



# Mercury biomagnification patterns in boreal and subarctic lake food webs

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## ABSTRACT

Climate change and land use are significant pressures on northern environments with the potential to influence mercury (Hg) biomagnification in lake food webs. How this process may differ along a north–south gradient, defined by simultaneously changing environmental characteristics, has not been thoroughly explored. Lake food webs, from primary producers to top predators, from 19 subarctic and 16 boreal lakes in Finland were tested for total Hg (THg) biomagnification through the linear regression of THg content ( $\log_{10}[\text{THg}]$ ) and trophic level derived from  $\delta^{15}\text{N}$ . Climate, productivity, lake, and catchment variables were combined and assessed in a principal component analysis (PCA), and the first three principal components (PC) (71.1% of overall variability) were individually regressed with regional trophic magnification slopes (TMS), and mercury baselines ([THg] baseline). PC1 (climate–productivity), PC2 (water bodies), and PC3 (catchment metrics) were used in stepwise multiple linear regression models to assess the combined influence of PCs on regional TMS and [THg] baseline. Subarctic TMS and [THg] baseline were positively and negatively important, respectively, along a climate–productivity gradient (PC1). The stepwise model for subarctic TMS included PC1 and PC2, which explained 42.3% of variation, while the model for boreal TMS included all three PCs, which explained 35.4% of variation. The notable complexity of influences on boreal lakes makes modelling and future predictions challenging for this region, while the ongoing and simultaneous influences of climate warming and land use intensification in the subarctic region suggest lower TMS in the future.

## 1. Introduction

Northern latitudes are significantly impacted by climate change through increases in temperature and precipitation, which are projected to continue in the coming decades (AMAP, 2021; IPCC, 2023). Climate warming has occurred nearly four times faster in the Arctic than in the rest of the world over the last decades (Rantanen et al., 2022). Concurrently, a general increase in annual precipitation has been identified across the Arctic, with current models projecting a strong shift from snow to rain for much of the annual precipitation in northern regions (Bintanja and Andry, 2017; Box et al., 2019). These changes are

significantly altering hydrological and nutrient cycles in northern catchments (Bring et al., 2016; Catalán et al., 2016; Chételat et al., 2022). Consequently, increased concentrations of dissolved organic carbon (DOC) have been identified in boreal catchments across Fennoscandia, and increasing precipitation is predicted to drive mobilisation of carbon and other nutrients into water bodies, resulting in increased browning and eutrophication (Monteith et al., 2007; De Wit et al., 2016; Räike et al., 2024). Mobilisation of carbon and nutrients from catchments to lakes has also been tied to expanding land use activities, especially forestry-related site preparation, clear-cutting, and peatland ditching (Monteith et al., 2015; Finér et al., 2021; Nieminen et al.,

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2021). Agricultural fertilisers and municipal sewage in particular have been linked to lake eutrophication, while ditched peatlands and forestry have been tied to browning, and both processes occur across northern landscapes (Taipale et al., 2016; Hayden et al., 2019). Changes in lake chemistry and productivity may modify the primary energy sources of the lake, thereby altering the structure and composition of lake food webs (Creed et al., 2018; Keva et al., 2021). While consequences of climate change and intensive land use are significant regarding eutrophication and browning, they may also alter contaminant dynamics in lakes (Post et al., 2009; Hayden et al., 2019; Kozak et al., 2021).

Mercury (Hg) is a toxic heavy metal originating from both anthropogenic and natural sources, posing a threat to the health of wildlife and human consumers of aquatic resources (Outridge et al., 2018; Wang et al., 2019; AMAP, 2021). Mercury represents a notable risk in the Northern Hemisphere due to high atmospheric deposition, where most emissions originate from sources including combustion for power generation and industry, and cement and ferrous metal production (AMAP, 2021). This has led to legacy Hg accumulation, even in remote catchments (Fitzgerald et al., 1998). Geologic sources of Hg in Finland are very limited, mainly due to leaching from black schist, while long-range transboundary air transport of Hg has been identified as its primary source (Ukonmaanaho et al., 2016; Braaten et al., 2019). While point source Hg loading from industrial sources has historically included chlor-alkali plants, power plants, and pulp mills in Finland (Kyllönen et al., 2014), these have been significantly reduced in recent decades due to improvements in policy and effluent treatment (Lodenius, 2013). Although atmospheric emission of Hg has declined in Europe over the past decade, emissions in the global south and particularly in Asia have increased (AMAP, 2021; Dastoor et al., 2022). Recently elevating accumulation rates of Hg in some northern lakes in contrast to the generally declining deposition trend in recent years highlight catchment-specific transport regimes and a higher representation of rain rather than snow as precipitation in colder months (Pelletier et al., 2021). Higher temperatures and precipitation influence atmospheric Hg wet deposition through variation in precipitation and snowfall, and dry deposition to surfaces and snowpack (Skov et al., 2006; Steffen et al., 2014). A warmer climate may also support more intensive mobilisation of Hg from snowpack and surface soils during spring melt (Douglas et al., 2017; Obrist et al., 2018; Lim et al., 2020).

Forestry activities have also been tied to increased leaching of DOC and Hg from catchments to water bodies (Morel et al., 1998; Porvari et al., 2003; Bishop et al., 2009; Lehnerr, 2014). DOC acts as a primary vector mobilising Hg from catchments to lakes, and higher amounts of available organic matter increases bacterial productivity in water bodies (Forsström et al., 2013; De Wit et al., 2016), thus promoting bacteria-driven methylation of Hg into the more bioavailable methylated Hg (MeHg) (Morel et al., 1998; Poste et al., 2015; Eagles-Smith et al., 2018). Within lakes, increased DOC hinders light penetration due to brownification, potentially promoting increased anoxia and methylation (Lehnerr, 2014). A warmer climate supports a more efficient methylation regime in sediments (Schaefer et al., 2020; AMAP, 2021). High concentrations of Hg have been measured in ditch water (Ukonmaanaho et al., 2016), highlighting peatland forestry as a potentially important source of Hg (Eklöf et al., 2016; Kozak et al., 2021), although less is known about Hg leaching from agricultural fields established on peatlands. Boreal catchments are mosaics of clear-cut areas, managed forests, peatlands, agricultural fields, and urban areas, which jointly influence the leaching of Hg and nutrients from catchments, thereby altering lake ecosystem dynamics. Additionally, morphometric attributes of catchment areas and lakes (e.g. size, land cover composition, lake volume, and retention time) can significantly influence concentrations of nutrients and Hg in lakes (Kidd et al., 2012; Clayden et al., 2013; Kozak et al., 2021; Keva et al., 2022). A greater proportion of catchments comprised of forest has been positively related to increased DOC in lakes and higher Hg content in fish (Watras et al., 1998; Sonesten, 2003; Keva et al., 2022), and a large catchment-to-lake

ratio, typical for small forest lakes, has also been linked to elevated Hg in fish (Aqdam et al., 2024). Intensive land use is more prevalent in southern boreal regions than in the subarctic north. However, as climate change increases accessibility, more opportunities for intensive land use further north will become evident.

Biomagnification of Hg refers to higher Hg content with increasing trophic level (TL), often modelled using the linear regression of Hg content and TL derived from stable isotope ratios of nitrogen ( $\delta^{15}\text{N}$ ) (Cabana and Rasmussen, 1994; Borgå et al., 2012; Kidd et al., 2012). The slope of this equation is termed as the trophic magnification slope (TMS), which describes the rate of biomagnification, while the intercept, termed as [THg] baseline, infers the basal Hg content (Borgå et al., 2012; van der Velden et al., 2013). Numerous factors influence TMS, such as latitude, nutrients, food web composition, as well as catchment and lake size, however, findings have been contradictory (Kidd et al., 2012; Clayden et al., 2013; Lavoie et al., 2013; Kozak et al., 2021). In Canadian boreal lakes, higher nutrient concentrations in lakes and larger lake surface area were linked to higher biomagnification (Kidd et al., 2012), while the opposite was found in a series of Finnish subarctic lakes (Kozak et al., 2021). In a global study, deposition magnitude of Hg was linked to latitude with TMS increasing along a latitudinal gradient (Lavoie et al., 2013), as also identified in Finnish subarctic lakes (Kozak et al., 2021). Dilution of Hg in more productive systems due to greater diversity and biomass within food webs has been observed in different lake types and regions, which likely influences the rate of Hg biomagnification (Wu et al., 2019; Kozak et al., 2021). Eutrophication and brownification may jointly, or contrastingly, influence biomagnification of Hg across spatial scales due to variations in Hg methylation and biomass dilution (Kozak et al., 2021). While eutrophication may reduce biomagnification through biomass dilution, brownification may increase it through dilution reduction by limiting primary production, however, these processes are complex and lake-specific (Seekell et al., 2015a, 2015b; Braaten et al., 2018). A holistic understanding involving the spatiality of Hg biomagnification in freshwater ecosystems which takes these pressures into account would be highly valuable for understanding this process (Kidd et al., 2012; Lavoie et al., 2013). More information is needed to understand how variability in climate, lake, and catchment properties comparatively influence Hg biomagnification in lake food webs.

