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Lichen thalli as substrates and microhabitats for slime moulds (Myxomycetes)

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ABSTRACT

Lichen thalli and plasmodial slime moulds often co-occur in cryptogam-rich microsites on bark, decaying wood and soil, where they form part of complex forest microhabitat systems. This evidence-led synthesis compiles published observations of myxomycete sporocarps developing on lichen thalli, together with evidence for trophic stages within thallus microzones and environmental studies describing lichen–myxomycete co-occurrence under shared abiotic drivers. The assembled evidence indicates that lichen thalli repeatedly act as microtopographically heterogeneous fruiting substrates, potentially linked to surface roughness and associated microbial films, and can harbour myxomycete trophic stages, whereas direct evidence of feeding on lichen symbionts is absent. *Licea parasitica* (Zukal) G.W. Martin is the most consistently documented taxon on lichen thalli and is also recorded on bare bark, indicating a facultative, substrate-flexible association. When lichen substrates are grouped ecologically, *L. parasitica* is reported predominantly from corticolous (epiphytic) lichen systems, whereas terricolous (epigeic) lichens are associated with recurrent records of other myxomycete taxa. Treating lichen thalli as myxomycete microhabitats can improve interpretation of cryptogam-associated forest biodiversity and guide targeted tests of trophic-stage activity within thallus microzones.

KEY WORDS

bark, cryptogam mosaics, epiphytic lichens, microhabitats, Myxogastria, sporocarps, trophic stages

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1. INTRODUCTION

In forest ecosystems, lichens and plasmodial myxomycetes frequently overlap in cryptogam-rich microsites on bark, decaying wood and soil. Lichens can buffer microclimate and provide structurally complex thallus surfaces, whereas myxomycetes contribute to microbial food webs through trophic grazing and episodic sporulation.

Lichens are self-supporting symbiotic systems in which a lichen-forming fungus (mycobiont) forms a persistent thallus with one or more photosynthetic partners (photobionts), typically green algae and/or cyanobacteria (Honegger 1998; Bock and Anderson 2015; Sanders 2024). The thallus also hosts structured microbial communities on its surface and within thallus microzones, creating microzones relevant to microbial predators and other microbial eukaryotes (Hawksworth and Grube 2020; Grimm et al. 2021; Morillas et al. 2022).

Within Amoebozoa, Eumycetozoa encompass several slime mould lineages, including Myxomycetes (Myxogastria), Protosporangiida and Dictyostelia (Adl et al. 2012, 2019; Tekle et al. 2022). Here, term myxomycetes refers to Myxogastria (acellular/plasmodial slime moulds), the group considered in this synthesis and known for producing macroscopic sporocarps. Although their sporocarps can resemble minute fungal fruit bodies, myxomycetes are not fungi (Adl et al. 2012, 2019). Myxomycetes alternate between microscopic trophic stages and macroscopic sporocarps; trophic stages graze on bacteria and other microorganisms in moisture-retentive substrates such as bark, decaying wood and leaf litter (Everhart and Keller 2008; Clark and Haskins 2015; Stephenson and Rojas 2017). Persistence across fluctuating hydric regimes is promoted by physiological plasticity and dormant structures that allow rapid activation and reproduction during brief favourable moisture windows (Everhart and Keller 2008; Stephenson 2023).

Myxomycete-lichen associations have rarely been synthesised explicitly, despite recurring reports of sporocarps developing on lichen thalli and microecological evidence that lichens can harbour myxomycete trophic stages (Bock and Anderson 2015; Grube 2018). Protist diversity on lichens is likely underestimated, and lichen thalli may provide spatially structured microbial prey fields intermittently accessible to plasmodia under favourable moisture conditions (Grube 2018). Occurrence records frequently mention *Licea parasitica*, and it is emphasised in several syntheses as a repeatedly reported taxon on lichen thalli (Lawrey and Diederich 2003; Czyżewska et al. 2008).

