

A call to reconceptualize lichen symbioses

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Several decades of research across disciplines have overturned historical perspectives of symbioses dominated by binary characterizations of highly specific species–species interactions. This paradigm shift has unlocked the previously underappreciated and overlooked dynamism of fungal mutualisms such as mycorrhizae. Lichens are another example of important fungal mutualisms where reconceptualization is urgently needed to realize their potential as model systems. This reconceptualization requires both an objective synthesis of new data and envisioning a revised integrative approach that unifies the spectrum of ecology and evolution. We propose a ten-theme framework that if pursued would propel lichens to the vanguard of symbiotic theory.

Success of lichen symbioses

Fungi that form mutualistic **symbioses** (see [Glossary](#)) are successful organisms, with high species richness, essential ecosystem functions, global geographic distribution, and abundance, even dominance, in many habitats, even extreme ones [1–6]. **Mycorrhizae** and **lichens** are two examples of broadly successful, keystone fungal symbioses with global importance [7,8]. Their success is attributed to benefits inherent in their lifestyles [9,10]. By and large mutualistic fungal symbioses are characterized by **symbiont flexibility**, in striking contrast to the specificity seen in many comparable plant and animal systems (e.g., corals or orchids and their pollinators [1,11–13]. Symbiont flexibility has long been recognized in mycorrhizal fungi, in part due to tractability of the symbiotic system to experimental study in diverse settings [6,8,14]. Until recently, symbiont flexibility was believed largely to be the exception in lichens, in part due to the intractability of the symbiotic system to experimentation in highly controlled laboratory conditions [15–17]. In fact, a growing body of evidence challenges this assumption as rapid advances in molecular data generation and analysis have led to increasing recognition that lichen symbioses are far more complex, diverse, and flexible than has long been assumed [18–23].

Narrow focus on studying the classical conception of the symbiosis (i.e., binary pairs of symbionts exclusively driven by the fungal species) has overshadowed overwhelming evidence that symbiont diversity and flexibility, rather than the symbiosis itself, is the causal mechanism for lichen success. New data and analytical tools have repeatedly forced reconceptualization of lichens for centuries [24,25], and recent reconceptualization has focused on the existence and nature of the symbiosis [26,27]. Current advances in understanding the implications and outcomes stemming from symbiont diversity and flexibility demand a novel perspective on the patterns and processes within lichens, the communities they form, and the ecosystems within which they function. Here, we present a transformational framework for lichen biology, ecology, and evolution through which the potential of these dynamic organisms can be unlocked and placed at the vanguard of science. This framework is organized around ten facets that illuminate the full spectrum of intrinsic characteristics and reciprocal interactions that exist within lichen symbioses.

Highlights

Partner flexibility is increasingly recognized as integral to successful mutualistic symbioses.

Fungi are some of the most diverse, impactful, and widespread mutualistic symbionts.

Growing evidence from lichen genomics, biochemistry, evolution, and ecology are challenging long-held perspectives on these key groups of mutualists.

We draw on this new research to present a framework for reconceptualizing lichens and propose lichen symbioses as ideal model systems.

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Lichen origins

Lichens have evolved more than ten times independently across the fungal tree of life [28]. Their forms are an exquisite example of **convergent evolution**, fulfilling congruent functions in unrelated evolutionary lineages. Yet, we lack a comprehensive understanding of their evolutionary and mechanistic origins from the perspectives of all the symbionts, including the primary fungus and its cohort of photosynthesizing partners [29,30]. How and why do lichens evolve? Do the fungi consistently transition from saprotrophs as appears to be the case in the Dothideomycetes [31]? Does the holobiont arise consistently through abrupt lichenization events or as stepping stones from partial to full lichenization? For the fungi, investigation of gene content and genome architecture supports the stepping-stone model [32,33], but analyses with multiple independent contrasts placed in a strong statistical framework are needed. Finally, do specific climatic conditions drive interactions between lichen symbionts and facilitate **trophic** transitions to lichenization [34]?

Speciation rates and mechanisms

There are more than 20 000 described species of lichen fungi belonging to over 100 fungal families [28]. These range from highly diverse lineages undergoing rapid radiations, to less diverse, ancient lineages that may be living fossils [35–40]. Species richness and evolutionary diversity of the photosynthesizing partners remains incompletely known, but recent advances suggest remarkable and previously underappreciated diversity across evolutionary scales [12,41]. Despite a wealth of phylogenetic study and robust higher-level evolutionary framework, the timing and processes that underlie diversity at and below the species level have been infrequently investigated [39–42]. Slow rates of speciation have been inferred or assumed across lineages of lichen fungi based on long-held assumptions of broad geographic distributions, slow growth rates, and unlimited dispersal ability [43]. These assumptions are contradicted by recent studies (see following section) and based on limited availability of fine-grain phenotypic, demographic, and genetic data across broad evolutionary and spatial scales. Integration of lichens into the general theoretical framework of speciation processes, validated by empirical genome-wide data, is urgently needed.

