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# Mapping and assessment of ecological vulnerability to wildfires in Europe

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## Abstract

**Background** Wildfires play a significant and complex role in ecosystems, influencing various aspects of their functioning and structure. These natural disturbances can positively and negatively impact ecosystems, shaping landscapes, nutrient cycles, biodiversity, and ecological processes. This study focuses on assessing and integrating the different factors that affect the ecological vulnerability to wildfires at the European scale. Our methodology follows three steps. Firstly, ecological values based on biological distinctiveness and conservation status were estimated to understand pre-fire conditions better. Secondly, we obtain vegetation's coping capacity (or resistance) to the impacts of fire, considering the functional traits of plants and fire characteristics through a fire extreme scenario. Finally, post-fire recovery time was calculated by considering the species-specific recovery time, recovery starting time, growth recovery rate, and the environmental constraints affecting the optimal vegetation response. These three variables were combined using a dynamic model that assumed the change of value due to wildfires integrated throughout the recovery time.

**Results** Our results indicate that the tundra biome emerges as the most ecologically vulnerable to fire, primarily due to its high ecological values and long recovery time, which outweigh its moderate coping capacity. Following closely, the temperate conifer forests also exhibit high vulnerability driven by their high recovery time, despite moderate ecological and coping capacity values. The boreal forests rank next, with moderate vulnerability due to their long recovery time and moderate coping capacity. The Mediterranean region, although having moderate ecological values and recovery time, shows a notable vulnerability influenced by lower coping capacity. The temperate broadleaf and mixed forests demonstrate relatively lower vulnerability owing to their balanced ecological values, moderate recovery time, and substantial coping capacity. Lastly, the temperate grasslands, savannas, and shrublands are the least vulnerable, benefiting from lower ecological values and the fastest recovery time, alongside moderate coping capacity, which collectively reduce their overall fire vulnerability.

Furthermore, we found that coping capacity is the factor that most influenced ecological vulnerability to wildfires.

**Conclusions** The study identifies key zones for European or national policies on fire prevention and post-wildfire regeneration. It offers insights into effective forest management and conservation policies, applicable to current conditions. Additionally, the methods can predict future ecological vulnerability to wildfires based on climatic and socio-economic trends.

**Keywords** Ecological vulnerability to wildfires, Recovery time, Ecological values, Coping capacity, Wildfires, Vulnerability assessment

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## Resumen

**Antecedentes** Los fuegos de vegetación juegan un rol significativo y complejo en los ecosistemas, influenciando varios aspectos de sus estructuras y funcionamiento. Estos disturbios naturales pueden impactar de manera positiva o negativa a los ecosistemas, modelando paisajes, ciclos de nutrientes, biodiversidad, y procesos ecológicos. Este estudio se enfoca a determinar e integrar los diferentes factores que afectan la vulnerabilidad a los incendios a escala europea. Nuestra metodología siguió tres etapas. En primer lugar, los valores ecológicos basados en distintivos biológicos y estatus de conservación fueron estimados para entender mejor las condiciones previas al fuego. Segundo, obtuvimos la capacidad de ajuste (o resistencia) de la vegetación a los impactos del fuego, considerando las características funcionales de las plantas y las características de los fuegos en un escenario de fuegos extremos. Finalmente, el tiempo de recuperación post fuego fue calculado considerando la recuperación específica de cada especie, el tiempo de inicio de la recuperación, la tasa de recuperación del crecimiento y de los condicionantes ambientales que afectan la respuesta óptima de la vegetación. Estas tres variables fueron combinadas usando un modelo dinámico que supuso el cambio de valor debido al fuego, integrado a través del tiempo de recuperación.

**Resultados** Nuestros resultados indicaron que el bioma de la Tundra emerge como el más ecológicamente vulnerable al fuego, debido fundamentalmente a sus valores ecológicos y altos tiempos de recuperación, lo que supera su moderada capacidad de afrontar los efectos de ese disturbio. A este ecosistema le siguen los bosques templados de coníferas, que también exhiben una alta vulnerabilidad debido a sus extensos tiempos de recuperación y su moderada capacidad de ajuste al fuego. Los bosques boreales se ubican en tercer lugar, con una moderada vulnerabilidad debido también a sus largos períodos de recuperación y moderada capacidad de ajuste a este disturbio. La región Mediterránea, aunque presenta valores ecológicos y tiempos de recuperación moderados, muestra una notable vulnerabilidad debido a su muy baja capacidad de adaptación. Los bosques deciduos y mixtos demostraron una vulnerabilidad relativamente más reducida debido fundamentalmente a sus valores ecológicos más balanceados y a una sustancial capacidad de adaptación. Por último, los pastizales templados, las sabanas y los arbustales, resultaron los menos vulnerables, que se benefician por su bajo valor ecológico y la más alta capacidad de recuperación además de su moderada capacidad de ajuste, lo que colectivamente reducen su vulnerabilidad total al fuego. Además, encontramos que la capacidad de ajuste es el factor que más influencia la vulnerabilidad ecológica a los fuegos de vegetación.

**Conclusiones** Este estudio identifica zonas clave para políticas a nivel nacional o europeo sobre prevención de incendios y en la regeneración post fuego. Ofrece perspectivas para el manejo efectivo de bosques y políticas de conservación aplicables a las condiciones actuales. Adicionalmente, los métodos pueden predecir la vulnerabilidad ecológica a fuegos de vegetación basados en tendencias climáticas y socio-económicas.

## Background

Wildfires play a significant and complex role in ecosystems, influencing various aspects of their functioning and structure. These natural disturbances can positively and negatively impact ecosystems, shaping landscapes, nutrient cycles, biodiversity, and ecological processes (Arrogante-Funes et al. 2024; Bond et al. 2005; Bowman et al. 2009; Guyette et al. 2002; Midgley & Bond 2015).

Ecosystems vary in their ability to withstand and recover from wildfires based on factors such as vegetation composition, fire history, and ecological processes. Some ecosystems have adapted to periodic fires (Naveh 1975) and even depend on them for functioning (Midgley & Bond 2015). For example, certain plant species have developed fire-adapted traits (Pausas et al. 2008), such as thick bark or serotine cones that require fire to open and release seeds (Baeza & Roy 2008). These fire-related traits allow plants to avoid, resist, or tolerate fire (individual, community or landscape level

(Archibald et al. 2019), strengthening ecosystem resistance or enhancing recovery.

However, many other ecosystems are less adapted to wildfires, mainly when they exceed historical conditions (i.e., more extreme or frequent fires) for which plants have not developed appropriate traits (Cochrane & Laurance 2002). For example, intense and large wildfires can cause significant damage to ecosystems, leading to habitat changes through landscape fragmentation (Driscoll et al. 2021) and changes in vegetation composition (Alcázar et al. 2016; Flannigan et al. 2009). The worst impacts of degradation induced by fire in the medium and long term include permanently disrupting natural processes, reducing biodiversity and impairing ecosystem functions (MMA 2006; Vallejo et al. 2009). In addition, the loss of vegetation cover after fire increases surface erosion because the bare soil is exposed to raindrop impact and surface runoff, especially in the first months after burning (Giovannini et al. 2001; Inbar et al. 1998) and promotes

the alteration of the nutrient pool (Vallejo et al. 2009). After a wildfire, the recovery process can be complex, depending on vegetation traits and environmental conditions, and it may take years or even decades for the ecosystem to recover its pre-fire state.

Several frameworks have been developed to study vulnerability to natural hazards. A vulnerability framework refers to a structured approach or model used to understand and assess the potential losses and resilience of communities and systems to the impact of natural hazards such as wildfires (UNISDIR, 2009; Williams & Kapustka 2000). The United Nations Office for Disaster Risk Reduction (UNDRR) promotes the implementation of the Sendai Framework for Disaster Risk Reduction (accessed: May 2023, <https://www.undrr.org/publication/sendai-framework-disaster-risk-reduction-2015-2030>), which serves as a comprehensive framework for understanding and addressing vulnerability and building resilience to disasters. Within the Sendai Framework, three elements are considered in natural hazards assessment: danger (probability that the event occurs), exposure to population, and vulnerability (capacity to experience damage caused by that hazard). Vulnerability assessment implies understanding and reducing the potential losses caused by a particular hazard. Assessing vulnerability is crucial for minimizing human and material damage from hazards. Often, preparedness efforts focus on reducing vulnerability by enhancing resistance or shortening recovery times for potentially affected communities. In the context of wildfires, vulnerability assessment involves estimating the various socio-economic and ecological factors that fires could impact, which implies considering the values at stake, the resistance of the system to the effects of fire (commonly termed coping capacity), and its regeneration ability (frequently measured in recovery time to recuperate the pre-fire values) (Chuvieco et al. 2023).

Different methodologies have appeared in the last two decades for assessing ecological vulnerability to wildfires, particularly the components of ecological values and resilience. Bisson et al. (2008) presented an index of plant community resilience to fire but did not contemplate water availability. Arianoutsou et al. (2011) evaluated the post-fire resilience of the *Pinus halepensis* in Cape Sounion National Park, Greece, using GIS and multi-criteria analysis. De la Riva et al. (2008), Alloza et al. (2006), and Duguay et al. (2012) produced a qualitative index of ecological vulnerability to wildfires in Mediterranean zones. Rodrigues et al. (2014) developed quantitative criteria for assessing ecological vulnerability in mainland Spain through recovery time based on land cover, NDVI trends, post-fire regeneration mechanisms (seeder or resprouter) of the dominant plant species, and local modifiers of

resilience such as climatic and soil factors. Rivière et al. (2023) evaluated the ecological vulnerability of South-Eastern France through a multi-criteria method based on the presence of forest covers and fuel load, fire interval and forest management tools. Although at the local scale Lecina-diaz et al. (2021) incorporate the factor coping capacity through tree bark thickness in the integral approach of vulnerability, the coping capacity of the ecosystem has not yet been well characterized in most studies. At the European scale, the European Forest Fire Information System (EFFIS) provides a map of ecological vulnerability to wildfires, considering only ecological values, which are understood as locations within the Natura 2000 network (San-Miguel-Ayanz et al. 2018).

The wildfire vulnerability assessment can be greatly benefited by using geographic information technologies, as they can provide a comprehensive characterization of vulnerable areas (Aretano et al. 2015; Chuvieco et al. 2023), helping to develop effective strategies for reducing potential damages in a certain territory.

The methodologies utilized in prior attempts to estimate ecological vulnerability to wildfires have exhibited limitations in comprehensively considering regeneration time, coping capacity, and the holistic characterization of ecological values. Typically, the assessment of ecological value focuses only on biodiversity, neglecting the conservation status, which plays a pivotal role in altering the intrinsic vulnerability of a location to fire (Arrogante-Funes et al. 2022; Dinerstein et al. 1995; Ricketts et al., 1999a). Moreover, the absence of a simulated fire scenario spanning the entire study area constrains the capacity to discern the total potential losses, constituting a fundamental point of origin for vulnerability assessment as it marks the initiation of the recovery process (UNISDIR, 2009; Williams & Kapustka 2000). Additionally, scant attention has been paid to existing studies on the inherent nature of species in terms of functional traits. These intrinsic characteristics significantly influence their ability to rebound from disturbances (Chuvieco et al. 2014a, b, 2023). As a result, key factors such as resistance or recovery time lack the requisite detailed characterization, impeding the establishment of a standardized process for different regions, thereby hindering the comparison of areas with varying levels of resilience to fire.

This study develops a method to assess the ecological vulnerability to wildfires at the European scale by characterizing its main components: ecological values, potential losses, and ecosystems' resistance and recovery (resilience). Our methodology presents a new holistic approach to estimating ecological vulnerability to fires based on three components: (a) computation of ecological values that could be potentially affected by fire by considering biological distinctiveness and conservation

status of these ecological values; (b) estimation of the coping capacity of the vegetation communities to the effects of fires, by assessing the functional traits of the plants that characterize the resistance to fire through a fire extreme scenario; and (c) calculation of the post-fire recovery time of vegetation by considering factors that allow plants to regrowth after fires, mainly those functional traits associated to regrowth and the local modifiers of those traits. These are integrated by estimating the total damages produced by the fires during the life cycle of their impacts. Our methodology uses biological knowledge, statistical pre-processed techniques, and heuristic methods, aiming to cover the complex interactions between wildfires, ecological values, vegetation composition, forest management, soil, climatic, topography factors, and vegetation functional traits. The combination of ecological diversity, fire-prone landscapes, human–environment interactions, climate variability, transboundary collaboration, historical records of wildfires, common policy frameworks, and socioeconomic implications make Europe an exceptional territory for studying vulnerability to wildfires and can provide valuable to develop fire management strategies in other regions facing similar challenges (Chuvieco et al. 2010, 2014a, b).

## Materials and methods

The study area covered the continental European territory and adjacent islands, excluding Cyprus (Fig. A1). Only terrestrial ecosystems were considered, as wildfires do not directly affect water bodies. Unburnable covers and croplands were removed from the analysis, as we were interested on wildland fires. The spatial resolution of this work was 1 km × 1 km, and the units per variable were discretized between 0 and 1000 to facilitate the integration with other variables generated within the FirEURisk project (last accessed: January 2024, <https://fireurisk.eu/>), in which this research is integrated.