This synthesis evaluates published observations of myxomycete sporocarps developing on lichen thalli and assesses whether these records support trophic exploitation of the lichen symbiosis or are more consistent with substrate use and microhabitat overlap. The objectives are to assess why lichen thalli may provide suitable microhabitats for myxomycetes, synthesise evidence for lichen-associated trophic stages and fructification, and compile and appraise published sporocarp-on-thallus records, with emphasis on *L. parasitica* (Lawrey and Diederich 2003; Kukwa and Czarnota 2006; Tsurykau 2017). Lichen substrates are also evaluated ecologically by grouping reported lichen taxa into epiphytic (corticolous) versus epigeic (terricolous) assemblages.

2. MATERIAL AND METHODS

2.1. Study design and source basis

We conducted a structured, evidence-led narrative synthesis rather than a PRISMA-compliant systematic review. Literature was retrieved from Web of Science Core Collection, Scopus and Google Scholar, supplemented by targeted searches in the Biodiversity Heritage Library and manual screening of reference lists in key sources. Searches were conducted up to 5 January 2026 without year limits. The objective was to compile documented observations of myxomycete sporocarps (fruiting bodies of Myxogastria, distinct from fruiting structures of the lichen-forming fungus) on lichen thalli and evidence of lichen-associated trophic stages, rather than to estimate prevalence.

Search terms were organised into three keyword categories and combined in database-specific syntax. The first category captured target organisms (e.g., “myxomycetes”, “Myxogastria”, “Eumycetozoa”, “slime moulds”, “slime molds”). The second category captured the lichen substrate and thallus context (e.g., “lichens”, “lichen thallus”, “thalli”, “lichenicolous”, “epiphytic”). The third category captured the interaction and observation context (e.g., “sporocarps on lichens”, “fruiting on lichen thalli”, “myxomycete on lichen”, “lichen microhabitat”, “corticolous”). Additional targeted searches addressed recurrent taxa and substrates reported in the literature (e.g., “*Licea parasitica*”, “*Physcia*”, “*Phaeophyscia*”, “*Physconia*”, “*Cladonia*”, “*Lobaria*”, “*Peltigera*”).

Records were screened in two stages. Titles and abstracts were first screened for relevance to myxomycetes and lichens; full texts were then assessed for explicit statements of sporocarps developing on lichen thalli, trophic stages detected within thallus-associated assemblages, or quantified co-occurrence patterns linked to shared abiotic drivers. Duplicate reports of the same observation were consolidated, retaining the earliest or most information-rich account.

2.2. Evidence handling and inference rules

Evidence was grouped into three classes. The first comprised records of sporocarps reported fruiting on lichen thalli in natural or managed habitats. The second comprised microecological detection or quantification of myxomycete trophic stages within lichen-associated microbial eukaryote assemblages, including studies reporting localisation within thallus microzones (Bock and Anderson 2015). The third comprised environmental-context studies documenting co-occurrence patterns of myxomycetes and lichens in bark-associated systems and relating these patterns to shared drivers such as air pollution and bark chemistry (Wrigley de Basanta 2000; Härkönen and Vänskä 2004).

Interpretation followed conservative rules. Parasitism was treated as unconfirmed unless a source provided direct evidence of feeding on lichen symbionts and/or measurable negative impacts on lichen condition attributable to myxomycete activity (Lawrey and Diederich 2003). The descriptor lichenicolous (occurring on or in association with lichens, unless direct trophic evidence is provided) was used cautiously because, in parts of the literature, it is applied in a purely occurrence sense (recurrent presence on lichen thalli) rather than demonstrated trophic exploitation of living lichen tissues (Lawrey and Diederich 2003; Kukwa and Czarnota 2006). Statements describing taxa as facultatively lichenicolous (recurrently associated with lichen thalli but not restricted to them) or reporting fructification on both lichen thalli and bare bark were treated as key qualifiers for inference (Kukwa and Czarnota 2006; Tsurykau 2017).

2.3. Data extraction and taxonomy

For each eligible sporocarp record, the following fields were extracted: myxomycete taxon; lichen thallus substrate taxon (genus or species, where provided); underlying substrate context (e.g., bark or soil where explicitly stated or ecologically implied by the lichen substrate group); source citation; and information on substrate flexibility (e.g., occurrence on bare bark as well as lichen thalli), lichen growth form (where stated), and habitat or regional context provided by the original authors. For microecological trophic-stage studies, extracted information included the lichen system studied and localisation context reported by the authors (Bock and Anderson 2015).

