Coarse-scale effects of land cover and fragmentation on Pyrodiversity

Sofia Bajocco^{1,*}, Daniela Guglietta^{2,*}, José Maria Costa-Saura^{3,4,7}, Gianna Vivaldo^{5,7}, Carlo Ricotta^{6,7}

¹Council for Agricultural Research and Economics, Research Centre for Agriculture and Environment (CREA-AA), Rome, Italy; ²Italian National Research Council, Institute of Environmental Geology and GeoEngineering (CNR-IGAG), Monterotondo, Italy; ³Department of Agricultural Sciences, University of Sassari, Sassari, Italy; ⁴Foundation Euro-Mediterranean Center on Climate Change (CMCC), Sassari, Italy; ⁵National Research Council, Institute of Geosciences and Earth Resources (CNR-IGG), Pisa, Italy; ⁶Department of Environmental Biology, University of Rome 'La Sapienza', Rome, Italy; ⁷National Biodiversity Future Center (NBFC), Palermo, Italy.

*Both authors contributed equally to this work and are listed in alphabetical order. Carlo Ricotta (<u>carlo.ricotta@uniroma1.it</u>)

ORCID

Sofia Bajocco <u>https://orcid.org/0000-0003-2301-9188</u> Daniela Guglietta <u>https://orcid.org/0000-0002-6117-2258</u> José Maria Costa-Saura <u>https://orcid.org/0000-0001-8460-6111</u> Gianna Vivaldo <u>https://orcid.org/0000-0003-4935-5710</u> Carlo Ricotta <u>https://orcid.org/0000-0003-0818-3959</u>

Abstract: Fire plays a crucial role in shaping ecosystem functions at multiple spatial and temporal scales. While traditional studies on fire regimes focus on central tendencies of fire attributes, such as average fire frequency, size, and seasonality, recent research highlights the importance of pyrodiversity as a critical ecological factor. Pyrodiversity reflects the variability in fire attributes across space and time and is thought to increase biodiversity. Although many authors have extensively studied the effects of pyrodiversity on ecosystem functioning, much less attention has been given to the factors driving pyrodiversity. In this paper we explore the influence of landscape drivers, such as land use/land cover (LULC) and fragmentation on the central tendencies and variability of fire regimes in Sardinia (Italy). We use multivariate redundancy analysis (RDA) to investigate how LULC and fragmentation affect the mean and variance of different fire attributes, including fire size and seasonality and the land cover diversity of the fire ignition points. Our results reveal that at the landscape scale, LULC types significantly influence both the central tendency and variability of fire regimes and that the different components of pyrodiversity are driven by distinct LULC types, thus highlighting the complementary nature of pyrodiversity to traditional fire regime parameters. These findings emphasize the need for integrating pyrodiversity into fire management strategies at the landscape scale.

Keywords: Fire attributes; Fire regimes; Landscape fragmentation; Land use/land cover; Redundancy analysis; Sardinia.

Introduction

Fire is a critical ecological process that significantly impacts ecosystem functions, biome distribution, and global biodiversity (Hoffman et al. 2012; Kelly & Brotons 2017; He et al. 2019; Moritz et al. 2023). Fire attributes strongly depend on climate, vegetation, and human activities. Therefore, substantial effort has been dedicated to quantifying the relationship between fire regimes and their climatic, ecological, and anthropogenic drivers (Chuvieco et al. 2008; Krawchuck et al.

2009; Archibald et al. 2013; Hantson et al. 2015). A fire regime is defined as the recurring pattern of fire in a particular area over a period of time and is characterized by a distinctive combination of fire attributes, including burn frequency, severity, seasonality, and spatial pattern (Gill 1975; Bond & Keeley 2005). Fire regime classifications typically focus on the central tendencies of these attributes, neglecting the variability in fire regime characteristics across space and time. However, this variability, referred to as pyrodiversity, is increasingly recognized as a crucial ecological driver, because it supports biodiversity (Maravalhas & Vasconcelos 2014; Jones & Tingley 2022), maintains ecosystem processes (Ulyshen et al. 2021), enhances resilience and stability (North et al. 2021), favors climate adaptation (Jones et al. 2022), and provides cultural and societal benefits (Greenwood et al. 2024).

