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SPECIAL ISSUE

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# Ecological significance of autotroph–heterotroph microbial interactions in freshwaters

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## Abstract

1. Ecologists often separate pathways of energy flow into those based on either autotrophy (green) or heterotrophy (brown). While these two pathways are easily separated by concept and methodology, increasing evidence shows a complex interplay between autotrophic and heterotrophic components of ecosystems.
2. In freshwater settings, autotroph–heterotroph microbial interactions range widely. Studies suggest that algal–bacterial and algal–fungal interactions can encompass competition, mutualism, and priming effects that depend on environmental factors and can alter ecosystem processes including energy flow and nutrient cycling. Other studies suggest that primary consumers do not feed exclusively in either brown or green food webs, blurring the distinctions between trophic pathways. This omnivory complicates trophic classification, and its nutritional significance is important to understand autotrophy, heterotrophy, and detritus as the basis of consumer growth and fitness.
3. This special issue addresses knowledge gaps regarding the breadth and complexity of the autotroph–heterotroph microbial interface in freshwaters. The nine manuscripts within this special issue showcase the range of topics crossing the boundary between green and brown food webs to understand organism- to ecosystem-level responses to light regime, nutrient availability, temperature, and other environmental factors that affect autotroph–heterotroph interactions.
4. We highlight knowledge gaps generated from this special issue, such as a need for additional field studies documenting autotroph–heterotroph microbial interactions particularly in lentic settings, and a need to scale interactions from the field up to food webs and ecosystems. We anticipate that this special issue will spur scientific interest in both autotrophy and heterotrophy in freshwaters, including how these energy flow pathways cannot be fully understood when studied in isolation.

KEYWORDS

algae, bacteria, energy flow, fungi, trophic interactions

## 1 | INTRODUCTION

Ecologists classically separate energy flow into either *green* autotroph-based or *brown* heterotrophic-based pathways (Hairston, Smith, & Slobodkin, 1960; Moore et al., 2004). This dichotomy has advanced ecology by simplifying development of laboratory and field techniques, focusing resources along distinct lines of inquiry, and easing development and testing of classic ecological theory.

  

However, contemporary research from terrestrial and aquatic settings points to an under-appreciation of the complex interplay between autotrophic and heterotrophic components of ecosystems (Guenet, Danger, Abbadie, & Lacroix, 2010; Ward, McCann, & Rooney, 2015; Zou, Thébault, Lacroix, & Barot, 2016). Given this interplay, ecologists cannot fully understand one component of the trophic system without considering the other. In freshwater settings, autotroph–heterotroph interactions may be important at multiple scales including: (1) within mixed-species syntrophic microbial biofilms (Battin, Besemer, Bengtsson, Romani, & Packmann, 2016; Wagner, Bengtsson, Findlay, Battin, & Ulseth, 2017); (2) at the consumer–resource interface where mixotrophy and multichannel feeding, including on aforementioned biofilms, are prevalent (Guillemete, McCallister, & del Giorgio, 2016; Wolkovich et al., 2014); and (3) top-down via animal release of organic and inorganic nutrient wastes that are differentially available to autotrophs and heterotrophs (Atkinson, Capps, Rugenski, & Vanni, 2017; Parr, Capps, Inamdar, & Metcalf, 2019). These and other examples highlight the need for further research at the interface of autotrophy and heterotrophy within a diverse array of freshwater ecosystems.

The complexity of the autotroph–heterotroph interface results from wide-ranging interactions between microbial autotrophs and heterotrophs, combined with a range of biotic and abiotic factors that influence these interactions. Autotrophic and heterotrophic microbes often coexist and share space within mixed-species periphyton communities (Carr, Morin, & Chambers, 2005; Rier & Stevenson, 2002; Scott, Back, Taylor, & King, 2008), where they share several resource pools for which they can directly compete, especially the dissolved nutrients nitrogen (N) and phosphorus (P). In turn, autotrophic and heterotrophic microbial groups differ fundamentally in both metabolic requirements and sources of carbon (C) acquisition, with autotrophy reliant upon light availability and inorganic C, and heterotrophy reliant on reduced organic C for both metabolism and C assimilation. Contrasting metabolic requirements may lead to co-metabolism or mutualism between autotrophs and heterotrophs (e.g. Hom & Murray, 2014) as the two groups exchange waste products, such as $CO_2$ and $O_2$, and potentially other chemical compounds (Calatrava, Hom, Llamas, Fernández, & Galván, 2018; Hom, Aiyar, Schaeme, Mittag, & Sasso, 2015). Co-metabolism is also a plausible mechanism underlying autotroph-mediated priming effects, whereby autotrophs exude fresh, labile organic C readily used by heterotrophs to enhance growth, enzymatic activity, and acquisition of recalcitrant organic C (Danger et al., 2013; Kuehn, Francoeur, Findlay, & Neely, 2014; Kuzyakov, 2010). Finally, autotrophs and heterotrophs may indirectly interact by changing their shared environmental milieu, e.g. photosynthesis-driven increases of pH which affect the activity of pH-sensitive degradative enzymes (Rier, Kuehn, & Francoeur, 2007), and allelopathic compounds produced by both fungi and algae, which may affect interactions (Allen et al., 2017; Hom et al., 2015; Leflaive & Ten-Hage, 2007).