Literature-derived lichen substrates were grouped into two ecological groups of lichen taxa on which myxomycetes were reported: epiphytic (corticolous) and epigeic (terricolous). Where a lichen taxon can occur in more than one ecological setting, assignment followed the dominant ecological affinity in the context of the cited record; epixylic occurrences were treated together with corticolous records as bark–wood surface substrates, because both represent the surface mosaic relevant to bark- and wood-associated microsites.

Higher-level placement and terminology for Eumycetozoa within Amoebozoa followed modern classification and phylogenomic frameworks (Adl et al. 2012, 2019; Tekle et al. 2022) and a phylogenetic classification of Myxomycetes (Leontyev et al. 2019). Nomenclature for myxomycetes was checked against an online nomenclatural information system for Eumycetozoa to reduce ambiguity due to synonymy and historical usage (Lado 2005–2026). Current names of lichen taxa were standardised according to Index Fungorum (Index Fungorum 2025); original names used in cited sources are retained in square brackets where they differ.

3. RESULTS

3.1. Lichen thalli as substrates for slime moulds

3.1.1. Microclimate and surface structure

Across forest and urban mosaics, cryptogam layers may function as humidity-buffering interfaces that expand microsites available to myxomycetes beyond bare bark and exposed wood, as well as ground-level substrates such as soil. Bryophyte mats and associated algal or cyanobacterial films may intercept propagules and dampen evaporative loss, creating moisture-retentive microrefugia that can support plasmodial development (Stephenson and Studlar 1985; Dudka and Romanenko 2006). Lichen thalli on bark and wood can operate analogously by creating growth-form-dependent surface microrelief, especially roughened or areolate surfaces, folds, fissures, lobes, podetia or branches, and by concentrating microbial surface films. Within the available evidence, surface roughness and related microtopography are the most plausible architectural features involved. The records do not support treating cilia, rhizines or hygroscopic properties as explanatory traits.

3.1.2. Sporocarp placement and microhabitat selection

Interpretation of sporocarps on lichens must account for the separation between trophic and reproductive phases in myxomycete life cycles. Because sporocarps are reproductive structures, their placement can be decoupled from the primary feeding substrate and may instead reflect microhabitat selection that favours exposure and dispersal. This distinction is relevant for lichens because many corticolous thalli provide elevated surfaces suitable for sporocarp placement even when feeding occurs in adjacent bark–thallus microzones. Consequently, sporulation on thallus surfaces does not by itself imply feeding on the lichen symbiosis, and claims about trophic use of lichen-associated microhabitats require trophic-stage evidence rather than sporocarp placement alone (Stephenson 2023).

3.2. Evidence for trophic stages and prey-mediated pathways

3.2.1. Microecological detection in thallus microzones

Evidence that lichens can harbour myxomycete trophic stages comes from a microecological study of rock-dwelling foliose lichens in which myxomycete trophic stages (amoebae, including “plasmodial amoebae” in the authors’ terminology) were recovered and quantified using a rehydration and culture observation protocol (Bock and Anderson 2015). Trophic stages were concentrated in the outer thallus segments, while middle and inner segments contained much lower abundances. Reported abundances were 272 ± 48, 12 ± 3 and 5 ± 2 individuals g^{-1} moist mass (outer, middle and inner segments, respectively), and 1127 ± 200, 49 ± 11 and 22 ± 9 individuals g^{-1} dry mass (Bock and Anderson 2015). These results demonstrate that myxomycete trophic stages can occur within lichen-associated microzones, but they do not, by themselves, demonstrate trophic exploitation of the lichen symbiosis.

3.2.2. Microbiome structure, prey availability, and broader protist communities

Studies of lichen microbiomes provide context for interpreting myxomycete occurrence on thalli. Contemporary work frames lichen thalli as multipartner systems with structured microbial communities on and within the thallus, including stable core components and context-dependent assemblages (Hawksworth and Grube 2020; Grimm et al. 2021; Morillas et al. 2022). Functional syntheses indicate that lichen-associated bacteria can contribute to nutrient provisioning, degradation of older thallus parts, biosynthesis of bioactive compounds, detoxification processes and protection against biotic and abiotic stress (Aschenbrenner et al. 2016).

