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Research article

# Comparing ecological classifications of freshwater lakes based on reference conditions for benthic invertebrates derived from spatial analogues and paleolimnological approaches

Simon Belle[a,*], Richard K. Johnson[a], Gary Free[b], Jens Folster[a], Brian Huser[a], Sandra Mingarelli[b]

[a] Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden
[b] European Commission, Joint Research Centre (JRC), Ispra, Italy

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ABSTRACT

A critical step in lake ecological assessment is establishing appropriate reference conditions, which enable the measurement of differences between the current status and these baseline conditions. To achieve this, spatial analogues and paleolimnology are two common approaches, each with strengths and limitations, but few studies have directly compared their performance. This study compares the ecological classification of Swedish lakes based on benthic invertebrate reference conditions derived from these two approaches. Overall, while both approaches yielded similar classifications, the key distinction lies in the emphasis on site-specific (sediment-based paleolimnology) versus type-specific (spatial analogues) conditions. As such, sediment-based estimates are generally more accurate and better suited to establish lake-specific baseline conditions. However, given the ongoing impacts of climate change, restoring lakes to their historical states may no longer be feasible due to climate-induced "shifting baselines". Spatial methods, by contrast, offer a more accurate representation of current conditions by accounting for climate-induced changes and by isolating human pressures. Nonetheless, the challenge of addressing human impacts, often presumed to be negligible, on reference lakes used in the spatial approaches remains unresolved. Our findings highlight the challenges of shifting ecological baselines, where climate change and anthropogenic pressures increasingly overlap. Consequently, there is a risk that current frameworks misclassify lake conditions by attributing climate-induced changes to anthropogenic pressures or overlooking them entirely. We recommend integrating paleolimnological records with current monitoring to improve ecological classification and better account for climate-driven changes in lake ecosystems, and improve assessment tools.

## 1. Introduction

The ecological status of freshwater ecosystems is a key component of water resource management policies, such as the Water Framework Directive of the European Union (WFD Directive, 2000), and is typically assessed by determining the degree of deviation between current status and reference conditions (Wallin and Wiederholm, 2003; Stoddard et al., 2006). These reference conditions represent the natural structure and function of aquatic ecosystems in the absence of significant anthropogenic stressors (Hawkins et al., 2010). However, numerous definitions have been proposed, differing slightly in terms of the acceptable levels of human impacts on ecosystems (Hughes, 1995; Reynoldson et al., 1997; Stoddard et al., 2006). A widely used method to quantify deviation from reference conditions is the use of the Ecological Quality Ratio (EQR), representing the ratio between the observed status and a reference value. An EQR close to 1 indicates that the current conditions are very similar to the reference state, while lower values reflect increasing levels of ecological degradation (van de Bund and Solimini, 2007; Poikane et al., 2015). A critical aspect of ecological assessment relies, therefore, on the establishment of appropriate reference conditions. Without accurate reference conditions, assessments may be misleading, potentially resulting in inappropriate management decisions, and ultimately a misuse of time and resources available (Koski et al., 2020).

Establishing reference conditions involves identifying undisturbed or

* Corresponding author.
*E-mail address:* simon.belle@slu.se (S. Belle).

