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Review

Could Hair-Lichens of High-Elevation Forests Help Detect the Impact of Global Change in the Alps?

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Abstract: Climate change and the anthropic emission of pollutants are likely to have an accelerated impact in high-elevation mountain areas. This phenomenon could have negative consequences on alpine habitats and for species of conservation in relative proximity to dense human populations. This premise implies that the crucial task is in the early detection of warning signals of ecological changes. In alpine landscapes, high-elevation forests provide a unique environment for taking full advantage of epiphytic lichens as sensitive indicators of climate change and air pollution. This literature review is intended to provide a starting point for developing practical biomonitoring tools that elucidate the potential of hair-lichens, associated with high-elevation forests, as ecological indicators of global change in the European Alps. We found support for the practical use of hair-lichens to detect the impact of climate change and nitrogen pollution in high-elevation forest habitats. The use of these organisms as ecological indicators presents an opportunity to expand monitoring activities and develop predictive tools that support decisions on how to mitigate the effects of global change in the Alps.

Keywords: biodiversity conservation; climate change; ecosystem functioning; fruticose-filamentose lichens; global warming; nitrogen pollution

1. Introduction

It is widely recognized that global change will impact ecosystems and society considerably [1,2]. The impact of global processes, including climate change and the anthropic emission of pollutants, is likely to accelerate for high-elevation mountain areas [3]. This phenomenon could cause negative consequences in the European Alps, which host high-priority habitats and species for conservation while also sustaining a relatively dense human population whose activities include summer and winter tourism, traditional agriculture, forest exploitation, and water extraction for energy production [4].

This scenario invokes the crucial task of detecting early warning signals of changes that can affect ecosystem stability and, in turn, human well-being in the alpine zone. In most cases this would facilitate the prompt adoption of local management solutions that could mitigate the negative effects of global change; however, there is still a lack of monitoring in high-elevation regions, mainly due to practical constrains in managing instrumental devices under challenging logistical and climatic conditions [3]. This information gap could be partially filled by detecting and monitoring functionally relevant organisms in relation to the main drivers associated with global change. This approach, based on ecological indicators, would allow the evaluation of early signs of ecosystem changes and help to manage the risks to biodiversity and its related ecosystem functions and services.

Epiphytic lichens are among the organisms most sensitive to climatic factors and air pollution and are increasingly used for biomonitoring purposes across Europe on the basis of standardized guidelines [5]. Recent studies have highlighted that the response of lichens to climate and pollution could depend on specific traits (e.g., photobiont type and thallus growth form), suggesting the usefulness of considering selected functional groups for evaluating environmental conditions [6]. Contrary to lichen monitoring approaches based on community diversity data [5], the use of functional groups would allow comparisons across wide areas and would not require high lichenological expertise, making it less problematic in terms of applicability.

In the alpine landscape, high-elevation forests provide a unique environmental setting that could take full advantage of the potential of epiphytic lichens as indicators for climate change and air pollution. In this regard, it has been demonstrated that in alpine ecosystems long-range pollution may impact the local biota and interactively exacerbate the effects of climate change. For example, together with bryophytes, lichen are among the most sensitive organisms to increased N input [7]. In high-elevation forests, due to the virtual absence of exploitative activities, lichen patterns are expected to be mainly controlled by factors acting on a large spatial scale, further underscoring their role in detecting the effects of global change.

This literature review is intended to provide a starting point for developing practical biomonitoring tools by examining the potential of hair-lichens, characteristically associated with high-elevation forests, as ecological indicators of global change in the Alps. In particular, we used an expert assessment approach for mining the available literature from the main scientific databases (Scopus and WOS), critically selecting the information necessary to investigate the potential of this lichen functional group in detecting the effects of climate change and nitrogen pollution, which are considered among the most challenging global threats to alpine environments [3,4,8,9]. The review includes a brief description of the main patterns of climate change and nitrogen pollution in the European Alps, while its core focus is on the lichen-climate and lichen-nitrogen pollution relationships with special emphasis on hair-lichen species (see Section 3).