Myxomycetes are phagotrophic protists whose trophic stages ingest bacteria and other microorganisms, making grazing on lichen-associated microbes a plausible mechanism for trophic-stage occupancy on thalli (Clark and Haskins 2015; Li et al. 2022). Work on bacterial communities associated with plasmodia documents close contact between trophic stages and microbial assemblages, supporting the relevance of microbially enriched substrates to myxomycete trophic stages (Li et al. 2022; Peng et al. 2024). In parallel, protist-focused syntheses emphasise that diverse protists, including myxomycete trophic stages, have been reported from lichen thalli, but evidence for lichen-specific relationships remains limited and detection can depend on moistening procedures and thallus region sampled (Grube 2018).

3.3. Documented occurrences and co-occurrence patterns

3.3.1. Compiled sporocarp-on-thallus records

Published observations document myxomycete sporocarps developing directly on lichen thalli across a range of lichen growth forms and substrate contexts. The compiled sporocarp-on-thallus records are summarised in Table 1, including the reported lichen substrate taxon, myxomycete taxon, underlying substrate context and source citation.

Table 1. Published records of myxomycete sporocarps reported on lichen thalli. Current lichen names follow Index Fungorum; original names used in the cited sources are given in square brackets where they differ. Lichen substrate taxa are assigned to two ecological groups: epiphytic (corticolous) and epigeic (terricolous).

Lichen substrate taxon	Ecological group of lichen substrate taxa	Myxomycete taxon	Underlying substrate context	Source(s)
Amandinea punctata	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Ronikier et al. 2017
Bacidia rubella	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Ronikier et al. 2017
Candelariella xanthostigma	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Drozdowicz et al. 2003; Ronikier et al. 2017
Coenogonium pineti [Dimerella pineti]	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000
Evernia prunastri	Epiphytic (corticolous) taxa	*Licea parasitica*	not stated	Etayo and López de Silanes 2024
Lecania cyrtella	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Ronikier et al. 2017; Kukwa and Czarnota 2006
Lecidella achristotera	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000
Lepraria elobata	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Drozdowicz et al. 2003
Lepraria jackii	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Drozdowicz et al. 2003
Lobaria pulmonaria	Epiphytic (corticolous) taxa	*Leocarpus fragilis*	not stated	Drozdowicz et al. 2003
Lobaria pulmonaria	Epiphytic (corticolous) taxa	*Didymium nigripes*	not stated	Kluša 2023
Melanelixia glabratula	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Notov et al. 2022
Melanohalea exasperatula	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Drozdowicz et al. 2003; Ronikier et al. 2017
Micarea nitschkeana	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Tsurykau 2017
Parmelia sulcata	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Tsurykau 2017
Parmeliopsis ambigua	Epiphytic (corticolous) taxa	*Licea parasitica*	not stated	von Brackel 2013
Phaeophyscia orbicularis	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000; Drozdowicz et al. 2003; Ronikier et al. 2017

cont. Table 1. Published records of myxomycete sporocarps reported on lichen thalli. Current lichen names follow Index Fungorum; original names used in the cited sources are given in square brackets where they differ. Lichen substrate taxa are assigned to two ecological groups: epiphytic (corticolous) and epigeic (terricolous).

