INTRODUCTION

The lichen symbiosis is one of the main life forms among fungi with 17% of the 110,000 described fungal species forming mutualistic relationships with eukaryotic algae or cyanobacteria (Lücking & Leavitt, 2016). This high number of lichenised fungi (mycobionts) highlights the ecological and evolutionary importance for fungi to form composite associations with autotrophs, so-called photobionts (Nash, 2008). Eukaryotic, unicellular trebouxioid green algae, that is species of the Trebouxiophyceae such as Trebouxiaceae and Coccomyxaceae, represent by far the largest proportion of photobionts, with approx. 70% of lichens (Rambold et al., 2001). The remaining proportions are represented by filamentous, trentepohlialean green algae (i.e. species of the Trentepohliales) with about 20% and prokaryotic cyanobacteria with about 8%–10% (Friedl & Büdel, 2008; Rambold et al., 2001; Zachariah & Varghese, 2018).

Photo- and mycobionts unequally depend on each other. The extracellularly located photobionts supply the heterotrophic mycobionts with photosynthetic carbon (Nash, 2008) but are sensitive to UV radiation, which can harm the algal photosystem and, thus, the entire symbiosis (Voytsekhovich & Kashevarov, 2010). Several studies proposed the type of photobiont to be important for the environmental response and spatial distribution of lichens (Aptroot & van Herk, 2007; Marini et al., 2011; Matos et al., 2015). Lichenised trebouxioid and trentepohlialean green algae not only show differences in their chemical properties of key metabolites determine the global distribution of lichens

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Abstract

In lichen symbioses, fungal secondary metabolites provide UV protection on which lichen algae such as trebouxiophycean green algae—the most prominent group of photobionts in lichen symbioses—sensitively depend. These metabolites differ in their UV absorbance capability and solvability, and thus vary in their propensity of being leached from the lichen body in humid and warm environments, with still unknown implications for the global distribution of lichens. In this study covering more than 10,000 lichenised fungal species, we show that the occurrence of fungal-derived metabolites in combination with their UV absorbance capability and their probability of being leached in warm and humid environments are important evolutionary drivers of global lichen distribution. Fungal-derived UV protection seems to represent an indirect environmental adaptation in which the lichen fungus invests to protect the trebouxiophycean photobiont from high UV radiation in warm and humid climates and, by doing this, secures its carbon source.

KEYWORDS
fungal secondary metabolite evolution, global trait distribution, indirect environmental adaptation, lichen symbiosis, macrophysiology

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UV protection but also in their global, latitudinal distribution. Trentepohlialean green algae show high abundance in tropical areas which decreases towards higher latitudes (Ahmadjian, 1967; Øvstedal & Smith, 2001; Tucker et al., 1991). They show active UV protection by producing chloroplast membrane-bound pigments such as β-carotene and haematochrome, which absorb UV radiation and thereby shield the photobiont (Iskandar & Syers, 2006; López-Bautista et al., 2002; Takei, 2005; Thompson & Wujek, 1997). Trentepohlialean green algae, which show a low abundance in the tropics that increases towards higher latitudes, lack such capabilities and mainly rely on passive UV protection provided by fungal-derived secondary metabolites, so-called ‘lichen substances’ and their metal complexes, which are deposited in the cortical and medullary layers of the lichen body (thallus) (Nguyen et al., 2013; Peksa & Škaloud, 2011; Solhaug & Gauslaa, 2012; Solhaug et al., 2003).

Lichen substances differ in their capability to absorb UV radiation and in their water solubility (Huneck & Yoshimura, 1996). They consequently do not only vary in their potential to provide UV protection to the photobiont, but also in their propensity for being leached from the lichen body by high precipitation and temperatures—climatic conditions typical for tropical regions. This is in contrast to the UV protective, mainly insoluble and intracellularly deposited pigments synthesised by trentepohlialean green algae (such as β-carotene) or by the mycobiont (such as melanin, Mafole et al., 2019). Consequently, a close relationship can be assumed between the chemical properties of lichen substances, the environmental conditions that influence their leaching and, thus, their occurrence probability and the global, latitudinal distribution of photobionts, which sensitively depend on the UV absorbance of these secondary metabolites. More specifically, high UV radiation might increase the importance of lichen substances for UV protection and, thus, promote their synthesis as shown for example for parietin in the genus Xanthoria (Gauslaa & Ustvedt, 2003). The role of UV protection by lichen substances (anthraquinones) for the occupation of high irradiation locations is furthermore emphasised by Gaya et al. (2015) for lichen-forming Teloschistaceae, which are exclusively associated with trebouxiod green algae. Environmental conditions that favour the leaching of lichen substances (i.e. high precipitation and temperatures) are likely to reduce the occurrence probability of these metabolites, which in turn might reduce the occurrence probability of photobionts in lichen symbioses that sensitively depend on these substances for UV protection (i.e. trebouxiod algae).

