km (Lizundia-Loiola et al. 2020). The FireCCI51 product is available for 2001-2019, at a global scale, in two spatial resolutions: 250 m and 0.25° grid cells. The latter dataset was used to compute the 19-year time-series of available FireCCI51 data which had three fire variables that were representative of fire regimes according to the classification proposed by García et al. (2022): (a) the proportion of burnt area (PBA), defined as the average ratio between the actual BA for each cell and the burnable area in that cell; (b) interannual variability (IV) in BA, measured as the coefficient of variation between the mean and the standard deviation of annual BA, and (c) fire intensity (FI), measured as the average fire radiative power in megawatts (MW) of the burnt patches in each cell. This last variable was obtained by running a previous contextual analysis to convert burnt pixels into burnt patches, following the methods described by Laurent et al. (2019).

The aim when selecting these three variables was to describe critical characteristics of the fire regime. The PBA highlights the importance of fire in each cell. The burnable area was obtained by adding together all the land covers that could potentially be burnable (forest,

shrub, grass, croplands...). The land cover data for this layer was obtained from the ESA Climate Change Initiative program (http://www.esa-landcover-cci.org/, last access: 10 January 2022). Interannual variability (IV) is an indicator of the duration of fires in a particular area, i.e., how long it takes to put them out (Archibald et al. 2013) and is related to the impact of climate cycles and anthropogenic activity on fire occurrence (Chuvieco et al., 2023). Finally, fire intensity (FI) is a surrogate of burn severity, in that fires have more severe impacts when they release more energy. This variable therefore indicates the seriousness of the damage caused by the fire.

Statistical analyses

The frequency distribution of each fire variable was examined as a function of the biome region to evaluate associations between the response variable (numeric and categorical BSD map) and the explanatory fire regime variables.

Next, inferential statistical tests were conducted to test the significance of the association between BSD numeric and categorical distribution and the explanatory fire regime variables. Spearman correlation coefficients were used to find out whether the association between the numeric BSD map and fire variables was positive or negative. Then, the Kruskal-Wallis test was used to test the significance of the association, as BSD was expressed as a categorical variable. A pairwise analysis called the

Bonferroni test was also performed. This test was used to evaluate whether there were any significant differences between the observed frequencies in the wildland bird diversity categories in relation with the different fire regime variables. Possible statistical errors were controlled by making multiple comparisons. Furthermore, these results allowed us to determine the behavior of fire regime variables within each biome, with a focus on identifying the biomes with the highest and lowest values of wildland bird species.

Results

Distribution of wildland bird diversity

Figure 3 shows the final output of the wildland bird species diversity model. Higher values are found in the tropical regions, particularly in the evergreen biomes, including Amazonia, the Congo Basin and the Gulf of Guinea, and Southeast Asia. High values are also observed in Central and Southeast America, South Africa and Madagascar, Southeast Australia, and several regions in Western Europe.

The MaxEnt integrated model obtained overall accuracy of 87.75% and a Kappa index value of 0.83 (both highly significant: p<0.001). The main explanatory variables were land cover, soil map, thermal amplitude, mean temperature, NDVI, precipitation accumulation, distance to water bodies, Palmer Drought Severity index,

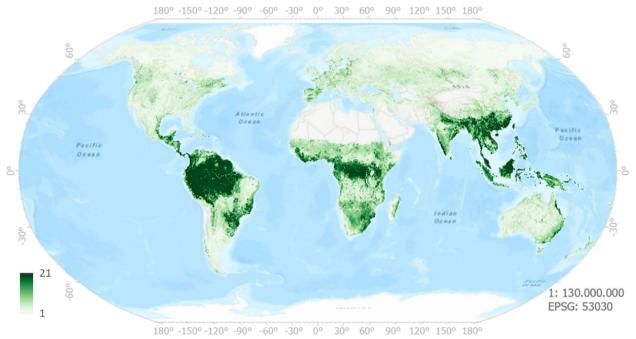


Fig. 3 MaxEnt integration model of the wildland bird species diversity. The values indicate the sum total of the probabilities of the presence of each species in each 0.25° cell

elevation, and road density, accounting for 90% of the model (Table 3).