Lichen substrate taxon	Ecological group of lichen substrate taxa	Myxomycete taxon	Underlying substrate context	Source(s)
Physcia adscendens	Epiphytic (corticolous) taxa	*Lamproderma arcyrioides*	not stated	Záhorovská and Lisická 2002
Physcia adscendens	Epiphytic (corticolous) taxa	*Licea parasitica*	not stated	Kukwa 2005; Ronikier et al. 2017
Physcia tenella	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Drozdowicz et al. 2003; Ronikier et al. 2017; Czyżewska et al. 2008
Physconia enteroxantha	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000; Drozdowicz et al. 2003; Ronikier et al. 2017
Poeltonia grisea [Physconia grisea]	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000
Physconia perisidiosa	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000; Drozdowicz et al. 2003; Ronikier et al. 2017
Rinodina efflorescens	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Ronikier et al. 2017
Scoliciosporum sarothamni	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Ronikier et al. 2017
Xanthoria parietina	Epiphytic (corticolous) taxa	*Lamproderma arcyrioides*	not stated	Záhorovská and Lisická 2002
Xanthoria parietina	Epiphytic (corticolous) taxa	*Licea parasitica*	bark	Kocourková 2000
Cetraria islandica	Epigeic (terricolous) taxa	*Leocarpus fragilis*	soil	Barsukova and Dunaev 1997
Cladonia cf. rangiferina	Epigeic (terricolous) taxa	*Listerella paradoxa*	soil	Kuhnt 2019
Cladonia gracilis	Epigeic (terricolous) taxa	*Didymium melanospermum*	soil	Drozdowicz et al. 2003
Cladonia (podetia)	Epigeic (terricolous) taxa	*Listerella paradoxa*	soil	Eliasson and Gilert 1982
Cladonia rangiferina	Epigeic (terricolous) taxa	*Comatricha laxa*	soil	von Brackel 2013
Cladonia portentosa [Cladonia sylvatica]	Epigeic (terricolous) taxa	*Listerella paradoxa*	soil	Kuhnt 2019
Peltigera canina	Epigeic (terricolous) taxa	*Leocarpus fragilis*	soil	Drozdowicz et al. 2003
Peltigera hymenina	Epigeic (terricolous) taxa	*Didymium squamulosum*	soil	Drozdowicz et al. 2003

3.3.2. Recurrent records of *Licea parasitica*

The compiled evidence (Tab. 1) shows a pronounced taxonomic skew, with *Licea parasitica* (Zukal) G.W. Martin representing the most consistently documented myxomycete on lichen thalli. A lichenological synthesis emphasises that most myxomycetes reported from lichens have not been regarded as strictly lichenicolous in a trophic sense, whereas *L. parasitica* is repeatedly encountered in corticolous contexts (Lawrey and Diederich 2003). Several accounts also indicate substrate flexibility, including fructification on bare bark as well as on lichen thalli (Kukwa and Czarnota 2006; Czyżewska et al. 2008; Tsurykau 2017). Within the compiled records, *L. parasitica* is associated primarily with epiphytic (corticolous) lichen systems, whereas terricolous (epigeic) lichen substrates are linked to other recurrent myxomycete taxa (Tab. 1).

Reported lichen substrates for *L. parasitica* include physcioid epiphytes such as *Physcia adscendens* (Fr.) H. Olivier and *Physcia tenella* (Scop.) DC. (Kukwa 2005; Czyżewska et al. 2008), crustose taxa such as *Lecania cyrtella* (Ach.) Th. Fr. (Kukwa and Czarnota 2006), and additional corticolous substrates including *Parmeliopsis ambigua* (Wulfen) Nyl. and *Evernia prunastri* (L.) Ach. (von Brackel 2013; Etayo and López de Silanes 2024).

Several sources note frequent association with physcioid epiphytes, but the records span crustose, foliose and fruticose thalli; therefore, they do not indicate a single lichen growth form as the main explanatory factor.

3.3.3. Other recorded taxa and ecological grouping

Table 1 also documents sporocarp development on lichen thalli by additional myxomycete taxa. Reported examples include *Leocarpus fragilis* (Dicks.) Rostaf. (e.g., on *Cetraria*, *Lobaria* and *Peltigera* thalli), *Listerella paradoxa* E. Jahn (recurrently on *Cladonia* thalli), *Lamproderma arcyrioides* (Sommerf.) Rostaf. (on *Physcia adscendens* (Fr.) H. Olivier and *Xanthoria parietina* (L.) Th. Fr.), *Comatricha laxa* Rostaf. (on *Cladonia rangiferina* (L.) F.H. Wigg.), and *Didymium* spp. (recorded on *Cladonia*, *Lobaria* and *Peltigera*) (Eliasson and Gilert 1982; Záhorovská and Lisická 2002; Drozdowicz et al. 2003; von Brackel 2013; Kluša 2023). Ultrastructural documentation records *Listerella paradoxa* sporocarps on *Cladonia* podetia (Eliasson and Gilert 1982).

