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Significance of sunlight for organic matter degradation in aquatic systems

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Abstract

Degradation of organic matter (OM) is generally considered to be primarily governed by biotic factors in aquatic environments. However, a number of abiotic processes also play key roles in mediating OM-degradation. Sunlight can act as a principal abiotic driver of the degradation of terrestrial organic matter, but its importance for freshwater ecosystems and possible interactions with biotic drivers remains poorly understood. We carried out two microcosm experiments which focused on the role of sunlight on microbial and invertebrate-mediated OM degradation using two species of plant leaves and the aquatic invertebrate *Asellus aquaticus*. Results indicated that sunlight was the primary driver of leaf mass loss during the early stages of decomposition, whereas microbial communities had a negligible effect. Sunlight was observed to strongly affect invertebrate behavior as invertebrates avoided direct illumination. This alteration of behavior resulted in a reduction in the consumption of a leaf surrogate (DECOTAB) by *A. aquaticus*. Together, these results indicate that sunlight has the potential to strongly influence structural and functional attributes of shallow freshwater systems, and hence serve as an appraisal to consider sunlight as a significant direct and indirect physical driver governing OM degradation in shallow aquatic systems.

1. Introduction

Riparian leaves fuel aquatic food webs with organic matter (OM) that serves as a food source for a diverse array of microorganisms and macroinvertebrates. The relative importance of key factors that govern the degradation of OM remains a central issue. In freshwater ecosystems, OM-degradation is typically considered to be primarily governed by biotic factors such as microbial decomposition and invertebrate consumption (Odum and de la Cruz 1963), in which key abiotic factors such as water current (physical abrasion) and temperature (promoting detritivore activity) are also considered to contribute to the overall process (Throop and Archer 2009). Despite the importance of detritivores for OM degradation, many studies have difficulties reconciling OM degradation rates with the composition of aquatic invertebrate communities (e.g. Gonçalves *et al* 2006, Lagrue *et al* 2011, Hunting *et al* 2016), suggesting other (abiotic) variables also contribute to OM-degradation in freshwater ecosystems. Studies in terrestrial environments, coastal areas and high altitude streams have provided increasing evidence that sunlight can act as a principal abiotic driver of OM degradation (Austin and Vivanco 2006, King *et al* 2012, Loayza-Muro *et al* 2014, Baker *et al* 2015, Bornman 2015), where it may affect OM directly by photodegradation or indirectly through facilitation of microbial degradation (Brandt 2007, Baker *et al* 2015). Yet, its relative importance for freshwater ecosystems remains poorly understood. Provided that sunlight is able to penetrate to the sediment in shallow freshwater bodies and fringe areas of lakes, where substantial amounts of

OM accumulate (Morris *et al* 1995), it is conceivable that sunlight could potentially affect OM degradation in aquatic systems.

A number of attributes of freshwater systems can be expected to interact with sunlight. Firstly, effects of sunlight likely depend on the chemical composition of leaves. Effects of sunlight on leaf decomposition in terrestrial systems have been observed to depend on variability among leaves, in which decomposition rates were observed to vary among plant species varying in leaf surface area and chemical constituents that may differ in their ability to absorb light (Hättenschwiler and Vitousek 2000, Cornwell *et al* 2008, Pan *et al* 2015). Secondly, it is known that sunlight can directly impair microbial communities through detrimental effects on DNA and extracellular enzymes (Santos *et al* 2013), or indirectly affect OM-associated microbial communities via photodegradation of OM into smaller palatable or harmful molecules depending on OM substrate (Mopper and Zhou 1990, Scully *et al* 1996, Obernosterer and Benner 2004, Hunting *et al* 2013a). This can be particularly relevant as besides their direct role in decomposing OM (Amado *et al* 2007), microbial communities also form an essential link towards invertebrates feeding on the OM by enhancing palatability and provisioning of nutrients (Graça *et al* 1993, Graça 2001, Danger and Robson 2004, Vonk *et al* 2016, Zhai *et al* 2018). Several invertebrates can detect resulting differences in food quality and select the most palatable food (Canhoto and Graça 2008, Hunting *et al* 2013a), and adverse effects of sunlight on OM-associated biofilms have been observed to impair invertebrate growth (Franken *et al* 2005, Albarino *et al* 2008). Thirdly, a potential mechanism that may underlie interaction effects between sunlight and leaf degradation is a behavioral response of invertebrates to sunlight. One of the few studies addressing the effect of solar radiation on invertebrate behavior provides clear indications that survival and performance of terrestrial isopods is negatively affected by sunlight (Morgado *et al* 2015). Likewise, aquatic invertebrates seem to avoid direct exposure to sunlight and take refuge in macrophyte rich areas (Loayza-Muro *et al* 2013, 2014), and hence avoidance behavior triggered by sunlight might potentially disrupt the relation between invertebrate feeding activity and OM-degradation. However, direct effects of sunlight on aquatic invertebrate behavior has not yet been tested, and inherently indirect behavioral effects OM-degradation decomposition remain unknown.

