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Cumulative effects of climate change and land use on the ecological status of Scandinavian lakes show contrasted interactions in different ecoregions: the role of pre-disturbance conditions in assessing ecological status

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A B S T R A C T

In this study, we used subfossil chironomids to assess temporal changes in lake ecological status over the last *ca.* 100 years in 30 lakes spread across different ecoregions in Sweden. By comparing Benthic Quality Index values and their temporal trends, we aimed to quantify the cumulative effects of climate change and land use on lakes and unravel how their effects may vary regionally. Results indicate that land use is the overarching driver of ecological changes in impacted lakes, in line with earlier studies showing that local pressures often suppress climate change effects on freshwaters. Furthermore, the known positive co-tolerance of chironomid species to temperature and eutrophication (e.g., cold stenotherm species also being indicators of oligotrophic condition, and conversely) was anticipated to induce antagonistic effects. However, the cumulative effects of climate change and land use differ across the landscape, being synergistic in the boreal forest ecoregion and antagonistic in the mixed forest ecoregion. We suggest that the pre-disturbance conditions (i.e., species composition and pressure sensitivities) play a key role in regulating the interactions between multiple pressures in freshwaters. Overall, this finding is encouraging as it implies that restoration of lakes that focuses on the most impactful pressure (e.g., nutrient loadings from agricultural fields and urban areas) remains a plausible restoration measure despite lake warming. Results also show that the net effect of climate change on the ecological status of the reference lakes varied regionally, being more pronounced in northern lakes due to the predominance of many cold water species which are more prone to disappear in response to small variations in temperature. As reference conditions are seldom revised, it is of fundamental importance to question whether the existing reference conditions are still applicable or need to be revised due to ongoing and future climate change.

1. Introduction

Aquatic ecosystems are increasingly affected by many environmental pressures, among which global changes such as climate change (e.g., altered temperature and precipitation) and eutrophication are often the main large-scale drivers of ecological changes in lakes (Jeppesen et al. 2010). As the rate of global change has drastically accelerated during the Anthropocene (Steffen et al. 2015), understanding the cumulative impacts of multiple pressures has gained attention from both ecosystem managers and scientists. Interactions among pressures can generate complex effects that reduce (i.e., antagonism) or compound (i.e., synergism) the sum of each pressure (Folt et al. 1999), and thus are inherently difficult to predict. Theoretical models that predict the cumulative impact of multiple pressures are often based on the co-tolerance concept defined by Vinebrooke et al. (2004). For exemple, models predict that if two pressures influence the same set of species in an assemblage (so-called positive co-tolerance), their cumulative impacts should be less than the sum of their individual effects (hereafter referred to as antagonistic effects). In other words, it is anticipated that exposure to one pressure combined with positive co-tolerance should reduce the impacts of the other pressure, thus resulting in antagonistic interactions between pressures. Earlier empirical studies reported the predominance of antagonistic effects in freshwater lakes (Côté et al. 2016; Jackson et al. 2016; Birk et al. 2020) and indicated that local pressures often suppress temperature effects on freshwaters (Morris et al. 2022). However, little is known regarding the impacts of multiple pressures on the ecological status of lakes, especially in Sweden.

Biological indices are often response-based approaches that use

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selected species, combinations of species, or whole communities to quantify the effects of pressures on aquatic ecosystems (e.g., Johnson et al. 1993). Considered relatively simple and reliable, these approaches are often used for evaluating the ecological status of aquatic ecosystems and are the cornerstone of many national monitoring programs (Poikane et al. 2016). The Benthic Quality Index (BQI; Widerholm 1980) is a frequently applied biological index for assessing the ecological status of lakes (Vitecek et al. 2021) and has been used in Swedish monitoring programs since the 1980s (Johnson and Goedkoop 2007). In brief, the BQI method uses Chironomidae larvae (Arthropoda; Diptera; Nematocera; non-biting midges with larvae living in superficial lake sediments), classified into 5 tolerance groups ranging from oligotrophic to eutrophic taxa, as indicator species. Although BQI was calibrated to quantify the effects of eutrophication on lakes (Wiederholm 1980), chironomids are also known to be strongly responsive to temperature fluctuations (Heiri et al. 2011; Stivrins et al. 2022). Accordingly, many chironomid taxa show a positive co-tolerance to eutrophication and climate change. On the one hand, chironomid taxa that indicate eutrophic conditions tend to be more resilient to changes in nutrient and oxygen conditions than the most sensitive species. For example, *Chironomus plumosus* typically tolerates a broader range of environmental conditions (e.g., oxygen and phosphorus concentrations) than *Heterotrissocladius marcidus* which persists under a specific and narrower range of conditions (Verbruggen et al. 2009; Luoto 2011). On the other hand, chironomid taxa indicating oligotrophic conditions are also cold water species, whereas eutrophic chironomid taxa tend to be warmer water taxa and can typically tolerate a wider range of temperatures (Heiri et al. 2011). In this context of positive co-tolerance, it is anticipated that land use and climate change should mutually reduce their individual impacts, thus leading to cumulative effects and antagonistic interactions.

