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ORIGINAL ARTICLE

Responses by benthic invertebrate community composition to dissolved organic matter in lakes decline substantially above a threshold concentration

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Abstract

1. Dissolved organic matter (DOM), often measured as dissolved organic carbon (DOC), plays a fundamental role in influencing the structure and function of lake ecosystems. Due to the myriad ecosystem effects of DOM, widespread observations of long-term increasing DOM concentrations have received much attention from ecologists. DOM positively influences primary production and consumer production at low concentrations due to the fertilising influence of bound nutrients. However, beyond a unimodal peak in production, a reduced light environment may result in a negative effect on production. This unimodal model has been largely developed and tested in lakes with low to moderate DOM concentrations (i.e., typically ≤10 mg/L DOC).
2. To understand ecological responses in lakes across a larger range in DOM concentrations, we examined the response of benthic invertebrate communities in 148 Swedish lakes with DOM concentrations ranging between 0.67 and 32.77 mg/L DOC.
3. We found that increasing DOM concentrations had a strong effect on invertebrate community composition below *c.* 10 mg/L. Across this range, abundances of individual taxa both increased and decreased, probably in response to environmental change induced by DOM. However, in lakes above this concentration, increasing DOM had minimal influence on community composition.
4. As DOM concentrations continue to increase, faunal communities in lakes below this 10 mg/L DOC threshold are likely to undergo substantial change whereas those above this threshold are likely to be minimally impacted.

KEYWORDS
benthic invertebrates, browning, dissolved organic matter, lake, light limitation

1 | INTRODUCTION

Terrestrial dissolved organic matter (DOM) in lakes, commonly measured as dissolved organic carbon (DOC), is a primary regulator of lake ecosystem function and strongly influences lake biota (Creed et al., 2018). Consequently, observations of long-term increases in DOM concentrations in many regions of the world, also termed *browning*, have received a lot of attention from ecologists (Evans et al., 2005; Monteith et al., 2007; Roulet & Moore, 2006). The response of lake biota to DOM is not simply linear but has been described as *unimodal*, where DOM reaches an optimum concentration for maximum productivity of primary producers and higher consumers (Finstad et al., 2014; Olson et al., 2020; Seekell, Lapierre, Ask, et al., 2015). In the absence of anthropogenic inputs, waters with low DOM concentrations are often nutrient poor. In these waters, additional inputs of DOM can stimulate productivity because DOM transports nutrients through the landscape by its strong binding capacity (Dillon & Molot, 1997; Kortelainen et al., 2006; Seekell, Lapierre, Ask, et al., 2015). Thus, DOM can have the effect of fertilising production in waters that are nutrient limited (Figure 1). However, this fertilising effect and the well-known negative influence of increasing DOM concentrations on the underwater light environment creates trade-offs (Figure 1). Beyond a threshold DOM concentration, effects on the light climate overwhelm the stimulating effects of added nutrients and DOM begins to depress production, resulting in the observed unimodal relationship (Seekell, Lapierre, Ask, et al., 2015; Seekell, Lapierre, & Karlsson, 2015).

Whether the hypothesised unimodal relationship is applicable to waterbodies with high DOM is unclear. Past research has been conducted primarily in low to moderate DOM systems (e.g., range < *c.* 10 mg/L; Finstad et al., 2014; Seekell, Lapierre, Ask, et al., 2015; Seekell, Lapierre, & Karlsson, 2015). This is problematic because a substantial number of lakes have concentrations exceeding this range, especially smaller lakes that are numerically dominant (Sobek et al., 2007). In addition, simulations project DOM concentrations will continue to increase in many regions due to changes in climate, hydrology, terrestrial vegetation, and land use (de Wit et al., 2016; Kritzberg, 2017; Weyhenmeyer et al., 2016).

Many of the DOM effects on lake biota are related to changes in both UV light and photosynthetically active radiation (PAR) (Williamson et al., 2015). The effects of DOM on depth of penetration of both UV light and PAR are exponentially decreasing so that at higher DOM concentrations, further increases in DOM have minimal additional affect (Figure 1a) (Morris et al., 1995; Williamson et al., 1996). Similarly, the strong nutrient effects of DOM may be dramatic at low DOM concentrations, but become less important at higher DOM concentrations (Figure 1a) (Seekell, Lapierre, & Karlsson, 2015). These DOM properties substantially impact lake biota by altering the chemical and physical environment. However, at concentrations approaching *c.* 10 mg/L, the food web is largely dominated by heterotrophy (i.e., chemoorganotrophy) rather than autotrophy (Jansson et al., 2000). Therefore, the effects of increasing DOM on lake biota may be relatively minor at higher concentrations (Figure 1b).

Although understanding DOM impacts on top fish consumers and primary producers is clearly important, understanding effects on benthic invertebrates can illuminate responses by an important pathway of energy transfer between benthic and pelagic habitats (Schindler & Scheuerell, 2002). Benthic invertebrates couple benthic and pelagic habitats by feeding on pelagic plankton that settle into the benthos (Hayden et al., 2019; Johnson & Wiederholm, 1992), and serving as prey for highly mobile consumers (Bartels et al., 2016; Schindler & Scheuerell, 2002). While much of the current understanding of the unimodal model has been developed by studying primary producers including phytoplankton and periphyton and consumers including zooplankton and fishes (Finstad et al., 2014; Kelly et al., 2014; Seekell, Lapierre, Ask, et al., 2015), DOM-darkened