## Framework

The general scheme and integration methodology of our approach to assessing ecological vulnerability is presented in Fig. 1. Ecological potential losses (EPL) were estimated considering the pre-fire ecological values, mediated by the ecological resilience (ER), which implies the capacity of the system to resist (coping capacity, CC). These losses after fire are integrated throughout time, considering the estimated time in which they will not be available (which depends on recovery time, RT). The different acronyms and terms used in the manuscript are included in Table 5. We termed potential losses and not actual losses, because this analysis is done before the

fire occurs, assuming a certain fire scenario. In our case, this scenario was computed from the 95% worst propagation conditions for those days when a fire larger than 2000 ha occurred in Europe, thus indicating extreme fire conditions.

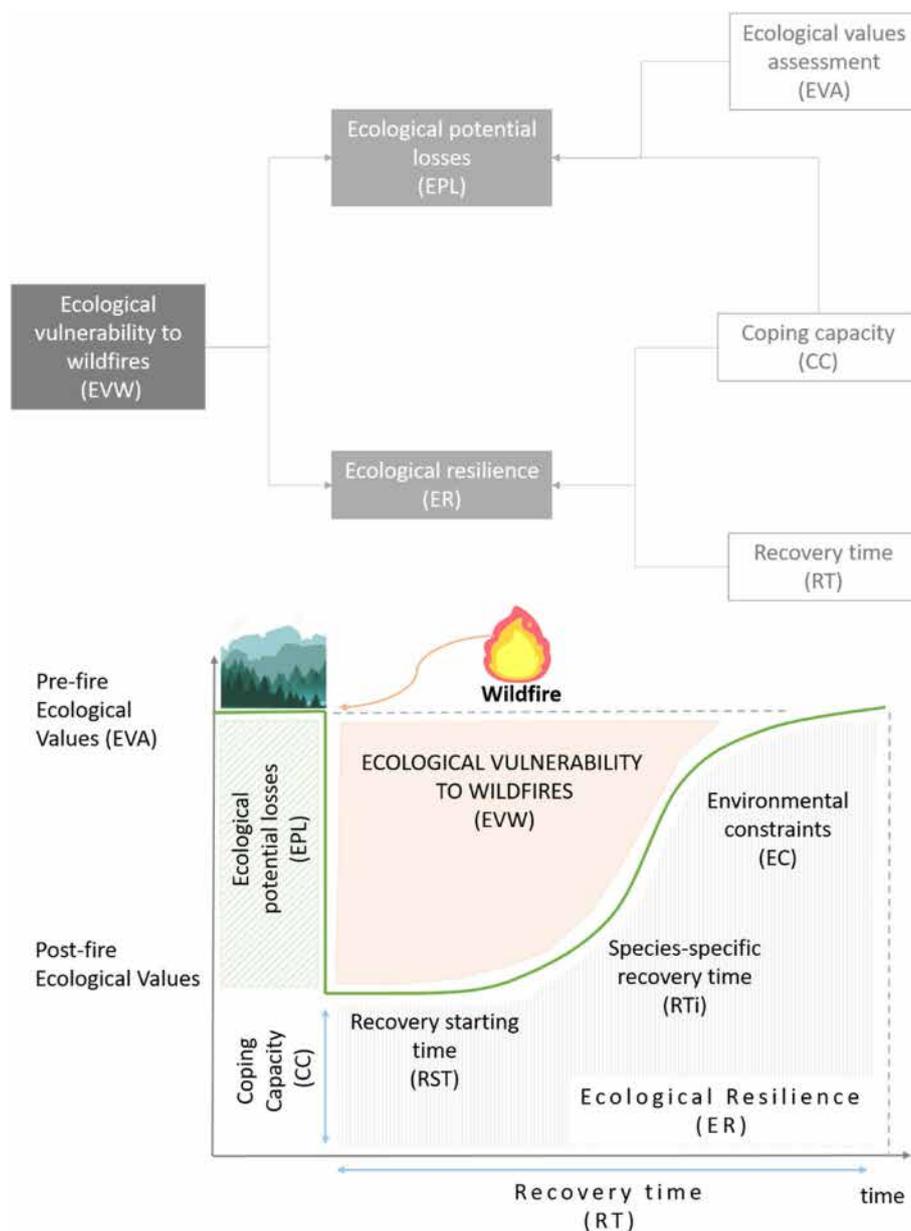
In the next paragraphs, we will review how the three main components of the ecological vulnerability were derived, first indicating the dimensions considered for estimating the ecological values, then the copying capacity and finally the regeneration time.

Figure 1 illustrates the dynamic process of ecological vulnerability assessment in the context of wildfire events. Initiated from the baseline ecological value, the occurrence of a wildfire leads to a reduction in this value, resulting in ecological losses within the affected area. However, amidst this devastation, the coping capacity of the vegetation plays a crucial role in determining what remains viable. Subsequently, a recovery phase ensues, marked by the activation of functional traits influenced by climatic and topographic factors as well as forest management practices. This process aims to restore the pre-fire values, mitigating the ecological impacts sustained during the wildfire event. This comprehensive vulnerability assessment, as described in earlier studies (Chuvieco et al. 2014a, b), quantifies these potential losses and acknowledges their persistence until the landscape returns to its pre-fire conditions.

## Ecological values assessment

The methodology used for ecological values assessment (EVA) is based on characterizing the ecosystems' biological distinctiveness (BD) and conservation status (CS) (Fig. 2) based on the methodology scheme proposed by Dinerstein et al. (1995) and Ricketts et al. (1999a) and previously used in the ecological vulnerability to wildfire at global scale by Arrogante-Funes et al. (2022). We stated that ecosystems hosting high taxonomic richness (Brun et al. 2019) or rare plant communities or habitats of endangered species highly contribute to their value through their enhanced functioning (Basile 2022; Leitão et al. 2016; Tang et al. 2023). The destruction or degradation of these valued ecological components, notably by fires, can have long-term implications for ecosystem health and conservation (Sriharan et al. 2022).

Biological distinctiveness (BD) refers to a particular biological group's uniqueness and distinct characteristics, emphasizing specific attributes at different ecological levels, from individuals to communities, thus characterizing structural biodiversity from the point of view of its exceptionality and in terms of ecosystem health (Ricketts et al., 1999a). The ecosystem's conservation status (CS) refers to its current condition and the threat it faces regarding degradation, loss or endangerment. Assessing the CS of



**Fig. 1** Components of the ecological vulnerability to wildfires and integration approach

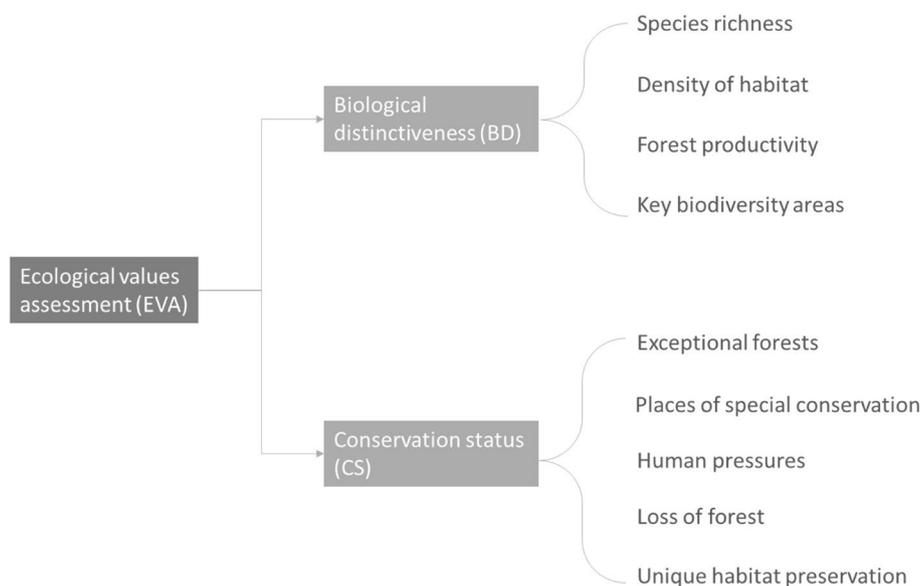
an ecosystem involves evaluating various aspects, including the state of its biodiversity and the presence of threats (Ricketts et al., 1999a).

**Biological distinctiveness**

Biodiversity, represented by biological distinctiveness, is essential for assessing the health of an ecosystem by reflecting the variability of life forms in a specific region (Dinerstein et al. 1995). Taxonomic richness favors the emergence of contrasted functional traits, thus maintaining vital ecosystem functions. Biological distinctiveness,

in preserving this functional diversity, ensures the continuity and effectiveness of crucial processes (Ricketts et al., 1999a). Beyond any direct benefit, each life form possesses a unique intrinsic value, contributing uniquely to the richness and complexity of our planet’s biological fabric. Consequently, considering biological distinctiveness when evaluating ecosystem ecological values becomes crucial (Dinerstein et al. 1995).

We built an integrated BD index based on previous studies by combining species richness, forest productivity, species abundance, and key biodiversity areas



**Fig. 2** Components of the estimation of ecological values

(Arrogante-Funes et al. 2022; Dinerstein et al. 1995; Ricketts et al., 1999a). The characterization of species richness is essential for understanding the biological diversity of an ecosystem, providing insights into the relative importance of each species and their contribution to the structure and function of the ecosystem (Ricketts et al., 1999a). Thus, species richness was estimated through potential habitat data for each species of mammals (278), birds (711), reptiles (156), amphibians (96), and vascular plants (20,000). Habitat maps were downloaded from the IUCN repository (<https://www.iucnredlist.org/resources/spatial-data-20download> last accessed: December 2023). For each species, a value of 1 was assigned to polygons where the presence of that species was confirmed and 0 otherwise. These binary data by species were transformed into rasters with a spatial resolution of 1 km. Then, all species' presences were added at the pixel level to obtain the species richness for Europe.

Characterizing vegetation density of habitat is crucial when estimating biological distinctiveness as it provides a more comprehensive understanding of the ecosystem's varied interactions, structures, and functions (Dinerstein et al. 1995). Utilizing biomass to indicate this abundance offers an effective approach, considering primary production and habitat structure. This strategy is particularly suitable when integrated with maps that assess individual species based on censuses, allowing for a more holistic approach in biodiversity assessment. For the density of habitat, a forest biomass density map at 100 m resolution for 2020 was used as a proxy (<https://data.jrc.ec.europa.eu/dataset/d1fdf7aa-df33-49af-b7d5-40d226ec0da3—last>

accessed: December 2023). This map comprises harmonized reference statistics regarding forest area in terms of biomass density ( $\text{gC}/\text{m}^2$ ) at national and subnational scales. The spatial resolution was initially set at 100 m but transformed to 1 km using a weighted average approach. This adjustment involved aggregating data and assigning greater importance to information nearer the center of each 1 km pixel. Such alterations in spatial resolution are common in spatial data processing, aiming to balance the trade-off between data precision and computational efficiency (Martínez-Gordón et al. 2021). The shift to coarser resolution facilitates analyses over larger areas while preserving essential spatial patterns.

Crowther et al. (2019) emphasize the significance of forest productivity through biogeochemistry in influencing the decomposition and turnover of soil organic matter and the fluxes with the health of the biodiversity and the ecosystem. Forest productivity, as a proxy from plant traits (Polley et al. 2022), was calculated by Moreno-Martínez et al. (2018) at 1 km spatial resolution based on biogeochemistry continuous data about specific leaf area (SLA) ( $\text{mm}^2 \text{mg}^{-1}$ ), leaf dry matter content (LDMC) ( $\text{g g}^{-1}$ ), leaf nitrogen content (LNC) ( $\text{mg g}^{-1}$ ), and leaf phosphorus content (LPC) ( $\text{mg g}^{-1}$ ). Ren et al. (2022) synthesized the positive relationship between carbon assimilation, SLA, and P/C leaf contents. Thus, the previous databases were used as a proxy for carbon, nitrogen, and phosphorus cycle productivity. The processing sequence of this database utilizes machine learning methodologies in conjunction with optical remote sensing data (MODIS/Landsat) and climate data to address

gaps and scale up in-situ measured leaf traits. Thus, the previous databases were used as a proxy for carbon, nitrogen, and phosphorus cycle productivity. After normalizing each variable, forest productivity was integrated as a sum at the pixel level of the carbon, nitrogen and phosphorus cycle production values.

Key biodiversity areas are characterized by exceptional biodiversity value stemming from their remarkable ecological integrity, globally significant ecosystems, and substantial populations of animals, fungi, and plants. They hold significant value for conserving biodiversity, and their identification and protection play a crucial role in combating global biodiversity loss. Key biodiversity areas were obtained from the database of Potapov et al. (2008) and can be viewed as biodiversity hotspots. The vector data layers were converted into raster binary data, assigning a value of 1 where a key biodiversity area was present and 0 where it was not.

### Conservation status

An ecosystem's conservation status (CS) refers to its current condition and the threat it faces regarding degradation, loss, or endangerment (Ricketts et al., 1999a). It is crucial in assessing its ecological value (Dinerstein et al. 1995). Firstly, a well-preserved ecosystem tends to be healthier and more resilient, enabling it to withstand disturbances and environmental changes (Ricketts et al., 1999a). The preservation of biodiversity in these ecosystems contributes to stability and resilience, promoting essential services and facilitating adaptation to changing conditions (Pausas et al. 2003). Healthy ecosystems offer a broader and more effective range of services.

Furthermore, establishing protected natural areas, driven by esthetic, recreational, and biological appeal, contributes to ecosystem conservation. In summary, an ecosystem's conservation status is essential for evaluating and appreciating its ecological value and significance for both nature and society (Ricketts et al., 1999a).