Recent studies suggest that the nature of autotroph–heterotroph microbial interactions can translate to altered ecosystem processes including energy flow and nutrient cycling. In shaded headwater streams where algae are often considered to play minimal ecological roles (Fisher & Likens, 1973; Vannote, Minshall, Cummins, Sedell, & Cushing, 1980), algae of low abundance can provide a high-quality resource, particularly of polyunsaturated fatty acids, supporting consumer nutrition (Crenier et al., 2017; Guo, Kainz, Valdez, Sheldon, & Bunn, 2016). In addition, periphytic algae can strongly inhibit or stimulate organic matter decomposition, with major consequences for long-term C storage and microbially mediated nutrient transformations (Halvorson et al., 2019; Halvorson, Scott, Entrekin, Evans-White, & Scott, 2016; Wyatt & Turetsky, 2015). This evidence underscores the need for more empirical research to understand the importance and impact of autotroph–heterotroph interactions on ecosystem processes in headwaters and other detritus-rich settings such as peatlands and lake littoral zones, which are major sites of C processing and storage (Cole et al., 2007; Kayranli, Scholz, Mustafa, & Hedmark, 2010). Furthermore, despite increasing studies of both autotrophic and heterotrophic responses to global change (Manning, Rosemond, Gulis, Benstead, & Kominoski, 2018; Welter et al., 2015), scientists remain challenged in how these autotroph–heterotroph interactions affect whole-system responses to increasing temperature, altered light regimes, and increasing nutrient availability (Gu & Wyatt, 2016; Wilken et al., 2018). Only when investigations have empirically tested underlying mechanisms, responses to environmental gradients, and ecological significance of the autotroph–heterotroph interface will we be able to understand the impact and importance of this interface within the broader discipline of ecology.

This special issue was organised to address knowledge gaps regarding the breadth and complexity of the autotroph–heterotroph microbial interface in freshwaters. Arising first from a special session at the 2018 Society for Freshwater Science meeting, this special issue addresses current fast-moving topics in ecology, including long-debated autochthonous versus allochthonous support of aquatic food webs (Brett et al., 2017; Tanentzap et al., 2017) and mixed support for the occurrence of priming effects during recalcitrant organic matter degradation across aquatic studies (Bengtsson, Attermeyer, & Catalán, 2018). The resulting nine manuscripts, the majority first-authored by students, showcase the range of settings in which autotroph–heterotroph interactions are (and are not) ecologically significant. The findings across studies provide a wide picture of microbial interactions, with a common theme to understand how microbial autotrophs and heterotrophs may separately and interactively respond to global change.

## 2 | OVERVIEW OF THIS SPECIAL ISSUE

The manuscripts in this special issue address autotroph–heterotroph microbial interactions, ranging from relatively controlled experiments testing the strength, direction, and mechanisms of interactions, to studies documenting how interactions affect organic matter breakdown and other microbial-mediated ecosystem functions, and finally to studies considering the wider implication of interactions for energy flow and nutrient cycling among higher trophic levels.

