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Environmental drivers of community composition in small boreal forest lakes

Aatu Turunen[1)]*, Hannu Huuskonen[1)], Petri Nummi[2)], Celine Arzel[3)], Mikko Olin[4)], Jukka Ruuhijärvi[4)], Kimmo K. Kahilainen[5)] and Anssi Vainikka[1)]

[1)] *University of Eastern Finland, Department of Environmental and Biological Sciences, P.O. Box 111, FI-80101 Joensuu, Finland*
[2)] *University of Helsinki, Department of Forest Sciences, P.O. Box 27, FI-00014 Helsinki, Finland*
[3)] *University of Turku, Department of Biology, FI-20014 Turku, Finland*
[4)] *Natural Resources Institute Finland, Latokartanonkaari 9, FI-00790 Helsinki, Finland*
[5)] *University of Helsinki, Lammi Biological Station, Pääjärventie 320, FI-16900 Lammi, Finland*
**corresponding author's e-mail: aatu.turunen@uef.fi*

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Faunal communities in small boreal lakes face large-scale stresses including eutrophication and browning. Here, we studied the community composition of macroinvertebrates, fish, and water birds in relation to lake morphometry and water quality in 25 small (< 40 ha) lakes in eastern and southern Finland to predict community-level responses to environmental drivers. Results indicated that phosphorus concentration, pH, and lake surface area are the main faunal drivers of community composition. While dissolved organic carbon (DOC) concentration did not explain faunal community composition, relative taxa composition was statistically significantly different when lakes were dissimilar in colour. Invertebrate orders Trichoptera and Isopoda were characteristic of high DOC lakes whereas Acari (water mites) and whitefish, *Coregonus lavaretus*, were characteristics of low DOC lakes. The results are generally consistent with previous studies but extend knowledge of community-level variation in boreal lakes.

Introduction

Boreal lakes are under increasing pressure from global climate change and intensive local land use that commonly increase the concentrations of organic substances and iron, leading to water brownification and subsequently altered thermal dynamics and hypolimnetic anoxia (Roulet and Moore 2006, Monteith *et al.* 2007, Albrecht *et al.* 2023). Small lakes are particularly affected, yet least monitored, compared to large lakes under the EU's water framework-based monitoring (Brönmark and Hansson 2005, Bhateria and Jain 2016). Changing aquatic environment can affect species composition and abundances not only within waterbodies but in the adjacent terrestrial environments as well (Knight *et al.* 2005, Schulz *et al.* 2015, Pilotto *et al.* 2019). This calls for understanding how species assemblages associated with small boreal lakes are shaped by environmental variables in general (Tonn *et al.* 1990, Lappalainen and Soininen 2006, Heino *et al.* 2010).

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A holistic view of how environmental variables drive aquatic communities is needed to conserve and manage freshwater biodiversity (Dahlin *et al.* 2021, Hermoso *et al.* 2021, Hill *et al.* 2021). The recent browning of boreal lakes requires both impact assessment and mitigation measures. Leaching of terrestrial dissolved organic matter (DOM) to boreal lakes is magnified by climate change that can increase precipitation, temperature, and terrestrial production, as well as intensive land use such as agriculture and forestry practices that disturb natural vegetation and soil cover (Hongve *et al.* 2004, Nieminen *et al.* 2015, Hayden *et al.* 2017). Often, studies on browning focus on food web interactions, productivity, or performance of individual species or taxonomic group under humic conditions (Estlander *et al.* 2012, Seekell *et al.* 2015, Arzel *et al.* 2020). Yet, comprehensive data on multiple taxonomic groups are needed to understand how dissolved organic carbon (DOC) and water colour explain variation in species assemblages in boreal lakes and their adjacent terrestrial habitats (Blanchet *et al.* 2022).

Species assemblages in small boreal lakes are most often studied by focusing on a single organismal group at a time (Tonn *et al.* 1990, Holmgren and Appelberg 2000, Paszkowski and Tonn 2006). Overall, the diversity of water birds, fishes and invertebrates reflects environmental characteristics and habitat diversity (Quinn and Hickey 1990, Welcomme *et al.* 2005, Pöysä *et al.* 2019) but also dispersal filters and historical factors (Tonn *et al.* 1990, Heino *et al.* 2017). For example, fish diversity is explained by lake surface area, depth, total phosphorus content, colour, and pH (Paszkowski and Tonn 2000, Eros *et al.* 2009, Sutela *et al.* 2010). Variables such as lake surface area, phosphorus content, alkalinity and DOC also explain species diversity of aquatic invertebrates (Fried-Petersen *et al.* 2020, Kesti *et al.* 2022). However, multiple faunal groups have only rarely been analysed together (but see Paszkowski and Tonn 2000, Nummi *et al.* 2016) to explore if animal communities would show predictable variation along certain environmental gradients or human-induced changes among small boreal lakes (Heino *et al.* 2005). Focusing only on one taxonomic group and its indicator power at a time may underestimate the total biological impact of certain drivers (Landres *et al.* 1988, Heino 2010), and weaken the ability to distinguish different lake types by their biota. Therefore, it is important to improve understanding of dynamics between different taxonomic groups and evaluate whether occurrence patterns emerge among the seemingly non-associated organisms (e.g., Heino *et al.* 2017, Heino *et al.* 2021).

The aim of this study is to investigate faunal community composition in small boreal lakes with respect to environmental variables, and particularly to DOC and water colour gradients. We hypothesize that environmental variables related to lake morphology and primary production explain the multitaxon assemblage composition while DOC forms an additional key gradient that mediates land-use and climate change driven changes in the community composition in small boreal lakes.

