

Review

Lobaria pulmonaria (L.) Hoffm.: The Multifaceted Suitability of the Lung Lichen to Monitor Forest Ecosystems

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Citation: Ravera, S.; Benesperi, R.; Bianchi, E.; Brunialti, G.; Di Nuzzo, L.; Frati, L.; Giordani, P.; Isocrone, D.; Nascimbene, J.; Vallese, C.; et al.

Lobaria pulmonaria (L.) Hoffm.: The Multifaceted Suitability of the Lung Lichen to Monitor Forest Ecosystems.

Forests **2023**, *14*, 2113. <https://doi.org/10.3390/f14102113>

Academic Editor: Cate Macinnis-Ng

Received: 10 August 2023

Revised: 2 October 2023

Accepted: 16 October 2023

Published: 22 October 2023



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Abstract: *Lobaria pulmonaria* (L.) Hoffm. is a tripartite, broad-lobed foliose lichen usually found on bark and on epiphytic and epilithic mosses in humid forests. Currently, the species is threatened in most European countries because of its sensitivity to environmental alterations. In this paper, a total of 107 previous studies across more than 50 years were analysed to gain insight into the multiple roles that *L. pulmonaria* plays in forest habitats, specifically relating to ecosystem services and as environmental bioindicator. Content analysis was employed to systematically characterise and classify the existing papers on the functions performed by *L. pulmonaria* into several groups mostly based on research topic and scope. Two main types of ecosystem services (N₂ fixation and feeding) offered by *L. pulmonaria* have been identified, with varying research aims and types of parameters measured in the studies. Two aspects of current biomonitoring applications using *L. pulmonaria* in forest habitats (concerning atmospheric pollution and forest management) were analysed, and it was found that the number of related studies increased significantly in recent years. Finally, the current practices of monitoring using *L. pulmonaria* as a biological indicator are discussed, and recommendations are provided.

Keywords: bioaccumulation; biodiversity; cyanolichen; ecosystem functioning; forestry practices; lichen herbivory; pollution; radioactivity; sensitive species; supporting services

1. Introduction

Epiphytic lichens are an integral component of many forest ecosystems. They provide food and habitats for animals, contribute to water and nutrient cycles, and represent a major part of species diversity (see for a review, e.g., [1]). For this reason, they can provide information on ecosystem integrity and on the impact of air pollution and climate change on the forest environment. Many studies have focused on forest-dwelling species, which are

usually sensitive to microclimatic variations and with poor dispersal ability, to monitor the effects of forest management and ecosystem functioning (see for a review, e.g., [1,2]). Lichen functional groups, such as macrolichens (namely, foliose and fruticose species) are widely used for exploring air pollution trends (nitrogen (N) and sulphur (S) depositions [3,4]) and climate gradients [2,5]. Moreover, the responses of single lichen species, either sensitive or tolerant to atmospheric pollution, are a suitable tool for forest monitoring [6,7]. In this regard, a particularly interesting species is *Lobaria pulmonaria* (L.) Hoffm. (Figure 1), a broad-lobed foliose lichen which is usually found on bark and on epiphytic and epilithic mosses in humid forests.



Figure 1. Fertile thallus of *Lobaria pulmonaria* from the Gargano beech forest, South Italy.

Its biogeographic, biological, and ecological features make it one of the most useful indicator species in forest monitoring:

1. It has a wide distribution, being present in boreal, temperate, mountainous, and oceanic regions of the northern hemisphere and in tropical forests of Eastern and Southern Africa [8].
2. Its long life cycle (the time to reach sexual fertility has been estimated up to 35 years) makes it an excellent indicator of undisturbed forest ecosystems, as well as forest areas with high ecological continuity (e.g., [9]).
3. It is a tripartite lichen, with the green alga *Symbiochloris reticulata* (Tschermak-Woess) Skaloud, Friedl, A.Beck and Dal Grande as its main photobiont and N-fixing cyanobacteria of the genus *Nostoc*, which are confined in structures called cephalodia inside the thallus [10]. This allows *L. pulmonaria* to actively contribute to the N balance of forest ecosystems [11,12].
4. It is very sensitive to air pollution. For this reason, its populations have declined considerably during the last century, and it is currently threatened in most European countries (see, e.g., [13–15]).
5. Compared to the usual small size of lichens, this species has a large thallus, often exceeding 20–30 cm in diameter, rather showy and easy to distinguish even by non-specialist personnel. For this reason, it can be used in large-scale monitoring networks involving numerous forest operators [16].

In light of these noteworthy features, we can include *L. pulmonaria* among some of the different definitions of the so-called *surrogate species*, which are suitable indicators of different facets of forest ecosystems [17]. In fact, it can be considered a *health indicator species* because it provides information on the integrity of forest habitats, especially from the point of view of forest management sustainability (see, e.g., [18,19]). In biological conservation, *L. pulmonaria* has been confirmed as a good biodiversity indicator, since various studies give evidence of its role as a proxy for the biodiversity of other lichen species characterising the epiphytic alliance *Lobarion pulmonariae* Ochsn., which is considered a climax lichen community on mature hardwood trees in old forests across Europe [13]. Moreover, since

the integrity of its populations guarantees the integrity of other species in the same habitat, it can also be considered an important *umbrella species* in forest sites [20–24].

Finally, *L. pulmonaria* is also viewed as a *flagship species*, thus capable of attracting a wider audience than insiders [25]. It may seem strange to consider a lichen as a charismatic species, but some projects have confirmed its effectiveness in environmental dissemination and education by improving public awareness on the issues of sustainable forest management, air pollution, and biodiversity conservation (see, e.g., the lichen campaigns included in the CSMON-LIFE project LIFE13 ENV/IT/842 [26]).

The aim of the present review is to provide insights into the current knowledge on the role of *L. pulmonaria* as a promising indicator in forest ecosystems. In particular, the discussion focuses on three main research fields: (i) ecosystem functioning and ecosystem services; (ii) air pollution monitoring in the context of remote forested areas; (iii) the effects of forest management and forest structure, as well as sustainable forest management.

2. Materials and Methods

A systematic review was carried out analysing all articles that appeared on Web of Science (<https://www.webofscience.com/wos/woscc/basic-search>, (accessed on 15 February 2023)) and Scopus (<https://www.scopus.com/search/form.uri>, (accessed on 15 February 2023)), as well as in Google Scholar (<https://scholar.google.com>, (accessed on 15 February 2023)). We used the catch terms ‘*Lobaria pulmonaria*’, first alone (yielding 385 articles), then combined with ‘acid rain’, ‘air’, ‘bioindication’, ‘biomass’, ‘C pool’, ‘forest’, ‘grazing’, ‘management’, ‘nitrogen’, ‘pollution’, ‘PTEs’, ‘role’, ‘sulfur/sulphur dioxide’, and ‘trace elements’, narrowing down the search, which resulted in 124 articles.

Only papers with full text in English were included. ‘Grey literature’, such as technical reports, and academic theses were not considered.

Some articles were rejected because they included *L. pulmonaria* only in relation to citations of other articles and/or focused on *Lobarion* communities. Also, studies about exclusively in-lab tests, lichenicolous fungi growing on *L. pulmonaria*, and bacteria as additional partners of the symbiosis were excluded.

The historical period investigated extends from 1970 to February 2023. The final selection of the systematic review consisted of 107 papers published between 1976 and 2023, concentrating solely on the multiple roles played by *L. pulmonaria* in forest habitats. Only research specifically aimed at (i) investigating ecosystem services by *L. pulmonaria*; (ii) monitoring *L. pulmonaria* in forest habitats; and (iii) studying *L. pulmonaria* as bioindicator/biomonitor in forest habitats were included. After duplicate removal, title screening, and abstract revision, the single papers were classified by topic, type of use, and spatial and temporal distribution.

A detailed list of these core articles is provided in Table 1.

Table 1. List of data references on studies including *L. pulmonaria* (role in forest ecosystems, as an air pollution biomonitor, and application related to forest management).