Martin & Sapsis (1992) first defined pyrodiversity as the "variety in interval between fires, seasonality, dimensions, and fire characteristics, producing biological diversity at the micro-site, stand, and landscape level". The concept of pyrodiversity thus encapsulates the idea that pyrodiversity begets biodiversity across various scales (Tingley et al. 2016). This perspective is supported by evidence indicating that variations in fire attributes can create heterogeneous landscapes composed of diverse habitats, thereby fostering biodiversity in all its forms (Brockett et al. 2001; Steel et al. 2019). As such, pyrodiversity is closely related to the intermediate disturbance hypothesis (Connell 1978; He et al. 2019), which suggests that intermediate disturbance levels maximize diversity by enhancing landscape heterogeneity and habitat diversity, enabling species from early and late successional stages to coexist. However, while the effects of pyrodiversity in determining ecological patterns and processes have been thoroughly explored by many authors (Taylor et al. 2012; Kelly et al. 2015; Steel et al. 2024), the landscape drivers of pyrodiversity remain largely untested.

At the landscape scale, several authors have demonstrated that different land use/land cover (LULC) types are associated with distinct fire regimes (Nunes et al. 2005; Bajocco & Ricotta 2008; Moreno & Chuvieco 2013). This is because LULC results from the complex interactions between climate, vegetation, and human influence, which are also the primary factors controlling fire occurrence. Climate determines the distribution of vegetation types, productivity (i.e., fuel load) and fuel moisture and flammability (Krawchuck & Moritz 2011; Bajocco et al. 2017) such that a close relationship between the type of land cover and the fuel characteristics is usually observed (Turner & Romme 1994; Bajocco & Ricotta 2008). Humans, in turn, have influenced LULC for millennia through their impact on natural vegetation and land-use change (Marlon et al. 2008; Aldersley et al. 2011; Kelly et al. 2020). Humans also extend the length of the fire season (Le Page et al. 2010) and alter the likelihood of fire occurrence, for example by accidental, or deliberate burning for grazing and agricultural practices (Moreira et al. 2011). Consequently, different LULC types are subjected to

distinct fire regimes based on anthropogenic pressure and the structure and flammability of the extant vegetation.

In this paper we will use a Mediterranean wildfire hotspot such as Sardinia (Italy) to explore whether LULC types, in addition to influencing the average conditions of fire regimes, also affect their variability, or pyrodiversity. For this purpose, we selected a set of fire attributes, easily derived from historical fire data, which allow us to characterize both the average behavior of fire regimes and their pyrodiversity. Specifically, this paper addresses the following questions:

Q1) How relevant is the influence of LULC on the central tendency and variability of fire attributes?Q2) Are different components of pyrodiversity influenced by different LULC types?

Materials and Methods

Study area

The island of Sardinia (Figure 1) covers roughly 24,100 km² and has a typical Mediterranean climate with a mild and rainy period from October to May and a warm and dry period from June to September. Annual precipitations range from less than 500 mm along the coast to 1200 mm on the mountains in the inner part of the island (Salis et al. 2015). The highest elevation is 1834 m. The mean annual temperature follows the same altitudinal gradient and ranges from 13 to 18°C.



Figure 1. Location of the study area. The inset represents the 26 Territorial Alert Areas (ATAs) of Sardinia.

Sardinia hosts high ecosystem diversity, encompassing habitats that span from coastal sand dunes to extensive maquis and forests in the mountains (Ricotta et al. 2018). Land cover is shaped by a long human history. Along the coast and in the main plains it is dominated by agriculture, whereas the interior areas are mainly covered by forests, shrublands, and pastures. The principal forest types include broadleaf Mediterranean oaks, such as *Quercus ilex*, and *Quercus suber*. At higher elevations, the sclerophyllous oak forests merge with broadleaved forests of *Quercus pubescens*, and *Castanea sativa*. Urban and industrial areas are concentrated primarily along the coasts and in major cities like Cagliari, Sassari, and Olbia. Tourism also significantly impacts on land use, particularly along the coastal zones during the summer season.