Material and methods

Study Lakes

We sampled 25 small state-owned boreal lakes: 17 lakes in Lieksa, eastern Finland (63.18ºN 30.67ºE), and 8 lakes in Evo, southern Finland (61.19ºN 25.10ºE) (Fig. 1, Vainikka *et al.* 2024). The lakes were selected based on their surface area (< 40 ha), accessibility (forest roads close enough to use a boat) and former history in research (Nummi and Pöysä 1993, Arvola *et al.* 2010, Turunen *et al.* 2023). The straight-line distance between the two furthest lakes was 26.4 km in Lieksa and 4.8 km in Evo region. Correspondingly, the straight-line distance between the closest two Lieksa and Evo region lakes was 347.5 km. Some of the lakes in Lieksa region were interconnected by small ditches or creeks that were not considered important for species abundances, yet they may facilitate dispersion (see also Vainikka *et al.* 2024). The lakes were surrounded by various types of forests ranging from intensively managed coniferous forests on peatlands to deciduous forests on mineral soils. The study lakes are open to recreational fisheries, but the impact of fishing on these rural lakes was assumed to be negligible. Whitefish (*Coregonus lavaretus*) has been introduced to some of

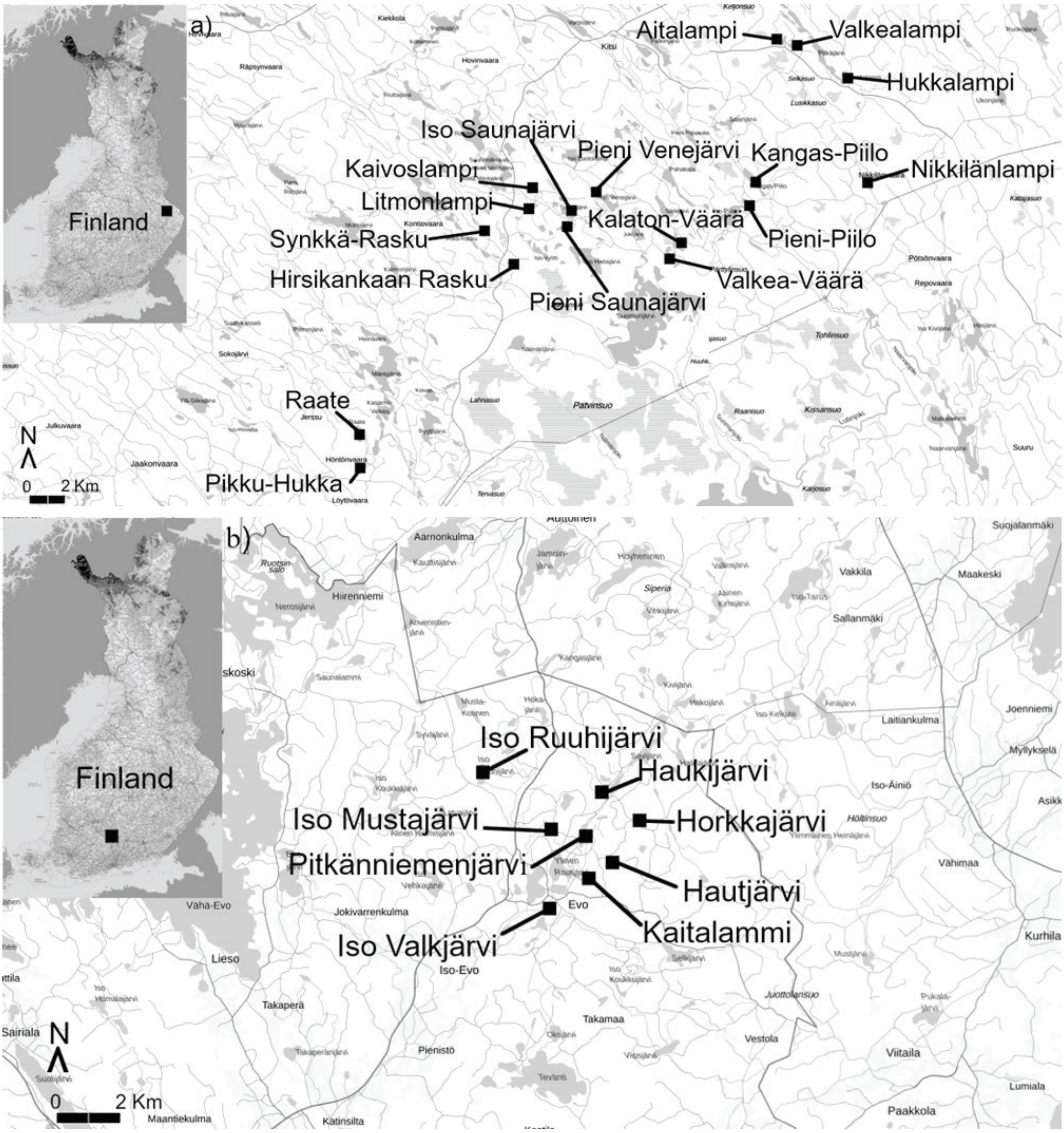

Fig. 1. Study lakes of **a**) Lieksa and **b**) Evo region. Background maps are from the open-source databank of National Land Survey of Finland, 1/2022 background map and topographic map set (CC 4.0) (NLS, 2022).

the lakes for recreational fishing; however, we lack knowledge about the extent of the stocking (Turunen *et al.* 2023). Fishing in the study lakes of Evo region was prohibited until recent years.

