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No evidence of biodiversity effects on stream ecosystem functioning across green and brown food web pathways

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Abstract

1. Biodiversity loss is known to affect the two fundamental and opposite processes controlling carbon and nutrient cycles globally, that is, primary production and decomposition, which are driven by green and brown food web compartments, respectively.

2. However, biodiversity in these two food web compartments has been mostly studied independently, and potential reciprocal effects of biodiversity loss on ecosystem processes remain unclear.

3. We conducted a 35-day stream mesocosm experiment with two levels of algal diversity (natural and diluted periphyton communities) and three levels of litter diversity (no litter, monocultures of poplar, maple, and oak, and the three-spp. mixture) to simulate changes in biodiversity in both the green and brown pathways of an aquatic food web. We then measured multiple ecosystem processes pertaining to carbon cycling.

4. We predicted that algal diversity would enhance decomposition and sporulation of fungal decomposers, while litter diversity would enhance algal growth and net primary production, due to the more diverse algal exudates or litter nutrients being released from more diverse mixtures.

5. In contrast to this hypothesis, we only found biodiversity effects on an ecosystem process within the green pathway: there was a relationship between algal diversity and biofilm carrying capacity. Nevertheless, we found that this relationship was affected by the presence or absence of litter (algal diversity increased the carrying capacity in presence of litter and decreased it in its absence), which also influenced the algal community structure.

6. Our mesocosm experiment did not evidence relationships between biodiversity and ecosystem processes across different food web compartments, but further studies in more realistic conditions would be necessary to confirm this result. If supported, the lack of biodiversity–ecosystem functioning relationships across compartments would facilitate the prediction of the impacts of biodiversity loss on ecosystems.

1 | INTRODUCTION

Studies focused on the relationship between biodiversity and ecosystem functioning have increased in recent decades due to concerns about the potential ecological consequences of biodiversity loss (Cardinale et al., 2012; Naeem et al., 1994; Tilman et al., 2014). Ecosystems are often valued for their capacity to maintain multiple processes, yet most studies assessing biodiversity–ecosystem functioning relationships have examined single processes in isolation (Hector & Bagchi, 2007). Among the different pathways of ecosystem functioning, biodiversity and ecosystem functioning studies have mostly focused on two opposite and fundamental processes controlling carbon and nutrient cycles globally (Field et al., 1998; Gessner et al., 2010): primary production, and how it is affected by the diversity of primary producers in the *green compartment* (Cardinale et al., 2011); and leaf litter decomposition, and how it is affected by the diversity of litter or consumers in the *brown compartment* (López-Rojo et al., 2019; Sanpera-Calbet et al., 2009). Biodiversity effects on these processes have mostly been considered separately, possibly because they are often dominant in different parts of the river network (Vannote et al., 1980). However, both processes generally co-occur, and studies should consider how biodiversity in both food web compartments and the processes occurring within them may interact to influence one another.

Microbial decomposers (mainly aquatic hyphomycetes) secrete extracellular enzymes that allow the decomposition of litter recalcitrant organic compounds (Marks, 2019). Microbial decomposition can be favoured by the presence of periphytic algae, which exude fresh, labile carbon (C) that, for example, can be used by fungi to invest in growth and enzyme production (Soares et al., 2017) in a phenomenon known as *priming effect* (Guenet et al., 2010; Löhnis, 1926). There is also evidence that algal accumulation in the epilithic biofilm increases the amount of organic substrates available for bacteria, and thus can enhance the use of organic matter by heterotrophic assemblages (Roman & Sabater, 1999). Similarly, when litter enters the stream, soluble compounds are released to the water column by leaching, including dissolved organic matter in the form of carbohydrates and nutrients (Bärlocher, 2005) that can enhance algal nutrient uptake and growth (Elser et al., 2007) and increase the C:nutrient ratios of algae (Stelzer & Lamberti, 2001), although some compounds may also inhibit algal photosynthetic activity (Ridge et al., 1999).

Some studies have addressed the complex interactions between primary producers and heterotrophic decomposers and found that the presence of diatoms increased microbial leaf litter decomposition rates (Danger et al., 2007; Daufresne & Loreau, 2001; Harte & Kinzig, 1993), but there is no evidence of whether such interactions across food web compartments are magnified by biodiversity. This could occur through the same mechanisms that operate within compartments, namely complementarity and selection effects (Loreau & Hector, 2001), which result from the greater number of biological traits associated with higher biodiversity (López-Rojo et al., 2021; Schindler & Gessner, 2009). For example, different algal taxa often produce chemically distinct exudates (Hamels et al., 2004; Widrig et al., 1996) that might be used more efficiently by microbial decomposers (i.e., a complementarity effect) promoting leaf litter decomposition and fungal growth and sporulation rates (Qiao et al., 2016); and the presence of more litter types could increase the chance that a nutrient-rich species might be present, with higher nutrient concentrations enhancing algal activity (i.e., a selection effect).

Here, we studied reciprocal effects between biodiversity and ecosystem processes between green and brown food web compartments (i.e., how biodiversity in the green compartment affected processes in the brown compartment, and vice versa). To do so, we completed a stream mesocosm experiment with two levels of both algal and litter diversity, where we examined rates of litter decomposition, fungal sporulation, algal growth, and net primary production. We hypothesised that: (1) algal diversity would enhance microbial activity (both microbial litter decomposition and fungal sporulation); and (2) the presence of litter and its diversity would promote biofilm growth, carrying capacity (i.e. the maximum potential population size; Berck et al., 2012) and net primary production. In both cases, we predicted (3) shifts in (fungal and algal) taxon diversity and assemblage composition, mediated by the differences in resource use (i.e. different strategies in the acquisition of nutrients; Frost et al., 2007).

