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Exploring the Role of Aquatic Fungal Communities in the Decomposition of Recalcitrant Plant Materials

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Abstract: Plant detritus that resists microbial attack, including lignified leaves, emergent macrophyte stems, woody debris and polyphenol-rich tissues, forms a large and persistent pool of organic carbon in streams, rivers, lakes and wetlands. The rate at which this material is processed shapes food-web energy supply, nutrient retention, oxygen dynamics and carbon storage, and is therefore a sensitive indicator of aquatic ecosystem health. This review synthesizes current understanding of how aquatic fungal communities, particularly aquatic hyphomycetes, chytrids, ascomycete and basidiomycete wood-decay fungi and yeasts, colonize and degrade recalcitrant plant polymers. Peer-reviewed field, mesocosm and laboratory studies addressing fungal diversity, biomass, enzymatic capacity and responses to environmental stressors were examined, and this evidence was combined with a first-order decay model to illustrate how substrate recalcitrance governs residence time. The evidence shows that fungi typically dominate microbial biomass and production on submerged coarse detritus, secrete cellulases, hemicellulases, pectinases and oxidative lignin-modifying enzymes, and condition litter so that it becomes palatable to invertebrate shredders. Bacteria contribute increasingly as particles fragment, and interactions between the two groups range from synergistic to antagonistic. Modelled half-lives increase from about 35 days for labile litter to nearly 700 days for woody debris, underscoring the slow turnover of lignified substrates. Moderate nutrient enrichment and warming accelerate fungal activity, whereas severe eutrophication, metals, pesticides, hypoxia and riparian degradation reduce diversity and impair decomposition. It is concluded that fungal-mediated breakdown of recalcitrant litter is a functional and integrative metric that should be incorporated into bioassessment, ecological restoration and integrated catchment management programmes.

Keywords: Aquatic Hyphomycetes; Lignocellulose; Leaf Litter Breakdown; Extracellular Enzymes; Ecosystem Functioning; Bioassessment.

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I. Introduction

Aquatic systems are dynamic, open systems. A high amount of organic material from the terrestrial "catchment" enters streams, rivers, lakes, ponds and wetlands, with terrestrial organic sources in many forested and agricultural catchments being greater than the carbon produced in the water body through algal and aquatic plant photosynthesis. New leaves and needles, twigs, bark, fruits, and fallen wood are added into the channels and littoral zones annually, and emergent and floating macrophytes contribute their senescent tissues to sediments and shorelines. All of these materials contribute to heterotrophic food webs, drive respiration in the ecosystem and affect retention and transport of carbon and nutrients across the river continuum and to receiving lakes and estuaries (Tank et al., 2010).

A lot of this debris is resistant to decay in terms of its chemical and structural properties. In plants, the cell walls are composed of cellulose microfibrils embedded in a matrix of hemicelluloses and pectins, with the matrix being further reinforced in vascular tissues by lignin, an irregular aromatic polymer which few organisms are able to depolymerize. Many leaves are further protected by the presence of waxy cuticles, tannins and polyphenols which bind to proteins and inhibit enzymes. This means that litters that are found to be recalcitrant remain in aquatic environments for months to years, acting as a long-term carbon pool and as a complex substrate for organisms. The processing rate and agents dictate the rate at which energy is delivered to consumers, the oxygen consumption rates of sediments, and the percentage of terrestrial carbon that is respired, transported downstream or buried (Tank et al., 2010; Gessner et al., 2010).

Initial comparative studies on lignocellulose showed that different microbial decomposers can break down the most resistant components of plant tissue, and that the proportion of prokaryotes and eukaryotes that do so were different in a variety of freshwater and marine environments (Benner et al., 1986). Since then, there has been extensive research revealing fungi as key players in the decomposition of submerged plant detritus. Aquatic hyphomycetes, a polyphyletic group of most ascomycete fungi with unique hyphal conidia, invade leaves within days of their submersion and other fungal groups, such as chytrids, basidiomycetes and yeasts, invade a variety of aquatic environments (Grossart et al., 2019; Krauss et al., 2011).