Community data

Abundance data on fishes were collected using standardized Nordic gillnet surveys (Olin *et al.* 2014) using a stratified random sampling design in July-August 2020 (Vainikka *et al.* 2024). Data are available in Fairdata, https://doi.org/10.23729/24986d9b-fff1-4cb7-87b5-467d1873369d. In this study, catch per unit effort (CPUE = individuals net^{-1} night^{-1}) by species was used to reflect the relative abundance of species in a lake.

Aquatic invertebrates were sampled from June-July 2020 (for details see Table S1 in Supplementary Information) using activity traps that consisted of a transparent plastic funnel attached to a transparent glass jar (funnel diameter narrowest point = 20 mm, jar diameter = 110 mm, jar length = 160 mm, volume = 1.5 L) with metal wire (Elmberg *et al.* 1992). Activity traps were set along the littoral zone with funnel opening facing to the centre of the lake (< 0.75 m depth). A total of 10 traps per lake per sampling session was used with a minimum distance of 3 m between traps. Five of the traps were set to a visually assessed densely vegetated microhabitat and the other five to a sparsely vegetated microhabitat (Elmberg *et al.* 1992). For logistic reasons, however, the traps were set to ca. 400 m part of the shoreline closest to the access point to each lake. The sampling time was 24 hours after which the contents of the traps were sieved through 0.5 mm mesh and the retained invertebrates were transferred into sample tubes filled with 70% ethanol. All individuals were identified to order level except for Ceratopogonidae and Chironomidae which were identified to family level due to their ecological differences between families (Wazbinski and Quinlan 2013, Strandberg *et al.* 2020). Also, Dytiscidae was separated from other Coleoptera families (Nilsson and Söderberg 1996). The total count of invertebrates caught by taxon was divided by the number of traps to form the average counts per jar (CPUE: individuals jar^{-1} 24 hours^{-1}).

Water bird pair survey (abundance as number of pairs) was conducted in spring 2020 and in spring 2022 (Table S1 in Supplementary Information) using an established national point counting method (Koskimies and Väisänen 1991). In short, lake shorelines were observed (approximately 3 minutes per spot) with binoculars by moving the point of vision slowly into one direction following the shoreline. Additional monitoring spots to cover blind spots were used if the whole lake could not be observed from one spot. Missing 2020 data for Iso Ruuhijärvi, Haukijärvi and Hautjärvi was supplemented with counting data from 2019 or 2021. For the Lieksa region lakes, we used the average number of pairs observed in 2020 and 2022 for our analyses.

Environmental data

Environmental variables were determined from water samples twice in the Lieksa region and once in the Evo region in the summer of 2020 as described in Vainikka *et al.* (2024) (Table S1 in Supplementary Information). In this study, we use the estimated mid-July values from (Vainikka *et al.* 2024) for total phosphorus (total-P) (μg L^{-1}), phosphate phosphorus (phosphate-P) (μg L^{-1}), total nitrogen (total-N) (μg L^{-1}), chlorophyll *a* (mg L^{-1}), dissolved organic carbon (DOC) (mg L^{-1}), colour (mg Pt L^{-1}), iron (mg L^{-1}), alkalinity (mmol L^{-1}), pH (5.29–7.56), water depth (m), surface area (ha), and Secchi depth (m). The water samples were taken at the deepest point of the lake from the depth of one meter using a Limnos sampler.

We categorized the lakes into three classes based on their DOC content. As lake type categorization in national monitoring of lakes according to the EU Water Framework Directive is based on water colour, the chosen categorization rather reflects the biological impact of organic carbon than integrative effects of colour. The first class represents clear-water lakes where DOC values have a predicted neutral or positive effect on lake's primary production (DOC < 10 mg L^{-1}, $n = 8$, Hanson *et al.* 2003, Solomon *et al.* 2015, Kelly *et al.* 2018). The second class includes slightly stained waters (DOC = 10–20 mg L^{-1}, $n = 14$) where DOC values may already decrease primary production. The third class represents browner lakes (DOC > 20 mg L^{-1}, $n = 3$) that are expected to show strongly depressed primary productivity due to decreased photic layer depth (Hanson *et al.* 2003, Solomon *et al.* 2015, Kelly *et al.* 2018).

Statistical analyses

Community composition was analysed using non-metric dimensional scaling (NMDS) using *vegan*-package (Oksanen *et al.* 2020) in R (ver. 4.1.0). NMDS rank orders entities in a dimensional space with the smallest stress possible. Stress measures the fit of the data to ordination, such that lower stress values indicate a better fit. The maximum number of random starts (999) was used to find a stable solution to a two-dimension projection ($k = 2$). If the stress measure was too high (> 0.2) (Clarke 1993), more dimensions were allowed. Community data were Wisconsin double standardized to reduce the effect on highly abundant taxa and to form ordination with data collected using multiple methods and as such on different scales (Bray and Curtis 1957). Bray-Curtis measure was used to form a dissimilarity matrix (Bray and Curtis 1957). Taxa observed in less than three lakes were omitted from the analysis. Individual taxa were projected to the ordination as weighted averages of site scores.