2. Main Patterns of Climate Change and Nitrogen Pollution in the Alps

The main patterns of climate change in the Alps were recently reviewed by Gobiel et al. [10]. In the European context, the Alps are located in a transitional and seasonally shifting zone influenced by a bipolar norths–south climate pattern, and with climate change scenarios predicting more warm–arid conditions in Southern Europe and increasing precipitation in Northern Europe. In the recent decades, the Alps have experienced dramatic climate changes and temperatures have risen at a rate about twice that of the northern hemisphere average, leading to a mean annual increase of about 2 °C [11]. This trend homogeneously spans the whole alpine region with higher rates of warming mainly at high elevations [4]. Climate changes associated with global warming also include changes in the precipitation regime. Less precipitation events are predicted for summer, mainly on the southern slopes of the Alps, and more precipitation in winter [12]. This pattern is consistent with a trend of relative humidity (positive relationship) and solar radiation (negative relationship).

The atmospheric deposition of reactive nitrogen (Nr) is among the major drivers of biodiversity loss across Europe [8], also impacting human health [13]. The Alps are surrounded by urban agglomerations and agricultural areas (e.g., the Padanian basin on the southern slopes and the Swiss Central Plain on the northern slopes), producing huge amounts of Nr that reach the alpine area by long-range transport [9]. This phenomenon may cause high concentrations of air pollutants, even at high elevations [14]. Several recent studies have documented the impact of nitrogen pollution on different organisms and ecosystems in the alpine area, as demonstrated by Humbert et al. [15] for mountain grasslands. Models of Nr deposition at the continental scale indicate that stronger impacts are currently affecting the northern and southern mountain borders and Alpine foothills, the greatly impacted areas being in Bavaria and Northern Switzerland (and part of Northern Austria [14]), according to Lombardy [9].

Both climate change and nitrogen pollution are therefore expected to directly impact the alpine biota. However, there is increasing evidence that their interactive effects should also be accounted for. Recently Hämmerlee et al. [16] proposed a new method to jointly assess the effects of climate change and nitrogen deposition on biodiversity. Nitrogen pollution is likely to have synergistic interactions with climate change that could affect soil carbon and nitrogen cycling in the soil with multiple consequences for autotrophic organisms [13,17]. In general, climate change may exacerbate the effects of nitrogen pollution [18]. Climate warming could amplify the negative effects of nitrogen in terms of diversity and compositional changes [15,19]. In addition changes in the precipitation regime are likely to interact with nitrogen deposition [20], with the impacts being enhanced by increasing rainfall [14].

From a lichen perspective, both factors may influence very different eco-physiological and ultra-structural parameters, as, for example, the process of rewetting and thallus water content in the case of climate, and the photobiont/mycobiont ratio in the case of nitrogen pollution. These are reflected by macro-ecological patterns of lichen communities. These effects will be elucidated in detail in the following sections.

3. Hair-Lichens

Hair-lichens are a morpho-functional group that includes pendulous epiphytic lichens with a fruticose-filamentose thallus, mainly belonging to the genera *Alectoria, Bryoria, Evernia, Ramalina*, and *Usnea*. While their identification at the species level can be problematic, they are clearly visible, identifiable by the naked eye, in the field as a distinct morphological guild. These lichens are known to play several ecological roles that contribute to forest ecosystem functioning, sustaining habitat quality, and resiliency [18]. For example, they provide winter forage for large herbivores [21,22], a habitat for canopy invertebrates that are consumed by passerine birds [23], nesting material for birds, and are involved in complex food webs (Figure 1).

In the Alps, hair-lichens are common in open high-elevation forests where they can locally envelope the branches (mainly on spruce and stone pine) or the higher part of the trunks (mainly on larch) of conifers, often accumulating a huge biomass (e.g., more than 900 Kg ha^{-1} for boreal forests [24]). Due to this tree-level colonization pattern and the high surface area to biomass ratio [25], hair-lichens are among the epiphytes most exposed to the atmosphere, emphasizing their potential use for the early detection of the effects of climate change and air pollution.