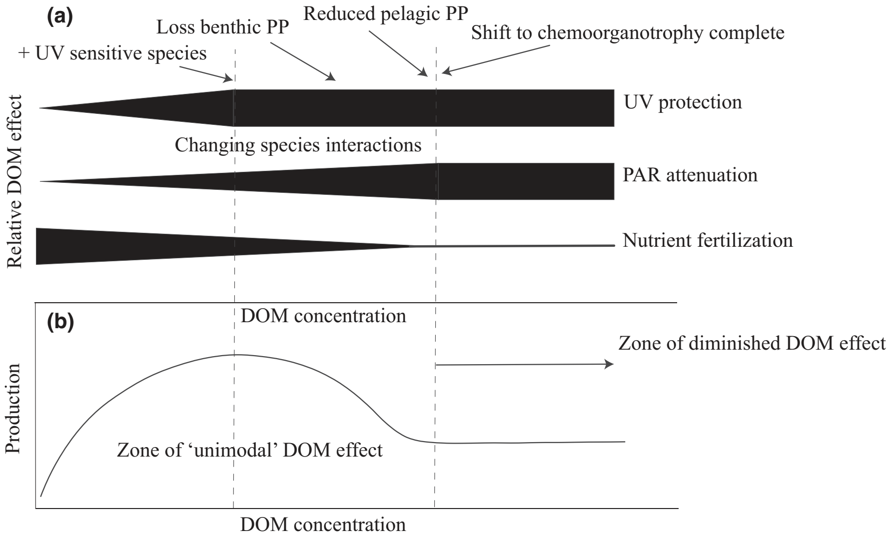

FIGURE 1 Conceptual figure of the effects of dissolved organic matter (DOM) on lake biota and how these effects operate through different mechanisms across a DOM concentration gradient. (a) DOM, acting through its effects on light, has a variety of effects on organisms at low to moderate concentrations. DOM effects on organisms include protection from harmful UV radiation, a fertilising effect of nutrients at low DOM concentrations, changes to species interactions such as predator–prey relationships with diminishing light, and loss of benthic and pelagic primary productivity (PP) as depth of 1% surface photosynthetically active radiation (PAR) declines with DOM concentrations. Line thickness represents the relative strength of that mechanism at the given concentration. (b) Theoretical and observational studies have demonstrated a unimodal relationship between DOM and both primary and secondary production in lakes.

waters can change the ability of visual feeding predators to efficiently locate benthic invertebrate prey and lead to diet shifts that alter benthic invertebrate community composition (Estlander et al., 2010; Koizumi et al., 2018). In addition, some benthic invertebrates are highly sensitive to UV light, causing them to be absent from ultra-clear, low DOM lakes (Lindholm et al., 2016). DOM may also partially reduce production of benthic invertebrates by reducing deep-water dissolved oxygen (DO) concentrations and therefore habitat availability (Craig et al., 2015).

We took advantage of a large dataset of benthic invertebrate community data to examine the effect of DOM, using DOC as a proxy, on lake benthic invertebrates across 148 Swedish boreal and hemiboreal lakes. In contrast to species-specific studies, or studies that aggregate total biomass across a group of species, we examined total benthic invertebrate community composition across DOC concentrations ranging from 0.67 to 32.77 mg/L. Accumulating evidence suggests the possibility of a DOM threshold around 10 mg/L at which DOM has maximally impacted consumer production (Jansson et al., 2000; Jonsson et al., 2015; Solomon et al., 2015). Therefore, we hypothesised that in the range of concentrations through which the unimodal response has been observed (primarily up to *c.* 10 mg/L) (Finstad et al., 2014), DOM strongly influences community composition but that, above this range, DOM has minimal additional effect (Figure 1).

2 | METHODS

2.1 | Lake data

We used water chemistry and benthic invertebrate community data from the Swedish freshwater inventory database http://www.slu.se/vatten-miljo and data available at https://miljodata.slu.se/MVM/Search (see table 1 in Fölster et al., 2014 for detailed sampling protocol information). Data in the Swedish freshwater inventory database included samples from all four seasons. To minimise differences in communities due to seasonal effects, yet maximise the amount of data available for analysis, we used data from 1982–2018, from which lakes were sampled during the months August to October. These were the months that yielded the largest number of samples. We excluded sample locations if they did not have at least 5 years of sampling data in the months specified, resulting in a total of 148 lake sites (Figure 2).

All data processing and analyses were conducted in the R programming environment version 3.5.0 (R Core Team, 2018).

2.2 | Data preparation for profundal benthic communities

Benthic invertebrates were collected using Ekman samplers from soft-bottomed profundal habitat (Fölster et al., 2014). Data indicated that sample stations were associated with a depth range, where the minimum depth of sampling could be different from the maximum depth of sampling during an individual sampling event. Within individual sample stations, the standard deviation of the minimum depth of independent samples (i.e., samples conducted during separate trips on different dates) tended to be under 1 m for shallow stations, but could be higher for deeper stations (Figure S1a). This is also the case for the maximum depth of sampling (Figure S1b). In most cases, the average minimum and maximum depths of benthic sampling were very close to the 1:1 line when plotted, indicating they were constrained to a small depth range (most often they were the same; Figure S1c). In most cases, the minimum depth of benthic sampling was substantially deeper than the mean lake depth (Figure S1d). The absolute depths sampled were correlated with mean lake depth.

To obtain abundance values for each taxon from unique sampling trips (i.e., those conducted on the same date and at the same location), five replicate samples were first sieved through 0.5-mm mesh and preserved in 70% ethanol. Samples were then identified in the laboratory using dissecting and light microscopy and enumerated to individuals/m^2. The average abundance values among the five replicate samples were taken as the sample abundance values. Nomenclature of the Swedish species (www.dyntaxa.se) was used to standardise taxonomy to operational taxonomic units. In most cases, taxon names were resolved to species, but in many cases were resolved to genus. However, in some cases taxa could not be resolved to these levels, in which case they were resolved to the most descriptive taxonomic classification possible. Out of 242 invertebrate taxa, 85.1% were resolved to species or genus.

To test our conceptual model (Figure 1) we used an average abundance value over the last 5 years of data in the available time series for each taxon. We created a taxa matrix for each lake by using all taxa names as columns in a matrix. For each lake, we then populated the abundance of each taxon with the calculated long-term average abundance.