Several manuscripts add to a growing list of evidence that microbial autotrophs directly stimulate heterotrophy within lotic and lentic aquatic settings, and further provide context that environmental factors can influence the degree of that stimulation. Two papers conduct short-term (minutes to hours) manipulations of algal activity using photosynthesis inhibitors or light gradients. The first demonstrates strong algal stimulation of fungal production and phosphatase activity associated with submerged *Typha* and *Schoenoplectus* litter in a wetland system (Francoeur, Neely, Underwood, & Kuehn, 2020). A second paper provides complementary findings, wherein greater algal-stimulated fungal production is contrasted by weak stimulation of bacterial or enzymatic activity on submerged *Typha* litter as temperature and light levels increase (Pope, Halvorson, Findlay, Francoeur, & Kuehn, 2020). Finally, in an 8-day laboratory experiment, Wyatt and Rober (2020) find that mixing algal- and peatland-derived dissolved organic C (DOC) results in greater DOC degradation, bacterial biomass, and DOC aromaticity than non-mixing treatments, a pattern which strengthens with warming expected for high-latitude regions. Together, these studies demonstrate the importance of labile autotroph-derived C in directly stimulating microbial heterotrophy and the importance of factors that control both autotrophy and heterotrophy, in particular temperature, which can magnify this stimulation.

A second suite of longer-term experiments focus on ecosystem processes, particularly leaf decomposition, as influenced by autotroph–heterotroph interactions. Howard-Parker, White, Halvorson, and Evans-White (2020) experimentally investigate algal priming effects during *Quercus* litter decomposition across a dissolved P gradient, and observe that higher P concentrations enhance algal priming, most strongly for recalcitrant litter fibre mass loss. In combination with the above three papers, this demonstrates that algal influences on microbial heterotrophy extend to the decomposition of recalcitrant particulate C. However, it remains unclear how heterotrophs may reciprocally influence litter-associated autotrophy. This notable gap is addressed by Allen et al. (2020) using extracts from leaf litter and fungi to show that fresh leaf leachates directly suppress autotrophy, but over the long-term, leaf litter and fungi weakly or even positively affect autotrophy in experimental streams. These studies highlight the diverse roles of algae in detrital–heterotrophic processes, which are still poorly understood in aquatic ecosystems.

Global change factors can shift the autotroph–heterotroph interface by stimulating the activity and biomass of one or both microbial groups. Two papers address effects of global anthropogenic change in the autotroph–heterotroph interface. In their artificial stream experiment, Gossiaux et al. (2020) show that higher temperatures and N additions weakly alter microbial heterotrophy, but warming negatively affects primary production and stimulates invertebrate feeding and growth, thus inducing an overall shift in energy flow pathways. In a separate field study, Eckert, Halvorson, Kuehn, and Lamp (2020) show how increased nutrients and light availability associated with land use change across streams can shift algal and fungal biomass, as well as litter stoichiometry, to influence the invertebrate community colonising leaf litter. While revealing the complexity of predicting autotroph–heterotroph responses to global change stressors based on controlled laboratory experiments, these papers imply far-reaching effects on higher trophic levels and ecosystem processes.

Autotrophs can provide a high-quality nutritional resource to primary consumers, a factor that studies increasingly address even in headwater streams dominated by detritus and heterotrophic biomass and activity. In their paper quantifying C flows from algae to the primary consumers *Ecdyonurus* and *Gammarus*, Kühmayer et al. (2020) show that algae provide essential polyunsaturated fatty acids to consumers, to a measurable degree even in streams containing plentiful leaf litter and minimal algal biomass. Animals can, in turn, influence the autotroph–heterotroph interface by directly removing algae via grazing and by excreting labile DOC available to heterotrophs. Parr, Vaugh, and Gido (2020) investigate the influence of fish, mussels, and snails on DOC availability in stream mesocosms, showing that animal grazing may reduce DOC by removing algae that exude DOC and therefore support heterotrophic activity, indicating that animal consumers can both directly and indirectly shift the balance between autotrophy and heterotrophy in aquatic systems.

## 3 | POTENTIAL INFLUENCE OF THIS SPECIAL ISSUE

Microbial autotrophy and heterotrophy directly influence the net balance of C storage versus processing within ecosystems, and are thus key to understanding the role of freshwater biota in the global C cycle (Cole et al., 2007). We hope that this special issue will heighten future scientific interest in both autotrophy and heterotrophy in freshwaters, including how energy flow pathways (green versus brown) cannot be fully understood when studied in isolation (Buchkowski, Leroux, & Schmitz, 2019; Wolkovich et al., 2014; Zou et al., 2016). For example, two studies in this special issue show that increased temperatures magnify algal influence on heterotrophy measured as fungal growth (Pope et al., 2020) and DOC degradation (Wyatt & Rober, 2020). In addition, higher temperatures can shift energy flow through both autotrophic and heterotrophic pathways simultaneously (Gossiaux et al., 2020). Understanding these dynamics is important to predict how global climate change will affect freshwater C stocks and fluxes at a global level, particularly considering the autotroph–heterotroph interface as a model for microbiome ecology (Cavicchioli et al., 2019; Demars et al., 2016; Guenet et al., 2018).