Here, we used a simplified aquatic microcosm experiments to begin to assess the significance of sunlight for leaf degradation in shallow aquatic systems in relation to the metabolic activity of the associated microbial community and consumption by a dominant macroinvertebrate. To this end, we performed an outdoor incubation to determine the impact of sunlight on leaf disk mass loss and activity and resource niche breadth of the leaf-associated microbial community using both labile and recalcitrant leaf material. In addition, we performed a laboratory incubation to determine the impact of sunlight on behavioral responses of the aquatic invertebrate *Asellus aquaticus*.

2. Materials and methods

2.1. Experimental setup

We carried out two microcosm experiments at the University of Leiden. These experiments focused on the role of sunlight on decomposition of two different leaf types through microbial activity as compared to sterile (formaldehyde-treated) leaves (experiment 1), as well as invertebrate-mediated leaf decomposition (experiment 2). The set up allows for obtaining a relative measure for the importance of sunlight for leaf degradation in relation to microbial metabolic activity and consumption of a dominant macrodetritivore, yet it is important to note that OM degradation also depends on season (e.g. leaf toughness) and various other variables (e.g. temperature, latitude) that could not be captured in this study.

2.2. Experiment 1: Effects of sunlight on OM degradation and OM-associated microorganisms

The experiment was conducted between 8 and 13 September 2016 in a total of 32 200-ml polyethylene containers filled each with 175 ml of demineralized water to which we added an undefined microbial community sourced from a ditch near Leiden University (N52.1601144°, E4.4970097°) (2 ml ditchwater per microcosm). The experiment included two plant species, which were exposed to shaded/unshaded conditions and microbial breakdown/no micro-organisms, resulting in a total of eight treatments. To investigate how effects of microbes and sunlight vary with leaf recalcitrance, we used two plant species that are known to vary in chemical constituents, in particular phenol concentration: the stinging nettle *Urtica dioica* and the oak *Quercus robur*. Mature leaves of both species were picked from plants surrounding the University of Leiden in September 2016. Phenolic compounds of both leaf species were extracted from 10 leaf disks using 50 ml of 70% aqueous acetone and an extraction time of 100 min. Total phenolics were determined using Folin-Ciocalteu reagents (Ragazzi and Veronese 1973). Prior to this assay, 10-μl extracts were put in open aliquots in a flow cabinet to allow vaporization of acetone. Phenolics were subsequently resuspended in 10-μl deionized water and assayed. Absorbance was measured at 740 nm (Nanodrop, ND1000). Since recalcitrant compounds typically strongly

Table 1. Characteristics of leaf disks used in this study. UV absorption and phenol content were measured in this study, other characteristics were derived from other studies and the TRY database.

	Urtica dioica	Quercus robur
UV absorption (A_{280})	0.096	0.236
Phenolic content (A_{470})	0.084	0.348
Leaf tannin content (%)[a]	0.93	12
Leaf lignin content (%)[b]	3.5–4.4	23.5–28.0
Leaf nitrogen content (%)[c]	4.1–4.3	1.8–2.2
Leaf carbon content (%)[c]	38–40	47.5–50.1
Leaf C:N ratio[c]	9.4	24.1

[a] Data derived from literature (Salminen *et al* 2004, Adhikari *et al* 2016).

[b] Data derived from literature (Sariyildiz and Anderson 2003, Bacci *et al* 2009).