Due to the scarcity of long-term monitoring data for most lakes, the effects of climate change and its combined effects with any other pressure on lake ecological status are difficult to quantify reliably. To circumvent this lack of monitoring data, one promising approach consists of using lake sediments as natural archives allowing us to assess lake ecological status by quantifying the degree to which present-day status deviates from historical conditions. By providing continuous biological records that cover a range of environmental conditions over a considerably larger time period than modern monitoring programs, the use of paleolimnological approach is key to disentangling to cumulative effects of climate change and eutrophication on lakes (Smol 2010). Specifically, chironomid larvae produce exoskeleton remains after each larval moulting that are usually well preserved in lake sediments (Walker 2001), allowing us to identify subfossil chironomids to the morphotype level. Subfossil chironomids can then be used to calculate the same biological indices as used in national monitoring programs, in particular the BQI; thus providing precious insights about past changes in lake ecological status (Ilyashuk et al. 2003). Furthermore, previous findings demonstrated that subfossil chironomids can serve as important bioindicator surrogates in aquatic ecosystems, as BQI calculated using subfossil data strongly correlate with the BQI values calculated from the contemporary communities (Jyväsjärvi et al. 2010).

This study aims to unravel the cumulative effects of climate change and land use on lakes and to determine regional variability across the landscape. We used subfossil chironomids identified from sediment cores covering the last *ca.* 100 years. These cores were retrieved from 30 lakes spread across different ecoregions in Sweden to assess temporal changes in lake ecological status and their response to climate change and land use. We tested the hypothesis that the known positive co-tolerance of chironomid species to temperature and eutrophication should lead to the prevalence of antagonistic effects. By producing novel results in the link between biological indicators, ecological status, and multiple pressures, we anticipate improving the monitoring of freshwaters under global change.

2. Material and methods

2.1. Site selection

Thirty small (area range 29–863 ha) and deep (maximum water depth range 15.4–47 m) lakes with relatively small catchments (ranging 1.3–57.3 km2) located across Sweden (56°45́N–64° 03́N) were studied. Lakes at southern latitudes belong to the mixed forest ecoregion, whereas lakes located at slightly higher latitudes and elevations (> 200 m a.s.L.) belong to the boreal forest ecoregion (Fig. 1). Lakes were grouped, hereafter defined as the pressure group, into reference (forested catchments considered largely unimpacted by agriculture and urban areas) and locally impacted lakes (Fig. 1) following a similar procedure developed by Johnson et al. (2018). Briefly, this classification accounts for the proportion of the catchment affected by clear-cut logging, agriculture, urban areas, as well as liming treatment (Table 1).

In June-July 2020, surface sediment cores were retrieved from the deepest point of the lakes using a gravity corer (9 cm in diameter: UWITEC). All sediment cores were then vertically split into two halves in the lab. One split core of each lake was continuously sliced into 1 cm thick samples and dated by ^{210}Pb, ^{137}Cs, ^{241}Am at Liverpool Universitýs Environmental Radioactivity Laboratory following Appleby et al. (1986)

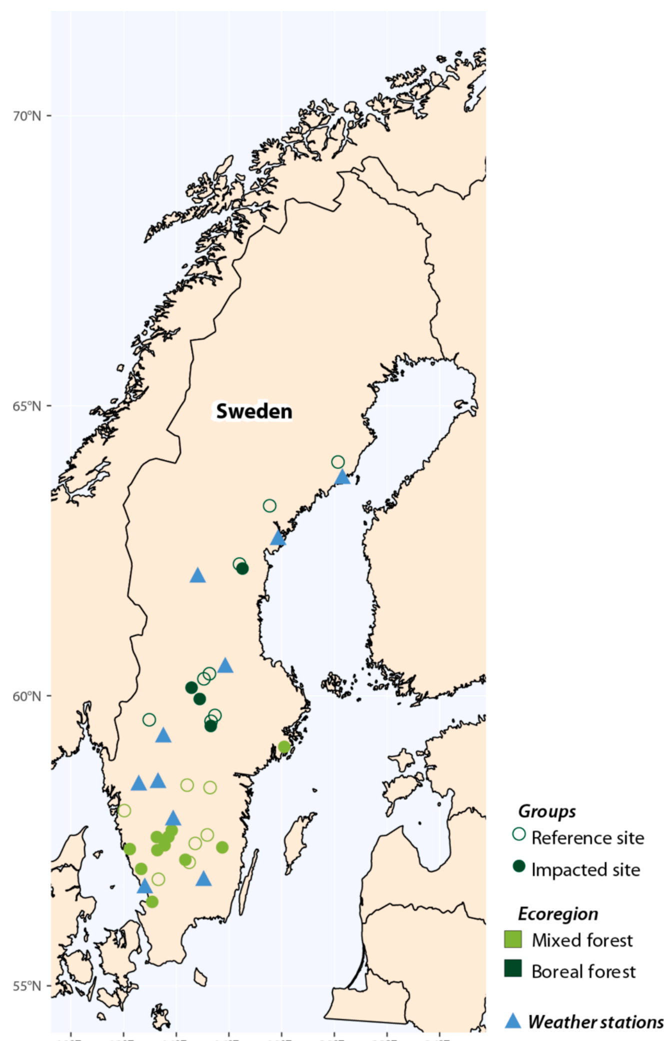

Fig. 1. Map showing the location of the study sites and weather stations. Open circles represent reference lakes and closed circles impacted sites whereas closed triangles show weather stations. Colours refer to the different mixed forest (light green) and boreal forest (dark green) ecoregions.