Causal relationships between the chemical characteristics of UV protective lichen metabolites, the physiological requirements of lichen symbioses and their global distribution can be deduced from recent studies on macroevolution and diversification of lichens (Gaya et al., 2015; Nelsen et al., 2020; Singh et al., 2021). However, such relationships have been never tested and the environmental requirements of lichenised photobionts have been only occasionally studied at regional scale (Ellis & Coppins, 2007; Nascimbene & Marini, 2015; Peksa & Škaloud, 2011). In this study, we investigate how the occurrence of globally abundant lichen substances modify the global, latitudinal distribution of lichen symbioses with trebouxoid algae. Our main hypotheses are (1) that the occurrence probability of lichenised Trebouxiothyceae decreases with warmer and more humid climates due to their sensitive dependence on lichen substances and their solubility and (2) that the occurrence probability of lichen substances increases with increasing UV-B radiation but decreases in environments that favour the leaching of these substances (see Figure 1 for the full set of hypotheses). We furthermore hypothesise a significant effect of the mycobiont phylogenetic relatedness on the relationship between the latitudinal distribution of lichens with trebouxoid algae and the UV absorbance / solvability of associated lichen substances.

To test our hypotheses, we combine global distribution information of lichens with information on symbiotic photo- and mycobionts and the chemical properties of related lichen substances (i.e. solvability and UV-absorbance). We furthermore included information on the phylogenetic history of lichenised Lecanoromycetes as the predominant group of host fungi of lichenised Trebouxiothyceae. We focus on trebouxiod algae because close links between the environment, lichen chemistry and global distribution have to be expected. We furthermore included trentepohlialean lichens as a control group, which do not sensitively depend on the UV protection by lichen substances and should therefore not show such close or contrasting dependencies as discussed above. In this study, we focussed on ultraviolet-B (UV-B) radiation (wavelengths of 280–315 nm) because strong evidence exists for adverse effects of UV-B radiation on the physiology, distribution and population dynamics of numerous organisms including lichens (Gaya et al. 2015; Gauslaa & Ustvedt, 2003; Voytsekhovich & Kashevarov, 2010; Beckmann et al., 2014).

**MATERIAL AND METHODS**

**Data**

We combined information on the global occurrence of 10,114 lichen fungal species and their associated photobionts and lichen substances with environmental information on UV-B radiation and the environmental dissolution potential. Global distribution information was retrieved from the Global Biodiversity Information Facility (GBIF) platform using the rgbif package (v.3.3.0; Chamberlain et al., 2021; references see Supporting Information). Data on lichen photobionts and associated
lichen substances were retrieved from the LIAS light trait database (Rambold et al., 2014). LIAS light covers all classes of ascomycota for which lichenised fungi are known. Taxonomic data (lichen names, synonyms and classification) are based on LIAS names (Triebel & Bensch, 2005) and the GBIF Backbone Taxonomy (GBIF Secretary, 2021) by following taxonomic concepts as currently accepted by lichenologists (e.g. http://www.speciesfungorum.org/; Wijayawardene et al., 2020). Information on the lichen substances was obtained from the LIAS metabolites database (Elix et al., 2012). The chemical structures of the lichen substances were compiled from Huneck and Yoshimura (1996) and references therein, were manually redrawn and transferred into SMILES line notation using ChemDraw Professional (v. 19.1).

The UV-B absorbance and solvability of the lichen substances were derived from the UV-Vis spectra and the solvation energy of the respective substance. Solvability is here defined as the negative solvation energy (kcal/mol) of a respective substance and provides a good proxy for the water solubility of this substance. Increasing solvability values correspond with decreasing (more negative) solvation energy, thus increasing water solubility. UV-B absorbance of the lichen substances was calculated as the integral of the compound-specific absorbance (UV-Vis) spectra estimated for wavelengths ranging between 280 and 315 nm.

The lichen substances of UV-Vis spectra and the solvation energy were quantified with a quantum chemical approach using the software Orca (v. 4.2.1; Neese, 2012, 2018). The 3D coordinates of the uncharged molecules were generated from SMILES using OpenBabel (O’Boyle et al., 2011). These geometries were pre-optimised using the functional BP86 with the def2-SVP basis set and afterwards optimised using B3LYP and the def2-TZVP basis set. Substance-specific absorption spectra were calculated by using time-dependent density functional theory (B3LYP; def2-TZVP) in the range of 12,500 to 50,000 cm\(^{-1}\) using Gaussians with widths of 500 cm\(^{-1}\). The solvation energy (kcal/mol) was calculated using B3LYP (def2-TZVP) in a continuum water as solvent using a conductor-like polarisable continuum model (CPCM) with default settings.