Mantel's test was performed to examine the correlations between community composition and browning-related variables: DOC, water colour, iron, and Secchi depth. The distance matrix of environmental variables was formed using Euclidean distance. Spearman's rank order correlation was used to assess correlations between ranked distances of sites in the environmental matrix and Bray-Curtis dissimilarity matrix. Permutations (n = 9999) were used to evaluate the significance of the correlation. Mantel's test was calculated using *vegan*-package (Oksanen *et al.* 2020) in R. The association between DOC (as a variable) and community dissimilarity was tested separately within the Lieksa and Evo regions to allow for potential regional differences. To further examine which taxa contribute to the dissimilarity of lakes with different DOC values, we divided lakes into three classes by DOC values (explained above). We used SIMPER-analysis (Clarke 1993) to investigate how taxa contribute to differences between lakes of different DOC classes using *vegan*-package (Oksanen *et al.* 2020) in R. SIMPER-analysis decomposes the Bray-Curtis dissimilarity matrix and tests how individual taxa contribute to the dissimilarity between groups, assessing the statistical significance by permutations (n = 999). We compared the taxa composition between DOC classes using the ANOSIM-function in *vegan*-package (Oksanen *et al.* 2020). The ANOSIM-function was used to test whether taxa composition differs among classes of lakes and assess the significance by forming a sampling distribution by permutating (n = 999) the grouping factor. We also tested whether the regional division caused differences in community composition (Bray-Curtis) by using ANOSIM-function, and examined which taxa contributed to dissimilarity between Lieksa and Evo lakes by using SIMPER-analysis.

Canonical correspondence analysis (CCA) was conducted using *vegan*-package (Oksanen *et al.* 2020) in R to examine the relationship between the abundance of aquatic taxa and the 12 environmental variables, and to obtain a projection of small boreal lakes with multiple taxa. CCA is a method for analysing the relation between two sets of variables and is suitable for examining data on species abundance and environmental variables in matrix form. CCA uses X^2 distance as a measure for assessing the distance between lakes and taxa. The statistical significance of environmental variables was assessed using permutational tests (n = 9999). Stepwise backward model selection was used to remove the non-significant environmental variables. The threshold for reduction of individual variable was assessed by permutation ($\alpha = 0.05$). Variables with a variance inflation factor (VIF) higher than 10 were omitted from the model selection to reduce the effect of multicollinearity (James *et al.* 2013). Due to this criteria, variables water colour, total-N, and chlorophyll *a* were omitted from the model. Before analyses, taxonomic abundance data were $\ln(1 + x)$ transformed. Taxa observed in less than three lakes were omitted from the analysis. The significance of individual axes of CCA was assessed using permutation (n = 9999). Kendall's τ was used to test individual taxa's relation to DOC. Kendall's τ is a non-parametric correlation coefficient that takes into account 0-values that were abundant in the dataset. Kendall's correlation analysis was performed using *Kendall*-package (McLeod 2022) in R. Bonferroni correction was applied to reduce the type 1 error caused by multiple tests.

Results

Lake biota

In total, six fishes, six water bird species and 14 invertebrate taxa were present in more than two study lakes (Table 1). In descending order of average abundance, the three most abundant fishes were perch (*Perca fluviatilis*) (present in all 25 lakes, average CPUE 15.1 ind. net^{-1} night^{-1}), roach (*Rutilus rutilus*) (20 lakes, average 7.8 ind. net^{-1} night^{-1}, mean in lakes present 10.0 ind. net^{-1} net^{-1}), and bleak (*Alburnus alburnus*) (7 lakes, average 0.5 ind. net^{-1} night^{-1}, mean in lakes present 2.0 ind. net^{-1} night^{-1}). The three most encountered bird species were the common gull (*Larus canus,* present in 5 lakes, average pairs 0.32, mean in lakes present 1.6 pairs), the common goldeneye (*Bucephala clangula*) (7 lakes, average 0.28 pairs, mean in lakes present 1.0 pairs), and the Eurasian teal (hereafter teal, *Anas crecca*) (4 lakes, average 0.28 pairs, mean in lakes present 1.75 pairs). The three most prevalent invertebrate taxa were Cladocera (present in 25 lakes, average CPUE 49.9 individuals jar^{-1} 24 hours^{-1}), Copepoda (25 lakes, average 15.2 ind. jar^{-1} 24 hours^{-1}), and Acari (25 lakes, average 6.4 ind. jar^{-1} 24 hours^{-1}).

Community composition and environmental variables

Visually observed separation of taxa optima (weighted averages) in NMDS projection of the first two axes (Fig. 2) suggested that Cladocera, Copepoda, Isopoda and Oligochaeta co-occur in the lakes of the Evo region. Similarly, Diptera, Ephemeroptera, Odonata, Arctic loon (Gavia arctica), and bleak co-occur in the lakes of the Lieksa region. Teal alone differed from other taxa in ordination, and Coleoptera and whitefish were mainly observed in the Lieksa region (Fig. 2). The data projection on the first and third NMDS axes formed a circular pattern, with Oligochaeta, Cladocera, and Copepoda being the most distinctive taxa (Fig. 2). The data projection on the second and third NMDS axes formed a circular pattern, with Ceratopogonidae and mallard. Lakes in Lieksa and Evo formed visually observable and statistically significant (Anosim, $R = 0.40$, $p = 0.001$) regional separation in ordination space (Fig. 2).

In Mantel's test (Table 2), individually tested water-colour related variables that statistically significantly related to community composition were DOC, colour, and Secchi depth. Total-P concentration was close to statistical significance ($r = 0.15$, $p = 0.053$) whereas iron was clearly a non-significant variable. Regionally tested, community composition changed along DOC gradient in Lieksa region lakes ($r = 0.24$, $p = 0.011$) but did not reach statistical significance in Evo region lakes ($r = 0.22$, $p = 0.143$).