Impacts of fire regime variables on BSD

At a global scale, there was no clear trend in terms of the association between the wildfire variables and BSD (Fig. 4). There was a significant difference between the PBA values for areas with low BSD and those for areas with medium or high BSD but not between medium and high. The PBA values were higher for the areas with low BSD than for the areas with medium or high BSD values, which means that more extensively burnt areas tend to have lower bird diversity. The Bonferroni tests revealed significant differences between the interannual variability (IV) values for the three BSD classes, which implies that fire duration is an important driver of wildland bird species diversity. The areas with higher BSD tended to have higher IV values. Finally, there were significant differences between the fire intensity (FI) values for the areas with low and high BSD, but the trends were not clear, with a very low negative correlation (spearman rho = -0.01).

More significant associations between BSD and the fire variables were found at biome scale. Figures 5, 6, and 7 include the spatial distribution of the Spearman correlation values between BSD and the fire variables for the different biomes. PBA showed significant negative correlations with BSD in tropical evergreen forest, tropical savannahs, and desert shrublands and positive correlations with BSD in temperate grasslands, including Central Asia and North America and South America and Australia (Fig. 5).

There were significant negative associations (Spearman rho values <-0.2) between interannual variability and BSD in boreal forest, temperate grassland, and montane grasslands (Fig. 6). This variable is positively associated with Tropical evergreen and tropical grassland and savannas. This suggests that the more frequently fires recur, the more diversity they promote in boreal and temperate forest, while in temperate

Table 3 The explanatory power of the input variables in the integrated MaxEnt BSD model accounts for 90% of the model. The variables that contribute to this explanation are shown in gray

	Trop. & Sub. Moist Broadleaf Forest	Trop. & Sub. Dry Broadleaf Forest	Temp. Broadleaf and Mix Forest	Boreal Forest	Trop. & Sub. Grasslands, Savannas, Shrubs	Temp. Grasslands, Savannas, Shrubs	Montane Grasslands, Shrubs	Mediterranean Forest, Woodlands	Desert Xeric Shrubs	Global
Land Cover										
Soil Map										
Thermal Amplitude										
Mean Temperature										
NDVI										
Precipitation										
Water Distance										
PDS Index										
Elevation										
Road Density										
Evapotranspiration										
Slope										
Aspect										
Pop Density										
Net Photosynthesis										
Biomass										
VCF										
BSCC										
Human Distance										
TCCC										

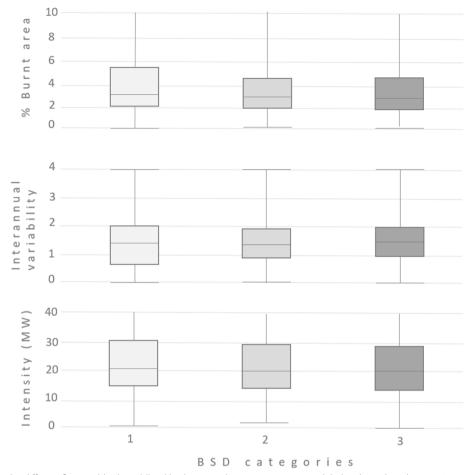


Fig. 4 Boxplots for the different fire variables by wildland bird species diversity categories at global scale. 1=low diversity, 2=medium diversity, and 3=high diversity

grasslands and tropical forest, the higher recurrence of fires reduces biodiversity.

Finally, the association between BSD and the average intensity of fires is much less clear (Fig. 7). The only significant positive Spearman correlations are in biomes with abundant dry vegetation, such as tropical dry forest and desert and xeric shrublands. Slightly positive relations were found for montane grasslands. The trends indicate that the more intense the fires are, the less biodiversity there is in areas that are better adapted to dry periods. These areas are probably covered by xerophytic species, which are more vulnerable to intense fire conditions. However, in montane areas, the more intense fires favor BSD.

