

Viewpoint

Flexible or fortified? How lichens balance defence strategies across climatic harshness gradients

Summary

Lichens play important roles in habitat formation and community succession in polar and alpine ecosystems. Despite their significance, the ecological effects of lichen traits remain poorly researched. We propose a trait trade-off for managing light exposure based on climatic harshness. In the harshest cold environments, where abiotic stress predominates over biotic pressures, lichens should rely on photostable, recalcitrant and immobile substances such as allomelanin and hydrophobic compounds. These compounds provide durable protection without the need for continual synthesis. In milder conditions where biotic interactions – for example, competition and pathogen presence – become increasingly pronounced, lichens should retain flexibility and produce simple protective secondary compounds that, in addition to functioning as light screens, can leach out to influence their direct environment. Preliminary empirical findings for Antarctic lichen species distribution are consistent with this hypothesised trade-off, in that lichens producing soluble compounds dominate in milder regions and are less represented at higher southern latitudes, where species producing insoluble compounds with a melanised thallus dominate. As climate change progresses, increasing temperatures and precipitation could make the currently coldest and driest areas more hospitable, allowing the ranges of lichens producing soluble compounds to expand, with cascading effects on rock weathering, nutrient cycling and other ecosystem processes.

Introduction

Lichens, a symbiosis between a fungus and a photosynthetic alga and/or cyanobacterium (Lücking *et al.*, 2017), form a key component of polar and high-altitude biomes. They make a large contribution to overall polar biodiversity (Kappen, 2000; Matveyeva & Chernov, 2000), host a great abundance and diversity of other organisms (Bokhorst *et al.*, 2015; Woltyńska *et al.*, 2023) and initiate ecosystem succession (Asplund & Wardle, 2017). With over 450 species in the Antarctic and 1750 in the Arctic, lichens show a remarkable ability to persist in some of the Earth's most challenging environments (Øvstedal & Smith, 2001; Dahlberg & Bultmann, 2013). Their success lies in a diverse range of

morphological and physiological adaptations (Armstrong, 2017), including the production of secondary compounds that defend against freezing temperatures, intense solar radiation, harmful UV-B exposure and desiccation (Lud *et al.*, 2001; Gautam *et al.*, 2011). These compounds, which can constitute 20–30% of the thallus dry mass (Huneck, 1973; Fahselt, 1994), represent a substantial biosynthetic effort, particularly in polar environments where the growth season is short, and activity patterns are limited by long periods of sub-zero temperatures and insufficient water availability (Raggio *et al.*, 2016). The amount and specific type of compounds synthesised thus likely reflect how lichens are adapted to their specific environments. Despite the discovery of *c.* 1050 unique secondary compounds in lichens (Molnár & Farkas, 2010), the full extent of their ecological roles and impacts on lichen distribution is not well understood, making it challenging to directly relate a lichen's metabolite profile to its ecological strategies.

Here, we explore the hypothesis that water solubility of secondary biochemical compounds shapes the ecological strategies of lichens and determines their distribution across polar and alpine environments. Lichen secondary compounds vary widely in their water solubility (Huneck & Yoshimura, 1996) (Fig. 1a), which likely affects the degree to which these compounds leach from the thallus into the environment (Schweiger *et al.*, 2022), impacting their availability for ecological interactions (Fig. 1b). We explore how environmental harshness could drive a trade-off between the flexibility that soluble secondary compounds may offer in a more benign or variable environment vs robust protection strategies involving insoluble compounds in environments where abiotic pressures consistently outweigh biotic pressures. The production of soluble compounds for stress (particularly excess light) protection is considered costly in the tropics, where high temperatures and humidity increase leaching losses (Schweiger *et al.*, 2022). Lichens associated with trentepohlialean algae, which are more frequent in the tropics, may mitigate these losses by relying on insoluble and intracellularly deposited pigments like beta-carotene (Schweiger *et al.*, 2022). Conversely, lichens in cold, dry environments where leaching is limited, can afford to produce secondary compounds with lower resource expenditure (Solhaug & Gauslaa, 2012). Furthermore, in the coldest and driest polar regions, lichen activity can be so low that it may be advantageous to invest in insoluble secondary compounds that provide guaranteed stress protection, rather than relying on the opportunity for rapid responsive synthesis. If so, lichen species distribution patterns in polar regions may, in part, be driven by their abilities to produce soluble or insoluble secondary compounds. Below, we examine the functional roles of lichen compounds and explore the potential trade-off between flexibility and robust protection. We hypothesise that (photo)stability and solubility of these compounds are critical