Data on mean annual UV-B radiation (J m\(^{-2}\) d\(^{-1}\)) were extracted from a global data set on UV-B radiation (gIUV; v.1.0; spatial resolution of 15 arc-minutes; Beckmann et al., 2014). To quantify the dissolution

**FIGURE 1** Hypothesised relationships between environmental conditions (UV radiation and environmental dissolution potential), chemical properties of lichen substances (i.e. solvability and UV-B absorbance) and the occurrence probability of these metabolites and the global distribution of lichenised trebouxiophycean green algae. Red, dashed lines indicate cases of hypothesised negative relationships while solid, black lines indicate hypothesised positive relationships. Grey lines indicate cases where we have no specific hypotheses about the direction of relationship.
potential of the environment as the probability for soluble substances to be leached from the lichen body we developed an index based on standard climatic variables, that is mean annual temperature * log (annual precipitation sum) at a given location. Spatial information on mean annual temperature and annual precipitation sum was extracted from the CHELSA bioclim data set (biol and bio12; v.1.2; spatial resolution of 30 arc-seconds; Karger et al., 2017, 2018).

Analyses

For analyses, we used global occurrence data and trait information of lichen fungal species co-occurring in grid cells with a spatial extent per grid cell of 1°. For each grid cell, we calculated the probability of occurrence for the two groups of photobionts as the sum of lichen fungal species associated with the respective photobionts divided by the total number of species occurring in the respective grid cell. We quantified mean UV-B absorbance and mean solvability of occurring lichen substances per grid cell based on the compound-specific values of each variable weight by the abundance of each lichen substance for the respective set of co-occurring lichen fungal species. We furthermore calculated the occurrence probability of lichen substances as the number of species in a grid cell with the respective lichen substance divided by the total number of species per grid cell. Besides this grid cell-based approach, we calculated species-specific mean UV-B absorbance and solvability for the two groups of photobionts as the arithmetic mean of the UV-B absorbance and solvability values of the lichen substances associated with the respective lichen fungal species.

All calculations were based on the 100 globally most abundant lichen substances. This threshold was chosen because of a clearly visible breakpoint in the number of global occurrences between the 100 most common and remaining metabolites (Figure S1). However, globally less abundant lichen substances, which we did not include in our analyses might deviate in their characteristics and might be more important for lichen occurrence at local scales. We did not differentiate between cortical and medullary lichen substances because the photobionts are predominantly located in the upper part of the medullary layer of the lichen body and hyphae in between the surface and this algal layer are often encrusted by lichen substances.

Differences in the average number and chemical properties of lichen substances between trebouxiod and trentepohlianean lichen fungal species were tested with parametric, two-sample t-tests. Latitudinal patterns in the occurrence probability of photobionts and the UV-B absorbance and solvability of the associated lichen substances were based on raw latitudinal values (−90° to 90°) and were analysed with Generalised Additive Models (GAMs) with integrated smoothness estimation using the gam() command of the mgcv R package (v.1.8-33; Wood, 2004). The optimal degrees of freedoms used for the smoothing spline interpolation were selected based on penalised regression splines. The same statistical approach was chosen to describe and test individual relationships between environmental conditions, the chemical characteristics and occurrence of lichen substances and the global distribution of lichenised green algae described in Figure 1.

Due to a spatial overrepresentation of lichen occurrence records for the northern mid-latitudes, the entire set of spatial co-occurrences was thinned before analysis. We therefore divided the entire data set into latitudinal bins of 1° width. From each bin, we randomly drew one grid cell with its co-occurring lichen fungal species, which resulted in a spatially balanced, subsampled co-occurrence data set. This subsampled data set was subsequently used for model estimations. This procedure was repeated 1000 times.