For the assessment of the CS, we estimated five indicators following previous studies (Arrogante-Funes et al. 2022; Dinerstein et al. 1995; Ricketts et al. 1999): presence of exceptional forests, places of special conservation, human pressures, loss of forest, and unique habitat preservation.

Exceptional forests were computed from an ecological point of view. Old-growth forests are important, albeit more structural than functional, in conserving most terrestrial diversity and enormously regulating the global climate (de Assis Barros et al. 2022). The intact forest landscapes cartography (Potapov et al. 2008) charts the location and extent of the forests and terrestrial ecosystems that remain unaltered by humans, with a minimum mapping unit of 500 km<sup>2</sup>.

Places of special conservation, mainly in national parks and reserves, play an essential role in conservation. We extracted the European territory from the World Database on Protected Areas (WDPA), which was generated as part of a project developed by the United Nations Environment Programme (UNEP) and by the IUCN, administered by the World Conservation Monitoring Centre (WCMC) and UNEP (<https://data-gis.unep-wcmc.org-last> access: December 2023). In this study, we only considered the terrestrial protected areas classified under IUCN categories I–IV as for these categories, there are reliable data verified on the ground, and they are managed similarly, thus enabling us to assume that they all have the same biodiversity conservation values. The vector data layer was converted to raster binary data by assigning 1 where a WDPA was located and 0 where it was not.

The human pressure indicator was collected from UNEP (<https://wesr.unep.org/index.php/article/biodiversity-and-nature-loss—last> accessed: January 2023). It was estimated through landscape fragmentation mapping based on the degree of fragmentation as a percentage through human infrastructures, roads, and railways. Human pressure varies between 0, the lowest to un-fragmented or homogeneous areas, to 1000, corresponding to highly degraded or heterogeneous landscapes.

The loss of forest indicator was obtained from global forest extent and change from the dataset of Hansen et al. (2013). This database compiles pixels based on Landsat satellite images that have experienced vegetation loss (2000–2013) due to various disturbances. For this study, we classify pixels within the database period that exhibit changes in vegetation cover as indicative of poor conservation status.

Finally, unique habitat preservation (Howard et al. 2020) was characterized based on potential habitat data for each species belonging to the category of “critically endangered,” “endangered,” and “vulnerable” of mammals, birds, reptiles, amphibians, and vascular plants. The dataset was downloaded from the IUCN repository (<https://www.iucnredlist.org/resources/spatial-data-%20download—last> accessed: December 2023). And we replicated the same process of species richness to obtain the final product of unique habitat preservation.

### Integration of EVA: principal components analysis

Principal component analysis (PCA) is a multivariate method that aims to reduce the complexity of a dataset by identifying the most important variables or “principal components” that explain the variation in the data (Andersen et al. 2009). Principal component analysis (PCA) represents a pivotal analytical tool employed by scientists to elucidate intricate relationships within

ecosystems, thereby enhancing the comprehension of ecological values (Janžekovič & Novak 2012). The first principal component represents the direction with the greatest variation among samples.

The first principal components are particularly important because they capture the largest amount of variability among the data. This means that they effectively summarize the essential information with fewer dimensions. The synergy effect between the variables is a key aspect here; by reducing the dimensionality, PCA helps to highlight the underlying structure and relationships within the data that may not be immediately apparent (Janžekovič & Novak 2012).

To assess variable reliability in PCA, Bartlett’s test of sphericity, Kaiser–Meyer–Olkin (KMO), and omega hierarchical asymptotic statistics were computed (Appendix 2).

The previously described indicators (from BD and CS) were introduced in the PCA model, taking the positive direction for values close to 1000 and negative for those close to 0. Species richness, forest productivity, density of habitat, key biodiversity areas, exceptional forest, unique habitat preservation, and places of special conservation conserve the original direction. In contrast, the human pressure and loss of forest indicators inverse the direction, taking values close to 1000 where human pressure and loss of forest values were low. Regarding the previous explanation, we selected the first PCA because it represents the synergies between conservation status and biological distinctiveness. For example, zones with fewer roads and railways and a loss of forest cover conserve better ecological values.

**Assessing ecological resilience**

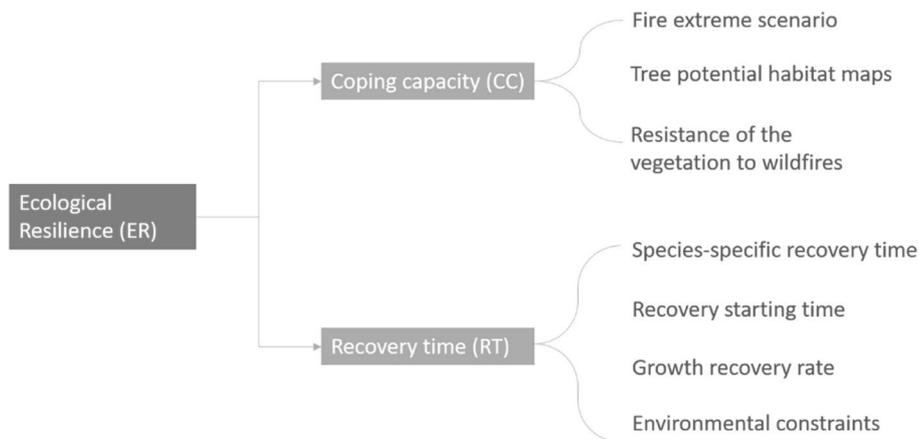
The methodology for estimating the ecosystem’s fire response comprises copying capacity and recovery time

(Fig. 3) for vegetation. An ecosystem’s copying capacity (CC) to wildfire refers to the ability to withstand or resist wildfire events and limit their impact. It encompasses the ecological characteristics and adaptations that enable an ecosystem to minimize damage and maintain its structure and functionality in the face of fire. Since plant CC depends on both its physiological characteristics and fire conditions, we estimated CC considering a particular fire scenario assuming extreme conditions.

On the other hand, ecosystem recovery time (RT) after a wildfire refers to the length required to regain pre-fire conditions. The recovery process involves restoring vegetation, forest management tools, ecological processes, and biodiversity affected by the fire. In this study, we estimate some relative indicators of the RT based on functional traits of the vegetation and local modifiers: species-specific recovery time, recovery starting time, growth recovery rate, and the environmental constraints.

**Fire scenario simulations**

Studying ecological resilience to fire entails integrating fire scenarios to understand better the potential impact of fire on ecological vulnerability (UNISDIR, 2009; Williams & Kapustka 2000). Through these simulations, the impact of various conditions on ecosystems, including vegetation, fauna, and soil, can be thoroughly analyzed. This understanding is crucial for assessing ecosystem resilience and devising effective fire management strategies. Exposure to these simulations provides insights into how components like vegetation, soil, and fauna respond and adapt (UNISDIR, 2009; Williams & Kapustka 2000), while also pinpointing weaknesses in environmental resistance and identifying vulnerable areas susceptible to significant damage during real wildfires.



**Fig. 3** Components of the estimation of ecological resilience

Within the FirEUrisk project, in which this research was developed, a fire simulation scenario was created by considering meteorological conditions of days in which at least 1 fire larger than 2000 hectares occurred in Europe within the time series 2001–2019. From those days, the 95th percentile of the worst weather conditions at noon (12 h) was computed. Weather parameters for the selected days were computed using ERA5-Land global re-analysis data. A topography-based transfer function was applied to the 1 km-resolution hourly ERA5-Land reanalysis data for variables such as temperature, dew point temperature, relative humidity, wind, and daily precipitation (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-land?tab=overview>, accessed: January 2023).

These weather conditions were input into the Behave program, along with fuels and topography (see Chuvieco et al. 2023), to estimate the fire line intensity (FI), which was selected as the main parameter to represent potential fire behavior conditions for the extreme scenario. The original value in kW/m was normalized to 0/1 using threshold values for fire suppression proposed by Rothermel (Rothermel 1983 [Table IV-18421]). Normalized values increased linearly from 0 to 0.5 for FI values between 0 and 346 kW/m (100 BTU/feet/s), implying fires that can be attacked by fire brigades with manual tools, from 0.5 to 0.75 for FI between 346 and 1731 kW/m (500 BTU/feet/s), where machines and aircraft can be used, and from 0.75 to 1 for values ranging from that threshold to the maximum FI. (Chuvieco et al. 2023).

### Coping capacity

CC was assessed through Fire Line Intensity and vegetation resistance to wildfires for the tree species present in a 1-km pixel based on the tree potential habitat maps (69 tree species) and the 7 non-forest land cover types (Table 6, Appendix 1).

Resistance of the vegetation to wildfires (RVW) was derived from a resistance index FTrvwi varying between 0 (non-resistant) and 1 (fully resistant), based on three criteria used in Stevens et al. (2020): (i) bark thickness (BT in cm), which protects the cambium and other living tissues against high temperatures from ground fires; (ii) tree height (THMAX in m); and (iii) basal crown height (BCH in m) as the capacities of trees to escape crown torching. These functional traits (FT) for each species are synthesized in Table 6 (Appendix 1). Each trait was rescaled between 0 (no resistance) and 1 (the most resistant), and the mean value of the three rescaled traits provided the aggregated final FTrvw for each species *i*. The criteria for selecting the tree species around Europe were based on the

general and specific plants related to the biomes (Dinerstein et al. 2017) (Table 6, Fig. 9 from Appendix 1).

The final calculation of the RVW was on the following model:

$$RVW = \frac{1}{\sum_{i=1}^n TPHMi} \times \sum_{i=1}^n TPHMi \times FTrvw_i \quad (1)$$

where *n* is the number of species on pixel *p*, and *i* is the species, TPHM is the tree potential habitat maps (extracted from <https://www.iucnredlist.org/resources/spatial-data-%20download—last> accessed: December 2023), and FTrvw is the functional trait related to the resistance of species *i*.

For non-forested pixels, we set CC=0 for grasslands, croplands, heathlands, and shrublands; none of the species in these land covers experience fire-resistant traits.

Pixel level CC was finally calculated as in Eq. 2

$$CC = RVW \times (1 - FI) \quad (2)$$

Finally, the CC result was normalized between 0 and 1000, where 0 represents areas with the least fire resistance, and 1000 represents the most resistant ones.

### Recovery time

RT comprises the species-specific recovery time (RT<sub>*i*</sub>), recovery starting time (RST), growth recovery rate (GR), and the environmental constraints (EC) affecting the optimal vegetation response, locally modified by climate, soil erosion, forest management, and topography (Seidl et al. 2011).

Firstly, for characterizing the RT (in years) of the 69 tree species and the 7 non-forested land cover types, we used each species' yearly growth rate (GR, m.year<sup>-1</sup>) and maximum tree height (THMAX, m) to derive the relative growth rate RGR (%HMAX.year<sup>-1</sup>) and the time needed for a species to reach its maximum height (RT in years) as 1/RGR (Table 6, Appendix 1). Information from observations (Schelhaas et al. 2018 among others) and forest growth models were used (Schworer et al. 2014; Morin et al. 2021; Rohner et al. 2018), assuming the starting point was a seedling (when data were missing in forest growth models or observations). BMAX and RG were derived from the tree species with the same taxa or the closest characteristics of tree height and wood density.

However, post-fire regeneration is more complex than a simple seed regeneration. We relied on the specific post-fire regeneration strategies from (Archibald et al. 2019) to define the species-specific regeneration starting time (RST<sub>*i*</sub>), a modifier, potentially anticipating or delaying the regeneration starting time (Table 6, Appendix 1). We collected information on tree species vegetative (resprouting) or seedling

emergence (serotiny, seed dispersal) response strategies. We attributed an RST value of  $-25$  years for fire-tolerant species regenerating from trunk buds and  $-10$  years for fire-tolerant species resprouting from belowground material (Table 6, Appendix 1). For species regenerating from the seed bank surviving the fire identified according to their level of serotiny and their facility to regenerate from the surviving seed bank found in the literature, we attributed an RST value of 0. Finally, for species without resprouting ability nor post-fire germination from the seed bank, regeneration relies only on seed dispersal from unburned areas (Liu 2021). We then accounted for colonization delays under inefficient dispersal strategy and time for the seed to be dispersed from neighboring unaffected ecosystems. Dispersal efficiency was related to seed mass and dispersal strategies and maximum distances (Vargas et al. 2023) (Table 6, Appendix 1). We attributed a dispersal index DI (in years) varying from 0 to 20 years according to their dispersal distance TDMAX. DI was calculated from dispersal distance rescaled rTDMAX between 0 (not dispersed) and 1 (long dispersal), so that  $DI = (1 - rTDMAX) * 20$  and DI varies between 0 for long distance dispersal and 20 years delay for short distance dispersal. For species carrying multiple strategies, we kept the lowest RST between the strategies.

Recovery time (RT, in years) was then calculated at the pixel level, as the mean value (over species in presence), of the cumulated species-specific regeneration starting time RST (in years) and species-specific recovery time (RTi in years) from biomass growth (Eq. 6).

$$RT = 1 / \sum_{i=1}^n TPHMi \times \sum_{i=1}^n TPHMi \times (RSTi \times ARSTm + (ARSTt + ARSTc) + RTi \times ARTic) \quad (3)$$

$$RT = 1 / \sum_{i=1}^n TPHMi \times \sum_{i=1}^n TPHMi \times (RSTi + RTi) \quad (4)$$

where  $n$  is the number of species on pixel  $p$ ,  $i$  is the species, and TPHM is the tree potential habitat map.