2 | MATERIALS AND METHODS

2.1 | Collection site and stream mesocosms

We collected the leaf litter, microbial inoculum, and periphytic algae from a section of the Huron River that runs through the University of Michigan's Nichols Arboretum in Ann Arbor, Michigan (42.283° N, 83.724° W). At this location, the Huron River is a fifth-order stream that drains 1,888 km^2 in southeast Michigan, with a mean annual discharge of 13.31 m^3/s. Conductivity was 716 µS/cm, dissolved oxygen concentration 10.40 mg/L, nitrogen (N) concentration 365 µg/L, and phosphorus (P) concentration 19 µg/L (data taken from USGS Station #04174500).

The experiment was conducted at the experimental flume facility of the University of Michigan, which is equipped with recirculating streams called flumes. Each flume was 0.6 m long × 0.1 m wide × 0.1 m deep, held 13.3 L of water, and had a 7-cm diameter propeller controlled by a DC motor attached to a TechPower HY3020E 3-amp voltage regulator that maintains water flow (set

at 20 cm/s [SD = 0.02]). Temperature was maintained at 13 ± 1°C (the temperature of Huron River site where the inoculums were collected, see below) by coolers, and lighting was provided by Coralife Aqualight T5 light fixtures (containing two 9-watt, 10K daylight spectrum fluorescent lamps) set to a 14:10-hr light:dark cycle.

2.2 | Experimental design

The experiment included two algal treatments (low and high diversity) and five litter treatments (no litter, three monocultures, and the three-spp. mixture), resulting in 10 treatments in total. Combinations with litter were replicated five times (n = 5; 40 flumes), while those without litter were replicated three times (n = 3; six flumes), for a total of 46 experimental flumes that were randomly assigned to treatments. We added 0.5 L of inorganic sediment, 400 ml of gravel-sized rocks (4 ± 1 cm Ø) and 100 ml of pea-sized gravel (1 ± 0.5 cm Ø), to a 220-cm^2 working section at the bottom of each flume, thus creating a heterogeneous substrate for colonisation and growth of periphytic algae that was consistent across all flumes. We also added four round ceramic tiles (1.9-cm Ø) to the working section as a substrate with a standardised area (2.84 cm^2) to simplify algal sampling and quantification. We filled the flumes with dechlorinated Ann Arbor city water (which comes from the Huron River) that was kept in an opaque holding tank recirculating through an ultraviolet steriliser (Aqua Ultraviolet, U.S.A.) for 72 hr before its use. Twenty-four hours before the experiment (i.e., when the flumes were filled for the first time and before each water replacement, see below), we added NaNO$_3$ and KH$_2$PO$_4$ to the water to achieve the ambient concentrations of nutrients in the Huron River (USGS Station #04174500).

2.3 | Algal communities

On 27 October 2019, we collected c. 14 L of cobbles that were evenly spaced along transects placed in both riffle and run habitats of the Huron River. We transported the cobbles to the laboratory in a cooler immersed in stream water, and then gently removed their biofilm with a soft toothbrush. We filtered the resulting biofilm slurry (7 L) through a 250-μm sieve to remove macroinvertebrates and large detritus. A 15-mL subsample of the slurry was preserved in 3% formalin for later determination of algal cell density and community structure using a Neubauer-improved haemocytometer in a binocular microscope at 400× magnification. The remaining slurry was used to prepare two solutions representing the two treatments of algal diversity: the initial slurry (i.e., the natural community, composed of 20 morphospecies) was used as the high algal diversity treatment, which was used to inoculate half of the flumes; and a serial six-fold dilution of the initial slurry (which progressively eliminated less abundant species, reducing diversity to six morphospecies, thus simulating extinction of rare species) (Costello et al., 2018) was used as the low diversity treatment, which was inoculated to

the other half of the flumes. All mesocosms were inoculated with the same number of algal cells (c. 30,000 per flume).

2.4 | Leaf litter and microbial inoculum

In October 2019, we collected recently abscised litter of three of the most common species in riparian habitat along the Huron river in south-eastern Michigan: *Populus deltoides* W. Bartram ex Marshall (hereafter poplar), *Acer saccharum* Marshall (hereafter maple), and *Quercus rubra* L. (hereafter oak). Litter was transported to the laboratory, air dried to constant mass, and leaf discs (1.27-cm Ø) were cut using a cork borer. Sets of 48 discs (belonging to one or three species; 16 discs per species in the latter case) were weighed to the nearest 0.0001 g and enclosed in 2-mm mesh bags. Each flume received five litter bags belonging to one of four treatments (i.e., monocultures of poplar, maple or oak, or the three-spp. polyculture), while others received no litter.

Additionally, we collected litter from natural leaf packs from the bed of the Huron river (dry mass [DM] = 37.80 g; 43.56% *Acer* spp., 27.83% *Quercus* spp., 7.14% *Platanus occidentalis*, 4.77% *Ulmus americana*, 4.20% *Populus deltoides*, 3.15% *Tilia americana*, and 9.35% unrecognised fragments and seeds) and associated natural foam (i.e. natural foam-like aggregates containing high density of aquatic hyphomycete conidia) to obtain a representative inoculum of the microbial decomposer community (Descals, 2005). We transported the material (litter and foam) to the laboratory within Ziplock bags filled with stream water in a cooler, and incubated it for 5 days in a plastic container with 7 L of water (the same used to fill the flumes) and constant aeration. Water was replaced every 24 hr until the start of the experiment (to ensure freshly detached conidia that were thus capable to develop; Chauvet, 2020), when we added 125 ml of this microbial inoculum (c. 3 × 10^3 conidia) to each flume. We also collected 8 subsamples of this inoculum and preserved them in 2% formalin to characterise the initial fungal community structure. For this purpose we added 150 μL of 0.5% Triton X-100 to each preserved sample, which was mixed with a magnetic stirrer in order to ensure a uniform distribution of conidia; 10–15 ml were filtered (25-mm diameter, pore size 5 μm, Millipore SMWP, Millipore Corporation; Descals, 2020) and stained with 0.05% trypan blue in 60% lactic acid, and conidia were identified and counted at 200× magnification (Gulis et al., 2005).