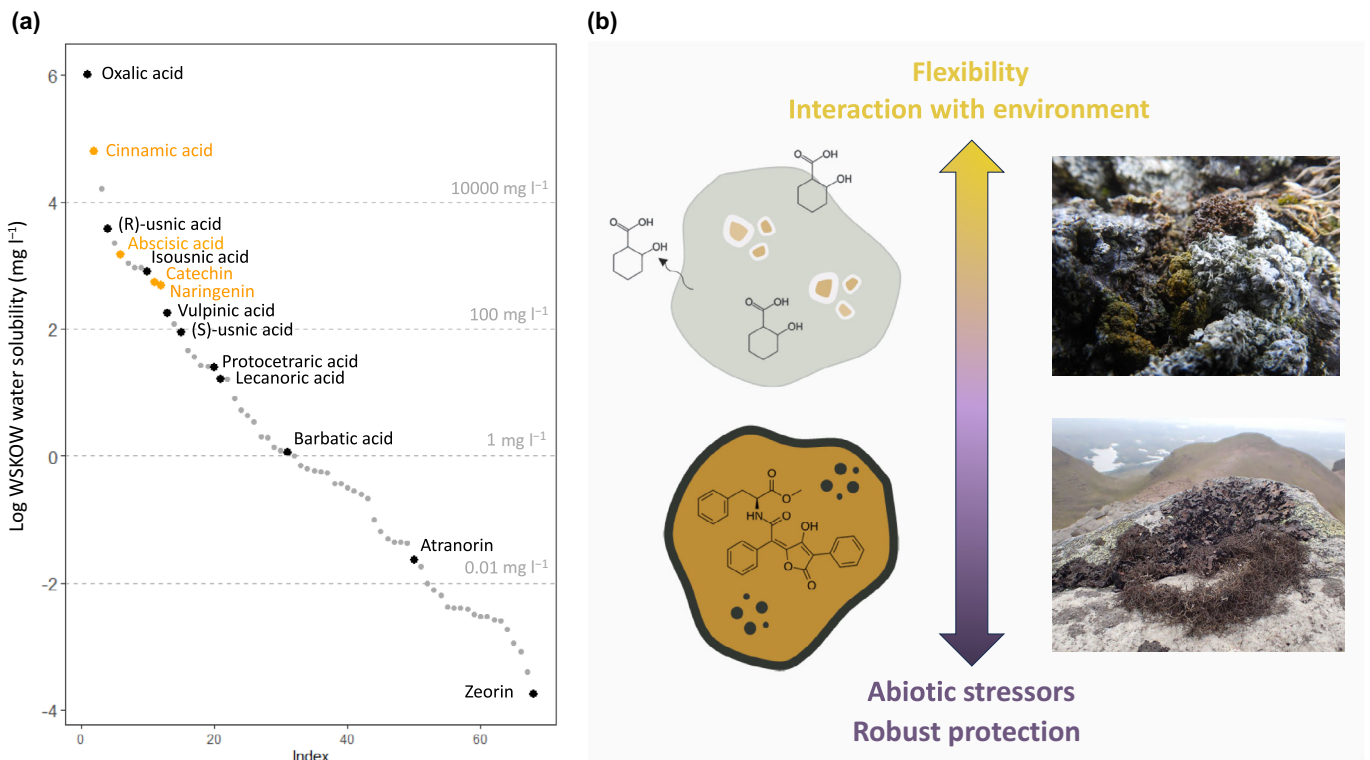


Fig. 1 Conceptual model illustrating how water solubility of secondary compounds (based on the Kow correlation method described by Meylan *et al.* (1996), computed through *WSKOW* v.1.41) found in Antarctic lichens (a) is expected to determine their ecological function (b). More soluble compounds leach to the environment where they could interact with other organisms or ecosystem processes (yellow arrow). Conversely, less soluble, more hydrophobic compounds, such as the triterpene zeorin and the biopolymer allomelanin, can accumulate in the lichen thallus and are expected to primarily be involved in helping lichens resist abiotic stressors, including light exposure and desiccation (purple arrow). Compounds found in Antarctic lichens are denoted in grey/black, while selected compounds from plants, identified as significant allelochemicals, are shown in orange. The solubilities of these well-characterised plant compounds all exceed 100 mg l⁻¹. Using this value as a benchmark, it is apparent that many lichen compounds show similar solubility levels. Photos: Inger de Jonge (top right) and Chris Cant (bottom right).

factors determining lichen distribution. We provide a preliminary empirical test of this hypothesis, using occurrence data and information on the specific compounds found in Antarctic lichens.

Multifunctionality of lichen compounds

Sunlight sustains life on Earth, yet its ultraviolet component, due to its high energy, can cause genetic defects and other damage to living cells. Lichens protect themselves against UV and excessive levels of photosynthetically active radiation (PAR) by synthesising protective secondary compounds, including those that act as screens (e.g. atranorin, usnic acid), have antioxidant properties (e.g. pulvinic lactone derivatives), or mitigate oxidative stress by scavenging reactive oxygen species (ROS) (e.g. stictic acids) (Elix & Stocker-Wörgötter, 2008; Nguyen *et al.*, 2013). Most of the 1050 currently identified lichen compounds can absorb UV radiation (Beckett *et al.*, 2021), a property largely attributable to their phenolic structure. This raises the question of how we can discern patterns in the selection and ecological roles of these compounds. The spatial location of compounds within the lichen is crucial for their function; those in the upper cortex are more likely

to serve as light screens (Solhaug & Gauslaa, 2012). Compounds also vary in the wavelengths they absorb or reflect; parietin, for instance, absorbs light and converts it to heat while atranorin reflects excess light (Solhaug *et al.*, 2010), affecting thermal regulation, which can itself be advantageous in polar regions. Moreover, while yellowish compounds such as vulpinic acid absorb blue light to protect against photoinhibition, they may compromise photosynthetic efficiency in low-light conditions (Phinney *et al.*, 2019). Finally, some compounds may be phylogenetically conserved and associated with specific lineages, such as the vibrant yellow-orange pigment parietin in the fungal order Teloschistales (Gaya *et al.*, 2015) (Fig. 2a).

Temperature, humidity and light intensity, thus, likely influence which compounds lichens employ for protection against excess light. These abiotic factors also control the relative importance of biotic interactions, such as competition with neighbouring cryptogams or higher plants, pathogen pressure and herbivory, which generally intensify in milder environments (Choler *et al.*, 2001; Rheubottom *et al.*, 2019; Delgado-Baquerizo *et al.*, 2020). If most lichen compounds protect against the harmful effect of light exposure, whether through light screening, antioxidant properties or ROS scavenging (Beckett *et al.*, 2021),

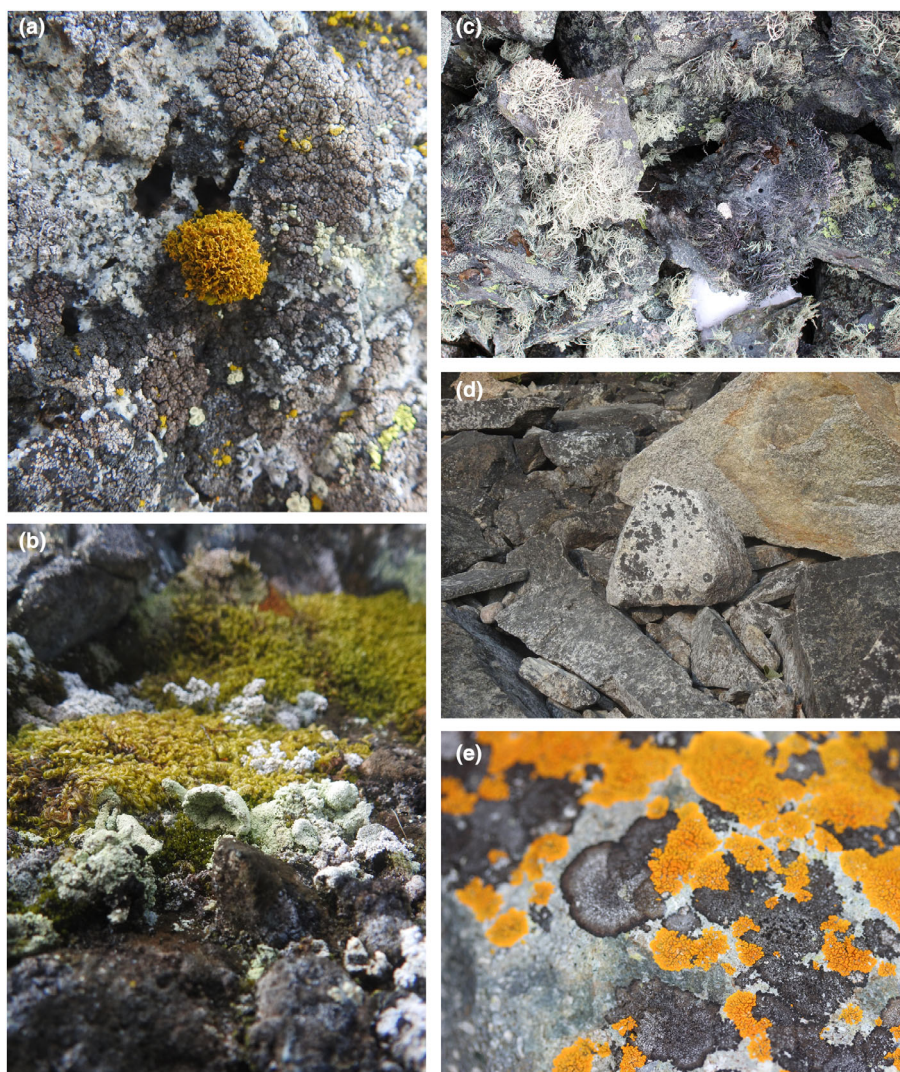


Fig. 2 Lichens *in situ*. (a) The secondary compound parietin gives *Polycauliona candelaria* its orange-yellow colour, Léonie island, Antarctica; (b) *Cladonia pleurota* tends to have a pale greenish colour due to the compound usnic acid, Léonie island, Antarctica; (c) rock with melanised *Usnea antarctica* individuals that were transplanted from a north-facing, sunny slope to a south-facing slope, Lagoon island, Antarctica; (d) crustose melanised lichens, Canada; (e) close contact between *Xanthoria* sp. and *Buellia* sp., Lagoon Island, Antarctica. Photos: Inger de Jonge (a–d) and Stef Bokhorst (e).