Table 4 shows the results of the Bonferroni test assessing whether there are significant differences between the three BSD categories (low-medium-high) for the three fire variables. The BSD in tropical evergreen forest increases with higher IV and FI and lower PBA values; for the tropical dry forest, FI is the only variable with a

significant association with BSD (in this case negative); for temperate forests, no significant associations could be found between BSD and any of the fire variables; for boreal forest, all three fire variables have negative associations with BSD, although the only significant one is IV. For tropical grasslands and savannas, the higher the PBA and FI values, the lower the BSD; for temperate grasslands, the greater the IV and the lower the PBA, the lower the BSD. For montane grasslands, IV is negatively related to BSD, while FI has a positive association with it. In the Mediterranean biome, no significant associations were observed between BSD and any of the fire variables, whereas in desert and xeric shrublands, BSD is negatively related with both PBA and FI.

Discussion

Potential wildland bird species diversity map: data and modeling issues

Using GBIF data and the MaxEnt algorithm, we managed to generate maps highlighting the probability of

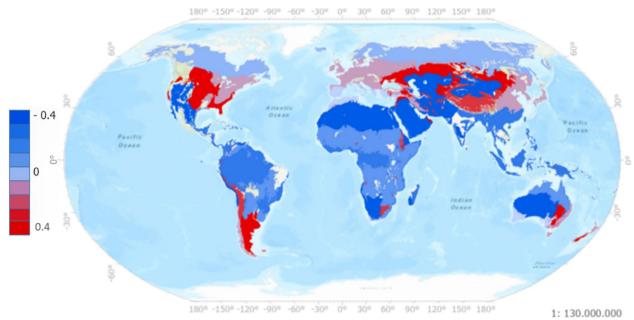


Fig. 5 Spearman correlation coefficient between BSD and PBA. The correlation was computed for all the cells in each biome

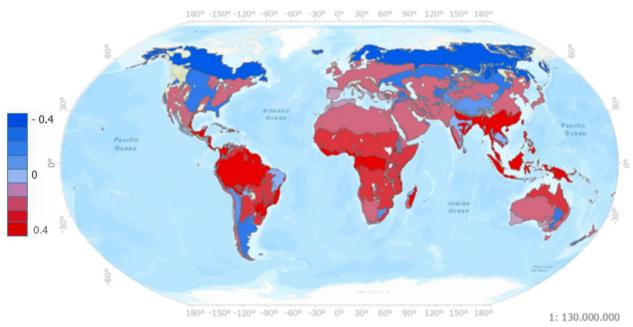


Fig. 6 Spearman correlation coefficient between BSD and IV. Correlation was computed for all the cells in each biome

occurrence (or potential habitat) of each bird species. In this study, we used a traditional approach based solely on data showing the presence of individual species in a particular biome as a sign of their fitness to inhabit such an environment (Hirzel and Le Lay 2008). However, the cost and effort involved in collecting data on this large scale, especially in remote or poor areas, is a challenge

for global studies (e.g., Rocchini et al. 2015). In regions where data are scarce, the only alternative is to use presence data (Anderson and Gonzalez 2011; Zaniewski et al. 2002). This is why we selected GBIF, a presence dataset, for the global analysis performed in this paper. It is important to note that the GBIF dataset has uncertainties arising from the fact that the observations were obtained

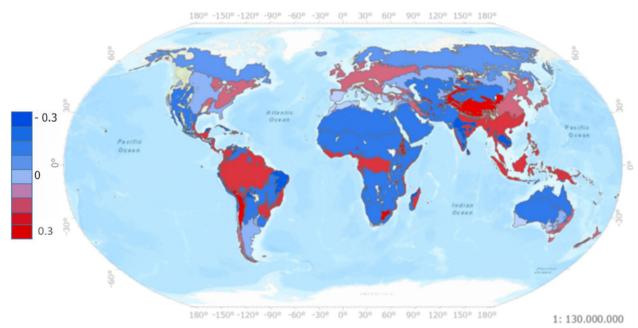


Fig. 7 Spearman correlation coefficient between BSD and Fl. The correlation was computed for all the cells in each biome