2.5 | Experimental procedure

On day 1 of the experiment (30 October 2019), litter bags were introduced in the flumes and attached to floating Styrofoam squares that suspended them in the water column and maintained separation from the sampling section in order to avoid shading. We then we added algal and microbial inocula, as described in the previous section. For the first 2 days, flow in the flumes was kept at a low velocity of 10 cm/s (half of the flow velocity during the rest of the experiment)

to facilitate algal settling and colonisation of the substrates. We replaced 50% of the water in each flume weekly in order to minimise nutrient depletion, and to maintain water pH. We collected one litter bag per flume on days 3, 6, 10, 16, and 32 to measure decomposition via mass loss, and one ceramic tile per flume on days 7, 11, 17, and 33 to measure algal biomass per unit area. Collection of litter bags and tiles was separated by one day to allow sample processing within the first 24 hr. We did not collect tiles on day 4 because it was too early to detect algal biomass accrual.

Upon collection, litter from each bag was dried (60°C, 72 hr), weighed, incinerated (550°C, 4 hr) and reweighed to measure the remaining ash-free DM. On day 3 (hereafter post-leaching), litter from each species was processed separately and, before incineration, we divided each sample in two subsamples; one was preserved to analyse nitrogen (N; Perkin Elmer series II CHNS/O elemental analyser) and phosphorus (spectrometer after autoclave-assisted extraction; APHA, 1998) contents (%DM) in order to calculate the amount of N and P leached. Specific leaf area (SLA; mm^2/mg) was also measured (by weighing five sets of five oven-dried 1.27-cm Ø discs per species) as a proxy of leaf toughness. We used extra non-incubated leaf discs (3–10 replicates per species) to calculate % moisture, initial ash and N and P contents and initial SLA (as above). Litter decomposition rate in each flume was estimated using the single-phase exponential decay model $M_r = M_i \times e^{-kt}$, where M_r = remaining mass at time t, M_i = initial mass, and k = decomposition rate. This model proved to be a good fit to mass loss, explaining an average 63% of the variation.

On day 32, we separated six discs from each bag (two per species in mixtures) before being dried to measure fungal sporulation rate, following 48 hr incubation of the discs in 25 ml of water from the corresponding flume placed on a shaker table that was set at 100 rpm at the same temperature as the flumes. We preserved the resulting conidial suspension to characterise the fungal community (as above) and processed the leaf discs and determined the final SLA (as above). Tiles were scratched with a soft toothbrush in *c.* 10 ml of water in order to obtain the biofilm. The resulting solution was filtered (pre-dried and weighed 0.7 μm GF/F glass fibre filters) and filters were oven-dried (60°C, 72 hr) and reweighed to calculate biofilm DM. Biofilm growth rate and carrying capacity were estimated for each flume (nls function, *stats* package) using the logistic growth model $dB/dt = r \times B \times (1 - (B/c))$, where B = biomass at time t, r = growth rate, and c = carrying capacity.

On days 34–35, after all bags and tiles had been collected, and only periphyton growing on the natural substrate remained in the flumes, we measured the change in oxygen concentration in 40 flumes; one replicate flume was excluded in treatments with litter monocultures due to equipment limitations. Flumes were deployed with an oxymeter (miniDOT Logger, PME, U.S.A,), totally filled with water removing air bubbles, and hermetically closed. We then recorded oxygen concentration every minute over the course of a 8-hr light, and 12-hr dark period. We calculated respiration rate as the slope of the decrease in oxygen concentration (mg O$_2$ L^{-1} hr^{-1}) during the dark period, and net primary production (*NPP*) as the slope of the increase in oxygen concentration; we then calculated gross primary production as the sum of NPP and respiration rate. Finally, we collected two gravel-sized and two pea-sized rocks from each flume, scratched them in 15 ml of flume-water and preserved and analysed (as explained above for the initial inoculum) to characterise the final algal communities.

2.6 | Data analyses

We examined the effect of algal and litter diversity on decomposition and sporulation rates, algal growth rate, biofilm carrying capacity and *NPP* with linear mixed effects (LME) models (lme function, *nlme* R package; Pinheiro et al., 2018). All models included litter (no litter, three monocultures, and the three-spp. mixture) and algal (low or high) diversity as fixed effects (fitted as an interaction to test whether algal diversity effects varied depending on litter diversity treatments and vice versa), litter species as a random effect, and the variance function structure varIdent, which allowed different variances for each algal diversity level (low or high); the need for this term was identified in initial data exploration and confirmed by comparison of the Akaike information criterion of models with and without this component. Additionally, we examined whether algal diversity effects differed between litter of different species (litter species as fixed factor) with linear models as above (lm functions, *nlme* R packages). When necessary, response variables where log-transformed to comply with model assumptions (Ieno & Zuur, 2015).

We analysed the effect of initial algal and litter diversity on the final fungal conidial and algal diversity with LME models (as above), and on taxonomic structure of fungal conidial and algal assemblages with non-metric multidimensional scaling and permutational analysis of variance (PERMANOVA) based on a Bray–Curtis dissimilarity matrix of Hellinger transformed data, (adonis function, *vegan* package); we determined the most representative taxa or morpho-species (simper, *vegan* package).