4. Lichen–Climate Relationships with Emphasis on Hair-Lichens

Epiphytic lichens are among the organisms most sensitive to climatic conditions, and evaluation of their distribution patterns along climatic gradients may provide early warning information that could be used to prevent the loss of forest diversity and ecosystem functions caused by climate change [26–28]. There is mounting evidence that changes in temperature and rainfall can severely affect epiphytic communities, leading to the local extinction of several species [29] and biomass loss [18]. Moreover, the contribution of lichens to ecosystem functioning in terms of net primary production depends on metabolic activity that, in turn, is influenced by climatic conditions, supporting the view that the analysis of lichen abundance patterns could provide relevant information on the effects of global change on ecosystem functioning [30–32].

The poikylohydric nature of lichens provides the main basis for their sensitivity to climate, which directly controls relevant eco-physiological processes influencing growth rates and species distributions [33]. In particular, lichen physiology is closely coupled with ambient temperatures and moisture conditions [34], which influence thallus water saturation and desiccation. Since lichens are photosynthetically active when wet, their growth rate, biomass accumulation and diversity are directly influenced by the amount of precipitation [25,28], even if other hydration sources, such as dew and air humidity, may be important [25]. Increasingly ambient temperatures may negatively affect lichens due to increased respiratory carbon loss [35]. High temperatures influence the process of rewetting and thallus water content and imply more frequent and severe desiccation events that hinder the photosynthetic activity of these poikilohydric organisms [33]. These effects could be exacerbated by decreasing precipitation (interaction between water and energy climatic factors), resulting in a stronger effect of temperature in dry mountains (modified conjecture of Reference [36]; see also Reference [37].

The particular response of lichens to climatic factors is mediated by their different functional traits (e.g., photobiont type, growth form, and thallus thickness), which affect species performance under given environmental conditions [6,38,39]. Photobiont type and thallus growth forms are among the most responsive traits explaining large-scale patterns of lichen diversity [25,28,40].

A recent study exploring the species–elevation relationship of epiphytic lichens in spruce forests of the Alps [39] stresses the sensitivity of hair-lichens to both increased temperature and precipitation. On a broader scale, Essen et al. [41] demonstrated that climate and nitrogen deposition are the main factors shaping the distribution of hair-lichens; their effects are greater than the response to forest structures. Hair-lichens have a high surface area to biomass ratio [25] and, in high-elevation forests, are physiologically active most of the year [42]. Studies conducted in boreal forests, mainly focused on the patterns of hair-lichens along a vertical gradient on the trees [24,42,43], provide a straightforward and robust eco-physiological basis for their sensitivity to climatic factors.

On the basis of sun-screening pigments accumulated in the thalli and protecting the photobiont from excessive solar radiation, hair-lichens can be split into two functional subgroups with contrasting responses to the climatic factors responsible for thallus hydratation. One group includes the species containing usnic acids (belonging to the *Usnea, Alectoria*, and *Evernia* genera), which are mainly restricted to the lower canopy, where they benefit from higher humidity and reduced air convection, prolonging the duration of thallus hydration after wetting events [42]. The other group includes species containing dark melanins (genus *Bryoria*) that mainly dominate the upper canopy, where they can replace "usnic lichens" that are impacted by photo-inhibition [44]. The authors' field of experience in alpine forests suggests that on poorly branched, deciduous conifers (i.e., on larch) the vertical distribution gradient of the two functional subgroups could have as its counterpart an exposure gradient, with *Bryoria* species prevailing on the more dry, sun-exposed sides of the trunks and "usnic lichens" prevailing on more sheltered and humid exposures. Other lichen compounds in hair-lichens, such as vulpinic acid in *Letharia vulpina*, have been shown to play a role in blue light screening [45], this pattern may vary elsewhere.