2.3 | Preparation for chemical and abiotic data

Chemical data were obtained from water samples that were collected in the surface water at 0.5 m water depth in the central and most commonly deepest part of a lake. The samples were kept cool during transport to the laboratory. Sampling and all further laboratory analyses were done according to international or European standards (Fölster et al., 2014, see also http://www.slu.se/vatten-miljo). For chemical data analysis, we used only chemical data that corresponded to the same months and years in which the corresponding benthic invertebrate community samples were collected, using the resulting long-term mean value. We retrieved the following information from the chemical data: total organic carbon (TOC), total phosphorus (total P), calcium (Ca), absorbance of a filtered sample at 420 nm (absorbance 420), pH, and DO. TOC was used as a proxy for DOC as has been done for other studies in Sweden (hereafter we refer to it as DOC), as the particulate contribution to TOC is considered to be less than 5% in Swedish boreal and hemiboreal lakes

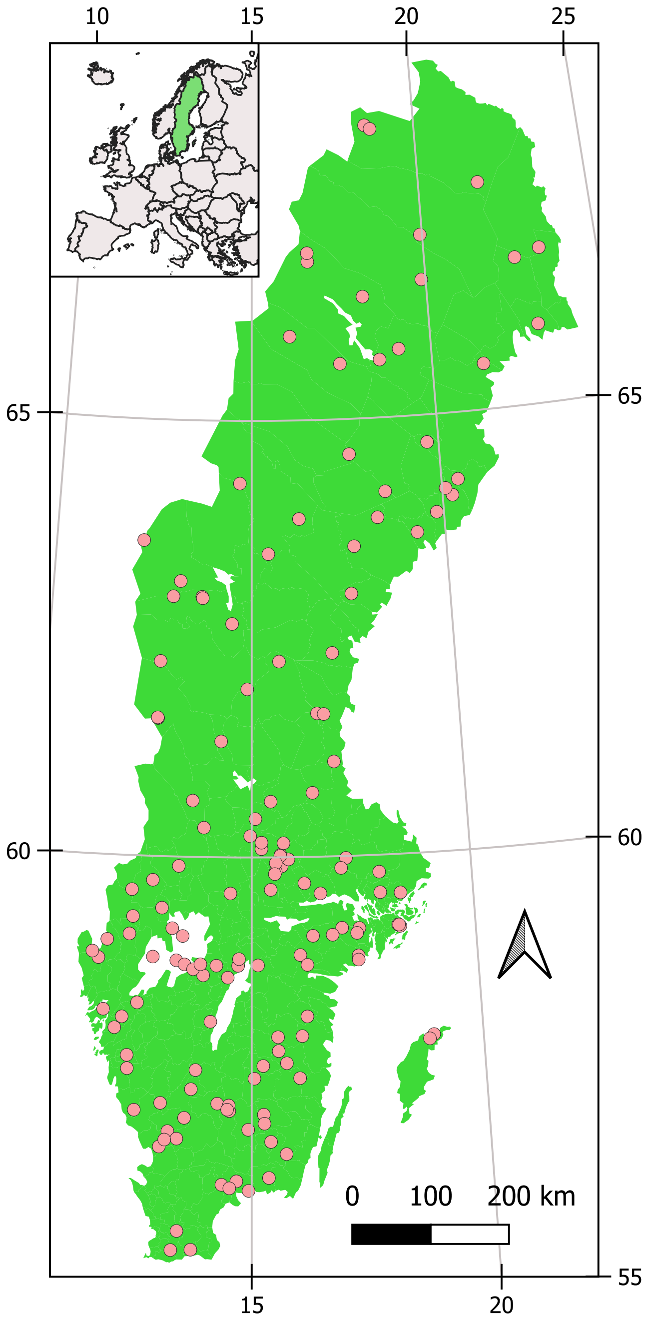

FIGURE 2 Locations of 148 Swedish lake sample sites used to analyse the response of profundal benthic invertebrate communities to lake dissolved organic carbon concentrations.

(Laudon et al., 2007; Nydahl et al., 2017). We used oxygen values from within 1 m of the minimum and maximum depth of benthic invertebrate community sampling for the corresponding sample site.

Other abiotic information used in our analysis included depth of benthic invertebrate community sampling, latitude, and lake surface area. For most lakes, lake surface area was retrieved from Corine Land Cover 2000 (https://land.copernicus.eu/en/products/corine-land-cover). For 22 lake sites, this information was not available. For 21 of the 22 lakes, we obtained lake surface area from the HydroLakes database (Messager et al., 2016).

2.4 | Statistical analysis of benthic profundal communities

We used non-metric multidimensional scaling (NMDS) in the *vegan* R package to test whether profundal benthic communities were more similar for lakes having similar DOC concentrations (Oksanen et al., 2019). This method provides a visual depiction of the distance, or degree of dissimilarity, between communities by plotting more similar communities closer together in 2d space. We conducted NMDS on the raw taxa abundance matrix, using the Bray–Curtis dissimilarity index. Values were square-root transformed and Wisconsin double standardised, which are the default options and appropriate for our analysis. We used the lowest number of dimensions that resulted in a stress value below 0.2 (Clarke, 1993). We conducted this analysis using only lakes having available DOC data ($n = 148$ lakes).

After performing the NMDS analysis we applied a random forest algorithm (Cutler et al., 2007), using the *randomForest* package in R (Liaw & Wiener, 2002), on the first axis scores of the NMDS analysis to determine the most important predictors of community position along this axis. We used the percent increase in mean squared error as a measure of variable importance. We included only predictors with no missing values. To maximise the number of lakes, we limited our analysis to complete values for the following set of predictors: Total P, DOC, Ca, pH, absorbance 420 (a measure of water colour), sample depth, latitude, and lake surface area ($n = 142$ lakes). DOC and absorbance 420 were highly correlated ($r = 0.82$). We ran the analysis with and without absorbance 420 and found that it did not change our results. We retained absorbance 420 in the analysis because we found that it was a reasonable indicator of the UV and visible light absorbing properties of DOC (Figure S2). Pearson correlations of all other predictors had an absolute magnitude <0.70 (Figure S3).

Many Swedish lakes are nitrogen limited, but we chose to use total P because some Swedish lakes are also phosphorus limited, some may be co-limited (Elser et al., 2009; Isles et al., 2020), and total N and total P are generally correlated at large spatial scales in Sweden (Kellerman et al., 2014; Kothawala et al., 2013). In addition, terrestrial DOM is typically associated with both bound nitrogen and phosphorus (Corman et al., 2018), so from the perspective of the fertilisation effect of DOM, using total P should also serve as a proxy for total N. Consequently, total P should be a reasonable indicator of both the fertilisation potential of DOM and the trophic status of lakes ranging from ultra-oligotrophic to eutrophic even though some unproductive lakes may be nitrogen limited (Bergström & Jansson, 2006) across the range of phosphorus concentrations in the lakes used in our study. We excluded lakes >60 µg/L total P from the analysis ($n = 5$) because they were probably dominated by the effects of nutrient pollution from urban or agricultural runoff.