[c] Data derived from TRY database (www.try-db.org; accessed September 2018).

absorb in the UV region of the light spectrum, we also measured UV-absorption at 280 nm (BIO- RAD SmartSpec™ Plus spectrophotometer) of extracts of the used OM sources. Together with data on tannin and lignin content derived from the literature (see table 1 for references), it was apparent that *U. dioica* was a relatively labile OM source compared to the more recalcitrant *Q. robur* (table 1). Leaf disks (diameter 0.5 cm) were prepared from fresh green leaves of both species. Microcosms received three fresh leaf disks of a particular species and were exposed to unshaded or shaded (covered with Aluminum foil) conditions for a period of seven days. An additional set of identical microcosms was used to test for OM decomposition in the presence of microbial activity and no microbial activity (1 ml of 37% formaldehyde per microcosms per day). Formaldehyde might degrade when exposed to sunlight, yet we do not expect this affected abiotic decomposition of leaf disks. Effectiveness of formaldehyde in inhibiting microbial growth was confirmed using Biolog® Ecoplates as described below. Oxygen levels were monitored over the course of the experiment and did not go below 90% saturation (Hach hq 40d electronic multiparameter). After seven days, disks were retrieved, dried at 60 °C for six days and weighed using a microbalance with 0.001 mg precision. Mass loss was determined comparing the mass loss of dried leaves after the experimental period with the average initial dry masses of 10 freshly cut leaf disks at the onset of the experiment considering mass loss as percentage of the initial mass loss. Initial mean mass of the leaf disks were determined with a separate set of leaf disks, and proved to be 0.74 mg and 1.25 for *U. dioica* and *Q. robur*, respectively. To detect differences in leaf disk mass loss (two levels: with and without microbes) and the direct effect of sunlight (two levels: full sun and shaded), we used a two-way ANOVA and a Tukey HSD test to determine pairwise differences computed in PAST. Homogeneity of variances was evaluated via Levene's test. Normality of the model residuals was confirmed using QQ-plots.

To investigate the effect of leaf traits and sterilization with formaldehyde on the metabolic diversity of microbial communities, microbial communities were sampled from a single leaf disk per microcosm for each of the treatments by vortexing for 30 s in 50 ml demineralized water. One ml of leaf-associated microorganism suspension was distributed over the Biolog® Ecoplates (Biolog Inc, Hayward, California, USA) to assess microbial utilizations of environmentally relevant substrates. The Biolog Ecoplate contains 31 of the most useful carbon substrates (e.g. carbohydrates and amino acids), replicated 3 times (Garland and Mills 1991). Each well of the Ecoplate contains a single carbon substrate and a tetrazolium that turns purple upon microbial respiration and dehydrogenation of the respective carbon source. The approach is limited as it is confined to a culturable fraction of the microbial community and it does not include e.g. recalcitrant substrates nor specific substrates typical of the plant leaves used in this study. It is thus impossible to directly relate the carbon substrates utilization to actual microbial density and community structure, as well as their relative metabolic activity and how they would function under natural conditions, yet the number of utilized substrates offers a proxy of the metabolic or functional diversity of a microbial community (Hunting *et al* 2013b, Zhai *et al* 2016), or the resource breadth utilized by the bacterial community (Hunting *et al* 2015, 2017). Plates were incubated for 96 h at 18 °C and absorbance was measured at 590 nm using a BIO- RAD SmartSpec™ Plus spectrophotometer. Microbial functional diversity was evaluated considering microbial resource niche breadth. Traditional measures of microbial functional diversity express functional diversity as metabolic diversity or overall functional diversity, reflecting the average number of substrates utilized and among treatment variation. Substrate identities of individual replicates are lost using this approach and thereby does not provide insights into within treatment variation in substrate utilization required to assess the breadth of resources utilized.

Therefore, we determined the breadth of resources utilized by the microbial communities by considering within treatment variability, in which we used Gower distances as a preferred distance measure for functional diversity as it allows for ecological variables and functional diversity measures to be both continuous or categorical (e.g. ability to utilize a specific substrate; Villéger *et al* 2008). To this end, we produced a treatment-constrained dendrogram based on Gower distances, and determined the square root of the nearest nodes of the Gower-distances between the replicates. These distances provide a measure of within treatment variability of the breadth of resources utilized and overcomes the problem that substrate identity is lost. We performed a permutational multivariate analysis of variance (PERMANOVA, 9999 randomizations) to detect differences between treatments in the obtained multivariate resource niche breadth.

