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REVIEW

Lichen ecophysiology in a changing climate

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Abstract

Lichens are one of the most iconic and ubiquitous symbioses known, widely valued as indicators of environmental quality and, more recently, climate change. Our understanding of lichen responses to climate has greatly expanded in recent decades, but some biases and constraints have shaped our present knowledge. In this review we focus on lichen ecophysiology as a key to predicting responses to present and future climates, highlighting recent advances and remaining challenges. Lichen ecophysiology is best understood through complementary whole-thallus and within-thallus scales. Water content and form (vapor or liquid) are central to whole-thallus perspectives, making vapor pressure differential (VPD) a particularly informative environmental driver. Responses to water content are further modulated by photobiont physiology and whole-thallus phenotype, providing clear links to a functional trait framework. However, this thallus-level perspective is incomplete without also considering within-thallus dynamics, such as changing proportions or even identities of symbionts in response to climate, nutrients, and other stressors. These changes provide pathways for acclimation, but their understanding is currently limited by large gaps in our understanding of carbon allocation and symbiont turnover in lichens. Lastly, the study of lichen physiology has mainly prioritized larger lichens at high latitudes, producing valuable insights but underrepresenting the range of lichenized lineages and ecologies. Key areas for future work include improving geographic and phylogenetic coverage, greater emphasis on VPD as a climatic factor, advances in the study of carbon allocation and symbiont turnover, and the incorporation of physiological theory and functional traits in our predictive models.

KEYWORDS

acclimation, algal physiology, carbon balance, climate change, cryptogam, functional trait, lichen physiology, poikilohydry, symbiosis, VPD, water relations

SETTING THE SCENE

What is a lichen (not exactly an easy answer)?

Lichens are among the most iconic and widely known symbioses, and yet, a lot has been recently debated on how to better describe them (Hawksworth and Grube, 2020; Allen and Lendemer, 2022; Spribille et al., 2022). Broadly speaking, lichens are morphologically and physiologically integrated associations between at least one fungus and at least one phototroph, typically a green alga (“chlorolichens”) or cyanobacterium (“cyanolichens”). Associations

with more than two components are not uncommon and may in fact be the norm for some lineages (Spribille et al., 2022). The nomenclature of lichens is based on the primary fungal component; however, such a myco-centric perspective has limitations (Ertz et al., 2018; Spribille et al., 2022). As such, understanding lichens involves both considering the whole-thallus physiology (integrated holorganism), and also the interactions between the component organisms. These two interacting perspectives guide the structure of this review.

The broad definition above encompasses a tremendous amount of diversity (Figure 1), as lichenizing fungi have

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FIGURE 1 Examples of the diversity of lichen bionts, morphologies, and habitats. Image margins reflect the mycobiont (solid: Ascomycota; dashed: Basidiomycota) and photobiont (green: green chlorococcoid; orange: green filamentous; blue: cyanobacterial; blue and green: tripartite). (A) crustose *Buellia* sp. on desert grit, Pan de Azúcar, Chile; (B) foliose *Xanthoria* and *Physcia* on urban tree, Paris, France; (C) fruticose *Usnea antarctica* on rock, King George Island, Antarctica; (D) diverse folioliculous lichens, near Tabatinga, Amazonas, Brazil; (E) crustose *Cryptothecia* on dry forest in the Pantanal biome, Mato Grosso do Sul, Brazil; (F) foliose *Leptogium* in lowland rainforest near Tabatinga, Amazonas, Brazil; (G) fruticose *Roccella peruensis* on mediterranean scrub, Santa Barbara, California, USA; (H) calicioid *Chaenotheca hispidula* from boreal forest, Minnesota, USA; (I) crustose *Collemopsidium* sp. on barnacle, Maine, USA; (J) foliose *Pseudocyphellaria vaccina* in temperate rainforest, Chaitén, Chile (arrow: cephalodia); (K) crustose *Placopsis* sp. and fruticose *Stereocaulon* sp. in road cut, Chaitén, Chile (arrow: cephalodia); (L) filamentous *Coenogonium* in subtropical forest, Mississippi, USA; (M) crustose *Multiclavula* in lowland rainforest near Tabatinga, Amazonas, Brasil; (N) foliose *Cora* sp. in tropical montane forest, Rio Grande do Sul, Brazil; (O) dimorphic *Cladonia* on sand dune, Mississippi, USA; (P) leprose *Lepraria* sp. in hyperarid desert, Alto Patache, Chile. Photo credits: A, D, F, G, I–K, M, P (D. Stanton); B, C, E, L, N, O (N. Koch); H (J. Thayer).

originated convergently in multiple lineages of Ascomycota and Basidiomycota, and lichenizing phototrophs derive from an even greater range of origins (Spribille et al., 2022). While some aspects of the lichen association are considered foundational, such as the exchange of carbon between fungus and phototroph, others may differ greatly depending on phylogenetic and/or ecological context.

The study of lichen physiology and ecology has largely prioritized larger lichens (“macrolichens”) in the temperate to boreal environments (Figure 2; Appendix S1) where most lichen researchers have historically been based, with additional attention to polar environments where lichens are apparent, abundant, and contribute to a large proportion of the biomass

(e.g., Figure 1C) (Asplund and Wardle, 2016). However, lichens are present in nearly all ice-free terrestrial environments and in some semiaquatic and tidal ecosystems. These biases arise not only from pragmatic considerations (ease of manipulation, proximity to laboratory facilities), but also from economic constraints and colonial legacies that have overlooked the diversity and importance of lichens at lower latitudes. This is a critical gap because these low-latitude ecosystems are of global ecological and biogeochemical importance and the lichens in the tropics can differ greatly phylogenetically and physiologically from the best-studied temperate taxa (Lange et al., 2000; Rivas Plata, Lücking and Lumbsch, 2008; Pardow et al., 2010; Dal-Forno et al., 2013).

