Ann. For. Res. 66(2): 17-32, 2023
https://doi.org/10.15287/afr.2023.2645

ANNALS OF FOREST RESEARCH
www.afrjournal.org

Conservation of unmanaged pan-European forest landscapes as a priority natural heritage for epiphytic lichens at different ecological and biogeographical scales - A review

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Vicol I., Sahlean T.C., 2023. Conservation of unmanaged pan-European forest landscapes as a priority natural heritage for epiphytic lichens at different ecological and biogeographical scales - A review. Ann. For. Res. 66(2): 17-32.

Abstract The European forestry landscape represents an important priority for biodiversity and needs adequate management strategies. The main focus of this review is the importance of European forest areas for epiphytic lichen richness under the impact of different management practices assessed in the biogeographical and ecological regions of Europe. In total, 88 scientific articles were reviewed (based on the first author's archive and by query in Web of Science), which examined epiphytic lichen richness within managed and unmanaged European forests. Biogeographical and ecological regions of Europe were not taken into account in the reviewed articles, but we used them for statistical analyses in the present work according to the geographical position of the investigated sites published in the reviewed articles. We also analysed the dissimilarities in epiphytic lichen richness among European biogeographical and ecological regions. Additionally, we analysed the impact of different silvicultural management practices (within assessed forests) on epiphytic lichen richness across the different biogeographical and ecological regions of Europe. The main results indicate that epiphytic lichen richness is significantly different across the biogeographical and ecological regions of Europe. Epiphytic lichen richness is significantly greater in Western European broadleaf forests in the Carpathian and Caledonian mountain areas and significantly lower in the Central European mixed forests and East European forest steppe. Management practices applied within studied forests had a negative impact on epiphytic lichen richness, while epiphytic lichen richness was higher within unmanaged forests. The main conclusion is that forests within highland areas of Europe that are not subjected to anthropogenic activities or management practices harbour greater epiphytic lichen richness and therefore should be conserved and protected due to their biological and ecological importance.

Keywords: abiogeographical regions, conservation of unmanaged forests, ecoregions, European forests, lichens.

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Manuscript: received October 13, 2022; revised September 19, 2023; accepted October 09, 2023

Introduction

Forests cover 35% of the European terrestrial surface, 46% being coniferous forests, 37% broadleaved forests, and 17% mixed forests (Forest Europe 2020). Consequently, European forests with high connectivity are currently regionally restricted (Wolseley et al. 2017), and some of them are subjected to economic conflicts (Blicharska et al. 2020).

The fragmentation of forestry landscapes is related to different unfavourable microclimates and a strong edge effect, which has a negative impact on epiphytic lichens (Esseen & Renhorn 1998; Brunialti et al. 2012; Maceda Veiga & Gómez-Bolea 2017; Cordero et al. 2021; Bartemucci et al. 2022). Generally, the conservation of biodiversity depends, to a high degree, on the good connectivity and continuity of forest landscapes, which provide varied environmental conditions for different biotic communities (Hanski 1999; Fritz et al. 2008; Świerkosz et al. 2017; Stăncioiu et al. 2018).

Lichens play important roles within forest habitats through their contribution to biological diversity and by driving ecological and biogeochemical processes (Asplund & Wardle 2017; Vondrák et al. 2019). Additionally, lichens provide additional biomass in forest habitats, are used as food and shelter for wildlife and are valuable forest continuity indicators (Asplund & Wardle 2017; Miller et al. 2020). Furthermore, lichens are traditionally used by humans as feed and for other purposes, such as therapeutic, ceremonial, religious, and veterinary (Devkota et al. 2017).

Lichens dwelling in forests, especially red-listed species, are affected by air pollution, fragmentation of forestry areas, and climate change (Kapusta et al. 2004; Nascimbene et al. 2013a; Łubek et al. 2021).