2.3. Experiment 2: Interacting effects of sunlight and invertebrate behavior

To investigate the significance of sunlight for litter degradation in relation to activity of dominant macroinvertebrates, we carried out an experiment with and without macroinvertebrates under shaded and unshaded conditions using solar lamps in standardized conditions in the laboratory. Prior to the experiment, individual *Asellus aquaticus* were collected from a pond near Leiden, Alphen aan den Rijn (N52.1276577°, E4.6688508°). To assess the single and combined effects on decomposition, we used Decomposition and COnsumption TABlets, DECOTABs (Kampfraath *et al* 2012, Van der Lee *et al* 2019; www.DECOTAB.org), that embed a homogenized and standardized mixture of particulate OM (POM) as a standardize substrate to determine detritivore consumption rate. DECOTABs were prepared with cellulose (25% agar and 75% cellulose) following the procedures as described by Kampfraath *et al* (2012), and DECOTAB mass loss was determined by subtracting the mass of dried (3 days at 60 °C) DECOTABs after the experimental period from dried freshly prepared DECOTABs (mean $\pm$ 1 SD $=$ 81.3 $\pm$ 3.1 mg, $n = 25$, accuracy 0.001 mg). Each microcosm contained 150 g sand and 300 ml Elendt M4 medium consisting of K_2HPO_4 (1.27 mM); KH_2PO_4 (1.27 mM); $NaHCO_3$ (1.27 mM); $(NH_4)_2SO_4$ (1.27 mM); NaCl (1.27 mM); Hepes (1.27 mM), with added yeast extract (0.5 gl^{-1}); Tryptone (0.5 gl^{-1}) 100X minerals (1%); 100X $CaCl_2$ (1%) and 40% sodium lactate (0.5%). Two DECOTABs were added to each microcosm (one on a side shaded with Aluminum foil, and one on an unshaded side). Collected invertebrates were variable in size, with insufficient invertebrates of comparable sizes to cover the entire experiment. Therefore, to obtain a comparable invertebrate body mass in each microcosm, twelve individuals of *Asellus aquaticus* of different sizes (two small 2–3 mm, six medium 3–4 mm, and four large $>$4 mm) were added to each microcosm. Both the treatment with and without *A. aquaticus* were replicated six times. Microcosms were exposed for 16 days to 160 W UV-mercury vapor lamp (Arcadia-D3, Redhill, UK: 160 W; luminous flux 1900 lm) that emits UV radiation of the following intensities: UV-B 1.75 Wm^{-2} at 310 nm; UV-A 10 Wm^{-2} at 365 nm; and PAR $<$1 Wm^{-2}: Light spectrum provided in figure S1 is available online at stacks.iop.org/ERC/1/101002/mmedia. Although these lamps do not provide an exact representation of natural intensities over the entire solar spectrum, the relative intensities of particularly UV radiation are commonly registered in temperate areas (e.g. Kelly *et al* 2003). A control experiment without invertebrates was run ($n = 10$) to assess the effect of illumination on biofilm formation on the DECOTABs as described above. During the experiment, visual observations were carried out daily to check whether *A. aquaticus* individuals developed a preference for the shaded or unshaded part of the microcosm. A number of individuals ($<$5) died during the initial stages of the experiment and replaced with an individual from the same batch of the same size. After 16 days, DECOTABS were retrieved, dried at 60 °C for 5 days and weighed. Differences in DECOTAB mass loss were tested using a non-parametric Kruskal-Wallis test because residuals were not normally distributed (Levene's test for homogeneity).

3. Results

For *U. dioica*, a difference in leaf disk mass loss was found between treatments, in which leaf disks exposed to sunlight degraded faster than leaf disks in shaded conditions (ANOVA: $F = 6.139, p = 0.029$; figure 1), but there was no significant impact of microorganisms or an interaction effect between sunlight exposure and presence of microorganisms. Microbial resource niche breadth in nettle was higher under shaded conditions compared to unshaded conditions (PERMANOVA: $F = 3.11, p = 0.030$) (figure 2), in which the number of substrates utilized in shaded conditions ranged 14–21, while in the illuminated it ranged 1–10 substrates. For oak, we found no effect of the interaction between sunlight and the presence of microorganisms (ANOVA: $F = 0.9443, p = 0.351$) on leaf disk mass loss (ANOVA: $F = 1.36, p = 0.266$; figure 1), and no effects of sunlight were observed on microbial resource niche breadth (figure 2). No substrates were utilized in microbial samples obtained from leaves that were incubated with formaldehyde.