The hydration requirements vary considerably across green algal lichen species [46,47]. Thin fruticose chlorolichens are well adapted to exploit humid air [48], and in the lower canopy they may depend more on humid air [49]. On the other hand, in the upper canopy, where water uptake mainly depends on precipitation [49], *Bryoria* species store a large amount of water on their surface (external water) in order to prolong the hydration after rain [47].

In general, there is agreement on the fact that the colonization pattern and abundance of different subgroups of hair-lichens in the canopy may reflect their interaction with the regional climate; in particular, the amount and precipitation regime influences the growth rate of hair-lichens [24] since rehydration from dewfall is not sufficient for physiological activation. Eriksson et al. [50] demonstrated that morphology and hydration traits influence distribution in several *Usnea* species. With similarities in the *Alectoria* and *Bryoria* genera and differences in *Usnea*, water storage increases with branch density, a strategy allowing prolonged hydration and, therefore, photosynthetically active periods [51]. Campbell and Coxon and Lange et al. [24,52] highlighted the importance of seasonal variations in the subalpine coniferous forests of British Columbia. In high-elevation forests snow melt events appeared crucial for thallus hydration during the winter period when both "usnic" and "melanic" lichens experienced the greatest duration of wetting (i.e., higher metabolic activity). Dark pigments in *Bryoria* species improved thallus heating, favoring snow melt and thallus hydration with the consequent activation of photosynthesis [42]. However, excessive heating by solar radiation could impact these lichens mainly found in cool–cold climates [39,44]. Moreover, *Bryoria* species suffer from excessive rewetting that depresses net assimilation [42,53]. For example, Coxon and Coyle [42] found an abrupt decline of *Bryoria* species after six days of continuous hydration, whereas the lichen *Alectoria sarmentosa* ("usnic lichen") declined more gradually. This phenomenon is reflected in the bio-geographic patterns of *Bryoria* biomass. For example, in Scandinavia *Bryoria* biomass is higher in inland regions with less rain than in coastal regions subjected to heavy rains [54,55]. Also in North America [56], *Bryoria* species are damaged by excessive rain or snowmelt that can cause biomass dieback [25]. Increasing rainfall is likely to favor the biomass accumulation of "usnic lichens" [43] that can adjust upwards in the canopy, or spread around the trunk, outcompeting *Bryoria* species. Thus, the species richness of lichens belonging to *Usnea* seems to increase from dry to oceanic areas [57].