Sardinia is a wildfire hotspot, experiencing over 2800 fire events annually on average (Bajocco & Ricotta 2008). The average annual burned area is more than 10,000 hectares. Like many other regions in southern Europe, most fires are directly caused by human activities. In recent decades, increased summer aridity, the abandonment of traditional agriculture, and the resulting accumulation of fuel have increased the risk of large and severe fires. Though most fires are of human origin, fire is a process largely driven by climate. More than 80% of fires occur between June and September, peaking in July. Fire size ranges over many orders of magnitude from 0.01 ha to >1000 ha, although less than 1% of total events gets larger than 100 ha (Ricotta et al. 2018).

Data and methods

For fire hazard monitoring and modelling, Sardinia has been divided by the regional Forest Service into 26 'Territorial Alert Areas' (ATA). To analyze the relationship between fires and land cover, for each ATA we extracted from the CORINE Land Cover map updated for the reference year 2018 the percentage cover of seven land cover types: (i) urban areas, (ii) arable land, (iii) permanent crops (mainly olive groves), (iv) mixed agriculture (heterogeneous agricultural areas), (v) forests, (vi) grasslands and pastures, and (vii) shrublands (Table 1). Bare soils, wetlands, and water bodies were excluded from the analysis. For details on the CORINE Land Cover products, see https://land.copernicus.eu/en/products/corine-land-cover.

The selected land cover types represent a synthetic expression of the anthropogenic and environmental factors that drive landscape structure and management. Due to the relative homogeneity in the amount and spatial continuity of fuel load within each LULC type, they were considered adequate to study fire occurrence patterns at the landscape scale (Bajocco & Ricotta 2008). To assess the degree of landscape fragmentation in the various ATAs, we calculated an empirical index expressed as the average number of land use patches within a standard area of 10 km² (frag_{LULC}). The higher the number of patches per unit area in a given ATA, the higher its degree of

fragmentation. Based on the fire database recorded by the regional Forest Service for the decade from 2012 to 2021, covering a total of 29,222 fires, we also extracted the following fire attributes for each ATA (Table 1):

- mean (mean_{FS}) and variance (var_{FS}) of fire size (after square root transformation of the fire sizes);
- mean (mean_{JD}) and variance (var_{JD}) of the Julian day of fire ignition;
- mean annual number of fires per 10 km² in each ATA (dens_{NR});
- mean annual burned area per 10 km² in each ATA (dens_{AREA}).

Finally, we also calculated the Simpson LULC diversity of the fire ignition points within each ATA. For categorical variables such as the LULC types, this indicator is regarded as a proxy for variance (Pavoine 2012) and is calculated as follows:

$$\operatorname{div}_{FI} = 1 - \sum_{i=1}^{K} f_i^2 \tag{1}$$

where f_i is the frequency of fire ignitions that occurred in land cover type i (i = 1, 2, ...K). That is, the number of fire ignitions in land cover type i (N_i) divided by the total number (N_{tot}) of fire ignitions in a given ATA: $f_i = N_i/N_{tot}$. In essence, div_{FI} tells us the probability that by randomly selecting two fires, the two fires were not ignited in the same land cover type. Therefore, the higher the value of the index ($0 \le \text{div}_{FI} \le 1$), the greater the diversity of land cover types in which the fires occur.

Variables mean_{FS}, mean_{JD}, dens_{NR}, and dens_{AREA} relate to the central tendency of fire regimes, whereas variables var_{FS}, var_{JD} and div_{FI} pertain to their variability, or pyrodiversity. To quantify pyrodiversity, we thus selected three distinct fire attributes addressing the following questions: When do the fires occur (how variable is their date of ignition)? How large are they (how variable is their size)? How diverse are they in terms of what they burn?

Note that the selected fire attributes can all be easily extracted from historical data on fire occurrences, such as the fire database maintained by the regional Forest Service of Sardinia. Other fire attributes that are less straightforward to extract from historical data, or that require more complex modelling efforts, such as fire intensity (see, e.g., Hempson et al. 2018), were excluded from the analysis. Apart from the theoretical aspects of this type of analysis, the use of readily available data allows for the operational application of the proposed approach for landscape management purposes in any region with an available fire data catalog.