The individual

Much like vascular plants, spatially discrete lichens have been assumed to be homogeneous throughout: consisting of a single haploid fungal genotype and a single genotype of a photosynthesizing partner [44–46]. This reflects a legacy of botanical study in which lichens were initially considered to be plants rather than fungi, the latter of which are widely recognized to form genetically heterogeneous colonies in nature [47]. Even direct comparative anatomical evidence to the contrary failed to shift this lichen–plant paradigm for nearly a century until DNA sequencing firmly integrated lichens to the fungal phylogeny [25]. Recent studies have demonstrated what appears to be a single, discrete, lichen individual composed of multiple distinct fungal genotypes [45,48] growing seamlessly together. The assumption that the absence of sexual reproductive structures implies complete fungal cellular haploidy has also been challenged [49] as has the absence of hybridization as an evolutionary process [50]. There is also substantial evidence that each lichen hosts a diverse community of photosynthesizing partners in varying levels of abundance [51–53] and degrees of **symbiont specificity** [21,54]. The aforementioned suggests that there is an urgent need to reconceptualize general theory about lichens, which has been based on incorrect assumptions about the homogeneous composition of the individual (Figure 1). This has direct implications for population genetics and speciation, especially in organisms that can have enormous population sizes (Figure 2).

Microbial microcosm

Until recently the internal portions of a lichen were thought to consist mostly of tissue from a single fungus and one, or rarely two, photosynthesizing partners [16,44]. There is now extensive

Glossary

Biosynthetic pathway: a series of chemical reactions in living organisms that are catalyzed by enzymes.

Biotic interactions: interactions between two or more living organisms.

Commensalism: a symbiotic relationship in which one partner benefits while the other is neither harmed nor benefited.

Convergent evolution: a character that arises independently in evolutionary unrelated organisms.

Ecological amplitude: the total breadth of multidimensional ecological conditions in which a species can survive.

Lichens: extraordinarily complex communities of microbial symbionts from a minimum of three evolutionarily distantly related phyla representing at least two kingdoms and that repeatedly form a phenotypically consistent, recognizable, mutually beneficial symbiosis. Taxonomically classified by the primary fungus and defined by a quintessential mutualistic relationship between that fungus and one or more photosynthesizing partners.

Mutualism: a symbiotic relationship in which all partners benefit.

Mycorrhizae: soil-dwelling fungi that form mutualistic symbiotic relationships with plants wherein hyphae connect directly to the roots.

Poikilohydry: when an organism remains at equilibrium with the moisture content of the surrounding environment.

Primary metabolite: substances that are generated through the processes that maintain the basic functions in cells and organisms.

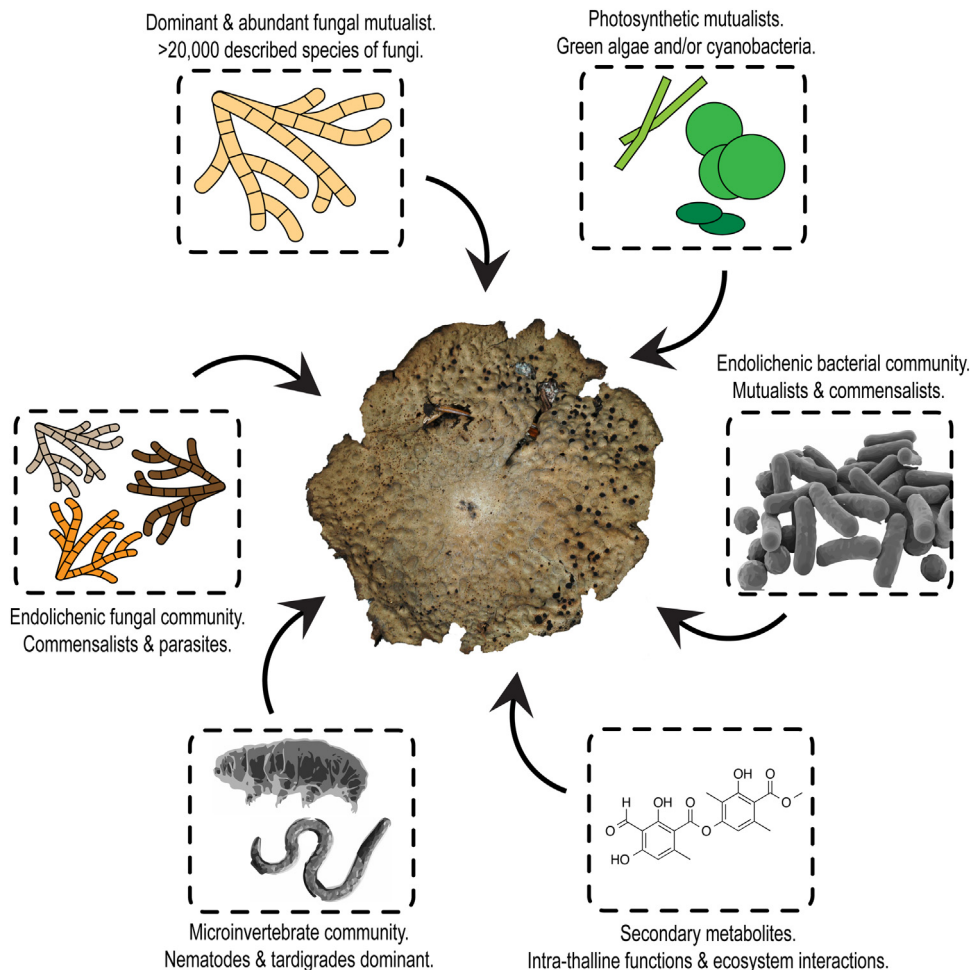
Secondary metabolite: substances produced by organisms that are not required for primary metabolism, vary between species, and with concentrations that can vary across tissues or growth stages.