Studies by Biome

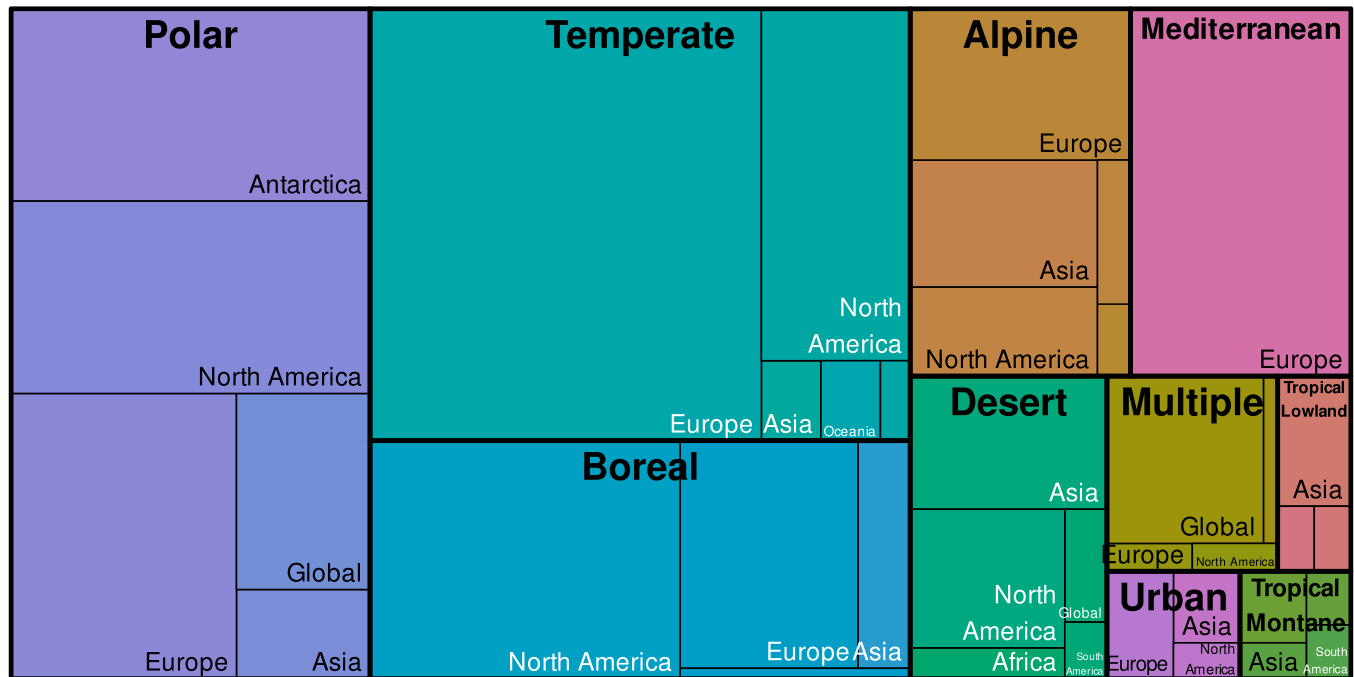


FIGURE 2 Geographic biases in current studies of lichens and climate change. A survey of current literature on lichens and climate change (see Appendix S1 for details) reveals a predominance of high latitudes climates (polar, boreal, and temperate) and European and North American study sites. Box size is relative to the number of studies.

Even the common assertion that lichens are most ecologically important at high latitudes is questionable, with Miranda-González, McCune (2020) estimating that the biomass of lichens in a Mexican tropical dry forest is equivalent to ~50% of leaf mass. In this review, we aim to highlight gaps in understanding arising from these historical biases, as well as recent work, which leads toward a more universal comprehension of lichen ecophysiology. We also draw attention to additional environmental factors (e.g., nutrients, pollution, biotic interactions) that can exacerbate or mask physiological responses to climate. By identifying and highlighting those gaps, we aim to compile a background to better describe and forecast lichen responses to climate change.

Whole-thallus physiology

Poikilohydry is the central dynamic concept in lichen physiology. In contrast to vascular plants, which have evolved mechanisms to decouple their metabolic activity from the surrounding climate, lichens, as poikilohydric organisms, equilibrate their internal water content with the surrounding atmosphere. Their activity is thus very dynamic, often changing on time scales of minutes to hours. This dynamic activity is often associated with desiccation tolerance, the ability to revive following periods of very low cellular water content (Kranner et al., 2008). It is worth noting that desiccation tolerance is different from drought tolerance,

which involves maintaining metabolism through periods of reduced water content (Proctor, 2000). Desiccation tolerance is a prominent feature for lichens from both hot and cold dry habitats (Gasulla et al., 2021), while lichens from humid environments have only very limited tolerance to full desiccation (Green and Lange, 1991; Kranner et al., 2008).

The water sources triggering physiological activity in lichens include rain, fog, dewfall (Gauslaa, 2014), and many lichens are also known to be reactivated by water vapor (Lange et al., 1986). Reactivation by water vapor seems to be a common feature of lichens growing in moist and humid habitats, where the air is naturally often carrying a high volume of water (high water potential) such as coastal and tropical forests (Pardow et al., 2010; Phinney et al., 2018) and, less intuitively, in drier systems. Parts of the Namib, Atacama, and Negev deserts, for example, sustain abundant lichen growth because here, the right combination of microclimatic factors (Jonsson et al., 2008) regularly triggers vapor-induced reactivation (Lange et al., 2006; Wilske et al., 2008; Maphangwa et al., 2012). Warm and hot climates may be particularly favorable to vapor usage, because the volume of available water (vapor pressure at saturation, e_{sat}) increases greatly with temperature (Figure 3A). Reactivation by vapor is facilitated by strongly negative water potentials in the photobiont cells (Figure 3B, and possibly mycobiont, but see Figure 5). This potential appears to vary across habitats (Figure 3B) although the number of studies has been quite limited (Appendix S2).