In this study, lake food webs from two distinct regions in Finland, including 16 southern boreal lakes and 19 northern subarctic lakes, were sampled during the open-water season. This enabled a large landscape level comparison of THg biomagnification in northern lake environments to give insight into potential region-specific influences of climate change and land use intensification. The following questions (Q) and predictions (P) were set.

Q1: What are the main drivers of the THg trophic magnification slope in boreal and subarctic lakes and how do they differ between these regions? P1: A strong climate–productivity gradient will show a positive trend towards colder lakes in subarctic trophic magnification slopes (Kozak et al., 2021), and boreal lake trophic magnification slopes are predicted to also follow this trend.

Q2: What environmental variables primarily influence the [THg] baseline in boreal and subarctic lakes, and how do their impacts vary between the two regions? P2: [THg] baselines will trend negatively towards colder lakes along a climate–productivity gradient in subarctic lakes (Kozak et al., 2021), and a similar trend is expected in boreal lakes.

## 2. Methods

### 2.1. Study area

Finland is a latitudinally extensive country, spanning from the hemiboreal south to the subarctic north. This landscape hosts diverse

ecosystems, comprising an array of species with differing habitat requirements at northern latitudes. Assessing gradients at the landscape level is valuable in understanding the potential impacts of climate change and land use intensification (Fukami and Wardle, 2005; Kozak et al., 2021). The Finnish subarctic region is characterised by generally lower annual temperatures and precipitation than the boreal region, with a longer, harsher winter and an extended period of lake ice-cover (Korhonen, 2006; Irannezhad et al., 2014). Variation in the duration of ice-cover has a notable influence on the aquatic communities of lakes. In the subarctic region, ice-cover may last from October to June, while in the boreal, it may last from November to May (Korhonen, 2006). Generally, the ice-covered period is decreasing in both regions (Sharma et al., 2019).

This space-for-time study was conducted on 35 Finnish lakes. Nineteen tributary lakes on the Tornio-Muonio watercourse in the subarctic region (66.5°N – 69.0°N, 20.5°E – 24.9°E) were sampled in August–September 2009–2013 (data from Kozak et al., 2021) and sixteen lakes in the boreal region (60.4°N – 61.6°N, 23.3°E – 27.2°E) were sampled in July–September 2020–2023 (Table 1; Fig. 1). Although acidification in some Finnish lakes has been tied to higher Hg content in fish (Rask et al., 2021), the study lakes are surface-water-fed and no acidified lakes were included.

## 2.2. Environmental variables

Surface water measurements for total nitrogen (TN;  $\mu\text{g L}^{-1}$ ), total phosphorus (TP;  $\mu\text{g L}^{-1}$ ), DOC ( $\text{mg L}^{-1}$ ), and water colour (Pt  $\text{L}^{-1}$ ) were either retrieved from the Finnish Environmental Institute (SYKE)

HERTTA database ([https://www.syke.fi/fi-FI/Avoin\\_tieto/Ymparistotietojarjestelmat](https://www.syke.fi/fi-FI/Avoin_tieto/Ymparistotietojarjestelmat)) or analysed in the laboratory immediately after lake sampling (see Vainikka et al., 2024). Lakes were organised into oligotrophic (TP  $\leq 10 \mu\text{g L}^{-1}$ ), mesotrophic (TP:  $10\text{--}30 \mu\text{g L}^{-1}$ ), and eutrophic (TP  $\geq 30 \mu\text{g L}^{-1}$ ) nutrient classifications based on TP as the limiting nutrient in lakes (Schindler, 1974; Nürnberg, 1996). Lake area, depth, and volume were taken from the same database or calculated using bathymetric maps (Hayden et al., 2017). Catchment metrics and land cover information within catchments were retrieved from the SYKE VALUE tool (<https://paikkatieto.ymparisto.fi/value/>), which is based on CORINE Land Cover (CLC) (2012). Observed land cover types included: sparse vegetation and rocks, wetlands, inland waters, urban, agriculture, and forest (Supplementary Table S1).