We used structural equation modelling to test the hypothesised network of direct and indirect relationships between the abiotic environment, the occurrence probability and chemical properties of lichen substances and the occurrence probability of the respective group of photobionts described in Figure 1. We applied non-spatial structural equation models by using the sem()-command implemented in the lavaan R package (v. 0.2.2; Rosseel, 2012). We furthermore applied spatially explicit structural equation models to account for spatial information in the analysed data set by using the sesem R package (Lamb et al., 2014). This method is based on the analysis of variance/covariance matrices calculated across a range of lag distances and thereby provides readily interpretable information of the change in path coefficients across spatial scale. To avoid distorting effects of spatially imbalanced sampling effort we applied the same random subsampling procedure as used for the GAM modelling approach with 100 repetitions. The change in path coefficients with increasing lag distances from these 100 repetitions was tested with GAMs. To account for the effect of host fungi phylogenetic relatedness, we calculated the Net Relatedness Index (NRI) for each set of co-occurring trebouxiophycean lichen fungal species using the ses.mpdl()-command of the picante R package (v. 1.8.2; Kembel et al., 2010) and included this as an additional predictor in the structural equation model. We performed this analysis based on a time-scaled ML phylogeny of lichenised Lecanoromycetes provided by Nelsen et al. (2020) and a reduced set of 1038 lichen fungal species present in the phylogeny and our trait data set. This resulted in a paraphyletic assemblage of lichenised Lecanoromycetes associated with trebouxiophycean algae. We did not perform this analysis for trentepohlianean lichens because of their strong under-representation in the phylogenetic tree.
We applied phylogenetic generalised least squares (PGLS) models (Grafen & Hamilton, 1989; Martins & Hansen, 1997) implemented in the pgls()-command of the caper R package (v.1.0.1; Orme et al., 2018) to test the effect of mycobiont phylogeny on the relation between the chemical properties of lichen substances and the species-specific latitudinal occurrence maxima of trebouxio- phycean lichens, that is the absolute latitude at which a lichen fungal species was found most frequently. We ran 1000 PGLS models using the ML tree with tip values randomly shuffled for each model to remove the phylogenetic structure. We compared the predictive power of these 1000 models to the original model based on the original ML tree using multiple $R^2$ as a measure of model performance. We assumed a significant difference between the shuffled and original models when the $R^2$ values from the shuffled models did not overlap with the $R^2$ values originating from the original model (Schweiger et al., 2021).

All analyses were performed in R (R Core Team, 2021) with a level of significance of $\alpha = 0.05$.

RESULTS

Lichens with trebouxioid green algae dominate at higher latitudes but decrease in occurrence probability towards the tropics (Figure 2a; $R^2 = 0.109 \pm 0.055$ with $p = 6.035 \times 10^{-3} \pm 8.94 \times 10^{-4}$; median ± median absolute deviation from 1000 model runs; see Supporting Information Figure S2a and b for details on the model statistics). This is in contrast to lichens with trentepohlialean green algae, which show higher occurrence probability in the tropics which declines towards higher latitudes (Figure 2b; $R^2 = 0.157 \pm 0.064$ with $p = 2.654 \times 10^{-5} \pm 3.935 \times 10^{-5}$; Figure S2c and d). Both, environmental dissolution potential and mean annual UV-B radiation, show maximum values in the tropics and decrease towards higher latitudes (Figure 2c and d; $R^2 = 0.919 \pm 0.018$ with $p = 0$ and $R^2 = 0.943 \pm 0.014$ with $p = 0$ respectively; Figure S2e–h).

Trebouxiophycean lichens show higher numbers of lichen substances than trentepohlialean lichens (average of 1.7 vs. 0.5 substances per species; $t = 42.1$, df = 8259.9, $p < 2.2 \times 10^{-16}$; based on the 100 globally most dominant lichen substances). Substances associated with trebouxiophycean lichens show higher mean UV-B absorbance and lower solvability than lichen substances from trentepohlialean lichens ($t = 6.7$, df = 1025.7, $p$-value = $4.371 \times 10^{-11}$ and $t = -4.6$, df = 1114.4, $p$-value = $5.35 \times 10^{-6}$ respectively; Figure 3).

The occurrence probability of trebouxioid photobionts is positively linked to the occurrence probability of