Description	Acronym
Variables related to land cover in each ATA	
1. Percentage cover of urban areas	CLCurban
2. Percentage cover of arable land	CLC <i>arable</i>
3. Percentage cover of permanent crops	CLC _{permcrops}
4. Percentage cover of mixed agriculture	CLC _{mixed}
5. Percentage cover of forests	CLC _{forest}
6. Percentage cover of grasslands and pastures	CLC grassland
7. Percentage cover of shrublands	CLC _{shrubs}
Variables related to landscape structure	
8. Landscape fragmentation within each ATA	frag _{LULC}
Variables related to the central tendency of fire regimes in each ATA	
9. Mean fire size	mean _{FS}
10. Mean Julian day of fire ignition	mean _{JD}
11. Mean annual number of fires per 10 km ²	dens _{NR}
12. Mean annual burned area per 10 km ²	dens _{AREA}
Variables related to the pyrodiversity of fire regimes in each ATA	
13. Fire size variance	var _{FS}
14. Variance of the Julian day of fire ignition	var _{JD}
15. Simpson Diversity of the fire ignition points	div _{FI}

Table 1. Summary table of all variables used in this study. For details on how the variables are calculated, refer to the main text.

To examine the influence of LULC on the fire regime characteristics of Sardinia, we employed redundancy analysis (RDA). This multivariate method, developed by Rao (1964) and introduced to ecological data analysis by ter Braak & Prentice (1988), is an asymmetric canonical ordination technique which quantifies the proportion of total variance in a set of response variables that can be explained by a set of explanatory variables. Essentially, RDA is a constrained principal component analysis (PCA), where the ordination axes are linear combinations of the response variables but are also constrained to be linear combinations of the explanatory variables (Legendre & Legendre 1998). Therefore, unlike PCA, redundancy analysis allows us to divide our data into a set of response variables and a set of explanatory variables, so that the RDA ordination axes represent the percentage of variance in the response variables explained by the predictors.

In fire ecology, redundancy analysis has been employed, for instance, by Elia et al. (2022) to examine the relationships between various climatic, biophysical, and socioeconomic factors and the fire regimes of distinct pyroregions in Italy. In our study, we aimed to understand how LULC influences fire attributes across Sardinia. Therefore, the predictor variables are related to landscape cover and structure in each ATA (variables 1-8 of Table 1), while the response variables were the different fire attributes (variables 9-15 of Table 1). Due to their high heterogeneity, all predictor and response variables were standardized before analysis by subtracting the mean and dividing by the standard deviation.

Results

Overall, the explanatory variables (the landscape attributes) account for 59% of the total variance in the response variables (fire attributes). A significant portion of this variance is captured by the first two axes of the RDA, which explain approximately 52% of the variance in the response variables. Given the coarse-scale approach of this study, this result supports the considerable influence of landscape cover and structure on the fire regimes characteristics of Sardinia and their pyrodiversity. The RDA triplot in Figure 2 reveals two main groups of fire attributes, each influenced by distinct predictor variables: mean fire size (mean_{FS}), variance in fire size (var_{FS}), and the mean Julian day of fire ignition (mean_{JD}) are primarily associated with the first RDA axis and increase with the proportion of heterogeneous agricultural areas and grasslands. In contrast, fire number density (dens_{NR}), burned area density (dens_{AREA}), variance in the Julian day of fire ignition (var_{JD}), and the diversity of ignition points (div_{FI}) are mainly associated with the second axis. dens_{NR} and dens_{AREA} increase with the percentage cover of anthropogenic LULC types, such as urban areas, arable land, and permanent crops, whereas var_{JD} and div_{FI} show the opposite trend: their values increase with the percentage cover of natural and semi-natural classes, such as forests and shrublands and decrease with the cover of anthropogenic land uses. As expected, landscape fragmentation (frag_{LULC}) positively affects var_{JD} and div_{FI}. This is because more fragmented ATAs tend to exhibit higher LULC diversity along with a higher variability in the seasonality of fire occurrence.