Fungi are now known to be more an important part of lake, wetland and river ecological functioning than a contaminant from land (Grossart et al., 2019; Wurzbacher et al., 2010). Nevertheless, there are some aspects of fungal-mediated decomposition which are not well integrated with the ecosystem-based approaches that support aquatic ecosystem health assessment and management. First, much classical research has been devoted to relatively palatable leaf species, while the more persistent components of the detritus, e.g., lignified macrophyte stems and wood, have been given less attention. Second, the interactions between fungi and bacteria and invertebrates with recalcitrant substrates are complex and dependent on context. Third, decomposition is sensitive to various anthropogenic factors, such as nutrient enrichment, warming, and contaminants as well as changes in riparian vegetation, and is sensitive in a non-linear manner (Gessner et al., 2010; Ferreira et al., 2015; Woodward et al., 2012).

Hence the aim of this review is to look at the role aquatic fungal communities play in the breakdown of recalcitrant plant materials with an ecosystem perspective. In particular, the review aims to describe: (i) the major recalcitrant plant materials entering aquatic ecosystems; (ii) summarize the diversity and ecological strategies of the fungi that colonize them; (iii) describe enzymatic mechanisms by which the fungi degrade resistant polymers; (iv) examine decomposition dynamics and interactions among fungi, bacteria and invertebrates; (v) evaluate how environmental drivers and human stressors will modify these processes; and (vi) identify implications for ecosystem health assessment, restoration and future research.

II. Methods of the Review

This article presents an integration of evidence from ecological and microbiological and management-oriented evidence using a narrative synthesis approach which is appropriate for the integration. Literature was retrieved by conducting searches in the major bibliographic databases of the scientific literature with the following combinations of terms: aquatic fungi, aquatic hyphomycetes, litter decomposition, leaf breakdown, lignocellulose, lignin, wood decay, macrophyte detritus, extracellular enzymes, fungal biomass, nutrient enrichment, stream ecosystem functioning. Key reviews were used as a reference list to find further primary studies. Studies were prioritized that quantified fungal biomass, fungal production, sporulation, or enzyme production on submerged plant material; studies that determined the relative contribution of fungi, bacteria and invertebrates to decomposition; and studies or syntheses that investigated the environmental or anthropogenic drivers at site or region level. Evidence was not arranged by habitat type, since all of the fungal processes are at work with varying strengths in lotic, lentic and wetland habitats. A comparative summary of the main plant polymers and associated fungal groups and enzymes degrading them in fungi, and of the main environmental constraints was put together (Table 1). To illustrate how the recalcitrance of the chemicals breaks down into detrital residence time, a single-pool negative-exponential model, was applied to four representative k values which cover the range of often reported values for labile leaves through to woody debris (Figure 1). Half-life (t50) and the time taken to achieve a 95 % mass loss (t95) were determined as ln(2)/k and ln(20)/k, respectively. These modelled curves are provided for illustration purposes and to show relative differences in turnover, and are not intended to predict turnover at any particular site. No field or lab data were collected for this review, as it draws on existing publications and follows a common analytical framework. The emphasis is on consistency in interpretation, with the provision of multiple independent studies supporting those interpretations, and explicit statements of areas

of disagreement and limited evidence. Demonstrate that the presence of recalcitrant plant materials can be beneficial to aquatic ecosystems.

III. Recalcitrant Plant Materials in Aquatic Ecosystems

Recalcitrance is a relative property of resistance of the organic matter to the process of biological degradation. It is the product of three interacting characteristics of plant detritus, which are: polymer chemistry, physical structure and inhibitory secondary compounds. Cellulose is the most abundant biopolymer found on earth, which is composed of linear chains of glucose, each chain forming crystalline microfibrils which limit enzyme access. Hemicelluloses are branched in structure, easily broken down, but are covalently bound to lignin, e.g. xylans and mannans. Lignin itself is one of the three-dimensional phenylpropanoid polymers that cannot be degraded by hydrolytic enzymes, and requires an attack with oxidizing agents (Benner et al., 1986; Krauss et al., 2011). These components can be present in very different proportions in the detrital sources. The leaves of riparian species including alder and willow are relatively low in lignin content, containing a relatively high amount of nitrogen; beech, oaks, eucalypts, conifers and many evergreen species have leaves that are tough, high in lignin, and rich in tannins. Emergent plants like reeds, cattails and sedges have a large amount of structural tissue in their stems, and produce a considerable amount of standing dead plant material that can decompose for long periods of time before falling to the bottom. The most recalcitrant fraction of woody debris is twigs, and can also include whole fallen trees, providing habitat, sediment and organic particle retention and influencing channel hydraulics for decades (Tank et al., 2010).