Lastly, given that litter and algal diversity did not explain variation in decomposition and sporulation rates, algal growth, biofilm carrying capacity or fungal community structure (see Results), we explored how those variables were affected by the leaf litter characteristics and the amount of leached N and P during the first 72 h of incubation. We constructed linear models (lm function in the *stats* package with initial and post-leaching N, P, ash [%], and SLA, final SLA and amount of leached N and P as response variables and then selected the model with the lowest Akaike information criterion using the step function [*stats* package]). We also analysed the potential effect of algal biomass and growth rate on litter decomposition with LME models (as above).

3 | RESULTS

Litter identity, but not diversity, had an effect on processes of the brown pathway. Thus, decomposition and sporulation rates and fungal conidial diversity varied among litter types (Figures 1a,b and 2a,
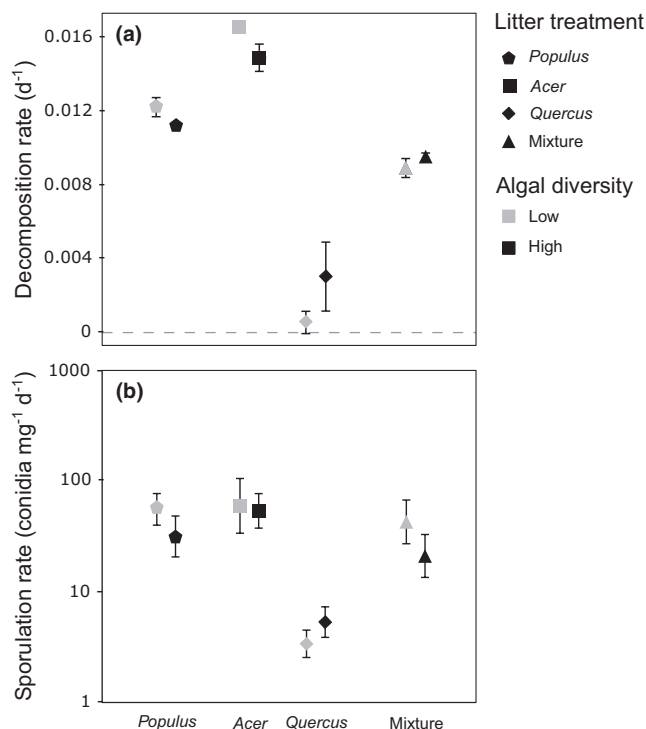
FIGURE 1 Litter decomposition rate (day^{-1}) and sporulation rate (conidia mg^{-1} day^{-1}, logarithmic scale) for treatment with low or high diversity of algae and with no litter, monocultures (*Acer*, *Populus* or *Quercus*) or the mixture (mean ± SE)

Table 1). Decomposition rates ranged from −0.001 to 0.017 d^{-1}, being highest for poplar and lowest for oak litter. Sporulation rates varied from 205.84 to 1.67 conidia mg^{-1} d^{-1}, being highest for poplar and maple and again, lowest for oak (Table S1). Litter samples (including the three-spp. mixture) presented an average of 5 ± 0.32 (mean ± SE) fungal conidial species. All litter types released N and P to the water during the first 72 hr (leaching period), with the exception of oak. Poplar was the species which released more N, while oak leached the highest amount of P (Tables 2 and 3).

Initial algal diversity increased algal carrying capacity and final diversity, but not algal growth rate or NPP (Table 4). The latter was generally low, ranging from −0.006 to 0.048 mg O$_2$ L^{-1} d^{-1}. At the end of the experiment, differences between algal diversity treatments were lower than initially but still significant ($t = -3.007$, $df = 40.696$, p-value = 0.004). Flumes corresponding to initial low and high algal diversity treatments presented 20.70 ± 0.70 and 23.85 ± 0.74 (mean ± SE) morphospecies respectively (Table S2).

We found no evidence that initial algal diversity enhanced rates of decomposition or fungal sporulation (Figure 1, Table 4), thus rejecting our first hypothesis. Similarly, neither litter presence nor diversity promoted algal growth, carrying capacity, or NPP (Figure 3, Table 4), rejecting our second hypothesis. However, we did find an interaction between the green and brown pathways: in the absence of litter, algal carrying capacity was higher at the low algal diversity treatment, and the pattern was opposite in its presence, regardless of diversity (Figure 3b).
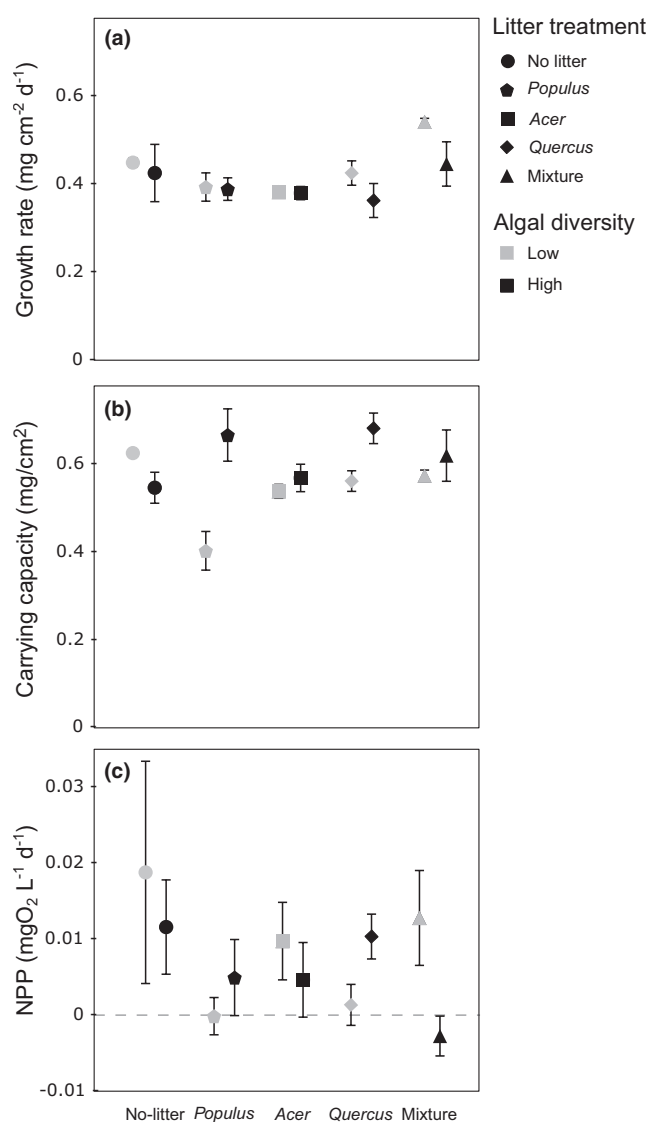

