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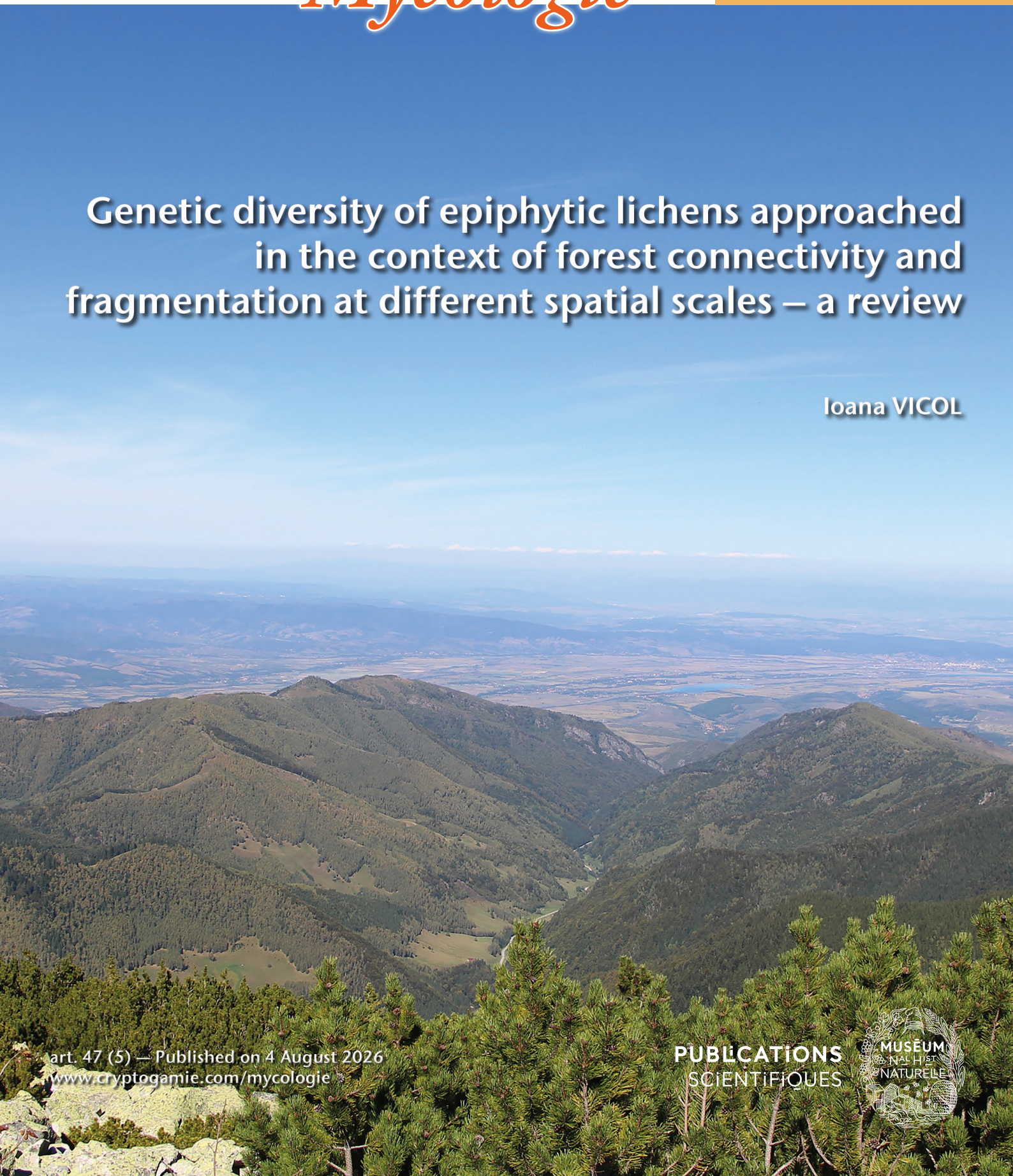

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Genetic diversity of epiphytic lichens approached in the context of forest connectivity and fragmentation at different spatial scales – a review

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ABSTRACT
To protect lichen species, habitats with large populations need to be conserved, alongside with genetic diversity. The genetic variation in lichen populations is significantly impacted by forest connectivity. Additionally, the genetic variation of populations is determined by the reproductive mode of lichens and their dispersal capacity. The microclimate and macroclimate shape symbiotic complexity supported by cryptic lineages of symbionts adapted to various environmental conditions. Climate and dispersal vectors, in the context of different adaptation strategies of symbiotic complexity, highlight an integrative biological connectivity framework with multiple interactions which occur at local and large spatial scales. Conservation genetic and forest management measures are important policy actions intended to prevent the extinction of lichens populations and species and to ensure their long-term survival within complex landscapes. In the context of the conservation and management of forest habitats, novel technologies (metagenomics, assisted migration and remote sensing) that provide important data are needed to identify refugia and hotspot areas for lichens. One of the planetary drivers with an imminent impact on biodiversity is global warming, which removes climatic barriers and could be implicated in the extinction of the genetic heritage of lichens in cold habitats. Therefore, conservation actions must be taken to reduce or avoid the risk extinction of lichen populations.