Detritus physical form also has an impact on decomposition in addition to chemical composition. The presence of thick cuticles, sclerenchyma, low surface to volume ratios and bark decrease the surface area available for microbial growth and decrease the leaching of soluble compounds. The oxygen level in the sediments and litter buried within can be low and prevent aerobic fungi, while the oxygen level in the water that comes into contact with litter trapped in a debris dam or riffle may be high and favour fungal growth and sporulation (Tank et al., 2010; Wurzbacher et al., 2010). Recalcitrant detritus is thus a heterogeneous resource that is influenced by the intrinsic properties of detritus and the environment where detritus accumulates. The ecosystem perspective of recalcitrant materials is that it gives temporal stability to detrital food webs. All labile leaves are colonized and eaten quickly after leaf drop in the fall, and all resistant leaves, remains of macrophytes, and wood provide energy and habitat in the next season(s). This is a staggered availability, which helps to protect consumer populations from seasonal shortages and adds to the resilience of heterotrophic food webs (Tank et al., 2010; Gessner et al., 2010). Knowledge of the agents which unlock this energy from the 'lumps' of recalcitrant detritus is therefore key to understanding ecosystem functioning.

IV. Diversity and Ecological Strategies of Aquatic Fungi

Fungi play diverse roles and are taxonomically diverse in aquatic ecosystems. The running water is most studied group of aquatic hyphomycetes. They are asexual stages of ascomycote fungi and the tetraradiate and sigmoid conidia are believed to be specialized for adhesion to submerged material in the flowing water. They quickly invade newly-submerged leaf tissue, develop within the leaf tissues, and produce copiously of conidia, which can be counted for community composition and reproductive activity. They are generally found in abundance and diversity in streams that are cool, well oxygenated and have a high quantity of leaf inputs (Krauss et al., 2011; Gulis & Suberkropp, 2003). In addition to aquatic hyphomycetes, molecular studies have shown that a much greater diversity of fresh water fungi exists. In lakes, Chytrids and other zoosporic fungi occur in abundance, and are known to parasitize phytoplankton, as well as particulate organic matter (such as pollen and plant fragments).

Submerged wood is colonized by ascomycete and basidiomycete fungi, many of which are not found on terrestrial wood and colonize wood over longer time periods. The fungi are generally represented by yeasts and filamentous fungi that are found in the water column, in sediments and biofilms and often in

environmental sequence surveys of unexplored lineages (Grossart et al., 2019; Wurzbacher et al., 2010). Lakes and wetlands are habitats different to streams in terms of flow, oxygen and light regime. Fungal communities are present in standing-dead macroorganisms in the littoral zone and wetlands, and the communities change in response to the collapse of the macroorganism into the water and sediments. Fungal activity in profundal sediments can be restricted due to oxygen depletion, but some fungi are able to grow under microaerobic conditions (Wurzbacher et al., 2010). These habitat differences produce different fungal communities and decomposition processes of similar plant materials. Aquatic fungi have several ecological strategies for the utilization of recalcitrant substrates.

The hyphal growth of fungi enables them to penetrate through intact plant tissues, to connect nutrient-poor and nutrient-rich microsites and to translocate resources within the mycelium. Extracellular enzymes secreted at hyphal tips pool within the substrate surface. Several aquatic fungi are also capable of absorbing dissolved inorganic nitrogen and phosphorus from the surrounding water, and use them for their growth, thereby improving the nutritional value of detritus for consumers (Krauss et al., 2011; Gulis & Suberkropp, 2003). It is well established from quantitative studies that fungi provide a large proportion of the microbial biomass and production in submerged coarse detritus. In a study that estimated the biomass of the shredders, fungi and bacteria on the decomposing leaves, most of the microbial biomass estimated was associated with the amount of leaf mass lost, and bacterial biomass was relatively small (Hieber & Gessner, 2002). In polluted rivers, fungi also seem to be important, dominating the bacterial production (Pascoal & Cássio, 2004). These results confirm the hypothesis that fungi play a major role in the primary decomposition of recalcitrant litter in many aquatic environments.

V. Enzymatic Mechanisms of Fungal Decomposition

Fungi have a wide variety of extracellular enzymes (Table 1) which enable them to decompose recalcitrant plant material. Cellulose is degraded by the cooperation of endoglucanases that act on amorphous regions and on the chain ends by cellobiohydrolases, and finally by beta-glucosidases that convert cellobiose to glucose. Endo-xylanases, beta-xylosidases and other side-chain-cleaving enzymes act on hemicelluloses in the middle lamella, which is degraded by polygalacturonases and pectin lyases. Pectinolytic activity is especially significant during the initial stages of decomposition since it will macerate the tissues and make cellulose available for other breakdown processes (Krauss et al., 2011).