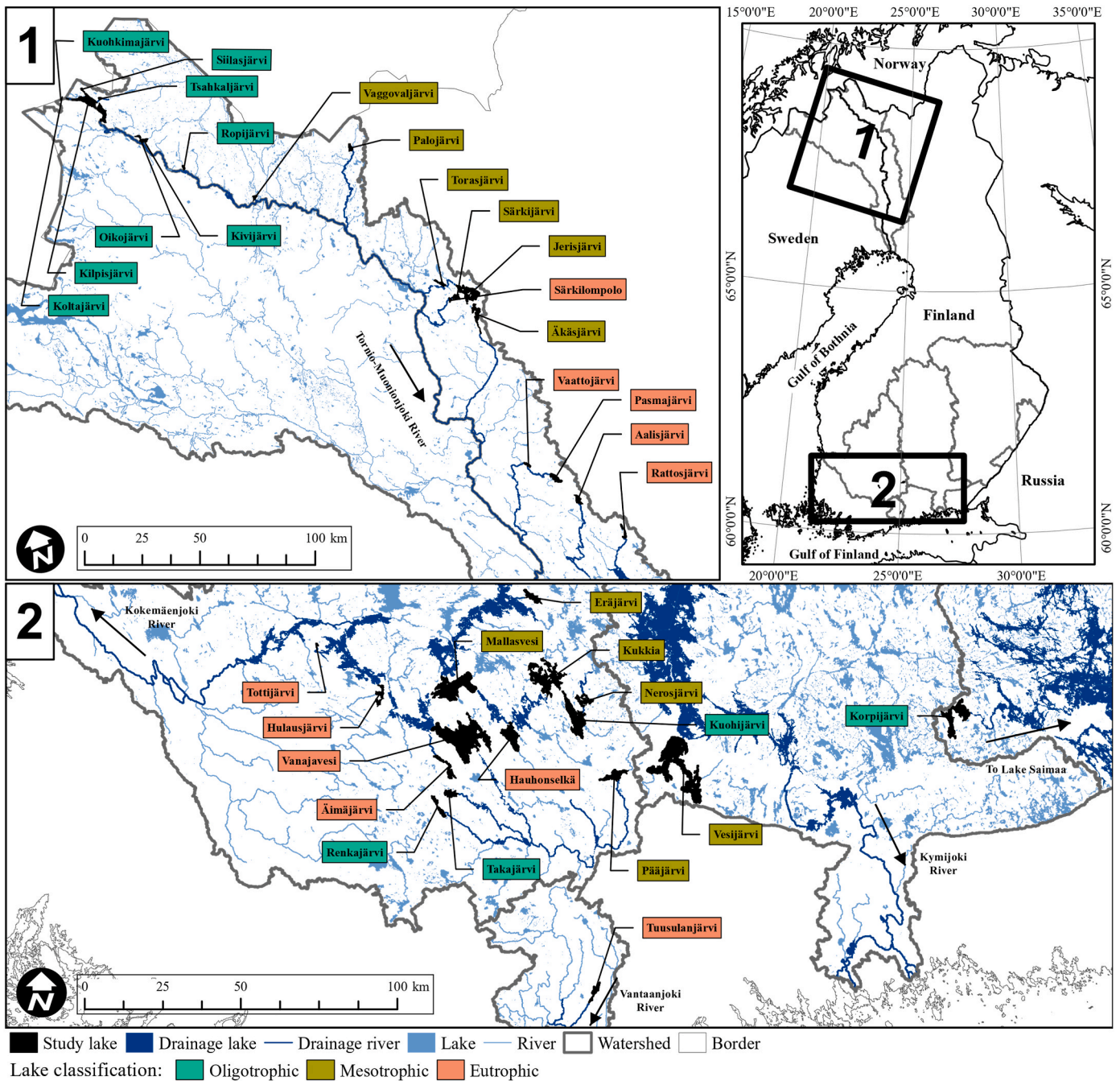
## 2.3. Biota sampling

Benthic algae, green filamentous algae, biofilm, and macrophyte samples were collected by hand from the lakebed and hard surfaces and manually cleaned in the laboratory, while pelagic algae were sampled directly from blue-green algal blooms with a plastic lid. Due to weather conditions and late growing season, collection of primary producers from ten lakes in the subarctic was not conducted. Pelagic zooplankton were collected using horizontal and vertical hauls with a zooplankton net. Littoral benthic macroinvertebrates (hereafter macroinvertebrates) were collected from the shoreline using handpicking and kick-nets (500  $\mu\text{m}$  mesh). Additionally, an Ekman grab (272  $\text{cm}^2$ ) was employed in the subarctic to collect supplementary benthic samples from littoral habitats (1–2 m) (Hayden et al., 2017), where combined samples from three

**Table 1**

Biomagnification regression intercepts ([THg] baseline) and slopes (trophic magnification slope (TMS)) with adjusted  $R^2$  values ( $\text{adj}R^2$ ) and  $p$ -values are presented for each lake with abbreviations (Lake Abb), organised by region and nutrient classification. Associated number of fish species captured in each lake (Species #), food chain length (FCL), basal total mercury content (Basal [THg]  $\text{mg kg}^{-1}$  dry weight (d.w.)), trophic magnification factor (TMF), principal component coordinates for climate–productivity (PC1), water bodies (PC2), and catchment metrics (PC3) are presented for each lake.

Region	Classification	Lake	Lake Abb	[THg] Baseline	TMS	$\text{adj}R^2$	$p$	Species #	FCL	Basal [THg] ( $\text{mg kg}^{-1}$ d.w.)	TMF	PC1	PC2	PC3
Boreal	Eutrophic	Äimäjärvi	ÄI	-2.793	0.607	0.57	<0.001	12	4.14	0.00161	4.05	-2.02	-0.60	0.48
		Hauhonselkä	HA	-2.277	0.637	0.64	<0.001	12	3.26	0.00529	4.34	-2.20	0.47	-1.19
		Hulausjärvi	HU	-2.457	0.483	0.69	<0.001	11	4.21	0.00349	3.04	-3.26	-2.10	0.09
		Tottijärvi	TO	-3.014	0.702	0.76	<0.001	7	3.95	0.00097	5.03	-1.75	-0.60	0.79
		Tuusulanjärvi	TU	-2.461	0.594	0.67	<0.001	11	3.74	0.00346	3.93	-3.07	-1.75	0.34
		Vanajavesi	VA	-2.424	0.487	0.67	<0.001	13	4.19	0.00376	3.07	-2.84	1.81	-2.19
	Mesotrophic	Eräjärvi	ER	-2.716	0.717	0.83	<0.001	9	3.76	0.00192	5.21	-1.38	-0.22	0.67
		Kukkia	KK	-2.503	0.584	0.82	<0.001	11	3.98	0.00314	3.84	-0.66	1.87	0.13
		Mallasvesi	MA	-2.618	0.573	0.73	<0.001	10	4.22	0.00241	3.74	-1.01	3.37	-3.07
		Nerosjärvi	NE	-2.000	0.543	0.69	<0.001	10	4.27	0.01001	3.49	-0.91	0.94	0.14
		Pääjärvi	PÄ	-2.162	0.502	0.48	0.003	12	4.35	0.00689	3.18	-2.30	-0.11	0.00
		Vesijärvi	VE	-2.462	0.498	0.61	<0.001	15	4.23	0.00346	3.15	-0.82	2.51	0.30
		Korpijärvi	KR	-2.196	0.553	0.50	0.006	9	3.81	0.00637	3.57	-0.42	2.54	1.04
		Kuohijärvi	KH	-2.055	0.617	0.81	<0.001	12	3.69	0.00880	4.14	-0.74	2.11	0.17
		Renkajärvi	RE	-2.846	0.713	0.80	<0.001	11	4.28	0.00142	5.16	-0.98	0.27	0.49
		Takajärvi	TA	-2.201	0.626	0.69	<0.001	11	3.80	0.00630	4.23	-0.91	0.35	0.45
Subarctic	Eutrophic	Aalisjärvi	AA	-2.070	0.630	0.84	<0.001	8	3.27	0.00851	4.26	-1.56	-1.74	0.34
		Pasmajärvi	PS	-1.908	0.498	0.82	<0.001	8	3.50	0.01236	3.15	-1.82	-1.88	0.22
		Rattosjärvi	RA	-2.076	0.499	0.87	<0.001	8	3.86	0.00840	3.16	-1.55	-1.29	0.26
		Särkilompola	SL	-2.182	0.443	0.77	<0.001	9	4.46	0.00657	2.77	-0.34	-0.32	0.72
	Mesotrophic	Vaattojärvi	VT	-1.997	0.532	0.85	<0.001	8	3.80	0.01007	3.40	-0.88	-2.84	-3.91
		Äkäsjärvi	ÄK	-2.350	0.478	0.79	<0.001	8	4.28	0.00447	3.01	0.54	0.11	1.01
		Jerisjärvi	JE	-2.139	0.430	0.96	<0.001	6	4.30	0.00726	2.69	-0.05	0.73	1.48
		Palojärvi	PL	-2.756	0.804	0.95	<0.001	7	3.11	0.00175	6.37	2.03	-1.90	0.05
		Särkijärvi	SÄ	-2.063	0.315	0.94	<0.001	6	4.53	0.00866	2.07	-0.26	0.74	1.71
		Torasjärvi	TR	-2.130	0.448	0.88	<0.001	10	4.01	0.00741	2.81	0.07	0.03	0.57
Oligotrophic	Vaggovaljärvi	VG	-2.393	0.651	0.91	<0.001	6	3.17	0.00405	4.48	1.76	-0.39	1.86	
	Kilpisjärvi	KP	-2.417	0.593	0.85	<0.001	7	3.89	0.00383	3.92	3.58	2.18	-0.32	
	Kivijärvi	KV	-2.049	0.661	0.96	<0.001	6	3.25	0.00892	4.58	2.81	-1.21	-0.41	
	Koltajärvi	KT	-2.476	0.848	0.83	0.008	3	2.64	0.00334	7.04	3.90	0.01	0.10	
	Kuohkimajärvi	KU	-2.361	0.615	0.97	<0.001	4	3.47	0.00436	4.12	3.72	-0.26	-1.06	
	Oikojärvi	OI	-1.930	0.484	0.88	<0.001	6	3.82	0.01176	3.05	2.54	-0.69	0.23	
	Ropijärvi	RO	-2.112	0.526	0.88	<0.001	11	3.81	0.00772	3.36	2.23	-1.49	-0.62	
	Siilasjärvi	SI	-2.238	0.633	0.91	<0.001	5	3.04	0.00579	4.30	4.79	-0.10	-0.69	
Tsahkaljärvi	TS	-2.073	0.581	0.78	<0.001	3	3.53	0.00845	3.81	3.74	-0.56	-0.19		



**Fig. 1.** Map indicating sampled subarctic lakes in northern Finland along the Tornio-Muoniojoki watercourse (1) and boreal lakes in southern Finland (2), with numbered regions identified on the map of Finland. Major catchments (Watershed) are delineated, primary drainage is named, and drainage water bodies relevant to the sample lakes are coloured. Lake names are coloured according to nutrient status (Lake Classification) in both regions.

replicates were used. All invertebrate samples were transported in cool boxes back to the laboratory for identification, sorting, and cleaning. Before storage in 2 ml plastic tubes, zooplankton samples consisting of cladocerans and copepods were composited, while macroinvertebrates were sorted to genus or family.