Table 4 Results of the Bonferroni test assessing the association between fire variables and BSD categories

	Trop. and sub. moist broadleaf forest	Trop. and sub. dry broadleaf forest	•	Boreal forest	Trop. and sub. grasslands, savannas, shrubs	Temp. grasslands, savannas, shrubs	Montane grasslands, shrubs	Mediterranean forest, woodlands	Desert xeric shrubs
PBA	***		**	**	***	***			***
IV	***			***	***	***	**		
FI	**	***			***	***	***		***

^{***} The test found significant differences between all 3 BSD categories

via crowd-sourcing, which should cause a bias towards regions with a higher density of bird watchers.

Given the global scale, the heterogeneity of the sources used, and the extensive area covered by an ecoregion, sometimes the uncertainty arises less from the method used to combine the databases and more from prior uncertainties in the databases themselves (Richards and Rowe 1999). It is also important to highlight that the global scale provides us with general information on what is happening, so enabling us to detect specific points where the results are unclear, which can then be studied at a more detailed local/regional scale (Goodchild et al. 1993). Despite the above, our approach follows the conceptual framework of essential biodiversity variables (EBVs) proposed by Kissling et al. (2018) which was based on (i) developing models to combine heterogeneous data sets from multiple sources and fill gaps in the geographic coverage data; (ii) integrating emerging data collection methods and technologies, such as citizen science and satellite remote sensing; and (iii) resolving major technical issues relating, among others, to the structure, workflow execution, and production process of the datasets.

Our BSD map contains more points of high species diversity than in previous research by Mittermeier et al. (2011) and Myers et al. (2010) despite being only threatened birds in our study. More specifically our work classifies the entire tropical zone and Southeast Australia as important points of high species diversity. Our results are also consistent with the findings of Neke and Du Plessis (2004) and Maseko et al. (2020) about the high levels of species diversity in the South African biome and with Recher (1969), Wiens (1992), and Razeng and Watson (2014), who found that the canopy cover of a patch, the density of shrubs, and the amount of litter and ground cover strongly influence the diversity of bird species in

^{**} The test only found significant differences between the low and high BSD categories

Southeast Australia. The fact that more areas show high bird species diversity values may be due to the fact that we used the extensive GBIF spatial database and the MaxEnt algorithm as a spatialization method as opposed to the heuristic models used by previous researchers.

Additionally, it is noteworthy that the use of threatened birds as unique observations in our study has identified diversity hotspots similar to previous authors, further contributing to the hypothesis that the use of protected species determines areas with higher ecological values and, consequently, species diversity (Connell et al. 2017; Lee et al. 2022; Lindenmayer et al. 2023).

As happens with the data obtained by Mittermeier et al. (2011) and Myers et al. (2010), GBIF information is not continuous in space and only offers points on the map where birds have been sighted. We therefore decided to complement the GBIF data with MaxEnt, which, unlike the heuristic methods used in the previous studies, facilitates the estimation of probability distributions from incomplete or partial information. Several authors have shown that the MaxEnt approach is more efficient, robust, accurate, and flexible than the heuristic methods (Phillips 1997; Bradie and Leung 2017).

While MaxEnt can handle categorical variables, there are some disadvantages to including them in the model (Phillips 1997). The greater complexity of the model and the correlation with other variables can lead to overfitting of the model. In our study, however, the land cover and soil map variables were processed by assigning arbitrary values to the categories. This ensures that the model accurately identifies the relationships between the variables and the outcome of interest.