FIGURE 2 Aquatic hyphomycete and algal diversity (no. of species and morphospecies respectively) for treatment with low or high diversity of algae and with no litter, monocultures (*Acer*, *Populus*, or *Quercus*) or the mixture (mean ± SE) and non-metric multidimensional scaling (NMDS) analysis of aquatic hyphomycete and algal community structure. A.acu: *Alatospora acuminata*; A.pul: *Alatospora pulchella*; A.tet: *Articulospora tetracladia*; F.cur: *Flagelospora curvula*; Fon: *Fontanella* sp.; G.inf: *Geniculospora inflata*; G/M: *Goniopila/Margaritispora*; L.aqu: *Lemonniera aquatica*; L.cen: *Lemonniera centrosphaera*; L.pse: *Lemonniera pseudofloscula*; L.cur: *Lunulospora curvula*; T.ele: *Tetrachaetum elegans*; T.fur: *Tetracladium furcatum*; T.mar: *Tetracladium marchalianum*; Tric: *Tricladium* sp.; T.var: *Tricladium varium*; Trid: *Tridentaria* sp.; T.acu: *Triscelophorus acuminatus*; T.mon: *Triscelophorus monosphorus*; T.cam: *Trypospermun camelopardus*; T.myr: *Trypospermun myrti*; V.gig: *Variocladium giganteum*. Ulo: *Ullothrix*; Fra: *Fragillaria*; Ach1-3: morphospecies of Achanthidiaceae; col1-3: colonial algae; Enc: *Encyonema*; nav1-6: morphospecies of naviculoid diatoms; Nit: Nitzschioid diatom; Cym: *Cymbellonitzschia*; Nei: *Neidium*; dia1-7: morphospecies of diatoms; Syn: *Synedra*; Diat: *Diatoma*; gre1-2: morphospecies of green algae; Cya: cyanobacteria; Lim: *Limnothrix*; Sce: *Scenodesmus*; Chl: *Chlorococcum*; Ped: *Pediastrum*; Des: *Desmodesmus*; Rho1-2: morphospecies of *Rhoicospenia*; Coc: *Cocconeis*; Amp: *Amphora*; Tet: *Tetraedron*; Clo: *Closterium*

TABLE 1 Results of linear effects models testing for the effect of algal diversity and litter species (*Acer*, *Populus*, or *Quercus*) and their interaction on decomposition and sporulation rate, biofilm growth rate and carrying capacity and net primary production

Response variable	Factor	df	F	p
Decomposition rate	Algal div	1	1.578	0.222
	Litter species	2	108.091	<0.001
	Algal div: Litter species	2	2.695	0.089
Sporulation rate	Algal div	1	0.325	0.574
	Litter species	2	24.070	<0.001
	Algal div: Litter species	2	0.770	0.474
Biofilm growth rate	Algal div	1	1.136	0.298
	Litter species	2	0.144	0.866
	Algal div: Litter species	2	0.771	0.474
Biofilm carrying capacity	Algal div	1	21.682	<0.001
	Litter species	2	3.299	0.056
	Algal div: Litter species	2	5.163	0.015
Net primary production	Algal div	1	0.829	0.374
	Litter species	2	0.753	0.485
	Algal div: Litter species	2	1.633	0.223
Aquatic hyphomycete conidial diversity	Algal div	1	0.708	0.408
	Litter species	2	3.285	0.055
	Algal div: Litter species	2	0.322	0.727
Algal final diversity	Algal div	1	9.062	0.006
	Litter species	2	0.498	0.614
	Algal div: Litter species	2	4.359	0.027

Abbreviations: *df*, degrees of freedom; *F*, *F* statistic value; *p*, *p*-value.

TABLE 2 Amount of nitrogen (N) or phosphorous (P) leached to the water (mg per flume) in treatments with litter of poplar (*Populus*), maple (*Acer*), oak (*Quercus*), or the three-spp. mixture

Litter treatment	Leached N (mg/flume)	Leached P (mg/flume)
Populus	4.99 ± 1.16	0.86 ± 0.05
Acer	2.24 ± 0.37	0.22 ± 0.02
Quercus	−1.70 ± 0.66	0.97 ± 0.02
Mixture	2.39 ± 0.24	0.68 ± 0.02

We did not find an effect of algal diversity on fungal conidial diversity or assemblage structure. The most abundant species were *Tetracladium marchalianum* and *Lemmoneira pseudofloscula* (Table S1). Litter diversity tended to increase final algal diversity, but the trend was not significant. However, the algal assemblage structure varied depending on litter presence and identity; flumes without litter and with oak litter differed from others. Diatoms were abundant in all samples, but simper analysis revealed that flumes without litter were characterised by the abundance of *Limnothrix*, while flumes with litter were characterised by the presence of *Fragilaria*, *Synedra*, *Nitzchia*, and diatom 4 (Figure 2d, Table S2).