their auxiliary ecological roles, particularly in biotic interactions, should contribute to their adaptive success and prevalence across gradients of climatic harshness. Such ‘multifunctionality’ is well exemplified by usnic acid, one of the most widely studied lichen compounds, which gives many lichens their characteristic green or pale yellow colour (Fig. 2b). Usnic acid acts as an antimicrobial agent (Huneck, 1999), a UV radiation screen (Nguyen *et al.*, 2013), an allelopathic agent (Goga *et al.*, 2017), a herbivore deterrent (Nimis & Skert, 2006) and an antioxidant (Molnár & Farkas, 2010). Producing compounds that can tackle various threats simultaneously is advantageous (Neilson *et al.*, 2013), and it seems reasonable to suggest that all lichens may depend on such multifunctional compounds. For a lichen compound to exert an ecological impact on its surroundings, it must leach from the thallus; a process dependent on molecular size, polarity and the presence of particular functional groups (Chiou & Kile, 1994). Such differences in compound properties suggest that a potential trade-off should exist in terms of ecological costs and benefits in the production of leachable as opposed to immobile, nonsoluble, secondary compounds.

Trade-off between robust protection and flexibility

Ecological theory often emphasises trade-offs, where trait variations among species have evolved as adaptations to different environments. Accordingly, the biochemical characteristics of secondary compounds, such as solubility, may reflect specific adaptations, each associated with distinct costs and benefits. In the harshest environments, where productivity is restricted by long periods of low temperature and limited liquid water availability (Raggio *et al.*, 2016), it could be costly for secondary compounds to be leached from lichen thalli as this necessitates continual synthesis to replenish the losses. Such losses may be exacerbated by photodegradation under exposure to intense solar radiation. Just as solubility varies among secondary compounds, so does their photolability, with some being more prone to photodegradation. For example, while the tridepsides gyrophoric acid and tenuiorin remain largely stable under UV exposure, the dibenzofurans didymic acid and usnic acid are more photolabile, breaking down under UV-B radiation (Begora & Fahselt, 2001). This breakdown necessitates *de novo* synthesis, which is facilitated by visible light,

helping to counterbalance the degradative effects of UV-B (Begora & Fahselt, 2001). However, in the harshest environments, the rate of synthesis may not fully compensate for that of degradation, potentially explaining observed reductions in phenolic concentrations with elevation (Swanson *et al.*, 1996). This logic suggests that compounds that are more robust against photodegradation should be selected for, but this hypothesis remains to be tested. Similarly, in conditions where resynthesis cannot compensate for the losses due to leaching, reliance on less soluble compounds would be advantageous. Along a climatic harshness gradient there could, thus, be a trade-off between producing compounds that can interact with the environment but require continual synthesis *vs* investment in longer lasting protection from compounds held within the thallus/cells in the harshest conditions.

An advantage of responsive synthesis of new compounds is that it allows increased flexibility in adaptation to varying environmental conditions. In milder polar environments where the growing season allows for extensive lichen growth, such as in the northern Maritime Antarctic (Sancho *et al.*, 2017) or alpine tundra, continual production may allow lichens to dynamically adjust their chemical defences in response to fluctuating levels of moisture, temperature and biotic interactions. Lichens with higher productivity and faster growth rates are likely better able to sustain the continual synthesis of soluble compounds, whereas slower-growing, low-productivity species may rely on more conservative, robust strategies involving insoluble compounds. Flexibility in compound production could enable a responsive strategy, whereby lichens can optimise their secondary metabolite profiles as required. If this is the case, compound concentration would be expected to fluctuate over time and across different spatial gradients. Indeed, the production of secondary compounds has been observed to be closely linked to water availability (Bjerke *et al.*, 2005a), with concentrations often fluctuating throughout the year and peaking during the season with the highest moisture availability (Taguchi *et al.*, 1969; Bjerke *et al.*, 2005b). During these periods, lichens may adjust their chemical outputs in response to specific environmental conditions, such as contact with neighbouring cryptogams or increased grazing by mites. Large intraspecific variation in secondary compound concentrations also exists across short environmental gradients, with significant increases in compounds such as gyrophoric acid under higher herbivore pressure (Bokhorst *et al.*, 2024).

These fluctuations in concentrations over time and space suggest that compounds do not simply passively accumulate but, rather, may reflect the phenotypic plasticity of lichens to different combinations of abiotic and biotic pressures. Loss of compounds, such as through leaching, may also form part of this strategy; in plants, a trade-off is recognised between the allocation of resources to growth, development and reproduction *vs* the biosynthesis, storage and maintenance of secondary compounds (Coley, 1988; Stamp, 2003). In other words, maintaining and storing unnecessary compounds is costly, so it may be more advantageous for lichens to allow these compounds to slowly degrade or leach away, freeing up resources for the production of those that are specifically required at any given time.

The alternative, robust approach includes build-up of compounds that do not leach and are highly photostable. For instance, allomelanin, a black or brownish pigment and likely the most common type of melanin in lichens, provides enduring protection against both UV radiation and high PAR (Mafole *et al.*, 2019). It is a complex and highly insoluble biopolymer, hard to dispose of once synthesised, meaning that lichens cannot easily revert to a lighter-coloured state if environmental conditions change, thereby reducing flexibility. Build-up of dark pigments in lichen tissues also reduces photosynthetic light-use efficiency (Mafole *et al.*, 2019), while their absorption of visible and near-infrared radiation (Nybakken *et al.*, 2004) warms lichen tissue and induces snowmelt which, in turn, facilitates hydration through the high microporosity of allomelanin (McCallum *et al.*, 2021), thereby activating photosynthesis (Coxson & Coyle, 2003). This may explain why *Usnea antarctica* on north-facing slopes, which receive more sunlight and are consequently drier, tend to be more melanised, indicating that this trade-off between flexibility and robust protection also occurs to some extent within species (Fig. 2c).

The warming effect of melanisation also accelerates water loss from the thallus, resulting in shorter active periods for melanised lichens (Phinney *et al.*, 2022). In polar and alpine regions, however, this warming alleviates the limitation of low-ambient temperatures (Kershaw, 1975), enhancing photosynthesis and enabling snowmelt-driven hydration. This may explain why melanic lichens thrive in the harshest cold environments but are less prevalent in temperate and tropical zones, where higher temperatures make warming unnecessary and faster drying becomes a greater disadvantage (Phinney *et al.*, 2022).