KEY WORDS
Epiphytic lichens, forest connectivity, forest fragmentation, forest management, genetic diversity.

RÉSUMÉ
La diversité génétique des lichens épiphytes abordée sous l'angle de la connectivité et de la fragmentation forestières à différentes échelles spatiales – une synthèse.
Pour protéger les espèces de lichens, il est nécessaire de préserver les habitats abritant des populations importantes, tout en préservant la diversité génétique. La variation génétique au sein des populations de lichens est fortement influencée par la connectivité forestière. De plus, cette variation génétique est déterminée par le mode de reproduction des lichens et leur capacité de dispersion. Le microclimat et le macroclimat façonnent la complexité symbiotique soutenue par des lignées cryptiques de symbiotes adaptées à diverses conditions environnementales. Le climat et les vecteurs de dispersion, dans le contexte des différentes stratégies d'adaptation de la complexité symbiotique, mettent en évidence un cadre de connectivité biologique intégratif comportant de multiples interactions qui se

produisent à l'échelle locale et à grande échelle spatiale. Les mesures de la conservation de la diversité génétique et de la gestion forestière constituent des actions politiques importantes visant à prévenir l'extinction des populations et des espèces de lichens et à assurer leur survie à long terme au sein de paysages complexes. Dans le contexte de la conservation et de la gestion des habitats forestiers, de nouvelles technologies (métagénomique, migration assistée et télédétection) fournissant des données importantes sont nécessaires pour identifier les refuges et les zones sensibles pour les lichens. L'un des facteurs planétaires ayant un impact imminent sur la biodiversité est le réchauffement climatique, qui supprime les barrières climatiques et pourrait être impliqué dans l'extinction du patrimoine génétique des lichens dans les habitats froids. Par conséquent, des mesures de conservation doivent être prises pour réduire ou éviter le risque d'extinction des populations de lichens.

MOTS CLÉS
Lichens épiphytes, connectivité forestière, fragmentation forestière, gestion forestière, diversité génétique.

INTRODUCTION

Forests have been exploited over millennia, and the impact of timber exploitation during this time is one of the anthropogenic drivers of the genetic diversity of forest dwellers (Ledig 1992). The concept of green infrastructure integrates the wide natural vegetation networks of the EU, which require conservation and restoration measures to ensure their sustainable development (Angelstam *et al.* 2018). Furthermore, the concept of green infrastructure is directly related to forest habitat quality, which is supported by the biodiversity of natural resources in forests (Angelstam *et al.* 2018). Thus, in the framework of this study, the genetic variation of lichen populations approached in the context of forest connectivity and fragmentation at different geographical scales (population, landscape, regional) under the influence of microecological and macroecological conditions represents one of the important targets of global biodiversity conservation (Otálora *et al.* 2011; Scheidegger *et al.* 2012; Belinchón *et al.* 2018). The footprints of ecological conditions are revealed in the genetics of populations at different temporal and spatial scales (Scheidegger *et al.* 2012). Thus, the consequences of human impacts on the ecology of forested landscapes are reflected in the perturbation of the genetic diversity of epiphytic lichen populations through the loss of rare alleles (Werth *et al.* 2006).

The reproduction mode and diaspore dispersal affect population genetic structure of epiphytic lichens (Scheidegger *et al.* 2012; Belinchón *et al.* 2018). Epiphytic lichen populations with reduced sizes have limited evolutionary potential due to their reduced gene flow, and a large chance to be extirpated by catastrophic events, while larger epiphytic lichen populations with developed dispersal abilities have greater gene flow causing low genetic differentiation (Hilmo *et al.* 2012). The local dispersal of clonal propagules of epiphytic lichens contributes to clustering at the host tree level (due to establishment abilities) being less efficient than propagules able to a long-distance dispersal, with the exception of when biotic and abiotic factors contribute to their spread over long distances (Solé *et al.* 2004; Werth *et al.* 2006; Werth 2010; Otálora *et al.* 2011; Hilmo *et al.* 2012; Belinchón *et al.* 2015, 2018). Moreover, sexual propagules are important for the genetic diversity of populations (Belinchón *et al.* 2018) due to their ability to disperse long distances and their high capacity to withstand to variations in environmental conditions (Solé *et al.* 2004; Werth *et al.* 2006; Werth 2010; Otálora *et al.* 2011; Hilmo *et al.* 2012; Belinchón *et al.* 2015, 2018).

The main objective of this study was to review studies of genetic diversity of epiphytic lichens conducted in connected and fragmented forests at different spatial scales which include the drivers that have an imminent impact on the genetic diversity of epiphytic lichens.