FIGURE 2 Global latitudinal patterns of the occurrence probability of (a) lichenised Trebouxiophyceae and (b) lichenised Trentepohliales as well as (c) environmental dissolution potential and (d) global UV-B radiation. The solid lines indicate median model predictions of generalised additive models fitted to the data from 1000 model runs generated by a sub-sampling procedure to circumvent spatial inhomogeneity in the global occurrence data. For more details, see the Methods section.
lichen substances (standardised path coefficient = 0.41, \( p = 0 \); Figure 4). Environmental dissolution potential showed a strong negative effect on the occurrence probability of trebouxioid green algae (standardised path coefficient = −0.32, \( p = 0 \)). The occurrence probability of lichen substances increases with UV radiation but decreases with increasing dissolution potential (standardised path coefficient = −0.07 and −0.09 with \( p = 0.004 \) and 0.001 respectively). We observed negative effects of mean solvability of lichen substances and mean UV-B absorbance on the occurrence probability of trebouxioid green algae (standardised path coefficient = −0.03 and −0.06 with \( p = 0.07 \) and 0.001 respectively). We furthermore observed a direct, negative effect of environmental dissolution potential and a positive effect of UV-B radiation on the occurrence probability of trebouxioid green algae (standardised path coefficients = −0.32 and 0.06 with \( p = 0 \) and 0.001 respectively). The response shapes of the individual relationships between the tested environmental conditions, the chemical characteristics and occurrence of lichen substances and the global distribution of lichenised green algae are depicted in the Figure S3. Phylogenetic relatedness of the Lecanoromycetes host fungi associated with trebouxiophycean algae showed positive effects on the occurrence probability of lichen substances and lichenised trebouxioid green algae but negative effects on mean UV-B absorbance and mean solvability of the tested lichen substances (Figure S4).

The occurrence of lichenised Trentepohliales was negatively correlated with the occurrence probability of lichen substances (standardised path coefficient = −0.18, \( p = 0 \); Figure S5). Environmental dissolution potential showed a strong positive effect on the occurrence probability of trentepohlialean green algae (standardised path coefficient = 0.31, \( p = 0 \)). The effect of UV-B radiation and mean solvability of lichen substances on the photobionts occurrence probability was observed to be positive (standardised path coefficient = 0.06 and 0.03 with \( p = 0 \) and 0.09 respectively), whereas we detected no correlation between photobiont occurrence probability and mean UV-B absorbance of lichen substances (standardised path coefficient = −0.007, \( p = 0.62 \); Figure S5).

The effects of UV-B radiation and environmental dissolution potential as well as of the occurrence probability and mean UV-B absorbance of lichen substances on the occurrence probability of lichenised Trebouxiophyceae showed a significant spatial structure (Table S1). The same was true for the effects of UV-B radiation and the occurrence probability of lichen substances on mean UV-B absorbance of lichen substances and the effect of the environmental dissolution potential in the mean solvability of the lichen substances (see Supporting Information Table S1 and Figure S6). Comparable spatial structure was observed when accounting for the phylogenetic relatedness of the host fungi and for lichenised Trentepohliales (see Tables S2 and S3 as well as Figures S7 and S8).

We observed a significant relationship between the species-specific latitudinal occurrence maximum and the mean solvability of lichen substances, with minimum solvability for trebouxiophycean lichens with maximum occurrence in the tropics, but increasing solvability for lichens with the maximum occurrence at higher latitudes (\( p < 0.01 \); see Figure S9a). The same pattern was observed for the mean UV-B absorbance of lichen substances (\( p < 0.001 \); see Supporting Information Figure S9c). For both relationships, we observed a significant effect of mycobiont phylogeny (Figure S9c and d).

**DISCUSSION**

**Environmental and physiological drivers of global lichen distribution**

Previous studies have identified atmospheric water availability and solar radiation as important environmental drivers for the spatial distribution of lichen fungi and algae (Gaya et al., 2015; Peksa & Škaloud, 2011; Rindi et al., 2003). However, the link between environmental conditions and species occurrence is rarely direct but is usually mediated by physiological traits that enable species to occur under certain environmental conditions (Kearney & Porter, 2009). In this study, we demonstrate the relevance of physiologically induced, chemical properties of lichen symbioses as important drivers of the global distribution of lichenised trebouxioid green algae—the most important group of lichen photobionts. As hypothesised, the occurrence probability of lichenised Trebouxiophyceae decreases in warmer and more humid climates, thus shows minimum occurrence in tropical regions, but increases towards higher latitudes. More specifically, the photobionts’ occurrence probability is positively affected by the occurrence of lichen substances, which in turn decreases in environments that favour the leaching of these substances (i.e. tropical regions). Still, the minimum occurrence probability of trebouxiophycean lichens in the tropics (0.6–0.8) is two to three times higher than the maximum occurrence probability of tentepohlialean lichens in the same latitudes (0.1–0.3, Figure 2). Thus, there is no complete replacement of trebouxiophycean symbionts with Trentepohliales but latitudinal turnover is still more extreme than suggested by other studies (e.g. Ahmadjian, 1967). Lichen substances associated with lichenised Trebouxiophyceae furthermore show higher UV-B absorbance and lower solvability than substances associated with lichenised Trentepohliales. Occurrence probability of this second most abundant group of photobionts was negatively related to the occurrence of lichen substances. All this suggests that the type of UV protection (active vs. passive) and the chemical properties of lichen substances are major ecological drivers of global lichen distribution.
Lichenised trebouxiophycean and trentepohlialean green algae show very different environmental limitations. Lichenised Trentepohliales have been reported to sensitively depend on high humidity and are therefore widespread in tropical regions (Marini et al., 2011; Rambold et al., 2016). Experiments showed that Trentepohlia-containing lichens are more susceptible to frost than Trebouxia-containing lichens, with strong depressions in photosynthesis associated with significant decreases in total chlorophyll being observed for Trentepohlia lichens (Nash et al., 1987). Most trebouxiophycean green algae synthesise ribitol rather than erythritol as mobile carbohydrate, which is not only more efficient for carbohydrate transport between the photobiont and mycobiont but also more protective against freezing than erythritol synthesised by Trentepohliales (Fontaniella et al., 2000; Richardson et al., 1968). These differences in frost protection of the photobiont could explain the differences between both groups of lichenised green algae in frost resistance and, thus, in latitudinal distribution. In our study, we observe environmental dissolution potential to be the most important direct, abiotic driver of global lichen distribution with opposite effects on trebouxiophycean and trentepohlialean lichens. Thus, a combination of indirect and direct effects of key abiotic drivers seem to be responsible for the contrasting, global distribution patterns we observed for trebouxiophycean and trentepohlialean lichens.