In the current context of forestry sustainability, inadequate forest management induces a lack of multi-aged forestry areas, which translates into reduced tree diversity (Dingová Košuthová et al. 2013). In addition, natural resources are critically affected, and as a consequence, the diversity of lichen species is poorly represented within these forest habitats (Dingová Košuthová et al. 2013; Bartemucci et al. 2022). Silvicultural practices (e.g., clearcutting and shelterwood systems) have a negative impact on epiphytic lichens because they create new harsh environmental conditions (Hilmo et al. 2005; Nascimbene et al. 2013b) with an especially harmful effect on species recognized as specialist groups and their communities (Lelli et al. 2019). Furthermore, the capacity and ability of lichens to inhabit woody substrates depends on adequate management of forest habitats (Johansson et al. 2012; Bouchard & Boudreault 2016). The ecology and genetics of lichens are strongly influenced by forest management, and therefore, massive forest fragmentation induces serious declines at the population level, with long-term ecological and genetic effects (Zoller et al. 1999; Otálora et al. 2011; Bouchard & Boudreault 2016). The main genetic effect of forest fragmentation is the high genetic differentiation of lichen populations at the landscape level (Hilmo et al. 2012).

Alpine forests not subjected to intensive management are natural refuges for a high number of lichen species, especially those included in red lists (Nascimbene et al. 2010; Nascimbene et al. 2014). Adequate forest management ensures that natural environmental conditions are maintained, which in turn supports the genetic variability of lichen species, especially specialist groups dependent on habitat quality, forest connectivity and forest continuity (Belinchón et al. 2018).

European old-growth forests are known to harbour a great diversity of epiphytic lichen species, especially rare and threatened ones, thanks to the heterogeneity, quality and continuity of micro- and macrohabitats (Otálora et al. 2011; Paltto et al. 2011;

Svoboda et al. 2011; Kiebacher et al. 2017). The native complexity of forest landscapes is clearly affected by forestry activities, but it could be offset by improving the environmental conditions to match those of native forests (Johansson et al. 2013a; Hämäläinen et al. 2021). The conservation of native forest continuity is the main support strategy for lichen richness and requires management actions such as the restoration of forest surroundings (Rosenvald & Lohmus 2008; Johansson et al. 2013b), leading to reduced edge effects (Caruso et al. 2011). Furthermore, increasing the forest network through high connectivity leads to a decrease in species extinction (Niculae et al. 2017), facilitates species dispersal through biological corridors (Beier & Noss 1998; Lindenmayer et al. 2000) and represents an important measure for biodiversity conservation (Stăncioiu et al. 2018; Palmero-Iniesta et al. 2020).

The matrix of fragmented forests represented by different woody formations has an important role in connectivity across the forestry landscape and represents an adequate management action for lichen communities (Belinchón et al. 2009).

This study aims to review epiphytic lichen richness at the spatial scale of biogeographical and ecological regions across Europe based on bibliographic sources clearly indicated in the Materials and Methods section. The main objectives of this review are (i) to describe the epiphytic lichen richness pattern across biogeographical regions and ecoregions in Europe and (ii) to highlight the best forest management strategies that enhance epiphytic lichen richness across the biogeographical and ecological regions of Europe.

Materials and Methods

Selection of reference materials

Article selection was performed based on the following requirements: (**i**) only scientific articles that clearly presented the number of epiphytic lichen species specifically for each studied forest site (each forest site should have their number of epiphytic lichen species) were considered; the total number of lichen species across all studied forest sites within one article was not taken into account because this study is based on forests assessed as a unit; (**ii**) it was important that each article contained a list of all epiphytic lichen species detailed for each forest site so that a list of all epiphytic lichen species could be created for this study; (**iii**) great importance was attributed to the applied silvicultural management practices such as clearcutting, selective clearcutting, shelterwood system, etc.; if the authors presented only the type of management such as timber harvesting and not a clear indication of management practices, the article was not considered for this study. Additionally, general information without a clear mention of management practices, such as managed forest, was also not considered for this study. In addition, two new variables were added for each forest site: biogeographical region (EEA 2017) and ecoregion (Dinerstein et al. 2017).

An important source of articles for the study was the first author's personal archive, which consisted of **878** scientific articles on lichenology; only **50** articles were deemed adequate for this study based on the above-mentioned requirements (**Table S1**). In addition, a query in Web of Science was conducted based on the following keywords:

1) forest/lichen species/Europe. A total of **96** results were returned, of which only **27** were taken into account (**Table S2**).
2) forest management/lichen species/Europe. A total of **77** results were returned, of which only **11** were considered (**Table S3**).

In the end, a total of **88** scientific articles met the inclusion criteria and were used for this review.

Additionally, **9** of the scientific articles found in the first author's personal archive of **137** articles on the topic of landscape ecology were used (**Table S4**).