Grouped ecologically, the compiled records suggest partial partitioning: epigeic (terricolous) lichen substrates are associated with recurrent records of *Listerella paradoxa* and *Leocarpus fragilis* (often on *Cladonia*, *Cetraria* and *Peltigera*), whereas corticolous (epiphytic) lichen systems include *L. parasitica* as the dominant repeatedly reported taxon in the compiled dataset (Tab. 1). At the species level, the compiled records include four unique myxomycete taxa recorded from epiphytic (corticolous) lichen substrates and five from epigeic (terricolous) lichen substrates; because one species-level taxon occurs in both groups, these are group-specific descriptive counts rather than additive estimates of total richness. Notably, *Leocarpus fragilis* is recorded in both ecological settings, while *Didymium* spp. are represented by different species across the two groups, indicating broader substrate breadth within the compiled records.

4. DISCUSSION

4.1. Evidence supports substrate use and microhabitat facilitation

Across the assembled evidence, the most defensible interpretation is substrate use and possible microhabitat-level facilitation, rather than obligate antagonism. Here, substrate use refers to the occurrence or placement of sporocarps on a lichen thallus without assuming trophic dependence on the lichen symbiosis, whereas microhabitat facilitation refers to locally favourable conditions created primarily by surface microrelief and microbial surface films. Sporocarp records across multiple taxa indicate that lichen thalli can act as microtopographically complex surfaces suitable for sporocarp placement and possibly for trophic activity in thallus-associated boundary layers (Kocourková 2000; Ronikier et al. 2017). Among architectural traits, surface roughness and related microrelief currently provide the most cautious explanation. In such cases, the thallus may function primarily as a fruiting platform rather than as the trophic substrate itself. This distinction is important because sporocarps are reproductive structures, and their position may reflect microhabitat selection for exposure and dispersal rather than the primary feeding substrate of preceding trophic stages (Stephenson and Studlar 1985; Ing 1994; Stephenson 2023).

Microecological work provides direct support for lichens as microhabitats capable of supporting trophic stages, with such stages detected and quantified in thallus microzones (Bock and Anderson 2015). At the same time, the available evidence does not justify interpreting these associations as parasitic, symbiotic or obligately dependent. This is particularly relevant for facultatively lichenicolous taxa, which occur recurrently on lichen thalli but are also known from non-lichenised substrates, such as bare bark. None of the reviewed sources provides direct evidence of feeding on lichen symbionts or measurable negative effects attributable to myxomycete activity. For this reason, lichenicolous should be used here only in the broad occurrence-based sense (Lawrey and Diederich 2003; Kukwa and Czarnota 2006; Czyżewska et al. 2008).

4.2. Taxonomic signal and substrate breadth in sporocarp-on-thallus records

The compiled records (Tab. 1) show a pronounced taxonomic signal, with *L. parasitica* emerging as the most consistently documented myxomycete associated with lichen thalli. This signal should be interpreted together with substrate flexibility: several accounts report fructification both on lichen thalli and on bare bark, supporting interpretation of *L. parasitica* as facultatively lichenicolous rather than obligately dependent on the lichen symbiosis (Kukwa and Czarnota 2006; Czyżewska et al. 2008; Tsurykau 2017). The range of recorded corticolous lichen substrates also suggests that ecological context within bark-associated mosaics may be more important than a narrow host range (Kukwa 2005; Kukwa and Czarnota 2006; Czyżewska et al. 2008; von Brackel 2013; Etayo and López de Silanes 2024).

Beyond *L. parasitica*, records of *Leocarpus fragilis*, *Listerella paradoxa*, *Lamproderma arcyrioides*, *Comatricha laxa* and *Didymium* spp. indicate that sporocarp development on lichen thalli is not restricted to a single myxomycete species. Macrolichen thalli and *Cladonia* podetia are particularly relevant in this respect because they provide exposed surfaces for sporocarp placement, but the present evidence remains occurrence-based rather than experimental (Eliasson and Gilert 1982; Záhorovská and Lisická 2002; Drozdowicz et al. 2003; von Brackel 2013; Kluša 2023).