Ecosystem Functioning and Services	Air Pollution Monitoring	Forest Management
N ₂ fixation: 12 [27–38]	Monitoring <i>L. pulmonaria</i> : 3 [39–41]	Monitoring <i>L. pulmonaria</i> : 10 [19,20,28,42–48]
C pool: 2 [29,49]	Biomonitoring PTEs, PAHs, HCHO: 14 [50–63]	Biomonitoring forest treatments: 15 [9,24,25,64–75]
Biomass: 6 [27–31,76]	Biomonitoring radioactivity: 6 [77–82]	Biomonitoring environmental and structural variables: 22 [23,25,43,83–101]
Feeding: 15 [102–116]	Biomonitoring phytotoxic pollutants and acid rains: 4 [117–120]	Biomonitoring historical or actual disturbances: 6 [121–126]

3. Results

3.1. Contextual Topics

The main research themes are related to forest management (Table 1). Papers dedicated to this topic were 50 in number: namely, related to monitoring forest management effects (15), the influence of environmental and structural variables (22), and historical or actual disturbances on *L. pulmonaria* (6); moreover, in 10 of them, *L. pulmonaria* is recognised and/or used as an environmental bioindicator. Studies on ecosystem services and the biomonitoring of air pollution were covered in 29 and 28 contributions, respectively (Table 1). Air pollution monitoring includes a wide range of research using *L. pulmonaria* both as an accumulator of potentially toxic elements (PTEs) (12), or other air pollutants, i.e., PAHs and HCHO (2); radioisotopes (mostly ^{137}Cs) (6); and as a bioindicator of the environmental effects of phytotoxic pollutants including acid rain (4); moreover, others (5) focused on the effects of multiple pollutants. Concerning ecosystem services, all the articles are dedicated to the role of *L. pulmonaria* in supporting N_2 fixation (12); C pool (2); biomass production (6); and providing food and microhabitats for other organisms, mostly gastropods (15). Some studies cover more than one topic.

3.2. Temporal and Spatial Distribution

The number per decade showed a gradual increase from 2 documents published between 1970 and 1979 to 41 documents between 2010 and 2019 (Figure 2).

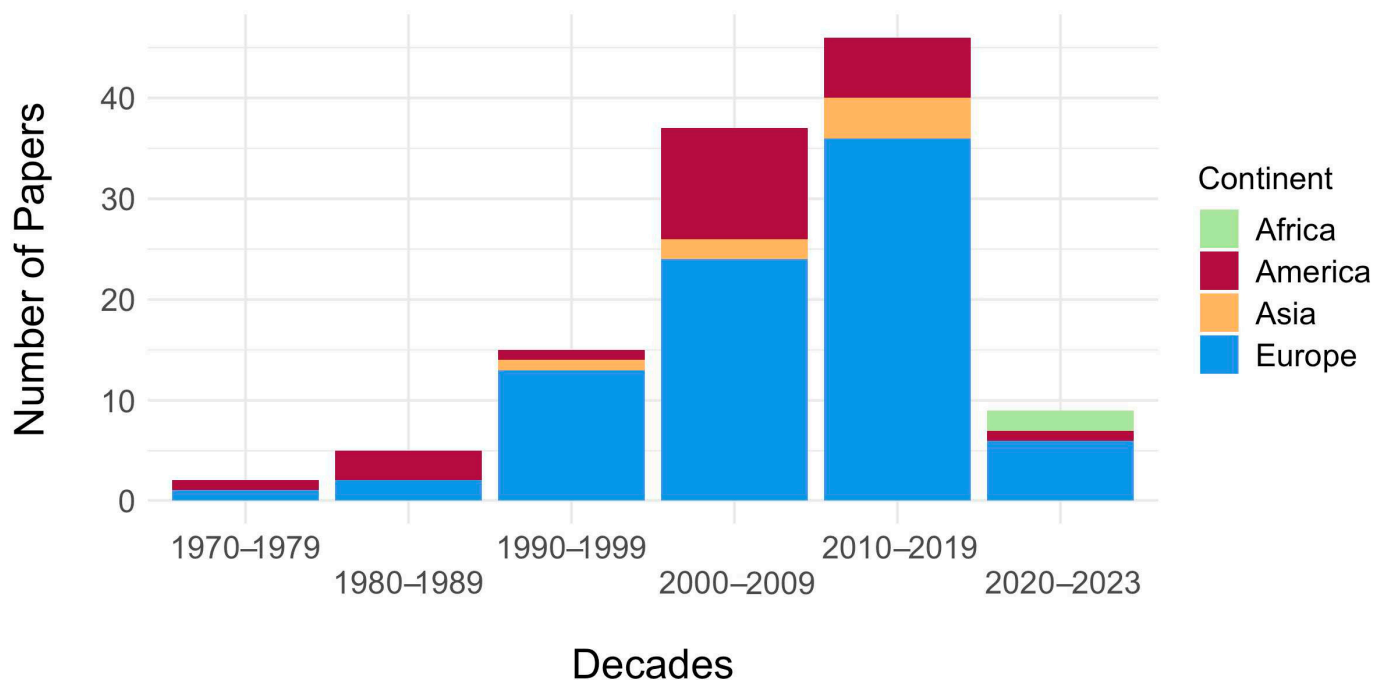


Figure 2. Distribution of the selected papers by their publication year and country.

The studies have almost always been carried out on a local scale, more rarely on a national scale, or including areas scattered in different countries. As regards the distribution of the papers across European countries, the greatest number concerns Norway (14), followed by Italy (11) and Switzerland (11), Great Britain (8), and Sweden (7) (Figure 3). Austria, Hungary, Montenegro, and Portugal are the countries for which the lowest number of papers (1) have been published. Most of the research carried out outside Europe is concentrated in North America, mostly in Canada (17), followed by Turkey (6). Additional papers have come from North Africa (2) (Figure 3).