A different approach is needed for lignin. Fungi synthesize the oxidative enzymes that generate reactive radicals that oxidize and break down aromatic structures, such as laccases and class II peroxidases (lignin peroxidase and manganese peroxidase). Basidiomycote white-rot fungi have the greatest lignin-degrading ability, whereas laccases and phenol oxidases are common in aquatic ascomycota, including some aquatic hyphomycota. During the initial stages of the aquatic decomposer process, the lignin is usually modified in some way and partially de-lignified, making the associated polysaccharides more available (Benner et al., 1986; Krauss et al., 2011). Microbial community functions linked to decomposition rates can be measured as extracellular enzyme activities on decomposing litter. Comparative experiments have revealed that fungi and bacteria colonizing the same litter have distinct enzyme profiles: fungi tend to exhibit higher levels of enzymes acting on structural polymers, and the presence of fungi may influence enzyme expression by the bacteria (Romaní et al., 2006).

Enzyme activities also are sensitive to the ratio of the substrate and the water present, and tend to rise with the availability of water and nutrients for microbial growth (Romaní et al., 2006; Gulis & Suberkropp, 2003). Recalcitrant leaves contain polyphenols and tannins that inhibit many hydrolytic enzymes and can bind to proteins, which decreases the microbial activity and nutrient content of litter. There are some aquatic fungi that are tolerant or detoxifying these compounds in addition, oxidative enzymes can participate in the transformation. During the first days of immersion, soluble phenolic load is leached out, and the fungal colonization proceeds usually at an accelerated rate (Krauss et al., 2011).

Coping with chemical defence is therefore an important trait that dictates taxa success on certain substrates, as is demonstrated by the cases of fungi.The case of fungi demonstrates the importance of coping with chemical defence as an important trait that dictates taxa success on certain substrates. The principal recalcitrant plant components, their sources, the fungal groups (and enzymes) most commonly associated with their degradation and the principal factors that limit decomposition in aquatic environments are summarised in table 1.

Table 1: Principal Recalcitrant Plant Components in Aquatic Detritus, Associated Fungal Agents and Enzymes, and Main Constraints on Their Decomposition (Compiled From [Benner et al., (1986); Grossart et al., (2019); Krauss et al., (2011); Wurzbacher et al., (2010); Romaní et al., (2006); Gulis & Suberkropp, (2003)])

Plant component	Typical sources in aquatic systems	Principal fungal agents	Key enzymes	Main constraints
Cellulose (crystalline)	All leaves, macrophyte stems, wood	Aquatic hyphomycetes; aquatic ascomycetes; basidiomycetes	Endoglucanase, cellobiohydrolase, β-glucosidase	Crystallinity; lignin shielding; low N and P in litter
Hemicellulose (xylans, mannans)	Leaves, grasses, sedges, reeds	Aquatic hyphomycetes; yeasts; ascomycetes	Endo-xylanase, β-xylosidase, mannanase	Cross-linking to lignin; side-chain substitution
Pectin (middle lamella)	Non-woody leaves and soft tissues	Aquatic hyphomycetes (early colonizers)	Polygalacturonase, pectin lyase	Inhibition by tannins; leaching losses
Lignin	Tough leaves, conifer needles, emergent macrophytes, wood	Basidiomycete white-rot fungi; aquatic ascomycetes	Laccase, manganese peroxidase, lignin peroxidase	Requires oxygen; slow kinetics; often only partial modification
Tannins and polyphenols	Oak, eucalypt, evergreen and many riparian leaves	Tolerant aquatic hyphomycetes and ascomycetes	Laccase, phenol oxidases, tannase	Enzyme inhibition; protein complexation
Cuticle and waxes (cutin)	Leaf surfaces, evergreen and aquatic plants	Ascomycetes; yeasts	Cutinase, lipases, esterases	Hydrophobic barrier delays colonization
Woody lignocellulose complex	Twigs, branches, fallen trees, roots	Submerged-wood ascomycetes and basidiomycetes	Full cellulolytic and ligninolytic suites	Low surface area; very slow turnover; burial and hypoxia