#### Adjustment of species-specific recovery time (ARTi) and recovery starting time (ARST) based on environmental constraints (EC)

As defined by RTi and RST, optimal post-fire dynamics can be locally modified by environmental or management constraints (Nolan et al. 2021). We used climatic (rainfall, temperature and solar radiation), topo-edaphic (soil erosion, topography), and management conditions as the main local adjustment modifiers (adjustment of

species-specific recovery time (ARTi) and recovery starting point (ARST)) as used in process-based forest models (Rohner et al. 2018) (Seidl et al. 2011).

The climatic, constraint on RST (ARSTc) was derived from the yearly mean annual precipitation (MAP) and potential evapotranspiration (PET) based on a 20-year time series from the 4-km resolution Terraclimate Observatory (Abatzoglou et al. 2018). We considered that these variables drive soil moisture and the subsequent seed germination (Chamorro et al. 2017), allowing plants to develop root systems after a wildfire for efficient water and nutrient uptake (Bakker et al. 1996). ARSTc was calculated as the PET/MAP ratio (varying from 0.2 for wet areas to 5 for dry areas) to modify the regeneration time RST so that dry areas ( $PET > MAP$ ) experience longer regeneration time (up to a 5-year delay) and wet areas ( $PET < MAP$ ) do not experience any regeneration delay.

We then considered post-fire soil erosion as an integrated topographic adjustment modifier for regeneration (ARSTt) that can reduce the seed bank, soil quality, and the subsequent regeneration capacity of the vegetation (Seidl et al. 2011). We used the soil erosion map (in t.ha<sup>-1</sup>) for Europe (<https://data.jrc.ec.europa.eu/dataset> -last accessed: December 2023), developed using the revised universal soil loss equation (RUSLE) with a spatial resolution of 1 km. The values were then transformed into a categorical variable, 1 to lower values and 4 to highest values according to the criterion for soil erosion due to water, proposed by the Food and Agriculture Organization of the United Nations (FAO) (FAO/UNEP/UNESCO,

1979): 1 to values between 0 and 20, 2 to values between 20 and 50, 3 to values between 50 and 200, and 4 to values over to 200, which is also applicable to fire erosion processes (Chuvieco et al. 2014a, b). We used these values as the potential delay in regeneration time (in years) due to topography (ARSTt).

Finally, humans might play a significant role in post-fire forest recovery by stimulating regeneration through tree plantations. We used the European forest management (FM) map from Hengeveld et al. (2012) (ranging from 1 for non-managed forests to 6 for highly managed forests), to derive the modifier ( $ARSTm = (6 - FM) / 5$ ) for the regeneration time RST so that RST is not delayed ( $ARSTm = 0$ ) when management was high (value = 6). Species RST was  $> 0$ , and kept as its initial value when management was low (value = 1).

A climate-driven adjusted recovery time (ARTic) was derived from mean annual temperature MAT, and the

monthly precipitation amount (MAP/12) (Abatzoglou et al. 2018) below soil available water capacity (AWC) as in Eq. 7 in a multiplicative combination as used in forest growth models (Schworer et al. 2014; Morin et al. 2021; Rohner et al. 2018). We set a minimum growth rate adjusted at 40% of the optimal for each climate control thus reaching a minimum of growth at 16%, when combined and reaching the observed 2 mm to 10 mm variation in tree growth observed at the European territory scale (Schelhaas et al. 2018). We obtained the climatic adjustment for recovery  $ART_{ic}$  as in Eq. 5.

$$ART_{ic} = (0.4 + 0.6 \times (MAT + 9)/29) \times (0.4 + 0.6 \times \min(MAP/12, AWC) \times 0.002) \quad (5)$$

We then modified Eq. 6 with management ( $ARST_m$ ), topographic ( $ARST_t$ ), and climatic ( $ARST_c$ ,  $ART_{ic}$ ) modifiers applied to recovery starting time (RST) or species-specific recovery time (RT $_i$ ), as in Eq. 6.

$$RT = 1 / \sum_{i=1}^n TP_{HMi} \times \sum_{i=1}^n TP_{HMi} \times (RST_i \times ARST_m + (ARST_t + ARST_c) + RT_i \times ART_{ic}) \quad (6)$$

where  $n$  is the number of species on pixel  $p$ , and  $i$  is the species.

### Integration of the ecological vulnerability to wildfires at the European scale

In this study, vulnerability assessment involved examining potential damages from an ecological perspective. In earlier projects (Chuvieco et al. 2014a, b), to determine potential losses caused by fires, we calculated the reduction in value (marginal loss) that occurs when an area is burned. These losses persist in the landscape until pre-fire conditions are restored, and the reduction of values was considered throughout the estimated recovery time.

Recognizing the greater importance of present values over future ones, as future benefits may be perceived as more uncertain, we estimated the equivalent present value of marginal losses using a discount rate. A common value of 2% was chosen for the discount rate, aligning with the valuation literature (Azqueta 2007). A hyperbolic factor was introduced in the marginal loss equation to prevent long-term effects from becoming negligible. This factor ensures that the penalty applied to the future diminishes asymptotically to zero, achieved by incorporating the Neperian logarithm instead of the absolute number of years for recovery (Azqueta 2007).

The three factors—EVA, CC, and RT—were integrated into ecological vulnerability to wildfires (EVW) using Eq. 7. This follows the interactions shown in Fig. 1, which we will describe below.

$$EVW = (EVA \times (1 - (CC/1000))) \times \frac{1 - (1 + r)^{-\ln RT}}{r} \quad (7)$$

where  $r$  is a discount rate of 2%; the EVW was normalized from 0 to 1000, with 0 indicating low vulnerability and 1000 indicating high vulnerability.

The first part of Eq. 9 represents the interaction

between EVA and CC and simulates the potential loss of ecological values when an extreme fire occurs. Thus, this part of the equation represents the starting point of recovery or the condition in which an ecosystem would be left after the fire (post-fire ecological values).

Ecosystems with high EVA but low CC may suffer significant losses in habitat destruction, species loss, and disruption of ecological processes. Conversely, an ecosystem with high CC may be better equipped to withstand wildfires, reducing potential ecological losses (Chuvieco et al. 2023).

The next part of Eq. 9 represents the fluctuation of recovery rates over time, as many authors reflect in post-fire regeneration trajectories through RT and  $r$  (Chu et al. 2016; Röder et al. 2008; Viana-Soto et al. 2017). Thus, this part of the equation simulates the recovery of ecosystems after a disturbance. While a logistic curve can represent the fluctuation of RT over time, the area under the curve can be used as one of many quantitative measures to assess the recovery dynamics or patterns of an ecosystem following a disturbance such as wildfires (Decò et al. 2013).

### Sensitivity analyses

The sensitivity analysis known as “one-at-a-time” is used to assess the individual impact of each factor in the ecological vulnerability integration equation to wildfires (Saltelli et al. 2000). Since the equation involves the interaction of four factors: ecological value assessment (EVA), coping capacity (CC), recovery time (RT), and a discount rate ( $r$ ), this type of analysis allows for the independent modification of each of these factors while keeping the others constant, observing how it affects the final result of ecological vulnerability.

The main purpose is to understand the relative sensitivity of each factor and its contribution to ecological vulnerability. By making changes one at a time, researchers can identify which factors significantly impact the overall result (Arrogante-Funes et al. 2022; Maes et al. 2023). This analysis helps researchers and scientists better understand the dynamics of the equation and prioritize areas of focus or improvement based on the relative influence of each factor.

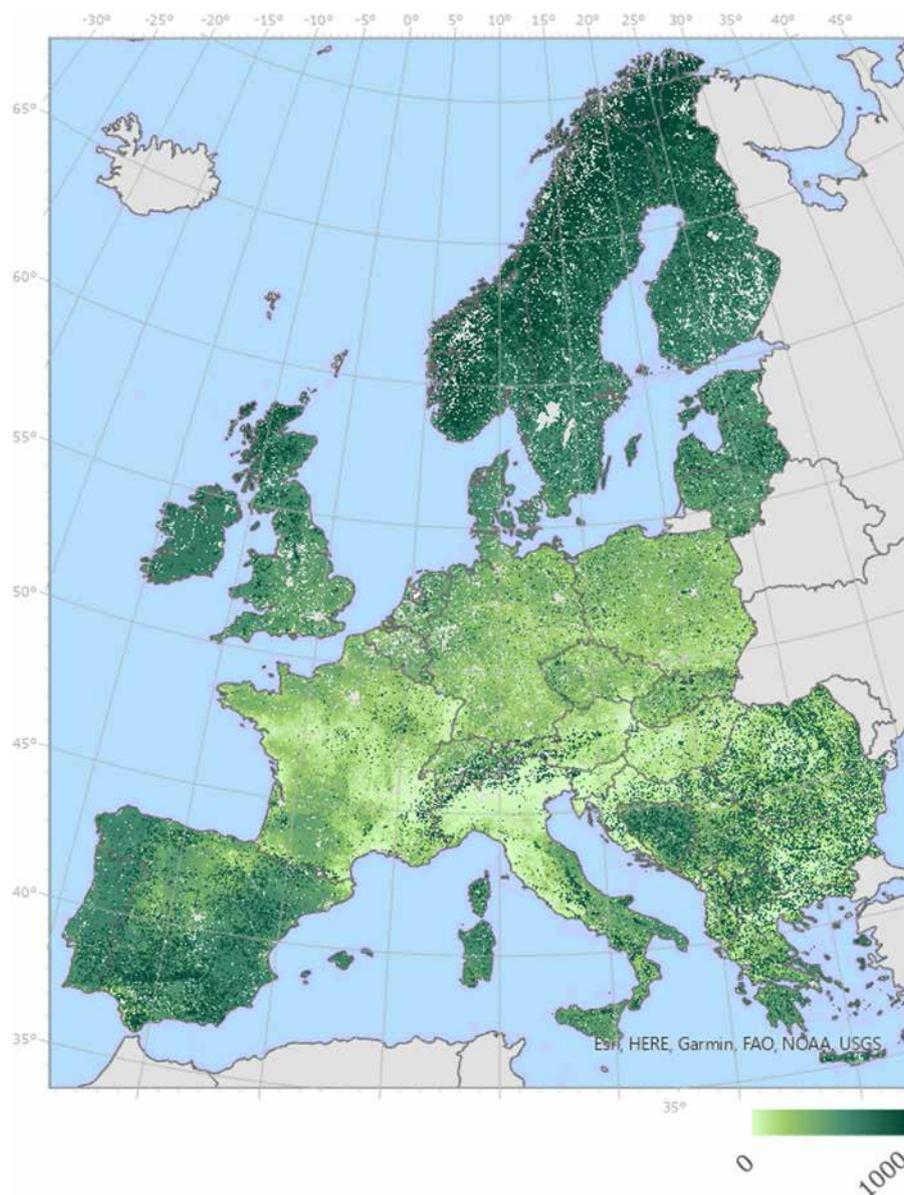
With this purpose, the weight of the four factors was individually modified, ranging from  $-50$  to  $50\%$  of each factor's value on the EVW equation.

## Results

### Ecological values

Figure 4 includes the EVA results based on the PCA's first axis. Table 1 provides a statistical summary of the results by biome.

This first principal component kept 0.79 of overall variability (Table 7, Appendix 1). The results of PCA statistical analyses are for KMO 0.83, Bartlett analyses  $p$  value 0, and omega hierarchical asymptotic 0.71. The results indicate that the data is suitable for conducting a principal component analysis. Significant relationships among the variables are evident based on the Bartlett test, and



**Fig. 4** Map of ecological value assessment (EVA) in Europe, scaled from 1 (low value) to 1000 (maximum value). Areas assigned to 0 were not assessed, indicating urban areas

**Table 1** Summary zonal statistics of the EVA per European biome

Biome	% Area	Min	Max	Mean	Std	Median	PCT90
Mediterranean region	19	0.10	983.90	340.42	276.60	379.74	722.66
Temperate conifer forests	5	27.20	973.32	303.06	362.48	50.59	821.67
Temperate broadleaf and mixed forests	56	25.50	994.38	153.97	255.88	51.60	795.73
Tundra	5	66.93	999.69	820.50	291.84	844	968.45
Temperate grasslands, savannas, and shrublands	1	37.64	925.76	467.57	372.46	794.70	799.29
Boreal forests	14	59.52	988.01	479.97	286.74	488.02	844.05

the scale utilized in the analysis demonstrates good reliability, as indicated by the omega value. The value of species richness (0.59), unique habitat preservation (0.52), places of special conservation (0.46), density of habitat (0.39), and key biodiversity areas reach the highest contribution to the ecological value assessment (Table 7, Appendix 1). Based on the PC1 axis, our EVA index identifies concomitantly biologically rich ecosystems with high biomass and recognized investment by nations to conserve them.

As shown in Fig. 4, the tundra had the highest ecological values. Half of the EVA values are above 844, with a mean of 820.50 (Table 1); 10% of the values exceed 968.45.

The next biome that stands out for its high yet moderate EVA is the temperate grasslands biome found in the Danube Delta in Romania (Fig. 4). Half of the ecological values are above 794.7. However, the mean value of 467.57 suggests the presence of many pixels with low EVA values (Table 1). Note that this biome is very scarcely distributed solely in this specific region of the Danube Delta.

Based on the development of the EVA, both regions host a unique biodiversity reflected by exceptional species and key biodiversity areas factors as well as good ecological health of the ecosystems represented through the conservation status indicator.