We then conducted a similar analysis on the second axis scores using the same set of predictors. To test our hypothesis that DOC had little effect on community composition in high DOC lakes, we reran the random forest analysis on the first axis scores for the subset of lakes where DOC exceeded 10 mg/L ($n = 61$). We selected

10 mg/L because several studies suggest that this concentration level may represent a threshold beyond which consumer production has already been severely reduced (Solomon et al., 2015). We used partial dependency plots for the top predictor variables to visualise the relationship of these predictors to community composition for the full dataset along NMDS axis 1. Partial dependency plots show the relationship of each individual predictor to the response while the values for all other predictors are held at their average (Friedman, 2001; Greenwell, 2017).

2.5 | Identification of taxa discriminating between high and low DOC lakes

We performed a SIMPER analysis using the *vegan* package in R to identify taxa most responsible for distinguishing between benthic invertebrate communities observed in low and high DOC lakes (Clarke, 1993; Oksanen et al., 2019). SIMPER identifies the taxa that contribute most to the dissimilarity between two or more groups. We considered lakes <5 mg/L DOC to be low DOC lakes and lakes >10 mg/L to be high DOC lakes. We based the 5 mg/L threshold on the response of UV penetration and lake productivity to DOC. Depth of UV penetration becomes shallower as DOC increases from low concentrations, reaching to within a few centimetres of surface by the time DOC concentrations approach 5 mg/L (Williamson et al., 1996). In addition, 5 mg/L appears to be a potential peak of the unimodal relationship between DOC and primary production (Seekell, Lapierre, Ask, et al., 2015). We considered DOC concentrations >10 mg/L high because this appears to be a concentration by which point available light has sufficiently reduced primary producer biomass that lakes are dominated by heterotrophy (Jansson et al., 2000). More lakes fell into the high than the low category (61 vs. 29 lakes). We randomly subsampled from the high DOC lakes to use an equal number of low and high DOC lakes. To minimise the possibility of getting a non-representative subsample of high DOC lakes, we subsampled 1,000 times, ran the SIMPER analysis each time and calculated the percent contribution of each taxon to discriminating between groups, and took the mean across all 1,000 samples. We present scatter plots of abundance of the nine most discriminating taxa plotted against DOC concentration, along with fitted loess smoothers.

Because our data included sample locations covering the entire length of Sweden from north to south, we checked for the possibility that findings from SIMPER analysis could be driven by regional differences. We ran a linear regression of DOC against latitude. In addition, we plotted the relationship between latitude and DOC and included natural log of abundance of each of the top six taxa that discriminated most between low and high DOC lakes in the SIMPER analysis. If, for example, low DOC lakes were only present in the northern most part of the country where high DOC lakes were absent, and a top discriminating taxon was present only in these lakes, it would suggest difficulty disentangling the effect of low DOC from a regional effect.

3 | RESULTS

3.1 | Benthic invertebrate community composition along a DOC gradient

Non-metric multidimensional scaling indicated that lakes with similar DOC concentrations tended to have benthic invertebrate community compositions more similar to one another than those that differed substantially in DOC concentrations. Lakes with low DOC concentrations tended to group to the left of the origin when plotted with NMDS axis 1 as the *x*-axis while those with high DOC concentrations grouped toward the right of the origin (Figure 3; Figure S4). Three dimensions were adequate to explain the observed data as indicated by a stress value of 0.19. DOC concentrations tended to increase gradually along axis 1 as the axis score increased while no obvious DOC pattern was evident along axis 2.

3.2 | Random forest important predictors

The eight tested predictors explained most (71.0%) of the variance in NMDS 1 axis scores, indicating that community composition along the *x*-axis was largely explained by these predictor variables. The top five predictors of community composition along this axis, in descending order of importance, were total P, DOC, latitude, absorbance 420, and lake surface area (Figure S5). Total P strongly affected community composition along this axis as values increased up to *c.* 15 μg/L, plateauing at higher values (Figure 4). DOC had relatively little effect until concentrations reached 5 mg/L, after which community composition rapidly changed until reaching just under 10 mg/L. Beyond 10 mg/L, further increases in DOC had minimal impact on community composition. Latitude was associated with variation in community composition between *c.* 57 and 64°. These same predictors explained somewhat less (53.3%) of the variance along axis 2, with the top five predictors in descending order of importance as follows: sampling depth, pH, total P, latitude, and Ca.

In the subset of high DOC lakes, the eight tested predictors explained 54.4% of the variance in community composition along NMDS axis 1. The top five predictors in descending order of importance for these lakes were: latitude, sample depth, pH, surface area, and Ca. DOC was the least important variable.

3.3 | Taxa associated with low and high DOC concentrations

SIMPER analysis indicated that the top nine taxa discriminating between lakes with low (<5 mg/L) and high (>10 mg/L) DOC concentrations, in decreasing order, were: *Chaoborus flavicans*, *Oligochaeta*, *Monoporeia affinis*, *Tanytarsus*, *Procladius*, *Pisidium*, *Stictochironomus rosenschoeldi*, *Zalutschia zalutschicola*, and *Chironomus tenuistylus*. The presence and abundance of *C. flavicans* and *C. tenuistylus* increased in high DOC lakes (Figure 5; Table 1). *Stictochironomus*

