



Lichen biodiversity in old-growth forests and on veteran trees: an overview with a focus on Italian forests

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Abstract: Lichens contribute significantly to forest biodiversity, both in terms of the number of species and their ecological roles that affect ecosystem functioning. Several species are threatened with extinction due to their sensitivity to both atmospheric factors and forest management. Solid scientific evidence indicates that forest management intensity strongly influences lichen patterns, suggesting a gradient of greater suitability from industrially managed forests to old-growth forests left to evolve according to natural dynamics. The invaluable role of old-growth forests for lichen diversity is increasingly recognized and parallels with that of veteran trees that are considered keystone for maximizing lichen diversity. Some lichen species consistently indicate the trees and forest stands of greatest interest for conservation. In temperate forests of Italy, *Lobaria pulmonaria* seems to have a good predictive potential for detecting remnants of old-growth forests and for prioritizing forest sites for conservation. This aspect, combined with its easy detectability in the field even by non-lichenologists, makes this species an excellent and promising indicator with practical applications in forest inventories. Old-growth forests are irreplaceable reservoirs of biodiversity, enabling the long-term conservation of currently threatened and extremely rare species. In this perspective, the strict conservation of these lichen hotspots should be mandatory.

Key words: lichen biota; *Lobaria pulmonaria*; old-growth forests; veteran trees.

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1. LICHENS: A COMPLEX SYMBIOSIS

Lichens are biotic systems resulting from symbiotic relationships between fungi (mainly Ascomycetes) and photosynthetic organisms (e.g. unicellular green algae and/or cyanobacteria) (Pichler et al., 2023). However, recent research indicates that lichens can be

interpreted as complex interaction networks involving many different organisms, including additional fungi, bacteria and viruses (Grimm et al., 2021). The compositional configuration of the network may vary depending on environmental conditions (Bogale et al., 2024). In other words, lichens may be also compared to self-sustaining microecosystems (Hawksworth

& Grube, 2020). However, the debate on the definition of a lichen is still open and future research will refine our interpretations (e.g. Sanders, 2024).

The lichenized life style of fungi independently evolved and was lost several times along their evolutionary history, thus lichens represent different lineages in the phylogeny of Ascomycetes (Lutzoni et al., 2001). Definitely, they are not a monophyletic group even though most of their diversity is included in the clade of Lecanoromycetes (Lücking et al., 2017).

The first fossils date back to the Devonian period (Honegger et al., 2013) and recent research based on the re-evaluation of the fossil *Spongiophyton* indicates that they played a major role in the colonization of terrestrial environments during the Devonian (Becker-Kerber et al., 2025). While the first clearly stratified chlorolichen dates back to the lower Cretaceous (Matsunaga et al., 2013), several fossils of forest lichens in the genus *Usnea* are included in Paleogene ambers (Kaasalainen et al., 2020). Most of the lichen biodiversity currently known globally originated after the last mass extinction, about 65 Ma, at the border between the Cretaceous period (end of the Mesozoic era) and Paleogene (Nelsen et al., 2020). The highest speciation rate seems to be related to macrolichens (i.e. foliose and fruticose lichens) and this is for example reflected in the extraordinary diversity in the families of Parmeliaceae and Cladoniaceae (Huang et al., 2019).

2. LICHENS IN FOREST ECOSYSTEMS

Overall, about 20,000 lichens are known at the global level (Lücking et al., 2017), even if similarly to fungi in general, this number likely provides a strong underestimate of their diversity. In Italy, which is one of the lichenologically best known country in the world,

about 3,000 species are known to occur, with new species added every year to the checklist (Martellos et al., 2023). Among these, about 900 are epiphytes, thus potentially colonizing trees in forest ecosystems.

Lichens contribute significantly to forest biodiversity, both considering the number of species and their ecological roles that impact ecosystem functioning and multiple ecosystem services (Ellis et al., 2021; Porada et al., 2023). Along with other epiphytes, such as bryophytes, lichens contribute significantly to the nitrogen cycle, since species with cyanobacteria are capable of fixing atmospheric nitrogen. They also participate significantly in the carbon and water cycles. Finally, they are key players in multiple food webs and provide habitats for numerous small invertebrates, thus sustaining forest biodiversity (Ellis et al., 2021).

Definitely, several species are threatened with extinction due to their sensitivity to environmental factors, such as air pollution and climate change, and forest management (Hauck et al., 2013). These drivers often act interactively, and while this can exacerbate negative impacts, appropriate management can also represent an opportunity to mitigate the effects of global change, whose trends depend on large-scale dynamics. Unfortunately, for reasons that go beyond a strictly scientific approach, lichens are not adequately protected at the European level by the Habitats Directive. In this context, it is therefore crucial to act promptly through parallel channels, starting especially with protected areas, to avoid significant species losses in a relatively short timeframe. Specifically, the challenge of conserving lichen biodiversity in forests lies in their explicit inclusion in management objectives, aiming, on the one hand, to protect the currently known hotspot of lichen diversity and rare species and, on the other, to improve

habitat conditions that can favor the spread of species for their long-term conservation.