Symbiont flexibility: the ability of one symbiont to associate with a diversity of other symbiont species or genotypes.

Symbiont specificity: the degree of taxonomic breadth and genetic diversity among partners in a symbiosis (e.g., one-to-one versus one-to-many).

Symbiosis: intimate, sustained biotic interactions with variable degrees of benefits for the partners involved.

Trophic (strategy): the means by which an organism acquires essential nutrients.



Trends in Ecology & Evolution

Figure 1. Lichen thallus deconstructed. Each individual lichen is comprised of a multitude of organisms that together constitute a miniature ecosystem. One primary mutualistic fungal symbiont contributes the majority of the biomass and structure to the thallus, and one or more photosynthesizing symbionts constitute the most important photosynthetic partners. Other species of fungi and microalgae, along with bacteria and micro-invertebrates, grow as commensalists in and among the scaffold of the dominant symbionts. Some species of fungi grow as pathogens and parasites. Secondary chemistry produced by the main fungal symbiont drives the functional interactions among organisms in the thallus and with the environment.

evidence that lichens host diverse and abundant bacterial communities throughout their bodies, and that these communities can be collectively dispersed as part of routine reproduction [55]. Lichens have also been shown to host diverse communities of non-lichen fungi whose functional roles vary across the entire symbiotic spectrum from **commensalism** and **mutualism** to parasites and pathogens [18,19,56–58]. Microbial communities are also known to be spatially structured and environmentally determined, with different lichen species sharing microbes and the same species having a varied microbiome across the range of habitats and locations where it occurs [59,60]. These advances follow the trend across biology of increased recognition of the essential role of microbial communities in the evolution, function, and health of macroscopic organisms [61,62]. Functional characterization of the lichen microbiome is needed to link a decade of robust descriptive work with the patterns and processes that have contributed to the remarkable success of lichens, as well as their characteristic sensitivity to disturbance.