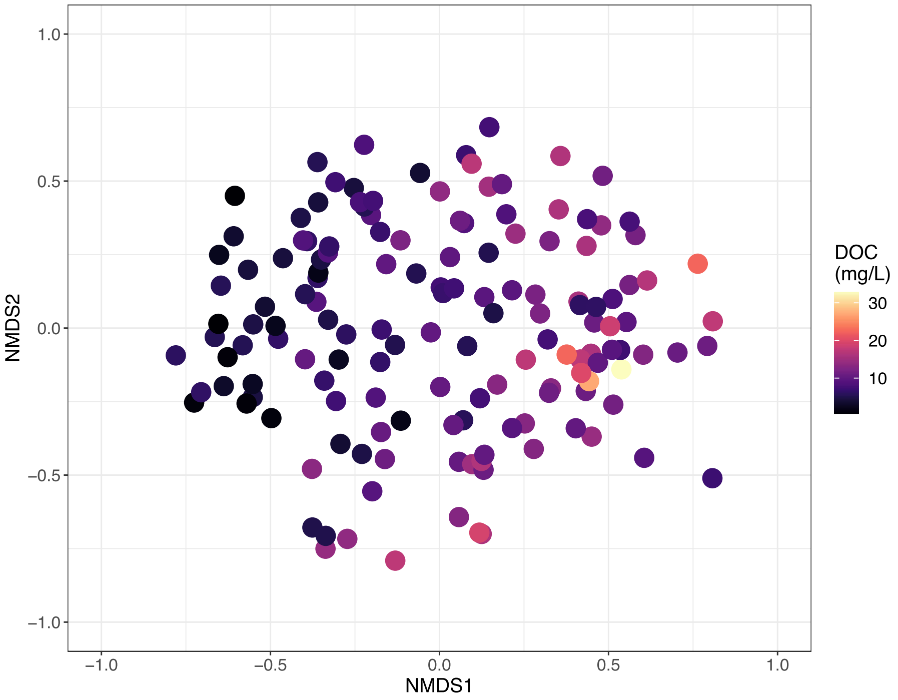

FIGURE 3 Results from a non-metric multidimensional scaling (NMDS) analysis conducted on abundance data from profundal benthic invertebrate communities sampled from Swedish lakes. Each point represents the benthic profundal invertebrate community from an individual lake sample location, colour coded by dissolved organic carbon (DOC) concentration. The *x*-axis represents NMDS axis 1 scores and the *y*-axis represents NMDS axis 2 scores.

rosenschoeldi and *Micropsectra* (tenth on list) demonstrated a clear trend of higher presence and abundance in low DOC lakes compared to almost complete absence from lakes with DOC concentrations >10 mg/L. Some taxa showed a less clear relationship to DOC concentration. For example, although *M. affinis* appeared only in low DOC lakes, the association with low DOC lakes was a result of its presence in only six low DOC lakes (20.7% of low DOC lakes). *Pisidium* was present in 25 out of 29 low DOC lakes (86.2%), but was only present in 37.7% of high DOC lakes (Table 1). Although presence of *Z. zalutschicola* was comparable in low (31.0%) and high (36.1%) DOC lakes, average abundance was 15 times greater in high DOC lakes.

The regression of DOC against latitude was significant but explained relatively little of the total variance ($r^2=0.18$). Few low DOC lakes were present south of 58° (range *c.* 56–68°) and extremely low DOC lakes (<3 mg/L) tended to be in the northern half of the country (Figure S6). However, *C. flavicans*, the most discriminating taxon, was present across the entire latitude of the country. Across the latitude range where low and high DOC lakes were commonly observed together, the pattern of absence of *C. flavicans* in low DOC lakes and presence in high DOC lakes was clear (Figure S6a). *Monoporeia affinis* was present in lakes across a small range of latitude, but even here, was clearly present in low DOC lakes and absent in high DOC lakes (Figure S6c). The remaining taxa displayed no patterns that suggested the effect was related to presence in only extremely low DOC northern lakes (Figure S6).

4 | DISCUSSION

Our results confirm our proposed hypothesis that increasing DOM strongly affects community composition at low to moderate DOC concentrations up to 10 mg/L, but above this threshold added DOM has a greatly diminished role in influencing community composition (Figure 1). Our results clearly show that the benthic invertebrate community composition did not present any further changes in lakes as DOC concentrations exceeded *c.* 10 mg/L. Consequently, the widely accepted and applied unimodal DOM response model (Figure 1b) requires some modification including the role of taxa abundances. We found that DOC effects on individual taxa were more complex than a general decrease in abundances with increasing DOC concentrations. Some taxa even exhibited increasing abundances along a DOC concentration gradient, which we discuss in more detail below.

One of the presumed primary drivers of the unimodal relationship between DOM and primary and secondary production is the fertilising effect of bound nutrients at low DOM concentrations (Seekell, Lapierre, Ask, et al., 2015) (Figure 1a). Partial dependency plots from our random forest analysis suggested the effect of a DOC increase was relatively minor at concentrations below 5 mg/L DOC (Figure 4). Such a pattern may be explained by the tight coupling between DOC and total P in low DOC lakes but a much noisier relationship in high DOC lakes (Figure 6a). Whereas the effect of DOC itself was minimal at low concentrations, total P had a large effect at low concentrations. This observation suggests that in these systems, 5 mg/L DOC may represent the *peak* of the unimodal response (Figure 1b), below which added DOM has a fertilising effect due to bound nutrients. In other words, DOM is the vehicle by which nutrients enter the system, which then serve to fuel primary production. The resulting increased biomass of primary producers then probably drives changes in biomass and production in the benthic invertebrate community that are reflected in community composition (Karlsson et al., 2009). The coupling of DOC and total P was tightest in ultra-oligotrophic lakes with total P concentrations <5 μg/L (Figure 6a).