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minimally impacted sites to define baseline conditions (Nijboer et al., 2004), and spatial analogues and paleolimnological approaches are among the most common approaches (Wallin and Wiederholm, 2003). Spatial analogues involve comparing a study site with other similar lakes that are deemed to be minimally impacted by human activities. These lakes, typically selected based on environmental characteristics like regional climate, land-use, morphology, and water chemistry, serve as reference sites (Chaves et al., 2006; Herlihy et al., 2013). For example, a "minimally impacted" lake with similar physical and chemical properties to a disturbed lake may serve as a spatial analogue. The primary advantage of this method is that it is relatively quick and easy to apply, especially when suitable reference lakes are available. However, its disadvantage lies in the assumption that all reference lakes are truly unaffected by human disturbances, which may not always be the case, and numerous lake types lack or have too few reference sites (Poikane et al., 2010), potentially leading to the establishment of inaccurate reference conditions (Pardo et al., 2012). In practice, reference sites are selected based on several criteria aimed at identifying "minimally disturbed" conditions (e.g., less than 10 % agriculture in the catchment area in the Swedish monitoring program; Johnson and Goedkoop, 2007). However, this approach inherently accepts a certain level of human impact within the establishment of reference conditions. Furthermore, establishing reference values for spatial analogues is usually only performed at a given time and under specific climatic conditions that prevailed during calibration; therefore, the established reference conditions may not be applicable under different environmental conditions. Paleolimnological approaches, by contrast, involve studying lake sediment cores to reconstruct past ecological conditions (Battarbee and Bennion, 2011) and use past empirical data to infer the reference conditions of a lake before significant disturbance has occurred, similar to the use of historical monitoring or observational data (Muxika et al., 2007). Analyzing different proxies preserved in sediments allows us to assess long-term changes in lake ecosystems, providing unique and detailed insights into ecological conditions in the absence of impactful local activities, thus defining site-specific reference conditions (Leira et al., 2006; Bennion et al., 2011). The key advantage of paleolimnology is that it offers a direct historical record of ecological status, largely exceeding the temporal range of possible observations given by monitoring data. However, it may often consider past environmental and climatic conditions that are likely not relevant to present-day ecosystems (Hiers et al., 2012). In this context, indicators of ecological quality, such as taxonomic composition, are likely to have shifted, a phenomenon often referred to as the "shifting baseline" (Free et al., 2024), and using their historical state as a reference value may no longer be appropriate. Each of these approaches has, therefore, its advantages and limitations, and in practice, they are often used in combination (Moss et al., 2003; Poikane et al., 2010) to provide a more comprehensive establishment of reference conditions in lakes, but few studies have compared the performance and similarities of these different approaches (Norberg et al., 2008; Johnson et al., 2010; Soranno et al., 2011).

Benthic invertebrates are among the most widely used biological indicators for assessing ecological status in lakes, due to their sensitivity to environmental changes and their important role in aquatic food webs (Poikane et al., 2016; Vitecek et al., 2021). Among these, the larvae of Chironomidae (Arthropoda; Diptera) are especially valuable, fulfilling many of the key criteria for an effective indicator group (Rossaro et al., 2007), and are used in national monitoring programs with the Benthic Quality Index in lakes of Northern Europe (BQI; Wiederholm, 1980). Among others, chironomid larvae are known for their well-documented taxonomic composition across various environmental conditions, including oxygen conditions (Brundin, 1949) and trophic status (Saether, 1979). They respond rapidly to environmental changes and have a relatively long period of larval development, particularly in the profundal zones of lakes, enabling them to integrate long-term ecological changes effectively. Another key advantage of chironomids is that their head capsules are morphologically robust and well-preserved in lake sediments, allowing them to be identified in paleolimnological studies (Walker, 2001). The preservation of subfossil chironomids in lake sediments makes them especially useful for reconstructing past environmental conditions, offering insights into long-term ecological changes that may not be captured by recent monitoring data. Subfossil chironomid assemblages can then serve as reliable indicator surrogates in aquatic ecosystems, providing critical information about historical water quality, temperature regimes, and trophic status (Brodersen and Quinlan, 2006; Millet et al., 2010; Luoto, 2011; Belle et al., 2025). As such, chironomids bridge contemporary monitoring and paleoecological reconstruction, enhancing our understanding of both present and past lake conditions, thus making them excellent indicator groups to quantify the extent to which outputs from different approaches of establishing reference conditions can differ.

This study aims to compare the ecological classifications of Swedish freshwater lakes based on reference conditions for benthic invertebrates derived from spatial analogues and paleolimnological approaches. We hypothesized that while the results from both approaches were expected to be similar, paleolimnological assessments were predicted to more accurately reflect lake-specific conditions. Additionally, differences in the prevailing climate conditions between both the calibration of reference conditions using spatial analogues and the reference period used in paleolimnology, and present-day conditions may influence classification outcomes, and ultimately increase the likelihood of misclassification if climate change impacts on ecological baselines are not adequately accounted for.