Table 1
Catchment characteristics and water chemistry variables. Study sites were grouped according to their ecoregion (boreal forest *vs.* mixed forest) and pressure types (locally impacted *vs.* reference lakes).

Catchment data		Lakes	Forestry – log(clear cut)				Urban (%)				Agriculture (%)			
Ecoregion	Group	*n*	Min	Max	Median	Mean	Min	Max	Median	Mean	Min	Max	Median	Mean
Boreal	Locally impacted	4	0.05	0.06	0.06	0.06	0.01	0.05	0.03	0.03	0.00	0.22	0.10	0.10
Boreal	Reference	8	0.00	0.09	0.04	0.04	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00
Mixed	Locally impacted	11	0.00	0.05	0.03	0.03	0.00	0.50	0.00	0.05	0.01	0.14	0.07	0.07
Mixed	Reference	7	0.03	0.05	0.04	0.04	0.00	0.03	0.00	0.00	0.00	0.15	0.02	0.04
Water data		**Liming**	**Absorbance 420 nm**				**Total Phosphorus ($\mu g.L^{-1}$)**				**Bottom oxygen concentration**			
Ecoregion	**Group**	***n***	**Min**	**Max**	**Median**	**Mean**	**Min**	**Max**	**Median**	**Mean**	**Min**	**Max**	**Median**	**Mean**
Boreal	Locally impacted	1	0.1	0.1	0.1	0.1	7.7	26.0	12.4	14.6	0.2	8.8	6.0	5.3
Boreal	Reference	2	0.0	0.3	0.1	0.1	2.5	8.8	6.2	6.1	0.0	9.9	6.7	6.2
Mixed	Locally impacted	5	0.0	0.5	0.1	0.2	3.6	37.8	7.0	8.7	1.1	6.4	3.6	3.5
Mixed	Reference	3	0.0	0.2	0.1	0.1	4.0	16.0	8.1	8.3	4.6	11.3	7.7	7.9

and Appleby et al. (1992). Dates were calculated using the Constant Rate of Supply model (Appleby and Oldfield 1978, Appleby 2002). Using the other half of the split core, the uppermost 1 cm of each sediment core was collected and represented present-day conditions (hereafter TOP samples). Using the age-depth models of each core, another 1 cm-thick sample was taken between 150 and 70 years ago in each sediment core (i.e., core depths vary depending on sedimentation rates) to represent historical conditions (called BOTTOM samples). No significant difference was found in the ages of BOTTOM samples between each pressure group and ecoregion (ESM. 1).

2.2. Climate change data

Long-term meteorological data was downloaded from the Swedish Meteorological and Hydrological Institute database (https://www.smhi.se), and weather stations were selected based on data availability (covering the 1895–2020 period) and distance to the study sites (with Halmstad, Karlstad, Skara, Vänersborg, Växjö and Jönköping stations representing the mixed forest ecoregion, and Umeå, Sveg, Falun, and Härnosand stations the boreal forest ecoregion; Fig. 1). Monthly average temperatures were then used to calculate the mean annual temperature for the 1895–1905 period (characterizing climate for the BOTTOM samples) and the 2015–2020 period (characterizing climate for the TOP samples), and differences were calculated to quantify temperature change over the period covered by the TOP and BOTTOM samples.

2.3. Chironomid analysis

Chironomid head capsules were hand-sorted and identified from each sample of wet sediment (*ca.* 15 g WW) following Walker (2001). Briefly, samples were successively rinsed with NaOH (10 %) solutions and sieved through a 100-µm mesh sieve. Chironomid remains were then hand-sorted from the sieving residue under a stereomicroscope and mounted in an aqueous agent on microscope slides. Chironomid assemblage composition was identified to the morphotype level (or the finest taxonomic unit) under a microscope using Brooks et al. (2007) and Rieradevall and Brooks (2011). We then calculated the Benthic Quality Index (Wiederholm 1980; Johnson and Goedkoop 2007) which classifies 12 indicator taxa into 5 tolerance groups with the highest weights assigned to indicators of oligotrophy and the lowest weights assigned to highly oxygen-tolerant species. The BQI is calculated as the abundance-weighted average of 12 indicator taxa scores (see below) and has values ranging between 0 (none of the 12 taxa recorded) and 5.

$$BQI = \sum_{i=0}^{12} \frac{(ki \times ni)}{N}$$

In which *i* represents each indicator taxon; k*i is* the weight of each indicator taxon reflecting its eutrophy affinity (Table 2); n*i* is the abundance of the indicator taxon *i*, and N is the sum of n*i*.