In terms of mean fire attributes, along the first axis of the RDA, the increase in mean_{FS} and mean_{JD} is primarily associated with the presence of grasslands, which in Sardinia are generally characterized by large, late-season fires (Bajocco et al. 2010). This is due to their location in more inland areas, at higher altitudes, and under less extreme climatic conditions (i.e., lower summer aridity), resulting in a delayed fire season compared to anthropogenic LULC types in coastal areas. In addition, grasslands are charaterized by fine, relatively continuous, and easily flammable fuels, which contribute to the large fires typically observed in this land cover type (Bajocco et al. 2010, 2017).

In terms of pyrodiversity, a higher proportion of grasslands is also positively related to an increase in fire size variance. This effect is associated with the characteristic power-law distribution of fire size, which is typically marked by a very large number of small fires and only a few large ones (Malamud et al. 1998; Ricotta et al. 1999). Therefore, an increase in the number of large fires leads to greater var_{FS} .



Figure 2. RDA ordination triplot illustrating the influence of land cover and fragmentation (explanatory variables) on fire attributes (response variables). The 26 Territorial Alert Areas (ATAs) are indicated by black squares. Blue dots represent fire attributes, while green vectors represent the landscape attributes. The length of the vectors indicates the strength of the influence of each landscape attribute on the fire attributes. The position of the fire attributes relative to the vectors of landscape attributes reveals the environmental preferences (in terms of LULC and fragmentation) of the different fire attributes. The abbreviations are explained in Table 1. The numbers in parentheses represent the percentage of variance explained by the two RDA axes.

Along the second axis of the RDA, fire number density (dens_{NR}) and the associated burned area density (dens_{AREA}) are both positively related to LULC types with high anthropogenic pressure, such as urban areas, arable land, and permanent crops, where the ubiquity of ignition sources related to human presence, together with more favorable climatic conditions, increase fire ignition probability (Ricotta et al. 2018). In arable land and permanent crops, a higher number of fires per unit area generally leads to a more pronounced increase in burned area density compared to urban areas. This

is because, in these intensive agricultural areas, the greater spatial continuity of fuel promotes fire spread, resulting in larger fires than in urban areas (Bajocco & Ricotta 2008). Conversely, in urban environments, earlier fire detection and more effective firefighting strategies often result in smaller fires, reducing the positive correlation between dens_{NR} and dens_{AREA}.

Looking at pyrodiversity, the variance in the day of fire ignition (var,D), and the diversity of ignition points (div,T) exhibit opposite patterns compared to dens,NR and dens,AREA. Both fire attributes increase with the presence of natural and semi-natural LULC types, and with greater landscape fragmentation, and decrease with increasing cover of urban areas, arable land, and permanent crops. This is because natural and semi-natural land use types, such as forests, shrublands, and to a lesser extent grasslands and mixed agricultural areas, are typically located in more fragmented interior regions with complex physiographic features. As a result, the LULC diversity at fire ignition points tends to be higher in these areas. Similarly, more fragmented landscapes are characterized by patches with varying fuel types, conditions, and availability, which contribute to increased variance in fire occurrence and seasonality.

Discussion and Conclusions

Due to the rising incidence of human-induced fires, whether intentional or accidental, understanding the influence of LULC patterns on wildfire regimes has become a critical area of research. This study explored the influence of LULC and fragmentation on the central tendencies and variability of fire regimes in Sardinia (Italy). Since land cover maps are one of the main tools used by environmental agencies for landscape management at various scales, understanding how LULC influences pyrodiversity has a direct impact on landscape planning and conservation strategies.