While this warming–desiccation trade-off (Gauslaa, 1984) may explain broad distributional trends, melanised lichens are still found in boreal and temperate regions. Their success in such environments may reflect the general robustness provided by melanisation, which also strengthens the thallus by thickening hyphal cell walls (Daminova *et al.*, 2022), forming a physical barrier that enhances resistance to environmental stress, including drought (Fernandez & Koide, 2013). Based on the hypothesised trade-off between flexibility and robust protection, we speculate that melanised lichens should thrive not just in cold, dry environments, but in any sun-exposed environment with consistently high-abiotic stress, where flexibility is less critical. This might explain, for instance, why black lichens also occur on otherwise bare rocks outside the polar regions (Fig. 2d).

The proposed trade-off may be particularly relevant for cortical compounds, which not only play a more direct role in light screening but also often crystallise on the thallus surface. Their exposed position may make them more prone to leaching, especially under physical forces such as raindrop impact (Pizňák & Bačkor, 2019). Consequently, the trade-off may primarily exist between soluble cortical compounds and insoluble compounds like melanin. Soaking or simulated dripping experiments could shed light on how cortical and medullary compounds differ in this respect.

Finally, many lichens lack both (cortical) secondary compounds and melanin yet thrive in both harsh and favourable conditions, suggesting that light screening through secondary compounds may

not be the only strategy for managing high-light environments. Alternative adaptations may include pale (white-greyish) thalli that reflect light, thicker cortices that provide better protection for photobionts (Hájek *et al.*, 2021), medullary compounds with strong ROS-scavenging properties to mitigate oxidative stress (Elix & Stocker-Wörgötter, 2008), and efficient DNA repair mechanisms to counteract the effects of UV damage (Begora & Fahselt, 2001). How lichens without secondary compounds fit into the proposed framework remains uncertain. They may represent an even more conservative strategy, as structural and physical defences are potentially less metabolically demanding when stress is persistent and long-lasting protection is required, as observed in plants (Eichenberg *et al.*, 2015). Further research is needed to better understand the adaptations and ecological significance of this relatively smaller group in polar and alpine regions.

The solubility of secondary compounds and their relevance for biotic interactions

A trade-off between flexibility and robust protection, driven by variable biotic pressures, would mean that biotic interactions, such as competition, could play an important role in lichen survival. However, based on their generally slow growth rates, longevity, and low-nutrient demands, lichens are not considered strong competitors (Grime, 1979), focusing energy on tolerating stress and survival rather than on overshadowing neighbours or producing offensive allelochemicals for competition (Armstrong & Welch, 2007). Despite this, lichens are often found growing in close proximity to, or even slightly overgrowing, one another (Fig. 2e), indicating that interactions between lichens do occur. It has been suggested that lichens rely on a 'contact avoidance strategy' (John, 1989) to manage these interactions with other organisms. This strategy can involve the use of secondary compounds to create a chemical buffer zone that deters encroachment by antagonistic neighbours (Armstrong & Welch, 2007), which likely function most effectively in the immediate space between the thallus and the encroaching organism. A zone of influence at the scale of, at most, millimetres would make sense in this context, although these interactions remain poorly studied, and helps explain why these compounds are often not detected further away, such as in the surrounding soil, where concentrations are generally low (Stark *et al.*, 2007).

This suggestion is supported by findings that compounds associated with strong anti-herbivore or antimicrobial effects tend to be relatively soluble. For example, lichens containing vulpinic acid are known for their reduced palatability to herbivores (Giez *et al.*, 1994; Gauslaa, 2005) and, with a solubility of 180 mg l^{-1} (WSKOW v.1.41), vulpinic acid ranks among the more soluble lichen compounds. Lichen compound solubilities span 10 orders of magnitude, with highly soluble compounds like oxalic acid at $1000\ 000 \text{ mg l}^{-1}$ and the hydrophobic triterpene zeorin at only $0.00018 \text{ mg l}^{-1}$. The solubility of vulpinic acid is comparable to well-known plant allelochemicals such as naringenin and cinnamic acid, which are typically sufficiently soluble to interact effectively with their surroundings and, thus, provide a useful reference for

evaluating lichen compound solubility (Fig. 1a). Another example is the antifungal activity of lecanoric acid, which inhibits the obligate fungal pathogen *Nectria parmeliae* from encroaching into the lichen *Punctelia rudecta* (Lawrey, 2000). However, when another common lichen inhabitant, an undefined *Fusarium* species, degrades lecanoric acid, this protection is lost, allowing *N. parmeliae* to invade. Though less soluble than vulpinic acid, lecanoric acid, at 16.08 mg l^{-1} , still ranks relatively high in solubility (Fig. 1a), suggesting that its ability to create a chemical barrier against *N. parmeliae* may be linked to its capacity to leach from the thallus. Finally, usnic acid has been suggested by some to play a role in suppressing neighbouring cryptogams and higher plants (Lawrey, 2009; Goga *et al.*, 2017). While allelopathy – the chemical suppression of one organism's growth by another (Inderjit & Callaway, 2003)—has been demonstrated in *in vitro* experiments (Hobbs, 1985; Lawrey, 2009; Sedia & Ehrenfeld, 2003; Melick & Seppelt, 1997), its ecological significance in natural lichen communities remains debated (Stark *et al.*, 2007) and seems to be species and context-dependent (Nystuen *et al.*, 2019). Notably, the solubility of usnic acid varies considerably depending on its form. While the (S)-usnic acid isomer has a solubility of 88.5 mg l^{-1} , the (R)-usnic acid isomer is much more soluble at 3671 mg l^{-1} , with isousnic acid falling between these values at 796.5 mg l^{-1} . This wide range – and solubility variations across different secondary compounds in general – could be key to re-evaluating the ecological roles of lichen compounds and clarify the inconsistencies observed in lichen-plant allelopathy research (Favero-Longo & Piervittori, 2010).

Some solubility values, such as for (S)-usnic acid, rely on experimentally measured parameters, while others, including for (R)-usnic acid, are estimated using computational tools like WSKOW v.1.41. Estimated values inherently carry some uncertainty, but they provide the only information currently available for many lichen compounds. Direct measurements of solubility under environmentally relevant conditions, such as varying pH, temperature, or humidity, would improve the accuracy of these estimates and may provide deeper insights into the ecological functions of lichen secondary compounds.

Preliminary test of the trade-off hypothesis: lichens producing soluble compounds decrease along an Antarctic climatic harshness index

To explore the validity of the proposed trade-off between flexibility and robust protection, we conducted a test across a gradient of climatic harshness. The Maritime Antarctic region serves as an ideal setting for this exploration, with milder conditions towards the South Orkney Islands (60°S) and harsher environments further south in Palmer Land (71°S). Survey records of lichen vegetation across the entire region are available, making it well-suited for testing our predictions:

- (1) lichens producing soluble compounds will be more frequent in the milder parts of the Maritime Antarctic, where biotic pressures are greater;
- (2) melanised lichens, representing the most robust protection strategy, will be most prevalent in the harshest areas; and

(3) if flexibility and robust protection are alternative strategies, lichen species in the Maritime Antarctic Region that produce soluble compounds will be less likely to have black or brownish upper thalli.

We combined information on the occurrence of 240 lichen species from the Global Biodiversity Information Facility (GBIF) with an Antarctic Climatic Harshness Index (ACHI), calculated using latitude and altitude across the Maritime Antarctic (Fig. 3a). Data on secondary compounds and upper thallus colour were obtained from the LIAS trait database (Rambold *et al.*, 2014). For each secondary compound, we calculated water solubility using AlogPS, computed from SMILES notation via the open-access software VCCLAB (Tetko *et al.*, 2005). For detailed data compilation and methods, see Supporting Information Methods S1.