The others presented lower values than these two high EVA regions (Table 1). Still, the boreal and Mediterranean regions stand out spatially (Fig. 4), being the former slightly higher than those of the latter (Table 1). In both regions, we find ecological values centered around 400 for Mediterranean areas and approximately 500 for boreal regions.

Furthermore, in Mediterranean regions, the range of EVA values is the most extensive compared to the six biomes, peaking at 983.8 (Table 1). This variation highlights significant differences in geographical distribution attributed to landscapes typically affected by human activity. This influence is accurately reflected in the

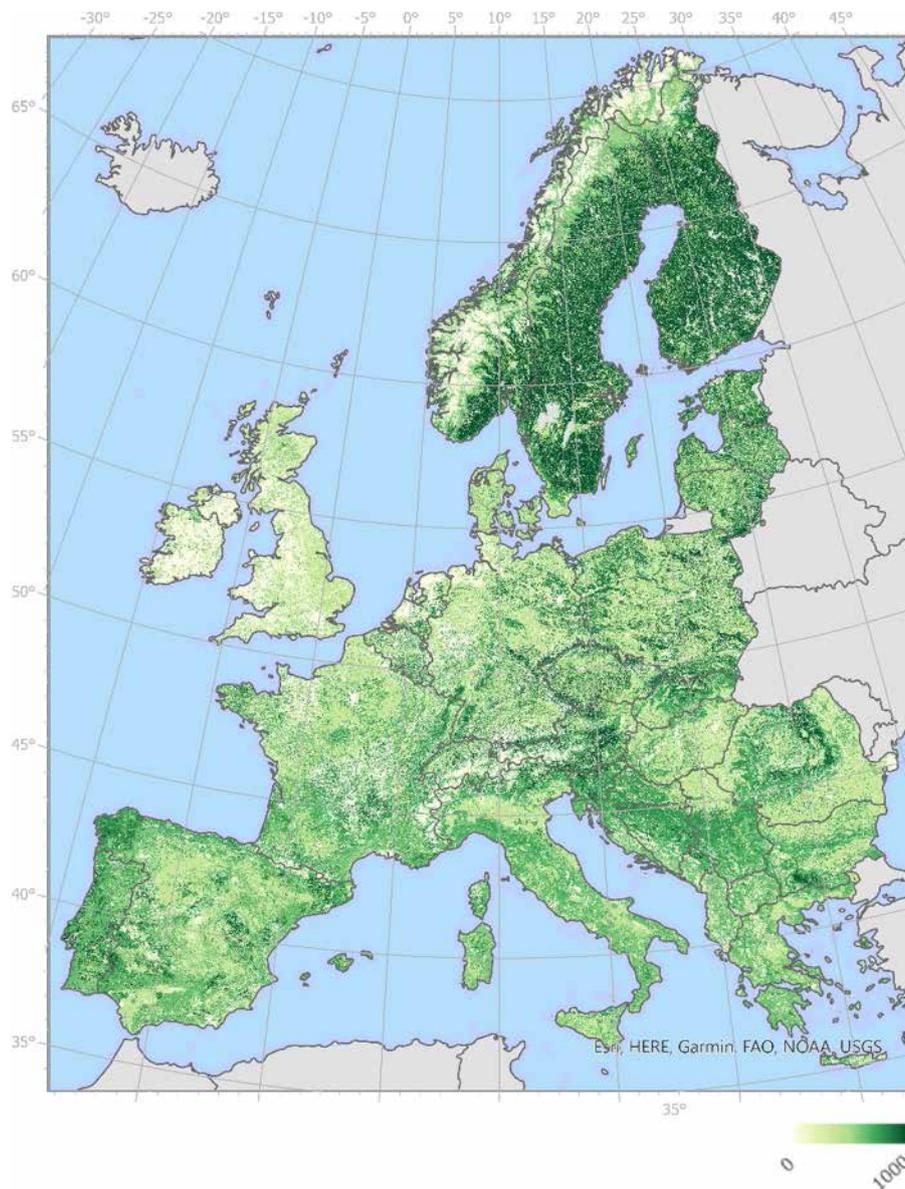
human pressure indicator, where even the more natural areas exhibit unique species conditions, as indicated by preserving unique habitats and key biodiversity areas. For example, the high EVA values in the Penibetic and Sierra Morena mountains in mainland Spain contrast with the low EVA values in the agroforestry landscapes of northern Italy (Fig. 4). Regarding the boreal forests, these zones suggest they contain many of Europe's general species but do not present higher ratios of the exceptionality diversity variable.

The results for the temperate broadleaf forests, conifer forests, and mixed forests generally experience lower EVA than the rest of Europe, as shown in the spatial distribution for the EVA (Fig. 4) and the statistics (Table 1). Despite this generality, we find areas with high ecological values in the Caledon forests of Ireland, the Alps, and the Danube Valley (Fig. 4).

#### Coping capacity and recovery time

The results obtained from applying the methodology for CC and RT are shown in Figs. 5 and 6 respectively, with their synthesis tables by biome (Tables 2 and 3). Notably, these results of CC stem from the interaction between the fire resistance functional traits for trees (while shrublands and grasslands have been considered similarly responding to fire) and a scenario of extreme fire in Europe.

As observed in the provided Table 2 and Fig. 5, the CC values were predominantly low to moderate across the different biomes in the EU. For instance, the Mediterranean region, which covers 19% of the EU area, exhibited a mean CC value of 180.73 on a 0–1000 scale, indicating a moderate resistance to extreme fire scenarios. The median CC value for this biome was 80.75, suggesting that many areas have lower fire resistance, but with significant variability as shown by a high standard deviation (193.95) and a 90th percentile (PCT90) value of 442.61. This indicates that about 10% of the Mediterranean region has high fire resistance, likely due to the presence of fire-resistant tree species.



**Fig. 5** Map of the ecosystems' coping capacity to fire over Europe (0 non-resistance, 1000 high resistance)

In contrast, the temperate conifer forests, covering 5% of the EU area, showed a higher mean CC value of 251.5 and a median of 216.6, with a notable PCT90 value of 611.46 (Table 2). This suggests that these forests generally exhibit higher fire resistance, with a substantial portion of the area having strong resistance due to the predominance of fire-resistant conifer species.

The temperate broadleaf and mixed forests, the most extensive biome covering 56% of the EU area, presented a mean CC value of 185.34 and a very low median of 21.44, indicating that while some areas have high fire resistance,

a large part of this biome has very low resistance, as reflected by the high standard deviation (231.3) and a PCT90 value of 508.6 (Table 2).

The tundra biome, which covers 5% of the EU area, showed low fire resistance with a mean CC value of 84.63 and a median of 21.29 (Table 2). The PCT90 value of 264.31 suggests that only a small portion of the tundra has moderately higher fire resistance, likely due to the sparse and low vegetation.

The temperate grasslands, savannas, and shrublands, covering 1% of the EU area, had the lowest mean CC value of 51.25 and a low median of 21.43 (Table 2).



**Fig. 6** Map of recovery time (in years after fire) over Europe

**Table 2** Summary zonal statistics of the CC

Biome	% Area EU	Min	Max	Mean	Std	Median	PCT90
Mediterranean region	19	0	999	180.73	193.95	80.75	442.61
Temperate conifer forests	5	0	999	251.5	250.24	216.6	611.46
Temperate broadleaf and mixed forests	56	0	1000	185.34	231.3	21.44	508.6
Tundra	5	0	1000	84.63	163.62	21.29	264.31
Temperate grasslands, savannas, and shrublands	1	0	999	51.25	119.51	21.43	64.31
Boreal forests	14	0	1000	411.99	290.75	590.96	639.05

**Table 3** Summary zonal statistics of the RT

Biome	% Area EU	Min	Max	Mean	Std	Median	PCT90
Mediterranean region	19	1	280.9	27.2	32.97	13.64	70.68
Temperate conifer forests	6	1	281	62.61	47.6	50.24	130.79
Temperate broadleaf and mixed forests	56	1	280.69	32.04	34.71	22.47	80.25
Tundra	5	1	280.89	21.45	25.63	14.33	46.61
Temperate grasslands, savannas, and shrublands	1	1	172.61	6.09	14.6	1.26	15.82
Boreal forests	14	1	280.89	29.66	18.2	28.64	51.25

The low PCT90 value of 64.31 reflects the very low fire resistance across this biome, consistent with the predominance of grasslands and shrublands for which we set the lowest resistance values.

The boreal forests, covering 14% of the EU area, demonstrated the highest fire resistance with a mean CC value of 411.99 and a median of 590.96 (Table 2). The PCT90 value of 639.05 indicates that a significant portion of this biome has very high fire resistance, due to the less presence of croplands in this biome since the croplands obtain 0 value in our approach.

In our methodology, we have focused on functional traits associated with trees, taking advantage of the available data on their habitat distribution. This approach is reflected in the spatial distribution of these values (Fig. 5): forested areas exhibit higher CC values, while, in contrast, grass or shrubland areas show lower CC values that we set to 0. Nevertheless, contrasted values within forests reflects the variety of resistance traits found across EU tree species.

The analysis shows that forested biomes, particularly boreal forests and temperate conifer forests, exhibit higher fire resistance due to the presence of fire-resistant tree species. Conversely, biomes such as temperate grasslands, savannas, and shrublands and tundra exhibit the lowest fire resistance, reflecting their sparse and non-resistant vegetation. The Mediterranean region and temperate broadleaf and mixed Forests show moderate resistance but with significant variability, highlighting the diversity of vegetation and its impact on fire resistance within these biomes.

As we can observe in Table 3 and Fig. 6, vegetation recovery time (RT) after a fire varies significantly across different biomes in the EU. This RT is influenced by several factors, including soil erosion, temperature, precipitation, human management practices, slope, and terrain aspect, as well as the functional traits of different species, such as resprouters and seeders. Grass and shrub species

generally recover faster than trees, as reflected in the following observations.

RT was estimated through years of tree recovery based on functional traits and local modifiers that facilitate or hinder recovery (Fig. 6, Table 3). A fixed value of 2 years was set for grasslands and 10 years for shrublands.

The Mediterranean region exhibits a moderate recovery time. The mean RT value in years is 27.2, indicating that vegetation recovery is neither fast nor slow on average (Table 3). The median RT of 13.64 suggests that a significant portion of the area recovers relatively quickly, but the high standard deviation (32.97) and PCT90 value (70.68) highlight considerable variability, with some areas taking much longer to recover, indicating spatial differences between higher and lower values (Fig. 6).

In contrast, temperate conifer forests show a relatively longer recovery time. The mean RT value of 62.61 and a high median of 50.24 indicate that these forests generally take longer to recover than the other biomes, likely due to the dominance of tree species with longer recovery periods. The high PCT90 value of 130.79 further emphasizes the extended recovery time for a significant portion of this biome.

Temperate broadleaf and mixed forests, which covers the largest area, has a mean RT value of 32.04 and a very low median of 22.47. This suggests that while many areas recover quickly (likely due to the presence of resprouting species and shrubs), significant portions take much longer, as indicated by the high standard deviation and PCT90 value, as in the Mediterranean region.

The tundra biome exhibits a generally fast recovery time with a mean RT of 21.45 and a low median of 14.33. However, the variability is high, as indicated by the standard deviation of 25.63 and PCT90 value of 46.61, reflecting some areas with significantly longer recovery times due to harsher conditions and limited vegetation types.

As in the previous case, temperate grasslands, savannas, and shrublands show the fastest recovery time with a mean RT of 6.09 and a median of 1.26. The low PCT90 value of 15.82 indicates that the majority of this biome recovers very quickly, likely due to the dominance of fast-recovering grass and shrub species.

Finally, boreal forests show the longest recovery times, with a high mean (29.66) and median (28.64). The high variability (Std: 18.2) and PCT90 value (51.25) indicate that recovery times are generally long, likely due to the slow growth rates of boreal tree species and harsh climatic conditions.

The biomes, from shortest to longest recovery time, are as follows. Temperate grasslands, savannas, and shrublands exhibit the fastest recovery times due to the rapid regrowth of grasses and shrubs. Next, the tundra also recovers quickly, reflecting the resilience of its hardy vegetation. Following this, the Mediterranean region shows moderate recovery times with significant variability, indicating a mix of fast-recovering shrublands and slower-recovering forested areas. Subsequently, temperate broadleaf and mixed forests have moderate recovery times, with a substantial portion recovering quickly due to the presence of resprouting species. In contrast, temperate conifer forests exhibit longer recovery times, reflecting the slow regrowth of coniferous trees. Finally, boreal forests have the longest recovery times, likely due to slow-growing tree species and harsh environmental conditions.

#### Integrated ecological vulnerability to wildfire

Based on the EVA, CC, and RT analyses, the ecological vulnerability to wildfires (EVW) across evaluated European lands shows moderate outcomes. Considering an extreme fire scenario around 500 mean value of EVW, the results reveal higher median values than the mean, indicating generally lower vulnerability (Table 4). The standard deviation surpassing the mean and median underscores distinct spatial distributions across regions, distinguishing between grasslands and wooded areas, among others (Fig. 7), and for RT, we computed the EVW

map (Fig. 7) and a summary of zonal statistics based on Europe's different biomes.