Fish were captured using either a gillnet series of eight randomly ordered 30 × 1.8 m nets (knot-to-knot: 12, 15, 20, 25, 30, 35, 45, and 60 mm) and one 30 × 1.5 m Nordic multimesh gillnet (12 × 2.5 m wide nets, mesh sizes: 5–55 mm), or only Nordic nets. Nets were set in littoral, pelagic, and profundal habitats overnight (10–12 h). In some lakes, bait traps, rod and line, and pelagic trawls (2–4 m height, 4–8 m width, 3 mm cod-end mesh (Thomas et al., 2016)) were used to ensure an effective capture of fish diversity and size categories. Representative subsamples

were taken from each lake for a total of 26 fish species, of which 17 were sampled in the subarctic and 19 in the boreal (Supplementary Table S2). European whitefish (*Coregonus lavaretus*) occur in two distinct morphs in the western subarctic (Supplementary Table S2): the large sparsely rakered whitefish (LSR), and densely rakered whitefish (DR) (Hayden et al., 2013). Whitefish morph separation is limited in the boreal, as southern populations originate from stocking of the planktivorous morph. Additionally, hybrid occurrence has been noted between whitefish and vendace (*Coregonus albula*) in some subarctic lakes (Supplementary Table S2) and between cyprinids in some boreal lakes. Fish were euthanized immediately after removal from the nets via cerebral concussion before being taken to the laboratory on ice. Fishing permits were obtained from lake owners and from the Regional Centre of

Economic Development, Transport and Environment. Fish were identified to species and measured for total length ( $\pm 0.1$  cm) and weight ( $\pm 0.1$  g). Representative subsamples of fish and composite samples of macroinvertebrates, zooplankton, and primary consumers were taken from each lake, totalling 6088 samples measured for [THg] and  $\delta^{15}\text{N}$  (Supplementary Table S2; S3). All primary producer, invertebrate, and fish dorsal muscle samples were freeze-dried at  $-50^\circ\text{C}$  for 48 h and pulverized.

#### 2.4. Mercury analysis

A Direct Mercury Analyzer (DMA-80) (Milestone S.r.l., Sorisole, Italy) was used to measure [THg] from individual freeze-dried samples (20–30 mg dry weight (d.w.)) (Supplementary Table S2; S3). Blank samples and certified reference materials (DORM-4, National Research Council Canada, mean  $\pm$  SD, Hg  $0.410 \pm 0.055$  mg  $\text{kg}^{-1}$  d.w.) (ERM-BB422, European Reference Materials, Hg  $0.601 \pm 0.030$  mg  $\text{kg}^{-1}$  d.w.) were used in the beginning and end of every run (DORM-4:  $0.408 \pm 0.022$  mg  $\text{kg}^{-1}$  d.w., mean recovery = 99.4%,  $n = 1138$ ; ERM-BB422:  $0.603 \pm 0.026$  mg  $\text{kg}^{-1}$  d.w., mean recovery = 100.3%,  $n = 196$ ). Sample duplicates were also used in every run (either every single or every fifth sample was duplicated depending on available sample amount), and averages of duplicates were used in subsequent analyses for those samples. A difference of  $<10\%$  was deemed acceptable for samples to be included in subsequent analyses. Average blank [THg] samples were subtracted from measured samples [THg] for correction (blank mean  $\pm$  SD:  $0.00126 \pm 0.00216$  mg  $\text{kg}^{-1}$ ,  $n = 1334$ ).

#### 2.5. Stable isotopes

Subsamples of freeze-dried primary producers, invertebrates, and fish dorsal muscle were weighed (animal tissue: 0.5–0.7 mg; plant material: 0.9–1.1 mg) in tin cups for measurement of  $\delta^{15}\text{N}$  using an elemental analyser connected to a continuous-flow isotope ratio mass spectrometer. Internal laboratory reference materials were calibrated to atmospheric  $\text{N}_2$ , which were included in every run to control for variability. The analytical error for  $\delta^{15}\text{N}$  runs was always  $\leq 0.2\%$ .

#### 2.6. Trophic level, biomagnification, and modelling calculations

The TL of each sample was calculated according to Post (2002):

$$TL = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / \Delta^{15}\text{N} + \lambda \quad (1)$$

where TL is the calculated trophic level of the organism,  $\delta^{15}\text{N}_{\text{consumer}}$  and  $\delta^{15}\text{N}_{\text{baseline}}$  are the isotope values of the consumer and a baseline organism (average primary producer  $\delta^{15}\text{N}$  value per lake),  $\Delta^{15}\text{N}$  is the trophic discrimination factor set to 3.4‰ (Post, 2002), and  $\lambda$  is the TL of the baseline organism (TL = 1 for primary producers). Variability in the trophic fractionation of  $\delta^{15}\text{N}$  among consumers across different TLs has been previously observed (Vander Zanden and Rasmussen, 2001; McCutchan et al., 2003; Bunn et al., 2013), which may influence TL estimations using a constant. However, using 3.4‰ as the trophic discrimination factor gives a reasonable approximate (Post, 2002) given that primary producers are the baseline organisms in all study lakes (Vander Zanden and Rasmussen, 2001; van der Velden et al., 2013).

Average TLs and [THg] were taken to represent each fish species and all available macroinvertebrate TLs and [THg] were averaged in each lake to avoid sample size bias. Primary producers were used as the base of the food web, however, this group was not available in every subarctic lake. Therefore, to infer a baseline organism for some subarctic lakes, average [THg] and  $\delta^{15}\text{N}$  for algae were taken from similar lake types nearby regarding nutrient concentration in water (oligotrophic, mesotrophic, eutrophic) and used for lakes lacking primary producer samples (indicated in Supplementary Table S2, Kozak et al., 2021). Primary producers were available in every boreal lake and lake-specific averaged

values of [THg] and  $\delta^{15}\text{N}$  were used. The highest species-specific mean TL was identified in each lake, which allowed for the identification of food chain length (FCL) (Cabana and Rasmussen, 1996; Post, 2002).

[THg] was  $\log_{10}$  transformed ( $\log_{10}[\text{THg}]$ ) to meet assumptions of normality and equal variance before calculating biomagnification by linear regression of taxa-specific average TLs and  $\log_{10}[\text{THg}]$  in every sampled lake (Table 1; Supplementary Table S4). The slope of this equation, termed as the trophic magnification slope (TMS), defines the rate of THg biomagnification, while the intercept, termed as the [THg] baseline, identifies the base  $\log_{10}[\text{THg}]$  in each lake. This is described by the following equation:

$$\log_{10}[\text{THg}] = a + b \cdot \text{TL} \quad (2)$$

where  $a$  is the estimated [THg] baseline,  $b$  is the estimated TMS (Borgå et al., 2012; Lavoie et al., 2013), and TL is the trophic level.

The biomagnification calculation then allows for calculation of the trophic magnification factor (TMF), which represents the average increase in [THg] per TL (Borgå et al., 2012) (Eq (3)), and basal [THg], which is the [THg] at the base of the food web (van der Velden et al., 2013) (Eq (4)):

$$\text{TMF} = 10^b \quad (3)$$

where  $b$  is the slope coefficient (Eq (2)).

$$\text{basal [THg]} = 10^a \quad (4)$$

where  $a$  is the [THg] baseline (Eq (2)).