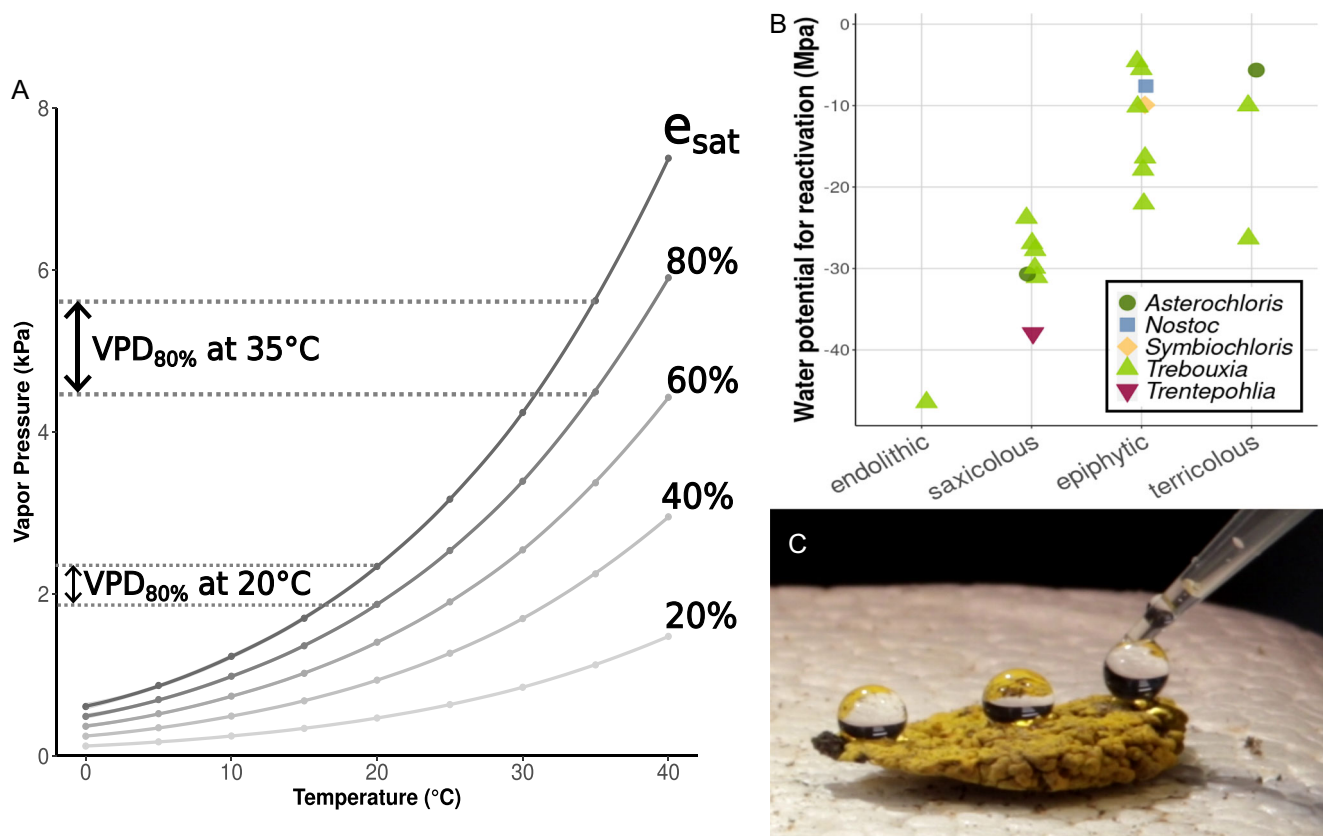


FIGURE 3 The role of vapor pressure deficit as an ecophysiological factor for lichens. (A) Illustration of the effect of temperature on saturating vapor pressure (e_{sat}) and vapor pressure at different relative humidities. (B) Water potential for reactivation by substratum and photobiont type based on available publications (see Appendix S2 for references). (C) Extreme hydrophobicity is observed for some lichen species adapted to high humidity environments, such as *Chrysothrix* from the Alto Patache fog oasis, northern Chile.

In contexts where the climate dynamics do not regularly sustain high water potentials, there is little evidence that water vapor reactivation is a realized trait (Pannewitz et al., 2003; del Prado and Sancho, 2007; Colesie et al., 2018). It should also be noted that distinguishing between water vapor and dew (liquid water deposited during temperature changes) in the field is often challenging, leading to frequent conflation of these mechanistically quite different water sources.

A challenge that emerges from lichens' ability to use multiple water sources is that commonly used climate metrics such as mean annual precipitation (MAP) are very poor predictors of lichen activity. As an integrator across air moisture and temperature, vapor pressure differential (VPD, Figure 3A; sometimes also referred to as saturation deficit) describes the difference between the amount of water vapor that the air is holding and the maximum at that temperature, and so it provides insight into both the drying stress and the potential for vapor uptake. Relative humidity (RH), which is sometimes reported instead of VPD, is far less physiologically informative; for example, drying stress increases greatly with temperature even when RH is held constant (Figure 3A). Fortunately, VPD is easily calculated from Temperature (T) and RH data as $0.611 \times e^{[17.502 T /$

$(T + 240.97)] \times (1 - RH/100)$ or similar parameterizations (Campbell and Norman, 1998). It is worth highlighting the duality of the impact of temperature: high temperatures greatly increase both the possible degree of drying stress (VPD) and the total pool of available vapor water when conditions are saturating (e_{sat}). The value of VPD for understanding lichen physiology is increasingly evident from long-term in situ studies made possible by technological advances such as the use of chlorophyll fluorescence monitoring systems (Schroeter et al., 2011; Raggio et al., 2017). These studies collectively demonstrate that thallus moisture content and activity are interconnected with temperature and VPD in a natural setting.

The isolated response of lichen physiology to hydration level depends on the water source and photobiont identity (Figures 3B, 4). Low levels of thallus hydration with liquid water can cause an overall negative carbon gain (resaturation respiration; Farrar and Smith, 1976); however, this phenomenon is not universal (Lange et al., 2006). With increasing thallus hydration, net photosynthesis (NP) increases until all cells are fully turgid (Figures 4, 5). In the case of rehydration by vapor, algal cells may achieve full turgor while fungal cells remain cavitated (Scheidegger et al., 1995), which is linked to very low respiration rates in the vapor-hydrated state