VI. Decomposition Dynamics and Fungal–Bacterial–Invertebrate Interactions

The process of decomposing plant litter in water typically involves three overlapping stages: leaching of soluble compounds; microbial conditioning/colonization; and physical breakdown by invertebrates and abrasion. Fungi are the main players during the conditioning phase where they raise the nitrogen content in the litter, soften the tissues and transform plant carbon into fungal biomass. Shredders selectively feed on well-conditioned litter, and fungus is a significant part of their food. The fungus-shredder interaction therefore increases the rate of detrital energy transfer to higher trophic levels, and the amount of mass loss (Gessner et al., 2010; Hieber & Gessner, 2002). The constant k is often used to describe the rate of decomposition of the process and is negative. Recalcitrant materials will have low k values and long residence times. This relationship is shown in figure 1 for four typical decay coefficients. Modelling with k = 0.020/day (representative of labile leaf litter) results in a half-life of about 35 days, and after one year only ~0.1 per cent of the initial mass is left.

The half-life is now ~92 days with k = 0.0075/day, and about 6 percent of the mass will be left after 1 year. The half-life varies between approximately 231 days for recalcitrant leaves and lignified macrophyte tissues, and approximately 693 days for woody debris. After one year, approximately 70 % of the mass remains for woody debris (k = 0.001 per day) and roughly a third remains for recalcitrant leaves and lignified macrophyte tissues (k = 0.003 per day). The duration of time that is required to achieve 95 % mass loss increases from approximately 150 days to nearly 3,000 days over this gradient. The modelled differences suggest that the fungal colonization of recalcitrant detritus occurs over longer periods of seasonal difference than happens for labile litter.

Fungal community succession should be longer on resistant substrates, with early colonizers able to use readily available polysaccharides being replaced by species that have a higher capacity for lignin modification. Long residence times further imply that the effects of environmental stressors on the activity of fungi can be cumulative, increasing differences among sites in carbon processing. The decomposition of litter into fine particulate organic matter (FPOM) increases the importance of bacteria. Fungi and bacteria may interact in a positive or negative way, such as when fungi produce some compounds that bacteria can use in decomposing litter; or when bacteria utilize fungal enzymes for nutrient uptake and/or the production of inhibitory products.

Antagonism between fungal and bacterial biomass and enzyme activities on litter has been demonstrated in laboratory experiments, where fungal and bacterial growth were inhibited when grown together as compared with when grown separately (Romaní et al., 2006). In rivers with high levels of pollution, the relative importance of bacteria in decomposition may also change but in these environments, the fungi may still be the most important decomposers on coarse material (Pascoal & Cássio, 2004). Diversity also matters. Complementarity and facilitation effects of decomposers and/or different litter types on decomposition rates have been demonstrated in experiments and syntheses, but are not consistent and dependent on the identity of the dominant decomposer species (Gessner et al., 2010). For difficult substrates, an ability to vary enzyme function may be especially significant as no single taxon is likely to have all the enzymes required for degradation of all the components of lignocellulose.

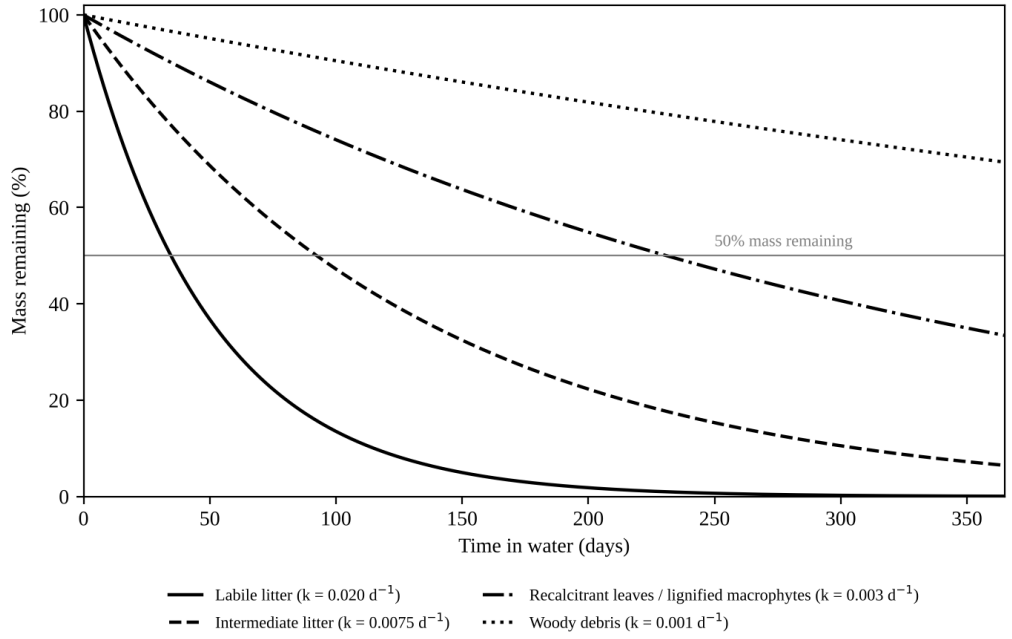


Figure 1: Predicted Mass Loss Profiles of Different Organic Materials During Aquatic Decomposition