Logistic regression confirmed that lichens producing relatively soluble compounds are more frequent in milder regions, with a low-climatic harshness index (Fig. 3b). The probability that a lichen produces at least one compound with a solubility of more than 20 mg l⁻¹ is around four times higher in the mildest areas, exceeding 0.8, compared to the harshest environments, where it drops to slightly above 0.2 ($\chi^2(1) = 178.5$, $P < 0.001$) (Fig. 3b). Exploring different thresholds for relative solubility, thresholds between 10 and 100 mg l⁻¹ yielded the best model fits, with the strongest fit at 20 mg l⁻¹ based on the log-likelihood ratio (Methods S2). An opposite pattern was observed for lichens with a melanised thallus: the probability of having a blackish or brownish upper thallus was just below 0.4 in the mildest regions and increased to nearly 0.7 in the harshest environments, reflecting a 1.7-fold increase ($\chi^2(1) = 33.5$, $P < 0.001$) (Fig. 3c). These results appear to be robust and not driven by the inclusion of specific species: running 64 824 models, each excluding a different combination of three species, consistently yielded significant relationships (Methods S2). Finally, a chi-square test of proportions shows that lichens that produce at least one compound with a solubility of 20 mg l⁻¹ less often had a blackish or brownish upper thallus ($P < 0.001$), whereas lichens lacking secondary compounds entirely were more likely to exhibit a blackish or brownish upper thallus ($P < 0.001$) ($\chi^2(2) = 59.2$, $P < 0.001$) (Fig. 3d). This result implies that lichen distribution patterns across climatic harshness gradients indeed reflect alternative strategies, as predicted, with some lichens favouring flexibility through the production of relatively soluble compounds, while others rely on robust protection via melanised thalli.

Concluding remarks and future directions

While the preliminary findings presented here support the hypothesised trade-off between flexibility and robust protection in lichens, the simplicity of this correlational analysis highlights the need for further experimental validation. Controlled experiments across environmental gradients could confirm these patterns and help to better understand the complex interplay between secondary compound production, climatic pressures, and biotic interactions. Although studying biotic interactions with lichens poses challenges due to their slow growth rates, previous research has successfully

provided insights by removing secondary compounds through acetone rinsing (Asplund *et al.*, 2015), which effectively strips compounds from lichens (Solhaug & Gauslaa, 2001).

Future experiments should aim to mimic real field conditions more closely. Specifically, to better understand how lichens interact with their immediate environment, a more appropriate approach would be to use leachates generated by simulating rainfall with a dripper system (see Pacé *et al.*, 2020), or by soaking lichens to mimic snowmelt conditions. This approach would allow the solubility of compounds to dictate what ends up in the leachate, better mimicking how lichens interact with their direct environment. Additionally, current studies often examine individual compounds in isolation during (allelopathy) experiments, even though the effects of one compound can be influenced by the presence of others (Inderjit Weston & Duke, 2005). Since soils and substrates are multi-solute systems, the specific combination of compounds determines which are absorbed onto organic matter or remain in solution (Tharayil *et al.*, 2006), and are thus available for ecological interactions.

In the context of microbial interactions, leached secondary compounds may not always have antagonistic effects but can also serve a facilitative role, acting as a carbon source for microbes (Stark & Hyvärinen, 2003). In this way, lichen communities may shape surrounding microbial communities (Leiva *et al.*, 2016). Lichens are also increasingly recognised as ‘miniature ecosystems’ themselves (Hawksworth & Grube, 2020), with their thalli containing multiple microbial partners such as bacteria, yeasts and lichenicolous fungi, all potentially producing further compounds. These organisms, often found in the lichen cortex, could also interact with the environment and contribute to the overall chemical ecology of lichens (Spribille *et al.*, 2016).

Although our results show strong patterns, some species do not fully align with the proposed framework, suggesting that additional environmental drivers and trait axes may influence lichen distributions. For example, *Himantormia lugubris* is melanised, which is associated with a robust strategy adapted to the harshest environments. Yet, its range is restricted to the climatically milder parts of the Maritime Antarctic, likely because it relies on a longer growing season to compensate for exceptionally low-photosynthetic rates (Sancho *et al.*, 2020). *Himantormia lugubris* appears to prioritise survival over growth, allocating resources to chitin for structural stability, which helps its fruticose thalli withstand strong winds – though at the cost of reducing algal cells needed for productivity (Sancho *et al.*, 2020). This suggests that beyond temperature and moisture – captured in our analysis through latitude and altitude – other factors such as high-wind exposure play a role in shaping species distributions, highlighting the need for broader trait-based frameworks to fully capture patterns in lichen occurrence.

Finally, the proposed trade-off between flexibility and robust protection may extend beyond polar and alpine systems, applying to any sun-exposed biome with stable vs variable environmental gradients, such as deserts or upper tropical forest canopies. In both cases, the harsh, dry conditions at the highest or most exposed areas will limit interactions with the environment. However, for instance, just a few meters lower in the forest canopy, humidity