All lichen species names were updated (last update on 04.05.2022) according to http://www.indexfungorum.org, and all synonyms were removed from the dataset.

Spatial data processing

Information regarding the location of the forest sites where the studies were conducted was added to the database directly if it was reported by the authors. For articles that did not include spatial data, we manually georeferenced the approximate location of the study site using Google Earth Pro v7.3 (https://earth.google.com), Google Maps (https://www.google.com/maps) or OpenStreetMap (https://www.openstreetmap.org). Spatial data regarding the distribution of the biogeographical regions of Europe were downloaded from the European Environmental Agency (https://www.eea.europa.eu). Ecoregions 2017 © Resolve (Direnstein et al. 2017) is a global database of the 846 ecoregions on Earth; the data were downloaded for free from the host website (https://ecoregions.appspot.com).

After adding coordinate information to all entries, the database was imported to ArcGIS 10.7.1 (ESRI 2019), which was used to create and export maps. The maps featuring ecoregions only show relevant ecoregions to limit the size of the legend and adhere to constraints regarding map format.

Statistical analysis

Regarding the variables taken into account in the statistical analyses, some necessary explanations are given as follows: (a) within this work, lichen richness is represented by the total number of epiphytic lichen species identified within a site represented by a forest; (b) management practices applied within each forest site were considered; (c) the type of forest is based on the map of the Earth's ecoregions (Dinerstein et al. 2017); and (d) biogeographical regions considered are those defined by the European Environment Agency (2017). The lichen richness and management practices were taken from reviewed materials, whilst ecoregions (Dinerstein et al. 2017) and biogeographical regions (EEA 2017) are new ideas first used in this study. The reference materials used for statistical analyses are listed in **Table S5** in the Supporting Information.

The ecoregions used for this study are as follows: Alps conifer and mixed forests, Apennine deciduous montane forests, Baltic mixed forests, Caledon conifer forests, Cantabrian mixed forests, Carpathian montane forests, Caucasus mixed forests, Celtic broadleaf forests, Central European mixed forests, Crimean Submediterranean forest complex, East European forest steppe, English Lowlands beech forests, Iberian conifer forests, Iberian sclerophyllous and semi-deciduous forests, Italian sclerophyllous and semi-deciduous forests, Northwest Iberian montane forests, Pannonian mixed forests, Scandinavian montane birch forests and grasslands, Scandinavian and Russian taiga, and Western European broadleaf forests (Dinerstein et al. 2017).

The biogeographical regions of Europe used in this study are Alpine, Atlantic, Boreal, Continental, Mediterranean, and Steppic (EEA 2017).

The management practices assessed in this study are clearcutting, coppicing, crop production, forest managed for its sustainable ecological and social functions, selective cutting, shelterwood system, thinning, and wood pastures (**Table S6, Table S8**). Additionally, unmanaged forests were considered in statistical analyses due to their conservation interest (**Table S7**). In the case of some reference materials, management practices were observed during field activities (**Table S8**).

The dataset includes the following variables: geographical coordinates, biogeographical region, ecoregion, management practice and epiphytic lichen richness. In this study, biogeographical region, ecoregion, and management practice were treated as binary variables, whilst epiphytic lichen richness was treated as a discrete variable.

All statistical analyses were conducted using PAST software (Hammer et al. 2001). First, to avoid autocorrelation between variables, biogeographical regions and ecoregions were correlated to geographic coordinates using spatial autocorrelation analysis based on Moran's *I* test (Hammer et al. 2001). The results showed (a) a significant correlation ($p < 0.05$) between geographical coordinates and the Boreal bioregion and (b) significant correlations ($p < 0.05$) between geographical coordinates and Baltic mixed forests, Crimean Submediterranean forest complex, English Lowlands beech forests, Iberian sclerophyllous and semi-deciduous forests, Italian sclerophyllous and semi-deciduous forests and Northwest Iberian montane forests. All correlated variables were not considered when running the statistical analyses. Afterwards, statistical analyses included Kendall rank-order correlation (Dytham 2011) and one-way ANOSIM (Hammer et al. 2001). Thus, correlations between lichen richness and each biogeographical region, each ecoregion, and each management practice were performed using the Kendall correlation coefficient (Hammer et al. 2001). The differences between different groups within the same variable (represented by ecoregions, biogeographical regions, and management practices) were tested using one-way ANOSIM. The one-way ANOSIM test was performed using the Bray–Curtis distance index based on 9,999 permutations (Hammer et al. 2001).