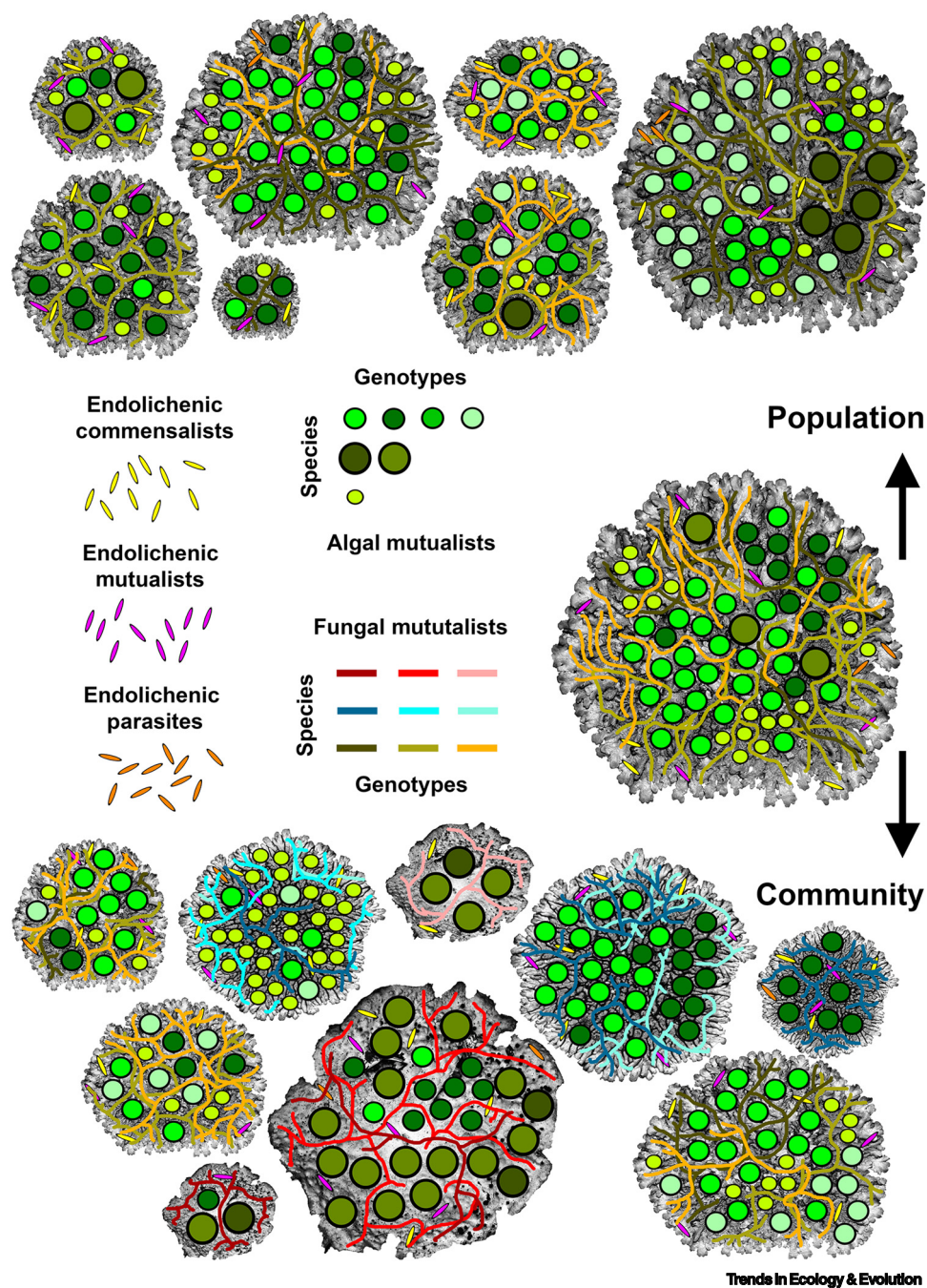


Figure 2. Recent research has shown lichen individuals, populations, and communities can be more diverse and dynamic than previously believed. Based on molecular sequence data and advanced microscopy techniques, it is increasingly clear that what is perceived as a visually discrete individual lichen (middle) is often home to multiple genotypes of the primary mutualistic fungal symbiont, multiple genotypes and/or species of mutualistic photosynthesizing symbionts, and a microbiome containing species with a range of symbiotic lifestyles. New methods and theory are required to account for ecological and evolutionary patterns and processes related to the complexities that result when this previously unrecognized diversity is extrapolated outwards within populations of a single species (top) and communities of multiple species (bottom).

Metabolite economy

Diverse scientific fields recognize lichens as quintessential mutualistic symbioses wherein the role and function of each symbiotic partner is clearly delimited. The photosynthesizing partner provides sugars to the heterotrophic fungus and in return the fungal partner provides an environment where the other partner is shielded from harsh extremes [63,64]. The symbiosis expands the **ecological amplitude** of the partners involved [34,43]. Polysaccharides and disaccharides are key symbiont signaling molecules [27,43,65], in addition to providing food and structures [4]. There is ample evidence that lichens host miniature ecosystems that include many organisms (e.g., microinvertebrates, parasitic fungi including yeasts, endolichenic fungi, bacteria, and archaea [66]). Without a holistic, integrated perspective of nutrient cycling and metabolic processes that incorporates the full range of **biotic interactions** within the entire intra-lichen community, it is not possible to completely characterize the functional roles of these diverse organisms. Shifting the conceptualization of lichens from a binary fungal-photosynthesizing partner interaction to a trophic network model could transform ecosystem ecology through development of tractable, small-scale, natural model systems.

Secondary metabolite biosynthesis

In addition to **primary metabolites**, many hundreds of unique secondary compounds are produced by lichen fungi and their associated microbiomes [26,67]. These compounds have been implicated in numerous functions essential to the lichen, mediating interactions with abiotic and biotic stressors both internally and externally. Although important to lichens, the evolutionary and ecological processes leading to the production of these compounds are similar to those in other fungi and plants [68]. Hence, from a systems perspective, lichen **biosynthetic pathways** are neither enigmatic nor functionally novel. Lichen **secondary metabolites** have been intensively characterized primarily for use in taxonomy and systematics [69,70]. However, the genetic underpinnings of these compounds and their biosynthesis remains both poorly characterized and little integrated with biosynthesis in other secondary metabolite-rich organisms. Detailed characterization of lichen biosynthesis, including heterologous expression of biosynthetic gene clusters in filamentous fungal systems, will prove indispensable in the search for novel compounds with application in medicine, industry, and the environment.

Reproductive biology

Lichens are characterized by a unique and complex reproductive biology that contrasts strongly with that of other organisms, especially vertebrates and plants [54,71]. The absence of sexual selection coupled with functionally indefinite life spans due to **poikilohydry**, vegetative reproduction, and rampant clonality results in organisms that completely defy classification using existing life history frameworks [72]. Lichen reproductive biology is not morphologically driven and gamete synthesis is not phenologically timed; however, existing understanding is shaped by theory from organisms that have highly structured and discrete life histories. Accounting for the unique aspects of reproduction across each lichen symbiont, as well as collectively for the holobiont, has profound implications for the calculation of key metrics such as generation length, population size, fecundity, migration, and gene flow. Transcending these constraints will vastly expand the horizon of evolutionary theory and computational biology by requiring a new conceptual framework and novel analytical tools. A lichen-derived framework and associated tools will provide a unique opportunity to elucidate an understanding of reproductive biology that is inclusive of all organisms.