Regional community dissimilarities and DOC classes

The largest significant contributors (SIMPER-analysis) to community dissimilarity between

Table 1. A list of studied taxa.

Invertebrates	Fish	Water birds
Ceratopogonidae	Bleak (*Alburnus alburnus*)	Common goldeneye (*Bucephala clangula*)
Chironomidae	Perch (*Perca fluviatilis*)	Common gull (*Larus canus*)
Cladocera	Northern pike (*Esox lucius*)	Arctic loon (*Gavia arctica*)
Coleoptera	Ruffe (*Gymnocephalus cernua*)	Mallard (*Anas platyrhynchos*)
Copepoda	Roach (*Rutilus rutilus*)	Whooper swan (*Cygnus cygnus*)
Diptera	Whitefish (*Coregonus lavaretus*)	Eurasian teal (*Anas crecca*)
Dytiscidae		
Ephemeroptera		
Hemiptera		
Acari		
Isopoda		
Odonata		
Oligochaeta		
Trichoptera		

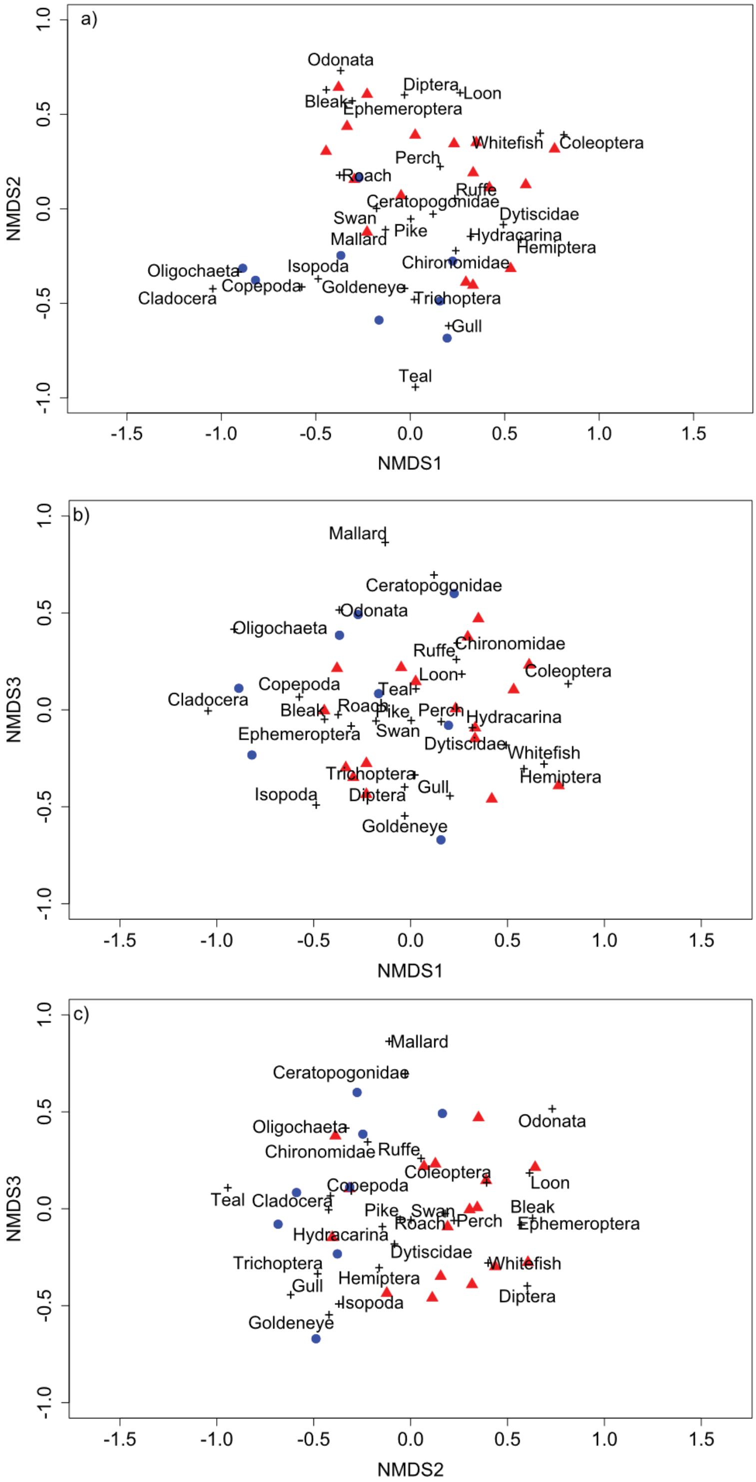

Fig. 2. Non-metric dimensional scaling of Bray-Curtis species dissimilarity in lakes (stress value = 0.17, dimensions (*k*) = 3). The red triangles represent the lakes in Lieksa the region (*n* = 17), while the blue circles represent the lakes in Evo (*n* = 8). Taxa are projected as weighted averages to lake ordination and indicated with black crosses.

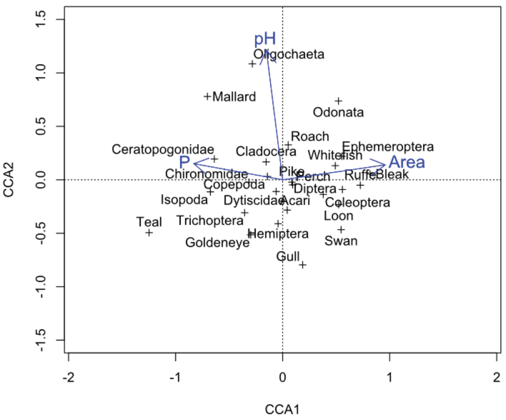

Fig. 3. Taxa distribution along the canonical axes and environmental variables.