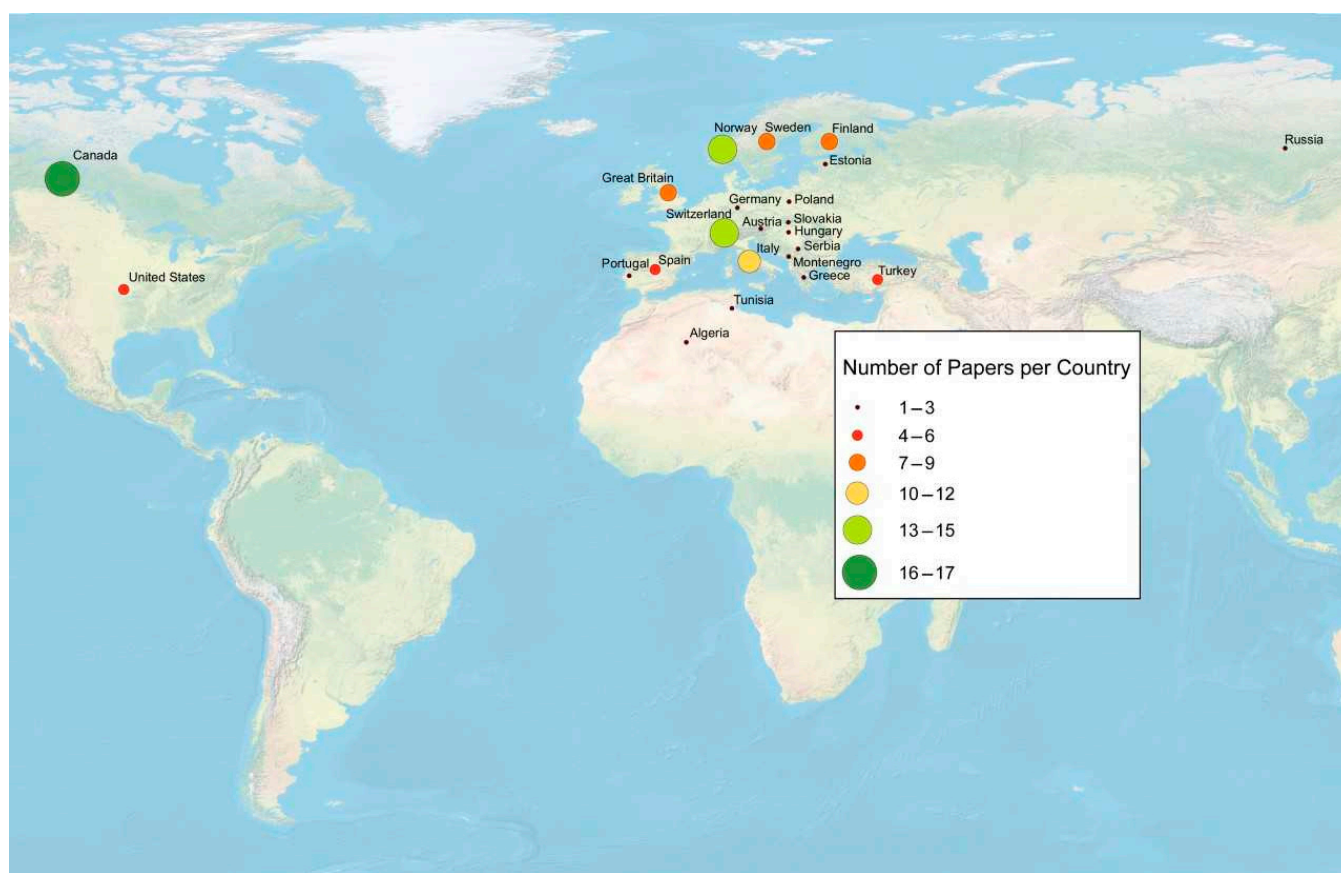


Figure 3. Distribution of the selected papers by country: world map.

4. Discussion

4.1. Ecosystem Functioning and Ecosystem Services

Lobaria pulmonaria provides regulating services mainly contributing to C cycle and N₂ fixation. Moreover, it supports the diversity of some organisms, e.g., by providing food for gastropods.

4.1.1. Carbon and Nitrogen Cycling

Most articles are dedicated to the importance of epiphytic cyanolichen abundance to N cycling. Some of these works also focused on the role of *L. pulmonaria* within forest biomass [27–32] and in the forest carbon cycle [29]. As an example, in a study that investigated the vertical distribution, biomass abundance, and N stocks of epiphytic macrolichens, it was demonstrated that both tree height and species influenced the biomass and the related N-stock [31]. Furthermore, *L. pulmonaria* appears to have a significant impact on the biomass of other lichen groups. Specifically, a high abundance of *L. pulmonaria* was found to be related to a lower biomass of foliose chlorolichens, especially in lower tree branches [31].

In terms of C stock, an experiment conducted under controlled climatic conditions revealed the optimal conditions under which *L. pulmonaria* achieves net positive photosynthesis (water content between 85 and 175% of the dry weight, light intensity above 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and temperature between 15 and 20 °C). In this work, *L. pulmonaria* was compared with one species of chlorolichen to model their net productivity in the field. Under the same conditions, there was a higher carbon gain in the chlorolichen than in *L. pulmonaria*, in which a greater investment and maintenance of photosynthetic units (i.e., photobiont cells and chloroplast proteins) can indirectly affect growth due to the increased respiration. However, the authors' attempt to model the carbon gain revealed some critical issues due to the excessive simplicity of the model itself [49]. We certainly know that *L.*

pulmonaria, especially in ancient forest ecosystems, can be quite large compared to other epiphytic lichens; however, its overall contribution to the forest's biomass and C stock is insignificant [29].

The opposite is true for N stock. In N fixation, atmospheric N gas (N₂) is converted into a usable form for plants and other organisms. This process is conducted by N-fixing cyanobacteria and is fundamental for soil nutrient cycling and ecosystem productivity. Many epiphytic cyanolichens are an important source of fixed N in forest ecosystems due to the symbiotic relationship with cyanobacteria that act as the photobiont partner [32,49,127–129]. The role of cyanolichens in maintaining N balance in forest ecosystems has been intensively studied in North America, highlighting the relevant contribution of *L. pulmonaria* [27,29,32] to N balance. As an example, in a forest of British Columbia, the N pools of *L. pulmonaria* in combination with the less abundant N-rich bipartite cyanolichens amounted to $7.5 \pm 1.9 \text{ kg N ha}^{-1}$ on fine-textured soils [29]. The ability of *L. pulmonaria* to fix N has also been found to be dependent on the age of the forest with a greater rate of fixed N in old-growth forests with respect to younger forests [28]. Additionally, in a study in sub-boreal conifer forests of Canada, where N is known to be a limiting factor, using stable isotope natural abundance techniques, the authors demonstrated a positive relationship between bipartite and tripartite cyanolichen abundances and host tree foliar N, thus providing greater N-inputs into N-limited conifer forests [32].

Nitrogen leaches from *L. pulmonaria* occur during rainfall [33,34]. By analysing the release of N in thalli of *L. pulmonaria* subjected to simulated episodes of heavy rainfall, Millibank [35] found that the total N fixed per day could be lost up to three times in one rainfall episode.

Another crucial role of *L. pulmonaria* is due to the contribution to the N supply through the decomposition of cyanolichen litter. Despite representing a small part of the total aboveground litter biomass (up to 2.3%), *L. pulmonaria* litter releases up to 11.5% of the total N input from aboveground litterfall. Moreover, *L. pulmonaria* has been shown to decay faster than green-algal lichens [30,35,76] due to high N content and low C/N ratio. The decomposition process of cyanolichens (particularly various bipartite cyanolichen species plus the tripartite *L. pulmonaria*) can release up to 2.1 kg of newly fixed N per hectare per year, which would otherwise remain unavailable [30].

Many of the large foliose cyanolichens are sensitive to high levels of nitrate and ammonia in the atmosphere [36]. Detrimental effects of acid rain, especially in the past, have been reported to affect both the rate of fixation and the distribution of *L. pulmonaria* from both field evidence [39] and laboratory experiments [37,38]. *Lobaria pulmonaria* populations growing on oak monitored in the 1980s in remote woodlands of Northern England, in a progressive bark acidification scenario [39], declined to such an extent that it eventually became extinct. Denison et al. [37] highlighted the potential effect of acid rain on N₂ fixation in *L. pulmonaria* and *L. oregana* (Tuck.) Müll. Arg. They found a decrease in fixed N in thalli after exposure to H₂SO₄ and after a five-week exposure to $50 \mu\text{g m}^{-3}$ of SO₂. Sigal and Johnston [38] found evidence that acidic rain at pH 2.6 caused thallus bleaching and significant reductions in N fixation and gross photosynthesis by 100% and 90%, respectively, whereas no significant modifications occurred at pH 4.2 and 5.6.

4.1.2. Growth, Dispersal, and Grazing

Among other organisms, the forest's food network is supported also by *L. pulmonaria*. In particular, the lobes of this foliose cyanolichen are frequently grazed by gastropods such as snails and slugs [102–107]. The palatability of lichens to gastropods may be enhanced by some lichen parasites that can indirectly reduce the fitness of their hosts [108].

Growth rates and survival of mature stands of *L. pulmonaria* are not inhibited by the grazing pressure of feeding gastropods if growth zones are not affected [102]. The same is not true for juvenile thalli [103]. In order to protect against herbivory, *L. pulmonaria* stores specific secondary compounds in the medullary layer [106,109,110], but a positive correlation occurs between thallus size and content of secondary compounds, making

juvenile thalli more vulnerable [103] but less palatable than senescent thalli [111]. There is not a single chemical race in *L. pulmonaria*. Culberson [130] described two chemical races in North America: the first has norstictic, stictic, and constictic acids and two unknown substances; the second one has norstictic acid and one unknown substance. Gastropods can discriminate between the two chemical races with a preference for the second with fewer secondary substances and a lower total concentration [112]. The number of secondary compounds has been shown to deter grazing by gastropods also in field transplant experiments [104,130]. As a matter of fact, with artificially reduced levels of metabolites, transplanted thalli resulted in being much more grazed than control thalli [104]. *Lobaria pulmonaria* has also developed a tissue repair mechanism consisting in the sealing of open wounds with a secondary cortex both on the thallus and above cephalodia [114].

Vatne et al. [105,110] focused their works on the role of some environmental factors such as pH and altitude on the abundance and species richness of herbivorous gastropods and the concentration of secondary compounds. The authors showed that gastropods may limit the distribution of *L. pulmonaria* in calcareous broad-leaved forests, where they are more abundant. Another interesting study, aimed at evaluating the possible influence of invertebrate grazing in modelling the communities of epiphytic lichens along a vertical gradient of the canopy, revealed that gastropods play a role in determining the lower limit of distribution of epiphytic lichens from the soil to the forest canopy top [115].