VII. Environmental Drivers and Anthropogenic Stressors

Fungal break down of plant litter is sensitive to various environmental factors such as temperature, dissolved nutrients, oxygen, pH, flow and substrate quality. Fungal growth rates and enzyme kinetics are related to temperature and microbial decomposition is generally accelerated by warming. Stream experiments conducted across the globe have shown that litter decomposition is generally promoted by nutrient enrichment and by warming, but the magnitude of the response depends on the type of litter and ambient conditions (Ferreira et al., 2015). The sensitivity to temperature of processing recalcitrant litter may be different to labile litter because the enzymes needed to break down the lignin-rich material have high activation energies and would be more sensitive to temperature; this requires further testing. Nutrients have a special influence on fungi in nutrient-poor litter, which use dissolved N and P from the water column. When a headwater stream was whole-reach experimental enrichment, the fungal biomass, sporulation rates and litter decomposition were greater than in an unaltered reach (Gulis & Suberkropp, 2003).

But not all responses are positive to nutrients. In a study that covered all streams in Europe, decomposition rates were found to rise with increasing levels of nutrient enrichment, but then to decrease at high nutrient enrichment levels related to eutrophication and associated stress (Woodward et al., 2012). This is a non-linear relationship and means that the decomposition can provide a signal of nutrient limitation and degradation of ecosystem functions. Fungal activity and diversity is generally suppressed by many anthropogenic stressors. Heavy metals, pesticides, pharmaceuticals and contaminants may decrease the fungal biomass, sporulation, and enzyme activities and may alter the fungal community towards tolerant taxa. Aerobic fungi are inhibited by organic pollution and slower anaerobic pathways are favoured. Fine sediment deposition may bury litter, limit oxygen supply and limit colonization. Fungal community structure is known to change significantly along pollution gradients in the polluted river systems studied (Pascoal & Cássio, 2004).

This redundancy could hide early signs of degradation, so it is important to use both structural and functional indicators. The amount and quality of detrital inputs change with riparian vegetation. Conifer plantation or other cover, including eucalypts, tend to increase the amount of recalcitrant litter entering streams, and deforestation tends to decrease the inputs. Both changes can affect the timing and nature of energy supply to the detritivores and fungal communities (Tank et al., 2010).

The effect of flow alteration, such as flow regulation and drought, on decomposition is also related to the alteration of oxygen conditions, exposure of litter and dispersal of fungal propagules. The frequency of drying in intermittent streams may be a factor that disrupts the activity of fungi and may result in the accumulation of unprocessed detritus (Grossart et al., 2019). These stressors are anticipated to be compounded by climate change. In lakes and slow flowing water, warmer water may decrease the availability of oxygen, while in water where nutrients and oxygen levels are sufficient the warmer water may speed up decomposition. Altered delivery and retention of recalcitrant material will occur with changes in precipitation and hydrology. These synergistic effects indicate the need for multi-stressor, integrated studies of fungal-mediated decomposition (Grossart et al., 2019; Ferreira et al., 2015; Woodward et al., 2012).

VIII. Implications for Ecosystem Health Assessment and Management

Bioassessment of aquatic ecosystems is usually based predominantly on structural parameters (macroinvertebrate, diatom and fish assemblages) and physicochemical data. Decomposition of plant litter is a complementary functional indicator that is dependent on both the microbial and invertebrate activities and is sensitive to several factors (Gessner et al., 2010; Woodward et al., 2012). Leaf litter breakdown assays conducted with coarse and fine litter bags can separate the role of microbes from invertebrates, and can be used at low cost to many sites. The addition of recalcitrant substrates to such assays would increase its diagnostic scope. The labile leaves are very sensitive to short-term changes and may be most sensitive to short-term changes, while the recalcitrant leaves, macrophyte stems or standardized wood sticks integrate

over longer time scales and reflect chronic stress and carbon storage changes. Additional data on fungal biomass (e.g. ergosterol) and spore production of aquatic hyphomycete fungi, extracellular enzyme activities and molecular community profiles may provide additional insights into the mechanisms of observed differences in decomposition rates (Krauss et al., 2011; Romaní et al., 2006; Gulis & Suberkropp, 2003).