In alignment with previous studies (Nunes et al. 2005; Bajocco & Ricotta 2008; Moreno & Chuvieco 2013), our findings demonstrate that, at the scale of our analysis, landscape attributes significantly influence both the central tendency and variability of fire regimes (Q1), and that the different components of pyrodiversity are associated with distinct LULC types (Q2). This is not surprising, as different land uses are complex indicators of distinct aspects of anthropogenic and environmental factors that shape landscape structure and management, as well as the available fuel load and typology (Bajocco et al. 2017). This relationship is primarily governed by two main complementary drivers: human pressure, which influences fire incidence patterns directly through fire ignition and indirectly through its impact on vegetation and fuel load, and climate, which determines the timing of the fire season. Together with the physiographic features of the landscape, climate also acts indirectly on fire regimes, determining the spatial distribution of LULC types (including human settlements), and thus the amount of fuel and its spatial arrangement (see Bajocco

and Ricotta 2008). Therefore, ecologically suitable LULC maps may be helpful for the development of strategies for fire risk assessment under changing climatic scenarios and evolving landscapes. In this context, as with other biological and ecological systems, pyrodiversity (i.e., variance) provides a complementary perspective rather than an alternative to the parameters controlling the central tendency (mean) of fire regimes, thereby offering a more comprehensive view of the complex interactions between fire and land cover.

Finally, in terms of the pyrodiversity-biodiversity relationship, while this paper makes a strong case that pyrodiversity is influenced by the underlying landscape structure, several other studies have observed that pyrodiversity fosters biodiversity at multiple spatial scales. This suggests that biodiversity in fire-prone regions is also linked to landscape structure. Can we disentangle the roles of fire and landscape structure in driving biodiversity? What specific contributions does pyrodiversity make to biodiversity? These are important questions, and their answers could provide valuable insights for developing effective strategies to promote biodiversity and enhance ecosystem resilience across landscapes.

References

- Aldersley, A., Murray, S.J., Cornell, S.E. (2011) Global and regional analysis of climate and human drivers of wildfire. Science of the Total Environment, 409: 3472–3481.
- Archibald, S., Lehmann, C.E.R., Gomez-Dans, J.L., Bradstock, R.A. (2013) Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Sciences, 110: 6442– 6447.
- Bajocco, S., Koutsias, N., Ricotta, C. (2017) Linking fire ignitions hotspots and fuel phenology: The importance of being seasonal., Ecological Indicators, 82: 433–440.
- Bajocco, S., Pezzatti, G.B., Mazzoleni, S., Ricotta, C. (2010) Wildfire seasonality and land use: when do wildfires prefer to burn? Environmental Monitoring and Assessment, 164: 445–452.
- Bajocco, S., Ricotta, C. (2008) Evidence of selective burning in Sardinia (Italy): Which land-cover classes do wildfires prefer? Landscape Ecology, 23: 241–248.
- Bond, W.J., Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution, 20: 387–394.
- Brockett, B.H., Biggs, H.C., van Wilgen, B.W. (2001) A patch mosaic burning system for conservation areas in southern African savannas. International Journal of Wildland Fire, 10: 169– 183.
- Chuvieco, E., Giglio, L., Justice, C. (2008) Global characterization of fire activity: toward defining fire regimes from Earth observation data. Global Change Biology, 14: 1488–1502.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. Science, 199: 1302–1310.
- Elia, M., Giannico, V., Ascoli, D., Arganaraz, J.P., D'Este, M., Spano, G., Lafortezza, R., Sanesi, G. (2022) Uncovering current pyroregions in Italy using wildfire metrics. Ecological Processes, 11: 15.
- Gill, A.M. (1975) Fire and the Australian Flora: A Review. Australian Forestry, 38: 4–25.