Facilitation and community establishment

Lichens are widely applied as bioindicators due to their nuanced responses to environmental change, disturbance, and pollutants [73,74]. Anthropogenic impacts reduce lichen species richness and community complexity [75,76]. Recovery from these impacts occurs over protracted

timescales beyond observational frameworks of the modern scientific era [77–79]. To date, complete recovery to preimpact conditions has yet to be documented [80]. Instead recovery results in novel communities missing sensitive species and skewed towards stress tolerant taxa [81,82]. Microbiome data have shown lichen symbiont pools to be highly structured at small scales and shared among locally occurring species [60,83]. Dispersal and migration limitations usually restrict successful establishment to small, local scales while establishment at long distances is rare or absent [37]. The challenges imposed by long-distance single-symbiont dispersal and migration are overcome by symbiont flexibility, by which the fungus may associate with an evolutionarily constrained variety of photosynthetic partners (e.g., a specific species, genus, or family) [84]. Symbiont flexibility is the general rule in lichens, and the few lineages that exhibit strict symbiont specificity are comparatively less resilient to disturbance, fragmentation, and other forms of change [83,85]. These phenomena suggest that healthy and diverse lichen communities require extensive ecological and symbiotic facilitation coupled with temporal habitat continuity. Full characterization of these processes, uniting perspectives from physiology, population genetics, microclimate ecology, and microbial interactions could unlock the fundamental basis of community assembly and specialization. Concurrently it could allow for the development of broadly applicable effective data driven conservation methods for sensitive symbiotic organisms.

Everything is not everywhere

Fungal biology has been dominated by a narrative that organisms are not dispersal limited and their distributions are entirely shaped by ecological requirements [86,87]. Despite decades of evidence to the contrary [88–90], this implicit bias is present in lichenology, pervasive in interdisciplinary environments, and has limited perspectives on lichen diversity across evolutionary and spatial scales. Molecular studies spanning an evolutionary gradient from populations to species have accelerated a paradigm shift away from ‘everything is everywhere’ [37,82,91,92], but the legacy continues to influence hypothesis development and data interpretation. A shift from this historical perspective to greater objectivity has the potential to uncover previously overlooked diversity and organizational complexity connected to fundamental biological concepts with broad relevance to all organisms with small propagules.

Integrate lichens into biodiversity science

Lichens are integral to ecosystems, the environment, and human society at large [7]. Yet, in the midst of the current planetary crisis and collapse of natural systems, comprehensive understanding of these essential organisms continues to be sabotaged by a synergy of multiple factors. There is a widespread, erroneous perception of lichens as having minor importance on the global stage of biodiversity. At the same time they are considered fundamentally unknowable, intractable study systems. Finally a legacy of academic discrimination, stemming from centuries old taxonomic misclassifications, continues to result in study of lichen symbionts by-and-large in isolation from their closest evolutionary relatives. Reinterpretation and reconceptualization of lichen biology is key to accurately integrating these remarkable symbioses into global biodiversity.

Concluding remarks

Fungal symbioses are diverse, dynamic interactions at the nexus between macroscopic and microscopic realms. These complex relationships weave throughout the evolutionary history of life on Earth, connecting diverse kingdoms and global ecosystems across space and time. Historical perspectives of symbioses were dominated by assumptions of strong symbiont specificity and binary species–species interactions. Ample evidence has now demonstrated that for mutualistic symbioses success lies in flexible trans-kingdom partnerships. We propose that lichens are iconic mutualisms poised to be the next model system that synthesizes and accelerates theory and practice in symbiotic ecology and evolution (see [Outstanding questions](#)).

Outstanding questions

What intrinsic and extrinsic factors lead to gains and losses of lichenization?

What molecular mechanisms underpin trophic shifts to and from lichenization?

What is the rate of accumulated genetic divergence between species and populations?

Among species and individuals, how frequently do lichens comprised of multiple genetically distinct symbiont partners form and how are compatible genotypes recognized?

How frequently does hybridization and polyploidy occur in lichenized fungi?

What is the interaction network of the microbial microcosm?

Which lichen secondary metabolites provide solutions to urgent challenges in human health, the environment, and industry?

What are the life history traits and population genetic structure of species of lichen symbionts, and how can these be characterized?

How do dispersal, establishment, and biotic interactions underpin species assemblages and distributions?

How does community reassembly differ between natural and anthropogenic disturbances?

How can generalized patterns and processes observed in lichens integrate with symbiotic theory broadly?

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Declaration of interests

No interests are declared.