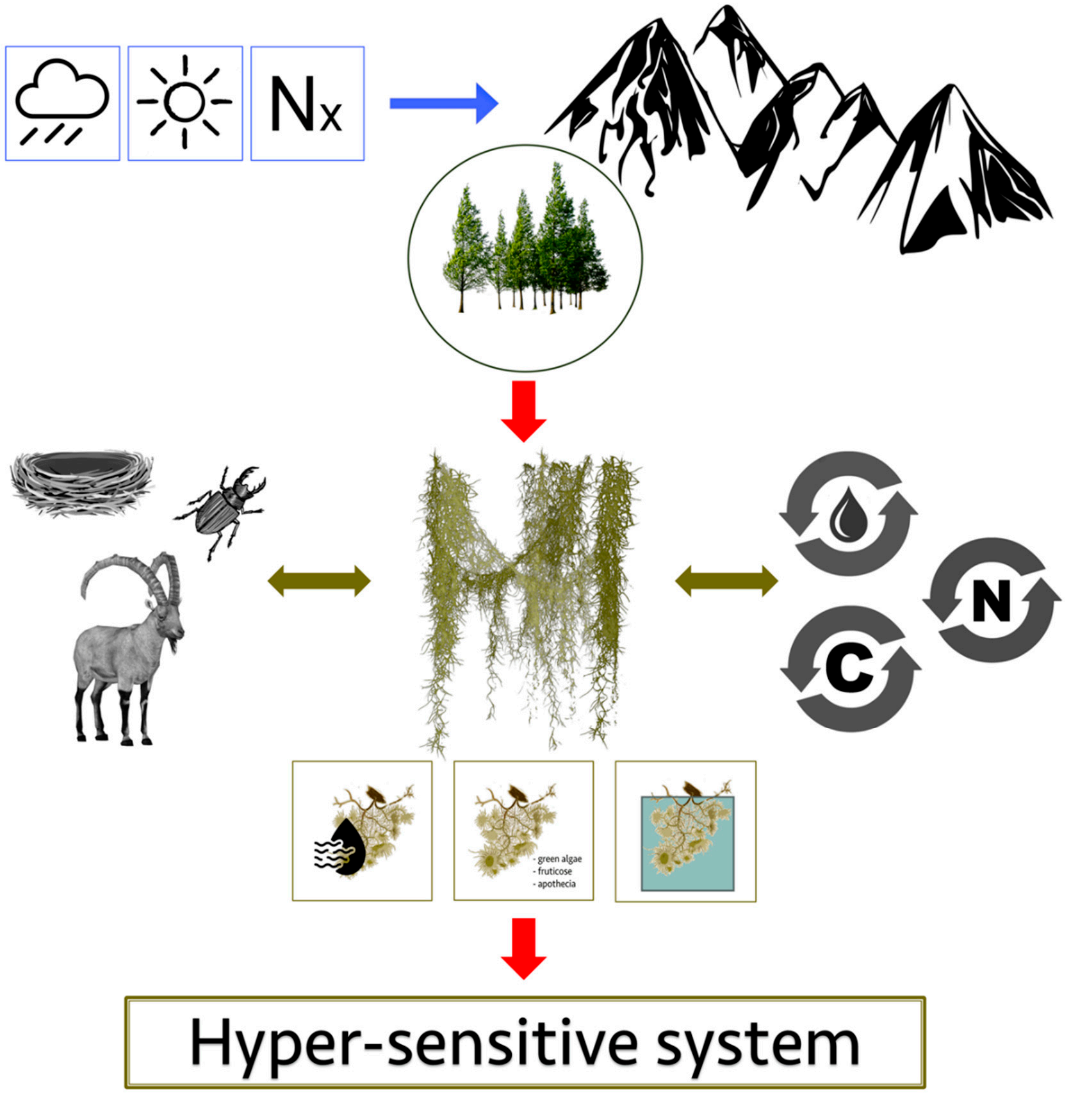

Figure 1. Conceptualization of the role and potential of hair-lichens as ecological indicators in high-elevation forests. Blue squares represent the variations in precipitation, global warming, and atmospheric deposition of reactive nitrogen (blue arrow), which are the main factors of global change threatening high-elevation ecosystems. The green arrows represent the ecological roles of hair-lichens that contribute to forest ecosystem functioning in sustaining habitat quality and resilience. The green squares on the left represent the poikylohydric nature of lichens; in the center is their main functional traits and on the right the high surface area is exposed to the atmosphere, which provides a basis for considering hair-lichens among the most sensitive organisms to high-elevation environments. The scheme stresses their potential for the early detection of the effects of climate change and air pollution.

5. Lichen–Nitrogen Pollution Relationships with Emphasis on Hair-Lichens

Epiphytic lichens are among the most sensitive organisms to eutrophication [8,58], the impact of which mainly includes shifts in lichen community composition (i.e., oligotrophic species are replaced by nitrogen-tolerant species [59,60]) and loss of community diversity and species cover across different ecosystems [8]. In forest ecosystems, these sensitive organisms may provide an early warning signal of potential threat to the entire biota [61].

Lichen functional groups with different nitrogen tolerances respond to different atmospheric pollutants, with both independent and joint effects, whereas the role of light and tree-related variables, such as bark pH, seems to vary depending on the habitat type and the level of nitrogen depositions [62,63].

A recent study in the Italian Alps revealed a pattern of lichen community changes related to the intensity of the agricultural management of alpine larch grasslands that was mirrored by a negative impact on other photo-autotrophic organisms [64]. Moreover, lichens accumulate substances directly from the atmosphere, including reactive nitrogen compounds, whose concentration in thalli is highly correlated with throughfall dissolved inorganic nitrogen deposition [65]. In alpine ecosystems, pasture derived nitrogen deposition is expected to significantly alter community composition and the diversity of many sensitive organisms, such as lichens. Giordani et al. [66] demonstrated that high cattle load reduced the species turnover and significantly increased similarity of the oligotrophic components of lichen communities.