TABLE 3 Initial and post-leaching nitrogen (N), phosphorous (P) and ash percentage (mean ± *SE*) and specific leaf area (SLA, mm^2/mg) of litter species (*Populus*, *Acer*, and *Quercus*)

Litter species	N%	P%	Ash%	SLA
Populus				
Initial	1.32 ± 0.08	0.08 ± 0.01	12.04 ± 0.16	11.06 ± 0.14
Post-leaching	1.38 ± 0.04	0.07 ± 0.00	9.45 ± 0.31	13.12 ± 0.15
Acer				
Initial	1.07 ± 0.02	0.06 ± 0.00	9.22 ± 0.22	21.28 ± 0.54
Post-leaching	1.13 ± 0.05	0.06 ± 0.00	11.00 ± 0.18	23.61 ± 0.30
Quercus				
Initial	0.90 ± 0.05	0.10 ± 0.01	5.23 ± 0.23	17.91 ± 0.33
Post-leaching	1.00 ± 0.05	0.04 ± 0.00	5.37 ± 0.30	16.39 ± 0.32

Response variable	Factor	df	F	p
Decomposition rate	Algal div	1,32	0.141	0.709
	Litter div	1,2	0.002	0.964
	Algal div: Litter div	1,32	0.127	0.724
Sporulation rate	Algal div	1,33	0.456	0.503
	Litter div	1,2	0.004	0.954
	Algal div: Litter div	1,33	0.337	0.565
Biofilm growth rate	Algal div	1,35	3.524	0.068
	Litter div	1,3	2.374	0.221
	Algal div: Litter div	1,35	1.757	0.139
Biofilm carrying capacity	Algal div	1,36	8.652	0.005
	Litter div	1,3	0.134	0.738
	Algal div: Litter div	1,36	0.032	0.859
Net primary production	Algal div	1,30	0.390	0.536
	Litter div	1,3	1.815	0.271
	Algal div: Litter div	1,30	1.416	0.243
Aquatic hyphomycete conidial diversity	Algal div	1,33	0.062	0.804
	Litter div	1,2	0.699	0.491
	Algal div: Litter div	1,33	1.975	0.169
Final algal diversity	Algal div	1,36	10.108	0.003
	Litter div	1,3	3.239	0.169
	Algal div: Litter div	1,36	0.576	0.453
Aquatic hyphomycete community	Algal div		0.859	0.519
	Litter div		1.468	0.188
	Algal div: Litter div		1.461	0.188
Algal community	Algal div		2.011	0.018
	Litter div		2.130	0.013
	Algal div: Litter div		0.682	0.777

TABLE 4 Results of linear-mixed effects models testing for the effect of algal diversity (low or high), leaf litter diversity (no litter, three monocultures, and the three-spp. mixture) and their interaction on decomposition and sporulation rate, biofilm growth rate and carrying capacity, net primary production, and aquatic hyphomycete and algal diversity, and PERMANOVAs testing for the effects on aquatic hyphomycete and algal community structure

Abbreviations: df, degrees of freedom; F, F statistic value; p, p-value.

The model selection procedure showed that decomposition rate was mainly explained by post-leaching ash content, sporulation rate was explained by final SLA and initial and post-leaching ash, and aquatic hyphomycete conidial diversity was explained by initial P. The model for algal growth rate included post-leaching N but its influence was non-significant ($p = 0.173$), and the same occurred for *NPP* with final SLA and initial P ($p = 0.07$ and 0.06 respectively) and gross primary production by final SLA (Table 5). None of measured litter characteristics included in the model (N%, P%, ash%, or SLA) explained the variation on algal carrying capacity or final algal diversity.

4 | DISCUSSION

Primary production and litter decomposition are key processes determining stream ecosystem functioning, and both can be altered by changes in biodiversity (Cardinale, 2011; López-Rojo et al., 2019; Sanpera-Calbet et al., 2009). However, studies have mainly focused on how primary producer diversity affects primary production (i.e., the green pathway of the food web) and how leaf litter diversity

affects decomposition (i.e., the brown pathway), mostly ignoring the reciprocal interaction between both pathways. Here, we addressed this issue through a stream mesocosm experiment, finding that leaf litter presence and identity (but not diversity) affected the green pathway, but no effects were significant in the other direction.