Despite this, the land cover and soil map variables were very important for modeling the potential habitats of birds, together with others such as thermal amplitude, mean temperature, NDVI, precipitation accumulation, distance to water bodies, Palmer Drought Severity index, elevation, and road density. In our study, these environmental, climatic, and anthropic factors affect the composition and structure of the forest, which in turn can have a significant impact on the distribution and abundance of bird species (Bradie and Leung 2017). Different bird species have adapted to different types of habitats, so the presence or absence of certain types of vegetation can determine which species are present in a particular area (Atauri and Lucio 2001). The presence of different forest types, such as mixed forests or deciduous forests, can also influence the composition of bird species (Farina 1997; Herrando et al. 2002). In addition, the fragmentation of forests due to human activities, such as the construction of roads and railways, can reduce the size of suitable habitats for some bird species, leading to a decline in their populations. As regards the soil map, the type of soil in an area can also affect the diversity of bird species. Certain soil types may be suitable for specific plant species that are important food sources or nesting habitats for particular bird species (Herrando et al. 2002). For example, acidic soils support the plants that attract the insects on which insectivorous birds can feed, while sandy soils are often a good option for ground-nesting birds. Soil type can also affect the availability of water, which can be critical for birds that require wetland or riparian habitats.

The effects of fire regime on wildland bird species diversity Several authors have shown that fires play a special role in maintaining ecosystem health and conserving biodiversity and pyrodiversity (Bowman et al. 2009; Krawchuk

in maintaining ecosystem health and conserving biodiversity and pyrodiversity (Bowman et al. 2009; Krawchuk and Moritz 2011; Pais et al. 2020).

If we look at wildfires at a global scale, our results indi-

If we look at wildfires at a global scale, our results indicated that the proportion of burnt area (PBA), interannual variability (IV), and fire intensity (FI) are important drivers of the distribution and the maintenance of wildland bird species diversity (BSD), as argued by several authors (Gosper et al. 2019; Jones et al. 2016; Lindenmayer et al. 2012; Parsons and Gosper 2011; San-Miguel-Ayanz et al. 2013; Williams 2013; Xaud et al. 2013). However, the relationship between them is quite complex and mediated by other external factors, such as climate and land cover.

The biomes with the greatest association between wildland bird diversity and fires were tropical forests, savannas, and grasslands, particularly in both tropical fringes of Africa, which host the vast majority of burnt areas worldwide (Lizundia-Loiola et al. 2020, 2022). The more frequent recurrence and low intensity of the wildfires reduce BSD in the tropical and subtropical moist broadleaf forests and grasslands, savannas, and shrubs, as indicated by recent studies of biodiversity by Buisson et al. (2019) and Pivello et al. (2021). According to Phillips (1997) and Laurance and Curran (2008), one of the factors altering bird diversity in tropical and subtropical regions is the current wildfire dynamics in deforested areas and the increasing use of fire in the land-clearing process, a finding reflected in our results in the low BSD values in areas with high PBA and FI. This may indicate that birds from tropical and subtropical evergreen forest prefer ecosystems with low fire activity (Alley et al. 2007). In short, this type of fire regime in which fires are deliberately started by humans suggests that historically there were few wildfires. The birds in these areas have therefore not adapted to the new situation and their populations are dwindling.

The highest values of BSD in boreal and xeric areas, in our study, occurred under low intensity fire regimes. In boreal forests, large and mega-fires are causing huge biodiversity losses due to their long duration and slow

recovery, which leads to the exile of birds and a decrease in the diversity of bird species in burnt boreal areas (Morissette et al. 2002; Schieck and Song 2006). Our results confirm these findings, in that BSD increased in areas with low-intensity fires (Puig-Girón et al. 2022). One example is the desert and xeric shrublands biome, where lower PBA values were associated with increases in BSD, probably because these areas have more insects and nutrients (Levin et al. 2012; Miller et al. 2012). Within a more general approach focused on four bird species, Pastro et al. (2014) studied the possible association between the diversity of bird species and fire regimes. Our study coincides with that of Sietz et al. (2011), who also found a negative association between fire variables and bird diversity, highlighting that these fires are mostly of human origin and are associated with the maintenance of organic matter for the crops.