Results

The final dataset comprised 128 records with the following data attached: biogeographical regions, ecoregions, management practices applied within studied forest sites, and richness of epiphytic lichens widely distributed across different European biogeographical (Fig. 1) and ecological (Fig. 2) regions.

A total of 936 epiphytic lichen species (**Table S9**) were recorded, geographically distributed across European biogeographical and ecological regions. The number of epiphytic lichen species was greater in the Alpine and Atlantic bioregions and lower in the Mediterranean and Steppic bioregions. Across the Boreal and Continental bioregions, a moderate number of epiphytic lichens were observed (**Table S10**). Within Europe's ecoregions, the number of epiphytic lichen species was greater across the Crimean Submediterranean forest complex, Carpathian montane coniferous forests, and Celtic broadleaf forests, moderate in English Lowlands beech forests, Central European mixed forests, Pannonian mixed forests, Western European broadleaf forests, and lower in Alps conifer and mixed forests, Apennine deciduous forests, Baltic mixed forests, Cantabrian mixed forests, East European forests steppe, Iberian conifer forests, Iberian sclerophyllous and

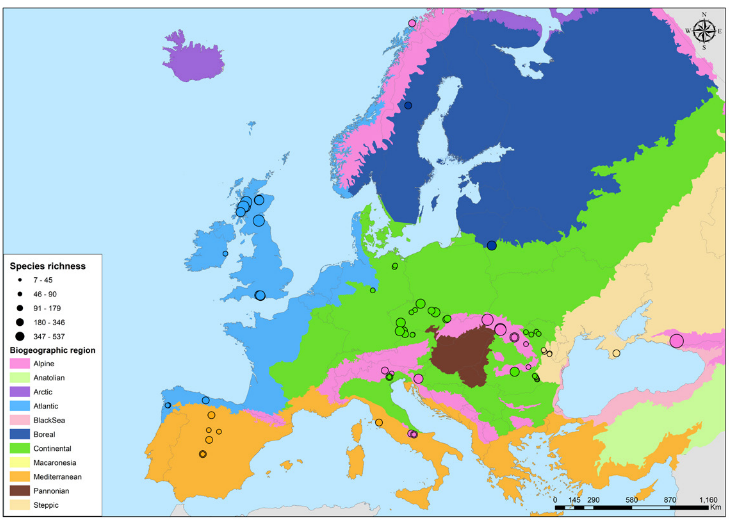

Figure 1 Geographical distribution of epiphytic lichen richness across European biogeographical regions.

semi-deciduous forests, Italian sclerophyllous and semi-deciduous forests, Northwest Iberian montane forests, Scandinavian and Russian taiga, and Scandinavian montane birch forests and grasslands (**Table S11**).

In particular, one-way ANOSIM of lichen richness between various biogeographical regions and ecoregions indicated significant differences for a great part of the variables attributed to these two categories (Table 1).

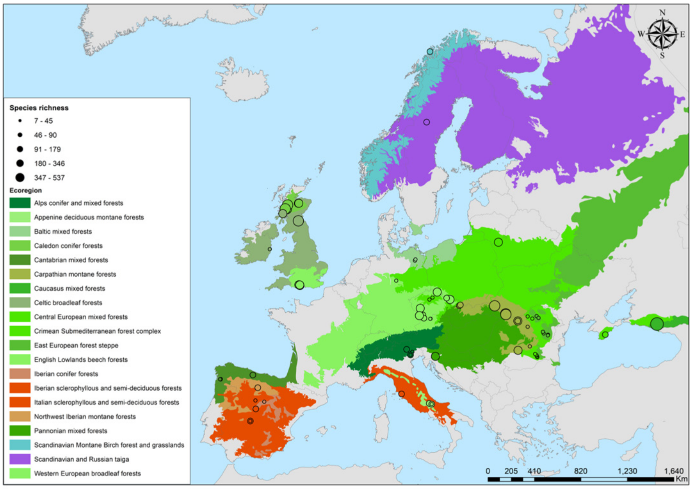

Figure 2 Geographical distribution of epiphytic lichen richness across European ecoregions. The large grey areas belong to other ecoregions not included in this study.