Table 2
Chironomid indicator taxa (i) and their corresponding coefficient (ki) reflecting their tolerance to eutrophication used to calculate the modified Benthic Quality Index (Wiederholm 1980; Johnson and Goedkoop 2007).

Indicator species (*i*)	*ki*
Chironomus plumosus-type	1
Chironomus anthracinus-type	2
Sergentia coracina	3
Stictochironomus sp.	3
Tanytarsus sp.	3
Micropsectra sp.	4
Paracladopelma sp.	4
Heterotanytarsus apicalis	4
Heterotrissocladius grimshawi	4
Heterotrissocladius marcidus	4
Heterotrissocladius maeaeri	4
Heterotrissocladius subpilosus	5

Furthermore, we collected sediment cores in another 10 small lakes located in Southern Sweden, analysed subfossil chironomid assemblages from the uppermost 1 cm of each sediment core, and calculated BQI as described above. Contemporary BQI data were retrieved from the Swedish National Monitoring Program database (https://miljodata.slu.se/mvm/) for all sites. When BQI data were available, datasets were then combined (with a total of 38 lakes), and we tested the extent to which the BQI calculated using subfossil chironomids correlated with contemporary measures of BQI.

2.4. Data analysis

Non-parametric Kruskal-Wallis tests were used to test the significance of temporal changes in BQI values for each pressure group and ecoregion. However, because it is challenging to obtain reliable *p*-values in such complex and strongly unbalanced experimental designs, *p*-values should be treated with caution. To quantify the net effects of climate change on lake ecological status and to test if these effects differed regionally, we calculated the mean of the differences between the BQI values of the TOP and BOTTOM samples of reference lakes in each ecoregion (Fig. 2A). The land use effects were estimated by calculating the difference between the average BQI values of the TOP samples of impacted and reference lakes in each ecoregion. Finally, to quantify the cumulative effects of climate change and land use on lake ecological status and to determine if these effects differed across the landscape, we calculated the mean of the differences between the BQI values of the TOP and BOTTOM samples of locally impacted lakes in each ecoregion (Fig. 2A). To identify potential non-additive interactions between pressures, we compared the sum of the impacts of the individual

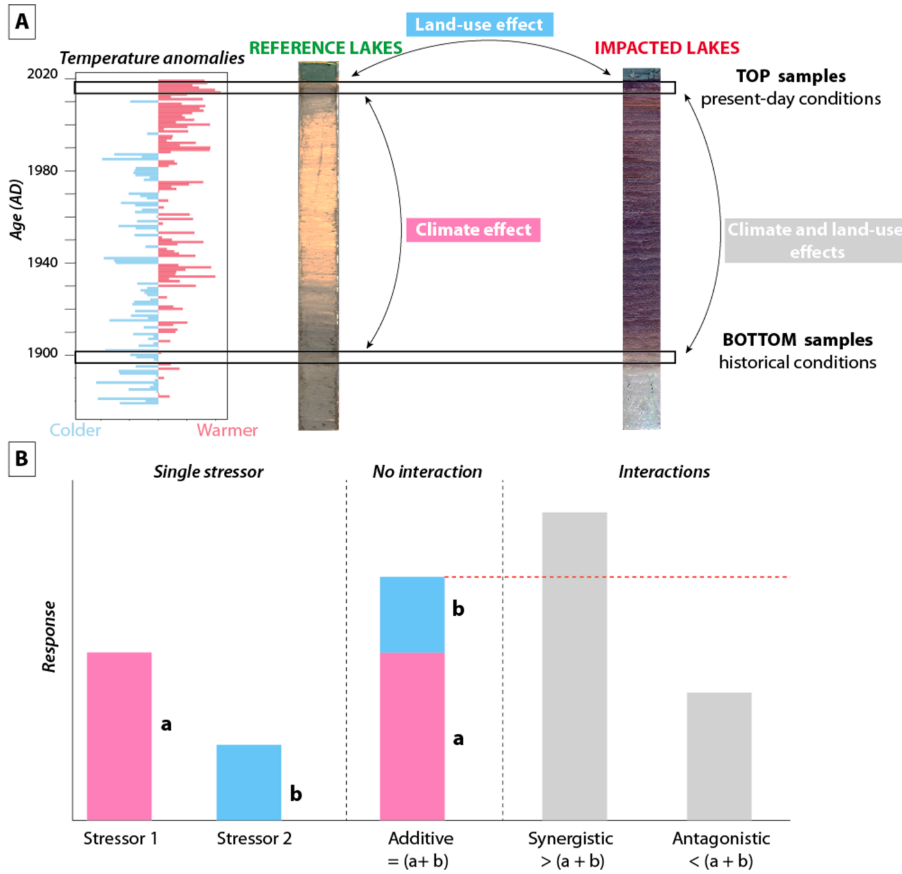

Fig. 2. (A) Conceptual view of the sampling strategy consisting of comparing present-day (TOP sample) and historical (BOTTOM sample) conditions between reference and locally impacted lakes in different ecoregions to quantify the net effects of climate change and land use and their combined effects. (B) Schematic view of responses to two pressures when they occur: separately (pressure 1, pressure 2), together with no interaction (additive), or together and with interaction (synergistic and antagonistic). The dotted line represents thresholds of non-additive interactions. Modified from Folt et al. (1999).

pressures (i.e., hypothetical additive effect) to their observed cumulative effects on BQI values (Fig. 2B). If the observed combined effect was larger than their hypothetical sum, interactions between pressures were defined as synergistic, and conversely, if the combined effects were smaller, interactions were defined as antagonistic. All statistical analyses and plots were performed using the R 4.4.0 software (R Core Team 2024).