This special issue also draws attention to the ecological significance of living autotroph biomass and activity in systems viewed as predominantly driven by heterotrophic processes, such as headwater streams. Five papers in this issue directly highlight autotrophic colonisation of organic matter in experimental or natural field settings, which is supported by an equal array of recent similar studies (e.g. Elosegi, Nicolás, & Richardson, 2018; Halvorson et al., 2019; Soares, Kritzberg, & Rousk, 2017). Several papers in this special issue also underscore the broader implications for

aquatic food webs through algal effects on invertebrate colonisation of leaf litter (Eckert et al., 2020) and C flow to primary consumers, particularly the provisioning of fatty acids (Kühmayer et al., 2020).

While this special issue highlights the ecological significance of the autotroph–heterotroph microbial interface, notable knowledge gaps still remain. We believe the following gaps will prove fruitful ground to disentangling the autotroph–heterotroph interface in freshwaters:

- Further research of autotroph–heterotroph interactions in lentic systems is needed, given the lotic bias within this special issue (six out of nine papers from lotic settings), and wide potential for autotrophs to interact with heterotrophs in well-lit lake pelagic and littoral zones and in wetlands (Paver et al., 2013; Wyatt & Turetsky, 2015).
- Although well-studied in terrestrial soils (Bastida et al., 2019; Kuzyakov, 2010) the influence of autotrophy on heterotrophy and C processing, such as the priming effect, remains poorly understood in submerged or water-saturated sediments (Bengtsson et al., 2018; Fortino, Hoak, & Waters, 2020; Gontikaki & Witte, 2019). This topic is not directly addressed within this special issue and remains a significant knowledge gap given the role of sediments in long-term C storage in aquatic settings.
- Several studies in this special issue document positive autotroph-mediated priming effects on heterotrophic activity or decomposition of recalcitrant organic matter. While these studies add to the literature, gaps persist regarding how interactions between labile and recalcitrant organic matter affect aquatic C cycling in both lotic and lentic ecosystems (Bengtsson et al., 2018; Bianchi & Ward, 2019).
- While this special issue highlights mechanistic tests of autotroph–heterotroph interactions, such tests are primarily derived from relatively controlled laboratory or mesocosm settings. To date, a limited number of direct field measures have documented autotroph–heterotrophic interactions under in situ conditions, a gap that must be resolved to address ecological significance (Demars, Friberg, & Thornton, 2020; Elosegi et al., 2018; Wyatt et al., 2019).
- This special issue frames autotroph–heterotroph interactions under environmental variation in elemental stoichiometry, temperature, and light availability, which are undergoing rapid global change. Future research efforts should investigate how interactions revealed here may explain ecological responses to warming, nutrient pollution, brownification, and interactions of these stressors (Manning et al., 2018; Song et al., 2018; Yvon-Durocher, Hulatt, Woodward, & Trimmer, 2017).
- Future emphasis on autotroph–heterotroph interactions will provide a novel framework to address the role of allochthony versus autochthony as the basis of freshwater food webs, namely addressing how complex interactions may blur distinctions between allocthony/autochthony and affect food web structure, energy flow, and nutrient transfer across ecosystems (Norman et al., 2017; Sitvarin, Rypstra, & Harwood, 2016).

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTION

All authors organised this special issue and aided in writing the initial issue proposal, soliciting manuscript submissions, and editing manuscripts. H.M.H. led writing of this introductory manuscript and all authors provided editorial feedback prior to submission.

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## REFERENCES

Allen, J., Laviale, M., Cellamare, M., Bachelet, Q., Felten, V., & Danger, M. (2020). Do leaf-litter decomposers control biofilm primary production and benthic algal community structure in forest streams? Insights from an outdoor mesocosm experiment. *Freshwater Biology*, *65*, 1256–1269. https://doi.org/10.1111/fwb.13475

Allen, J. L., Leflaive, J., Bringuier, C., Ten-Hage, L., Chauvet, E., Cornut, J., & Danger, M. (2017). Allelopathic inhibition of primary producer growth and photosynthesis by aquatic fungi. *Fungal Ecology*, *29*, 133–138. https://doi.org/10.1016/j.funeco.2017.07.001