GENETIC VARIATION IN EPIPHYTIC LICHENS AT DIFFERENT SPATIAL SCALES IN THE CONTEXT OF CONNECTED AND FRAGMENTED FORESTED AREAS

Genetic diversity and structure of epiphytic lichens in connected and fragmented forests

Forest connectivity and habitat quality provide important support for the population genetics of epiphytic lichens (Scheidegger & Werth 2009; Belinchón *et al.* 2018), while forest fragmentation affects the area of woody habitats and leads to an increasing number of isolated epiphytic lichen populations being subjected to genetic drift, which induces a sharp decline in genetic diversity (Otálora *et al.* 2011; Hilmo *et al.* 2012). Consequently, the destruction of woodlands leads to local extinction of epiphytic lichen populations because the habitat is destroyed (Hilmo *et al.* 2012). The survival of populations of epiphytic lichens in forests requires forest dynamics operating on different forest stands, where a suitable amount of epiphyte habitat is present continuously (Hilmo *et al.* 2012). Surprisingly, even throughout intensively logged forest areas, genetic diversity is well represented due to the better spatial distribution of epiphytic lichen populations (Werth *et al.* 2006). This could be explained by the contributions of sexual and asexual reproduction, which counteract genetic drift (Otálora *et al.* 2011). Additionally, this situation could also be explained by the interaction of genetic and ecological processes; for instance, the high genetic diversity of epiphytic lichen populations is supported by the availability of their habitat (especially available trees), and more importantly, immigrations over time have significant contributions to the increase in genetic diversity in epiphytic lichen populations (Werth *et al.* 2006). Furthermore, the

pattern of genetic diversity and structure of epiphytic lichens can be determined by geographical factors such as altitude, in cases where forests are not subjected to harsh human impacts (Nadyeina *et al.* 2014; Devkota *et al.* 2019). In the context of forest connectivity, epiphytic lichen populations capable of sexual reproduction can disperse over long distances and colonize other forest habitats (Singh *et al.* 2012).

The connectivity including lichen species habitats, climate gradient, and geographical aspect such as altitude induce genome differentiation in lichens (Rolshausen *et al.* 2023; Wong *et al.* 2024) which is accompanied and supported by reproductive mode and physiological mechanisms of lichens (Wong *et al.* 2024; Dal Grande *et al.* 2017). We analyse populations of two lichen symbioses, *Umbilicaria pustulata* (L.) Hoffm. and *Umbilicaria hispanica* (Frey) Davydov, Peršoh & Rambold, along an elevational gradient spanning 2100 altitudinal metres and covering three major biomes. Our study shows (i.e. Wong *et al.* 2024), which is accompanied and supported by the reproductive mode and physiological mechanisms of lichens (Dal Grande *et al.* 2017; Wong *et al.* 2024). In a study performed on *Umbilicaria phaea* Tuck. and *Umbilicaria pustulata* under different climatic conditions, genetic differentiation was supported by physiological mechanisms (cytoprotectant chemical compounds) and reproductive modes (asexual reproduction for *U. pustulata* and sexual reproduction for *U. phaea*), which ensure their adaptive capacity to climatic (especially harsh temperature) gradients (Wong *et al.* 2024). Lichen adaptation to harsh climatic conditions could involve the progressive loss of genes accompanied by the low selectivity of photobionts, which are highly evolutionarily important with respect to tolerance to different environmental conditions (Merges *et al.* 2023). Thus, these findings strongly support that forest connectivity not only is a simple driver of gene flow across distances between lichen populations but also represents complex environmental interactions involved in the distribution and resilience of lichens (Rolshausen *et al.* 2023; Wong *et al.* 2024).

The lichen symbionts underpin the distribution and resilience of symbiotic associations in forest habitats

The genetic composition of lichen thalli, represented by associated symbionts (fungal, algal, and bacterial components), is shaped by both abiotic (microenvironmental and macroenvironmental conditions) and biotic drivers (interactions among components of the lichen thallus), which determine adaptive responses in terms of geographical and climatic distributions (Rolshausen *et al.* 2023).

Photobiont diversity is an important attribute for lichen distribution and resilience under different environmental conditions (Saini *et al.* 2019; Pino-Bodas & Stenroos 2021; Berlinches de Gea *et al.* 2024) and enhances partnership strategies to cope with variations in environmental conditions by strengthening the relationship between photobiont and mycobiont (De Carolis *et al.* 2022). The availability and compatibility of photobionts are actively implied in the constitution of lichen holobionts, which are able to expand their habitat and cope with different environmental conditions at small and large spatial scales (Saini *et al.* 2019). In fragmented forests, photobiont pools may be affected by management measures and edge effects, which can lead to a low-selectivity process in terms of symbiotic associations due to the high similarity of photobionts (Berlinches de Gea *et al.* 2024). Additionally, the associations between photobionts and mycobionts in fragmented forests are influenced by growth forms and reproductive modes subjected to environmental conditions (Berlinches de Gea *et al.* 2024); furthermore, the specialisation and selectivity processes of mycobiont – photobiont associations are modulated by habitat quality and availability, which influence the local colonisation and wide dispersal of holobionts (De Carolis *et al.* 2022; Berlinches de Gea *et al.* 2024). Compared with lichens with asexual reproductive modes, which are more specialised highly reflected in both ecological and evolutionary processes, forest fragmentation determines a lower degree of specialisation in lichens with sexual reproductive modes (Blázquez *et al.* 2022; Berlinches de Gea *et al.* 2024).