Evo and Lieksa regions were Cladocera ($p = 0.005$), Copepoda ($p = 0.001$), mallard ($p = 0.023$), and teal ($p = 0.033$). All taxa showing statistical differences had higher average abundance in Evo region compared to the Lieksa region (Table S2 in Supplementary Information).

Community composition (Bray-Curtis dissimilarity) was statistically significantly different (*Anosim*, $R = 0.22$, $p = 0.008$) across the three categories of lakes based on their DOC concentration (low < 10 mg L^{-1}, 10 mg L^{-1} ≤ medium ≤ 20 mg L^{-1}, high > 20 mg L^{-1}) (Table 3). The statistically significant taxa contributing to dissimilarity between low DOC lakes and medium DOC lakes (SIMPER-analysis) were whitefish ($p = 0.002$) and Acari ($p = 0.007$) (Table S3 in Supplementary Information). Statistically significant contributors to dissimilarity between medium and high DOC lakes were Trichoptera ($p = 0.021$), Isopoda ($p = 0.027$), and for low and high DOC; Isopoda ($p = 0.019$) and Trichoptera ($p = 0.033$). Kendall's τ was used to assess the correlation between individual taxa abundance and DOC concentration (Fig. S1 in Supplementary Information). None of the correlations was statistically significant after correction for multiple testing (Bonferroni-corrected $\alpha = 0.0019$).

Canonical correspondence analysis

The final model included total-P, surface area, and pH ($x^2 = 0.21$, $F = 2.08$, $p = 0.001$; Table 4), and explained 22.9% of the total variance. The first canonical axis (eigenvalue = 0.11) explained 11.6% of the total variation and 50.9% of the constrained variation and was statistically significant ($x^2 = 0.11$, $F = 3.17$, $p = 0.008$). The second axis (ev.= 0.07) explained 7.2% of the total variation and 31.4% of the constrained variation, and was not statistically significant ($x^2 = 0.07$, $F = 1.96$, $p = 0.192$). The third axis (ev.= 0.04) explained 4.1% of the variation and 17.7% of the constrained variation and was not significant ($x^2 = 0.03$, $F = 1.11$, $p = 1$). The environmental variables with the most explanatory power for the first axis were total-P and surface area (Table S4 in Supplementary Information, Fig. 3). The environmental variable with the most explanatory power for the second axis was pH (Table S4 in Supplementary Information, Fig. 3).

Abundance of bleak, ruffe (*Gymnocephalus cernua*), whitefish, Coleoptera, Diptera, Ephemeroptera, Odonata, Arctic loon, and whooper swan (*Cygnus cygnus*) was positively related to surface area, and negatively to total-P (Table S5 in Supplementary Information, Fig. 3). Taxa that

Table 2. Mantel's test results of the relationship between Bray-Curtis dissimilarity and environmental variables including water colour, DOC, iron, Secchi depth, and phosphorus. Spearman rank order correlation was used with 9999 permutations. Statistically significant (Bonferroni corrected $\alpha = 0.01$) variables are in bold.

Variable	Mantel's *R*	*p*	90%	95%	97.5%	99%
DOC	**0.24**	**0.002**	**0.11**	**0.14**	**0.17**	**0.20**
Colour	**0.25**	**0.003**	**0.11**	**0.14**	**0.17**	**0.20**
Secchi	**0.25**	**0.002**	**0.11**	**0.14**	**0.17**	**0.20**
Fe	0.06	0.273	0.12	0.16	0.20	0.23
Total-P	0.15	0.053	0.12	0.16	0.19	0.23

were positively associated with high nutrient concentration were Ceratopogonidae, Isopoda, teal, and mallard (*Anas platyrhynchos*) (Table S5 in Supplementary Information, Fig. 3). Taxa such as roach, Odonata, Oligochaeta, and mallard were positively related to pH (Table S5 in Supplementary Information, Fig. 3). Abundances of Dytiscidae, Hemiptera, Trichoptera, common goldeneye, common gull, teal, whooper swan associated with lower pH values (Table S5 in Supplementary Information, Fig. 3).

Discussion

Lake area, pH, and total phosphorus were the best variables in explaining the variation in the community composition among the study lakes. DOC can be considered as one of the main drivers of aquatic production (Seekell *et al.* 2015, Arzel *et al.* 2020), but it did not have significant effect on community composition at the studied taxonomic resolution based on CCA. However, Lieksa region lakes sorted by DOC showed a significant change in community composition in Bray-Curtis dissimilarity. Between DOC categories, the most important taxa contributing to the dissimilarity between low DOC and medium DOC lakes were whitefish and Acari, whereas between medium and high DOC and low and high DOC, they were Trichoptera and Isopoda. However, as whitefish has no natural recruitment in the study lakes, their occurrence pattern rather reflects human preference in stocking whitefish to clearwater lakes. Correlation analyses did not reveal strong associations between the abundance of individual taxa and DOC.