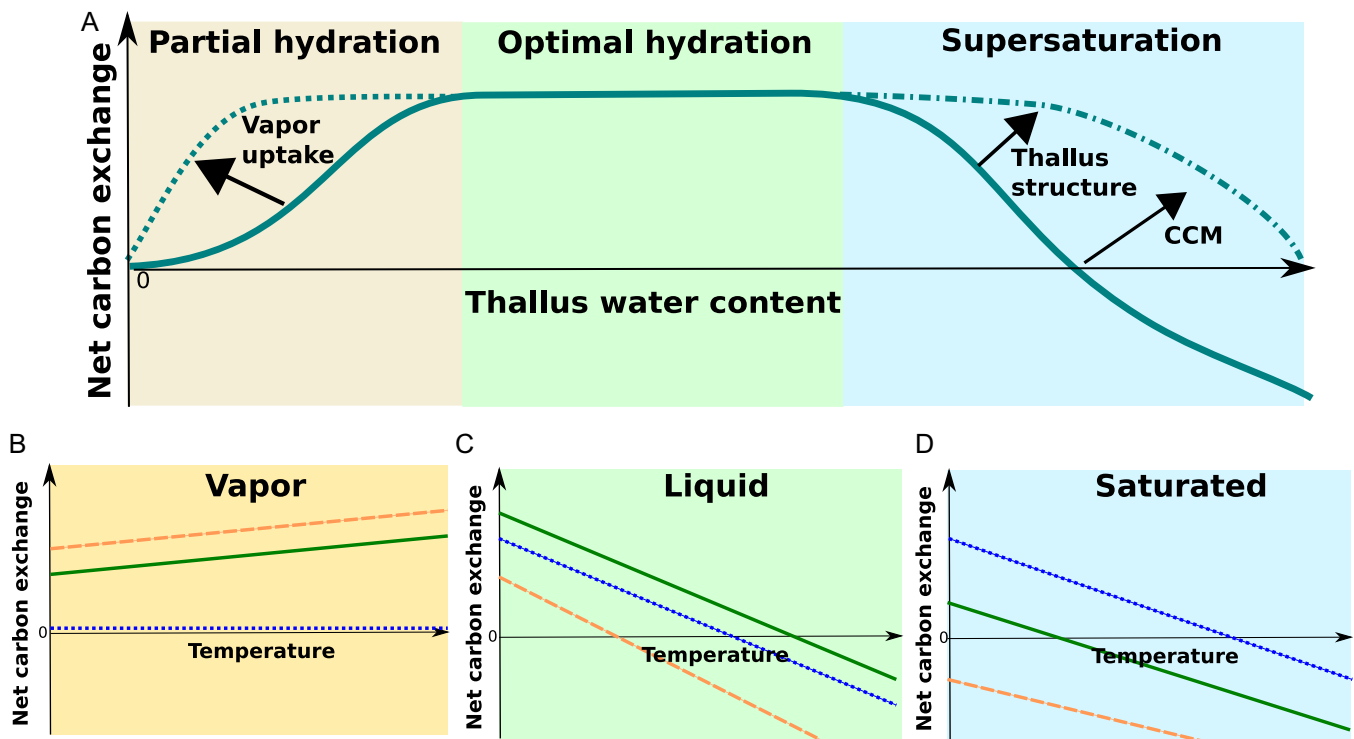


FIGURE 4 Idealized lichen thallus physiological responses to water content and temperature. (A) Lichen physiological activity in response to thallus water content. Net carbon exchange varies with the state of thallus hydration and can be affected by thallus structure and photobiont physiology, as the presence of carbon-concentrating mechanisms. Solid line represents the standard response to liquid water, with dashed lines representing the differing responses arising from vapor uptake, carbon-concentrating mechanisms and complex thallus structure. (B–D) Putative responses of net carbon exchange to temperature for different hydration states from vapor (B) to optimal (C) and saturating liquid (D), highlighting potential differences driven by photobiont physiology (blue: cyanobacterial, green: green algal with pyrenoids, orange: green algal without pyrenoids).

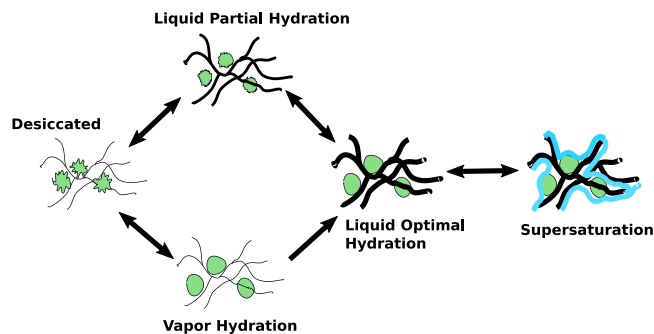


FIGURE 5 Variation in cell turgor with hydration state. Recovery from a low-turgor, desiccated state can involve partial turgor recovery of both mycobiont and photobiont (liquid partial hydration) or turgor recovery of the photobiont only (vapor hydration). Drying from optimal hydration leads to partial hydration of both bionts. In supersaturation, the presence of extracellular water may interfere with gas exchange.

(Lange et al., 1986; del Prado and Sancho, 2007). Once fungal and algal cells have reached full turgor, any additional water will remain extracellular (Esseen et al., 2017), which can lead to a depression in NP rates through limited CO₂ diffusion on the algal cell wall (Lange et al., 1996) (Figure 4C). The degree of saturation depression depends on photobiont physiology (see section 1.3). Many lichen species present adaptations to saturation through thallus-level properties such as

hydrophobic surfaces (Figure 3C), specialized tissues retaining air (medulla) and/or pores (such as cyphellae, pseudocyphellae, and similar structures).

The isolated response of lichen physiology to temperature shows that respiration increases with increasing temperature (Figure 4; Lange and Green, 2005), whilst gross photosynthesis increases until about 30°C before beginning to decline. As a consequence, lichen net photosynthesis has an optimal temperature above which further increases of respiration depress net carbon gain. The optimal temperatures for photosynthesis can vary with seasonal acclimation (MacKenzie et al., 2001; Lange and Green, 2005), as well as across climates (Domaschke et al., 2013; Colesie et al., 2016), and it has been shown that daily net CO₂ exchange can become negative at moderately elevated temperatures especially when the lichen is active and hydrated during the night (e.g., Lange et al., 2000; Lange and Green, 2005; Alam et al., 2015).

Other than high temperatures, high light levels can also cause significant stress in hydrated and active lichens via a process called photoinhibition and the formation of reactive oxygen species (Barták et al., 2004; Bianchi et al., 2019; Beckett et al., 2021). Species including *Lobaria pulmonaria* are able to increase synthesis of pigments that protect against light-associated photoinhibition (Gauslaa and Solhaug, 2004), but this defense mechanism is dependent

on the thallus hydration status and the species. For example, hydration can increase photoinhibition in sun-adapted species, but decrease in shade-adapted species (Gauslaa and Solhaug, 2004). This highlights the three-dimensional character of lichen physiology. Lichen net photosynthesis is a complex response to varying water content, temperature, and light availability, and optimum response curves can only display responses to individual factors, which limits the interpretability for natural settings especially in the climate change context.

Photobiont physiology

Although much of the physiology of lichens is driven by the association as an integrated whole, some aspects are specific to the photosynthetic symbiont, particularly those related to carbon assimilation. Lichen photobionts derive from a number of phylogenetically and physiologically disparate lineages, and this diversity can be quite consequential for lichen physiology. An important distinction is often made between lichens with eukaryotic photobionts (typically green algae) and those with cyanobacteria as the primary photobiont (Palmqvist, 2000). The latter differ in their photo-physiology, but also in that they are also capable of nitrogen-fixation, typically in differentiated cells. The competing needs for carbon and nitrogen fixation introduce a trade-off in photobiont functions that is absent in chlorolichens.