3. Results

Temporal changes in mean annual air temperature revealed increases up to 2.4 °C between the 1895–1905 and 2015–2020 periods, and temperature increases were slightly higher in the boreal forest ecoregion (2.3 ± 0.1 °C) than in the mixed forest ecoregion (1.9 ± 0.3 °C; Fig. 3).

Results showed that subfossil BQI values correlated strongly with the BQI values calculated from the contemporary chironomid data (ESM 2.A), thus confirming that subfossil chironomids can serve as important bioindicator surrogates in Swedish lakes. In total, 3697 head capsules were identified to the morphotype level. No major differences in BQI calculated for BOTTOM samples were observed between pressure group (impacted *vs.* reference lakes) or ecoregion (e.g., reference and impacted lakes had similar BQI_bottom values in the mixed forest ecoregion; Fig. 4A). However, BQI_bottom values were higher in lakes in the boreal forest ecoregion than in the mixed forest ecoregion (Fig. 4A). When calculated using subfossil chironomid data from TOP samples, BQI_top values did not differ with pressure group in the different ecoregions (e.g., impacted lakes had similar BQI_top in both mixed and boreal forest ecoregions; Fig. 4B). However, BQI_top values of impacted lakes were generally lower than reference lakes in both ecoregions (e.g., impacted lakes had lower BQI_top than reference ones in the boreal forest ecoregion, Fig. 4B).

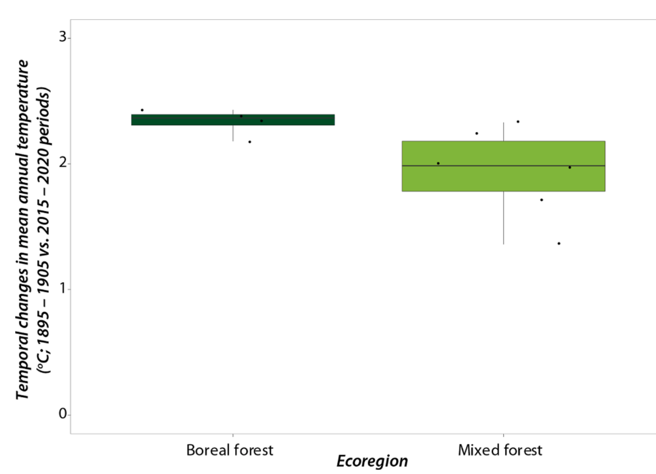

Fig. 3. Temporal changes in mean annual temperature between the 1895–1905 and 2015–2020 periods (Swedish Meteorological and Hydrological Institute; https://smhi.se). Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions.

Overall, BQI_top values were generally lower than BQI_bottom values, resulting in negative BQI_delta values (with BQI_delta = BQI_top − BQI_bottom) observed in both pressure groups and ecoregions (Fig. 5).