An explicit account of fungal-mediated decomposition also can be used to benefit the management and restoration strategy. Native riparian vegetation provides protection and restoration and results in a more diverse supply of litter types (labile and recalcitrant) that leads to a diversity of fungi and more continuous energy pulses to detritivores. Retention of woody debris and debris dams in channels increases the storage of organic matter and provides long-lived substrates for fungi and invertebrates (Tank et al., 2010). Maintenance of natural flow regimes, fine sediment load reductions, and control of nutrient and contaminant inputs are important for maintaining conditions for effective fungal community function (Gulis & Suberkropp, 2003; Woodward et al., 2012).

Macrophyte stands (vegetation) and water levels, in wetlands and lake littoral zones, can be influenced by the nutrient loading and can influence the accumulation and decomposition of plant detritus. Too much poorly decomposed matter can lead to oxygen depletion and to an excessive loading of nutrients into the internal waters of the lake, while the right amount of decomposition will lead to better nutrient cycling and productivity. The monitoring of fungal mediated decomposition in these habitats can then provide a guide for measures to be taken to maintain water quality and habitat integrity (Wurzbacher et al., 2010). Last, the ability of aquatic fungi to break down lignocellulose and to transform pollutants indicates potential use in bioremediation and biotechnology. Aquatic fungi enzymes could be applied to wastewater containing phenols or plant biomass processing; however, their applications under realistic conditions have yet to be evaluated (Krauss et al., 2011).

IX. Research Gaps and Future Directions

From this synthesis, there are several research priorities that can be derived. First, the breakdown of the most refractory fractions of detritus, especially aquatic wood and lignified macrophyte tissues, has been relatively unstudied, and knowledge of the fungal taxa involved in long-term lignin transformation in aquatic environments is quite incomplete. Successional dynamics and final fate of lignin derived carbon require long-term studies beyond the early stages of decomposition. Second, combining molecular tools with process measurements provides opportunities to relate the structure and composition of fungal communities to function. Metabarcoding, metagenomics, metatranscriptomics and proteomics can be used to determine which taxa are active and which are not, as well as the expression of genes and enzymes on hard to break down detritus, and carbon flow from detritus to fungi and consumers can be tracked using stable isotopes (Grossart et al., 2019; Wurzbacher et al., 2010).

This approach across habitat types could be useful to create some rules of thumb. Third, fungal decomposers' reaction to the several interacting stressors needs to be explored further. In order to establish thresholds where decomposition is affected and to determine additive, synergistic and antagonistic effects, factorial experiments and large-scale field surveys along gradients of nutrients, temperature, contaminants and land use should be conducted (Ferreira et al., 2015; Woodward et al., 2012).

Fourth, information on the role of fungi in lakes, wetlands, estuaries, and groundwater-fed systems is not as well-known as is the role in small forested streams. These ecosystems present a great opportunity for comparative studies that would better define the role of the hydrology, oxygen regime and salinity on the development of fungal community and their ability to break down plant recalcitrant materials (Benner et al., 1986; Wurzbacher et al., 2010). Lastly, standardized protocols for decomposition assays, including recalcitrant substrates, would allow comparison of results among studies and allow the integration of the results into monitoring programmes.

X. Conclusion

This review illustrates the aquatic fungi as key players in the breakdown of resistant plant matter in streams, rivers, lakes and wetlands. Phytoplankton and aquatic hyphomycetes are among the fungi that can rapidly colonize submerged detritus, penetrate structurally resistant tissues with their hyphae and produce a wide range of hydrolytic and oxidative enzymes which break down cellulose, hemicelluloses and pectins, as well as modifying lignin and polyphenols. These activities lead to the microbial biomass and production being dominated by fungi, the immobilization of dissolved nutrients, and the effect of fungi on the litter so that it could be utilized by the aquatic invertebrate shredders, thus transferring carbon from terrestrial and macrophyte sources to aquatic food webs. Modelled decay curves indicate that recalcitrance has a profound influence on the detrital residence time, for example, weeks for labile leaves, years for woody debris, and these materials can serve as a carbon reserve and a long-term habitat for fungi. Decomposition by fungi is influenced by temperature, nutrients, oxygen, flow, substrate quality and is modified by eutrophification, contaminants, sedimentation, riparian alteration, hydrological alteration and climate warming, frequently in non-linear ways. The decomposition of recalcitrant litter along with measurements of fungal biomass, sporulation and enzyme activity provides a valuable functional measure of aquatic ecosystem health, as it incorporates the effects of a number of stressors. The use of indicators like this in bioassessment, conservation of native riparian vegetation and the retention of woody debris and management of nutrient and contaminant inputs will help maintain the decomposition processes. Future studies should include: a) long term decay of lignified substrates, b) molecular relationships between fungal community structure and function, and c) multi-stress thresholds in a variety of freshwater and coastal aquatics.