Despite this pattern, we can find areas with the highest EVW values in the Scandinavian Peninsula (Fig. 7). Table 4 illustrates that the tundra biome emerges as the most vulnerable to wildfires based on its high mean EVW, reflecting substantial susceptibility primarily due to climate-related factors and vegetation characteristics. The considerable standard deviation (188.67) indicates variability in vulnerability levels across tundra regions. The median (399.86) and PCT90 (547.4) values highlight areas within the tundra biome with elevated vulnerability.

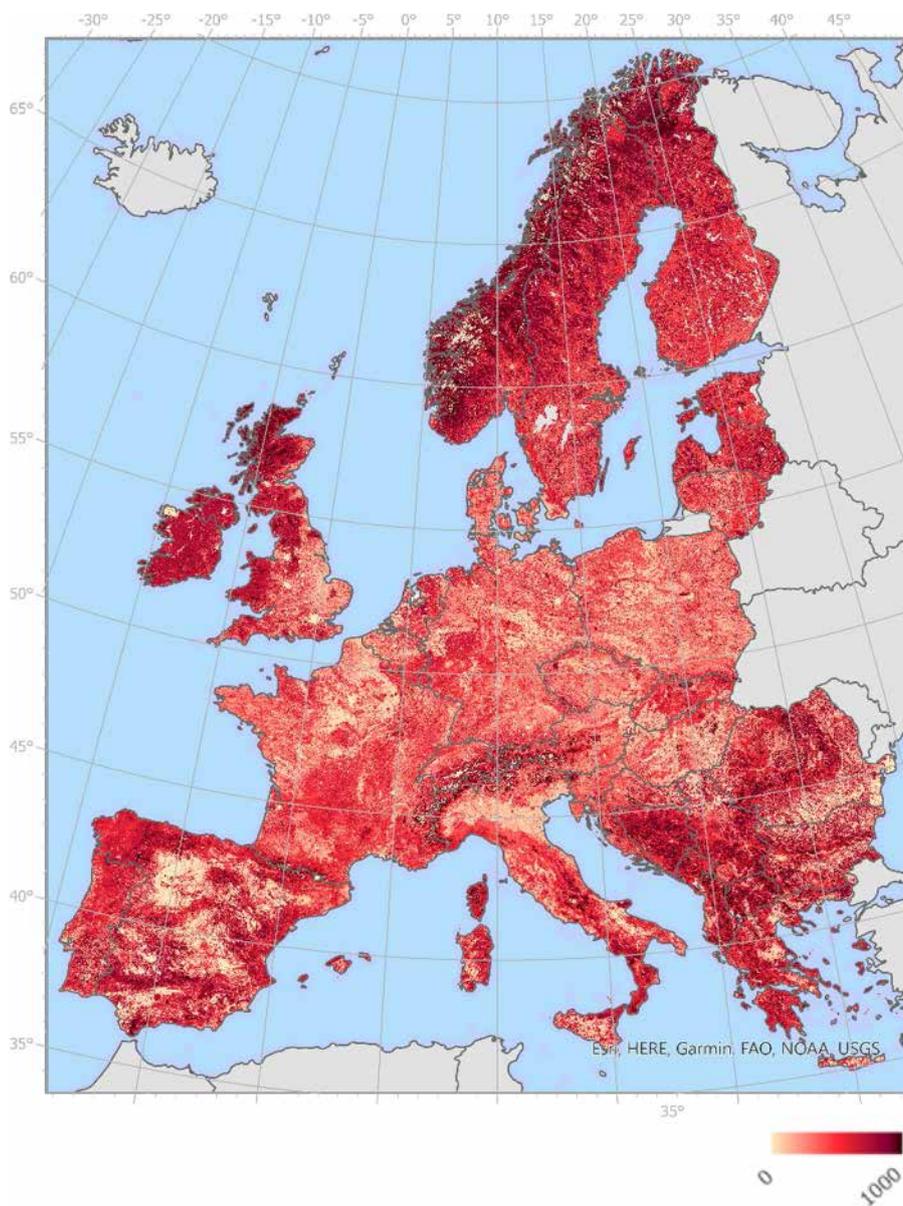
The next more vulnerable biome was temperate conifer forests exhibit significant vulnerability to wildfires, characterized by a relatively high mean EVW (157.51) and substantial standard deviation (211.08). This vulnerability is influenced by the prevalence of fire-prone coniferous species and climatic conditions conducive to fire spread, particularly in northern Europe and mountainous regions (Fig. 7). Furthermore, the elevated PCT90 (527.6) value indicates localized areas with heightened vulnerability.

Boreal forests show moderate vulnerability to wildfires, with a mean EVW (145.66) influenced by slow-growing tree species and environmental conditions prone to fire outbreaks. The standard deviation suggests varying susceptibility across boreal landscapes (162.58), with the PCT90 (426.68) value highlighting regions of elevated vulnerability, particularly in North Scandinavia.

The next biome, but with lower EVW compared to boreal forests, was the Mediterranean region, displaying moderate vulnerability to wildfires, characterized by a mean EVW (of 81.91) influenced by diverse landscape types from fire-prone shrublands to more fire-resilient forests (Fig. 7). The variability in vulnerability levels across the region it was also indicated by the standard deviation (141.88). The PCT90 value highlights areas with heightened vulnerability, such as the Alps, stand out in the Iberian sclerophyllous and semi-deciduous forests,

**Table 4** Zonal statistics of the EVW values per biome in Europe

Biome	% Area EU	Min	Max	Mean	Std	Median	PCT90
Mediterranean region	19	0	893.05	81.91	141.881313	24.57	339.39
Temperate conifer forests	6	0.02	956.23	157.51	211.079439	31.13	527.60
Temperate broadleaf and mixed forests	56	0	882.55	65.39	125.325281	21.10	217.97
Tundra	5	0.02	1000	339.56	188.673707	399.86	547.40
Temperate grasslands, savannas, and shrublands	1	0	714.90	55.07	102.944104	11.81	150.67
Boreal forests	14	0	870.67	145.66	162.581745	40.19	426.68



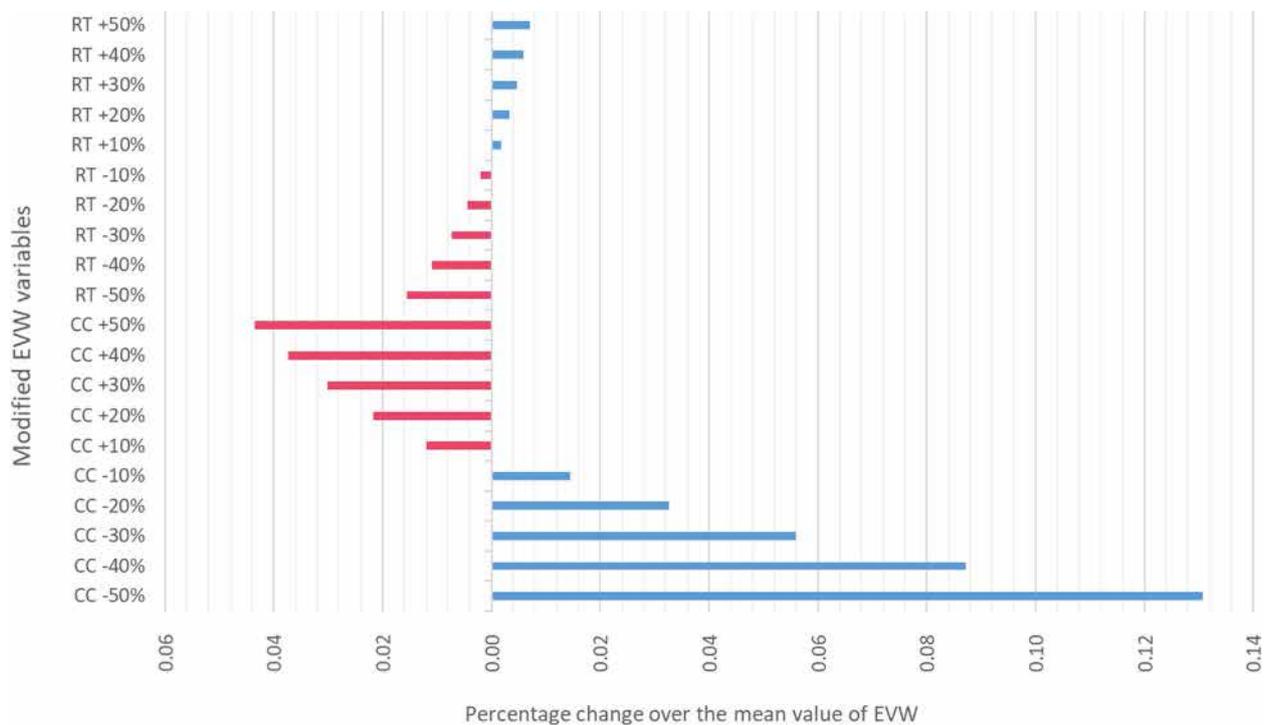
**Fig. 7** Map of ecological vulnerability to wildfire (EVW) integrating coping capacity (CC), recovery time (RT), and ecological value assessment (EVA) over Europe (with 0 = low vulnerability, 1000 = high vulnerability)

such as the Penibetic mountain range, or the case of temperate conifers.

The last two less vulnerable biomes were temperate broadleaf and mixed forests and temperate grasslands, savannas, and shrublands. The first shows a mean EVW (65.39) influenced by a mix of deciduous and evergreen species. The standard deviation (125.33) indicates variability in vulnerability levels across temperate Europe, as we can observe in France and Germany (Fig. 7), with the median (21.1) and PCT90 (217.97) values highlighting

regions with elevated vulnerability due to forest composition and climatic factors.

The last biome, temperate grasslands, savannas, and shrublands, exhibits the lowest vulnerability to wildfires among the assessed biomes, characterized by a relatively low mean EVW (55.07) and standard deviation (102.94). The resilience of grasslands, savannas, and shrublands to fire is evident in the minimal variability in vulnerability levels across these landscapes. The median (11.81) and PCT90 (150.67) values reinforce the overall



**Fig. 8** OAAT sensitivity analyses result in changing weights of each variable by separating from  $-50$  to  $50\%$  over the EVW integration

low susceptibility to wildfires in temperate grassland and shrubland ecosystems, as we can observe in the last lands of the Danube River (Fig. 7).

### Sensitivity analyses

The sensitivity of the methodology to estimate the integrated ecological vulnerability to wildfire (EVW) was assessed through induced changes in the factors involved in its estimation: ecological value assessment (EVA), coping capacity (CC), recovery time (RT), and rate of discount ( $r$ ). Figure 8 shows the sensitivity of the EVW integration method to changes in these factors by recalculating the EVW while perturbing the parameters one by one from  $-50$  to  $+50\%$  of their baseline value. The results demonstrate that, after inducing different intensities of change in the parameters, the average EVW result barely varies. Thus, it was found that the EVW integration method showed good stability in the face of variations in its factors, as the percentage change was below  $0.3\%$  (Fig. 8). The most significant impact on EVW was obtained by modifying coping capacity (CC), which establishes potential ecological losses based on the initial ecological value (EVA). A  $50\%$  decrease in coping capacity resulted in a  $0.13\%$  increase in EVW, while a  $50\%$  increase in coping capacity resulted in a  $0.4\%$  decrease in

EVW. The complete figure for all results is in the Appendix 1 (Fig. 10).

### Discussion

#### Ecological values: first steps and toward further conceptual frameworks

We used the concept of ecological value assessment (EVA) as an integrated index of ecosystem functioning potentially affected by fires, informing about priority regions to be protected from or managed after fires. The concept of ecological value assessment is in fact still loosely defined, so that independent studies assembled contrasted information as reviewed in Amador-Cruz et al. (2021). Our framework is informed by the key information list, adapted to fit the constraints of the European-scale study area and data availability (Perrone et al. 2023).

Based on this raw information, we computed species richness as the number of species. This first choice is a simple approach when current new indices based on functional richness (Legras et al. 2018) or rarity-weighted richness (Albuquerque & Beier 2015) could integrate species endemism or rarity and functional redundancies between species. To maintain consistency in the information across both plants and animals,

we utilized the number of species, with plants benefiting from extensive documentation of their traits from the TRY database (Kattge et al. 2020), while animals, which have been less thoroughly investigated, are also accounted for (Tobias et al., 2022). Further improvements using a functional biogeography framework (Violle et al. 2014) and refined species distribution will certainly improve this ecological value assessment.

Despite our assumptions guided by technical and conceptual constraints, we could propose a first attempt to provide an ecological value assessment map for Europe. Our final map illustrates how the European continent encompasses diverse ecosystems and landscapes with contrasted ecological values. Particularly, as many studies reflect, the boreal forests of Scandinavia, the Carpathian Mountains, Atlantic coastal areas, the Danube River Basin, and the South Iberian Peninsula present higher EVA due to the presence of particular species, such as endemism, plus the general species supported in central Europe ecosystems, considered being rich biodiversity areas (Habel et al. 2013; Kayes et al. 2020; Mamos et al. 2021; Manzano et al. 2019).

Our approach suggests the tundra has very high ecological values compared to the rest of the biomes, in contrast to previous studies (Walker et al. 2001). The tundra landscapes in the northern part of the Scandinavian Peninsula showcase biodiversity that stands out for having exceptional species in good condition compared to other biomes with only widespread species (Hofgaard et al. 2012). Many studies highlight that fires can negatively impact the tundra's high EVAs (Bret-Harte et al. 2013; Mccarty et al. 2021).