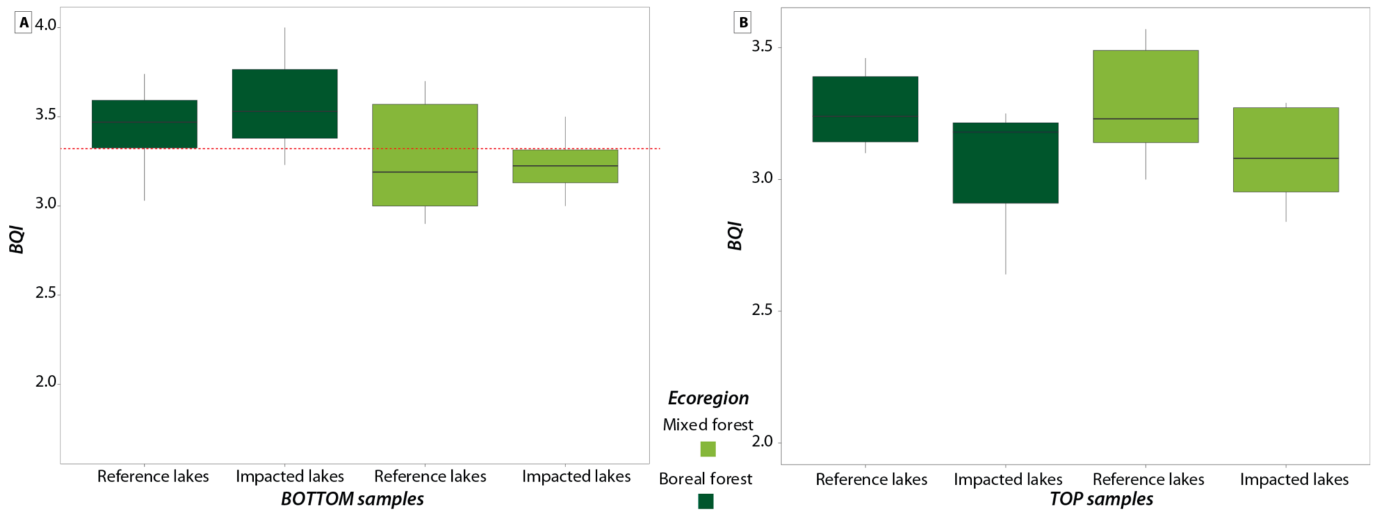

Fig. 4. Boxplots showing the Benthic Quality Index (BQI) values for BOTTOM (**A**) and TOP (**B**) samples of the different lake groups (reference *vs.* impacted) in the two ecoregions. Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions. In panel A, a dotted line has been drawn to better visualize discrepancies between ecoregions.

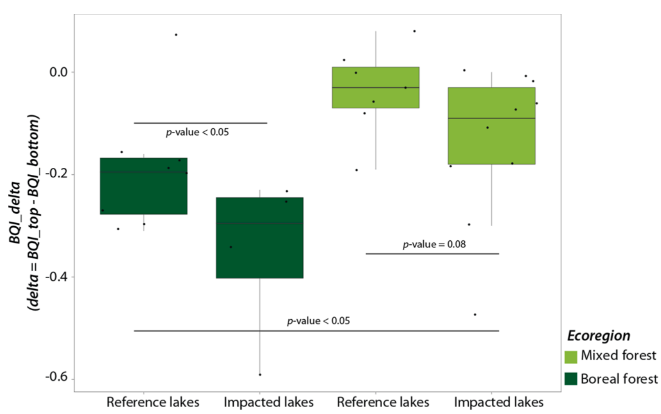

Fig. 5. Boxplots showing temporal changes in Benthic Quality Index (BQI; BQI_delta = BQI_top–BQI_bottom) for the different lake groups (reference *vs.* impacted) in the two ecoregions. Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions. *P*-values from Kruskal-Wallis tests are shown for each paired comparison.

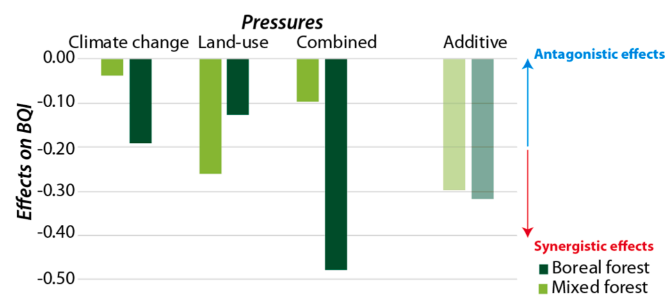

Fig. 6. Changes in Benthic Quality Index (BQI) in response to climate change and land use when they occur separately or combined. In each ecoregion, the effects of each pressure taken separately were summed to calculate a hypothetical additive effect and compared to the observed cumulative effects of the two pressures. If the observed combined effect is larger than their hypothetical sum, interactions between pressures are defined as synergistic, and conversely, if the combined effects are smaller, interactions are defined as antagonistic. Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions.

Furthermore, larger BQI_delta values were reported for impacted lakes within each ecoregion (Kruskal-Wallis tests, with p-value < 0.05 and p-value $= 0.08$ for mixed forest and boreal forest ecoregions, respectively). In most cases, larger BQI_delta values were also observed for lakes located in the boreal forest ecoregion, regardless of their pressure groups (Kruskal-Wallis test, p-value < 0.05, Fig. 5). Interestingly, temporal changes in BQI reported in reference lakes of the boreal forest ecoregion are much larger than those observed for impacted lakes in the mixed forest ecoregion.

The individual effect of each pressure was calculated and their sums were compared to their observed cumulative effects on BQI values to identify potential non-additive interactions between pressures. In the mixed forest ecoregion, results showed that the individual effect of climate change on BQI values was much lower than the land use effect, and the cumulative effects of climate change and land use were lower than their hypothetical additive effects (Fig. 6), indicating antagonistic interactions between climate change and land use. In contrast, the results of boreal forest lakes showed a lower individual effect of land use on BQI values than climate change, whereas the cumulative effects of climate change and land use were higher than their hypothetical additive effects (Fig. 6), indicating synergistic interactions between climate change and land use.

4. Discussion

We compared BQI values and their temporal trends to quantify the cumulative effects of climate change and land use on lakes and unravel how these two pressures may interact to affect BQI values across the landscape. Chironomid species are known to show positive co-tolerance to temperature and eutrophication (e.g., cold stenotherm species also being indicators of oligotrophic conditions, and conversely). We, therefore, expected to find antagonistic effects of climate change and land use, similar to studies that reported the predominance of antagonistic effects for other taxonomic groups in freshwater lakes (Coté et al. 2016; Jackson et al. 2016; Birk et al. 2020; Morris et al. 2022).