Table 1 Results of one-way ANOSIM of lichen richness between different European biogeographical and ecological regions.

European biogeographical regions	
Test statistic R and its *p* value	Pairwise post hoc *p* value
R = 0.35 *p* = 0.0001	ALP vs. MED (*p*=0.0001) ALP vs. STE (*p*=0.008) ATL vs. CON (*p*=0.01) ATL vs. MED (*p*=0.0001) ATL vs. STE (*p*=0.006) CON vs. MED (*p*=0.0001) MED vs. STE (*p*=0.0001)
European ecological regions	
Test statistic R and its *p* value	Pairwise post hoc *p* value
R = 0.31 *p* = 0.0001	ACMF vs. CCF (*p*=0.0002) ACMF vs. CRMF (*p*=0.004) ACMF vs. CBF (*p*=0.02) ACMF vs. CEMF (*p*=0.001) ACMF vs. EEFS (*p*=0.001) ACMF vs. WEBF (*p*=0.02) CCF vs. CMF (*p*=0.004) CCF vs. EEFS (*p*=0.0001) CCF vs. SMBFG (*p*=0.03) CCF vs. WEBF (*p*=0.02) CMF vs. EEFS (*p*=0.009) CRMF vs. EEFS (*p*=0.0001) CBF vs. EEFS (*p*=0.01) CEMF vs. EEFS (*p*=0.0003) EEFS vs. SMBFG (*p*=0.01) EEFS vs. WEBF (*p*=0.003)

Legend: European biogeographical regions: ALP-Alpine; ATL-Atlantic; CON-Continental; MED-Mediterranean; STE-Steppic. European ecological regions: ACMF-Alps conifer and mixed forests; CBF-Celtic broadleaf forests; CRMF-Carpathian montane forests; CCF-Caledon conifer forests; CEMF-Central European mixed forests; EEFS-East European forest steppe; CMF-Cantabrian mixed forests; SMBFG-Scandinavian montane birch forests and grasslands; WEBF-Western European broadleaf forests.

At the biogeographical level, major differences in lichen richness were noted in the Alpine versus Mediterranean and Steppic bioregions, followed by Atlantic versus Continental, Mediterranean, and Steppic bioregions, Continental versus Mediterranean, and Mediterranean versus Steppic bioregions (Table 1).

In the case of Europe's ecoregions, lichen richness was significantly different across various types of European forests from mountain areas, especially the Alps and Carpathian Mountains, to the western, central and eastern forest ecoregions of Europe (Table 1). Additionally, the lichen richness of the Caledon forest area was significantly different from that of the Cantabrian, Scandinavian and West European forest ecoregions and from the

Eastern forest steppe (Table 1). The Carpathian and Celtic forest areas were significantly different from the Eastern forest steppe of Europe with regard to their lichen richness (Table 1). The eastern forest steppe of Europe was significantly different in lichen richness from the central, northern and western forest areas of Europe (Table 1).

Lichen richness was significantly related togeographical distribution across various European biogeographical and ecological regions (Table 2). Additionally, lichen richness was significantly correlated with forest management practices applied within the studied forest sites (Table 2).

The lichen richness increased across the Alpine and Atlantic bioregions, whilst across the Continental and Steppic bioregions, the lichen richness decreased (Table 2). Western European broadleaf forests, Carpathian montane forests and Caledon conifer forests supported a higher lichen richness, whilst across Central European mixed forests and East European forest steppe, the lichen richness was lower (Table 2).

Table 2 Relationships between lichen richness and distribution across different European biogeographical and ecological regions based on the Kendall correlation coefficient (τ). Additionally, relationships between lichen richness and forest management practices developed within the studied forests are given based on the Kendall correlation coefficient (τ).