- Greenwood, L., Bliege Bird, R., McGuire, C., Jadai, N., Price, J., Skroblin, A., van Leeuwen, S., Nimmo, D. (2024) Indigenous pyrodiversity promotes plant diversity. Biological Conservation, 291: 110479.
- Hantson, S., Pueyo, S., Chuvieco, E. (2015) Global fire size distribution is driven by human impact and climate. Global Ecology and Biogeography, 24: 77–86.
- He, T., Lamont, B.B., Pausas, J.G. (2019) Fire as a Key Driver of Earth's Biodiversity. Biological Reviews, 94: 1983–2010.
- Hempson, G.P., Parr, C.L., Archibald, S., Anderson, T.M., Courtney Mustaphi, C.J., Dobson, A.P., Donaldson, J.E., Morrison, T.A., Probert, J., Beale, C.M. (2018) Continent-level drivers of African pyrodiversity. Ecography, 41: 889–899.
- Hoffmann, W.A., Geiger, E.L., Gotsch, S.G., Rossatto, D.R., Silva, L.C.R., Lau, O.L., Haridasan, M., Franco, A.C. (2012) Ecological thresholds at the savanna–forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology Letters, 15: 759–768.
- Jones, G.M., Ayars, J., Parks, S.A., Chmura, H.E., Cushman, S.A., Sanderlin, J.S. (2022) Pyrodiversity in a Warming World: Research Challenges and Opportunities. Current Landscape Ecology Reports, 7: 49–67.
- Jones, G.M., Tingley, M.W. (2022) Pyrodiversity and biodiversity: A history, synthesis, and outlook. Diversity and Distributions, 28: 386–403.
- Kelly, L.T., Bennett, A.F., Clarke, M.F., Mccarthy, M.A. (2015) Optimal fire histories for biodiversity conservation. Conservation Biology, 29: 473–481.
- Kelly, L.T., Brotons, L. (2017) Using fire to promote biodiversity. Science, 355: 1264–1265.
- Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Batllori, E., Bennett, A.F., Buckland, S.T., Canelles, Q., Clarke, M.F., Fortin, M.J., Hermoso, V., Herrando, S., Keane, R.E., Lake, F.K., McCarthy, M.A., Morán-Ordóñez, A., Parr, C.L., Pausas, J.G., Penman, T.D., Regos, A., Rumpff, L., Santos, J.L., Smith, A.L., Syphard, A.D., Tingley, M.W., Brotons, L. (2020) Fire and biodiversity in the Anthropocene. Science, 370: eabb0355.
- Krawchuk, M.A., Moritz, M.A. (2011) Constraints on global fire activity vary across a resource gradient. Ecology, 92: 121–132.
- Krawchuk, M.A., Moritz, M.A., Parisien, M.A., Van Dorn, J., Hayhoe, K. (2009) Global pyrogeography: the current and future distribution of wildfire. PloS ONE, 4: e5102.
- Le Page, Y., Oom, D., Silva, J.M.N., Jönsson, P., Pereira, J.M.C. (2010) Seasonality of vegetation fires as modified by human action: observing the deviation from eco-climatic fire regimes. Global Ecology and Biogeography, 19: 575–588.
- Legendre, P., Legendre, L. (1998) Numerical Ecology; Elsevier, Amsterdam.
- Malamud, B.D., Morein, G., Turcotte, D.L. (1998) Forest fires: an example of self-organized critical behavior. Science, 281: 1840–1842.
- Maravalhas, J., Vasconcelos, H.L. (2014) Revisiting the pyrodiversity-biodiversity hypothesis: longterm fire regimes and the structure of ant communities in a Neotropical savanna hotspot. Journal of Applied Ecology, 51: 1661–1668.
- Marlon, J.R., Bartlein, P.J., Carcaillet, C., Gavin, D.G., Harrison, S.P., Higuera, P.E., Joos, F., Power, M.J., Prentice, I.C. (2008) Climate and human influences on global biomass burning over the past two millennia. Nature Geoscience, 1: 697–702.