In our study, climate change and land use showed, however, contrasted interactions across the landscape, with antagonistic effects observed in the mixed forest ecoregion and synergistic effects observed in the boreal ecoregion. We hypothesize that the observed contrasted interactions between pressures can be explained by differences in historical chironomid assemblage composition and potential asymmetric relationships between the sensitivities to the studied pressures (Fig. 7). Chironomid assemblages of lakes from the mixed forest ecoregion are

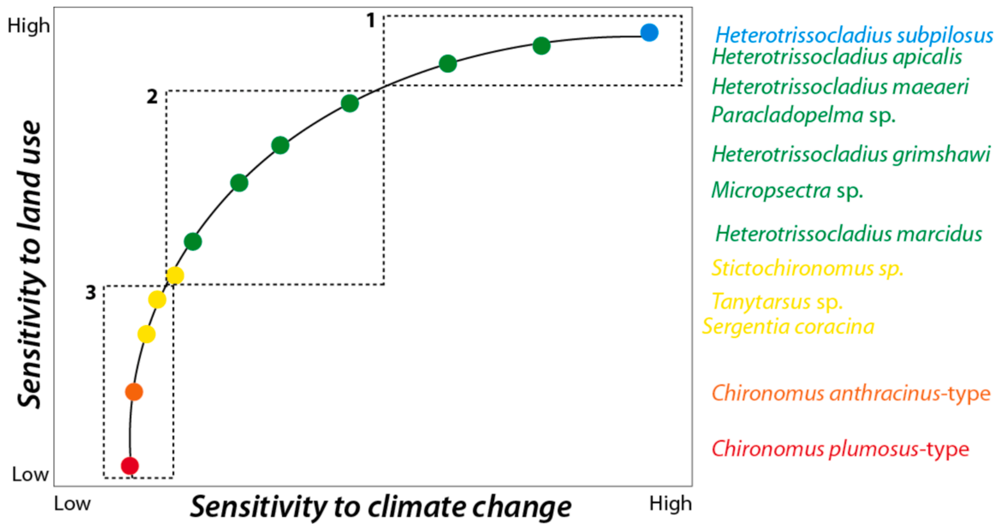

Fig. 7. Hypothetical sensitivities to climate change and land use of the indicator taxa used in the Benthic Quality Index. The colours of the indicator taxa listed on the right side reflect their scores in the BQI (see methods). Lakes predominated by species belonging to box 1 should exhibit synergistic interactions between climate change and land use, whereas lakes predominated by species from boxes 2 and 3 should show antagonistic effects.

mainly composed of more warm water and thermo-tolerant taxa (Fig. 7; zones 2 and 3). In such ecosystems, climate change and land use impact the same set of taxa within the assemblage, leading to typical antagonistic effects. In contrast, chironomid assemblages of boreal lakes are historically predominated by cold stenotherm species (Fig. 7; zones 1 and 2), which are more prone to decrease in abundance or disappear with increasing temperatures. As a result, land use mainly affects the remaining warmer water species which are only marginally affected by changes in climate conditions. Climate change and land use likely impact distinct groups of chironomid species within the assemblage leading to higher taxonomic turnover and synergistic effects. The historical conditions of ecosystems (i.e., nature and ecology of pre-disturbance species) appear to play a key role in determining the interactions between multiple pressures.

The ecological status of lakes assessed using chironomid assemblages appears strongly responsive to land use, with consistently lower BQI values reported for impacted lakes (similarly to Kansanen et al. 1990; Hynynen et al. 2004; Jyväsjärvi et al. 2010). Our study confirms that BQI is a reliable indicator of the ecological status in Scandinavian lakes (see also Poikane et al. 2016), as present-day BQI values were similar in lakes similarly affected by land use (see pressure criteria in Table 1). Results also suggest that agricultural land use is the overwhelming driver of change affecting in-lake water conditions (often characterized by low bottom water oxygenation and high nutrient concentrations, Akinnawo 2023), ultimately driving chironomid community assembly and associated decreases in BQI. Overall, these findings are consistent with earlier studies reporting that local pressures often suppress the effects of climate change on lakes (Nõges et al. 2016; Morris et al. 2022). Our findings are, therefore, encouraging as they indicate that management actions should focus on mitigating the effects of local pressures (e.g., nutrient loadings from agricultural fields and urban areas), as these interventions should lead to substantial improvements in lake ecological status (see also Brown et al. 2013). In case of synergistic effects between temperature change and land use, this management strategy should be particularly efficient (i.e., leading to an even larger recovery than expected), but the presence of many cold stenotherm species combined with more pronounced changes in climate in the boreal regions, makes defining appropriate targets to gauge restoration challenging (see also Free et al. 2024). Furthermore, when interactions are antagonistic, mitigation of local pressures may result in a greater impact of increasing temperatures on lakes and their communities.