Temperate broadleaf and mixed forests do not stand out with the highest ecological values compared to other biomes, reducing their intrinsic vulnerability. This goes against what was reported by Marín et al. (2021) reporting a biodiversity hotspot in Central Europe but only assessing the entire European territory by quantifying biodiversity solely based on tree species. Although using simple indices, our study considers an extensive database of plant and animal taxa to characterize each biome as recommended by previous ecological value assessment frameworks (Dinerstein et al. 1995; Ricketts et al. 1999).

However, landscape variability also plays a significant role, as spatial differences suggest that the observed low vulnerability is not uniform across the extensive territory of the biome. In those zones, our study coincides with the findings of Marín et al. (2021). In some areas, such as the lands near the Danube Valley and the Carpathians, the highly biodiverse

composition of the forest may influence local vulnerability, emphasizing the importance of studying variability at the regional level to fully comprehend the dynamics of ecological vulnerability by biome, as many authors highlighted about the frameworks of vulnerability (Blaikie et al. 1994).

#### **Coping capacity, post-fire recovery and ecological vulnerability to wildfires: beyond vegetation**

Beside the geographical variety of EVAs contributing to EVW, contrasted vegetation responses during fires themselves (Midolo et al. 2023) and after fire during regeneration (Nolè et al. 2022) could be integrated in our framework.

While some ecosystems, such as Mediterranean forests, have developed adaptations that confer higher CC values over the forested areas (Kühn et al. 2021), others, like the tundra, exhibit lower CC due to the less efficient functional traits of their flora to cope with high temperatures reached during combustion (Lashchinskiy et al. 2020).

The tundra landscapes of the Scandinavian Peninsula are highly ecologically vulnerable to fire due to the interaction between their rich ecological values, low resistance capacity, and medium regeneration times. A typically highly flammable organic horizon that spreads fires rapidly increases the likelihood of intense fires reaching these areas and reducing CC (Lashchinskiy et al. 2020).

In general, the Mediterranean region also exhibits a notable values of ecological vulnerability to wildfires, attributed to its prominent ecological values, moderate coping capacity, and recovery times. These regions showcase characteristics that reduce potential losses and recovery times based on their resistance and regeneration functional traits, making them among the most adapted ecosystems (Baeza & Roy 2008). However, the region displays high variability in the values of EVW due to its heterogeneous landscape, where general values may not fully represent this diversity, as also argued by Pausas and Vallejo (1999).

Specifically, certain zones in the Mediterranean, like Spanish or Italian sclerophyllous and semi-deciduous forests, exhibit lower RT values for forested areas compared with other forested zones of Europe owing to the presence of resilient resprouter communities and higher water availability from ocean and sea climate conditions (Rodrigo et al. 2004; Rodrigues et al. 2014).

Like the Scot and Alp forests, the temperate coniferous biome in Europe shows a significant ecological

vulnerability to wildfires, as the literature over *Pinus spp.* suggested (Adámek et al. 2016). While they do not possess high ecological values throughout their extent, they exhibit a moderate coping capacity combined with extended regeneration times under an extreme fire scenario, contrasting with previous studies (Adámek et al. 2016; Engelmark & Hytteborn 1999). The conifers of these ecosystems do not have specific fire regeneration functional traits, making them less effective in extreme fire-prone environments (Aubin et al. 2016). Broad-leaved forests show moderate coping capacity and recovery time values, indicating a moderate ability to cope with and recover from fires, as previously stated (Maringer et al. 2016; Moris et al. 2017).

The boreal forest ecosystems that dominate the countries of Finland, Sweden, and Norway exhibit a more moderate ecological vulnerability to wildfires compared with the previous biomes. This is due to the biome's outstanding ecological values, with extensive regeneration times according to other authors (Héon et al. 2014; Weldon & Grandin 2019), but with high coping capacity due to the coarse bark-thickness of these species. While boreal forest species have developed some functional resistance traits to fire throughout their evolution as canopy height, the overall regeneration is not as pronounced as in more fire-prone ecosystems, which are more fire-adapted (Kühn et al. 2021).

The temperate broadleaf and mixed forests biome in Europe demonstrates the lowest ecological vulnerability to wildfires among the biomes studied that contains tree species due to its regular ecological values and its diverse tree species, including fire-resistant deciduous and evergreen trees, and resprouting species that recover quickly post-fire as Adie and Lawes (2023) illustrated too. According to Bauhus et al. (2017), this resilience is enhanced by the favorable climatic conditions prevalent in temperate regions, such as moderate temperatures and adequate rainfall, which support rapid vegetation recovery.

Additionally, the biome's mosaic of forested areas and grasslands as in the case of the Mediterranean region, with the latter recovering quickly due to rapid regrowth of grasses and herbaceous plants, further reduces overall vulnerability (Bauhus et al. 2017; Hamilton & Burton 2023).

In Europe, temperate grasslands, savannas, and shrublands such as the temperate grasslands of the Danube Delta are among the ecosystems with the lowest ecological vulnerability to wildfire. These ecosystems exhibit diverse landscapes internally caused by an equilibrium between nature and humans, similar to

what occurs in Mediterranean regions (Gastescu 1993). Thus, the limited area of this biome in the Danube Delta ecosystem in Romania shows a low EVW due to the short regeneration period despite assembling high EVA and very low CC.

European grasslands, in general, show no fire resistance. Grasses are highly flammable and would be completely consumed in fire (aboveground), unlike tree structures, but grass structures experience shorter regeneration times than trees (Keeley et al. 2011). Hence, the grasslands may have the ability to regenerate quickly after a fire (Gang et al. 2019; Ruprecht et al. 2015).

We did not differentiate CC and RT between grassland and shrubland species. Still, expanding the information in our database of species distribution for grasses or shrubs would be necessary. As proposed by Keeley et al. (2011), this would allow us to more accurately determine the ecological vulnerability of these areas, where tree cover does not represent all ecosystems.

In our framework, we limited CC and RT assessment to vegetation, whose response to fire is the most direct and which constitutes the main habitat for animal species. We then hypothesized here that animal diversity was equally affected and equally recovered after fires as vegetation. This might not be fully true as animal recovery is slower than vegetation (Jacquet & Prodon 2009; Prodon & Diaz-Delgado 2021), and fire size affecting landscape fragmentation might significantly affect the recovery rate (Puig-Giron et al. 2022). Further improvements should assemble animal traits related to fire-affected habitat specificities, as well as landscape fragmentation indices.

### Uncertainties

Our EVW framework relies on multiple data sources and assumptions, potentially sources of uncertainties. Our sensitivity analysis results revealed that CC and RT were both similarly relevant, as the extensive literature reflects (Yi & Jackson 2021), but with the CC factor standing out, a key factor to refine and pay attention to. We could show that Europe exhibits contrasted vulnerability to extreme fires throughout its territory. The following ranking of ecosystems most vulnerable to fire could be established: tundra, boreal forests, temperate coniferous forests, Mediterranean regions, temperate grasslands, and temperate deciduous and mixed forests. Interestingly, in line with the study on the vulnerability of forest ecosystems to climate change in Europe by Lindner et al. (2010), the most vulnerable regions coincide as the boreal and coniferous forests in the northern UK, while Mediterranean areas are identified

as moderately vulnerable, so that increasing fires with climate change might enhance these already identified vulnerable regions.

Our framework provides a static map of EVW, assuming constant species distribution maps and climate modifiers. Based on these climate effects, we could provide climate-responsive RT following observations. For example, the tundra undergoes a short growing season due to low temperatures, shortening the time for vegetation to recover and regenerate and contributing to a reduced regenerative capacity after a fire (Boucher et al. 2020; Bret-Harte et al. 2013; Strengbom et al. 2001). Similarly, many areas in the Mediterranean region report higher RT values due to low water availability from insufficient rainfall and consequent soil degradation caused by drought episodes (Baeza et al. 2007; Bisson et al. 2008). Adequate water availability post-fire is crucial for the germination of most seeders (Moreno & Oechel 1992), as dry conditions can delay post-fire regeneration in seeding communities, as suggested by Rodrigo et al. (2004). Despite being a region with most European fires and so considered good fire response, it does not emerge as the least vulnerable region based on the extreme fire scenario. In turn, as argued by Pausas et al. (2008), the extreme fire scenario with high temperatures and prolonged fire exposure results in a challenge to overcome even by fire-adapted vegetation of the Mediterranean. This can severely impact seed viability and soil quality and hinder plant species' successful germination and regrowth (Moreira et al. 2011). Furthermore, the loss of vegetation cover, soil degradation, and dry weather with limited water availability after fire can impede seed germination, making it challenging for new plants to establish themselves (Seidl et al. 2011). Here, we used simple linear relationships between mean annual precipitation/temperature and CC or RT that could be further used in future climate change scenarios and forest species distribution (Mauri et al. 2022).

A more dynamic EVW approach, re-evaluating CC, RT, and EVA yearly, could consider potential cascading effects (Ibanez et al. 2022) when fire recurrence reaches short-term intervals below species maturity thresholds. Depending on the time since the last fire, non-linear responses could highly increase RT and the subsequent EVW.

Our methodological framework can finally be applied at a regional scale with fine-resolution data improving biodiversity information (Diví & Chytrý, 2018), fire scenario (Chuvienco et al. 2023), plant functional traits (Kattge et al. 2020), biomass assessment

(Vallet et al. 2023), and topo-climates (Ackerly et al. 2020), for more local fire management strategies and stakeholder concerns or empirical knowledge (Rivière et al. 2023).

### Applicability

Despite the disparity in spatial databases, inherent assumptions and the uncertainty of the integration methods inherent to these kinds of studies (Heuvelink 1998; Heuvelink et al. 1989), we have proposed a standardized methodology for assessing ecological vulnerability to wildfires across Europe, developing the current assessment of wildfire vulnerability available at the European Forest Fire Information system San-Miguel-Ayanz et al. (2018), relying on the Natura 2000 network alone. This latter initial approach lacks fire scenarios and fails to consider the key component of ecosystem resilience.

Our achievement is a significant step for the scientific community in consolidating a standardized approach and holds significant importance for the EU stakeholders. A comprehensive framework allows for a holistic assessment of vulnerability, considering multiple factors such as biodiversity richness and conservation status, vegetation resilience to fire, and bioclimatic conditions affecting regeneration. This integrated approach facilitates a deeper understanding of how different ecosystems respond to wildfires and their potential for recovery, thus providing a scientific basis for informed decision-making. Standardized methodologies enable comparative evaluations of vulnerability across different European regions, which is essential for identifying areas requiring prioritized attention and additional resources. This optimizes the allocation of funds and mitigation efforts.

The ability to map these ecologically vulnerable zones provides a valuable tool for society, legislation, and decision-making to solve the current concerns of UNESCO World Heritage (Durrant et al. 2023) and the specific biodiversity (Biodiversity Strategy for 2030) (<https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52020DC0380>—last accessed: December 2023) and forest (New EU Forest Strategy for 2030) (<https://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:52021DC0572>—last accessed: December 2023) targets in risk reduction of the European Green Deal. Moreover, the assessment of ecological vulnerability enhances fire risk information systems, by extending the traditional concept of danger evaluation with new dimensions, reminding that risk assessment should include both aspects, the physical probability of the event and the potential damages that it may cause.

Based on the vulnerability maps, the European Union can allocate funds specifically to countries and regions with higher vulnerability. This ensures that resources are used efficiently to reduce wildfire risk and enhance ecological resilience. The data derived from these studies can guide the development of specific wildfire management policies, including forest management and ecosystem restoration practices.

Examples of effective measures include the selective clearing of vegetation to reduce available biomass, managed grazing to control vegetation sustainably, and the planting of shrubs and trees to restore degraded areas with fire-resilient species (Jucker Riva et al. 2018). These measures promote ecological recovery and protect against erosion, contributing to the overall resilience of ecosystems. Additional conservation practices, such as the protection of specific species and the provision of forage, can further enhance ecosystem resilience (Jucker Riva et al. 2018).

Areas identified with higher vulnerability can benefit from more detailed studies using precise databases that allow for a fine-grained identification of priority areas. This facilitates more effective and targeted investments in mitigation measures.

## Conclusions

This study aims to present a first methodological framework for assessing ecological vulnerability to wildfires at European scale based on the concepts of ecological values, coping capacity, and recovery time after wildfires. The method is based on map algebra, which could ensure replicability on other regions and scales. Coping capacity was a prominent factor when estimating vulnerability. As a preliminary approximation, it can be further refined to address uncertainties in the model within specific areas.

In conclusion, the tundra biome emerges as the most ecologically vulnerable to fire, primarily due to its high ecological values and significant recovery time, combined with a moderate coping capacity. Temperate conifer forests also exhibit high vulnerability to wildfires driven by extensive recovery time, despite moderate ecological and coping capacity values. The boreal forests rank next, with considerable vulnerability due to their long recovery time and moderate coping capacity. The Mediterranean region, although having moderate ecological values and recovery time, shows a notable vulnerability influenced by lower coping capacity. The

temperate broadleaf and mixed forests demonstrate relatively lower vulnerability owing to their balanced ecological values, moderate recovery time, and substantial coping capacity. Lastly, the temperate grasslands, savannas, and shrublands are the least vulnerable, benefiting from lower ecological values and the fastest recovery time, alongside moderate coping capacity, which collectively reduce their overall fire vulnerability.

The proposed method contributes a step forward to a European-scale mapping of ecological vulnerability. This component of the full framework includes additional vulnerabilities such as those related to the socio-economic values (ecosystem services, human infrastructure, and houses) (Chuvienco et al. 2023).