Atkinson, C. L., Capps, K. A., Rugenski, A. T., & Vanni, M. J. (2017). Consumer-driven nutrient dynamics in freshwater ecosystems: From individuals to ecosystems. *Biological Reviews*, *92*, 2003–2023. https://doi.org/10.1111/brv.12318

Bastida, F., García, C., Fierer, N., Eldridge, D. J., Bowker, M. A., Abades, S., … Delgado-Baquerizo, M. (2019). Global ecological predictors of the soil priming effect. *Nature Communications*, *10*, 3481. https://doi.org/10.1038/s41467-019-11472-7

Battin, T. J., Besemer, K., Bengtsson, M. M., Romani, A. M., & Packmann, A. I. (2016). The ecology and biogeochemistry of stream biofilms. *Nature Reviews Microbiology*, *14*, 251–263. https://doi.org/10.1038/nrmicro.2016.15

Bengtsson, M. M., Attermeyer, K., & Catalán, N. (2018). Interactive effects on organic matter processing from soils to the ocean: Are priming effects relevant in aquatic ecosystems? *Hydrobiologia*, *822*, 1–17. https://doi.org/10.1007/s10750-018-3672-2

Bianchi, T. S., & Ward, N. D. (2019). Editorial: The role of priming in terrestrial and aquatic ecosystems. *Frontiers in Earth Science*, *7*, 321. https://doi.org/10.3389/feart.2019.00321

Brett, M. T., Bunn, S. E., Chandra, S., Galloway, A. W. E., Guo, F., Kainz, M. J., … Wehr, J. D. (2017). How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? *Freshwater Biology*, *62*, 833–853. https://doi.org/10.1111/fwb.12909

Buchkowski, R. W., Leroux, S. J., & Schmitz, O. J. (2019). Microbial and animal nutrient limitation change the distribution of nitrogen within coupled green and brown food chains. *Ecology*, *100*, e02674. https://doi.org/10.1002/ecy.2674

Calatrava, V., Hom, E. F. Y., Llamas, Á., Fernández, E., & Galván, A. (2018). OK, thanks! A new mutualism between Chlamydomonas and methylobacteria facilitates growth on amino acids and peptides. *FEMS Microbiology Letters*, *365*, fny021. https://doi.org/10.1093/femsle/fny021

Carr, G. M., Morin, A., & Chambers, P. A. (2005). Bacteria and algae in stream periphyton along a nutrient gradient. *Freshwater Biology*, *50*, 1337–1350. https://doi.org/10.1111/j.1365-2427.2005.01401.x

Cavicchioli, R., Ripple, W. J., Timmis, K. N., Azam, F., Bakken, L. R., Baylis, M., … Webster, N. S. (2019). Scientists' warning to humanity: Microorganisms and climate change. *Nature Reviews Microbiology*, *17*, 569–586. https://doi.org/10.1038/s41579-019-0222-5

Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., … Melack, J. (2007). Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems*, *10*, 172–185. https://doi.org/10.1007/s10021-006-9013-8

Crenier, C., Arce-Funck, J., Bec, A., Billoir, E., Perrière, F., Leflaive, J., … Danger, M. (2017). Minor food sources can play a major role in secondary production in detritus-based ecosystems. *Freshwater Biology*, *62*, 1155–1167. https://doi.org/10.1111/fwb.12933

Danger, M., Cornut, J., Chauvet, E., Chavez, P., Elger, A., & Lecerf, A. (2013). Benthic algae stimulate leaf litter decomposition in detritus-based headwater streams: A case of aquatic priming effect? *Ecology*, *94*, 1604–1613. https://doi.org/10.1890/12-0606.1

Demars, B. O. L., Friberg, N., & Thornton, B. (2020). Pulse of dissolved organic matter alters reciprocal carbon subsidies between autotrophs and bacteria in stream food webs. *Ecological Monographs*, *90*, e01399. https://doi.org/10.1002/ecm.1399

Demars, B. O. L., Gíslason, G. M., Ólafsson, J. S., Manson, J. R., Friberg, N., Hood, J. M., … Freitag, T. E. (2016). Impact of warming on $CO_2$ emissions from streams countered by aquatic photosynthesis. *Nature Geoscience*, *9*, 758–761. https://doi.org/10.1038/ngeo2807

Eckert, R. A., Halvorson, H. M., Kuehn, K. A., & Lamp, W. O. (2020). Macroinvertebrate community patterns in relation to leaf-associated periphyton under contrasting light and nutrient conditions in headwater streams. *Freshwater Biology*, *65*, 1270–1287. https://doi.org/10.1111/fwb.13473.