Our results suggest that wildfires that burn intensely, steadily, and persistently over time support higher wildland bird species diversity (BSD) in the temperate and montane grasslands and scrub shrub biomes, as evidenced in the study of Pons et al. (2003). However, there are few studies on fire regimes and bird diversity in temperate and mountain grass ecosystems, so it would be necessary to delve into this with more regional or local studies. In grassy areas, the fires burn fast but the grass grows back quickly. The birds can resist for a few weeks, and when the pasture comes back, they can return to carry out their biological role in the same places (Coppedge et al. 2008; Daubenmire 1968).

In this context, the type of cover plays an important role, as in the biomes with forests mentioned earlier, low FI and PBA contribute to greater bird species diversity, while in the biomes with grasslands, high FI and PBA values have similar results. The birds in the burnt forests with intense and severe fire regimes cannot complete their biological cycle because the insects (a source of nutrients) (Nilsson 1992) have been killed, and regeneration takes too long (Auclerc et al. 2019; Carbone et al. 2019). In temperate broadleaf forests, intense wildfires promote the canopy's opening and maintain the landscape's heterogeneity (Brotons et al. 2005; Herrando et al. 2002; Puig-Giron et al. 2022). According to previous research (Atauri and Lucio 2001; Farina (1997); Herrando et al. (2002), a heterogeneous plant composition allows the ecosystem to host numerous species of birds. However, in areas with greater fire intensity, the diversity of wildland birds is reduced because they are unable to maintain and carry out their biological cycle in these places because the plant structure takes too long to recover (Brotons et al. 2005; Herrando et al. 2002).

By contrast, in Mediterranean ecosystems no clear association could be found in our study between wildfire

variables and wildland bird diversity, as suggested in other studies by Brotons et al. (2005), Buddle et al. (2000) or Pons and Clavero (2010), among others. This may be due to the fact that this study has a resolution of 0.25° which makes it difficult to capture the great heterogeneity of the ecosystems and therefore the association between wildfire and wildland bird diversity. This is the main vulnerability highlighted by the methodological frameworks (Turner et al., 2003). In this case, it would be of great interest to expand the scale applied in these biomes in order to be able to identify associations between wildfires and the ecological values of these areas.

Understanding the spatial association between wildfires and wildland bird diversity should enable us to identify ecosystems that are ecologically vulnerable to fire. This global-scale study is valuable for identifying issues and guiding more localized research in these critic areas, enabling a more precise characterization of patterns between fire regimes and bird diversity. Thus, this contributes to enhancing conservation strategies and aids in preserving critical habitats for the survival of wild birds worldwide (Connell et al. 2017) and to develop sustainable landscape management practices which can help conserve the priority ecological zones in these ecosystems (Brown et al. 2004; Gilliam 2007). The potential wildland bird diversity map and the differentiation between the three fire regimes will be useful in the selection of new priority areas for protection against fires.

Conclusions

The MaxEnt algorithm was used with GBIF data to develop a Potential Wildland Bird Species Diversity (BSD) map on the basis of limited data at a global scale. Kruskal-Wallis, Bonferroni, and Spearman statistical analyses were used to demonstrate (i) the association between the PBA, IV, and FI and (ii) the fire regimes associated with higher BSD values.

On a global scale, our results show that bird diversity is highly sensitive to fire in moist tropical regions, with negative correlations for PBA and positive for IV and FI. This suggests that BSD increases in areas with varying but intense fire regimes (forest clearing) and decreases as the burnt area increases. In tropical dry regions, an increase in the number of fires, and in their frequency and intensity, has negative effects on BSD. In temperate savannah or grassland covers, higher FI and PBA values tend to promote BSD, while in boreal or temperate zones, low FI and PBA values also benefit BSD. No clear association could be found between BSD and wildfires in Mediterranean ecosystems.

This research could help identify ecologically vulnerable areas to wildfires. It could also be useful in guiding regional studies aligned with the development of

sustainable landscape management practices and the conservation of priority ecological zones in tropical ecosystems.

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Authors' contributions

FAF designed the study, organized and oversaw data collection, developed the analysis approach, and implemented the analysis. IAS and EC obtained funding, drafted the manuscript, and contributed editorial input during manuscript preparation. The authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed here are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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