Future research should try to better incorporate the ecology of species of pre-disturbance communities (specifically their differential sensitivity to the pressures) when aiming to quantify the effects of multiple pressures on freshwaters (e.g., Johnson et al. 2017; Jonsons et al. 2018), as species within each community often have asymmetric affinities and sensitivities to the targeted pressures. Our study also assumes a strictly synchronous scenario (i.e., climate change and land use pressures overlapping) and similar intensities in both ecoregions, which is likely an oversimplification of the dynamic that prevails during the Anthropocene. For example, higher magnitudes and seasonal variability of temperature changes are expected at higher latitudes, and the order and timing of exposures may also have changed over time (e.g., land use intensification happening earlier and later in different ecoregions/catchments; see also MacLennan and Vinebrooke (2021) for a theoretical framework about ecology memory). As paleolimnological approaches can provide a continuous record of pressure history and their impacts on aquatic communities, future research should therefore better integrate temporal dynamics of pressures and their associated ecological responses, thus allowing us to identify the mechanisms underpinning lake responses to multiple pressures. Overall, these findings provide novel insights about the responses of lakes and their ecological status to multiple pressures, therefore, contributing to improving the monitoring of freshwater lakes under global change.

Finally, we also reported a strong net effect of climate change on the ecological status of lakes, reflected by large decreases in BQI in reference lakes and between-ecoregion differences. Overall, lakes in the boreal forest ecoregion (i.e., situated at higher latitudes and elevations) had higher historical BQI values as assemblages are typically composed of taxa found in colder environments and also have the highest scores in the BQI (Wiederholm 1980; Johnson and Goedkoop 2007). As temperature increased between early 1900 to present-day (Schimanke et al. 2022), periods represented by BOTTOM and TOP samples, respectively, chironomid assemblages of boreal reference lakes typically lost their cold water taxa, resulting in the relatively large climate-induced decreases in BQI values observed in these boreal lakes. However, whereas the taxa with the highest scores are strictly cold water species (e.g., *Heterotrissocladius subpilosus*; Luoto 2009; Heiri et al. 2011), chironomids with lower scores are more warm water taxa that tolerate a wider range of environmental conditions such as temperature and other stressors (e.g., *Chironomus anthracinus*-type; Stivrins et al. 2021). As a result, reference lakes in the southern mixed forest ecoregion were often predominated by more temperature-tolerant chironomids and, as such, were less impacted by climate change in the last *ca.* 100 years. Finally, climate change is expected to be non-uniform across the landscape (i.e., typically exacerbated at higher latitudes and elevations; Schimanke et al. 2022; Lind et al. 2023) which could further reinforce the observed patterns, with higher amplitudes of climate change impacting cold stenotherm communities of northernmost aquatic ecosystems.

Because the ecological status of lakes is usually assessed as the deviation between present-day status and reference conditions, the appropriateness of the reference conditions is of paramount importance to providing reliable ecological status and defining realistic restoration targets. However, reference conditions are seldom revised, thus excluding the potential effects of climate change on lakes and their communities. The climatic conditions that prevailed when the reference conditions were established decades ago, often differ from conditions that occur when the ecological status is being assessed. As we demonstrated that climate change can exert a significant influence on aquatic communities (so-called shifting baselines), using reference conditions established decades ago in monitoring and/or restoration programs could be inappropriate due to experienced warming, thus potentially leading to misinformed management decisions (see also Free et al. 2024). It is, therefore, of fundamental importance to question whether the existing reference conditions are still applicable in the context of climate change.

5. Conclusion

Our study contributes to understanding the combined effects of multiple pressures on lakes. We found that climate change and land use showed contrasted interactions across the landscape, discrepancies that could be explained by differences in historical chironomid assemblage composition and sensitivities to pressures. These findings indicate that understanding co-tolerance of species to different pressures plays a pivotal role when predicting the combined effects of multiple pressures on freshwater lakes. Results also confirmed that land use often suppresses temperature effects on Swedish lakes. This finding is encouraging as it implies that restoration of lakes that focuses on the most impactful pressure (e.g., nutrient loadings from agricultural fields and urban areas) remains a plausible restoration measure despite lake warming.

Results also show that the net effect of climate change on the ecological status of the studied lakes varied regionally, being more pronounced in northern lakes. As climate change is forecasted to be a key driver of environmental and biological changes shortly, our study stresses the urgent need to better understand and quantify the net effects of climate change on lakes and especially on the biological metrics used to assess their ecological status (i.e., shifting baselines). As reference conditions are often seldom revised, thus excluding the potential effects of climate change on lakes and their communities, it is of fundamental importance to question whether the existing reference conditions are still applicable or need to be revised due to ongoing and future climate change. Otherwise, we risk over-correcting a pressure like land-use change (and wasting resources) to try and reach a reference condition that is based on a different climate, and associated biological metrics, that are not relevant to current conditions.

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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.ecolind.2024.112879.

Data availability

Data will be made available on request.

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