Elosegi, A., Nicolás, A., & Richardson, J. S. (2018). Priming of leaf litter decomposition by algae seems of minor importance in natural streams during autumn. *PLoS ONE*, *13*, e0200180. https://doi.org/10.1371/journal.pone.0200180

Fisher, S. G., & Likens, G. E. (1973). Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecological Monographs*, *43*, 421–439. https://doi.org/10.2307/1942301

Fortino, K., Hoak, J., & Waters, M. N. (2020). Evidence for positive priming of leaf litter decomposition by contact with eutrophic pond sediments. *Hydrobiologia*, *847*, 137–149. https://doi.org/10.1007/s10750-019-04077-0

Francoeur, S. N., Neely, R. K., Underwood, S., & Kuehn, K. A. (2020). Temporal and stoichiometric patterns of algal stimulation of litter-associated heterotrophic microbial activity. *Freshwater Biology*, *65*, 1223–1238. https://doi.org/10.1111/fwb.13442.

Gontikaki, E., & Witte, U. (2019). No strong evidence of priming effects on the degradation of terrestrial plant detritus in estuarine sediments. *Frontiers in Marine Science*, *6*, 327. https://doi.org/10.3389/fmars.2019.00327

Gossiaux, A., Rollin, M., Guérold, F., Felten, V., Laviale, M., Bachelet, Q., … Danger, M. (2020). Temperature and nutrient effects on the relative importance of brown and green pathways for stream ecosystem functioning: A mesocosm approach. *Freshwater Biology*, *65*, 1239–1255. https://doi.org/10.1111/fwb.13474.

Gu, L. Y., & Wyatt, K. H. (2016). Light availability regulates the response of algae and heterotrophic bacteria to elevated nutrient levels and warming in a northern boreal peatland. *Freshwater Biology*, *61*, 1442–1453. https://doi.org/10.1111/fwb.12783

Guenet, B., Camino-Serrano, M., Ciais, P., Tifafi, M., Maignan, F., Soong, J. L., & Janssens, I. A. (2018). Impact of priming on global soil carbon stocks. *Global Change Biology*, *24*, 1873–1883. https://doi.org/10.1111/gcb.14069

Guenet, B., Danger, M., Abbadie, L., & Lacroix, G. (2010). Priming effect: Bridging the gap between terrestrial and aquatic ecology. *Ecology*, *91*, 2850–2861. https://doi.org/10.1890/09-1968.1

Guillemete, F., McCallister, S. L., & del Giorgio, P. A. (2016). Selective consumption and metabolic allocation of terrestrial and algal carbon determine allochthony in lake bacteria. *The ISME Journal*, *10*, 1373–1382. https://doi.org/10.1038/ismej.2015.215

Guo, F., Kainz, M. J., Valdez, D., Sheldon, F., & Bunn, S. E. (2016). High-quality algae attached to leaf litter boost invertebrate shredder growth. *Freshwater Science*, *35*, 1213–1221. https://doi.org/10.1086/688667

Hairston, N. G., Smith, F. E., & Slobodkin, L. B. (1960). Community structure, population control, and competition. *The American Naturalist*, *94*, 421–425. https://doi.org/10.1086/282146

Halvorson, H. M., Barry, J. R., Lodato, M. B., Findlay, R. H., Francoeur, S. N., & Kuehn, K. A. (2019). Periphytic algae decouple fungal activity from leaf litter decomposition via negative priming. *Functional Ecology*, *33*, 188–201. https://doi.org/10.1111/1365-2435.13235

Halvorson, H. M., Scott, E. E., Entrekin, S. A., Evans-White, M. A., & Scott, J. T. (2016). Light and dissolved phosphorus interactively affect microbial metabolism, stoichiometry and decomposition of leaf litter. *Freshwater Biology*, *61*, 1006–1019. https://doi.org/10.1111/fwb.12763

Hom, E. F., Aiyar, P., Schaeme, D., Mittag, M., & Sasso, S. (2015). A chemical perspective on microalgal–microbial interactions. *Trends in Plant Science*, *20*, 689–693. https://doi.org/10.1016/j.tplants.2015.09.004

Hom, E. F., & Murray, A. W. (2014). Niche engineering demonstrates a latent capacity for fungal–algal mutualism. *Science*, *345*, 94–98. https://doi.org/10.1126/science.1253320