Conflict of Interest

The authors have no financial or personal conflict of interest to report.

Data Availability Statement

There was no generation of new empirical data for this review. The first-order decay model and decay coefficients presented in Section 2 are used in figure 1, which can be reproduced completely from the provided equations.

References

[1] Tank, J. L., Rosi-Marshall, E. J., Griffiths, N. A., Entrekin, S. A., & Stephen, M. L. (2010). A review of allochthonous organic matter dynamics and metabolism in streams. *Journal of the North American Benthological Society, 29*(1), 118–146. https://doi.org/10.1899/08-170.1

[2] Gessner, M. O., Swan, C. M., Dang, C. K., McKie, B. G., Bardgett, R. D., Wall, D. H., & Hättenschwiler, S. (2010). Diversity meets decomposition. *Trends in Ecology & Evolution, 25*(6), 372–380. https://doi.org/10.1016/j.tree.2010.01.010

[3] Benner, R., Moran, M. A., & Hodson, R. E. (1986). Biogeochemical cycling of lignocellulosic carbon in marine and freshwater ecosystems: Relative contributions of procaryotes and eucaryotes. *Limnology and Oceanography, 31*(1), 89–100. https://doi.org/10.4319/lo.1986.31.1.0089

[4] Grossart, H.-P., Van den Wyngaert, S., Kagami, M., Wurzbacher, C., Cunliffe, M., & Rojas-Jimenez, K. (2019). Fungi in aquatic ecosystems. *Nature Reviews Microbiology, 17*(6), 339–354. https://doi.org/10.1038/s41579-019-0175-8

[5] Krauss, G.-J., Solé, M., Krauss, G., Schlosser, D., Wesenberg, D., & Bärlocher, F. (2011). Fungi in freshwaters: Ecology, physiology and biochemical potential. *FEMS Microbiology Reviews, 35*(4), 620–651. https://doi.org/10.1111/j.1574-6976.2011.00266.x

[6] Wurzbacher, C. M., Bärlocher, F., & Grossart, H.-P. (2010). Fungi in lake ecosystems. *Aquatic Microbial Ecology, 59*(2), 125–149. https://doi.org/10.3354/ame01385

[7] Hieber, M., & Gessner, M. O. (2002). Contribution of stream detrivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology, 83*(4), 1026–1038. https://doi.org/10.1890/0012-9658(2002)083[1026:COSDFA]2.0.CO;2

[8] Pascoal, C., & Cássio, F. (2004). Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Applied and Environmental Microbiology, 70*(9), 5266–5273. https://doi.org/10.1128/AEM.70.9.5266-5273.2004

[9] Romaní, A. M., Fischer, H., Mille-Lindblom, C., & Tranvik, L. J. (2006). Interactions of bacteria and fungi on decomposing litter: Differential extracellular enzyme activities. *Ecology, 87*(10), 2559–2569. https://doi.org/10.1890/0012-9658(2006)87[2559:IOBAFO]2.0.CO;2

[10] Gulis, V., & Suberkropp, K. (2003). Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology, 48*(1), 123–134. https://doi.org/10.1046/j.1365-2427.2003.00985.x

[11] Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., & Graça, M. A. S. (2015). A meta-analysis of the effects of nutrients and temperature on litter decomposition in streams. *Biological Reviews, 90*(3), 669–688. https://doi.org/10.1111/brv.12125

[12] Woodward, G., Gessner, M. O., Giller, P. S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B. G., Tiegs, S. D., Cariss, H., Dobson, M., Elosegi, A., Ferreira, V., Graça, M. A. S., Fleituch, T., Lacoursière, J. O., Nistorescu, M., Pozo, J., Risnoveanu, G., … Chauvet, E. (2012). Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science, 336*(6087), 1438–1440. https://doi.org/10.1126/science.1219534