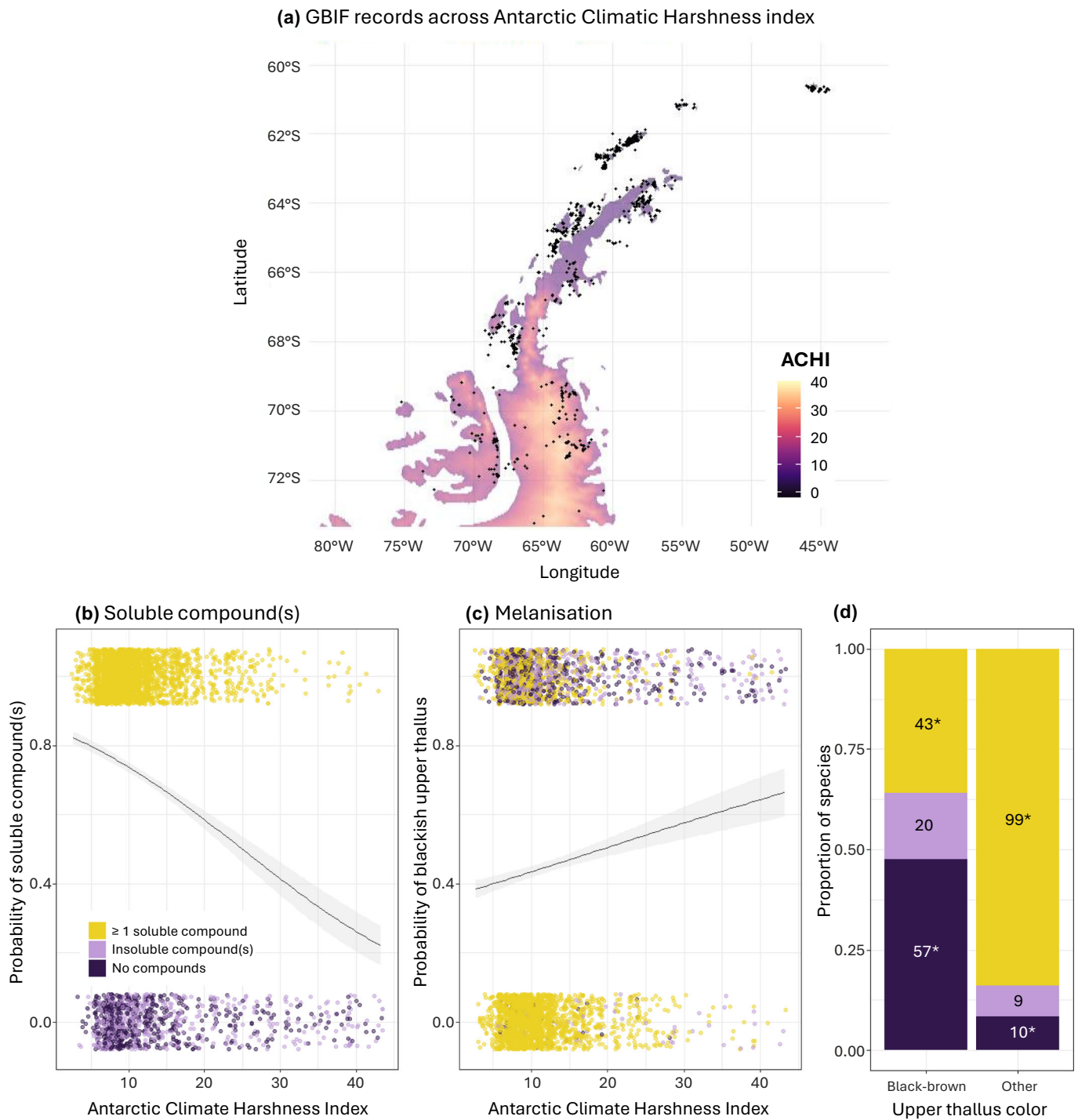


Fig. 3 Lichen observations and trait patterns across climatic harshness gradients. (a) Map showing lichen observations across the Maritime Antarctic, extracted from Global Biodiversity Information Facility (GBIF) using the `RGBIF` package (v.3.8.0; Chamberlain *et al.*, 2022). (b) Results of logistic regression showing the probability of presence of a species with at least one compound exceeding a solubility of 20 mg l^{-1} across the Antarctic Climatic Harshness Index (ACHI), calculated as $\text{ACHI} = (\text{abs}(\text{Latitude} - 55)) + (\text{Altitude}/100)$, following Cornelissen *et al.* (2001). (c) Probability of presence of species with a blackish or brownish upper thallus along the ACHI gradient. Each dot in (b) (soluble compounds, $n = 2724$; insoluble/no compounds, $n = 1122$) and (c) (blackish or brownish upper thallus, $n = 1713$; other thallus colour, $n = 2120$) represents one occurrence of one species. The shaded area in (b, c) represents the 95% confidence intervals of the predicted probabilities derived from the logistic regression model. (d) The proportion of species with at least one compound with a solubility of 20 mg l^{-1} is significantly lower for species with a blackish/brownish upper thallus, which more often produce no other secondary compounds compared to those that are not melanised. Asterisks indicate pairwise comparisons with significant differences ($P < 0.05$). Sample sizes differ slightly due to the availability of secondary compound and thallus colour data in the LIAS trait database (Rambold *et al.*, 2014).

increases, and conditions become more variable, much like the transition zones where deserts meet drylands.

In conclusion, we propose that the solubility and stability of secondary compounds can offer key insights into the ecological strategies of lichens in one of Earth's most challenging habitats. As polar and alpine biomes become warmer and (in many regions) wetter, we anticipate lichens that produce leachable compounds will increase in abundance and range, potentially leading to cascading effects on communities and biogeochemical cycling, as these compounds interact more extensively with the environment. Further experimental and monitoring studies are now required to investigate in detail the ecological roles, costs and benefits of producing leachable compounds and their broader impacts on ecosystem processes.

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Competing interests

None declared.

Author contributions

IKdJ, PC, IJK, JHCC and SB conceived the ideas. IKdJ analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ORCID

Stef Bokhorst  <https://orcid.org/0000-0003-0184-1162>
Peter Convey  <https://orcid.org/0000-0001-8497-9903>
Inger K. de Jonge  <https://orcid.org/0000-0001-6729-8145>
Ingeborg J. Klarenberg  <https://orcid.org/0000-0002-9548-9069>

Data availability

Data (de Jonge, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.14497379>.

Inger K. de Jonge^{1*} , Peter Convey^{2,3,4,5} ,
Ingeborg J. Klarenberg¹ , Johannes H. C. Cornelissen¹
and Stef Bokhorst¹ 

¹Amsterdam Institute for Life and Environment (A-LIFE), Section Systems Ecology, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081HV, Amsterdam, the Netherlands;

²British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET, UK;

³Department of Zoology, University of Johannesburg, Auckland Park, 2006, South Africa;

⁴Millennium Institute – Biodiversity of Antarctic and Sub-Antarctic Ecosystems (BASE), Santiago, 8331150, Chile;

⁵School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK

(*Author for correspondence: email ingerdejonge@gmail.com)

References

- Armstrong RA. 2017. Adaptation of lichens to extreme conditions. In: Shukla V, Kumar S, Kumar N, eds. *Plant adaptation strategies in changing environment*. Singapore: Springer, 1–27.
- Armstrong RA, Welch AR. 2007. Competition in lichen communities. *Symbiosis* 43: 1–12.
- Asplund J, Bokhorst S, Kardol P, Wardle DA. 2015. Removal of secondary compounds increases invertebrate abundance in lichens. *Fungal Ecology* 18: 18–25.
- Asplund J, Wardle DA. 2017. How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews* 92: 1720–1738.
- Beckett RP, Minibayeva F, Solhaug KA, Roach T. 2021. Photoprotection in lichens: adaptations of photobionts to high light. *The Lichenologist* 53: 21–33.
- Begora M, Fahselt D. 2001. Photolability of secondary compounds in some lichen species. *Symbiosis* 31: 3–22.
- Bjerke JW, Elvebakk A, Domínguez E, Dahlback A. 2005b. Seasonal trends in usnic acid concentrations of Arctic, alpine and Patagonian populations of the lichen *Flavocetraria nivalis*. *Phytochemistry* 66: 337–344.
- Bjerke JW, Gwynn-Jones D, Callaghan TV. 2005a. Effects of enhanced UV-B radiation in the field on the concentration of phenolics and chlorophyll fluorescence in two boreal and arctic–alpine lichens. *Environmental and Experimental Botany* 53: 139–149.
- Bokhorst S, Asplund J, Convey P. 2024. Intra-specific variation in lichen secondary compounds across environmental gradients on Signy Island, maritime Antarctic. *Polar Biology* 47: 833–843.
- Bokhorst S, Asplund J, Kardol P, Wardle DA. 2015. Lichen physiological traits and growth forms affect communities of associated invertebrates. *Ecology* 96: 2394–2407.
- Chamberlain S, Oldoni D, Waller J. 2022. rgbif: interface to the global biodiversity information facility API. *Zenodo*. doi: [10.5281/zenodo.6023735](https://doi.org/10.5281/zenodo.6023735).
- Chiou CT, Kile DE. 1994. Effects of polar and nonpolar groups on the solubility of organic compounds in soil organic matter. *Environmental Science & Technology* 28: 1139–1144.
- Choler P, Michalet R, Callaway RM. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82: 3295–3308.
- Coley PD. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* 74: 531–536.
- Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik D, Hobbie S, Press M, Robinson C *et al.* 2001. Global change and Arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* 89: 984–994.
- Coxson DS, Coyle M. 2003. Niche partitioning and photosynthetic response of alectorioid lichens from subalpine spruce–fir forest in north-central British Columbia, Canada: the role of canopy microclimate gradients. *The Lichenologist* 35: 157–175.
- Dahlberg A, Bultmann H. 2013. Fungi. In: Meltofte H, ed. *Arctic biodiversity assessment. Status and trends in Arctic biodiversity*. Akureyri: Conservation of Arctic Flora and Fauna, Arctic Council, 303–319.
- Daminova AG, Rogov AM, Rassabina AE, Beckett RP, Minibayeva FV. 2022. Effect of melanization on thallus microstructure in the lichen *Lobaria pulmonaria*. *Journal of Fungi* 8: 791.
- de Jonge I. 2024. Data for paper 'Flexible or fortified? How lichens balance defense strategies across climatic harshness gradients'. *Zenodo*. doi: [10.5281/zenodo.14497379](https://doi.org/10.5281/zenodo.14497379).