## 2. Material and methods

### 2.1. Calibration of sediment-based BQI against monitoring data

Thirty-seven 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 $km^2$) located across Sweden (56°45′N – 64°03′N) were studied. Lakes were selected to represent a gradient of ecological conditions based on the land use in their catchment areas, ranging from minimally disturbed sites (e.g., forested catchments) to heavily impacted sites (e.g., situated in agricultural and urban catchments).

Contemporary Benthic Quality Index data (Wiederholm, 1980; Johnson and Goedkoop, 2007), which classifies 12 chironomid taxa into 5 tolerance groups with the highest weights assigned to indicators of oligotrophy and the lowest weights assigned to highly oxygen-tolerant species (Table 2 and Wiederholm, 1980; Johnson and Goedkoop, 2007), were retrieved from the Swedish National Data Host (https://miljodata.slu.se/mvm/) for all these 37 sites. Briefly, benthic invertebrate samples were collected from the profundal zones of lakes using an Ekman grab (256 $cm^2$), washed through a 0.5 mm mesh sieve, and preserved in 70 % ethanol (final concentration). The chironomid larvae were identified to the genus/species level and reported as individuals per $m^2$. BQI values using monitoring data were calculated as the abundance-weighted average of 12 indicator taxa scores and have 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; n$i$ is the abundance of the indicator taxon $i$, and N is the sum of n$i$. To allow comparisons with sediment core data, mean BQI values (if sufficient data existed) were calculated using the number of years encompassed by the first cm of each sediment core given by the age-depth models (see below).

In 2017 (10 lakes) and 2020 (27 lakes), sediment cores were retrieved from the deepest point of these lakes using a gravity corer (9 cm in diameter: UWITEC). The uppermost 1 cm of each sediment core was collected and represented present-day conditions (hereafter TOP samples). Chironomid head capsules were hand-sorted and identified from each sample of wet sediment (*ca.* 15g wet weight) following Walker (2001). Briefly, samples were successively rinsed with NaOH (10 %) solutions and washed through a 100-μm mesh sieve. Chironomid remains were then hand-sorted from the sieved residue under a stereo-microscope 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 calculated the BQI using subfossil data as the abundance-weighted average of 12 indicator taxa scores (see above and Table 2).

To visually represent the distribution of subfossil chironomid species abundances with each sediment sample, Whittaker rank-abundance diagrams were constructed by plotting the overall abundance of morphotypes against their rank in the samples (Whittaker, 1965). The relationship between the occurrence of the taxa (i.e., the relative frequency of each morphotype among all samples) and their mean relative abundance when present was also plotted.

As minor differences between the taxonomic composition of subfossil chironomids and their extant counterparts have been frequently reported in the profundal zones of lakes (van Hardenbroek et al., 2011; Frossard et al., 2013), sediment-based BQI values are expected to differ slightly from BQI values derived using traditional monitoring data. The relationship between monitoring and sediment-based BQI values must be established using a linear regression approach, providing a statistical framework for understanding how sediment-based values align with monitoring observations. For sediment-based data, only the TOP sediment samples (corresponding to present-day conditions, see above) were included in this analysis to enable comparison with the most recent monitoring data from the same lakes. The final model utilized sediment-based BQI data to infer BQI values comparable to those obtained through traditional monitoring.

### 2.2. Calculation of ecological quality ratios using sediment-based data

We used a subset of 30 lakes, cores collected in 2020, from these study sites. Selected lakes were then grouped following the lake typologies implemented in the status classification of Swedish lakes (Johnson and Goedkoop, 2007). The majority of lakes are situated in the south and belong to the mixed forest ecoregion, whereas ten lakes located at slightly higher latitudes and elevations (>200 m a.s.l.) belong to the boreal forest ecoregion (Table 1). Lakes were also grouped into reference (forested catchments considered largely unimpacted by agriculture and urban areas) and locally impacted lakes (Table 1) following a similar procedure developed by Johnson et al. (2018), and hereafter defined as the pressure group.