Besides the negative impacts of herbivory on *L. pulmonaria*, an interesting work by Boch et al. [116] underlined the role of invertebrates as vectors for lichen dispersal. During their experiment, *L. pulmonaria* regenerated from 29% (out of 379) snail faecal pellets investigated, indicating that the lichen fragments passed the snail guts without being digested and developed into juvenile thalli. Similarly to seed plants, in epiphytic lichens, the endozoochory also plays a prominent role in dispersal.

4.2. *Lobaria pulmonaria* in Air Pollution Monitoring

4.2.1. Monitoring *Lobaria pulmonaria*

The sensitivity of *L. pulmonaria* to atmospheric pollution, especially to SO₂ and heavy metals, has been traditionally acknowledged in lichen monitoring (e.g., [131]). On the whole, the scientific literature highlighted that toxic air pollutants such as SO₂, NO_x, and acid rain have a double detrimental effect, both by direct phytotoxicity and by secondary bark acidification [39], which in the past caused the disappearance or the substitution of *Lobaria* vegetation with other, more acid-tolerant, lichen communities [132]. Rose [40] related the rapid decline of sensitive indicator species to the rising levels of air pollution by SO₂, as well as the disturbance of the woodland microclimate. Gilbert [39] observed that the increase in rainfall acidity was damaging lichen-rich communities in forests of the UK and reported field evidence for an acid rain effect between 1969 and 1984 on two lichen populations in remote woodlands of N England: *L. pulmonaria* on oak, and *Sticta limbata* (Sm.) Ach. on ash trees. Both species were observed to decline to the point of extinction, and this phenomenon was accompanied by progressive bark acidification.

Nowadays, the presence of *L. pulmonaria* populations within a certain site is associated 'by default' to a condition of low environmental pollution. In this sense, the scientific research highlighted the link between deteriorated air quality and the retreat of this species. In a recent review, Paoli et al. [41] summarised works carried out by the Slovak lichenologist Ivan Pišút and colleagues about the retreat of air pollution sensitive lichens in Central Europe, with a focus on *L. pulmonaria* in the Western Carpathians. Such works highlighted the importance of large-scale monitoring of common and rare indicator species over space and time to demonstrate the influence of various factors, especially the acidification of the environment due to past air pollution by SO₂ (see Paoli et al. [41] for references). It was already in 1894 when Zahlbruckner referred for the first time to the retreat of *L. pulmonaria* from the surroundings of Bratislava (Slovakia), where it completely vanished during the 1930s, in parallel with the industrialisation of the area. During the 20th century, it was evident that the retreat was also accompanied by a significant reduction of colonised

habitats and a shift of the distributional range (in Slovakia between 150 and 1400 m) to more remote and higher mountain regions (lower altitude about 600 m, with only few exceptions). Several other species linked to natural/semi-natural forests of higher altitudes and requiring higher air humidity shared a similar pattern and exhibited a dramatic reduction of their distributional range, which was evident especially in the 1970s. The combined effects of air pollution, intensive agriculture, forest management, and habitat fragmentation were among the most relevant factors explaining the decline of epiphytic lichens and the extinction or retreat of rare species (such as *L. pulmonaria*) from previously colonised areas in Central Europe (e.g., [133]).

Similarly, Farkas et al. [134] reported *L. pulmonaria* as widely occurring in the past, in beech forests and various broad-leaved trees in mountainous regions of Hungary (94 records up to 1967), while only three recent records were found in 2008 and 2016. The past retreat of *L. pulmonaria* and other sensitive species was also associated with SO₂ levels, which increased until the middle of the 1980s contributing to acidic depositions in Central Europe.

Hence, air pollution (especially in the past) and habitat fragmentation (nowadays) appeared as the main anthropogenic factors influencing epiphytic lichen diversity in forests of the Western Carpathians [41].

Recently, Paoli et al. [50] carried out a translocation experiment in beech forests of the Western Carpathians to investigate whether current air quality potentially limits the recolonisation in sites where *L. pulmonaria* disappeared during the last century. About 125 thalli were transplanted on selected trees at the foot of the Malé Karpaty Mts and the Nízke Tatry Mts (Slovakia). Prior to the translocation and after one year, the content of trace elements (Al, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb, S, and Zn), photosynthetic performances (by chlorophyll *a* fluorescence emission analysis), and ultrastructural-morphological features of the thalli were considered. The accumulation of heavy metals was used as a proxy of the effects of air pollution. After one year, the translocation ensured an effective survival of the thalli in remote beech forests characterised by a negligible or low contamination by heavy metals (Nízke Tatry Mts). The thalli attached by themselves to the bark of the host trees, looking overall healthy, without evident symptoms of alteration. Four years later, newly formed individuals were also found. On the other hand, the translocation was not successful in the Malé Karpaty Mts, where the thalli did not attach by themselves and showed visible symptoms of damage, consisting in discoloration and the presence of necrotic parts and holes in the surface. A partial alteration of the photosynthetic performance and an accumulation of trace metals (mostly As, Mn, Ni, Pb, S, Sb, and Zn, occasionally Cd, Cr, and Cu) were also reported. A last check completed in February 2020 revealed that only 10–15% of the thalli remained attached to the trees in sites concerned by heavy metal accumulation (Malé Karpaty Mts) and about 60% in unpolluted sites (Nízke Tatry Mts). Hence, the results indicated a link between the failure of the translocation and air pollution and suggested that current air quality in the Western Carpathians still limits the possibility of recolonisation by sensitive threatened species typical of clean environments, such as the forest lichen *L. pulmonaria*, actually extinct from most localities in Slovakia.

4.2.2. Monitoring with *Lobaria pulmonaria*

Lobaria pulmonaria has been employed as a monitoring tool (as a biomonitor and/or as a bioindicator) in studies carried out in forest habitats around specific pollution sources [50–54,117,118]; in remote forest sites [55–57]; and in sites concerned by the long-range transportation of pollutants, such as radionuclides [77–82], acid rain depositions [119,120], or under controlled conditions in relation to specific pollutants [58–63].

4.2.3. Monitoring the Effects of Acid Rain

To demonstrate the effects of acid rain depositions on lichens, Farmer et al. [119] transplanted sensitive species, including *L. pulmonaria*, from a woodland in W Scotland to two woodlands in SW Scotland and NW England, where the species had shown a previous decline. Lichens were exposed from November 1988 to 1991 (for an overall period

of about 940 days). The first signs of stress (chlorosis or necrosis) were observed in *L. pulmonaria* after 12 months. It was concluded that wet deposited acidity was the most likely explanation of the loss of vitality, particularly at the site in NW England. Previous work had shown adverse effects due to low pH but could not exclude the possibility that high SO₂ levels at an earlier period may have caused the decline [119]. In another study [120], the seasonal variation of acidic pollutants was assessed in *L. pulmonaria* from three oak woodlands in the UK. Gaseous pollutants (ozone, S- and N- compounds), acidity and volume of precipitations, bark chemistry, and elemental content (Ca, K, Mg, and N) in lichen tissues were considered. The results showed that *L. pulmonaria* responded rapidly to the changing bark ionic environment in relation to nutrient availability and acidity as well. At the time, the study highlighted the importance of establishing critical loads concerning the acidification of the environment, necessary to promote the conservation of *Lobaria* species.