Generally, lichen fungi seem to benefit from associations with trebouxiophycean green algae, which are characterised by more efficient carbon acquisition and translocation. To gain this benefit, the mycobiont has to invest in UV protective metabolites. The production of these lichen substances is metabolically very costly for the mycobiont (Calcott et al., 2018). Thus, UV protection of trebouxiophycean green algae seems to be only beneficial for the mycobionts as long as the benefits from this symbiotic association (i.e. photosynthetic carbon gain) does not outweigh the costs associated with UV protection (i.e. costs for producing lichen substances with high UV absorbance but low solubility).

Despite the clear global distribution patterns we observe, a significant ecological variation might exist at local scale which deviates from the global scale observations. Foliicolous lichens occurring in densely shaded rainforest understories are, for example described to be mainly characterised by trentepohlialean green algae whereas the foliicolous light-gap communities are reported to be characterised by trebouxiophycean algae (Pinokiyo et al., 2006; Rindi & López-Bautista, 2008). This dominance of trebouxiophycean lichens might be related to the higher photosynthetic efficiency (higher electron transport rates) and faster movement of mobile carbohydrates between the photobiont and mycobiont (Polishchuk & Voytsekhovich, 2014; Richardson et al., 1968). Both physiological characteristics might be beneficial in the highly variable light environments realised in light gaps of tropical rain forests and might outweigh the negative effects related to a high dissolution potential characterising these environments.

Most of the dominant lichen substances such as usnic acids, depsides, depsidones, pulvinic acids, anthraquinones have traditionally been considered insoluble or poorly soluble (Huneck & Yoshimura, 1996). However, other evidence demonstrates dominant lichen substances such as usnic and perlatolic acids can be leached out in ecologically important quantities (Dawson et al., 1984; Garcia-Junceda & Filho, 1986). These findings
in combination with our observations indicate that the water solubility of major lichen substances is sufficient to be washed out in humid and warm environments such as the tropics.

Sufficient leaching of lichen substances is crucial for the antibiotic effectiveness of these compounds. About 50% of all lichen fungal species produce lichen substances with antibiotic properties (Malhotra et al., 2013). Thus, a trade-off might exist between the antibiotic effectiveness and the UV protection potential of lichen substances, which is linked to the solubility of these substances and which might have major implications for the occurrence of lichens in different environments but also for the biochemical evolution of lichen symbioses in general. Furthermore, several studies report that the major lichen substances are sufficiently water soluble to act as metal-complexing agents in rock weathering or to enter the soil and subsequently contribute to soil formation and other soil processes (Dawson et al., 1984; Iskandar & Syers, 1971; Zagoskina et al., 2013). Thus, water solubility of lichen substances facilitating rock weathering and soil formation is a crucial trait of lichens regarding the global biogeochemical cycles. The spatio-temporal intensity of this ecological function might be strongly linked to the eco-evolutionary significance of the trade-off between antibiotic effectiveness and UV protection potential of lichen substances.