In any case, we consider the proposed method sufficiently strong to be valuable for the European Community since it is valid for identifying ecological priority zones against wildfires, promoting successful regeneration after wildfires, and promoting effective forest management practices and conservation policies.

## Appendix 1

**Table 5** List of terms through the manuscript with its acronyms

Terms	Acronyms
Biological distinctiveness	BD
Conservation status	CS
Coping capacity	CC
Discount rate	r
Ecological potential losses	EPL
Ecological resilience	ER
Ecological values assessment	EVA
Ecological vulnerability to wildfires	EVW
Environmental constraints	EC
Fireline intensity	FLI
Principal component analyses	PCA
Recovery time	RT
Recovery starting time	RST
Species-specific recovery time	RTi
Resistance of the vegetation to wildfires	RVW
Tree potential habitat maps	TPHM
Adjustment of recovery starting time	ARST
Adjustment of species-specific recovery time	ARTi



**Fig. 9** The study area of Europe is classified into the biomes proposed by Dinerstein et al. (2017)

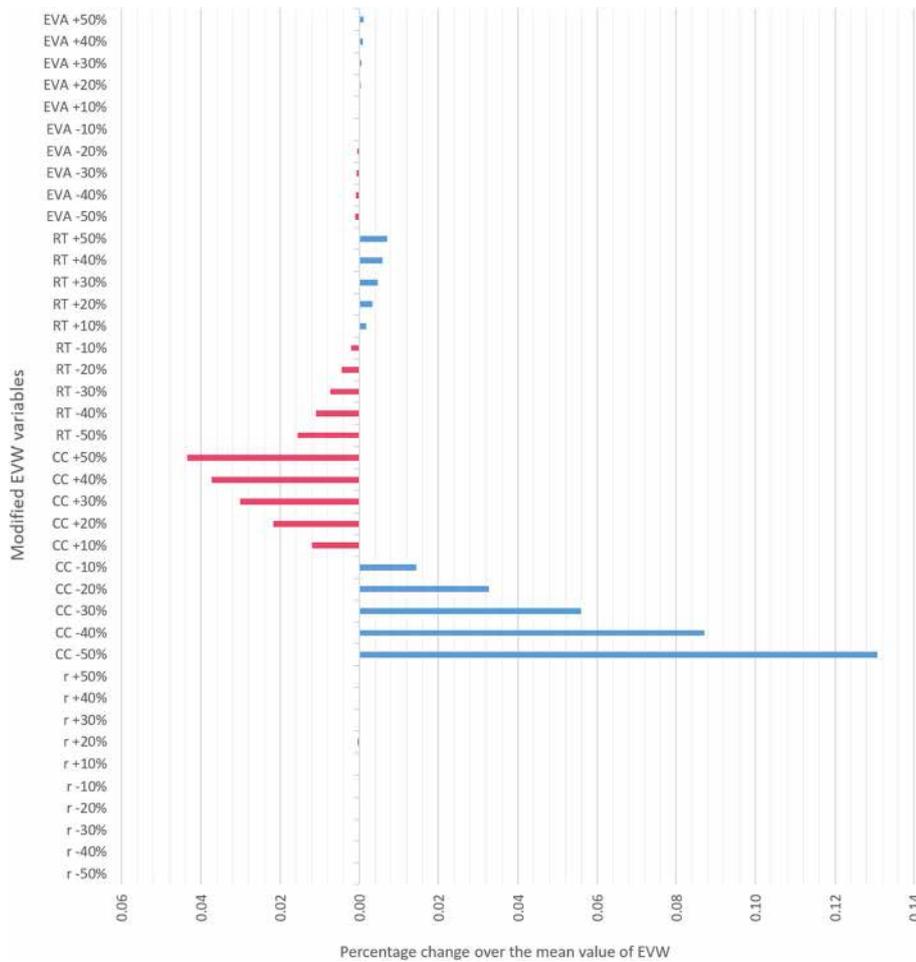
**Table 6** List of plant species used to characterize the CC and RT

Species	Sub	Land cover	Resistance (FTrw)	Regeneration starting time (years) RST	Maximum growth rate (GR) (m.year <sup>-1</sup> )	Biomass max (BMAX) (MgDW. ha)
Grass	grass	1	0.00	0	0.10	5
Crop	crop	2	0.01	0	1.00	5
Peat	peat	3	0.01	0	0.10	50
Heath	heath	4	0.02	-2	0.20	50
Shrub	shrub	5	0.02	-2	0.20	50
Orchard	orchard	6	0.08	-10	0.09	300
Vineyard	vineyard	7	0.03	-2	0.10	60
Forest	broadleaves	8	0.30	12	0.96	1
Forest	needleleaves	9	0.13	-10	0.21	1
<i>Abies</i>	<i>alba</i>	9	0.17	-10	0.21	391
<i>Acer</i>	<i>campestre</i>	8	0.13	-10	0.25	71
<i>Acer</i>	<i>opalus</i>	8	0.32	-10	0.22	71
<i>Acer</i>	<i>platanoides</i>	8	0.23	-10	0.24	69
<i>Acer</i>	<i>pseudoplatanus</i>	8	0.16	-10	0.24	201
<i>Alnus</i>	<i>glutinosa</i>	8	0.09	-10	0.50	85
<i>Alnus</i>	<i>incana</i>	8	0.10	-10	0.10	121
<i>Arbutus</i>	<i>unedo</i>	5	0.23	-10	0.31	50
<i>Aria</i>	<i>edulis</i>	8	0.22	-10	0.31	120
<i>Betula</i>	<i>pendula</i>	8	0.10	12	0.09	89
<i>Betula</i>	<i>pubescens</i>	8	0.13	-10	0.51	89
<i>Borkhausenia</i>	<i>intermedia</i>	8	0.16	-10	0.51	89
<i>Carpinus</i>	<i>betulus</i>	8	0.27	-10	0.14	163
<i>Carpinus</i>	<i>orientalis</i>	8	0.20	-10	0.51	163
<i>Castanea</i>	<i>sativa</i>	8	0.16	-10	0.15	371
<i>Celtis</i>	<i>australis</i>	8	0.12	-10	0.11	163
<i>Ceratonia</i>	<i>siliqua</i>	8	0.09	-10	0.07	163
<i>Cormus</i>	<i>domestica</i>	8	0.23	17	0.20	163
<i>Corylus</i>	<i>avellana</i>	8	0.29	-25	0.29	163
<i>Cupressus</i>	<i>sempervirens</i>	9	0.41	-10	0.72	163
<i>Eucalyptus</i>	<i>spp</i>	10	0.33	-10	0.26	300
<i>Fagus</i>	<i>sylvatica</i>	8	0.24	-10	0.33	385
<i>Fraxinus</i>	<i>angustifolia</i>	8	0.13	-10	0.10	126
<i>Fraxinus</i>	<i>excelsior</i>	8	0.21	-10	0.50	126
<i>Fraxinus</i>	<i>ornus</i>	8	0.27	10	0.15	126
<i>Juglans</i>	<i>regia</i>	8	0.27	15	0.34	200
<i>Juniperus</i>	<i>thurifera</i>	5	0.05	-10	0.10	50
<i>Larix</i>	<i>decidua</i>	8	0.09	11	0.09	232
<i>Laurus</i>	<i>nobilis</i>	8	0.15	-10	0.12	50
<i>Malus</i>	<i>sylvestris</i>	8	0.07	-10	0.48	90
<i>Olea</i>	<i>europaea</i>	11	0.42	10	0.94	400
<i>Ostrya</i>	<i>carpinifolia</i>	8	0.52	0	0.23	100
<i>Picea</i>	<i>abies</i>	9	0.28	1	0.17	272
<i>Pinus</i>	<i>brutia</i>	9	0.40	0	0.49	542
<i>Pinus</i>	<i>cembra</i>	9	0.50	3	0.60	542
<i>Pinus</i>	<i>halepensis</i>	9	0.45	0	0.70	294
<i>Pinus</i>	<i>nigra</i>	9	0.45	0	0.70	289
<i>Pinus</i>	<i>pinaster</i>	9	0.48	11	0.31	559
<i>Pinus</i>	<i>pinea</i>	9	0.07	-10	0.36	559

Species	Sub	Land cover	Resistance (FTrw)	Regeneration starting time (years) RST	Maximum growth rate (GR) (m.year <sup>-1</sup> )	Biomass max (BMAX) (MgDW. ha)
<i>Pinus</i>	<i>sylvestris</i>	9	0.07	-10	0.36	208
<i>Pistacia</i>	<i>lentiscus</i>	5	0.14	-10	0.47	50
<i>Pistacia</i>	<i>terebinthus</i>	5	0.27	-10	0.48	50
<i>Populus</i>	<i>alba</i>	8	0.30	-10	0.44	225
<i>Populus</i>	<i>nigra</i>	8	0.16	-10	0.23	225
<i>Populus</i>	<i>tremula</i>	8	0.16	12	0.23	87
<i>Prunus</i>	<i>avium</i>	8	0.92	9	2.16	90
<i>Prunus</i>	<i>padus</i>	8	0.09	11	0.09	90
<i>Pseudotsuga</i>	<i>menziesii</i>	8	0.36	-10	0.25	266
<i>Pyrus</i>	<i>communis</i>	8	0.09	-10	0.30	90
<i>Quercus</i>	<i>cerris</i>	8	0.31	-10	0.17	400
<i>Quercus</i>	<i>coccifera</i>	8	0.30	-10	0.25	50
<i>Quercus</i>	<i>faginea</i>	8	0.18	-10	0.10	400
<i>Quercus</i>	<i>frainetto</i>	8	0.35	-10	0.63	400
<i>Quercus</i>	<i>ilex</i>	8	0.24	-10	0.30	443
<i>Quercus</i>	<i>petraea</i>	8	0.16	-10	0.17	409
<i>Quercus</i>	<i>pubescens</i>	8	0.34	-10	0.63	258
<i>Quercus</i>	<i>pyrenaica</i>	8	0.43	-25	0.11	400
<i>Quercus</i>	<i>robur</i>	8	0.29	-10	0.48	433
<i>Quercus</i>	<i>suber</i>	8	0.18	-10	0.25	450
<i>Robinia</i>	<i>pseudoacacia</i>	8	0.12	-10	0.19	400
<i>Salix</i>	<i>alba</i>	8	0.22	-10	0.20	123
<i>Sorbus</i>	<i>aucuparia</i>	8	0.14	-10	0.20	33
<i>Taxus</i>	<i>baccata</i>	8	0.27	-10	0.40	514
<i>Tilia</i>	<i>cordata</i>	8	0.18	-10	0.15	246
<i>Tilia</i>	<i>platyphyllos</i>	8	0.38	-10	0.38	243
<i>Torminalis</i>	<i>glaberrima</i>	8	0.35	-10	0.38	243
<i>Ulmus</i>	<i>glabra</i>	8	0.32	-10	0.38	202
<i>Ulmus</i>	<i>laevis</i>	8	0.00	0	0.10	202
<i>Ulmus</i>	<i>minor</i>	8	0.01	0	1.00	202

**Table 7** Results of PCA based on ecological values assessment and its explanatory variables

Number of PCA	Axis 1
Explicability	0.79
Eigenvectors	259.3
Input layer	Ecological values assessment (EVA)
Species richness	0.59
Abundance of species	0.39
Forest productivity	0.35
Key biodiversity areas	0.38
Exceptional forests	0.29
Places of special conservation	0.46
Human pressures	-0.32
Loss of forest	-0.34
Unique habitat preservation	0.52



**Fig. 10** Results of the sensitivity analyses OAAT

**Appendix 2**

PCA methodology: extra

Bartlett’s test of sphericity evaluates redundancy between variables by comparing the observed correlation matrix with the identity matrix. The alternative hypothesis suggests sufficient correlation for data reduction (Andersen et al. 2009). The test is represented by Eq. 8, where  $\det(R)$  is the determinant of the correlation matrix,  $N$  is the number of observations, and  $p$  is the number of variables.

$$\text{Bartlett} = -\log(\det(R)) * (N - 1 - \frac{2p + 5}{6}) \quad (8)$$

KMO is a statistical measure determining data suitability for factor analysis; values below 0.5 indicate inadequate sampling (Andersen et al. 2009). Equation 9 defines the KMO test, where  $r_{jk}$  is the correlation between the

variable in question and another, and  $p_{jk}$  is the partial correlation.

$$\text{KMO} = \frac{\sum \sum_{j \neq k} r_{jk}^2}{\sum \sum_{j \neq k} r_{jk}^2 + \sum \sum_{j \neq k} p_{jk}^2} \quad (9)$$

Omega hierarchical asymptotic assesses the internal consistency reliability of data, indicating the overall consistency of a measure. This test was chosen for its appropriateness in this context (Andersen et al. 2009). The equation for omega hierarchical asymptotic is given in Eq. 10, representing the ratio between true score variance and the sum of variances and covariances of the data.

$$\omega = \frac{(\sum \lambda_j)^2}{(\sum \lambda_j)^2 + (\sum \sigma_{ej})^2} \quad (10)$$

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## Authors' contributions

FAF designed the study, organized and oversaw data collection, developed the analysis approach, implemented the analysis, drafted the manuscript, and contributed editorial input during manuscript preparation. FM organized and oversaw data collection, implemented the analysis, and contributed with the improvement of the manuscript. BM organized and oversaw data collection and contributed to the improvement of the manuscript. IAS and EC obtained funding, designed the study, 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 upon 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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