- Delgado-Baquerizo M, Guerra CA, Cano-Díaz C, Egidi E, Wang JT, Eisenhauer N, Singh B, Maestre F. 2020. The proportion of soil-borne pathogens increases with warming at the global scale. *Nature Climate Change* 10: 550–554.
- Eichenberg D, Purschke O, Ristok C, Wessjohann L, Bruelheide H. 2015. Trade-offs between physical and chemical carbon-based leaf defence: of intraspecific variation and trait evolution. *Journal of Ecology* 103: 1667–1679.
- Elix JA, Stocker-Wörgötter E. 2008. Biochemistry and secondary metabolites. In: Nash TH, *Lichen Biology, 2nd edn*. Cambridge, UK: Cambridge University Press, 104–133.
- Fahsel D. 1994. Review article secondary biochemistry of lichens. *Symbiosis* 16: 117–165.
- Favero-Longo SE, Piervittori R. 2010. Lichen-plant interactions. *Journal of Plant Interactions* 5: 163–177.
- Fernandez CW, Koide RT. 2013. The function of melanin in the ectomycorrhizal fungus *Cenococcum geophilum* under water stress. *Fungal Ecology* 6: 479–486.
- Gauslaa Y. 1984. Heat resistance and energy budget in different Scandinavian plants. *Ecography* 7: 5–6.
- Gauslaa Y. 2005. Lichen palatability depends on investments in herbivore defence. *Oecologia* 143: 94–105.
- Gautam S, Singh J, Pant AB. 2011. Effect of UV-B radiations on the pigments of two Antarctic lichens of Schirmacher Oasis, East Antarctica. *Polish Polar Research* 32: 279–287.
- Gaya E, Fernández-Brime S, Vargas R, Lachlan RF, Gueidan C, Ramírez-Mejía M, Lutzoni F. 2015. The adaptive radiation of lichen-forming Teloschistaceae is associated with suncreening pigments and a bark-to-rock substrate shift. *Proceedings of the National Academy of Sciences, USA* 112: 11600–11605.
- Giez I, Lange OL, Proksch P. 1994. Growth retarding activity of lichen substances against the polyphagous herbivorous insect *Spodoptera littoralis*. *Biochemical Systematics and Ecology* 22: 113–120.
- Goga M, Antreich SJ, Bačkor M, Weckwerth W, Lang I. 2017. Lichen secondary metabolites affect growth of *Physcomitrella patens* by allelopathy. *Protoplasma* 254: 1307–1315.
- Grime JP. 1979. Primary strategies in plants. *Transactions of the Botanical Society of Edinburgh* 43: 151–160.
- Hájek J, Hojdová A, Trnková K, Váci P, Bednaříková M, Barták M. 2021. Responses of thallus anatomy and chlorophyll fluorescence-based photosynthetic characteristics of two Antarctic species of genus *Usnea* to low temperature. *Photosynthetica* 59: 95–105.
- Hawksworth DL, Grube M. 2020. Lichens redefined as complex ecosystems. *New Phytologist* 227: 1281.
- Hobbs RJ. 1985. The persistence of *Cladonia* patches in closed heathland stands. *The Lichenologist* 17: 103–109.
- Huneck S. 1973. Nature of lichen substances. In: Ahmadjian V, Hale ME, eds. *The lichens*. London, UK: Academic Press, 495–522.
- Huneck S. 1999. The significance of lichens and their metabolites. *Die Naturwissenschaften* 86: 559–570.
- Huneck S, Yoshimura I. 1996. *Identification of lichen substances*. Berlin: Springer.
- Inderjit, Callaway RM. 2003. Experimental designs for the study of allelopathy. *Plant and Soil* 256: 1–11.
- Inderjit Weston LA, Duke SO. 2005. Challenges, achievements and opportunities in allelopathy research. *Journal of Plant Interactions* 1: 69–81.
- John EA. 1989. An assessment of the role of biotic interactions and dynamic processes in the organization of species in a saxicolous lichen community. *Canadian Journal of Botany* 67: 2025–2037.
- Kappen L. 2000. Some aspects of the great success of lichens in Antarctica. *Antarctic Science* 12: 314–324.
- Kershaw KA. 1975. Studies on lichen-dominated systems. XII. The ecological significance of thallus color. *Canadian Journal of Botany* 53: 660–667.
- Lawrey JD. 2000. Chemical interactions between two lichen-degrading fungi. *Journal of Chemical Ecology* 26: 1821–1831.
- Lawrey JD. 2009. Chemical defense in lichen symbioses. In: White JF, Torres MS, eds. *Defensive Mutualism in Microbial Symbiosis*. Boca Raton, FL, USA: CRC Press, 185–200.
- Leiva D, Clavero-Leon C, Caru M, Orlando J. 2016. Intrinsic factors of *Peltigera* lichens influence the structure of the associated soil bacterial microbiota. *FEMS Microbiology Ecology* 92: fw178.
- Lücking R, Hodkinson BP, Leavitt SD. 2017. The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota—Approaching one thousand genera. *The Bryologist* 119: 361–416.
- Lud D, Huiskes AHL, Moerdijk TCW, Rozema J. 2001. The effects of altered levels of UV-B radiation on an Antarctic grass and lichen. *Plant Ecology* 154: 87–99.
- Mafole TC, Solhaug KA, Minibayeva FV, Beckett RP. 2019. Occurrence and possible roles of melanic pigments in lichenized ascomycetes. *Fungal Biology Reviews* 33: 159–165.
- Matveyeva N, Chernov Y. 2000. Biodiversity of terrestrial ecosystems. In: Routledge, ed. *The Arctic: Environment, people, policy*. Amsterdam, the Netherlands: Harwood Academic Publishers, 233–274.
- McCallum NC, Son FA, Clemons TD, Weigand SJ, Gnanasekaran K, Battistella C, Barnes B, Abeyratne-Perera H, Siwicka Z, Forman C *et al.* 2021. Allomelanin: A biopolymer of intrinsic microporosity. *Journal of the American Chemical Society* 143: 4005–4016.
- Melick DR, Seppelt RD. 1997. Vegetation patterns in relation to climatic and endogenous changes in Wilkes Land, continental Antarctica. *Journal of Ecology* 85: 43–56.
- Meylan WM, Howard PH, Boethling RS. 1996. Improved method for estimating water solubility from octanol/water partition coefficient. *Environmental Toxicology and Chemistry: An International Journal* 15: 100–106.
- Molnár K, Farkas E. 2010. Current results on biological activities of lichen secondary metabolites: a review. *Zeitschrift für Naturforschung. Section C* 65: 157–173.
- Neilson EH, Goodger JQ, Woodrow IE, Möller BL. 2013. Plant chemical defense: at what cost? *Trends in Plant Science* 18: 250–258.
- Nguyen KH, Chollet-Krugler M, Gouault N, Tomasi S. 2013. UV-protectant metabolites from lichens and their symbiotic partners. *Natural Product Reports* 30: 1490–1508.
- Nimis PL, Skert N. 2006. Lichen chemistry and selective grazing by the coleopteran *Lasioderma sericorne*. *Environmental and Experimental Botany* 55 (1–2): 175.
- Nybakken L, Solhaug KA, Bilger W, Gauslaa Y. 2004. The lichens *Xanthoria elegans* and *Cetraria islandica* maintain a high protection against UV-B radiation in Arctic habitats. *Oecologia* 140: 211–216.
- Nystuen KO, Sundsdal K, Opedal ØH, Holien H, Strimbeck GR, Graae BJ. 2019. Lichens facilitate seedling recruitment in alpine heath. *Journal of Vegetation Science* 30: 868–880.
- Øvstedal DO, Smith RL. 2001. *Lichens of Antarctica and South Georgia: a guide to their identification and ecology*. Cambridge, UK: Cambridge University Press.
- Pacé M, Paré D, Fenton NJ, Bergeron Y. 2020. Effects of lichen, *Sphagnum* spp. and feather moss leachates on jack pine and black spruce seedling growth. *Plant and Soil* 452: 441–455.
- Phinney NH, Asplund J, Gauslaa Y. 2022. The lichen cushion: a functional perspective of color and size of a dominant growth form on glacier forelands. *Fungal Biology* 126: 375–384.
- Phinney NH, Gauslaa Y, Solhaug KA. 2019. Why chartreuse? The pigment vulpinic acid screens blue light in the lichen *Letharia vulpina*. *Planta* 249: 709–718.
- Pizňák M, Bačkor M. 2019. Lichens affect boreal forest ecology and plant metabolism. *South African Journal of Botany* 124: 530–539.
- Raggio J, Green TGA, Sancho LG. 2016. In situ monitoring of microclimate and metabolic activity in lichens from Antarctic extremes: a comparison between South Shetland Islands and the McMurdo Dry Valleys. *Polar Biology* 39: 113–122.
- Rambold G, Elix JA, Heindl-Tenhunen B, Köhler T, Nash TH III, Neubacher D, Reichert W, Zedda L, Triebel D. 2014. LIAS light—towards the ten thousand species milestone. *Mycologia* 8: 11–16.
- Rheubottom SI, Barrio IC, Kozlov MV, Alatalo JM, Andersson T, Asmus AL, Baubin C, Brearley FQ, Egelkraut DD, Ehrlich D *et al.* 2019. Hiding in the background: community-level patterns in invertebrate herbivory across the tundra biome. *Polar Biology* 42: 1881–1897.
- Sancho L, De Los Ríos A, Pintado A, Colesie C, Raggio J, Ascaso C, Green A. 2020. *Himantormia lugubris*, an Antarctic endemic on the edge of the lichen symbiosis. *Symbiosis* 82: 49–58.
- Sancho LG, Pintado A, Navarro F, Ramos M, de M, Blanquer JM, Raggio J, Valladares F, Green T. 2017. Recent warming and cooling in the Antarctic