Howard-Parker, B., White, B., Halvorson, H. M., & Evans-White, M. A. (2020). Light and dissolved nutrients mediate recalcitrant organic matter decomposition via microbial priming in experimental streams. *Freshwater Biology*, *65*, 1189–1199. https://doi.org/10.1111/fwb.13503

Kayranli, B., Scholz, M., Mustafa, A., & Hedmark, Å. (2010). Carbon storage and fluxes within freshwater wetlands: A critical review. *Wetlands*, *30*, 111–124. https://doi.org/10.1007/s13157-009-0003-4

Kuehn, K. A., Francoeur, S. N., Findlay, R. H., & Neely, R. K. (2014). Priming in the microbial landscape: Periphytic algal stimulation of litter-associated microbial decomposers. *Ecology*, *95*, 749–762. https://doi.org/10.1890/13-0430.1

Kühmayer, T., Guo, F., Ebm, N., Battin, T. J., Brett, M. T., Bunn, S. E., … Kainz, M. J. (2020). Preferential retention of algal carbon in benthic invertebrates: Stable isotope and fatty acid evidence from an outdoor flume experiment. *Freshwater Biology*, *65*, 1200–1209. https://doi.org/10.1111/fwb.13492.

Kuzyakov, Y. (2010). Priming effects: Interactions between living and dead organic matter. *Soil Biology and Biochemistry*, *42*, 1363–1371. https://doi.org/10.1016/j.soilbio.2010.04.003

Leflaive, J. P., & Ten-Hage, L. (2007). Algal and cyanobacterial secondary metabolites in freshwaters: A comparison of allelopathic compounds and toxins. *Freshwater Biology*, *52*, 199–214. https://doi.org/10.1111/j.1365-2427.2006.01689.x

Manning, D. W. P., Rosemond, A. D., Gulis, V., Benstead, J. P., & Kominoski, J. S. (2018). Nutrients and temperature additively increase stream

microbial respiration. *Global Change Biology*, *24*, e233–e247. https://doi.org/10.1111/gcb.13906

Moore, J. C., Berlow, E. L., Coleman, D. C., Ruiter, P. C., Dong, Q., Hastings, A., … Wall, D. H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, *7*, 584–600. https://doi.org/10.1111/j.1461-0248.2004.00606.x

Norman, B. C., Whiles, M. R., Collins, S. M., Flecker, A. S., Hamilton, S. K., Johnson, S. L., … Webster, J. R. (2017). Drivers of nitrogen transfer in stream food webs across continents. *Ecology*, *98*, 3044–3055. https://doi.org/10.1002/ecy.2009

Parr, T. B., Capps, K. A., Inamdar, S. P., & Metcalf, K. A. (2019). Animal-mediated organic matter transformation: Aquatic insects as a source of microbially bioavailable organic nutrients and energy. *Functional Ecology*, *33*, 524–535. https://doi.org/10.1111/1365-2435.13242

Parr, T. B., Vaugh, C. C., & Gido, K. B. (2020). Animal effects on dissolved organic carbon bioavailability in an algal controlled ecosystem. *Freshwater Biology*, *65*, 1298–1310. https://doi.org/10.1111/fwb.13438.

Paver, S. F., Hayek, K. R., Gano, K. A., Fagen, J. R., Brown, C. T., Davis-Richardson, A. G., … Kent, A. D. (2013). Interactions between specific phytoplankton and bacteria affect lake bacterial community succession. *Environmental Microbiology*, *15*, 2489–2504. https://doi.org/10.1111/1462-2920.12131

Pope, C. A., Halvorson, H. M., Findlay, R. H., Francoeur, S. N., & Kuehn, K. A. (2020). Light and temperature mediate algal stimulation of heterotrophic activity on decomposing leaf litter. *Freshwater Biology*, *65*, 1210–1222. https://doi.org/10.1111/fwb.13465.

Rier, S. T., Kuehn, K. A., & Francoeur, S. N. (2007). Algal regulation of extracellular enzyme activity in stream microbial communities associated with inert substrata and detritus. *Journal of the North American Benthological Society*, *26*, 439–449. https://doi.org/10.1899/06-080.1

Rier, S. T., & Stevenson, R. J. (2002). Effects of light, dissolved organic carbon, and inorganic nutrients on the relationship between algae and heterotrophic bacteria in stream periphyton. *Hydrobiologia*, *489*, 179–184.