4.3. Forest bark-lichen mosaics, shared drivers, and priorities for targeted tests

The evidence base indicates that lichen thalli should be treated as a distinct microhabitat compartment within bark-lichen mosaics, especially in forest contexts where bark, dead branches and decaying wood jointly structure cryptogam layers and moisture dynamics. Three non-exclusive pathways can be distinguished conceptually: sporulation on thallus surfaces, possible microbiome-mediated trophic use of thallus-associated boundary layers and shared abiotic filtering across bark-lichen systems. The microbiome-mediated pathway is plausible because lichen thalli host structured microbial communities and surface films whose distribution and accessibility may be shaped by thallus microrelief (Aschenbrenner et al. 2016; Hawksworth and Grube 2020; Grimm et al. 2021; Morillas et al. 2022), while myxomycete trophic stages are phagotrophic and embedded in microbial food webs (Clark and Haskins 2015; Li et al. 2022; Peng et al. 2024). Shared abiotic filtering is supported by studies showing concordant responses of corticolous lichens and myxomycetes to bark-associated environmental conditions. A long-term comparison from Helsinki reports concurrent increases in corticolous myxomycete richness and corticolous lichen richness over decades, alongside improvement in air quality and stabilisation of bark pH (Härkönen and Vänskä 2004). A gradient study from Madrid similarly reports fewer corticolous myxomycetes in more polluted zones on holm oak (*Quercus ilex* L.) bark, supporting a shared-sensitivity framework in which both groups respond to abiotic constraints on bark microhabitats (Wrigley de Basanta 2000). In this framing, lichen thalli are not only potential microhabitats in their own right but also indicators of broader bark-surface conditions that may constrain both groups.

Future work should prioritise designs that explicitly discriminate boundary-layer grazing on lichen-associated microbiomes, opportunistic use of adjacent bark–lichen mosaics with sporulation on thallus surfaces and possible direct trophic interaction with lichen symbionts. This requires time-resolved microscopy and controlled in situ observations on living thalli coupled with stratified sampling of thallus microzones, alongside surveys that compare forest, plantation and urban systems under contrasting bark chemistry and pollution regimes (Bock and Anderson 2015; Grube 2018; Morillas et al. 2022). Integrating lichen growth form, surface roughness or microrelief and microzone sampling into myxomycete field protocols would test whether the apparent prominence of physcioid epiphytes and macrolichen substrates in published records reflects an ecological association or observation bias (Czyżewska et al. 2008; Ronikier et al. 2017). Given the current evidence base, the most cautious working hypothesis is that *L. parasitica* is more often reported from corticolous lichen systems, whereas terricolous lichen systems more often contain records of taxa such as *Listerella paradoxa* and *Leocarpus fragilis*.

5. CONCLUSIONS

Lichen thalli repeatedly function as substrates for myxomycete sporocarp development, and available microecological evidence demonstrates that myxomycete trophic stages can occur within thallus-associated microzones. Across the reviewed evidence, the association is best interpreted as substrate use and possible microhabitat-level facilitation, whereas direct evidence of trophic exploitation of lichen symbionts is absent. A pronounced taxonomic signal is present, with *Licea parasitica* (Zukal) G.W. Martin emerging as the most consistently documented taxon on lichen thalli and showing substrate flexibility through additional records on bare bark. Several other taxa also recurrently fruit on macrolichen substrates, supporting the view that lichen thalli form part of the substrate mosaic used by myxomycetes.

Recognising lichen thalli as a distinct microhabitat compartment can improve interpretation of cryptogam biodiversity, particularly in forest ecosystems where bark, dead wood and ground-level substrates structure moisture dynamics and microbial prey fields. Explicit incorporation of lichen thalli into myxomycete sampling and biodiversity assessments may improve detection of lichen-associated records and help clarify the role of surface microrelief and thallus-associated microbial films across corticolous, epixylic and terricolous cryptogam mosaics.

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