4.1 | Algal diversity did not affect the brown pathway

Our experiment did not reveal any effect of algal diversity on microbially mediated litter decomposition or aquatic hyphomycete sporulation. This lack of effect was unexpected, as we had hypothesised that algal diversity would increase the variety of algal exudates and thus, the priming intensity (i.e., the magnitude of the priming effect on heterotrophic activity; Halvorson et al., 2019). However, the difference between our two algal diversity treatments at the end of the experiment (a mean of 20 vs. 24 morphospecies respectively), albeit significant, was not as large as it was initially (6 vs. 20), possibly due to unwanted colonisation of additional algal species through the
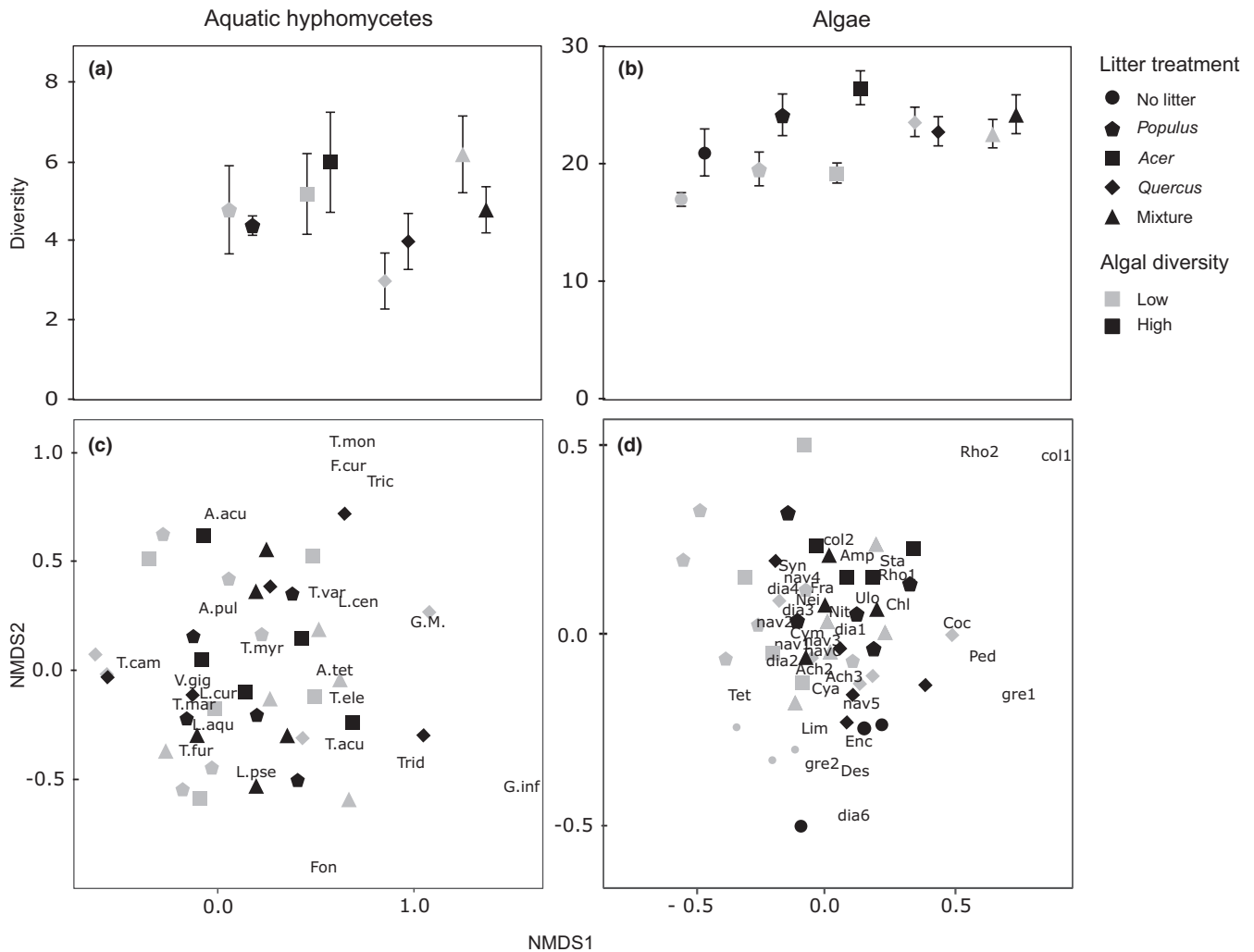
FIGURE 3 Biofilm growth rate (mg cm^2 day^{-1}) and carrying capacity (mg cm^2) and net primary production (NPP, mgO$_2$ L^{-1} day^{-1}) for treatment with low or high diversity of algae and with no litter, monocultures (*Acer*, *Populus*, or *Quercus*) or the mixture (mean ± *SE*)

microbial inoculum. This smaller-than-expected difference between our low and high algal diversity treatments may have precluded the occurrence of a diversity effect on the brown pathway. Further studies analysing the evolution if both algal and fungal communities during the decomposition process will be needed to confirm this hypothesis and better understand the relationship between both pathways. We did not show any relationship between algal biomass ($F = 0.008$; $p > 0.05$) or growth rate ($F = 0.957$; $p > 0.05$) and litter decomposition (algal growth rate was similar in flumes of acer and oak leaf litter, the species presenting highest and lowest decomposition rates, respectively). A relationship between decomposition and algal biomass could indicate a priming effect due only to the presence of primary producers and not to their diversity, pointing to some redundancy between algal species. This issue should be further explored by including treatments in absence of primary producers.

There are other possible explanations for the lack of effect of algal diversity on the brown pathway. The overall low net primary production rates measured at the end of the experiment suggests an important contribution of heterotrophic bacteria to the composition of biofilm in the flumes. These bacteria could monopolise the organic exudates excreted by algae (Marshall, 1989) and prevent the

detection of positive effects on litter decomposition, which is mainly driven by fungal decomposers in those environments (Pascoal & Cássio, 2004). However, as bacterial communities play an important role in the degradation of dissolved organic matter (Tranvik, 1992), which is increased by exudates from primary producers, future studies should examine the effect of algal diversity also in bacterial communities. Also, fungal decomposers often show high functional redundancy (Gessner et al., 2010), which may have precluded any complementary effect derived from the existence of a higher variety of algal exudates.