Dispersal strategies supported by sexual and clonal means could shape the genetic structure and genetic diversity of *Lobaria pulmonaria* (L.) Hoffm. across various habitats characterised by different geographical and climatic conditions (Dal Grande *et al.* 2012; Otálora *et al.* 2015). Dispersal via the clonal reproductive mode retains the diversity of photobionts and increases the probability of holobiont habitat expansion (Onuţ-Brännström *et al.* 2018).

Landscape genetics of epiphytic lichen populations

Epiphytic lichens are successfully used in landscape genetics because they represent an important experimental model due to their occurrence on host tree islands, which are clumped within forest stands, and because the latter are integrated within forested landscapes (Belinchón *et al.* 2018). At the landscape level, the population genetics of symbiotic epiphytes, such as lichens, is strongly supported by population dynamics, which are influenced by core and fringe species – categorized according to dispersal mode (clonal dispersal in core species and spore dispersal in fringe species) which depend on each other due to the availability of compatible genotypes shared by core species and required by fringe species (Belinchón *et al.* 2015). Forest connectivity may lead to high genetic diversity of both core and fringe epiphytic lichen species due to their habitat quality (suitable environmental conditions and associated old trees), which has a significant effect on population dynamics across forest habitats (Otálora *et al.* 2011; Hilmo *et al.* 2012; Belinchón *et al.* 2018). In contrast, the reproduction mode of epiphytic lichens is affected by forest fragmentation, which, induces a decrease in genetic diversity and an increase in population differentiation (Otálora *et al.* 2011). The genetic diversity of epiphytic lichens is indeed influenced by reproductive mode (Belinchón *et al.* 2018). Epiphytic lichens with a clonal reproductive mode often exhibit high genetic structure (Walser *et al.* 2004; Scheidegger *et al.* 2012). Furthermore, lichens that undergo asexual reproduction contribute to genetic diversity through cryptic support based on occasional sexual

reproduction and somatic mutations within the genome of the clonal thallus (Belinchón *et al.* 2018).

The cryptic lineages of lichen symbionts can be structured along different environmental gradients as adaptive strategies necessary to expand the niche of symbiotic associations (Rolshausen *et al.* 2018, 2020). Furthermore, cryptic lineages can show greater genetic differentiation in terms of both generalists and specialists (Rolshausen *et al.* 2018). Remnant forests characterised by long-term continuity with adequate microhabitats and microclimates are microrefugia for specialised mycobiont and photobiont lineages (Singh *et al.* 2019). The interaction between highly specialised mycobiont-photobiont lineages can be significantly shifted by environmental gradients, which are implied in their survival and movement (Dal Grande *et al.* 2018; Kosecka *et al.* 2021) across environmentally structured niches, highlighting that connectivity means more than contiguous forest habitats at broad spatial scales (Rolshausen *et al.* 2018).

Regional genetic structure of epiphytic lichen populations

The genetic diversity and structure of epiphytic lichens combined with their ecology and biogeography at larger spatial scales are highly important in the global biogeographical context (Del-Prado *et al.* 2016). The genetic diversity of epiphytic lichens could represent an evolutionary adaptation to land history in response to important environmental drivers (Walser *et al.* 2004; Belinchón *et al.* 2018). Thus, at the regional scale, the genetic variation in epiphytic lichens could be attributed to postglacial events related to geographical refugia represented by vast natural forest habitats (Scheidegger *et al.* 2012; Allen *et al.* 2021). Due to the long persistence on phorophytes, forest fragmentation effects may be reflected in the genetic diversity of epiphytic lichens (Werth *et al.* 2006). Sometimes, the genetic diversity of epiphytic lichen communities within fragmented forests could be high despite the effect of genetic drift, which may not yet have come into play due to the longevity of lichens (Otálora *et al.* 2011). Bottlenecks and geographical isolation of ancient habitats may lead to low genetic diversity over time and a significantly differentiated genetic structure of epiphytic lichens represented by small populations (Walser *et al.* 2004; Werth 2010). However, there are geographical areas with high genetic diversity even in recently fragmented forests (Otálora *et al.* 2011; Hilmo *et al.* 2012). Species can disperse over large distances with small propagules like ascospores (Ronnås *et al.* 2017) and if long-distance dispersal is common, populations of the respective species may exhibit panmixia. Panmixia over large geographic scales has indeed been found in a predominantly sexually reproducing lichen (Alors *et al.* 2017). Comparatively heavy propagules like soredia, on the other hand, disperse over shorter distances than ascospores (Ronnås *et al.* 2017) which can be reflected in spatial autocorrelation in genotypes (Wagner *et al.* 2005; Werth *et al.* 2006). The genetic structure at large geographical scale is related to evolutionary processes (glacial and postglacial events) and ecological conditions (Werth 2010; Widmer *et al.* 2012; Allen *et al.* 2021).