Sediment cores were dated by $^{210}Pb$, $^{137}Cs$, $^{241}Am$ at Liverpool

**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 |

**Table 1**
Lake names and IDs, pressure group classification (reference or impacted), and associated ecoregions. The BQI column presents data obtained through the traditional monitoring approach, along with corresponding type-specific reference conditions established using a spatial approach (BQI_ref). BQI_bottom represents sediment-based BQI values derived from subfossil chironomid assemblages in BOTTOM sediment layers. Corresponding site-specific reference conditions (BQI_ref2) were inferred using a model linking sediment-based BQI with monitoring-based BQI data. Ecological Quality Ratios (EQR) calculated using type-specific reference conditions from the spatial approach are shown in the EQR_spatial column, while those based on historical, sediment-based (site-specific) reference conditions are shown in the EQR_time column.

| Lake ID | Lake name | Group | Ecoregion | BQI_ref | BQI | BQI_bottom | BQI_ref2 | EQR_spatial | EQR_time |
|---|---|---|---|---|---|---|---|---|---|
| SE656793-163709 | Drevviken | Impacted | Mixed forest | 2.68 | 1 | 1.67 | 0.83 | 0.37 | 1.2 |
| SE636365-136675 | Södra Gussjö | Reference | Mixed forest | 2.68 | 2.7 | 3 | 2.36 | 1.01 | 1.14 |
| SE670275-146052 | Tryssjön | Reference | Boreal forest | 3 | 3.03 | 3.06 | 2.44 | 1.01 | 1.24 |
| SE651973-149250 | Bleklången | Reference | Mixed forest | 2.68 | 2 | 3.18 | 2.61 | 0.75 | 0.77 |
| SE652412-143738 | Långsjön | Reference | Mixed forest | 2.68 | 2 | 3.21 | 2.66 | 0.75 | 0.75 |
| SE633959-144217 | Skärlen | Reference | Mixed forest | 2.68 | 3.1 | 3.21 | 2.66 | 1.16 | 1.17 |
| SE633344-130068 | Skärsjön | Impacted | Mixed forest | 2.68 | 2.02 | 3.22 | 2.67 | 0.75 | 0.75 |
| SE638665-129243 | Lilla Öresjön | Impacted | Mixed forest | 2.68 | 2 | 3.22 | 2.68 | 0.75 | 0.75 |
| SE634447-144024 | Holmeshultasjön | Impacted | Mixed forest | 2.68 | 3 | 3.24 | 2.7 | 1.12 | 1.11 |
| SE635334-135239 | Majsjön | Impacted | Mixed forest | 2.68 | 3 | 3.24 | 2.71 | 1.12 | 1.11 |
| SE638014-136892 | Lagmanshagasjön | Impacted | Mixed forest | 2.68 | 1.3 | 3.25 | 2.72 | 0.49 | 0.48 |
| SE663216-148449 | Lien | Impacted | Boreal forest | 3 | 3 | 3.25 | 2.72 | 1 | 1.1 |
| SE631309-134951 | Södra Färgen | Impacted | Mixed forest | 2.68 | 1.5 | 3.3 | 2.79 | 0.56 | 0.54 |
| SE637379-137645 | Norra Vallsjön | Impacted | Mixed forest | 2.68 | 1.31 | 3.31 | 2.81 | 0.49 | 0.47 |
| SE668161-145410 | Bysjön | Impacted | Boreal forest | 3 | 2 | 3.32 | 2.82 | 0.67 | 0.71 |
| SE639047-149701 | Hökesjön | Impacted | Mixed forest | 2.68 | 3.21 | 3.35 | 2.87 | 1.2 | 1.12 |
| SE642122-148744 | Glimmingen | Reference | Mixed forest | 2.68 | 3 | 3.37 | 2.89 | 1.12 | 1.04 |
| SE638409-138549 | Rasjön | Impacted | Mixed forest | 2.68 | 1.53 | 3.37 | 2.89 | 0.57 | 0.53 |
| SE711365-171748 | Täftesträsket | Reference | Boreal forest | 3 | 2.98 | 3.36 | 2.89 | 0.99 | 1.03 |
| SE629489-133906 | Gyltigesjön | Impacted | Mixed forest | 2.68 | 3 | 3.5 | 3.1 | 1.12 | 0.97 |
| SE691365-156127 | Väster-Rännöbodsjön | Impacted | Boreal forest | 3 | 3.03 | 3.5 | 3.1 | 1.01 | 0.98 |
| SE664620-148590 | Västra Skälsjön | Reference | Boreal forest | 3 | 3.28 | 3.51 | 3.12 | 1.09 | 1.05 |
| SE663532-148571 | Övre Skärsjön | Reference | Boreal forest | 3 | 3 | 3.57 | 3.21 | 1 | 0.93 |
| SE666703-147051 | Haggen | Impacted | Boreal forest | 3 | 3 | 3.59 | 3.24 | 1 | 0.93 |
| SE641603-144848 | Försjön | Reference | Mixed forest | 2.68 | 3 | 3.62 | 3.28 | 1.12 | 0.91 |
| SE644180-127892 | Torrgårdsvatten | Reference | Mixed forest | 2.68 | 3.63 | 3.65 | 3.34 | 1.35 | 1.09 |
| SE672467-148031 | Spjutsjön | Reference | Boreal forest | 3 | 3.02 | 3.73 | 3.46 | 1.01 | 0.87 |
| SE704955-159090 | Hällvattnet | Reference | Boreal forest | 3 | 3 | 3.77 | 3.53 | 1 | 0.85 |