4.2.4. Monitoring around Pollution Sources

Riga-Karandinos and Karandinos [51] investigated the effects of air pollution from a lignite power plant in the valley of Megalopolis (Greece) using *L. pulmonaria* (and other lichens) growing on deciduous oaks as biomonitors. The study focused on 22 forest stands at different elevations, exposures, and distances from the source. Several chemical elements (Ca, Cd, Cu, Fe, Mn, Pb, S, and Zn) were determined in native samples, together with biochemical parameters. The results indicated a significant uptake of elements (particularly Cd, Cu, and S), decrease in thallus pH, alteration of total proteins, and breakdown of polysaccharides, as well as chlorophyll degradation to phaeophytin, especially in the sensitive species *L. pulmonaria*. The authors highlighted the use of more than one species to obtain a reliable assessment of air pollution effects and a cross-calibration between species, which is useful in case that one (*L. pulmonaria*) is rare or disappears due to its high sensitivity to environmental pollution. Kouadria et al. [54] used *L. pulmonaria* transplants to monitor heavy metal (Cd, Cr, Pb) depositions in NW Algeria and assessed the detoxification activities of the enzymes catalase (CAT), ascorbate peroxidase (APX), and guaiacol peroxidase (GPX), considered as antioxidant systems in response to heavy-metal-induced stress. Samples were exposed at 12 selected sites in the urban area of Oran and retrieved monthly (from December 2018 to June 2019). According to the concentrations presented, all study sites appear heavily polluted, with a progressive increase in concentrations from the first up to the seventh month of exposure. Heavy metal concentrations were correlated with the overexpression of detoxification enzymes.

Lobaria pulmonaria (together with other species) has been used also in biomonitoring studies of air pollution by means of transplants to polluted environments. Çiçek et al. [52] exposed thalli of several lichens (taken from unpolluted forests) for monitoring purposes (Cu, Cr, Fe, Ni, Pb) in the urban area of Erzurum (Turkey). Samples were exposed for 8 months. Heavy metal concentrations reflected the influence of traffic pollution and were significantly higher in *Peltigera praetextata* (Flörke ex Sommerf.) Zopf with respect to other species (including *L. pulmonaria*). In another study [117], the same species, exposed for 4, 8, and 12 months in the same area, were used to investigate genotoxic effects due to traffic pollution using total soluble protein content and DNA integrity by the random amplified polymorphic DNA (RAPD) method as markers. The total soluble protein content did not change with exposure time, while after 8 months, all species showed relevant DNA changes. The ratio of band differences in *P. praetextata* was higher than that in other lichens, highlighting its potential as an indicator of genotoxicity [117]. In a nearby area, the genotoxic effects and total soluble protein content after exposure to airborne pollutants were assessed around a cement factory (in Aşkale-Erzurum) [118]. The lichen species *Pseudevernia furfuracea* (L.) Zopf, *L. pulmonaria*, *Cetraria islandica* (L.) Ach., and *Usnea longissima* Ach. were exposed at increasing distances (50, 100, 200 m) from the source (downwind from the combustion unit of the plant) for 4, 8, and 12 months (in 2008) using lichen-bags. The response of soluble proteins was species specific: in *L. pulmonaria*, they were affected only in

the closest site, after 8 months, while in *P. furfuracea*—the most responsive—after 4 months at all sites. Yemets et al. [53] investigated the dispersal of airborne-traffic-related elements using lichen transplants (*L. pulmonaria* and other species) along three transects of increasing distance (10, 15, 30, 50, and 100 m) from a highway in SE Norway. The concentrations of most measured elements (Ca, Mg, Na, Fe, Al, Zn, Ba, Cu, V, Cr, Ni, Co, Sn, As, Mo) increased with the proximity to the highway. *Lobaria pulmonaria* was the only species with pollutant-dependent reductions in growth, chlorophyll a fluorescence emission, and chlorophyll content. Measurement of metal accumulation in the thalli revealed more clearly the impact of traffic emission than lichen vitality parameters.

4.2.5. Manipulative Experiments in Relation to Specific Pollutants

Lichen abundance in coniferous forests of Europe and North America can be, among other factors, controlled by the supply with Mn: field observations carried out in spruce forests of Montana (US) suggested that epiphytic cyanolichens could be particularly sensitive to Mn levels (being more frequent on barks with low Mn concentration) when compared with *L. pulmonaria*, which was found also on barks characterised by higher Mn depositions [60]. Based on these considerations, Mn uptake (from MnCl_2 solutions) and toxicity (investigated by chlorophyll fluorescence emission) were tested in cyanolichens and the tripartite *L. pulmonaria* [61,62]. After short-term treatments, cyanolichens showed an alteration of chlorophyll fluorescence, indicating that even short exposures to Mn in the field, e.g., via stemflow, could affect the physiology of the species. On the other hand, *L. pulmonaria* appeared more tolerant to Mn, suggesting that different mechanisms could be responsible for Mn and SO_2 toxicity in lichens. In another experiment, Muir and Shirazi [58] investigated the biological effects of formaldehyde (HCHO) dispersed in fog-water in Oregon (US). They tested the response of *L. pulmonaria* thalli to fog-water enriched with HCHO (3–30 ppm), simulating ecologically relevant concentrations under controlled (green-house) conditions. The experiment lasted between October 1993 and May 1994, with misting sessions separated by about 45 days, when lichens were returned to their native forest. In *L. pulmonaria*, nitrogenase activity decreased in those samples treated at the highest HCHO concentration, after all but the first mist session, but without significant effects on their growth.

Yemets et al. in 2011 [63] tested the sensitivity of *L. pulmonaria* to salt (NaCl, up to 0.6 M) and metal (Cu and Zn, up to 500 μM) stress. Conductivity methods (i.e., electrolyte leakage as marker of cell membrane integrity, especially from the mycobiont biomass) and chlorophyll fluorescence emission (as an indicator of the vitality of the photobiont) were used as response markers. High salt concentrations adversely affected cell membrane integrity, whereas the effects on the potential quantum yield of PSII (here represented by the parameter F_v/F_m) appeared less evident. Similarly, both metals (Cu and Zn) altered membrane integrity, with limited effects on the photobionts. Overall, the results suggested that membrane integrity of the mycobiont is more sensitive to salt and heavy metal stress than the potential photosystem II efficiency of its autotrophic partners. Branquinho et al. [59] demonstrated the sensitivity of *L. pulmonaria* to Pb exposure under controlled conditions by the assessment of chlorophyll a fluorescence emission 24, 48, 72, 96, and 120 h after incubation in solutions with different Pb concentrations (up to 4.8 mM). The effects of Pb were shown to be dependent on the nature of the photobiont, with green algal lichens being less sensitive than the cephalolichen *L. pulmonaria* and the cyanolichen *Peltigera canina* (L.) Willd. The study also demonstrated the displacement of extracellular exchangeable ions (Ca^{2+} and Mg^{2+}) by Pb^{2+} at the cell wall level.

4.2.6. Monitoring Radionuclides

Lobaria pulmonaria has been employed as a biomonitor of radionuclides (^{137}Cs —half-life about 30 years) in remote forests. In a chestnut forest of Central Italy, Loppi and De Dominicis [78] evaluated ^{137}Cs activity concentration in *L. pulmonaria* and *Flavoparmelia caperata* (L.) Hale harvested before (1978) and after (1993) the Chernobyl disaster (1986).

Results highlighted a significant rise of concentration activity of ^{137}Cs from 1978 to 1993 in both *L. pulmonaria* (from 570 to 970 Bq kg^{-1}) and *F. caperata* (from 290 to 490 Bq kg^{-1}). The authors explained the differences in ^{137}Cs activity between the species on the basis of their ecological requirements: *L. pulmonaria* is much more aerohygrophytic and may have absorbed much more water and/or air moisture (and consequently much more ^{137}Cs) during rainfall events within the first 10 days after Chernobyl. On the other hand, Baysal and Yazici [77] reported low values of ^{137}Cs activity (280 Bq kg^{-1}) in *L. pulmonaria* harvested in 1993 from the Eastern Black Sea region (Turkey) in comparison with other species from the same area, e.g., *Xanthoria parietina* (L.) Th. Fr. (1030–2810 Bq kg^{-1}) or *Parmelia* s.l. (3340–3940 Bq kg^{-1}). Unfortunately, they reported values without a description of collection sites (and of rainfall data) to clarify their results. In 1988 and 1996, Riga-Karandinos and Karandinos [80] investigated ^{137}Cs activity concentration in the valley of Megalopolis (Greece) using *L. pulmonaria* (and other lichens) growing on deciduous oaks as biomonitors. Values in *L. pulmonaria* overall decreased from 1988 (660–1250 Bq kg^{-1}) to 1996 (120–280 Bq kg^{-1}). Kahraman et al. [82] investigated radionuclides in four native lichens from a remote area in the Marmara region (Turkey), 24 years after the Chernobyl accident. Their results indicated that ^{137}Cs was still present in the study area (37–53 Bq kg^{-1}). On the other hand, Celik et al. [79] compared various lichens and mosses collected in 2006 from the Eastern Black Sea region and reported that the ecological half-lives (years) of ^{137}Cs followed the order *L. pulmonaria* (2.74) > *X. parietina* (2.42) > various *Usnea* species (2.15–1.75) > *F. caperata* (1.93). > *Parmelia sulcata* Taylor (1.88). Dragović and Janković Mandić [81] reported data on radionuclides in soils, ants, mosses, and lichens harvested from undisturbed semi-natural ecosystems in Serbia and Montenegro. Among lichens, they also measured ^{137}Cs activity concentration in *L. pulmonaria* (with values in the range of 80–1318 Bq kg^{-1}).