Scott, J. T., Back, J. A., Taylor, J. M., & King, R. S. (2008). Does nutrient enrichment decouple algal–bacterial production in periphyton? *Journal of the North American Benthological Society*, *27*, 332–344. https://doi.org/10.1899/07-108.1

Sitvarin, M. I., Rypstra, A. L., & Harwood, J. D. (2016). Linking the green and brown worlds through nonconsumptive predator effects. *Oikos*, *125*, 1057–1068. https://doi.org/10.1111/oik.03190

Soares, M., Kritzberg, E. S., & Rousk, J. (2017). Labile carbon 'primes' fungal use of nitrogen from submerged leaf litter. *FEMS Microbiology Ecology*, *93*, fix110. https://doi.org/10.1093/femsec/fix110

Song, C., Dodds, W. K., Rüegg, J., Argerich, A., Baker, C. L., Bowden, W. B., … Ballantyne, F. (2018). Continental-scale decrease in net primary productivity in streams due to climate warming. *Nature Geoscience*, *11*, 415–420. https://doi.org/10.1038/s41561-018-0125-5

Tanentzap, A. J., Kielstra, B. W., Wilkinson, G. M., Berggren, M., Craig, N., del Giorgio, P. A., … Pace, M. L. (2017). Terrestrial support of lake food webs: Synthesis reveals controls over cross-ecosystem resource use. *Science Advances*, *3*, e1601765. https://doi.org/10.1126/sciadv.1601765

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*, 130–137. https://doi.org/10.1139/f80-017

Wagner, K., Bengtsson, M. M., Findlay, R. H., Battin, T. J., & Ulseth, A. J. (2017). High light intensity mediates a shift from allochthonous to autochthonous carbon use in phototrophic stream biofilms. *Journal of Geophysical Research: Biogeosciences*, *122*, 1806–1820. https://doi.org/10.1002/2016JG003727

Ward, C. L., McCann, K. S., & Rooney, N. (2015). HSS revisited: Multichannel processes mediate trophic control across a productivity gradient. *Ecology Letters*, *18*, 1190–1197. https://doi.org/10.1111/ele.12498

Welter, J. R., Benstead, J. P., Cross, W. F., Hood, J. M., Huryn, A. D., Johnson, P. W. et al (2015). Does $N_2$ fixation amplify the temperature dependence of ecosystem metabolism? *Ecology*, *96*, 603–610.

Wilken, S., Soares, M., Urrutia-Cordero, P., Ratcovich, J., Ekvall, M. K., Van Donk, E., & Hansson, L.-A. (2018). Primary producers or consumers? Increasing phytoplankton bacterivory along a gradient of lake warming and browning. *Limnology and Oceanography*, *63*, S142–S155. https://doi.org/10.1002/lno.10728

Wolkovich, E. M., Allesina, S., Cottingham, K. L., Moore, J. C., Sandin, S. A., & de Mazancourt, C. (2014). Linking the green and brown worlds: The prevalence and effect of multichannel feeding in food webs. *Ecology*, *95*, 3376–3386. https://doi.org/10.1890/13-1721.1

Wyatt, K. H., & Rober, A. R. (2020). Warming enhances the stimulatory effect of algal exudates on dissolved organic carbon decomposition. *Freshwater Biology*, *65*, 1288–1297. https://doi.org/10.1111/fwb.13390.

Wyatt, K. H., Seballos, R. C., Shoemaker, M. N., Brown, S. P., Chandra, S., Kuehn, K. A., … Sadro, S. (2019). Resource constraints highlight complex microbial interactions during lake biofilm development. *Journal of Ecology*, *107*, 2737–2746. https://doi.org/10.1111/1365-2745.13223

Wyatt, K. H., & Turetsky, M. R. (2015). Algae alleviate carbon limitation of heterotrophic bacteria in a boreal peatland. *Journal of Ecology*, *103*, 1165–1171. https://doi.org/10.1111/1365-2745.12455

Yvon-Durocher, G., Hulatt, C. J., Woodward, G., & Trimmer, M. (2017). Long-term warming amplifies shifts in the carbon cycle of experimental ponds. *Nature Climate Change*, *7*, 209–213. https://doi.org/10.1038/nclimate3229

Zou, K., Thébault, E., Lacroix, G., & Barot, S. (2016). Interactions between the green and brown food web determine ecosystem functioning. *Functional Ecology*, *30*, 1454–1465. https://doi.org/10.1111/1365-2435.12626

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