Phylogenetic relationships between the host fungi could be responsible for some of the observed effects but were just partly corrected for in this study due to a restricted availability of phylogenetic information. This highlights the need of future studies with a special focus on the so far phylogenetically underrepresented Trentepohliales-associated lichen fungi. Spatial taxonomic bias based on a geographic variation in taxonomic methods and expertise (Freeman & Pennell, 2021) might additionally affect our results. We believe that this bias is of minor importance for lichens which are often characterised chemotaxonomically in addition to macromorphological descriptions (and since recently species DNA barcoding). This standardised, chemical approach should minimise a spatio-taxonomic bias for lichens. We furthermore argue, that our spatial subsampling procedure, which we used to reduce distorting effects of spatially imbalanced sampling effort, also helps to reduce the spatio-taxonomic bias.

The eco-evolutionary significance of lichen substances

The environmental limitation associated with high UV radiation appears to be not only of ecological relevance for the global distribution of lichens, but also to be phylogenetically important (cf. Gaya et al., 2015; Singh et al., 2021). Previous studies have shown that genetic variation and phylogenetic history of lichen photobionts closely correlate with environmental (climatic) factors, but less so with mycobiont phylogeny (Fernández-Mendoza et al., 2011). In our study, we observe significant effects of the phylogenetic history of the Lecanoromycetes mycobionts on the relationship between the spatial distribution of lichenised Trebouxiophyceae and the UV absorbance and solvability of associated lichen substances. We furthermore observe that the phylogenetic relatedness of co-occurring fungal species seems to play a significant role in determining the occurrence probability of lichen substances. All this suggests a close eco-evolutionary association between trebouxiophycean green algae and their mycobionts, with UV protection by fungal secondary metabolites being a major driver of this association.

Tolerance to high UV radiation, along with freezing tolerance, has been assumed to be an important trait of photobionts that provides a selection advantage for lichen symbioses (Singh et al., 2016). The low content of UV-protective intracellular β-carotene and xanthophylls characteristic of Trebouxiophyceae are described by Voytsekhovich and Kashchevav (2010) as the result of long-term co-evolution with lichen-forming fungi, where fungal hyphae and lichen substances increasingly substituted intracellular carotenoids to protect the algal
chlorophyll from photodamage by high UV radiation. These authors argue that partial reduction of carotenoids could be a reason for the rare occurrence of Trebouxia species in the free-living state and for the fact that any mutation that reduces the content of carotenoids is considered lethal for this group of algae (Gudvin & Merser, 1986; Siefermann-Harms 1987). However, some species groups of the genus Trebouxia (i.e. the T. corticola and T. impressa groups) still show comparably high contents of carotenoids. Such lichens are known to often occur at high elevations or latitudes (Beck, 2002; Opanowicz & Grube, 2004). The production of carotenoids is thereby assumed to be an adaptation to these specific abiotic conditions, namely high UV radiation but relatively low liquid precipitation and low temperatures, thus, relatively low environmental dissolution potential (Voytsekhovich & Kashevarov, 2010). We observe trebouxiophycean lichens with a distribution maximum in the tropics to have comparably low solvability and UV-B absorbance of lichen substances as compared to trebouxiophycean lichens with distribution dominance in higher latitudes. This might hint towards tropical trebouxiophycean photobionts still having higher active UV-protection and goes in line with recent findings that the T. corticola group, which is characterised by still comparably high contents of carotenoids, seems to generally occur in warmer and wetter habitats (Nelsen et al., 2021).

CONCLUSIONS

Organisms adapt to environmental conditions, which in turn affects their global distribution. This direct environmental adaptation applies not only to individual organisms, but also to mutualistic interactions such as lichen symbioses, where one of the partners shows environmental adaptations to protect itself, as in our case the active photobiont (i.e. the mycobiont) sensitively depends on the perfor-

drivers of the global distribution of organisms and highlight the potential of such approaches to be broadly important to the study of biodiversity gradients.

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AUTHORSHIP

A.H.S and G.R. designed the research; A.H.S. performed the research with major input by G.R., G.M.U., DT and R.S.; A.H.S. analysed the data; A.H.S. and G.R. wrote the paper with major input by all authors.

OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at: https://doi.org/10.5281/zenodo.5159337.

DATA AVAILABILITY STATEMENT

Data on lichen photobionts and associated lichen substances were retrieved from the LIAS light trait database (www.lias.net). More details see re3data under https://www.re3data.org/repository/r3d10001872. Data used in this study (distribution data incl. citation information; lichen traits incl. information on photobiont and secondary metabolite occurrence; geographic location, climatic conditions and chemical properties of lichen co-occurrences) and scripts used for analyses are archived at Zenodo (https://doi.org/10.5281/zenodo.5159337).

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REFERENCES

Ahmadjian, V. (1967) The lichen symbiosis. Waltham, Massachusetts: Blaisdell Publishing, p. 152.