- Peninsula region has rapid and large effects on lichen vegetation. *Scientific Reports* 7: 5689.
- Schweiger AH, Ullmann GM, Nürk NM, Triebel D, Schobert R, Rambold G. 2022. Chemical properties of key metabolites determine the global distribution of lichens. *Ecology Letters* 25: 416–426.
- Sedia EG, Ehrenfeld JG. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. *Oikos* 100: 447–458.
- Solhaug KA, Gauslaa Y. 2001. Acetone rinsing—a method for testing ecological and physiological roles of secondary compounds in living lichens. *Symbiosis* 30: 301–315.
- Solhaug KA, Gauslaa Y. 2012. Secondary lichen compounds as protection against excess solar radiation and herbivores. In: Lüttge U, Beyschlag W, Büdel B, Francis D, eds. *Progress in botany*. Berlin, Heidelberg, Germany: Springer, 283–304.
- Solhaug KA, Larsson P, Gauslaa Y. 2010. Light screening in lichen cortices can be quantified by chlorophyll fluorescence techniques for both reflecting and absorbing pigments. *Planta* 231: 1003–1011.
- Spribille T, Tuovinen V, Resl P, Vanderpool D, Wolinski H, Aime MC, Schneider K, Stabentheiner E, Toome-Heller M, Thor G *et al.* 2016. Basidiomycete yeasts in the cortex of ascomycete macrolichens. *Science* 353: 488–492.
- Stamp N. 2003. Out of the quagmire of plant defense hypotheses. *Quarterly Review of Biology* 78: 23–55.
- Stark S, Hyvärinen M. 2003. Are phenolics leaching from the lichen *Cladonia stellaris* sources of energy rather than allelopathic agents for soil microorganisms? *Soil Biology and Biochemistry* 35: 1381–1385.
- Stark S, Kytöviita MM, Neumann AB. 2007. The phenolic compounds in *Cladonia* lichens are not antimicrobial in soils. *Oecologia* 152: 299–306.
- Swanson A, Fahselt D, Smith D. 1996. Phenolic levels in *Umbilicaria americana* in relation to enzyme polymorphism, altitude and sampling date. *The Lichenologist* 28: 331–339.
- Taguchi H, Sankawa U, Shibata S. 1969. Biosynthesis of natural products. VII. Biosynthesis of usnic acid in lichens. Seasonal variation observed in usnic acid biosynthesis. *Chemical and Pharmaceutical Bulletin* 17: 2061–2064.
- Tetko IV, Gasteiger J, Todeschini R, Mauri A, Livingstone D, Ertl P, Prokopenko VV. 2005. Virtual computational chemistry laboratory—design and description. *Journal of Computer-Aided Molecular Design* 19: 453–463.
- Tharayil N, Bhowmik PC, Xing B. 2006. Preferential sorption of phenolic phytotoxins to soil: implications for altering the availability of allelochemicals. *Journal of Agricultural and Food Chemistry* 54: 3033–3040.
- Woltyńska A, Gawor J, Olech MA, Górniak D, Grzesiak J. 2023. Bacterial communities of Antarctic lichens explored by gDNA and cDNA 16S rRNA gene amplicon sequencing. *FEMS Microbiology Ecology* 99: fiad015.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Methods S1 Data compilation and methods.

Methods S2 Sensitivity and robustness analyses.

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