References

- Selosse, M.A. *et al.* (2006) Mycorrhizal networks: des liaisons dangereuses? *Trends Ecol. Evol.* 21, 621–628
- Watkinson, S.C. (2016) Mutualistic symbiosis between fungi and autotrophs. In *The Fungi* (3rd edn) (Watkinson, S.C. *et al.*, eds), pp. 205–243, Academic Press
- Martin, F.M. *et al.* (2017) Ancestral alliances: plant mutualistic symbioses with fungi and bacteria. *Science* 356, eaad4501
- Khokhani, D. *et al.* (2021) Deciphering the chitin code in plant symbiosis, defense, and microbial networks. *Annu. Rev. Microbiol.* 75, 583–607
- Elliott, T.F. *et al.* (2019) A global review of the ecological significance of symbiotic associations between birds and fungi. *Fungal Divers.* 98, 161–194
- Rimington, W.R. *et al.* (2020) The distribution and evolution of fungal symbioses in ancient lineages of land plants. *Mycorrhiza* 30, 23–49
- Asplund, J. and Wardle, D.A. (2016) How lichens impact on terrestrial community and ecosystem properties. *Biol. Rev. Camb. Philos. Soc.* 92, 1720–1738
- Powell, J.R. and Rillig, M.C. (2018) Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytol.* 220, 1059–1075
- Naranjo-Ortiz, M.A. and Gabaldón, T. (2019) Fungal evolution: major ecological adaptations and evolutionary transitions. *Biol. Rev. Camb. Philos. Soc.* 94, 1443–1476
- Genre, A. *et al.* (2020) Unique and common traits in mycorrhizal symbioses. *Nat. Rev. Microbiol.* 18, 649–660
- Suggett, D.J. *et al.* (2017) Symbiotic dinoflagellate functional diversity mediates coral survival under ecological crisis. *Trends Ecol. Evol.* 32, 735–745
- Sanders, W.B. and Masumoto, H. (2021) Lichen algae: the photosynthetic partners in lichen symbioses. *Lichenologist* 53, 347–393
- van der Kooij, C.J. *et al.* (2021) Mutualisms and (a)symmetry in plant-pollinator interactions. *Curr. Biol.* 31, R91–R99
- Ward, E.B. *et al.* (2021) Ericoid mycorrhizal shrubs alter the relationship between tree mycorrhizal dominance and soil carbon and nitrogen. *J. Ecol.* 109, 3524–3540
- Athukorala, S.N. *et al.* (2014) Identification and comparison of the 3 early stages of resynthesis for the lichen *Cladonia rangiferina*. *Can. J. Microbiol.* 60, 41–52
- Brodo, I.M. *et al.* (2001) *Lichens of North America*, Yale University Press
- Trembley, M.L. *et al.* (2002) Morphological and molecular analysis of early stages in the resynthesis of the lichen *Baeomyces rufus*. *Mycol. Res.* 106, 768–776
- Sprille, T. *et al.* (2016) Basidiomycete yeasts in the cortex of ascomycete macrolichens. *Science* 353, 488–492
- Tuovinen, V. *et al.* (2019) Two basidiomycete fungi in the cortex of Wolf Lichens. *Curr. Biol.* 29, 476–483
- Hawksworth, D.L. and Grube, M. (2020) Lichens redefined as complex ecosystems. *New Phytol.* 227, 1281–1283
- Dal Forno, M. *et al.* (2021) Extensive photobiont sharing in a rapidly radiating cyanolichen clade. *Mol. Ecol.* 30, 1755–1776
- Pardo-De la Hoz, C.J. *et al.* (2022) Phylogenetic structure of specialization: a new approach that integrates partner availability and phylogenetic diversity to quantify biotic specialization in ecological networks. *Ecol. Evol.* 12, e8649
- Grimm, M. *et al.* (2021) The lichens' microbiota, still a mystery? *Front. Microbiol.* 12, 714
- Mitchell, M.E. (2007) Signposts to symbiosis: a review of early attempts to establish the constitution of lichens. *Huntia* 13, 101–120
- Honegger, R. (2000) Simon Schwendener (1829–1919) and the dual hypothesis of lichens. *Bryologist* 103, 307–313
- Calcott, M.J. *et al.* (2018) Secondary metabolism in the lichen symbiosis. *Chem. Soc. Rev.* 47, 1730–1760
- Nazem-Bokaei, H. *et al.* (2021) Towards a systems biology approach to understanding the lichen symbiosis: opportunities and challenges of implementing network modelling. *Front. Microbiol.* 12, 667864
- Lücking, R. *et al.* (2016) The 2016 classification of lichenized fungi in the Ascomycota and Basidiomycota – approaching one thousand genera. *Bryologist* 119, 361–416
- Ametrano, C.G. *et al.* (2022) Should we hail the Red King? Evolutionary consequences of a mutualistic lifestyle in genomes of lichenized ascomycetes. *Ecol. Evol.* 12, e8471
- Nelsen, M.P. *et al.* (2020) No support for the emergence of lichens prior to the evolution of vascular plants. *Geobiology* 18, 3–13
- Schoch, C. *et al.* (2009) The Ascomycota tree of life: a phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Syst. Biol.* 58, 224–239
- Wedin, M. *et al.* (2004) Saprotrophy and lichenization as options for the same fungal species on different substrata: environmental plasticity and fungal lifestyles in the *Stictis-Conotrema* complex. *New Phytol.* 164, 459–465
- Armaleo, D. *et al.* (2019) The lichen symbiosis re-viewed through the genomes of *Cladonia grayi* and its algal partner *Asterochlorella glomerata*. *BMC Genom.* 20, 1–33
- Nelsen, M.P. *et al.* (2021) Macroecological diversification and convergence in a clade of keystone symbionts. *FEMS Microbiol. Ecol.* 97, fiab072
- Leavitt, S.D. *et al.* (2012) Miocene divergence, phenotypically cryptic lineages, and contrasting distribution patterns in common lichen-forming fungi (Ascomycota: Parmeliaceae). *Biol. J. Linn. Soc.* 107, 920–937
- Kaasalainen, U. *et al.* (2017) A Caribbean epiphyte community preserved in Miocene Dominican amber. *Earth Environ. Sci. Trans. R. Soc. Edinb.* 107, 321–331
- Allen, J.L. *et al.* (2018) First genome-wide analysis of the endangered, endemic lichen *Cetrionia linearis* reveals isolation by distance and strong population structure. *Am. J. Bot.* 105, 1556–1567
- Simon, A. *et al.* (2018) High diversity, high insular endemism and recent origin in the lichen genus *Stictis* (lichenized Ascomycota, Peltigerales) in Madagascar and the Mascarenes. *Mol. Phylogenet. Evol.* 122, 15–28
- Itten, B. and Honegger, R. (2010) Population genetics in the homothallic lichen-forming ascomycete *Xanthoria parietina*. *Lichenologist* 42, 751–761
- Allen, J.L. *et al.* (2021) Population genetics and biogeography of the Lungwort lichen in North America support distinct eastern and western gene pools. *Am. J. Bot.* 108, 2416–2424
- Muggia, L. *et al.* (2020) Formally described species woefully underrepresent phylogenetic diversity in the common lichen photobiont genus *Trebouxia* (Trebouxiophyceae, Chlorophyta): an impetus for developing an integrated taxonomy. *Mol. Phylogenet. Evol.* 149, 106821
- Alonso-García, M. *et al.* (2021) population genomics of a reindeer lichen species from North American lichen woodlands. *Am. J. Bot.* 108, 159–171
- Nelsen, M.P. *et al.* (2020) The macroevolutionary dynamics of symbiotic and phenotypic diversification in lichens. *Proc. Natl. Acad. Sci. U. S. A.* 117, 21495–21503
- Ahmadjian, V. (1967) *The Lichen Symbiosis*, Blaisdell Publishing
- Nadyeina, O. *et al.* (2017) Polymorphic fungus-specific microsatellite markers of *Bactrospora dryina* reveal multiple colonizations of trees. *Lichenologist* 49, 561–577