4.2.7. Major and Trace Elements and PAHs in Remote Areas

Several studies highlighted the chemical content of major and trace elements in *L. pulmonaria* from remote forest areas. Bolshunova et al. [56] detected the concentrations of 56 chemical elements using inductively coupled plasma mass spectrometry in native thalli from the Barguzin Nature Reserve (Baikal Lake). In 2015, samples from cedar pine forests were collected and analysed. The samples overall presented background concentrations, but were enriched in Al, Ca, K, Mg, Na, P, Si, and Ti, probably determined by soil particle transportation, as well as the transfer of aerosols from Baikal Lake, whose waters contain high concentrations of Ca, Na, Mg, K, Si, and P.

Paoli et al. [134] characterised the chemical composition (Al, As, Cd, Cr, Cu, Fe, Mn, Ni, Pb, S, and Zn) of *L. pulmonaria* populations from remote oak forests in Central Italy, which was found to correspond to the background of clean environments. Chahloul [57] assessed the bioaccumulation capacity of PTEs (Al, As, Cd, Cr, Cu, Fe, Ni, Pb, Sb, and Zn) in the native thalli of *L. pulmonaria* (and other species) from two remote sites in Tunisia. Results showed species-specific differences, with *L. pulmonaria* accumulating the highest amounts of PTEs. On the whole, all values reflected a condition of a clean environment. A practical outcome of the above studies was the possibility of using those sites as suitable for harvesting uncontaminated lichen material for biomonitoring studies based on lichen transplants.

Blasco et al. [55] assessed the behaviour of different lichen species as biomonitors of air pollution by persistent organic pollutants, such as PAHs in natural ecosystems (Central Pyrenees). Samples were collected in 2005 from pine and oak trees at increasing distances from the main road of the area, including sites where up to six lichen species could be compared. Nevertheless, *L. pulmonaria* could be found only in 13 sites out of 47. The study highlighted the influence of traffic emissions in PAH accumulation: on the whole, *L. pulmonaria* showed a low concentration of total PAHs, especially those associated to combustion processes, although with the greatest three-ring percentages (over 50%, especially acenaphthene). Three-ring PAHs are low-molecular-weight compounds, mainly

present in the gas phase and relevant due to their abundance in the air. The authors hypothesised that, with *L. pulmonaria* being aerohygrophytic, it absorbed more water and air moisture and consequently reflected airborne PAHs (like the three-ring compounds) when compared with other species (e.g., a less aerohygrophytic lichen, *P. sulcata*), which better accumulated PAHs associated with particulate matter.

4.3. Forest Management

4.3.1. Monitoring *Lobaria pulmonaria*

It is well known that *L. pulmonaria* depends on specific microclimatic conditions, such as humidity with moderate light intensity, as well as the presence of fit substrates, such as large and mature trees (particularly oak and beech) [9,64,135,136]. All these factors are influenced by forest management. Destruction and fragmentation of large parts of forest ecosystems produce changes both at structural and functional levels, and a fragmented landscape may have different effects on lichen communities, especially on rare or endangered species such as *L. pulmonaria* [9,25,135]. Understanding the effects of disturbances on *L. pulmonaria* populations is important also for the conservation of those threatened species sharing the same habitats [42,65]. For such reasons, several studies focused on the spatial distribution and dynamics of *L. pulmonaria* populations in relation to different degrees of forest management and alteration (e.g., [43,66,67,83,121]) also due to the presence of invasive species [137].

4.3.2. Influence of Forest Management

Several studies were carried out in Mediterranean mixed oak forests to assess the impact of forest management on *L. pulmonaria* populations [24], the alteration in vitality and growth due to logging [68], the influence of local microclimate modifications introduced after logging [69], and the importance of retaining unlogged forest aggregates to preserve vital populations [70]. The direct consequences of forest logging on *L. pulmonaria* consisted in the loss of biomass (−40%), in changes of the composition of the population (most of the remaining thalli were small and sterile, while most of the largest fertile-ones disappeared), and in the loss of several lichens of conservation concern. Furthermore, it was demonstrated that individuals on retained isolated trees within the logged stand had lower photosynthetic performances compared to those of the unlogged stand, and their vitality was significantly reduced. Bianchi et al. [68] reported a significant reduction of photosynthetic performances and the absence of growth in *L. pulmonaria* (both young meristematic and adult fragments) transplanted for one year on isolated *Quercus cerris* L. to simulate the effects of logging, with respect to samples exposed within an uncut forest. Several transplants appeared melanised [68] since thallus melanisation represents a relevant character in response to light stress. Hence, Di Nuzzo et al. [69] showed that south-exposed samples in the logged stand had low probability to grow (compared to north-exposed samples), and in general, higher growth rates were observed in young thallus fragments when compared with adult ones. Fačková et al. [70] compared thalli from isolated trees with those from retained-forest patches in the same area, demonstrating that thalli on the trunks of retained-isolated trees were thinner (−35%) and showed lower vitality (F_v/F_m and PI_{ABS} —the former known as performance index, an indicator of the overall photosynthetic performance), as well as lower water holding capacity. On the other hand, thalli from forest patches had performances comparable to those of healthy samples from unlogged forests. The study clearly indicated the efficacy of retaining small forest aggregates in mixed oak forests as suitable to preserve vital populations of *L. pulmonaria*, since the species generally avoids both excess exposure to light irradiance and full shading.

Studies on the survival of *L. pulmonaria* were carried out especially in Northern Europe in relation to retention forestry: in 1994, a transplantation experiment with *L. pulmonaria* was set up on 280 aspens at 35 sites in Sweden to assess the habitat suitability of retained aspens using adjacent forest trees as a control [71]. The results showed that the northern side of trunks is more favourable than the southern side. After 14 years, 23% of *L. pulmonaria*

transplants still remained, with a significantly higher survival on retained aspens than on aspens in the surrounding forest, especially on the northern side of the stems [72]. Larsson et al. [73] simulated forest logging in boreal forests collecting *L. pulmonaria* thalli in old stands and transplanting them into clear-cuts in different seasons, demonstrating that logging in winter was less harmful and could be associated to higher growth rates than logging in summer, which was associated with higher chlorophyll degradation and lower growth. This study demonstrated the sensitivity of *L. pulmonaria* to the effects of logging and the consequent increase in habitat dryness even in boreal forests.

Pioneering studies on the ecophysiology of *L. pulmonaria* (e.g., [74]) revealed that treatments with increasingly high light irradiance were detrimental (in some cases irreversibly) to the photosynthetic activity of such species, especially in the dry state (decreased F_v/F_m and increased chlorophyll degradation).

Gauslaa et al. [84] transplanted 600 thalli of *L. pulmonaria* to three boreal forest habitats: even-aged young and closed canopy stand, old forest with gaps, and open clear-cut areas. Mean biomass growth over 100 days varied from 8.3% in the dark young spruce forest to 16.0% in the old forest, reaching 23.1% in the clear-cut area. Nevertheless, some bleaching and changes in thalli (i.e., increasing thickness and chlorophyll a/b-ratio) in clearcuts suggested some high-light-induced chlorophyll degradation, showing how biomass growth is controlled by a delicate balance between light availability and desiccation risk. Muir et al. [85] transplanted 60 thalli of *L. pulmonaria* in a *Fraxinus latifolia* Benth. undisturbed forest (Oregon, US) for 3 years and measured seasonal changes in biomass. Most of the transplants survived, growing mainly during the wet seasons (November to June) and with a maximal growth rate in spring, hence reflecting the balance between appropriate water and light availability.