- Martin, R.E., Sapsis, D.B. (1992) Fires as agents of biodiversity: pyrodiversity promotes biodiversity.In: Kerner, H.M. (Ed.), Symposium on Biodiversity in Northwestern California. Wildland Resources Centre, University of California, Berkeley, pp. 150–157.
- Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., Bilgili. E. (2011) Landscape–wildfire interactions in southern Europe: implications for landscape management. Journal of Environmental Management, 92: 2389–2402.
- Moreno, M.V., Chuvieco, E. (2013) Characterising fire regimes in Spain from fire statistics. International Journal of Wildland Fire, 22: 296–305.
- Moritz, M.A., Batllori, E., Bolker, B.M. (2023) The role of fire in terrestrial vertebrate richness patterns. Ecology Letters, 26: 563–574.
- North, M.P., York, R.A., Collins, B.M., Hurteau, M.D., Jones, G.M., Knapp, E.E., Kobziar, L.,McCann, H., Meyer, M.D., Stephens, S.L., Tompkins, R.E., Tubbesing, C.L. (2021) Pyrosilviculture Needed for Landscape Resilience of Dry Western United States Forests. Journal of Forestry, 119: 520–544.
- Nunes, M.C.S., Vasconcelos, M.J., Pereira, J.M.C., Dasgupta, N., Alldredge, R.J., Rego, F.C. (2005) Land-cover type and fire in Portugal: do fires burn land cover selectively? Landscape Ecology, 20: 661–673.
- Pavoine, S. (2012) Clarifying and developing analyses of biodiversity: towards a generalisation of current approaches. Methods in Ecology and Evolution, 3: 509–518.
- Rao, C.R. (1964) The use and interpretation of principal components analysis and applied research. Sankhya, 26: 329–358.
- Ricotta, C., Avena, G.C., Marchetti, M. (1999) The flaming sandpile: self-organized criticality and wildfires. Ecological Modelling, 119: 73–77.
- Ricotta, C., Bajocco, S., Guglietta, D., Conedera, M. (2018) Assessing the influence of roads on fire ignition: does land cover matter? Fire: 1, 24.
- Salis, M., Ager, A.A., Alcasena, F.J., Arca, B., Finney, M.A., Pellizzaro, G., Spano, D. (2015) Analyzing seasonal patterns of wildfire exposure factors in Sardinia, Italy. Environmental Monitoring and Assessment, 187: 4175.
- Steel, Z.L., Campos, B., Frick, W.F., Burnett, R., Safford, H.D. (2019) The effects of wildfire severity and pyrodiversity on bat occupancy and diversity in fire-suppressed forests. Scientific Reports, 9: 16300.
- Steel, Z.L., Miller, J.E.D., Ponisio, L.C., Tingley, M.W., Wilkin, K., Blakey, R., Hoffman, K.M., Jones, G. (2024) A roadmap for pyrodiversity science. Journal of Biogeography, 51: 280–293.
- Stillman, A.N., Siegel, R.B., Wilkerson, R.L., Johnson, M., Tingley, M.W. (2019) Age-dependent habitat relationships of a burned forest specialist emphasise the role of pyrodiversity in fire management. Journal of Applied Ecology, 56: 880–890.
- Stillman, A.N., Wilkerson, R.L., Kaschube, D.R., Siegel, R.B., Sawyer, S.C., Tingley, M.W. (2023) Incorporating Pyrodiversity into Wildlife Habitat Assessments for Rapid Post-Fire Management: A Woodpecker Case Study. Ecological Applications, 33: e2853.
- Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F., Clarke, M.F. (2012) Landscapescale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? Diversity and Distributions, 18: 519–529.

- ter Braak, C.J.F., Prentice, I.C. (1988) A theory of gradient analysis. Advances in Ecological Research, 18: 271–317.
- Tingley, M.W., Ruiz-Gutierrez, V., Wilkerson, R.L., Howell, C.A., Siegel, R.B. (2016) Pyrodiversity promotes avian diversity over the decade following forest fire. Proceedings of the Royal Society B: Biological Sciences, 283: 20161703.
- Turner, M.G., Romme, W.H. (1994) Landscape dynamics in crown fire ecosystems. Landscape Ecology, 9: 59–77.
- Ulyshen, M.D., Hiers, J.K., Pokswinksi, S.M., Fair, C. (2021) Pyrodiversity Promotes Pollinator Diversity in a Fire-Adapted Landscape. Frontiers in Ecology and the Environment, 20: 78–83.

Acknowledgements: JMCS, GV and CR acknowledge the funding support of the National Biodiversity Future Centre (NBFC), funded by the National Recovery and Resilience Plan (NRRP) of the Italian Ministry of University and Research (MUR) through European Union funds – NextGenerationEU.

Author Contributions: SB: Conceptualization, Methodology, Data collection and analysis, Writing – review & editing; DG: Conceptualization, Methodology, Data collection and analysis, Writing – review & editing; JMCS: Data analysis, Writing – review & editing; GV: Data analysis, Writing – review & editing; CR: Conceptualization, Methodology, Writing – original draft.

Conflicts of Interest: The authors declare no conflicts of interest.