46. Tripp, E.A. *et al.* (2017) A review of existing whole genome data suggests lichen mycelia may be haploid or diploid. *Bryologist* 120, 302–310
47. Smith, A.L. (1922) In *Lichens. Cambridge Botanical Handbooks* (Seward, A.C. and Tansley, A.G., eds), University Press
48. Mansournia, M.R. *et al.* (2012) Genotypic analysis of the foliose lichen *Parmotrema tinctorum* using microsatellite markers: association of mycobiont and photobiont, and their reproductive modes. *Lichenologist* 44, 419–440
49. McKenzie, S.K. *et al.* (2020) Complete, high-quality genomes from long-read metagenomic sequencing of two wolf lichen thalli reveals enigmatic genome architecture. *Genomics* 112, 3150–3156
50. Keuler, R. *et al.* (2020) Genome-scale data reveal the role of hybridization in lichen-forming fungi. *Sci. Rep.* 10, 1497
51. Muggia, L. *et al.* (2014) Photobiont selectivity leads to ecological tolerance and evolutionary divergence in a polymorphic complex of lichenized fungi. *Ann. Bot.* 114, 463–475
52. Molins, A. *et al.* (2021) Thallus growth stage and geographic origin shape microalgal diversity in *Ramalina farinacea* lichen holobionts. *J. Phycol.* 57, 975–987
53. Blázquez, M. *et al.* (2022) The role of photobionts as drivers of diversification in an island radiation of lichen-forming fungi. *Front. Microbiol.* 12, 784182
54. Steinhová, J. *et al.* (2019) Reproductive and dispersal strategies shape the diversity of mycobiont-photobiont association in *Cladonia* lichens. *Mol. Phylogenet. Evol.* 134, 226–237
55. Aschenbrenner, I.A. *et al.* (2014) Microbial cargo: do bacteria on symbiotic propagules reinforce the microbiome of lichens? *Environ. Microbiol.* 16, 3743–3752
56. Petrini, O. *et al.* (1990) An analysis of fungal communities isolated from fruticose lichens. *Mycologia* 82, 444–451
57. Arnold, A.E. *et al.* (2009) A phylogenetic estimation of trophic transition networks for ascomycetous fungi: are lichens cradles of symbiotrophic fungal diversification? *Syst. Biol.* 58, 283–297
58. Diederich, P. *et al.* (2018) The 2018 classification and checklist of lichenicolous fungi, with 2000 non-lichenized, obligately lichenicolous taxa. *Bryologist* 121, 340–425
59. Aschenbrenner, I.A. *et al.* (2017) Differential sharing and distinct co-occurrence networks among spatially close bacterial microbiota of bark, mosses and lichens. *Mol. Ecol.* 26, 2826–2838
60. Fernández-Mendoza, F. *et al.* (2017) ITS1 metabarcoding highlights low specificity of lichen mycobiomes at a local scale. *Mol. Ecol.* 26, 4811–4830
61. Integrative HMP (iHMP) Research Network Consortium (2019) The Integrative Human Microbiome Project. *Nature* 569, 641–648
62. Trivedi, P. *et al.* (2020) Plant-microbiome interactions: from community assembly to plant health. *Nat. Rev. Microbiol.* 18, 607–621
63. Honegger, R. (1992) Lichens: Mycobiont-photobiont relationships. In *Algae and Symbioses: Plants, Animals, Fungi, Viruses, Interactions Explored* (Reisser, W., ed.), pp. 255–275, Biopress
64. Palmqvist, K. (2000) Carbon economy in lichens. *New Phytol.* 148, 11–36
65. Piercey-Normore, M.D. and Athukorala, S.N. (2017) Interface between fungi and green algae in lichen associations. *Botany* 95, 1005–1014
66. Hawksworth, D.L. and Grube, M. (2020) Lichens redefined as complex ecosystems. *New Phytol.* 227, 1281–1283
67. Parrot, D. *et al.* (2016) Lichen-associated bacteria as a hot spot of chemodiversity: Focus on uncialamycin, a promising compound for future medicinal applications. *Planta Med.* 82, 1143–1152
68. Culberson, C.F. (1969) *Chemical and Botanical Guide to Lichen Products*, University of North Carolina Press
69. Culberson, W.L. (1969) The use of chemistry in the systematics of the lichens. *Taxon* 18, 152–166