Another major difference between photobiont lineages is their response to water saturation (Figure 4). Many green algal lineages and all lichenized cyanobacterial lineages have carbon-concentrating mechanisms (CCMs) that mitigate carbon-limitation in saturating conditions. These anatomical adaptations are not, however, universal and have been convergently lost in multiple algal lineages, especially in terrestrial/subaerial environments (e.g., *Trentepohlia*, *Symbiochloris*). Lichenized algae lacking CCMs are therefore more susceptible to carbon limitation by water saturation (Palmqvist et al., 1997) but potentially more tolerant of low light (Koch et al., 2022) and better able to utilize water vapor (Phinney et al., 2019), with consequences for distributions along environmental gradients (Koch et al., in press).

Component interactions

For lichens to grow as a symbiotic system, resource allocation and the transfer of fixed carbon from a photosynthesizing symbiont to the fungus needs to be controlled within the thallus. Growth depends on photosynthetic carbon assimilation minus respiratory CO₂ losses. In a lichen thallus, carbohydrate acquisition is directly related to photobiont photosynthesis, while carbon is lost through myco- and photobiont respiration (and leachates). It has long been accepted that even though the mycobiont appears to dominate in terms of biomass, the metabolic demands of this fungal tissue must be lower than that which can be supported by the photobiont. However, this

relationship is now refined by the suggestion that some lichens may augment fixed CO₂ with carbon from external sources (Resl et al., 2022). Within the thallus, lichens can optimize resource investments between carbohydrate input and expenditure tissue (Colesie et al., 2016) according to the growth differentiation balance theory, and/or invest in nitrogen resources so that their maximal carbon input capacity was increased (Palmqvist et al., 2002).

WHAT IS AT STAKE IN A CHANGING ENVIRONMENT?

Observed changes in response to climate

Climate change is placing increasing pressure on lichens; however, many of the observed responses appear to be habitat and/or species specific, making it difficult to identify universal responses. In cold environments such as Antarctica, species responses to increased temperature are mixed, with some species sensitive and others seemingly unaffected or enhanced (Bokhorst et al., 2016), although growth rates may be positively associated with temperature (Sancho et al., 2017, 2019). In temperate and mediterranean environments warming has more often been found to have negative effects, such as reducing species numbers (Aptroot and van Herk, 2007), cover (Escobar et al., 2012) and growth (Smith et al., 2018), often attributed to degradation of photosynthetic capacity (Pisani et al., 2007) and photobiont loss (Meyer et al., 2023).

Many species experiencing climate warming respond by shifting their spatial distribution and migrating into cooler climates (Parmesan, 2006; Allen and Lendemer, 2016; Devkota et al., 2019). The distribution broadens when climate change results in a greater availability of suitable bioclimatic space, as seen in warm-temperate species (Rubio-Salcedo et al., 2017). Responses are highly species-specific and dependent on life history traits such as dispersal, leading to community composition changes. Limited dispersal capacity in asexually reproducing species (Löbel et al., 2006) or photobiont availability in sexually reproducing species (Belinchón et al., 2014) may limit ability to track the changing climate. However, as discussed above, it is important to remember that warming is often conflated with increased VPD, leading to shortened periods of hydration and increased respiratory demands.

The interaction of temperature and hydration (typically reflected as precipitation in macroclimatic studies, which may fail to capture VPD dynamics) has significant impacts on lichen community composition (Ellis et al., 2007). For example, a shift toward lichens with *Trentepohlia* as the photobiont, that have a southerly distribution, was seen in the Netherlands as a direct response to climate warming (Aptroot and van Herk, 2007). Given that *Trentepohlia* lacks a carbon-concentrating mechanism (see Photobiont physiology section), this community shift can be seen as favoring a warm-adapted and vapor-using photobiont. However, warm-adapted does not mean climate-resilient;

Smith et al. (2020) found that most vulnerable North American lichen communities are from low-elevation and southerly sites. There is a complex interaction of microclimatic factors, including aspect, shading from plants, snow cover and soil moisture content in determining lichen species response to macroclimate (Veres et al., 2020).

Observed changes in response to nutrient availability

In addition to direct, climate-related effects, the availability of nutrients may influence lichen growth and physiological responses. Increased N availability may lead to increased photobiont proportions and photosynthetic rates in some lichens (Johansson et al., 2011), whilst increased P availability can increase growth, particularly of cyanolichens (Benner and Vitousek, 2007, 2012; McCune and Caldwell, 2009), especially in habitats with low background levels of P (McCune and Caldwell, 2009). On the other hand, elevated N levels can have deleterious effects on the symbiotic equilibrium, with green algal photobionts benefiting disproportionately and causing both intra- (Palmqvist et al., 2017) and interspecific (Gaio-Oliveira et al., 2005) competition. Such changes can leave the lichen disadvantaged during heavy rain events, which can cause physical disruption and expose the lichen to parasitic fungal attack (Johansson et al., 2012). Conversely, heavy precipitation can also dilute N deposition onto lichens and potentially increase leaching rates (Geiser et al., 2010), allowing physiological processes that fix N to continue. Nitrogen fertilization might have wider, ecosystem-scale implications also, for example, through altering gastropod-grazing regimes (Asplund et al., 2010), which have the potential to ultimately alter N inputs into the habitat. The effects of N and P availability are often interacting (e.g., Johansson et al., 2011; Ochoa-Hueso et al., 2013; Wang et al., 2019), and micronutrients associated with N fixation, such as Mo and V, can also influence activity and growth rates of some lichens (Darnajoux et al., 2017). However, there is a pressing need for more such studies, as well as the inclusion of more phylogenetic and geographic breadth.

The effects of increasing ambient CO₂ on lichens has been shown to be variable, with some species increasing photosynthetic rates and growth, whilst in others there is little or no fertilization effect (Lange and Green, 2008; Smith et al., 2018; Meyer et al., 2023). Baldauf et al. (2021) suggest that CO₂ fertilization in *Diploschistes diacapsis* is able to mitigate the negative effects of reduced moisture associated with climate change. Considering the interacting effects of CO₂, temperature and moisture changes may result in the masking or exacerbation of any one given climate factor.

Observed changes in response to pollution

Lichens are directly affected by changes in air quality, as shown in multiple studies globally, although some of them are

good at accumulating heavy metals and used as biomonitors for this type of air pollutants (Conti and Cecchetti, 2001). Disentangling the effects of climate change and air pollution is not always an easy task (Munzi et al., 2014), since they may mask or amplify the negative effects of each other, and can be particularly challenging with pollutants that can also be nutrients, such as N (Gutiérrez-Larruga et al., 2020). Besides, different lichen species have different responses to air quality changes (Pinho et al., 2008; Koch et al., 2016).