On the basis of these responses, lichens are increasingly being used in biomonitoring studies to detect patterns and effects of nitrogen pollution in different ecosystems in relation to both long-distance transport of pollutants and local management [59,67]. Recent research has provided valuable tools that improve the lichen biomonitoring approach by (a) determining critical loads of reactive nitrogen for different ecosystems [18,60,61,68], (b) selecting indicator species for the assessment of nitrogen deposition and source identification [69] and (c) selecting lichen functional groups that are highly responsive to nitrogen loads, such as macrolichens (i.e., foliose and fruticose/hair-lichen thallus growth forms [61]). Interestingly, in the larch grasslands of the Alps [64], 85% of the species associated with low nitrogen input are macrolichens and 25% are hair-lichens species belonging to *Bryoria* and *Usnea*.

Empirical patterns of community changes and species distributions in relation to nitrogen pollution are likely to be related to differential physiological species responses [70,71]. Using an experimental approach, Johansson et al. [70,71] evaluated the response of selected species to increasing nitrogen deposition across time slices, revealing that hair-lichens belonging to *Bryoria* and *Alectoria* are extremely sensitive to nitrogen pollution. They also provided an eco-physiological basis for interpreting the mechanism behind the observed decrease of *Alectoria sarmentosa* with increasing nitrogen loads, invoking reduced thallus stability (by increasing the photobiont/mycobioint ratio) [70] or increasing susceptibility to diseases, favoring the development of parasitic fungi that damage the cortical layer [71] as plausible drivers. These experimental results are reflected in the bio-geographical patterns of certain hair-lichens species. For example, *Alectoria sarmentosa* is most likley extinct in the north-western regions of Central Europe due to excessive eutrophication and habitat destruction [72]. *Bryoria fuscescens* is nearly extinct in the Netherlands where it is currently restricted to remote sites far from nitrogen pollution sources [67]. In the Pacific Northwest, McCune and Geiser [73] found a frequency peak of *Bryoria* species at low levels of nitrogen deposition (1.9–2.3 Kg N ha^{-1} yr^{-1}). This load is consistent with that observed in European forests [61], where a significant critical load for epiphytic lichens was calculated at 2.4 Kg N ha^{-1} yr^{-1}. [67]. An exploration of lichen patterns in forest monitoring plots across Europe established a decrease in the probability of occurrence of *Bryoria* and *Usnea* species at very low nitrogen loads (e.g., 0.3 mg N L^{-1} precipitation).

6. Conclusions and Perspectives

Recent research has demonstrated that lichen-based monitoring methods can be effective in detecting the effects of climate change and nitrogen pollution [74]. We identified sound scientific support for the practical use of hair-lichens in detecting the impact of these factors in high-elevation areas of the Alps, the environmental and economical heritage of which is increasingly threatened by global change. The use of these sensitive and functionally relevant organisms as ecological indicators provides an opportunity to fill a gap in the instrumental monitoring of high-elevation areas, and in the development of predictive tools that could sustain an evidence-based decision process that mitigates the effects of global change in the Alps.

This could be developed in future projects testing and elucidating the response of hair-lichens in terms of different biological metrics describing the status of the target indicator species. In particular, researchers should test whether the abundance patterns of hair-lichens are influenced by climatic factors, with possible contrasting responses between green–yellow colored (usnic-acid containing) species and dark colored (melanic) species, and the interactive effects of temperature and precipitation. Moreover, spanning a gradient of nitrogen pollution across the Alps, researchers should test whether the abundance patterns of hair-lichens are negatively influenced by nitrogen deposition, reflecting the sensitivity of the species composing this functional group to nitrogen pollutants. This trend is expected to interact with climatic factors; we hypothesize a stronger impact in wetter areas.

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