In the current study, the first CCA axis reflected phosphorus and surface area gradients, while the second CCA axis, reflecting pH variation, was not statistically significant. The observation that only a small number of environmental variables may explain community composition aligns with the study of Paszkowski and Tonn (2000) and suggests that few key environmental gradients dominate community formation. With increasing lake size, the diversity of different microhabitats increases as well as the absolute carrying capacity of the limited environment (Heino 2013, Fried-Petersen *et al.* 2020). For example, compared to small ponds with relatively steep shore slopes, larger lakes may provide wider vegetated littoral habitats for macroinvertebrates such as Ephemeroptera and Odonata (Tolonen *et al.* 2003, Bartels *et al.* 2021), which were associated with a large surface area in our study (range of our lakes 1.2–37.7 ha). While Trichoptera showed a weak association with small surface area in our study, the presence of caddisflies likely rather reflects some fine-scaled environmental characteristics

Table 3. Distribution of environmental variables and lake counts in DOC classes.

	DOC < 10 mg L^{-1}	10 ≤ DOC ≤ 20 mg L^{-1}	> 20 mg L^{-1}
Total-P (µg L^{-1})	6.0–20.0	11.5–52.6	14.6–29.6
Area (ha)	3.9–18.0	2.2-37.7	1.2–14.4
Depth (m)	2.4–14.5	1.5–12.0	5.2–13.0
Colour (mg Pt L^{-1})	8.7–108.7	87.6–218.3	214.5–293.4
Lakes (*n*)	8	14	3

Table 4. Statistical significance of environmental variables in the most optimal backward selected CCA model (permutations = 9999).

Variable	X^2	*D.F.*	*F*	*p*
Total-P	0.07	1	2.01	0.019
Area	0.08	1	2.29	0.006
pH	0.06	1	1.93	0.018

that were not assessed in this study. Because small lakes tend to have low habitat diversity (Heino 2013), they may be inhabited mostly by generalist taxa (Paszkowski and Tonn 2000). In our study, small lake size was weakly associated with generalist taxa such as Isopoda (Lau *et al.* 2013) and Chironomidae which is a species-rich and widely distributed group of insects that can inhabit various niches (Pinder 1986). Acidity, i.e. pH is a well-known driver for invertebrate community composition in aquatic ecosystems (Feldman and Connor 1992, Fried-Petersen *et al.* 2020). High pH values generally have a positive influence on species abundance and richness (i.e. pH range = 4.3–6.6; Bowman *et al.* 2014), whereas low pH values tend to have the opposite effect (Stendera and Johnson 2008). In our results, higher pH values were associated with Oligochaeta which is shown to prefer high pH (Bowman *et al.* 2014). However, the observed pH range was rather narrow (pH = 5.29–7.56) suggesting that clear negative effects of low pH may not have appeared in this dataset. It is important to note that using low taxonomic resolution in analyses (e.g. Cladocera and Copepoda) overlooked variation in community structure, for example within zooplankton communities.

Fish species diversity generally increases with lake size (Barbour and Brown 1974, Helminen *et al.* 2000, Paszkowski and Tonn 2000) as a result of increasing depth and shoreline diversity on microhabitat diversity (Eros *et al.* 2009, Heino *et al.* 2010) and potentially increasing connectivity with other lakes. Likewise, fish species composition was associated with surface area and phosphorus concentration in this study. Large lakes with large pelagic habitats support pelagic plankton-feeding species, such as bleak and whitefish (Liu and Uiblein 1996, Kahilainen *et al.* 2005). This was supported by our observation of their positive association with the lake surface area. Ruffe, as a benthic insectivore, is often relatively rare in small lakes and may simply benefit from larger surface area as that could better maintain a genetically and demographically sustainable population size (Hölker and Thiel 1998). The main effect of phosphorous on fish species richness is unimodal, meaning that species richness (mainly cyprinid diversity, Helminen *et al.* 2000, Olin *et al.* 2002) increases with eutrophication at low phosphorus concentrations but decreases with very high concentrations (Jeppesen *et al.* 2000). In this study, no clear associations between fish species and environmental gradients were observed.

The composition of water bird community was related to the lake surface area, pH, and phosphorus concentration which is mainly in line with the previous studies (Paszkowski and Tonn 2000, Paszkowski and Tonn 2006, Epners *et al.* 2010). The surface area has a strong positive effect on the number of water bird species that can inhabit a lake (Paszkowski and Tonn 2000, Roach and Griffith 2015). Usually, also the body size of the species increases with lake surface area (Paszkowski and Tonn 2000), which is visible in the CCA ordination of the current study (e.g., whooper swan and Arctic loon in large lakes, teal in small lakes). The size of the lake may limit large avian species that need a long runway to take off (e.g., Arctic loon, whooper swan). Lake shallowness accompanied by large surface area is related to an increase especially in duck species (Paszkowski and Tonn 2000). The general effect of pH on water birds is weak but associated with patterns in feeding guilds (Elmberg *et al.* 1994, Paszkowski and Tonn 2006). In our study, mallard was the only duck species that showed some association with high pH. Phosphorus concentration, as a proxy for primary productivity, was suggested to have a positive effect on the density of breeding and moulting water birds in the previous study (Epners *et al.* 2010). However, phosphorus (range = 6.0–52.6 μg L^{-1}) did not explain variation in the composition of breeding water bird communities but explained the composition of moulting water bird communities (Epners *et al.* 2010). We quantified the breeding pairs suggesting that the composition of water bird communities in the study lakes were mostly driven by lake size.