4.3.3. Genetic Diversity

The consequences of repeated disturbances (such as intensive logging and fragmentation) that alter forest structure, density, and tree species diversity may also affect the genetic diversity and the reproductive strategies of this heterothallic species (sexual reproduction occurs only when opposite mating types come in contact), affecting the frequency and distribution of mating types. This fact could compromise the potential for sexual reproduction and may lead to clonal vegetative reproduction, which could have long-term negative effects on the distribution, abundance, and genetic diversity of *L. pulmonaria* populations [86,122,123]. In fact, Zoller et al. [86], in Switzerland, found the highest genetic diversity in populations where the fungal symbiont is reproducing sexually and suggested that such populations should have a higher rank in terms of conservation priority than strictly asexual populations. Less intensive forest management (e.g., selection cutting) has been also reported as detrimental to the fertility of *L. pulmonaria* [75], even if moderate logging (as in uneven-aged forestry) does not significantly impact its genetic diversity [125]. Although fragmentation and reduction of suitable habitats suggest a possible erosion of the genetic diversity for *L. pulmonaria* populations, in Mediterranean forests, a relatively high level of genetic diversity was reported at plot level in old forest patches [87]. On the other hand, habitat quality seems to influence local genetic diversity, highlighting that time is an important factor in dispersal and colonisation processes for long-lived species such as *L. pulmonaria* [126,138].

4.3.4. Forest Edges

Forest edges are components of forested landscapes where abiotic factors, such as radiation, wind, humidity, and dust deposition, differ from the forest interior and influence the organisms that live therein [139]. While natural edges are reported to be gradual and complex [139], human-induced forest edges are in general homogeneous and abrupt [88,139,140]. Lichens, being sensitive to microclimatic variations, are strongly influenced by forest edges [141]. Moreover, most of the abiotic factors that change with the approximation of a forest edge are strictly related to lichen physiology [140]. In general, *L.*

pulmonaria seems to withstand moderate disturbances [125], in particular those determining a slight increment in solar radiation. However, logging could determine a sudden and strong variation in microclimatic conditions between the forest interior and the logged area, which could affect organisms several metres inside the remaining forest [139]. The ‘forest edge’ effect has a different impact on *L. pulmonaria*, which, however, could vary depending on the local conditions.

Lobaria pulmonaria seems to be positively affected by forest edges by having a higher growth rate close to the edge, both considering small (0.07 g) and large thalli (1.41 g) in ‘soft’ edges, i.e., those that border areas with lower tree density. By contrast, in situations with ‘hard’ edges, i.e., forest edges in contact with open clear-cut, small thalli showed none or little enhancement near the edges [88]. In accordance, Belinchon et al. [89] found that *L. pulmonaria* had higher cover and higher probability of occurrence near the edge of the forest patches, except for those surrounded by heath matrices. Gauslaa et al. [90] measured chlorophyll content and fluorescence as well as specific thallus mass (STM) in 23 thalli of *L. pulmonaria* along five transects in different forest patches retained after clear-cut logging in Kispiox Valley, British Columbia. They reported a reduction in chlorophyll content and chlorophyll fluorescence with increasing distance from the edge. However, they did not find any variation in STM with increasing distance, and probably their measured STM values reflect pre-logging conditions. The distances from the edges at which the ‘edge effect’ seems to fade out has been reported to be 12 m [91], 7.5–15 m [88], and up to 120 m [90]. This quite large difference could be due to different climatic conditions and methodologies in the studies considered. In order to provide more detailed suggestions for conservation, further studies are needed to disentangle the effects of climate, type of forest, and surrounding conditions on the growth rate and survival of *L. pulmonaria* at forest edges.

4.3.5. Tree-Level Factors

Comprehending which factors at tree and stand levels influence *L. pulmonaria* colonisation and survival is fundamental for developing conservation-oriented forest management. Belinchón et al. [92] investigated which factors may drive the future metapopulation size of *L. pulmonaria* in a managed forest landscape. Considering the limited dispersal capacity of the species, the study highlighted the importance, for a successful colonisation, of an adequate number of host trees located in shady conditions, which should not be isolated from occupied trees and the necessity for a long rotation cycle of the host trees, with negative effects set by tree mortality and tree cutting by forestry. It is well known that *L. pulmonaria* is associated with old-growth forests with long ecological continuity [94]. Light, water availability, and temperature are the most important factors in determining the growth and survival of *L. pulmonaria*, also considering the contest of climate change [142]. Nevertheless, ecological requirements vary during its life cycle [83,95]. Benesperi et al. [95] suggested that the probability of occurrence is influenced by an interplay between forest habitat type and some biotic and abiotic factors, whose effect changes during the life cycle of *L. pulmonaria*. In fact, small thalli can colonise a wider range of ecological conditions with respect to the sites where adults survive, as adult thalli are less frequent in the southern part of the trunks and more abundant in the higher parts.

4.3.6. Forest Type

Forest type influences the presence of *L. pulmonaria* as, for instance, in the Mediterranean area, *Quercus* forests are more suitable than a montane mixed forest, with *Castanea* forest in an intermediate position [95]. Within such forest types, *L. pulmonaria* is associated with old trees with large circumference and basal area [23,96]. Such preference could be the result of a combination of conditions on older and larger trees, together with higher cumulative probability of colonisation that results from a longer presence [23]. Nevertheless, such results seem to be strongly influenced by local climatic conditions [96]. In fact, if climatic conditions are optimal, *L. pulmonaria* is reported as able to colonise trees with small diameters [44,96,97] and to have a high population rate development [98].

Forest type and the position on the trunk are linked to the availability of light. In British Columbia's inland rainforest, the growth rate of *L. pulmonaria* is positively associated with increasing canopy openness, with an optimum between 30% and 40% for large thalli and close to 30% for smaller thalli [88]. In a similar setting Coxson and Stevenson [93] found comparable results, showing that growth rate is strongly associated with increasing light transmission. In fact, the dry matter gain over a two-year period ranged from less than 5%, in thalli exposed in a close canopy, to up to 20% in thalli on branches under canopy gaps. Similarly, Juriado et al. [97] reported a higher probability of occurrence of *L. pulmonaria* with increasing light availability. The presence of deciduous shrubs is positively associated with *L. pulmonaria*, and the authors hypothesised that the presence of these shrubs could give shelter to the diaspore of *L. pulmonaria*, aiding their attachment and colonisation. Even adult *L. pulmonaria* could be favoured by the presence of deciduous shrubs, as they protect the trunk from desiccating winds and direct sunlight during the summer periods. Although these findings are likely to be influenced by climatic conditions and latitudinal factors even in Mediterranean oak forests, it seems that a small increase in solar radiation could positively affect the growth rate of *L. pulmonaria* [68].

4.3.7. Dispersal Capacity

The dispersal capacity of a species is a fundamental factor to consider in forest management aimed at species conservation. In fact, a species with low range dispersal is favoured by habitat continuity, size, and connectivity between habitat patches [99]. By re-surveying 12 forest sites in southern Sweden with a nine-year interval, Ockinger et al. [99] found that the dispersal ability of *L. pulmonaria* has a stronger effect on dispersal than habitat quality at a large distance, while at a small distance, habitat quality could be more important. The estimated mean dispersal distance was 35 m with a maximum of 75 m. Considering propagules sampled in snow, the maximum dispersal distance was over 200 m, suggesting that *L. pulmonaria* is not dispersal limited but that there are some ecological factors that could hinder the establishment of propagules [100]. A study comparing several populations of *L. pulmonaria* in the Iberian Peninsula confirms the absence of an isolation pattern due to distance [143]. Similarly, Kiebach et al. [96] found no evidence of isolation in *L. pulmonaria* populations in the Alps. Nevertheless, the distance at which the propagules are able to effectively establish is normally lower than the maximum distance at which they can be found. Juriado et al. [101] indicated in 15–30 m the effective dispersal distance of vegetative diaspores of *L. pulmonaria* and over 21–50 m the dispersal based on sexual reproduction which takes over vegetative dispersal. These results suggest that dispersal limitation hinders the expansion of *L. pulmonaria*. Thus, the source and suitable host trees should not be further than 30 m. In addition, the genetic dissimilarity is influenced by tree species and trunk diameter, and in managed forests, there were fewer juvenile thalli, indicating an effect of management on the population structure of this species. Vegetative propagules disperse over a shorter distance and ascospores are able to reach larger distances [125]. The type of forest management, or disturbance, seems to also influence the genetic structure of the population. For instance, Werth et al. [125] found a stronger clonal structure in fire-disturbed forests.