DECOTAB mass loss was higher under shaded conditions than under unshaded conditions (Kruskal-Wallis: H-Chi-square $= 9.9$; $p = 0.002$; figure 3A). This was confirmed by daily visual observations, where we observed

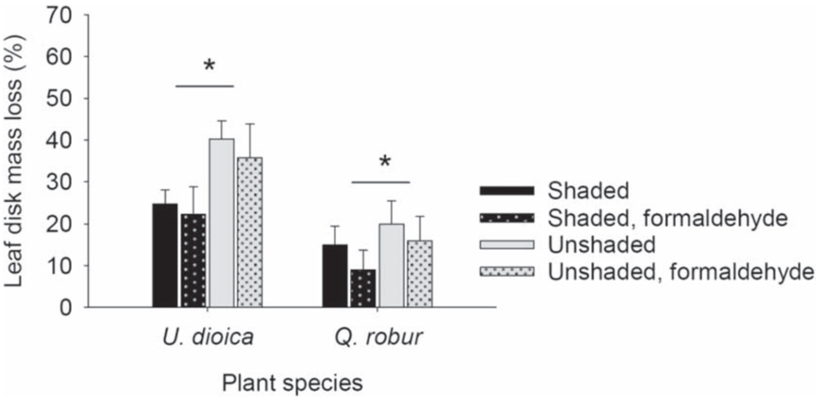

Figure 1. Leaf disk decomposition (mean ± standard error) for *Urtica dioica* (stinging nettle) and *Quercus robur* (oak) after exposure to microorganisms and no microorganisms (with formaldehyde) under shaded and unshaded conditions. Asterisks indicates significant difference at $a = 0.05$.

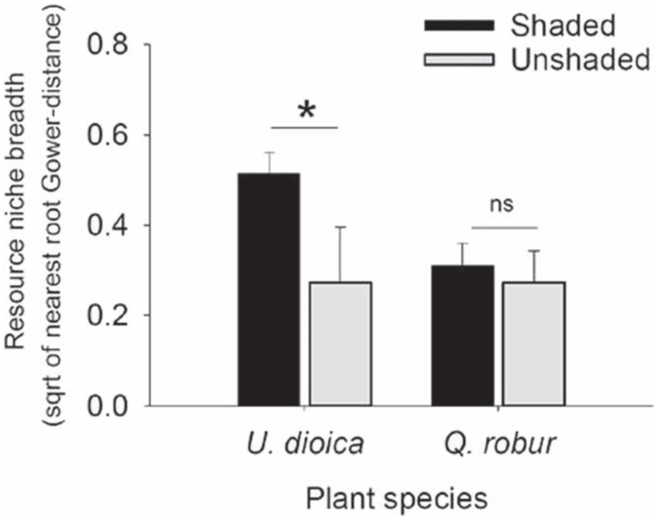

Figure 2. The effect of shaded and unshaded conditions on microbial resource niche breadth (mean ± standard error) for *Urtica dioica* (stinging nettle) and *Quercus robur* (oak). Asterisks indicate significant differences at $a = 0.05$. ns: not significant.

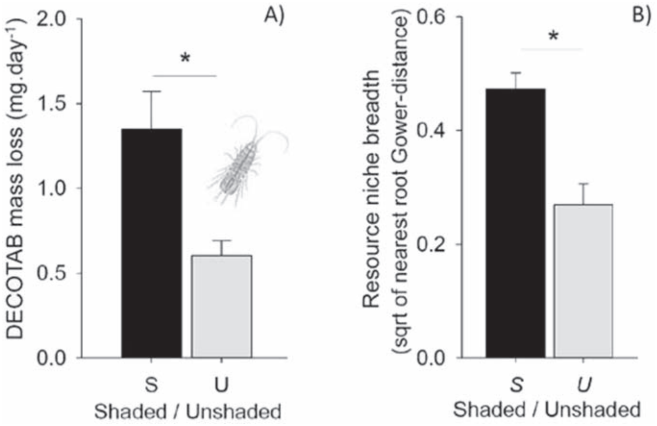

Figure 3. The effect of shaded and unshaded conditions on DECOTAB consumption by *Asellus aquaticus*. Asterisks indicate significant differences at $a = 0.05$.