European biogeographical region	τ -Test	*p* value
ALP	τ = 0.17	*p* = 0.003
ATL	τ = 0.24	*p* = 0.00003
CON	τ = -0.13	*p* = 0.01
STE	τ = -0.18	*p* = 0.001
European ecological region	**τ -Test**	***p* value**
CCF	τ = 0.25	*p* = 0.0001
CEMF	τ = -0.27	*p* = 0.000004
CRMF	τ = 0.15	*p* = 0.01
EEFS	τ = -0.23	*p* = 0.0008
WEBF	τ = 0.19	*p* = 0.001
Management practice	**τ -Test**	***p* value**
FMSESF	τ = -0.20	*p* = 0.0008
SC	τ = -0.16	*p* = 0.004
UMF	τ = 0.24	*p* = 0.00004

Legend: European biogeographical regions: ALP-Alpine; ATL-Atlantic; CON-Continental; STE-Steppic. European Ecological Regions: CRMF-Carpathian montane forests; CCF-Caledon conifer forests; EEFS-East European forest steppe; CEMF-Central European mixed forests; WEBF-Western European broadleaf forests. Management practices: FMSESF-forest managed for its sustainable ecological and social functions; SC-Selective-cutting; UMF-Unmanaged forests.

Management practices such as forests managed for their sustainable ecological and social functions and selective cutting applied within studied forests caused a decrease in the number of lichen species (Table 2). Great importance was attributed to unmanaged forests that supported high lichen richness within the studied forests (Table 2; Fig. 3).

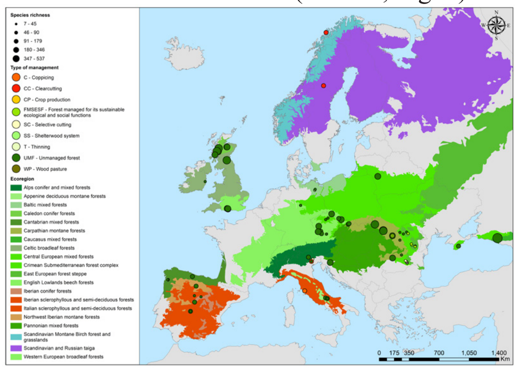

Figure 3 Epiphytic lichen species distribution based on forest management across Europe's ecoregions. The large grey areas belong to other ecoregions not included in this study.

Discussion

Conservation of European forest landscapes

Within Europe, all forested areas (managed and unmanaged forests) are important as enclaves of remnant biodiversity (Malíček et al. 2019). All European forests are sanctuaries for both human society and patches of wilderness, the latter being permanently subjected to anthropogenic conflicts (Blicharska et al. 2020).

In the context of European forest conservation, it is important to highlight that the significant results obtained on epiphytic lichen richness across European biogeographical and ecological regions could be attributed to geographical location (longitude and latitude) within the European continent, geomorphology, various climate conditions, low level of air pollution and different forest vegetation types (EEA 2017; de Rigo et al. 2016; Fatima et al. 2019; Cervellini et al. 2020; Forest Europe 2020; Surian 2022).

In Europe, there is a great complexity of forest types (habitats and ecosystems) represented by different tree species (EEA 2017; Forest Europe 2020), which harbour a high epiphytic lichen richness within the wildest forested areas (Vondrák et al. 2018; Malíček et al. 2019; Vondrák et al. 2019; Hofmeister et al. 2022). The most important conservation attributes of European highland and lowland forest habitats are represented by the oldest and multi-layered components, which provide adequate microhabitats efficient in supporting higher lichen richness (Dymytrova et al. 2014; Vicol 2020b). Carpathian and Caledonian forests comprise ancient woodlands recognized, among other aspects, for their richness in lichen species (Çobanoğlu et al. 2009; Çobanoğlu et al. 2011; Ardelean et al. 2013; Dymytrova et al. 2014; Vondrák et al. 2018; Hofmeister et al. 2022). Additionally, Carpathian and Caledonian forests are among the rare forestry areas characterized by uneven-aged forests (Dymytrova et al. 2014; Hofmeister et al. 2022).

Management strategies

Maintaining unmanaged forests across Europe

At the European level, multi-aged forests occupy 25% of the total land area (Forest Europe 2020). Generally, unmanaged European forests are uneven-aged and therefore should be important for conservation (Barredo et al. 2021) due to their capacity to harbour high epiphytic lichen richness (Dymytrova et al. 2014; Vondrák et al. 2018; Hofmeister et al. 2022). Historically, unmanaged European forests have been subjected to traditional activities maintained for centuries in European countries, and as such, traditional activities are important conservation strategies, actively implied in scenarios targeting the continuity of ancient forests that harbour a remarkable lichen diversity (Aragón et al. 2012; Hofmeister et al. 2016; Wolseley et al. 2017; Czerepko et al. 2021a). The higher lichen richness in unmanaged forest habitats could be attributed to their ecosystem quality, structural complexity and heterogeneity and is further supported by proper conservation measures, an adequate regime of protected areas and traditional management developed over time (Paillet et al. 2010; Aragón et al. 2012; Wolseley et al. 2017; Hofmeister et al. 2022).