Since the end of the industrial revolution and associated S and N deposition, lichen populations have not recolonized to their pre-pollution levels and compositions, likely a result of reduced genetic diversity within the remaining population and poor dispersal capabilities (Weldon and Grandin, 2021). Within mediterranean climates, elemental (Zn, Ti, Mg) and NO₂ pollution has resulted in significant changes in species composition, with a shift from oligotrophic-dominated communities to nitrophytic-dominated (Pinho et al., 2008). In subtropical regions, lichen communities from lower to higher air pollution towns showed contrasting patterns as well, with shifts not only in species composition, but richness and cover (Koch et al., 2016).

Furthermore, previous air quality effects are found to exacerbate current and ongoing climate effects. Past SO₂ pollution and ongoing N pollution is still preventing the succession of lichen communities within urban areas in the UK due to persistent acidification of bark pH (Llewellyn et al., 2020). The shift toward *Trentepohlia*-dominated lichen communities initiated by warming is more pronounced within previously heavily polluted areas. Niches left vacant after pollution-induced species decline are now being utilized by species that were able to persist in less favorable climates, preventing communities from returning to their pre-pollution composition (Aptroot and van Herk, 2007; Geiser et al., 2021).

Observed change in response to ecosystem interactions

Frequently, predictions of the effects of climate change on biodiversity are obtained from studies at macroscales, often without consideration of fine-scale microclimatic conditions in which small, immobile species experience their environment (Frey et al., 2016). When considering the forest habitat, suitable microclimates are determined by features including habitat structure, light exposure, tree age, species, bark structure, and associated pH. These features are often found to be more important than macroclimate in increasing lichen growth and diversity (Johansson et al., 2007; Moning et al., 2009).

Light availability is often determined by habitat structure. High light levels such as those found along forest edges and in open habitats can reduce lichen photosynthetic activity and growth (Gauslaa et al., 2006; Pardow et al., 2010; Veres et al., 2020), often attributed to associated reduced

moisture availability (Gauslaa et al., 2006). Low light levels found within dense forest canopies (Gauslaa et al., 2006), for example, along with shading from competitive vascular vegetation, plant litter (Cornelissen et al., 2001; Serpe et al., 2013), or snow cover (Bjerke et al., 2011) result in reduced photosynthetic performance and growth.

Herbivory pressure, in particular from gastropods, is known to constrain growth and reduce lichen cover (Greiser et al., 2021) and influence the distributions of epiphytic lichen species (Asplund et al., 2010). When considering the interactive effect of climate change on herbivory pressure, it is difficult to quantify a direct response. Post et al. (2022) showed that *Peltigera* sp. was less common within an experimentally warmed system lacking herbivores, yet increased with the introduction of large herbivores, possibly explained by warming in the absence of herbivores, allowing uncontrolled vegetation growth. These results contrast with those of other studies showing negative effects of large herbivores through trampling damage, especially in dry conditions (Heggenes et al., 2020). More studies are needed to disentangle the direct (e.g., consumption, trampling) and indirect (changing light and nutrient availability) effects of herbivores on lichens.

Lichens are often sensitive to and have species-specific host and/or substratum requirements, which can be problematic when considering, for example, pathogens such as the one that causes ash dieback, which typically results in the death of ash trees and their associated lichens (Jönsson and Thor, 2012). In this case, there is some hope that climate-mediated range shifts will decouple ash trees from their pathogen (Goberville et al., 2016), benefitting lichen communities, but in other contexts climate change may drive mismatches between epiphytic lichens and their host trees (Zhao et al., 2019).

MECHANISTIC UNDERSTANDING

Lichen acclimation pathways

Lichen acclimation to changing conditions can occur at multiple scales: within individual symbionts, in the interactions between symbionts, and in the realized collective phenotype of the symbiosis, and even in the genetic identity of the symbionts constituting the lichen (Figure 6). These pathways to acclimation are not mutually exclusive, but reflect some of the conceptual challenges associated with the physiological ecology of symbiotic associations.

Acclimation within an individual symbiont has been documented in both photo- and mycobiont components. Multiple studies have reported seasonal patterns in the photosynthetic properties of lichenized green algae, primarily through shifts in chlorophyll fluorescence parameters such as F_v/F_m (MacKenzie et al., 2001; Pisani et al., 2007; Vivas et al., 2017) and temperature responses of assimilation rates (MacFarlane et al., 1983; Colesie et al., 2018), but other studies have found no seasonal effects on algal components (Tegler and Kershaw, 1980). In considering such studies, it can be important to distinguish between “true” acclimation, i.e., changes in temperature or light optima when measured under standard conditions, and seasonal variation in performance, which may or may not derive from acclimation. Seasonal acclimation in dark respiration rates, which are primarily attributable to the mycobiont, have also been documented (Lange and Green, 2005), these often reduce seasonal variation in realized respiration rates. Studies of acclimation by algal or fungal components are nearly all from mid to high latitudes where seasonality primarily affects temperature and day length. Equivalent studies of