In the temporal context of adaptation, it is generally recognized that lichens often have slow growth rates (Spribille *et al.* 2022) and long generation times (Hämäläinen & Fahrig 2024) and are able to cope with climatic changes due to their adaptation to the environmental conditions of new habitats (Søchting 2004; Aptroot & van Herk 2007; Aptroot 2009). Otherwise, the climatic native niche could be unique for distinct lichen genotypes and therefore cannot track rapid climatic changes by dispersing to new habitats (Williams *et al.* 2017).

The cryptic pattern of lichens is widely reflected in their adaptation to environmental gradients, which is strongly supported by genetic markers, as described in a few selected articles as follows:

1) single Nucleotide Polymorphisms (SNPs), which may be involved in physiological adaptation to environmental conditions and reproductive mode (Dal Grande *et al.* 2017);

2) the second region of the Internal Transcribed Spacer (ITS2) of the ribosomal RNA of the photobiont and the fungal gene MCM7 (DNA minichromosome maintenance complex component 7), which confer adaptive genetic support for symbiotic associations to cope with different environmental conditions (Dal Grande *et al.* 2018);

3) the nuclear ITS of the ribosomal DNA is used as a genetic marker to explore the diversity of different lineages of photobionts associated with mycobionts under harsh environmental conditions, which support and enhance cryptic adaptation to expand their spatial distribution (De Carolis *et al.* 2022);

4) A complex of DNA genetic regions (nuclear ribosomal internal transcribed spacer, nuclear large subunit region, the largest subunit of RNA polymerase II, and the mitochondrial small subunit) was used to infer mycobiont phylogeny. Moreover, the second part of the internal transcribed spacers was used to identify the community composition of the photobiont. This complex of genetic markers reveals a cryptic pattern of lichen genetic diversity, which supports complex interactions between the growth form and reproductive mode of lichens within their habitats; furthermore, the genetic markers mentioned above increase the symbiotic association capacity to cope with environmental changes and the effects of forest fragmentation (Berlinches de Gea *et al.* 2024);

5) lichen species with multiple symbionts could highlight structured adaptive genotypes developed under environmental conditions supported by SNPs for fungal components, the ITS2 spacer of ribosomal RNA for photobionts, and the 16S ribosomal RNA gene for bacteria; in addition, genetic markers of lichen symbionts support their cryptic distribution pattern, which is clearly reflected in survival and movement strategies across a range of habitats with distinct environmental conditions (Rolshausen *et al.* 2023);

6) the genetic diversity of the mycobiont assessed by the ITS of ribosomal DNA (rDNA) and the genetic diversity of the photobiont assessed through the ITS of rDNA and the actin type I gene represent a genetic complex that highlights adaptive strategies to local and global environmental conditions of different species included in the *Cladonia* genus (Pino-Bodas & Stenroos 2021);

7) the Internal Transcribed Spacer of rDNA was used to highlight adaptive genotypes of both mycobionts and photobionts to various microhabitats and macrohabitats subjected to different forest management regimes (protected stands, managed stands, and disturbed stands) within Białowieża Forest (Poland). The diversity of the cryptic pattern was highly supported by photobionts associated with mycobionts within all types of forest management regimes (Singh *et al.* 2019);

8) microsatellites are adequate genetic markers used to highlight the genetic diversity and genetic structure of lichen populations influenced by climate, forest attributes (connectivity and microhabitat quality) and reproductive mode (Belinchón *et al.* 2018). Microsatellite markers have also been successfully used to highlight the importance of old-growth forests, which support a high diversity of cryptic lineages of *Lobaria pulmonaria* compared with managed forest habitats (Scheidegger *et al.* 2012).

Highly adapted cryptic lineages of a new photobiont to a wide range of environmental conditions strengthens the symbiotic associations across its spatial distribution with different microclimate conditions (Pino-Bodas & Stenroos 2021).