Aptroot, A. & van Herk, C.M. (2007) Further evidence of the effects of global warming on lichens, particularly those with Trentepohlia phycobionts. Environmental Pollution, 146, 293–298.

Beck, A. (2002) Photobionts: diversity and selectivity in lichen symbioses. International Lichenological Newsletter, 35, 18–24.

Beckmann, M., Václavík, T., Manceur, A.M., Šprõtvá, L., von Wehrden, H., Welk, E. et al. (2014) glUV: a global UV-B radiation data set for macroecological studies. Methods in Ecology and Evolution, 5, 372–383.

Calcott, M.J., Ackerley, D.F., Knight, A., Keyzers, R.A. & Owen, J.G. (2018) Secondary metabolism in the lichen symbiosis. Chemical Society Reviews, 47, 1730–1760.
Pinokiyo, A., Singh, K.P. & Singh, J.S. (2006) Leaf-colonizing lichens: their diversity, ecology and future prospects. *Current Science*, 90, 509–518.

Polischuk, O. & Voytekovich, A. (2014) Photosynthetic properties of some green free-living and lichenized terrestrial algae. *Algologia*, 24, 1–7.

R Core Team (2021) R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rambold, G., Davydov, E., Elix, J.A., Nash, H. III, Scheidegger, C. & Zedda, L. (2001) LIAS light—A Database for Rapid Identification of Lichens. Available at: liaslight.lias.net/. Last accessed 17 April 2021.

Rambold, G., Elix, J.A., Heindl-Tenhenun, B., Köhler, T., Nash III, T.H., Neubacher, D. et al. (2014) LIAS light—Towards the ten thousand species milestone. *MycoKeys*, 8, 11–16.

Rambold, G., Zedda, L., Coyle, J.R., Peršoh, D., Köhler, T. & Triebel, D. (2016) Geographic heat maps of lichen traits derived by combining LIAS light description and GBIF occurrence data, provided on a new platform. *Biodiversity and Conservation*, 25, 2743–2751.

Richardson, D.H.S., Hill, D.J. & Smith, D.C. (1968) Lichen physiology. *New Phytologist*, 67, 469–486.

Rindi, F., Guiry, M., Critchley, A. & Gall, E. (2003) The distribution of some species of Trentepohliaceae (Trentepohliales, Chlorophyta) in France. *Cryptogamie Algologie*, 24, 133–144.

Rindi, F. & López-Bautista, J.M. (2008) Diversity and ecology of Trentepohliales (Ulvophyceae, Chlorophyta) in French Guiana. *Cryptogamie Algologie*, 29, 13–43.

Rosseel, Y. (2012) lavaan: an R package for structural equation computing. *Vienna, Austria: R Foundation for Statistical Computing.*

Solhaug, K.A., Gauslaa, Y., Nybakken, L. & Bilger, W. (2003) UV-induction of sun-screening pigments in lichens. *New Phytologist*, 158, 91–100.

Takaichi, S. (2011) Carotenoids in algae: distributions, biosyntheses and functions. *Marine Drugs*, 9, 1101–1118.

Thompson, R.H. & Wujek, D.E. (1997) Trentepohliales: cephalears, phycolepsis, and stomatochroon: morphology, taxonomy, and ecology. Enfield, New Hampshire: Science Publishers.

Triebel, D. & Bensch, K. (2005) LIAS names—A Database with Names of Lichens, Lichenicolous Fungi and Non-Lichenized Ascomycetes. Available at: http://liasnames.lias.net. Last accessed 4 April 2021.

Tucker, S.C., Matthews, S.W. & Chapman, R.L. (1991) Ultra-structure of subtropical crustose lichens. In: Galloway, D.J. (Ed.) *Tropical lichens: their systematics, conservation and Ecology*. Oxford, UK: Clarendon Press, pp. 171–191.

Voytsekhovich, A.A. & Kashevarov, G.P. (2010) Pigment content of photosynthetic apparatus of green algae (Chlorophyta)—the photobionts of lichens. *International Journal on Algae*, 12(3), 282–292. https://doi.org/10.1615/InterJAlgae.v12.i3.60.

Wood, S.N. (2004) Stable and efficient multiple smoothing parameter estimation for generalized additive models. *Journal of the American Statistical Association*, 99, 673–686.

Zachariah, S.A. & Varghese, S.K. (2018) The lichen symbiosis: a review. *International Journal of Scientific Research and Reviews*, 7, 1160–1169.

Zagoskina, N., Nikolaeva, T., Lapshin, P., Zavarzin, A. & Zavarzina, A. (2013) Water-soluble phenolic compounds in lichens. *Microbiology*, 82, 445–452.

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