A Call To Reconceptualize Lichen Symbioses

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Abstract

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.

Keywords

Anthropocene resiliency, multi-omics, network biology, systems theory, transdisciplinary.

Main Text

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], recent reconceptualizations have 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.

1. 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]?

2. 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 [e.g., 43]. These assumptions are contradicted by recent studies (see below) 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.

3. 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 wherein 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 can be 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 above suggests that there is an urgent need to reconceptualize general theory about lichens which has been based on incorrect assumptions about the homogenous 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).

4. 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 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.

5. 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], 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.

6. 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 environment.

7. Reproductive Biology

Lichens are characterized by 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 (e.g., [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, among others. 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.

8. 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 pre-impact 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, wherein 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 would unlock the fundamental basis of community assembly and specialization. Concurrently it would allow for the development of broadly applicable effective data driven conservation methods for sensitive symbiotic organisms.

9. 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.

10. 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 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).

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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/s is/are 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.

Lichen(s) - 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.

Figure Captions

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.

Figure 2. Recent research has shown lichen individuals, populations and communities can be much 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 the result when this previously unrecognized diversity is extrapolated outwards within populations of a single species (top) and communities of multiple species (bottom).