GLOBAL THREATS WITH AN IMMINENT IMPACT ON THE GENETIC VARIABILITY OF EPIPHYTIC LICHEN SPECIES

Genetic diversity of epiphytic lichen species in the global warming context

Forests worldwide are actively being used to mitigate greenhouse gases due to their capacity to store carbon (Blattert *et al.* 2023). The impact of global warming is critically amplified by different anthropogenic activities, which are reflected in the reduction of the genetic diversity of epiphytic lichens (Aptroot & van Herk 2007; Ralimanana *et al.* 2022). Thus, sensitive species, such as lichens, are among the most threatened species (Ralimanana *et al.* 2022). If they are able to adapt to changed environmental conditions, lichens could counteract the harmful effects of global warming and conserve their genetic diversity; however, global warming induces a large edge effect at the biosphere level that could cause major extinction of lichens adapted to lower temperatures and cause sensitive species to migrate towards the boreal and austral hemispheres (Parmesan & Yohe 2003; Aptroot & van Herk 2007). The pattern of species distribution across local populations and at the landscape, regional, continental, and global scales is now critically affected by global warming and the reduction of their wild habitats, which had been well conserved for millennia (Parmesan & Yohe 2003; Antonelli *et al.* 2022). Furthermore, global warming removes climatic barriers between biogeographical realms and forces lichens adapted to cold climate to migrate towards their survival limits (Aptroot & van Herk 2007).

Natural selection is the fundamental process through which strongly adapted individuals endowed with significant genotypic variability are able to cope with major changes in the environment and climate (Callaghan *et al.* 2004; Ewens 2013). Lichens are of special interest because of their wide latitudinal and altitudinal distribution (Parmesan & Yohe 2003; Callaghan *et al.* 2004; Leavitt *et al.* 2014). Lichen species adapted to xeric environmental conditions are being induced by global warming to migrate northwards, and high altitudes are being successfully used as refugia by cold-adapted species due to niche availability (Parmesan & Yohe 2003; Callaghan *et al.* 2004; Leavitt *et al.* 2014). The altitude and latitude gradients include diverse millennial wild habitats and specific environmental conditions that support different genetic patterns of lichen species (Semenova *et al.* 2015; Medeiros *et al.* 2021). Therefore, strategies for the conservation of the complexity of wild habitats under the impact of global warming should be applied by considering genetic diversity as one of the important biological attributes recognized by the International Union for Conservation of Nature (Galetti 2018).

The warming of the climate in cold areas of the Earth affects different ecosystem services, especially food chains, at diverse hierarchical levels (Semenova *et al.* 2015). It is well recognized that the genetic variability of lichens improves their response to changing environmental conditions (Singh *et al.* 2014), but the increasing impact of global warming on genetic variability leads to their retrenchment and limits the ability of lichens to provide resources in the context of ecosystem services (Semenova *et al.* 2015).

The genetic structure of lichens across their spatial distribution could be shaped by habitat fragmentation (Berlinches de Gea *et al.* 2024), which is related to variations in climatic factors, especially temperature and precipitation (Núñez-Zapata *et al.* 2015; Oh *et al.* 2019; Moya *et al.* 2021).

In the phylogeographic context, the range of symbiotic associations could be shaped by an evolutionary pattern of adaptive divergence, whereas in the population and species context, environmental drivers shape the range of compatible photobiont pools towards the mycobiont (Rolshausen *et al.* 2018). The different preferences of diverse lineages of photobionts across a large geographic scale are structured by environmental and climate conditions and represent different spatial pools of compatible photobionts available for association with mycobiont (Rolshausen *et al.* 2018). The ecological resilience of lichens across fragmented habitats could be enhanced by the adoption of various adaptation strategies to cope with local extinction and to expand their geographical distribution across available dispersal corridors (Berlinches de Gea *et al.* 2024). The cryptic adaptation of lichens to the environment and climate change has significant implications for habitat conservation strategies, which implies effective measures for vulnerable lichen species (Núñez-Zapata *et al.* 2015; Rolshausen *et al.* 2018; Lagostina *et al.* 2021; Berlinches de Gea *et al.* 2024).

Genetic diversity of epiphytic lichen species in the forest management context

Ancient forests are recognized as valuable heritage sites for their associated lichen species (Werth *et al.* 2006). Management practices such as stand-replacing logging lead to the loss of suitable microhabitats for lichens represented by century-

old trees (Werth *et al.* 2006). Forest management that does not take into account the spatial configuration of trees and does not retain at least some old trees negatively affects the genetic diversity of lichen populations (Scheidegger *et al.* 2012); therefore, for their conservation, it is recommended that old trees be retained as preferred microhabitats for lichens and that adequate management measures be implemented for forest stands (Zoller *et al.* 1999; Scheidegger *et al.* 2012). Forest management, especially fragmentation, enhances genetic drift and leads to low genetic diversity (Scheidegger *et al.* 2012). Furthermore, low genetic diversity in managed forests compared to non-managed forests reflects predominantly clonal reproduction (Scheidegger *et al.* 2012). Within strongly disturbed forests, immigration and the dispersal of vegetative propagules are important drivers that could influence genetic diversity, especially if there is a great availability of nearby sources of propagules (Werth *et al.* 2006).

Conservation measures implemented for managed forests are based on the retention of old trees across a large forest area, and such trees are needed to decrease the distance between host trees of lichens, enabling lichen dispersal from tree to tree (Scheidegger *et al.* 2012). Furthermore, management practices affect the genetic diversity of lichen populations over time and may cause their local extinction, especially if the pool of locally available propagules is small (Werth *et al.* 2006).