that *A. aquaticus* avoided unshaded conditions and preferred shaded conditions. The control experiment without invertebrates to assess the effect of illumination on biofilm formation on the DECOTABs revealed a reduced (Wilcoxon signed rank test: $V = 0, p = 0.002$) number of substrates used by the microbial community in the illuminated area compared to the shaded area (figure 3B).

4. Discussion

Sunlight was observed to be the primary driver of the initial stages of leaf degradation in our aquatic experimental incubations, while the microbial community contributed minimally. This corroborates earlier observations on abiotic controls on early stages of leaf degradation, which often seems governed by various abiotic drivers such as photodegradation and autolysis in the first days after abscission, while microbial decomposition becomes progressively more important during later stages of degradation (Baldy and Gessner 1997, Whittaker *et al* 2014). Photo-degradation was observed to be most pronounced in nettle, which showed a significantly higher degradation rate as compared to oak leaves. This is likely due to differences in leaf chemistry, as nettle is known to be less recalcitrant than oak and contains less lignin and phenols (e.g. Feeny 1970, Otles and Yalcin 2012). The importance of leaf chemical composition for OM degradation in general is well known for both aquatic and terrestrial systems, and effects of sunlight on leaf breakdown have been observed to depend on leaf quality and toughness in terrestrial systems (e.g. Cornelissen 1996, Biasi *et al* 2016). Since our study was conducted in summer using freshly collected leaves, our results mimic decomposition of green leaf input during storm events which do not necessarily reflect the texture and chemical composition of the bulk of senescent leaves that enters the aquatic food web during autumn. This is important considering leaf chemistry is known to be a driver of leaf decomposition by affecting leaf palatability and colonization potential of leaf-associated microbial communities (Feeny 1970, Vonk *et al* 2016, Biasi *et al* 2016). Despite this, the observed differences between two leaf species that vary in multiple quality attributes seem to hint that leaf chemical composition can interact with sunlight and microorganisms to collectively drive leaf degradation. This encourages future studies considering leaf chemistry in examining the relative contribution of sunlight in leaf degradation in aquatic systems.

Sunlight was found to negatively affect leaf-associated microbial communities. Sunlight is known to impair microorganisms through detrimental effects on DNA and extracellular enzymes (e.g. Santos *et al* 2013), in which indirect effects of sunlight can also affect OM-associated microbial communities via photo-oxidation of OM and its degradation into smaller palatable or harmful molecules depending on OM substrate (Mopper and Zhou 1990, Scully *et al* 1996, Obernosterer and Benner 2004, Albarino *et al* 2008, Hunting *et al* 2013b). Adverse effects of shorter wavelengths (e.g. UV-A and UV-B) on microbial communities are well described, but also photosynthetically active radiation (PAR) has been observed to adversely affect microbial community structure and performance, suggesting synergistic effects of UV-B, UV-A and PAR on leaf associated communities (Muela *et al* 2000). Effects of sunlight on leaf-associated microbial communities also appeared to co-vary with leaf type, hinting that leaf quality (e.g. phenolic content) also seems to negatively affect microbial resource niche breadth. The observed negative effects of sunlight on OM-associated microbial communities also likely reduce overall microbial respiratory activity and microbial biomass production, which itself may already retard microbially-mediated OM degradation (Tlili *et al* 2017) and growth of invertebrates that consume microbially-conditioned OM (Zhai *et al* 2018).