4.2 | Leaf litter presence and identity (but not diversity) affected the green pathway

Litter diversity had no effect on algal growth, carrying capacity or net primary production, which again contradicted our expectations of enhanced algal activity in the presence of a higher variety of nutrients in the water as a result of leaching. It is also possible that any potential effects of more diverse nutrients may have been counteracted by the also higher variety of toxic compounds (e.g., condensed tannins,

Response variable	Selected factors	Retained variance	F value	p-value
Decomposition rate	Post-leaching ash (+)	84.64%	305.11	<0.001
	Leached N (+)	2.35%	8.46	0.006
	Final SLA (+)	2.05%	7.39	0.010
	Initial P (−)	1.19%	4.28	0.046
	Initial ash (+)	0.89%	3.22	0.081
Sporulation rate	Final SLA (+)	20.99%	15.32	<0.001
	Initial ash (+)	15.97%	11.66	0.001
	Post-leaching ash (−)	15.11%	11.03	0.002
Biofilm growth rate	Post-leaching N (+)	9.52%	1.99	0.173
Net primary production	Initial P (−)	13.99%	3.82	0.067
	Final SLA (−)	13.37%	3.65	0.072
	Post-leaching SLA (+)	10.48%	2.86	0.108
Gross primary production	Final SLA (+)	19.11%	5.11	0.036
	Post-leaching SLA (−)	13.60%	3.63	0.072
Aquatic hyphomycete conidial diversity	Initial P (−)	12.04%	5.06	0.030

TABLE 5 Results of linear models examining the variability of decomposition and sporulation rates, algal growth rate and carrying capacity, net primary production, gross primary production, and aquatic hyphomycete conidial diversity based on initial and post-leaching N, P, and ash (%) and SLA, final SLA, and amount of leached N and P (mg per flume)

Note: Retained variance: percentage of the variance retained by each factor. (+) and (−) indicate positive and negative relationships, respectively.

which are present in high concentrations in species form the family Fagaceae as oak; López-Rojo et al., 2021) inhibiting algal growth (Ridge et al., 1999), resulting in a net lack of effect. Strikingly, the above variables did not even differ between treatments with and without litter, despite the fact that most litter types released N and P to the water (except for oak, which immobilised N). Algal biomass production is usually enhanced as a result of N and P enrichment related to anthropogenic activities (Artigas et al., 2013), but here nutrient enhancement was due to leaching, which may be expected to be lower in magnitude than enrichment due to other sources. In our case, the concentration of N and P in the water during the first days ranged from 237 to 740 µg/L and 35 to 91 µg/L, respectively (taking in account both the N and P content of the water and the nutrients leached from the leaves); studies analysing the water quality of rivers in agricultural or urban areas have reported higher levels (for example, Gücker et al., 2011 measured concentrations of total phosphorous up to 553 ± 113 µg/L in urban streams). Despite a trend for algal growth to be higher in presence of the litter mixture (especially in treatments with low algal diversity), this trend was not significant and thus did not indicate an effect of litter diversity. Again, the lack of effects could be related to the low rates of net primary production found in the flumes. This situation might be similar to that of many detritus-based streams, where algal production is generally low (Fisher & Likens, 1973). The high variability of net primary production values, especially in flumes without litter that was the treatment with lowest replication, could be precluding the detection of significant differences.

Interestingly, the presence of litter modulated the relationship between algal diversity and algal carrying capacity. This relationship was negative in the absence of litter (i.e., carrying capacity was higher in less diverse algal communities, which were mainly characterised by high numbers (both richness and abundance) of green algae and lower numbers of diatoms) and was positive in the presence of litter (i.e., carrying capacity was higher in more diverse algal assemblages). This difference may be related to the fact that more diverse algal assemblages can take greater advantage of nutrients leached from litter (trough resource partitioning), allowing the coexistence of more species at higher population sizes (Cardinale, 2011; Chapin et al., 1997).

Finally, we found differences in algal community structure depending on litter treatments. The presence of diatoms such as *Fragillaria* on treatments with poplar, maple or the litter mixture agrees with other studies that related the presence of these species with high contents of water N (Costello et al., 2018). Others have related higher abundances of other diatoms (i.e. *Rhoicosphenia* and *Nitzchia*, which in our case were more abundant in flumes with litter) with nutrient enriched conditions (Artigas et al., 2013). In contrast, green algae were more abundant in flumes without litter. A plausible explanation could be the scarcity of elements that are necessary for diatom growth in the water (e.g., silicon, which is common in leaf litter structural compounds) (López-Rojo et al., 2021; Zhang et al., 2019); but unfortunately, we cannot confirm this as we did not measure those elements. Measurements of inorganic content and micronutrients of leaf litter might provide a better understanding of litter identity effects on algal community structure, as observed for microbial decomposers (Purahong et al., 2016).

5 | CONCLUSIONS AND INSIGHTS

Our results revealed notable effects of litter presence and identity on algal assemblages, although we did not detect any change in algal biomass or in net primary production, which was low overall. Similarly, algal diversity had no effects on the brown compartment, which agrees with other field and laboratory studies finding no or little evidence of algal priming effects on decomposition (Bengtsson et al., 2014; Elosegi et al., 2018). As a whole, these results point to greater biodiversity–ecosystem functioning relationships within food web compartments than between them, which may facilitate the prediction of the impacts of biodiversity loss on these ecosystems. However, this result should be taken with caution due to the experimental drawbacks of our study. Specifically, laboratory mesocosms are useful because they allow experiments with high degree of control and replication, but their size is too small to be realistic depictions of stream ecosystems. An important result of our research is that nutrients leached from leaf litter can modify the structure of algal communities, which could drive further changes in the green compartment in the longer term. Further studies should ideally include detritivorous invertebrates and examine the whole microbial community (including bacteria) to better understand biodiversity effects across different food web compartments. Given that algae and microbial decomposers compete for the same inorganic nutrients (Gossiaux et al., 2020), and that algae are often worse competitors (Currie & Kalff, 1984) and seasonality dependent (Francoeur et al., 1999), interactions between both types of organisms may vary with light and nutrient availability and thus change throughout the year, which also merits further attention.

CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data supporting all the analyses of this study is available upon request from the corresponding author.

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