A large distance between host trees of lichens generally leads to reduced gene flow followed by reduced genetic diversity at the tree level (Scheidegger *et al.* 2012). Furthermore, genetic drift reduces allelic richness, and over time, small epiphytic lichen populations may go extinct because they are more likely to be maladapted and not be able to evolve to changed conditions or be affected by catastrophic events (Frankham 1995; Werth *et al.* 2006).

The genetic diversity of epiphytic lichen species depends on their population size in the context of current environmental changes to ensure long-term survival (Zoller *et al.* 1999; Singh *et al.* 2012). Adequate resolution requires forest management to be performed so that forest dwelling species are not affected and to achieve long-term restoration or regeneration of forest habitats (Angelstam *et al.* 2018).

INTERACTION BETWEEN LICHENS AND DISPERSAL VECTORS IN A BROADER CONNECTIVITY CONTEXT

The biotic vectors involved in the dispersal of epiphytic lichen propagules could include hymenopteran insects, dipteran insects, and insectivorous birds, which are more effective in ancient forest habitats due to the availability of microhabitats (Ronnås *et al.* 2017). Ants have a significant effect on epiphytic lichen dispersal, favouring lichens with clonal reproduction by the transport of vegetative propagules during movement across forest habitats (Di Nuzzo *et al.* 2022). Woodpeckers are dispersal vectors for lichen propagules (soredia and ascospores) and free-living green photobionts and could contribute to the dispersal of lichen propagules over large spatial scales through their migratory patterns (Johansson *et al.* 2021). Endozoochory mediated by gastropods is another important dispersal vector of lichen propagules that facilitates lichen establishment within local populations (Boch *et al.* 2011).

Lichen thallus components can be dispersed over long distances by wind and birds at the intercontinental scale, which has significant implications for phylogenetic studies (Lebreton *et al.* 2025). Components of lichen thalli, such as photobionts, can be transported by wind, rain, and insects (Sanders & Masumoto 2021). Additionally, lichen propagules can be dispersed by wind to enhance and diversify their habitats (Keepers *et al.* 2019). Otherwise, the dispersal of lichens within aquatic habitats could be performed by wind and the flow of water (Doering *et al.* 2020).

The dispersal of lichen propagules by different vectors has significant importance for species conservation in disturbed habitats (Johansson *et al.* 2021; Lagostina *et al.* 2021). At the microscale level, tree bark is an important driver that can interact with local climate (temperature, air humidity, and wind) and environmental factors (tree and forest variables) and can facilitate epiphytic lichen establishment on trees (Nunes *et al.* 2019). Interactions between the dispersal vectors of lichens and climate involve a complex network that provides a significant support to expand their distribution into new habitats (Sork & Werth 2014; Lebreton *et al.* 2025).

NOVEL TECHNOLOGIES APPROACHED IN A WIDER CONTEXT OF ENVIRONMENTAL CONNECTIVITY, CONSERVATION AND MANAGEMENT OF FOREST HABITATS

Metagenomics is a successful genetic approach because it allows sequencing of symbionts represented by bacteria, cyanobacteria, green algae, protists, and other lichen-forming fungi considered "co-mycobionts" and invertebrates at lower taxonomic levels (Graham *et al.* 2018). Metagenomics is widely used to identify and highlight symbiotic lineage components in lichens such as fungi, algae, nonphotosynthetic (Smith *et al.* 2020) and photosynthetic bacterial lineages (Tagirdzhanova *et al.* 2024), and virus genotypes assessed within the bacterial and algal components of lichen thalli (Merges *et al.* 2021).

Metagenomics is a useful tool for exploring holobiont components to identify genes involved in metabolic activities (Graham *et al.* 2018; Puvar *et al.* 2020; Vecherskii *et al.* 2022). Thus, metagenomic studies on lichen intrathalline components such as bacteria have revealed their role in symbiosis to provide vitamins and minerals and their capacity in increase tolerance to environmental variations (Graham *et al.* 2018; Puvar *et al.* 2020). Additionally, metagenomics has revealed the tolerance of lichens to different climate conditions through variations in protein kinases across an elevation gradient (Merges *et al.* 2023). The resilience of lichens in diverse habitats with different environmental conditions is enhanced by metabolic interactions, which provide cryptic support for lichens to cope with environmental pressures (Puvar *et al.* 2020; Merges *et al.* 2023).

In the context of lichen diversity, metagenomics is better at identifying more lichen species than other inventory methods across habitats on the basis of their propagules via whole-genome shotgun sequencing (Keepers *et al.* 2019). Furthermore, metagenomics, which is based on whole-genome shotgun sequencing, is an adequate genetic tool for exploring the environmental drivers of species distribution, where habitat conservation and habitat restoration is concerned, as well as for the development and improvement of conservation policies that safeguard lichen habitats (Keepers *et al.* 2019).