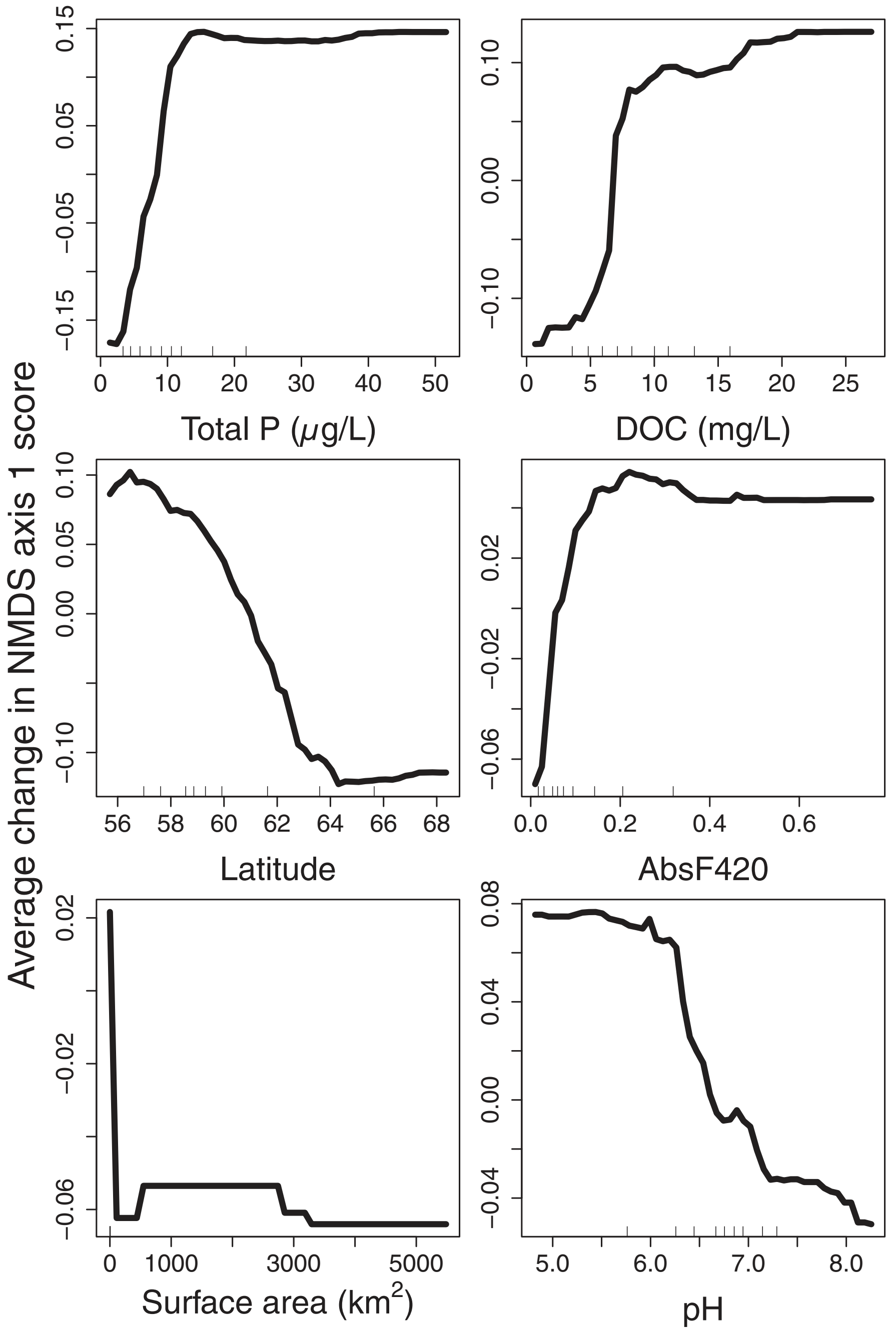

FIGURE 4 Partial dependency plots for the variables having the greatest importance in determining non-metric multidimensional scaling (NMDS) axis 1 scores based on random forest analysis. Upper *x*-axis tick marks indicate the deciles of the data distribution (i.e., the spaces between ticks contain 10% of the data).

We suggest that a DOC range between 5 and 10 mg/L represents the downward slope of the unimodal response in our study lakes (Figure 1b), where negative DOM effects on the light climate begin to dominate. Other studies have also suggested that roughly 5 mg/L may be a threshold where the light-limiting role of DOM begins to dominate over any stimulatory effect of added nutrients in subarctic and boreal lakes (Seekell et al., 2015b). Partial dependency plots demonstrated a strong effect of DOC on the benthic invertebrate community across this concentration interval. This general pattern of a DOC impact up to roughly 10 mg/L with minimal further impact thereafter was also reflected among some individual taxa, including two of the most differentiating taxa *Micropsectra* and *S. rosenschoeldi* (Figure 5g). Both of these taxa exhibited steady declines in abundance up to 10 mg/L, after which they were essentially absent from lakes. Their steady declines until 10 mg/L are consistent with the increased attenuation of PAR over this range (Williamson et al., 1996) (Figure 1).

The observation that some taxa increased in abundance as DOC concentrations increased may be due to the protective role of DOM against the damaging effects of UV radiation (Bukaveckas & Robbins-Forbes, 2000; Lindholm et al., 2016; Morris et al., 1995) (Figure 1a). In very clear lakes, UV may penetrate to substantial depths whereas at moderate DOC concentrations most UV is attenuated within a few centimetres of the surface (Williamson et al., 1996). UV radiation may adversely affect organisms at all trophic levels, with reduced survival of eggs and larvae of some