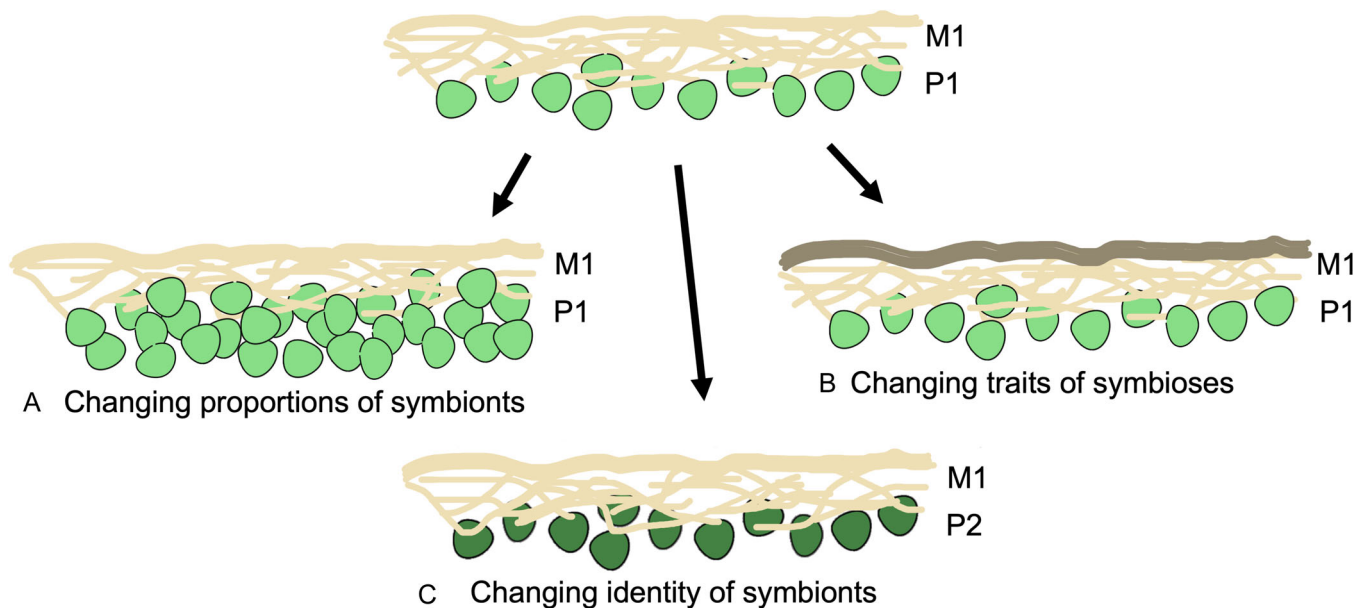


FIGURE 6 Pathways for lichen acclimation at the thallus scale, illustrated with an idealized lichen composed of one mycobiont (M1) and one photobiont (P1 or P2).

acclimation at low latitudes where seasonality more often affects water availability and in deciduous forests where seasonality greatly affects light levels are currently lacking and sorely needed.

While acclimation through biochemical changes within symbionts is well documented, acclimation can also take the form of changes in the symbiotic association. Because only the photobiont contributes to carbon gain, at least in our current understanding of lichen symbiosis (but see Spribille et al., 2022) for a discussion of alternative perspectives), the relative proportions of the symbionts (Figure 6A) have a big impact on carbon balance. Greater fungal to algal ratios are associated with higher respiration and lower net assimilation. Shifting ratios of symbionts are therefore a pathway to acclimation, which has been observed as changes in photobiont density with season (Tretiach et al., 2013), across environmental gradients (Sun and Friedmann, 2005; Colesie et al., 2017; Williams et al., 2017) and in response to nutrient additions (Johansson et al., 2011; Palmqvist et al., 2017). Nutrient availability can also affect the abundance of secondary symbionts such as the cyanobacteria in tripartite lichens, in which decreased biomass of cephalodia as in *Peltigera aphthosa* thalli exposed to high N deposition occurs (Palmqvist et al., 2017).

Acclimation can further occur through changes in the realized phenotypes of the lichen association (Figure 6B), which may or may not overlap with changing proportions of the symbionts. This scale of acclimation would encompass many of the observations of intraspecific variation in response to environmental gradients, including variation in functional traits (see below).

Lastly, acclimation through symbiont turnover (Figure 6C) has also been proposed but is less certain. A tendency for mycogenic perspectives on lichens means that most reported cases involve changes in photobionts, but changing mycobiont identity should also be considered possible (Spribille et al., 2022). The dominant genotypes of photobionts within a given lichen association have been observed to vary across local and regional environmental gradients (Vargas Castillo and Beck, 2012; Rolshausen et al., 2020), and even possibly within-thallus gradients (Casano et al., 2011). However, these observational studies cannot distinguish between within-thallus turnover and changing associations across generations, and little is known about the rates of individual algal cell turnover within thalli. A transplant experiment was unable to induce photobiont turnover in the soil crust lichen *Psora decipiens* (Williams et al., 2017), although a recent climate change experiment suggests temperature-induced photobiont genotype changes in the boreal epiphyte *Evernia mesomorpha* (Meyer et al., 2023). Novel techniques are needed to adequately document photobiont (and possibly mycobiont) cell and genotype turnover.

Functional traits as integrative approach

Describing the physiological, anatomical, and morphological responses of lichens to environmental context is often

complicated by the vast array of lineages and forms that fall within the category of lichen association. As with many other organisms, a functional trait perspective that emphasizes shared attributes in a mechanistic framework has proven to be a powerful approach. In its ideal form, a functional trait framework would enable predictions of future responses on a mechanistic basis, without the need for taxon-specific studies. While a unifying framework on the scale of the leaf economic spectrum (LES) is still lacking, a few traits have been shown to bridge effectively across lineages (Ellis et al., 2021). Given the centrality of water content to physiology (see above), water-holding capacity (WHC) has been found to be a good predictor of the duration of physiological activity and even, to an extent, water sources (Gauslaa, 2014). In addition to being relatively easy and inexpensive to measure (especially for macrolichens), it is quite closely related to the equally simple specific thallus mass (STM; mass/area) and water content at maximum assimilation.

Additional traits are needed if we are to develop a more universal functional framework. Water relations are driven not only by WHC, but also by rates of water acquisition and loss. Water-holding capacity may be impacted by surface properties (Lakatos et al., 2006) and photobiont physiology (Phinney et al., 2019; Koch et al., 2022), while the latter may be quite responsive to thallus temperature and therefore albedo (color/albedo studies). It is also important to recognize that not all potential traits will be universally applicable. Current efforts have prioritized larger foliose and fruticose lichens, due to their greater visibility and ease of manipulation, but these only represent a subset of the overall diversity of lichen associations. Future efforts should broaden the taxonomic coverage of trait measurements and evaluate their interaction with other factors such as pollution and herbivory.

RESEARCH GAPS

Practical and historical biases

Our current understanding of lichen physiology is constrained by significant practical and conceptual biases. Although observational studies of community shifts and responses to climate have at times considered all growth forms, physiological studies have been largely confined to the larger taxa that are most amenable to experimentation. Often the evidence for particular phenomena is based on studies of one or a very few taxa. While quite understandable from a practical standpoint, this narrow evidence base limits our predictive abilities and mostly constrains studies to a limited set of lineages, almost all in the Lecanoromycetes clade of Ascomycota. The applicability of these findings to other lineages and even other growth forms is often uncertain. These taxonomic biases are a problem worldwide, but particularly pronounced for tropical and subtropical areas where microlichens make up the majority

of the diversity and biomass. There is a pressing need to adapt existing methodologies and develop new ones for measurements on microlichens and other growth forms.