In addition, eDNA metabarcoding is a suitable tool for surveying lichen diversity in forest habitats, which could be shaped as traditional surveys by changes in climate and forest management (Dreyling *et al.* 2024).

Metagenomics has clearly demonstrated that lichens are microhabitats for multiple symbionts with important roles to their survival and for inferring evolutionary processes (Graham *et al.* 2018).

Assisted migration is an effective conservation action applied to avoid species extinction in extreme cases (IUCN/SSC 2013) and assumes that all the environmental conditions of a species range are provided and maintained over a long period of time (Brooker *et al.* 2018; McMullin *et al.* 2019). A study performed on *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell over five years in the Cairngorm Mountains of Scotland (United Kingdom) indicated that the transplanted samples were influenced by climate and environmental drivers (Brooker *et al.* 2018). Lichen species are shaped by climate; therefore, assisted migration is highly important in the context of climate change and conservation because climate has an important effect on lichen survival, especially at the limits of species ranges such as arctic and alpine lichen species (Brooker *et al.* 2018). Furthermore, epiphytic lichens are dependent on their forest habitats; therefore, assisted migration should be performed by the translocation or identification of suitable trees at sites similar to their natural habitats (Grady *et al.* 2015; McMullin *et al.* 2019). In a global approach to lichen migration under current climate change conditions, the dispersal ability of lichen species indicates lower values of natural migration rates to appropriate new habitats; therefore, assisted migration represents an important tool to maintain lichens in future suitable habitats (Mallen-Cooper *et al.* 2023).

Remote sensing techniques are used to map land covered with lichens and can be used to locate and conserve their microrefugia (Casanovas *et al.* 2015) in the context of climate change and forest management (Waser *et al.* 2004; Palmroos *et al.* 2023).

CONSERVATION GENETICS IN THE CONTEXT OF FOREST CONNECTIVITY TO PREDICT THE RISK OF POPULATION AND SPECIES EXTINCTIONS

Conservation genetics is becoming increasingly important because habitat connectivity is reduced or lost over time which strongly affects genetic diversity and the adaptive potential of populations (Ledig 1992; Otálora *et al.* 2011). Conservation genetics relies primarily on policy actions that contribute to enhancing genetic diversity, particularly to avoid species extinctions (Frankham 2019); therefore, the International Union for Conservation of Nature recognizes genetic diversity as one of the hierarchical levels of biodiversity (Galetti 2018). Additionally, long-term assurance of habitat connectivity is an important management measure that is directly involved in enhancing the genetic diversity of epiphytic lichens (Belinchón *et al.* 2018). Conservation genetics approaches in fragmented forest landscapes have focused mainly on the dispersal of epiphytic lichen propagules (Werth 2010; Belinchón *et al.* 2018). Thus, the dispersal ability of lichens within fragmented habitats is important for their survival because it contributes to genetic diversity, which enhances the adaptive capacity and genotypic diversity (Walser *et al.* 2004; Werth 2010; Hilmo *et al.* 2012). Old-growth forests and non-managed forests are important because they support high genetic diversity (Scheidegger *et al.* 2012). Generally, within old-growth forests, the genetic diversity of lichen populations is greater than the genetic diversity within managed forests, which is rather low due to the altered environment (Walser *et al.* 2004; Scheidegger *et al.* 2012). In the context of epiphytic lichen reproduction, asexually reproducing lichen populations are sensitive to changes in forest management because no new genetic combinations arise from sexuality; asexually reproducing lichen populations are nevertheless locally important in the context of conservation (Singh *et al.* 2012). Furthermore, sexual reproduction is related to high genetic variability; therefore, this reproductive mechanism of epiphytic lichens is important both in the context of evolutionary potential and as an important criterion within international conservation programs (Zoller *et al.* 1999; Singh *et al.* 2012). Conservation strategies to preserve epiphytic lichens should moreover consider that heterothallic species of lichen-forming fungi need both mating types in a population for sexual reproduction to occur (Singh *et al.* 2012). This would increase the adaptive potential of the population (Singh *et al.* 2012). So, when designing conservation programmes, homothallism and heterothallism should be taken into account, so that the extinction of populations can be prevented when environmental conditions are critically modified (Singh *et al.* 2012).

CONCLUSIONS

Genetic variation ensures the capacity of lichen species to survive and reproduce in their forested habitats; therefore, forest connectivity is important for lichens because it helps the long-term survival of lichen populations with their genetic heritage. The conservation of genetic variation in epiphytic lichen populations requires adequate forest management and a reduced socioeconomic impact on forested landscapes at different spatial scales. A broader approach to connectivity at different spatial scales includes not only continuous forest cover itself but also different climate niches, ecological

interactions, anthropogenic pressure, and dispersal vectors, which highly affect the genetic complexity of lichens.

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