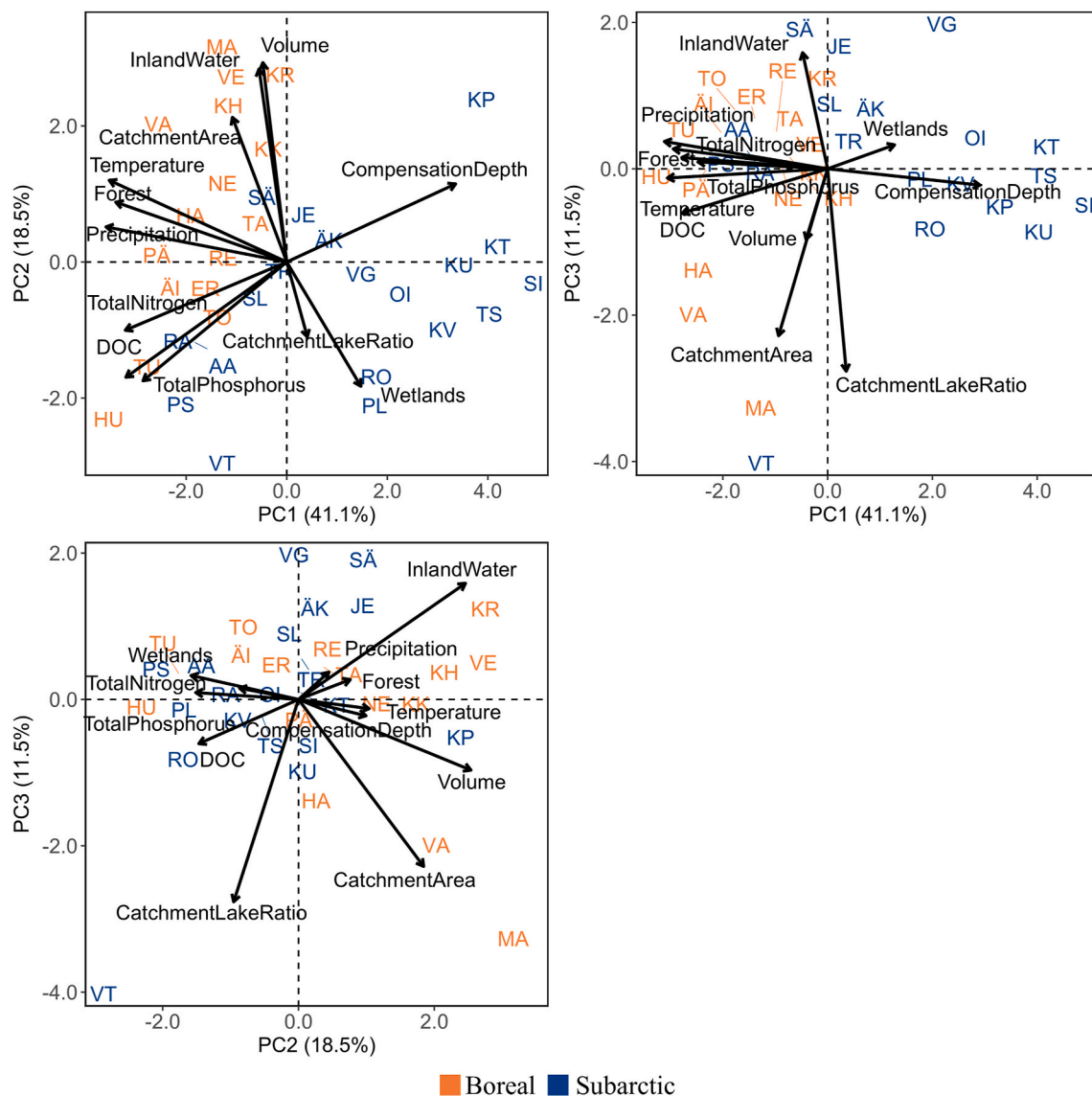
Environmental, lake, and catchment metrics were assessed in a correlation matrix using Pearson's coefficient (Supplementary Table S5) before subsequent inclusion in a principal component analysis (PCA) to reduce environmental dimensions. Agriculture, urban, and sparse vegetation and rocks land cover were excluded from the PCA due to the notable disparity in representation between regions, thereby limiting bias. Principal components with  $>9\%$  contribution explaining variance in the metrics (PC1–PC3) were considered the most important variables for further analyses (Fig. 2; Supplementary Table S6). To assess the influence of the principal components (PC1–PC3) on boreal and subarctic TMS and [THg] baseline, linear regression analyses were performed. Stepwise multiple linear regression models were also used to assess region-specific TMS and [THg] baseline using forward and backward stepwise direction based on the Akaike Information Criterion (AIC) with selection for best direction to identify the influence of PC1, PC2, and PC3 on biomagnification in the study regions.

All statistical analyses were conducted using R version 4.2.3 (R Core Team, 2019) and the significance limit was set to  $p = 0.05$ . The FactoMineR package (Husson et al., 2006) was used to compute PCAs and the factoextra package (Kassambara and Mundt, 2016) for extracting and visualising results, the MASS package (Ripley and Venables, 2009) was used for stepwise models, and the ggplot2 package (Wickham et al., 2007) was used in data visualisation.

### 3. Results

#### 3.1. THg biomagnification

Biomagnification of THg was significant in all assessed lakes ( $p < 0.05$ ) (Table 1; Supplementary Table S4; Supplementary Fig. S1; S2). The TMS average  $\pm$  SD across all lakes was  $0.574 \pm 0.109$  (boreal:  $0.590 \pm 0.078$ , subarctic:  $0.561 \pm 0.130$ ) with a range of 0.315 to 0.848 (range: boreal: 0.483 to 0.717, subarctic: 0.315 to 0.848). The [THg] baseline average  $\pm$  SD across all lakes was  $-2.309 \pm 0.281$  (boreal:  $-2.449 \pm 0.294$ , subarctic:  $-2.192 \pm 0.212$ ) with a range of  $-3.014$  to  $-1.908$  (boreal:  $-3.014$  to  $-2.000$ , subarctic:  $-2.756$  to  $-1.908$ ). Subarctic TMS tended to be higher in oligotrophic and mesotrophic lakes than in eutrophic lakes, however, this trend was not observed in the boreal lakes (Supplementary Fig. S3; S4; S5).



**Fig. 2.** The first three principal components explaining most of the variation (71.1%) in the principal component analysis across the assessed landscape gradients. The arrow length and direction identify the importance of a variable for the PCs, and loadings are on the axes of each plot. Lake abbreviations are used (Table 1) with region-specific colour identified in the legend, and PC scores and loadings are found in Supplementary Tables S6, S7, and S8.

### 3.2. Principal component analysis and linear regressions

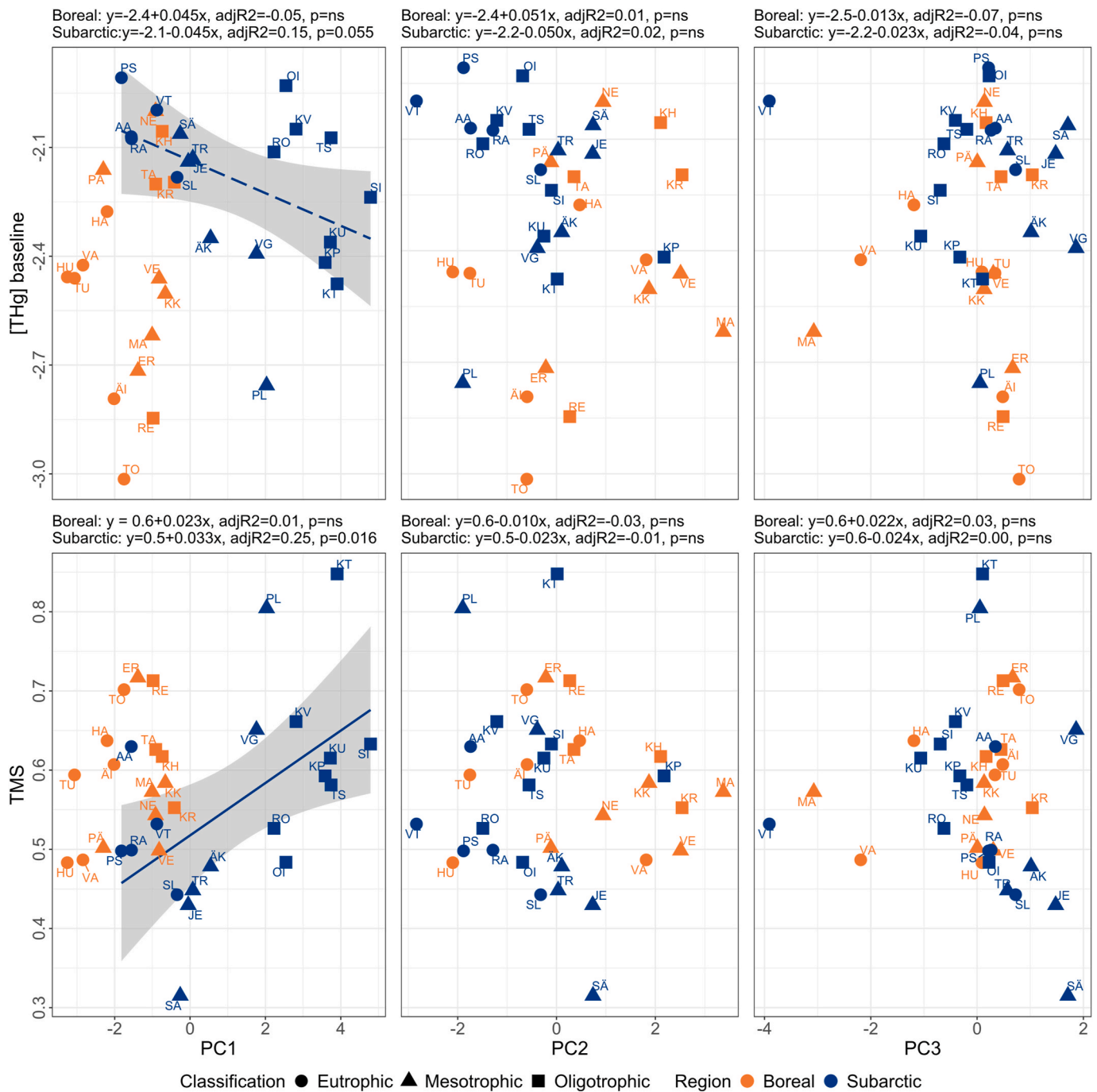
The first three principal components of the PCA (PC1–PC3) explained 71.1% of variance in the environmental, lake, and catchment attributes data (Fig. 2; Supplementary Table S7). The first principal component (PC1: climate–productivity) explained 41.1% of variation and was primarily comprised of climate and productivity variables (Supplementary Table S6; S7; S8). PC1 thus forms a climate–productivity gradient, with warmer and more productive lakes with a greater proportion of forest cover on the left and colder and less productive lakes with a lower proportion of forest cover on the right (Fig. 2). The second principal component (PC2: water bodies) explained 18.5% of variation and was primarily determined by lake volume and catchment variables (Supplementary Table S6; S7; S8). A gradient related to water bodies is formed by PC2, as lakes with lower volumes and lower proportions of their smaller catchments containing inland water and wetlands on the left, and lakes with larger volumes and a greater proportion of their larger catchments containing inland water and wetlands on the right (Fig. 2). The third principal component (PC3: catchment metrics) explained 11.5% of variation and was determined by