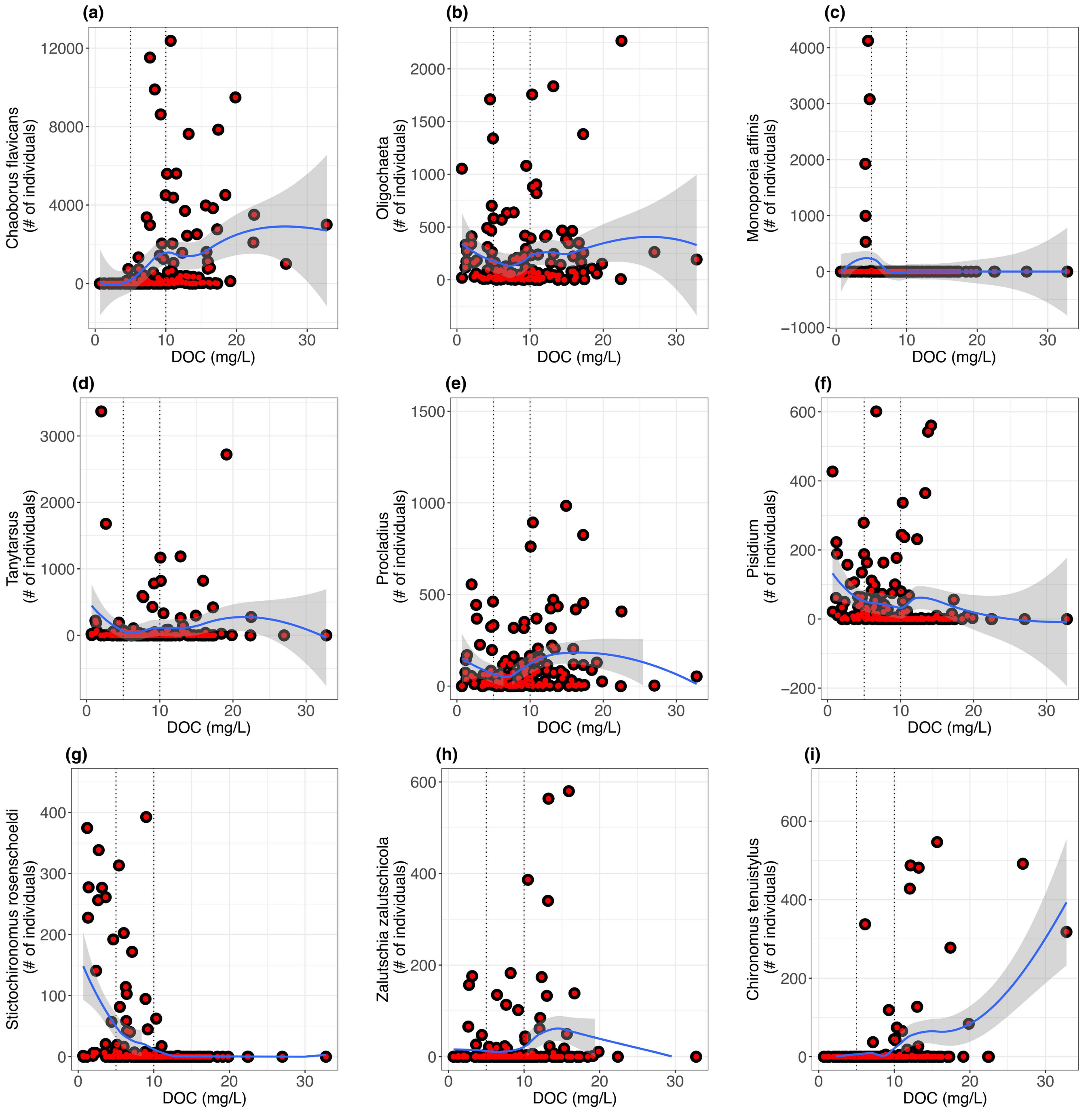

FIGURE 5 Abundance by dissolved organic carbon (DOC) for taxa most discriminating between high and low DOC lakes as determined by SIMPER analysis, plotted in decreasing percent contribution from top left to lower right. Dotted vertical lines mark 5 and 10 mg/L DOC concentrations. Blue line is a fitted loess smoother. Abundances for a) *Chaoborus flavicans* b) *Oligochaeta* c) *Monoporeia affinis* d) *Tanytarsus* e) *Procladius* f) *Pisidium* g) *Stichtochironomus rosenschoeldi* h) *Zalutschia zalutschicola* i) *Chironomus tenuistylus*.

zooplankton and fishes observed with high UV exposure (Häder et al., 2011). Our most sensitive taxon to varying DOC concentration, *C. flavicans*, might be a good example for such a mechanism as its abundance increased with increasing DOC concentration. *Chaoborus flavicans* was present at relatively low abundances in all lakes until DOC concentrations exceeded roughly 5 mg/L, after which abundances were dramatically higher in many lakes. In Norwegian lakes, *C. nyblaei* was absent from lakes where DOC concentrations were less than *c.* 4 mg/L (Lindholm et al., 2016). Many studies have found *Chaoborids* to be highly sensitive to UV radiation (Nagiller & Sommaruga, 2009; Persaud & Yan, 2003; Williamson et al., 1999), suggesting this may be the mechanism driving the observed response of *C. flavicans*. However, we cannot rule out the possibility that other factors, such as increased ability to avoid visual predators or a greater tolerance for low DO conditions, drive the response of *C. flavicans*. In either case, those taxa

TABLE 1 Top taxa discriminating between low and high dissolved organic carbon (DOC) lakes determined by SIMPER analysis.

Taxa	% low DOC lakes present	% high DOC lakes present	Average abundance low DOC lakes	Average abundance high DOC lakes
Chaoborus flavicans	13.8	86.9	30.5	1633.2
Oligochaeta	100	95.1	306.1	279.8
Monoporeia affinis	20.7	0	367.8	0
Tanytarsus	69.0	50.8	206.0	147.4
Procladius	93.1	93.4	120.2	222.6
Pisidium	86.2	37.7	74.3	47.3
Stictochironomus rosenschoeldi	62.1	6.6	84.8	1.4
Zalutschia zalutschicola	31.0	36.1	16.6	249.0
Chironomus tenuistylus	0	34.4	0	129.6

Note: Values in abundance columns indicate the average number of individuals observed per lake in the respective subset of lakes (low DOC or high DOC).

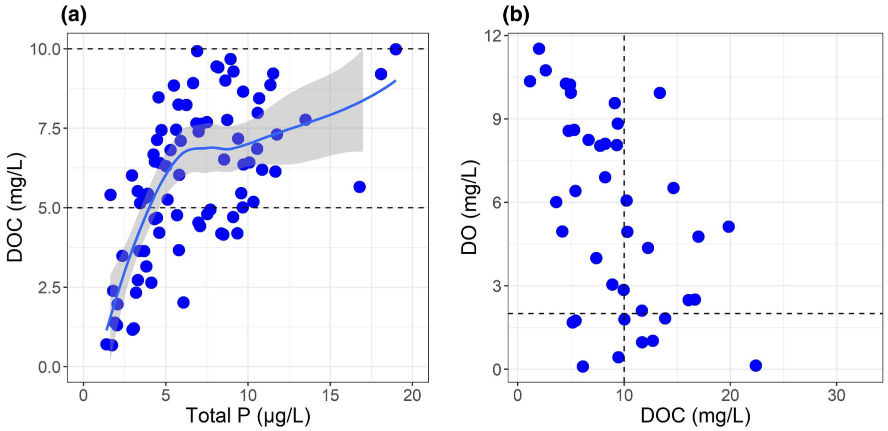

FIGURE 6 (a) Dissolved organic carbon (DOC) concentration as a function of total P. Dashed horizontal lines represent 5 and 10 mg/L DOC while the blue line is a fitted loess smoother along with 95% confidence intervals. *X* and *Y* axes are restricted to the ranges indicated to enhance viewing in the critical range of DOC concentration less than 10 mg/L DOC. (b) Dissolved oxygen (DO) concentration as a function of DOC. The dashed horizontal line is the 2 mg/L threshold for hypoxia and the vertical line represents 10 mg/L DOC.

that are sensitive to UV, as well as those that experience release from predation pressure, are likely to expand their ranges into some currently low DOM lakes if browning continues (Lindholm et al., 2016).