Sustainable forest management across Europe

European forests provide many services consisting of wood and non-wood products used in various ways by human society (Forest Europe 2020). In this study, we show that forests managed for timber harvesting harbour a lower lichen richness, unlike unmanaged forests, which support a higher lichen richness. Retaining the complexity of forest structure is an efficient management practice that enhances lichen diversity (Sorrell 2006; Klein et al. 2020; Czerepko et al. 2021b). Adequate wood harvesting within forests, aimed at maintaining a heterogeneous structure, represents a management strategy that supports lichen species associated with ancient forest landscapes (Lommi et al. 2010); at this level, the structural complexity of forests plays an important role in enhanced lichen richness (Runnel et al. 2013; Oksuz et al. 2020; Czerepko et al. 2021b) as a result of the mosaic pattern of forest vegetation (Giordani 2006; Paltto et al. 2006; Giordani & Incerti 2008; Cardós et al. 2018). An important role is attributed to forest continuity, closely related to long rotation cycles as the main management strategy that offers support for high lichen diversity, reflected in species considered ecological continuity indicators (Rolstad & Rolstad 1999; Sorrell 2006).

Forest connectivity network across Europe

Forest connectivity has decreased over time, and currently, forest areas are overwhelmingly represented by different sized fragments with poor or absent connectivity (Stănciou et al. 2018). Forest fragmentation is caused by natural calamities (e.g., geological effects, climatic changes, volcanic eruptions) and by human activities such as the conversion of forests to agricultural fields, industrial areas, and buildings (Mullu, 2016). Generally, at lower altitudes, where forests are predominantly fragmented, especially in continental Europe, biodiversity is affected by human activities, as opposed to mountainous areas, where a high degree of forest connectivity exists, biodiversity is well represented and human impact is low (Stăncioiu et al. 2018). This could explain the higher richness of lichens identified in the Carpathian and Caledonian mountain forests, as opposed to the Central European mixed forests and East European forest steppe, where a lower lichen richness was observed, which could be influenced by climate conditions, such as longer drought periods in forest steppe areas (Lukanina et al. 2022). In this study, the Western European broadleaf forests included only unmanaged forests represented by diverse tree species that harbour a greater epiphytic lichen richness (Dittrich et al. 2014; Hofmeister et al. 2016; Malíček et al. 2019). Forested areas situated within the Central European mixed forests and East European forest steppe are subjected to human impacts accompanied by a severely lacking degree of connectivity (Stăncioiu et al. 2018). The mountain ranges of Europe are one of the largest forested areas of the biosphere and are characterized by high heterogeneity, continuity, and connectivity of forest habitats that are traditionally managed and can, therefore, support high lichen richness (Dilkina et al. 2016). Generally, epiphytes are well represented within forest habitats, but red-listed lichen species depend on the habitat quality offered by old-growth forests with a significant connectivity between patches (Paltto et al. 2006; Fritz & Brunet 2010). Forest connectivity is important for lichen diversity conservation since it reduces the risk of species extinction and enhances propagule dispersal (Fritz & Brunet 2010; Ellis & Coppins 2019). The connectivity between conserved forest habitats and the matrix represented by managed forest habitats should be enhanced to reduce edge effects across managed forests (Caruso et al. 2011; Liepa et al. 2020).

Size of forest fragments across Europe

Forest fragmentation reduces the widespread distribution of species, induces the loss of forest habitats and, consequently, leads to the extinction of species (Cardós et al. 2017). Afforestation with representative forest patches around intensively managed forestry areas creates a buffer zone that reduces the edge effect; thus, sensitive lichen species associated with undisturbed forests are less likely to be affected (Carlsson & Nilsson 2009; Jüriado & Liira 2009; Paoli et al. 2019; Bartemucci et al. 2022).

Forest fragmentation plays an important role in decreasing lichen richness (Marmor et al. 2011; Malíček et al. 2019). The lower lichen richness observed across the East European forest steppe could be caused by inadequate timber harvesting, accompanied by a critical level of fragmentation (Sârbu et al. 2007; Vicol 2020a). One of the more efficient management measures in strongly fragmented forests is a well-defined matrix of distinct natural vegetation communities (e.g., shrub and forest belts) and even plantations, which are important for mature forests because they act as a buffer against anthropogenic disturbance (Calviño-Cancela et al. 2013).