It is important to recognize that community patterns are affected by many regional and historical filters in addition to contemporary environmental factors (Tonn *et al.* 1990, Heino *et al.* 2017). In our study, however, environmental variables were most likely the dominating drivers of community composition, since we included avian species and several invertebrate taxa (with aerial adult stages for example) that can select and move along different habitats over annual or shorter time scales (De Bie *et al.* 2012). Bleak, whitefish, Hemiptera, whooper swan, and common gull, were not observed in the study lakes of Evo region. These species occur commonly in southern Finland surrounding Evo and the other lakes in the area (Olin *et al.* 2010, Holopainen *et al.* 2022) implying that their scarcity was most likely caused by environmental differences rather than their restricted dispersal. Also, the small sample of Evo lakes (n = 8) may explain the absence of individual taxa. However, the community composition (Bray-Curtis) was significantly different between Evo and Lieksa regions, indicating the potential importance of regional filters and climate conditions on community composition. It is noteworthy that a species itself may work as a filter for other taxa (Väänänen *et al.* 2012, Nummi *et al.* 2016). For example, water bird abundance is positively related to food availability (e.g., invertebrates) (Nummi and Pöysä, 1993, Setash *et al.* 2024), and predatory fish can negatively affect the abundance of water birds (Paasivaara and Pöysä, 2004, Elmberg *et al.* 2010). Fish and water birds both compete for the same food resources (invertebrates, juvenile fish) (Väänänen *et al.* 2012, Nummi *et al.* 2016). However, Paszkowski and Tonn (2000) suggested that environmental variables are more central drivers for fish and water bird assemblages than biotic interactions.

The most interesting difference in community composition was caused by variables that are involved in browning of the waters. DOC, water colour, and Secchi depth had significant effect on community composition. This result agrees with previous studies highlighting the significance of browning on the structure and functioning of aquatic ecosystems (Arzel *et al.* 2020, Blanchet *et al.* 2022). However, the community composition had a statistically significant association with DOC only among Lieksa lakes. This result may be due to smaller sample size of Evo region lakes (n = 8) which reduces statistical power, or higher average of DOC in those lakes (15.8 ± 5.5 mg L^{-1}) compared to Lieksa lakes (n = 17, DOC = 11.4 ± 5.5 mg L^{-1}). These results might also support the idea that the most prominent effects of DOC occur at concentration values close to 10 mg L^{-1} (Kelly *et al.* 2018). However, it is important to recognize that most of the study lakes (n = 14) were medium DOC class lakes and high DOC class comprised only three lakes. As such, future studies should include a larger number of lakes presenting high and low DOC concentrations to better evaluate the structural variation of aquatic communities along DOC gradients.

CCA analysis did not suggest any strong relationship between DOC-related variables and community composition. However, the effect of DOC might be hidden by other environmental covariates with similar but stronger impacts e.g., positive correlation with nutrients (Vainikka *et al.* 2024). For example, phosphorus has similar positive effects on primary production as DOC in small concentrations (Solomon *et al.* 2015, Kelly *et al.* 2018). However, prolonged browning leads to lower primary productivity and reduced macroinvertebrate species abundance, with potential cascading effect on secondary consumers such as fish and water birds (Arzel *et al.* 2020). Forestry practices and land use can increase both nutrient and dissolved organic carbon (DOC) loads to lake ecosystems through ditches and forest drainages (Miettinen *et al.* 2020, Finér *et al.* 2021, Holopainen and Lehikoinen 2022), which may explain the similar effects observed. Regionally, the surrounding areas of lakes in the Lieksa region were heavily used for forestry (Kärkkäinen *et al.* 2019), whereas the Evo area had quite limited agricultural land use in addition to the less intensively used forested areas (Forsius *et al.* 2016).

Decomposition of Bray-Curtis dissimilarity of lakes divided to classes by DOC revealed taxa that had the largest contribution to differences between classes. Between low and medium DOC lakes, whitefish and Acari were significant contributors to these differences, both associating with low DOC lakes. Aquatic mites can occur in a variety of different environmental conditions (Di Sabatino *et al.* 2000) but generally, they can be used as indicators of good water quality (Goldsmidt 2016), and our results suggest that the relative abundance of water mites is higher in low DOC lakes. Trichoptera and Isopoda had the strongest significant contribution to differences between both medium and high DOC lakes, and between low and high DOC lakes. It is most likely due to capability of these taxa to use detritus (Bjelke and Herrmann 2005), which may be abundant in high DOC lakes. Isopoda includes the freshwater isopod *Asellus aquaticus* that is a common species in boreal lakes and capable of feeding on detritus (Kesti *et al.* 2022, Strandberg *et al.* 2023). None of the taxa with significant contribution to differences had the highest average abundance in medium DOC lakes which suggests that medium DOC class may be too wide in the context of DOC values or that only extreme values in DOC induce differences in community composition.

The effects of primary production, water quality and lake morphometry on community composition are generally well known in large lakes (Tonn *et al.* 1990, Pöysä *et al.* 2019, Cohen *et al.* 2020). Small boreal lakes may be particularly vulnerable to rapid community changes due to immediate effects of climate change related weather events and land uses including intensive forestry practises (Roulet and Moore 2006, Monteith *et al.* 2007, Albrecht *et al.* 2023). The current study increases our knowledge on these potential responses by providing data on little-studied small but numerous boreal forest lakes, where browning and associated changes can be major determinants of changes in community composition. Overall, increasing DOC is related to the deterioration of the overall quality of the aquatic environment, which also affects the quality of fish that boreal lakes can provide to humans (Strandberg *et al.* 2016). We highlight the importance of governing human land-use induced leaching of organic and inorganic material that can affect the whole faunal community of small boreal forest lakes.

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