4.3.8. Monitoring with *Lobaria pulmonaria*

Being easily recognised even by non-specialists, *L. pulmonaria* has been largely tested as an indicator of stand characteristics, overall lichen diversity, and the presence of endangered lichen species. In British Columbia, the abundance of *L. pulmonaria* was found to be strongly correlated with macrolichen diversity and with stand age scale [28]. Similarly, in Switzerland, the presence of *L. pulmonaria* was found to be a positive indicator of forest autochthony, i.e., those forests that have a natural tree species composition, with no evidence of significant management and having existed for at least 120 years [45,46]. Gauslaa [42] found *L. pulmonaria* as a suitable indicator of forests with a high number of rare species and forest continuity in Norway. Kuusinen [47] confirmed the role of indicators

of forest continuity for Finland. Ojala et al. [48] found the abundance of *L. pulmonaria* (and bryophytes) on *Populus tremula* L. forests associated with its regional abundance (alpha-diversity) and the size of host trees in Finland. On the other hand, Kalwij et al. [43] noticed that in forests of Switzerland heavily disturbed until the end of the eighteenth century, *L. pulmonaria* populations recovered to a previous condition of an undisturbed environment. Moreover, their results show that some disturbances that determine a partial increase in light and higher availability of trees, following, for example, post-logging re-sprouting of trees, could be even beneficial for this species. *Lobaria pulmonaria* has been tested also as an indicator of the presence of red-listed lichens and wood beetles: considering beetles, it was positively associated with those dependent on hollow trees, while the overall number was not. On the other hand, the presence of *L. pulmonaria* was strictly associated with red-listed lichens in hemiboreal forests in Southern Sweden [20]. Of note, the authors report that in areas with higher precipitation, *L. pulmonaria* can colonise more exposed situations, where other red-listed lichens cannot. Thus, it is fundamental to consider the abundance of the species, as well as the fertility of the populations, and not only its presence. In fact, the abundance of *L. pulmonaria* varies according to the biogeographic area and was associated with red-listed lichens in different bioclimatic conditions in Italy [19]. Moreover, in abandoned old-growth chestnut orchards, it is associated with sensitive species such as those of the order *Caliciales* [144]. As previously discussed, in optimal conditions, *L. pulmonaria* could have a high demographic rate and colonise quite exposed situations. In addition, old trees with a high abundance of *L. pulmonaria* can maintain their presence and abundance, even if the surrounding trees have been clear cut. In such cases, other more shade- and humidity-demanding species, which are often red-listed lichens, can be locally extinct. Finally, the research in the Mediterranean area outlined the great importance of ensuring the safeguard of forest ecosystems hosting fertile populations of this model species, especially in the case of unprotected forests [24], and its usefulness as an indicator of forest sites worthy of conservation.

5. Conclusions

Three main research fields were examined: (i) ecosystem functioning and services; (ii) air pollution monitoring; and (iii) the effects of forest management and forest structure.

- In terms of ecosystem functioning and services, *L. pulmonaria* contributes to C cycle and moreover N₂ fixation (thanks to the presence of cephalodia). *Lobaria pulmonaria* is important for the forest's food network, especially for snails and slugs, and it supports the diversity of some organisms, e.g., offering suitable microhabitats for several small animals. However, the interaction between *L. pulmonaria* and lichen-eating animals still requires investigations.
- *Lobaria pulmonaria* is considered to be extremely sensitive to pollution. Its application in air pollution monitoring refers to past acid rain and SO₂ depositions, heavy metals, radionuclides, and PAHs in forest habitats. Hence, air pollution (especially in the past) and habitat fragmentation (nowadays) appear as the main anthropogenic factors influencing *Lobaria* vegetation. On the other hand, its use to monitor air pollution is in fact limited by its sensitivity and rarity. Actually, there is particular interest in understanding whether current air quality still limits the possibility of recolonisation in forest sites where *L. pulmonaria* disappeared, as well as the interaction between pollution, microclimatic parameters, and forest structure and dynamics in a conservation perspective. In this sense, recent research also highlighted the possibility of translocation practices for conservation purposes in relation to potential anthropogenic impact on *L. pulmonaria* in threatened habitats.
- We discussed the impact of forest management on *L. pulmonaria*, a sensitive species to the variation of microclimatic conditions. Forest management practices, such as logging and fragmentation, can negatively affect *L. pulmonaria* populations, leading to a loss of biomass, changes in population composition, and reduced vitality. Retaining unlogged forest aggregates is essential to preserve vital populations of *L. pulmonaria*.

Genetic diversity in *L. pulmonaria* can be influenced by forest disturbances, potentially leading to clonal vegetative reproduction. Genetic dissimilarity is influenced also by tree species and trunk diameter, and forest management can impact population structure also at a genetic level. We also discussed the impact of forest edges on *L. pulmonaria*, with varying effects depending on edge type and local conditions. The species tends to have a higher growth rate near ‘soft’ forest edges but may not show the same enhancement near ‘hard’ edges. Factors at tree and stand levels, such as tree age, canopy openness, and habitat continuity, play a crucial role in *L. pulmonaria* colonisation and survival. The species is associated with old-growth forests with long ecological continuity, and the ecological requirements vary during its life cycle. Forest type, light availability, and climatic conditions also influence the presence and growth of *L. pulmonaria*. The species is more likely to colonise older trees with large circumferences, but it can adapt to different conditions, especially with optimal climatic conditions. Finally, *L. pulmonaria* is used as an indicator species for assessing forest characteristics and the presence of endangered species. Its abundance is often correlated with forest continuity and the presence of specific (and often desirable) ecological conditions. Hence, the complex relationship between forest management, microclimatic conditions, genetic diversity, and the ecological role of *L. pulmonaria* in forest ecosystems further highlight the need for sustainable and modern forest management practices.

As a concluding remark, *Lobaria pulmonaria* is an excellent candidate for monitoring forest ecosystems due to its biological characteristics. Over more than 50 years, a considerable amount of data have been collected on the ecology of *L. pulmonaria* throughout its range. However, this review highlights a clear gap between scientific knowledge on the potential of Lung lichens as forest biological indicators and their actual use in monitoring plans in at least two contexts:

- The conservation of the species per se, and as an umbrella species for epiphytic communities of conservation concern. Future efforts should focus on regular, standardised, and harmonised monitoring of the conservation status of *L. pulmonaria* at continental and global scales to ensure its adequate protection in the context of climate change scenarios;
- as part of monitoring the effects of forest management plans in order to provide biological data to support policymakers’ decisions and to guide the use of forest resources to be both economically and environmentally sustainable.

Author Contributions: Conceptualisation, G.B., L.F., L.P. and S.R.; methodology, G.B., L.F., L.P. and S.R.; formal analysis, C.V. and S.R.; investigation, S.R.; data curation, S.R.; writing—original draft preparation, R.B., E.B., G.B., L.D.N., L.F., P.G., D.I., C.V., L.P. and S.R.; writing—review and editing, R.B., E.B., G.B., L.D.N., L.F., P.G., D.I., J.N., C.V., L.P. and S.R.; visualisation, C.V. and S.R.; supervision, L.P. This article is part of the project “Effects of forest management on threatened macrolichens” developed by the Working Group for Ecology of the Italian Lichen Society, coordinator L.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no funding.

Data Availability Statement: Not applicable.

Acknowledgments: S.R. acknowledges the support of University of Palermo (PJ_GEST_FFR_2023). G.B. and L.F. have been partially supported by the LIFE Programme of the European Commission under Grant Agreement LIFE20 GIE/IT/000091—LIFE MODERn (NEC) (New Monitoring system to Detect the Effects of Reduced pollutants emissions resulting from NEC Directive adoption).

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

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