Role of protected areas

Protected forests cover 23.6% of the total European forest surface and play an important role in halting biodiversity loss (Forest Europe

2020). European forests should be preserved not only because of their lichen richness but also their biodiversity and environmental attributes, which, as a whole, represent a continuity of the undisturbed state of nature (Felton et al. 2020; Łubek et al. 2020; Marin et al. 2020). The last ancient forests of Europe are typically represented by deciduous and coniferous patches situated within undisturbed areas, some of which are located within protected areas (Marín et al. 2021) with a high priority for biodiversity conservation thanks to their status as biodiversity hotspots (Blicharska et al. 2020). In the present context of forestry landscapes, the diversity of both lichen species and their communities needs a network of forest areas (Johansson et al. 2013b) with a certain integral protection regime for sustainable forest conservation as one of the important EU nature strategies for 2030 (Barredo et al. 2021). Additionally, restoration of degraded habitats in protected areas should be based on adequate forest management, such as the retention of an old-growth mosaic represented by multi-aged trees; this also leads to the long-term conservation of lichen species, especially those dependent on natural old forests (Johansson et al. 2013b; Wolseley et al. 2017; Bartemucci et al. 2022).

Current threats to lichen species and their forest habitats

The niches of species across different types of European forests depend on various factors, such as climatic conditions, climate change, air pollution, fire regimes, forest landscape structure and dynamics, management measures, and conservation actions, which are important determinants of species dynamics (Wolseley 1995; Kapusta et al. 2004; Han et al. 2022).

At the global level, a serious and imminent threat is represented by climate change, which has grave consequences for biodiversity (Reed 2012). As with other groups of organisms, lichen species are also threatened by global warming, and as a consequence, they are becoming extinct in their millennial forest habitats (van Herk et al. 2002). Additionally, air pollution is another important global threat responsible for species extinction (Bellard et al. 2022).

Conclusions

At the pan-European level, lichen richness was significantly different across various bioregions and ecoregions. Furthermore, lichen richness was significantly greater across the Alpine and Atlantic bioregions whilst across the Continental and Steppic bioregions, lichen richness was significantly lower. The Western European broadleaf forest, Carpathian montane forest and Caledon conifer forest ecoregions were significantly well represented with regard to their lichen richness, whilst Central European mixed forests and East European forest steppe supported a lower lichen richness. An important finding is that unmanaged forests across Europe supported a greater lichen richness, in contrast to managed forests, which showed a lower lichen richness. Thus, an important aspect of this review is focused on unmanaged pan-European forests, which are generally a veritable core (hotspot) for biodiversity conservation. Unmanaged European forests are the last natural remnant refugia for lichen species, and therefore, it is critical to enhance their conservation and protection regimes. Furthermore, at the European Union level, political stakeholders should prioritize the conservation and protection of unmanaged forests because they represent the last natural heritage of Europe.

Acknowledgements

The study was funded by project RO1567-IBB04/2022 from the Institute of Biology Bucharest of the Romanian Academy. The authors would like to thank American Journal Experts, who improved the English language.

Description of the Supporting Information

Table S1. Scientific articles included in the first author's personal archive (Lichenology database) used in the present review article.
Table S2. Reference materials retrieved from the Web of Science platform according to the following topics: forest/lichen species/Europe.
Table S3. Reference materials retrieved from on the Web of Science platform according to the following topics: forest management/lichen species/Europe.
Table S4. Scientific articles included in the first author's personal archive (Landscape Ecology database) used in the present review article.
Table S5. Reference materials used in the statistical analyses based on selected variables such as lichen richness and management practices.
Table S6. Reference materials used in the statistical analyses based on management practices.
Table S7. Reference materials for unmanaged forests used in the statistical analyses.
Table S8. Management practices observed during field activities used in the statistical analyses.
Table S9. Total epiphytic lichen richness recorded based on reviewed articles.
Table S10. Variation in the number of epiphytic lichen species across biogeographical regions and corresponding references.
Table S11. Variation in the number of epiphytic lichen species across European ecological regions corresponding references.

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