catchment variables (Supplementary Table S6; S7; S8). PC3 formed a gradient showing similar patterns in catchment area and inland waters in the lake catchment as PC2, although the primary variable in PC3, catchment-to-lake ratios, delineates lakes with smaller ratios on the top with larger ratios on the bottom (Fig. 2).

PC1 (climate–productivity) was the only principal component found to be significant with any region-specific TMS or [THg] baseline: in regression with subarctic TMSs ( $p < 0.05$ ) and near-significant in regression with subarctic [THg] baseline ( $p = 0.055$ ) (Fig. 3; Table 2; Supplementary Table S9).

### 3.3. Stepwise models

Stepwise multiple linear regression models for region-specific [THg] baseline and TMS were assessed for prediction using PC1, PC2, and PC3 (Table 3; Supplementary Table S10). Models for subarctic biomagnification variables performed better than those for boreal and relied heavily on PC1 for predictive power. PC2 and PC3 were not included in the final subarctic [THg] baseline model, which was near-significant (adjusted  $R^2 = 0.15$ ,  $p = 0.055$ ) and only included PC1 in a



**Fig. 3.** Linear regressions between principal components and biomagnification metrics (trophic magnification slope (TMS) and [THg] baseline). If significance or near-significance was detected, regression lines (significant: solid, near-significant: dashed) and 95% confidence intervals (grey shaded area) are shown. Lake abbreviations are used (Table 1). Shapes identify nutrient status of the lakes (Classification), and colour indicates region. Region-specific linear regression equations are given above each plot with adjusted R<sup>2</sup> values (<sub>adj</sub>R<sup>2</sup>) and p-values, where ns indicates no significance. Regressions details can be found in Table 2 and Supplementary Table S9.

negative direction. However, the model for boreal [THg] baseline was non-predictive, as backward selection excluded all variables (Table 3; Supplementary Table S10a). The boreal TMS model included PC1 in a positive direction, and PC2 and PC3 in a negative direction (adjusted R<sup>2</sup> = 0.35, p < 0.05). The subarctic TMS model performed the best out of all variables assessed (Table 3; Supplementary Table S10b), including PC1 in a positive direction and PC2 in a negative direction (adjusted R<sup>2</sup> = 0.42, p < 0.05). Findings from the TMS models in both regions demonstrate that while the climate–productivity (PC1) and lake volume and land cover (PC2) gradients were significant in the subarctic, the

boreal required all three PCs to enable predictive power and did not perform as well as the subarctic TMS model.

#### 4. Discussion

##### 4.1. Biomagnification

The PCA conducted in this study agrees with previous similar approaches conducted for Finnish subarctic lakes, where climate and productivity-, lake morphology-, and catchment-related principal

**Table 2**

Region-specific linear regression models describing the relationship between trophic magnification slope (TMS), [THg] baseline (Baseline), and principal components PC1 (climate–productivity), PC2 (water bodies), and PC3 (catchment metrics) are depicted for boreal and subarctic regions. The residual standard error (RSE), F-statistic with degrees of freedom ( $F_{(d.f.)}$ ), and  $p$ -value are depicted.

Region	Comparison	Intercept	Slope	adjR <sup>2</sup>	RSE	$F_{(d.f.)}$	$p$
Boreal	Baseline vs PC1	−2.378	0.045	−0.050	0.301	$F_{(1,14)} = 0.3$	0.602
	Baseline vs PC2	−2.484	0.051	0.009	0.292	$F_{(1,14)} = 1.1$	0.306
	Baseline vs PC3	−2.450	−0.013	−0.069	0.304	$F_{(1,14)} = 0.0$	0.860
	TMS vs PC1	0.626	0.023	0.010	0.773	$F_{(1,14)} = 1.2$	0.302
	TMS vs PC2	0.597	−0.010	−0.027	0.079	$F_{(1,14)} = 0.6$	0.448
	TMS vs PC3	0.592	0.022	0.032	0.076	$F_{(1,14)} = 1.5$	0.242
Subarctic	<b>Baseline vs PC1</b>	<b>−2.136</b>	<b>−0.045</b>	<b>0.152</b>	<b>0.197</b>	<b><math>F_{(1,17)} = 4.2</math></b>	<b>0.055</b>
	Baseline vs PC2	−2.224	−0.050	0.018	0.212	$F_{(1,17)} = 1.3$	0.264
	Baseline vs PC3	−2.194	−0.023	−0.039	0.218	$F_{(1,17)} = 0.3$	0.575
	<b>TMS vs PC1</b>	<b>0.518</b>	<b>0.033</b>	<b>0.254</b>	<b>0.112</b>	<b><math>F_{(1,17)} = 7.1</math></b>	<b>0.016</b>
	TMS vs PC2	0.548	−0.023	−0.014	0.130	$F_{(1,17)} = 0.8$	0.396
	TMS vs PC3	0.563	−0.024	0.001	0.129	$F_{(1,17)} = 1.0$	0.329

**Table 3**

Final stepwise multiple linear regression models using best direction to explain trophic magnification slope (TMS) and [THg] baseline using principal components PC1 (climate–productivity), PC2 (water bodies), and PC3 (catchment metrics) are depicted for boreal and subarctic regions. The Akaike Information Criterion (AIC), residual standard error (RSE), F-statistic with degrees of freedom ( $F_{(d.f.)}$ ), and  $p$ -value for final models are depicted.