Invertebrate behavior was observed to be strongly affected by sunlight. *A. aquaticus* avoided areas in the microcosms that were exposed to solar lamp illumination. This resulted in higher OM degradation rates in the shaded areas. While performance of terrestrial isopods has been observed to be negatively affected by sunlight (Morgado *et al* 2015), the results presented here provide a first clue that invertebrates in aquatic ecosystems avoid direct exposure to sunlight. This corroborates previous observations of invertebrates using macrophytes as a physical refuge to avoid direct exposure to sunlight in high altitude streams (Loayza-Muro *et al* 2013, 2014). Invertebrates can be very important for overall OM-degradation rates as they can consume large amounts of OM, while macrofaunal locomotive activity is also known to affect ecosystem functioning by altering sediments, particulate OM availability and microbial activity through, for instance, the introduction of oxygen (Mermillod-Blondin 2003, Nogaro *et al* 2009, Hunting *et al* 2012). Sunlight-induced avoidance behavior may thus feed through to changes in ecosystem processes, as a preference for shaded conditions could be expected to translate to reduced leaf consumption and bioturbation activities in irradiated sediments.

Here we observed that leaf disk mass loss and microbial resource niche breadth were strongly governed by sunlight, and invertebrates were observed to avoid direct illumination with solar lamps, and this alteration of behavior resulted in reduced invertebrate contributions to leaf degradation. This hints that sunlight has the potential to strongly influence structural and functional attributes of shallow aquatic food webs, and hence this study serves as an appraisal to consider sunlight as a potentially significant physical driver affecting OM

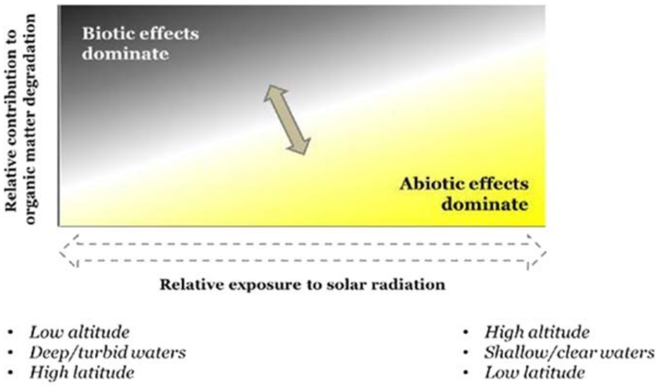

Figure 4. Conceptual figure showing relative importance of solar radiation mediating OM degradation, depending on key attributes of freshwater ecosystems.

degradation and (metabolic) activities of microorganisms and invertebrates. We used a limited number of species and a simplified setting, and hence it remains uncertain whether patterns observed here reflect those occurring in natural systems where many important drivers of OM degradation (e.g. chemical composition) are highly variable. However, sunlight can penetrate clear waters and has even been observed to alter shallow sediment OM and their associated microbial communities (Morris *et al* 1995, Albarino *et al* 2008), and therefore our results suggest that sunlight may be more important as driver and modifier of OM degradation in shallow freshwater bodies than previously anticipated. Natural ecosystems are spatially heterogeneous, in which OM can be directly exposed to sunlight, but also can provide shading for invertebrates, and hence results presented in this study might overestimate the effect of sunlight on invertebrate behavioral responses and inherent effects on OM consumption. Ultimately, the degradation of OM is a complex interplay between resource diversity, microbial and invertebrate diversity and activity, and community responses to physico-chemical variables that largely influence its spatio-temporal properties. The relative contribution of sunlight likely also depends on latitude and altitude (as conceptually depicted in figure 4), which strongly dictates both sunlight intensity and the relative abundance and contributions of macroinvertebrates. The relative contribution of biota to OM degradation is likely equally dependent, although our current understanding of biodiversity effects on OM degradation remains ambiguous. Diverse communities of microorganisms and macroinvertebrates have often been predicted and observed to positively influence litter degradation, suggesting close links between functional diversity and the functioning of aquatic ecosystems (Gessner *et al* 1999). However, these links are scarcely observed in natural environments where plant litter degradation ultimately relies on complex interactions between microbial and invertebrate diversity and various abiotic factors. A disparity between OM-degradation in streams that are exposed to sunlight or shaded due to dense riparian canopy cover has indeed been observed (Lagrue *et al* 2011), suggesting sunlight could potentially overrule diversity effects on ecosystem functioning.

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Author’s contributions

EH conceived the study. SdJ performed the experiments. EH, SdJ, MS analyzed the data. EH and MS drafted the manuscript, and SdJ contributed to revisions of the manuscript.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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