70. Culberson, C.F. and Elix, J.A. (1989) Lichen substances. In *Methods in Plant Biochemistry* (Vol. 1. *Plant Phenolics*) (Harborne, J.B., ed.), pp. 509–535, Academic Press
71. Tripp, E.A. and Lendemer, J.C. (2017) Twenty-seven modes of reproduction in the obligate lichen symbiosis. *Brittonia* 70, 1–14
72. Will-Wolf, S. and Jovan, S. (2019) Lichen species as element bioindicators for air pollution in the eastern United States of America. *Plant Fungal Syst.* 64, 137–147
73. Smith, R.J. *et al.* (2020) Climatic niche limits and community-level vulnerability of obligate symbioses. *J. Biogeogr.* 47, 382–395
74. Ellis, C.J. *et al.* (2018) Quantifying the anthropocene loss of bioindicators for an early industrial region: an equitable baseline for biodiversity restoration. *Biodivers. Conserv.* 27, 2363–2377
75. Tripp, E.A. *et al.* (2019) Habitat quality and disturbance drive lichen species richness in a temperate biodiversity hotspot. *Oecologia* 190, 445–457
76. Ellis, C.J. (2017) When is translocation required for the population recovery of old-growth epiphytes in a reforested landscape? *Restor. Ecol.* 25, 922–932
77. Price, K. *et al.* (2017) Long-term recovery of epiphytic communities in the Great Bear Rainforest of coastal British Columbia. *For. Ecol. Manag.* 391, 296–308
78. Goward, T. and Arseneault, A. (2018) Calicioid diversity in humid inland British Columbia may increase into the 5th century after stand initiation. *Lichenologist* 50, 555–569
79. McMullin, R.T. and Wiersma, Y.F. (2019) Out with old growth, in with ecological continEWity: new perspectives on forest conservation. *Front. Ecol. Environ.* 17, 176–181
80. Rose, C.I. and Hawksworth, D.L. (1981) Lichen recolonization in London's cleaner air. *Nature* 289, 289–292
81. Hawksworth, D.L. and McManus, P.M. (1989) Lichen recolonization in London under conditions of rapidly falling sulphur dioxide levels, and the concept of zone skipping. *Bot. J. Linn. Soc.* 100, 99–109
82. Dal Grande, F. *et al.* (2017) Adaptive differentiation coincides with local bioclimatic conditions along an elevational cline in populations of a lichen-forming fungus. *BMC Evol. Biol.* 17, 93
83. Vančurová, L. *et al.* (2018) The complexity of symbiotic interactions influences the ecological amplitude of the host: A case study in *Stereocaulon* (lichenized Ascomycota). *Mol. Ecol.* 27, 3016–3033
84. Leavitt, S.D. *et al.* (2015) Fungal specificity and selectivity for algae play a major role in determining lichen partnerships across diverse ecogeographic regions in the lichen-forming family Parmellaceae (Ascomycota). *Mol. Ecol.* 24, 3779–3797
85. Nelsen, M.P. *et al.* (2022) Contrasting patterns of climatic niche divergence in *Trebouxia*—a clade of lichen-forming algae. *Front. Microbiol.* 13, 791546
86. Baas-Becking, L.G.M. (1934) *Geobiologie of Inleiding tot de Milieukunde*, W.P. Van Stockum & Zoon
87. Bisby, G.R. (1943) Geographical distribution of fungi. *Bot. Rev.* 9, 466–482
88. Tedersoo, L. *et al.* (2014) Global diversity and geography of soil fungi. *Science* 346, 1078
89. Peay, K.G. *et al.* (2010) Not every fungus is everywhere: scaling to the biogeography of fungal-plant interactions across roots, shoots and ecosystems. *New Phytol.* 185, 878–882
90. Větrovský, T. *et al.* (2019) A meta-analysis of global fungal distribution reveals climate-driven patterns. *Nat. Commun.* 10, 5142
91. Branco, S. *et al.* (2017) Continental-level population differentiation and environmental adaptation in the mushroom *Suillus brevipes*. *Mol. Ecol.* 26, 2063–2076
92. Magain, N. *et al.* (2018) Species delimitation at a global scale reveals high species richness with complex biogeography and patterns of symbiont association in *Peltigera* section *Peltigera* (lichenized Ascomycota: Lecanoromycetes). *Taxon* 67, 836–870