Variable	Intercept	PC1	PC2	PC3	AIC	adjR <sup>2</sup>	RSE	$F_{(d.f.)}$	$p$
Boreal [THg] Baseline	−2.955							$F_{1,15} = 0.3$	
Var. Sig.	<0.001								
Std. Error	0.073								
95% CI L	−2.606								
95% CI U	−2.293								
<b>Boreal TMS</b>	<b>0.813</b>	<b>0.114</b>	<b>−0.068</b>	<b>−0.039</b>	<b>−85.30</b>	<b>0.353</b>	<b>0.062</b>	<b><math>F_{3,12} = 3.7</math></b>	<b>0.042</b>
Var. Sig.	0.001	0.012	0.016	0.146					
Std. Error	0.076	0.038	0.024	0.025					
95% CI L	0.648	0.030	−0.121	−0.095					
95% CI U	0.978	0.198	−0.015	0.016					
<b>Subarctic [THg] Baseline</b>	<b>−2.136</b>	<b>−0.045</b>			<b>−59.81</b>	<b>0.152</b>	<b>0.197</b>	<b><math>F_{1,17} = 4.2</math></b>	<b>0.055</b>
Var. Sig.	<0.001	0.055							
Std. Error	0.054	0.022							
95% CI L	−2.249	−0.091							
95% CI U	−2.023	0.001							
<b>Subarctic TMS</b>	<b>0.474</b>	<b>0.044</b>	<b>−0.052</b>		<b>−85.43</b>	<b>0.423</b>	<b>0.098</b>	<b><math>F_{2,16} = 7.6</math></b>	<b>0.005</b>
Var. Sig.	<0.001	0.002	0.027						
Std. Error	0.032	0.012	0.021						
95% CI L	0.405	0.019	−0.098						
95% CI U	0.542	0.068	−0.007						

components explained much of the variance in the environmental data (71.1%) (Ahoen et al., 2018; Kozak et al., 2021; Keva et al., 2021). Here, PC1 (climate–productivity) encompassed much of the predictive power of the PCA (41.1%) and show a positive relationship with TMS in the subarctic lakes as previously observed (Kozak et al., 2021), however, no relationships between boreal TMS and any individual PC were found, contrasting with the first prediction. A global study (Lavoie et al., 2013) identified a positive relationship between TMS and latitude in lakes. This was supported by this study in the Finnish subarctic lakes, although not in boreal lakes due to a narrower latitudinal range. A negative relationship with PC1 and [THg] baseline was observed in the subarctic lakes (Kozak et al., 2021), however, no relationships were found between boreal [THg] baseline and any individual PC, contrary to the second prediction. In general, TMS and [THg] baseline in both regions are similar to those measured in the Gulf of the St. Lawrence in Canada (Lavoie et al., 2010) and the Canadian Arctic (van der Velden et al., 2013).

#### 4.2. Climate and productivity variables

A negative climate–productivity gradient relationship with TMS was found in the subarctic (Kozak et al., 2021). This contrasts work

conducted on Canadian lakes, where TMS was positively related to lake productivity in some lake types (Kidd et al., 2012; Finley et al., 2016). In the boreal region, a combination of lake morphometrics, agricultural land use, and DOC has been previously used to model [THg] in perch (*Perca fluviatilis*) (Strandberg et al., 2016; Keva et al., 2022). This potentially explains the inclusion of PC1 in the boreal TMS stepwise model in the context of productivity. PC1 incorporates lake chemistry variables which are likely influenced by inputs from forested land cover, forestry operations, agriculture, and urban sources within the catchment.

The significance of PC1 in the subarctic, and in both regions' stepwise models, is especially interesting considering the stark contrast between the sparsely populated low impact areas in the northern subarctic compared to the heavily modified catchments in the southern subarctic and boreal regions. A strong climate–productivity gradient was not observed in the boreal region due to the generally warmer climate, higher population density, historical modification, and watercourse management across catchments (Virkkala and Toivonen, 1999; Korhonen et al., 2021).

Forestry operations have been linked to nutrient mobilisation into water bodies in Finland (Kortelainen and Saukkonen, 1998; Finér et al., 2021), and forest land cover and nutrients were prominent in the PC1 of

this study. Higher forest land cover enables greater opportunity for forestry operations, where intensive ditching of peatlands is perhaps the most significant landscape pressure in Finland with a high potential for mobilising Hg and nutrients stored in the catchment (Porvari et al., 2003; Lepistö et al., 2021). Ditched drainage networks to enhance forest growth have been previously identified as an obvious source of Hg and nutrients in these southern subarctic lakes (Kozak et al., 2021) and are also present in the boreal region (Korhonen et al., 2021; Härkönen et al., 2023). This directly adds Hg and MeHg to water bodies and may also increase productivity and methylation in lakes (Porvari et al., 2003; Finér et al., 2021). The methylation potential in ditches and other stagnant anoxic waters, such as those created by vehicular disturbance and stump holes caused by forestry operations, can be high, thereby enhancing MeHg availability in aquatic ecosystems (Porvari et al., 2003; Eklöf et al., 2016). Additionally, higher conifer representation and poor litter quality combined with other factors generating wet and cold soils decreases decomposition, suggesting that higher DOC concentrations are present in boreal soils (Kritzberg et al., 2020). DOC mobilisation from catchments is closely linked to Hg and MeHg supply, and photo-reduction of MeHg via demethylation is reduced in dark water lakes (Watras et al., 1998). These factors likely influence [THg] baseline, including nutrient and Hg source inputs with resulting methylation processes. Along the north–south gradient in the subarctic, southern catchments in the region are exposed to significantly higher run-off from peatland ditching than in the north (Kozak et al., 2021). This supports the parallel relationship in the [THg] baseline stepwise model in the subarctic, although other influences within the subarctic are likely also relevant due to the near significance of this model. The lacking predictive power in the boreal [THg] baseline stepwise model likely originates from diverse boreal catchment land use mosaics which include agricultural, forestry, and urban inputs to different extents.

The community shift from salmonid to percid, and finally to cyprinid dominance with broader ecosystem alterations towards a more productive regime along the PC1 climate–productivity gradient was previously documented in these subarctic lakes (Hayden et al., 2017) and along a productivity gradient from percids to cyprinids in boreal lakes (Persson et al., 1991; Olin et al., 2002). In these boreal lakes, a high representation of percids was noted in oligotrophic lakes, shifting to cyprinids with increasing productivity (Olin et al., 2002), likely due to higher temperatures and a generally weaker climate gradient than in the subarctic. In oligotrophic subarctic lakes with low biodiversity, energy transfer efficiency is high due to fewer trophic links, likely corresponding to Hg primarily derived from diet (Thomas et al., 2016). While increased biomass in productive lakes has been tied to THg biodilution and lower TMS in the subarctic (Kozak et al., 2021), this remains unclear in the assessed boreal region, potentially due to relatively higher biodiversity and trophic links within lakes.

#### 4.3. Lake size, elevation, and wetlands

In conjunction with climate and productivity, lake volume and inland water within catchments are determinant in a negative relationship with TMS across Finland. PC2 (water bodies) includes a lake size gradient, where the observed negative association in the stepwise models suggests higher TMS with less volume (smaller lakes) and fewer water bodies and wetlands within the catchment in both regions. Higher Hg content has been measured in fish from smaller lakes compared to larger ones in Canada (Evans et al., 2005; Finley et al., 2016) and in boreal lakes in Finland (Rask et al., 2021, 2024). Larger lake size has been linked to higher TMS, while the opposite relationship has been observed in [THg] baseline (Kidd et al., 2012). Both subarctic and boreal TMS stepwise models included PC2, indicating that lake morphology in conjunction with geographic position of the catchment influence biomagnification metrics across Finland. Previously assessed Canadian lakes tend to be larger with more diverse food webs than in Finland, and differences between these regions also include catchment

morphometrics and composition, lake physicochemical properties, and nutrient source (Kidd et al., 2012; Kozak et al., 2021). Larger lakes in this study also appear to have more diverse food webs, as boreal lakes contained a higher number of fish species on average (11) than subarctic lakes (7) and were generally larger in volume (mean  $\pm$  SD  $10^6$  m<sup>3</sup>, boreal:  $197.6 \pm 244.2$ , subarctic:  $51.7 \pm 164.9$ ). This could also be expected due to the region's postglacial history and current north–south climate–productivity gradient limiting species distribution (Tammi et al., 2003). More diverse food webs in the boreal region may indicate biodilution through larger biomass pools with greater aquatic diversity in larger lakes, which are additionally influenced by more intensive land use.

The inland water land cover in PC2 is tied to elevation, as size distribution of water bodies tends to decrease at higher elevation (Verpoorter et al., 2014). This is apparent along the Finnish latitudinal gradient as elevation increases northward. Additionally, less vegetation at higher altitudes not only reduces the amount of nutrients available for run-off, but also limits forestry activity above 67°N in the studied subarctic gradient (Zhang et al., 2013; Blackwell and Driscoll, 2015). This is especially relevant in contrast to the high DOC concentrations in boreal soils (Kritzberg et al., 2020). Most of the boreal catchments here are comprised of forest (>50%) (PC1), in contrast to subarctic catchments, which instead have a much higher percentage of wetlands (PC2). Peatland cover percentage in catchments has been linked to higher Hg content in perch in boreal lakes (Strandberg et al., 2016), and approximately 80% of all peatlands have been ditched in the boreal region where this study took place (Sallinen et al., 2019; Härkönen et al., 2023).