DOM may reduce benthic invertebrate productivity by reducing the availability of well-oxygenated habitat as DOC concentrations exceed 10 mg/L (Craig et al., 2015). Increases in DOM tend to decrease hypolimnetic DO by strengthening stratification and subsequently reducing deep-water DO replenishment, and by providing added substrate for ecosystem respiration (Read & Rose, 2013; Williamson et al., 2015). A subset of 40 of our lakes had DO data available (mean DO available for the same years and months, and within 1 m, of benthic invertebrate samples). Of these lakes, only two were completely anoxic (Figure 6b). Nine of the lakes had DO levels ≤2 mg/L, a commonly used threshold for hypoxia known to detrimentally impact fisheries (Vaquer-Sunyer & Duarte, 2008). Of these nine lakes, four had relatively low DOC concentrations <10 mg/L. Recently, 3.5 mg/L was proposed as a DO concentration that will preserve populations for all but the most sensitive invertebrate taxa in marine systems (Steckbauer et al., 2011). This threshold appears to be consistent with findings in freshwater systems (Jónasson, 1984). Roughly half of high DOC lakes with oxygen data exceeded this DO concentration (Figure 6b). *Procladius* had higher average abundance in high DOC lakes (Table 1; Figure 5e) and has been associated with low oxygen conditions (Quinlan & Smol, 2001). Similarly, *Micropsectra* has been associated with high oxygen conditions and this taxon had steadily declining abundance up to 10 mg/L DOC and was essentially absent from lakes with higher concentrations (Quinlan & Smol, 2001). Nonetheless, even though DO loss probably explains some of the benthic invertebrate response in these lakes, these observations suggest that DO related habitat loss is not the sole driver of our benthic community DOC response.

As we anticipated, DOC and benthic invertebrate community composition were unrelated at DOC concentrations >10 mg/L. We believe this largely reflects the asymptotic nature of the relationship between DOM and PAR attenuation, with its manifold consequences for lake systems (Morris et al., 1995). For example, the ability of visual predators to locate invertebrate prey may diminish dramatically as a lake transitions from clear to brown, resulting in diet shifts (Estlander et al., 2010). However, beyond this 10-mg/L threshold, DOM-related diet shifts may largely have been established while the diminishing influence of DOM on light climate is insufficient to drive further diet changes. A DOC threshold of 10 mg/L may represent the transition from an autotrophic based food web to chemoorganotrophy (Jansson et al., 2000). This suggests that loss of sedimenting organic detritus as a food source should occur rapidly as lakes transition from clear to brown as DOC approaches this threshold, with little additional loss beyond this threshold (Johnson & Wiederholm, 1992).

Our findings imply that in many lakes, 10 mg/L may represent a DOC concentration at which benthic and pelagic food webs become decoupled (Bartels et al., 2016). Zoobenthos often make up a large portion of the diet of many fish species and because fish are highly mobile, this resource use often couples pelagic and benthic habitats (Vadeboncoeur et al., 2002; Weidel et al., 2008). Evidence suggests that benthic food resources are more efficiently utilised by fish consumers than pelagic resources (Vander Zanden et al., 2011). Loss of this benthic–pelagic coupling may have consequences for trophic biomass distribution, food web stability, and trophic control (Post et al., 2000; Tunney et al., 2012). Given the importance of benthic–pelagic coupling to lake food webs (Schindler & Scheuerell, 2002), if loss of benthic–pelagic coupling does occur in this 5–10 mg/L transition zone, this could further explain the observation that increases in DOC above 10 mg/L have minimal additional influence on benthic invertebrate community composition.

We note that our results are based on profundal data with possible deviations in the littoral zone or in shallow lakes where more light at similar DOM is available for benthic invertebrates (e.g., Olson et al., 2020). Such deviations are supported by the random forest analysis of NMDS axis 2 scores, in which sampling depth was the most important variable separating lakes along this axis. The peak of the observed unimodal relationship between fish yield and DOM shifts depending on lake depth (Finstad et al., 2014). In shallow lakes, this peak occurred at higher DOM concentrations. We anticipate that our threshold concentration of 10 mg/L DOC would probably be higher in the littoral zone and in very shallow lakes.

Our observations have important implications when DOM continues to increase. Lakes that fall into the *unimodal zone* where DOC stays between 0 and 10 mg/L will see changes in community composition, with consequent changes to species interactions including predator–prey dynamics. However, our results suggest that for lakes outside the *unimodal zone*, further increases in DOM are likely to have relatively minimal impact. In terms of management implications, our results suggest that managers may be able to identify lakes that should be relatively resilient to future increases in DOM concentrations. In low DOM lakes, future browning may lead to the establishment of new predators and altered abundance of existing predators, with consequent changes to the food web, as well as the decline in abundance of other species related to decreased production with increasing DOM. In contrast, lakes already in the high DOM category are likely to be relatively resilient to future browning.

AUTHOR CONTRIBUTIONS

Conceptualisation: Stephen F. Jane and Gesa A. Weyhenmeyer. Developing methods: Stephen F. Jane and Gesa A. Weyhenmeyer. Conducting the research: Stephen F. Jane. Data analysis: Stephen F. Jane. Data interpretation: Stephen F. Jane, Gesa A. Weyhenmeyer, Peter Eklöv, Richard K. Johnson and Kevin C. Rose. Preparation of figures and tables: Stephen F. Jane. Writing: Stephen F. Jane, Gesa A. Weyhenmeyer, Peter Eklöv, Richard K. Johnson and Kevin C. Rose.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest relating to the content of this work.

DATA AVAILABILITY STATEMENT

Data used in this study is publicly available and can be accessed at http://www.slu.se/vatten-miljo and downloaded directly at https://miljodata.slu.se/MVM/Search.

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SUPPORTING INFORMATION

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