The phylogenetic/morphological bias in knowledge is further compounded by very strong geographic biases in studies, that have prioritized the northern hemisphere, mid to high latitudes where most researchers have historically been based, with the addition of concentrated studies on polar regions in both hemispheres. In contrast, tropical regions, and the global south are very poorly represented in the existing literature (Figure 2), with limited but notable exceptions. Many of these understudied regions are not only exceptionally diverse, they are also projected to be amongst the most strongly impacted by future climate change. Closing this critical knowledge gap will require not only an increase in studies in those regions, but also concerted efforts to promote local research activity in lichen physiology and functional ecology, as well as the development of low-cost and efficient methodologies that can be more widely adopted.

Misconception of the importance of VPD

Throughout this review, the profound importance of the atmospheric moisture budget as a factor affecting lichen ecophysiology shines through. However, most studies emphasize mostly aspects of temperature change when examining climate change effects. This focus has left a significant gap in understanding the effects of VPD as a climate driver, notably the effects on periods of activity and the relationship between drying rate and stress. For vascular plants, VPD has long been identified as an increasingly important driver of plant functioning and has been established as a major contributor in recent drought-induced plant mortality (Grossiord et al., 2020). For lichens, we can reasonably suggest that negative effects of increased VPD might have even more significant (and potentially lethal) consequences, given the poikilohydric lifestyle of these organisms. Therefore, climate projections for the next 100 years showing VPD to increase on an even steeper slope than temperature (McDowell et al., 2022) paint a grim picture and underline the need for further research into this topic.

Determination of photobiont turnover rates

One of the more exciting developments in the past decade in lichenology has been increased understanding of the genetic diversity within thalli (Piercey-Normore, 2006; Casano et al., 2011) and the degree to which the genetic identity, especially of photobionts, can vary across environmental gradients (Dal Grande et al., 2018; Rolshausen et al., 2020). These findings raise the intriguing possibility of climate acclimation at the thallus level through turnover of photobiont strains, which is a major mechanism for

acclimation to climate change in another iconic photosynthetic symbiosis, marine corals (Sampayo et al., 2016). However, although we increasingly understand symbiont switching at evolutionary and generational timescales, there is still no understanding of the turnover rates of algal cells and genotypes within established thalli. We posit this as a critical area for future research if we are to understand the potential for lichen acclimation and adaptation to changing climates.

Determination of thallus internal carbon allocation

Studies on thallus internal carbon allocation patterns date back to 1978, when Farrar (1978) described that photosynthetically produced sugars can be allocated to different pools within the thallus. Palmqvist et al. (2002) proposed that lichens are able to optimize their resource investments between carbohydrate input and expenditure, suggesting that a carbon economy view might be a fruitful way to compare and understand the performance and acclimation of different lichens (Palmqvist, 2000). However, this approach has only very rarely been used (Colesie et al., 2014), and to our knowledge, no experimental study has tested these mechanisms in a climate change context. This knowledge gap is especially relevant now, where new findings suggest that within the complexities of the lichen symbiosis, even external carbohydrate sources might be of relevance (Resl et al., 2022) and the functional roles of photosynthates may differ from common assumptions (Spribille et al., 2022).

Multifactor interactions

The responses of lichens to climate change rarely happen in a vacuum: physiological responses to climate interact with numerous other factors such as pollution, nutrient availability and biotic context. These factors may mitigate negative impacts, as has been suggested with CO₂ fertilization or moderate increases in nutrient supply. They may also mask or exacerbate effects, as when poor air quality interferes with climate-driven successional shifts in lichen communities or unavailability of adequate host trees prevents climate migration. There is a need for more studies of these interactions, in particular where physiological and functional traits may predict responses (e.g., thallus hydrophobicity and susceptibility to wet deposition, N. Koch, University of Minnesota, personal communication).

Any lichen trait framework that emerges in coming years must be capable of accommodating the fact that many physiology-related traits also interact with other factors. For example, pigments may influence albedo and mitigate light stress, but many of those same compounds also reduce invertebrate and microbial attack (Asplund and Wardle, 2016).

Surface properties such as hydrophobicity, which can reduce the risk of saturation, may also reduce exposure to wet deposition of nutrients and pollutants. A unifying trait framework, which makes cross-species comparisons possible, will make it easier to discern which factors are driving trait selection in different environments and communities.

Mechanistically informed modeling of future changes

Disentangling drivers of species interactions and responses is difficult as interactive effects are complex, and lichens may respond to spatial and temporal scales that are poorly represented by current climate data. Models often focus on macroclimate and overlook local scale drivers such as species-specific functional traits (e.g., dispersal capacity, host specificity) and biotic habitat features that alter the microclimatic space (Ellis, 2019; Nascimbene et al., 2020). These drivers will further interact with past and present pollution and management to constrain present and future distributions. Only with consideration of the interaction of these local drivers alongside macroclimate data can models be reliable across broad scales (Eaton and Ellis, 2012).

Furthermore, predictive models would benefit from more explicit inclusion of ecophysiological theory. The responses to increased temperature and water availability are likely to differ considerably across photobiont lineages and physiologies (see Photobiont physiology section; Figure 4), and yet these distinctions are rarely explicitly included. Some of the most physiologically important factors, such as time spent in vapor hydration or saturation occurs at time scales (hours) that are poorly captured by macroclimate data (monthly and annual averages). Longer timescales are also important to consider: The adaptive responses of the algal symbiont *Trebouxia* to increases in temperature and reduced moisture availability have been found to evolve slower than the current rate of climate change and be less adaptive to hot and dry conditions (Nelsen et al., 2022).

KEY CONCLUDING MESSAGES

The study of lichens as “sentinels of climate change” has progressed greatly in recent years, but some significant knowledge gaps and biases persist. Even though lichens are ubiquitous and easily observed, future studies will need to account for their biological complexity (as multiorganismal assemblages), physiological attributes (poikilohydry and interspecific interactions) and evolutionary diversity (paraphyletic combinations of fungi and phototrophs forming structurally and ecologically diverse associations). Embracing this diversity and complexity is the key to overcoming historical biases and building physiologically informed predictions for this most iconic of symbioses.

AUTHOR CONTRIBUTIONS

D.E.S., A.O., and C.C. designed the study; D.E.S. and C.C. wrote the sections Setting the scene, Mechanistic understanding, and Research gaps with input from N.M.K. and A.O.; A.O. wrote the section What is at stake in a changing environment? with input from D.E.S., N.M.K., and C.C.; D.E.S. and N.M.K. developed figures with input from C.C. and A.O.; all authors revised and edited the manuscript.

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DATA AVAILABILITY STATEMENT

All data (data sources for Figures 2 and 3) used in this review is included in the supplementary information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Overview of existing literature database search methods.

Appendix S2. Data sources for Figure 3B.

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