#### 4.4. Catchment size and lake size ratio

The boreal TMS stepwise model also included PC3, which is mainly comprised of the catchment-to-lake ratio, catchment area, and inland water proportion in the catchment. This PC is negatively associated with boreal TMS, suggesting that smaller catchment systems with fewer but larger water bodies are linked to higher TMS. As with the previously discussed lake size, catchment size and variability in the boreal is much higher (mean  $\pm$  SD km<sup>2</sup>,  $787.9 \pm 1256.8$ ) than in the subarctic ( $114.0 \pm 144.7$ ), while the catchment-to-lake ratio is lower (boreal:  $28.9 \pm 24.9$ , subarctic:  $42.6 \pm 63.7$ ). This trend suggests that biodilution may occur in these lakes through food webs formed by higher productivity due to greater inputs from catchments to relatively smaller lakes (Kozak et al., 2021; Aqdam et al., 2024). Food webs with higher productivity tend to be denser and more diverse, potentially indicating higher biodilution of Hg. However, growth rate is slower with longer life span, which is typical in low productivity lakes and colder climate, implying reduced growth dilution and increased Hg content in fish (Kozak, 2023). In addition, fishing pressure is generally higher in the boreal region, which may increase the growth rate of fish, thereby potentially increasing growth dilution and food web biodilution processes (Verta, 1990). For example, two boreal lakes in this study, Lake Tuusulanjärvi and Lake Vesijärvi, have been intensively fished and have undergone mass removals since the 1990's (Rask et al., 2020; Salonen et al., 2020). However, as PC3 encompassed only 11.5% of the variation within the PCA, one must take caution in such interpretations.

#### 4.5. Caveats

Studies on lake food webs must endeavour to capture a representative sample of all TLs to come to accurate conclusions. As seen here and in other efforts, collection of lower TLs, pelagic fish, and top predators is challenging, and future work must attempt to include a representative abundance and diversity of these groups (Jackson and Füreder, 2006; Gozlan et al., 2019). Additionally, measurement of the water Hg concentration would provide a valuable understanding of the background Hg in the system, which may prove important in biomagnification

studies. Assessing seasonality in these studies may also be necessary, as [THg] and bioaccumulation fluctuations in fish species throughout the seasons have been previously identified (Keva et al., 2017; Piro et al., 2023). Although biomagnification does not appear to fluctuate seasonally in a deep, humic boreal lake, further investigation should be conducted in different lake types (Piro et al., 2025). Potential interannual variability in Hg metrics and environmental data is apparent between and within regional sampling, which may have influenced results (Braaten et al., 2019; Thomas et al., 2020; AMAP, 2021). However, all data here falls within a 30-year period (WMO, 2017), and further assessment of such variability is not feasible without more precise yearly data on all variables assessed. While this study used bulk stable isotope analysis to assess TLs, compound-specific isotope analysis of  $\delta^{15}\text{N}$  in amino acids has shown potential in measuring more accurate TLs (Chikaraishi et al., 2009; Ohkouchi et al., 2017; Elliott et al., 2021; Piro et al., 2025). This method is, however, more costly and time intensive, drawing limitations when working with large datasets. Additionally, this study analysed [THg], and variability has been observed in the percentage of [MeHg] throughout the food web and between lakes. This percentage can range from 5 to 30% in lower TLs to 60–90% in the higher TLs, with the highest TLs exceeding 90% (May et al., 1987; Watras et al., 1998; Arcagni et al., 2018; Lescord et al., 2018). TMS measured using [MeHg] is typically steeper than those measured using [THg] due to a lower [MeHg]/[THg] ratio at lower TLs compared to higher TLs (Lavoie et al., 2013; van der Velden et al., 2013; Lescord et al., 2018; Moslemi-Aqdam et al., 2023).

#### 4.6. Implications for the future

Changes along the continuum of subarctic lakes signal a transformation of ecosystems and chemical compositions towards greater similarity with the boreal south. There is a growing probability that the mesotrophic and oligotrophic lakes along the subarctic continuum may follow this trend under the assumption of continuous land use intensification and climate change. As currently observed, northward expansions of southern fish species will likely continue (Hayden et al., 2017). Changing community composition likely implies alterations to Hg biomagnification within these systems through changing food web dynamics (Thomas et al., 2016), as observed in the southern subarctic study lakes. In the boreal region, ongoing transformative impacts on lakes through brownification and eutrophication are likely, as increasing temperatures and productivity appear to be continuing pressures. Findings here demonstrate a need for greater focus on boreal lakes to more specifically identify variables with the greatest influence on Hg biomagnification across different lake types. Additionally, most lakes in this study are  $>1\text{ km}^2$ , although most Finnish lakes are smaller. As high Hg levels in some small headwater boreal lakes in Finland have been identified (Rask et al., 2024), future investigations exploring landscape gradients, which include these smaller lakes, should be considered. Space-for-time methods, as used here, may be confounded by ongoing development of aquatic communities and notable differences in lake physicochemical characteristics (Jeppesen et al., 2014). While this method is valuable in providing an initial idea on potential trends in these regions, reassessing sites using long-term monitoring would be of significant value to confirm or refute these predictions. Increasing pressures on Finnish aquatic ecosystems demonstrate the need for improved methods and management to assess and mitigate impacts on freshwater ecosystems, including broader and more sustainable catchment planning (Marttila et al., 2020; Härkönen et al., 2023). Additionally, special consideration should be given to discerning nutrient and Hg inputs from forestry operations and other sources.

## 5. Conclusions

This study assessed regional patterns and differences in factors potentially influencing total mercury biomagnification in Finnish

subarctic and boreal lake food webs. Patterns of total mercury biomagnification along environmental gradients show differences between these regions. Subarctic trophic magnification slopes and total mercury baselines were correlated with a climate–productivity gradient, with higher trophic magnification slopes and lower total mercury baselines in the more pristine northern oligotrophic lakes decreasing and increasing, respectively, into more heavily impacted eutrophic southern lakes. The northern lakes also contained fewer fish species, whereas boreal lakes were more diverse. Boreal trophic magnification slopes incorporated three environmental gradients encompassing climate and productivity, water body, and catchment metrics in stepwise multiple linear regression models to gain explanatory power, while no predictive measures could be generated for boreal total mercury baseline. Generally higher fish diversity in boreal lakes increases trophic links and energy flows, which may suggest that biodilution is linked with nutrient status to a less extent than in subarctic lakes. Mercury dynamics in boreal lakes are likely influenced by the mosaic of land cover in these catchments, including forest, agriculture, and urban land use, which jointly affect biomagnification with catchment and lake morphology. Differences in biomagnification patterns of subarctic and boreal lakes along environmental gradients indicate a high complexity and variation of pressures across the Finnish landscape. Results suggest that ongoing climate change and intensive land use in subarctic lakes may lead to lower trophic magnification slopes and higher total mercury baselines in the future, however, such trends may not be evident in boreal lakes. Further time series of mercury biomagnification should be conducted in both subarctic and boreal lakes food webs to evaluate the long-term impacts of a changing climate and land use regime.

## CRediT authorship contribution statement

**Alexander J. Piro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Natalia Kozak:** Writing – review & editing, Software, Methodology, Data curation. **Ossi Keva:** Writing – review & editing, Methodology, Investigation, Data curation. **Emmi S. Eerola:** Writing – review & editing, Investigation, Data curation. **Katja Kulo:** Writing – review & editing. **Timo J. Ruokonen:** Writing – review & editing. **Jan Weckström:** Writing – review & editing, Resources. **Tommi Malinen:** Writing – review & editing, Investigation, Data curation. **Mikko Kiljunen:** Writing – review & editing. **Sami J. Taipale:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Kimmo K. Kahilainen:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

## Declaration of competing interest

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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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envres.2025.122352>.

## Data availability

Data will be made available on request.

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