Solid scientific evidence, resulting from studies over thirty years, indicates that forest management intensity strongly influences lichen patterns, suggesting a gradient of greater suitability from industrially managed forests to old-growth forests left to evolve according to natural dynamics (Nascimbene et al., 2013a; Vicol & Sahlean, 2023). The invaluable role of old-growth forests for lichen diversity is increasingly recognized and parallels with that of veteran trees that are considered a keystone for maximizing lichen diversity (Fritz et al., 2009; Lie et al., 2009; Marmor et al., 2011; Zemanová et al., 2017). In fact, on veteran trees many species accumulate over time, including many lichens of conservation interest that for example are extremely rare in Italy, precisely because of the rarity of this type of microhabitat (Nascimbene et al., 2009). Due to the combined effect of the temporal stability of the substrate (which therefore increases the probability of colonization), the larger available surface area (the number of species depends on the available area), and the microenvironmental conditions related to both the characteristics of the bark (heterogeneity with cracks, holes, etc.) and the canopy, old trees can be thought of as biodiversity lifeboats providing valuable refugia to several threatened species that may potentially disperse into the surrounding forests.

Moreover, results of a recent study (Nascimbene et al., 2025) reveal a further, previously undocumented, effect of veteran trees on lichen biodiversity: they are not only “accumulators of species”, but also seem able to mitigate the rate of compositional change in lichen communities over time. The results of this study, based on the resampling of approximately 100 trees at five sites, 15 years after the initial sampling, highlight greater compositional changes in lichen communities on

young trees than on old trees. This aspect is particularly relevant in the current scenario characterized by global changes that are causing rapid shifts in the distribution of many species, which is reflected in changes in community composition. This for example applies to those lichens commonly referred to as “beard lichens” (filamentous lichens of the genera *Usnea*, *Bryoria*, *Evernia*, and *Alectoria*), which are declining across Europe (Esseen et al., 2022; Ellis et al., 2025).

Finally, old growth forests usually host large amount of different types of deadwood in different decomposition stages. Similarly to many forest organisms, deadwood is robustly documented to be a unique microhabitat for many specialized lichens (Spribille et al., 2008; Nascimbene et al., 2013b; Nirhamo et al., 2026). Probably, snags are the most important deadwood type for lichens (e.g. Nascimbene et al., 2008a), even if both stumps and logs host peculiar species, thus contributing to maximize the diversity of the forest lichen biota. Recent research indicates that conservation of deadwood-dwelling lichens should not only be related to the release of deadwood in managed forests, but should maintain adequate habitat conditions in the surrounding landscape (Hämäläinen et al., 2023).

3. INDICATOR SPECIES

Some lichen species consistently indicate the trees and forest stands of greatest interest for conservation. This is the case of the charismatic lung lichen, *Lobaria pulmonaria*, universally recognized as an indicator of forest conservation interest (Ravera et al., 2023), especially in sub-optimal climatic regions where its occurrence and abundance is mainly related to forest structure, rather than to macro-climatic conditions. While in the past this

species was relatively common across European forests, currently it is locally extinct or threatened in many countries, being included on the red-lists. Its decline reflects both the increasing atmospheric pollution and the intensification of forest management that reduced forest continuity, availability of veteran trees, and forest heterogeneity (Ravera et al., 2023).

While Italy (especially southern Italy) is among the main European centers of genetic diversity of this species (Widmer et al., 2012), recent research indicates its sensitivity to climate change whose effects may negatively interact with management intensity, thus exacerbating its potential decline across Italian forests (Nascimbene et al., 2016). Interestingly, climate change may even indirectly affect the species in the future, causing a distributional mismatch between the lichen and its preferred host tree species (Nascimbene et al., 2020).

In temperate forests of Italy, *Lobaria pulmonaria* seems to have a good predictive potential for detecting remnants of old-growth forests and for prioritizing forest sites for conservation, since its occurrence and abundance are indicative of the occurrence of several overlooked and threatened species (Nascimbene et al., 2010). This aspect, combined with its easy detectability in the field even by non-lichenologists, makes this species an excellent and promising indicator with practical applications in forest inventories.

Besides the potential of the flagship species *Lobaria pulmonaria* for temperate forests, in subalpine forests of the Alps, additional indicator species or lichen guilds may be effectively used. This is for example the case of the wolf lichen *Letharia vulpina* that is typically related to *Larix decidua* forests at the tree-line, under continental climate. Despite the fact that several cryptic species were recently documented in the Alps (Ament-Velásquez et al., 2021) the

abundance of this easily detectable lichen was demonstrated to be positively related with tree age (Nascimbene et al., 2008b), thus representing a good indicator of forest conservation value for lichens.

Despite the impossibility of working in detail on the species, due to objective taxonomic difficulties that would not allow a non-specialist approach, the group of hair lichens is also very promising as an indicator in the coniferous forests of the Alps (Nascimbene et al., 2019). In particular, these lichens are demonstrated to be sensitive to climate and pollution, thus being excellent candidates to monitor the effects of global change on tree-line forests.

4. CONSERVATION

For the lichen biota, old-growth forests are irreplaceable reservoirs of biodiversity, enabling the long-term conservation of currently threatened and extremely rare species. In this perspective, the strict conservation of these lichen hotspots should be mandatory. However, since forests managed for timber production dominate the forest landscape of Europe, including Italy, it is necessary to rapidly develop management guidelines that address the protection of this sensitive and threatened component of biodiversity. This should especially apply to forest areas where biodiversity conservation is explicitly included among the management objectives, such as in protected areas and, in general, in the Natura 2000 network.

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