University's Environmental Radioactivity Laboratory, and age-depth models, linking the depth of a sample within a sediment core to its estimated age, were previously discussed in Belle et al. (2024). Using the age-depth models of each core, one 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 (Kruskal-Wallis test, $p > 0.05$, Fig. 1). Subfossil chironomid analysis and BQI calculation using subfossil data were calculated as described above.

EQRs were calculated using historical reference values established using sediment-based BQI data. First, sediment-based BQI data from BOTTOM samples were used as input in the developed model that links sediment-based and monitoring BQI values (see "*Calibration of sediment-based BQI against monitoring data*"), in order to infer historical BQI values. Then, these reconstructed historical BQI values, along with present-day monitoring BQI values from the same lakes, were used to calculate the EQR. Finally, the results were further compared with class boundaries outlined in monitoring programs, as shown in Table 3, to evaluate the current ecological status relative to historical conditions. These results will contribute to the paleolimnology component of this study.

### 2.3. Calculation of ecological quality ratios using spatial analogue reference conditions

Using the same subset of 30 lakes, EQRs were also calculated using the ecoregion-based framework outlined by Johnson and Goedkoop (2007), which employs spatial analogy to establish reference conditions. In the calibration study (Johnson and Goedkoop, 2007), monitoring data from 2006 were used to estibale ecoregion-specifc BQI reference values. The calculated EQRs were then compared with intercalibrated class boundaries (see also Sandin et al., 2014; Poikane et al., 2016), with further details provided in Table 3. These results will contribute to the spatial analogue component of this study. Spearman's rank correlation test was conducted across different ecoregions to assess the agreement between spatial analogue conditions and paleolimnological reconstructions of ecological quality ratios. All statistical analyses and plots were performed using the R 4.5.0 software (R Core Team, 2025).

**Table 3**
Class boundaries. Following Johnson and Goedkoop 2007.

| Ecoregion | Reference value | EQR class | Classification |
|---|---|---|---|
| Mixed | 2.68 | ≥0.75 | High |
| | | 0.6–0.75 | Good |
| | | 0.4–0.6 | Moderate |
| | | 0.2–0.4 | Poor |
| | | ≤0.2 | Bad |
| Boreal | 3.00 | ≥0.9 | High |
| | | 0.7–0.9 | Good |
| | | 0.45–0.7 | Moderate |
| | | 0.25–0.44 | Poor |
| | | ≤0.25 | Bad |

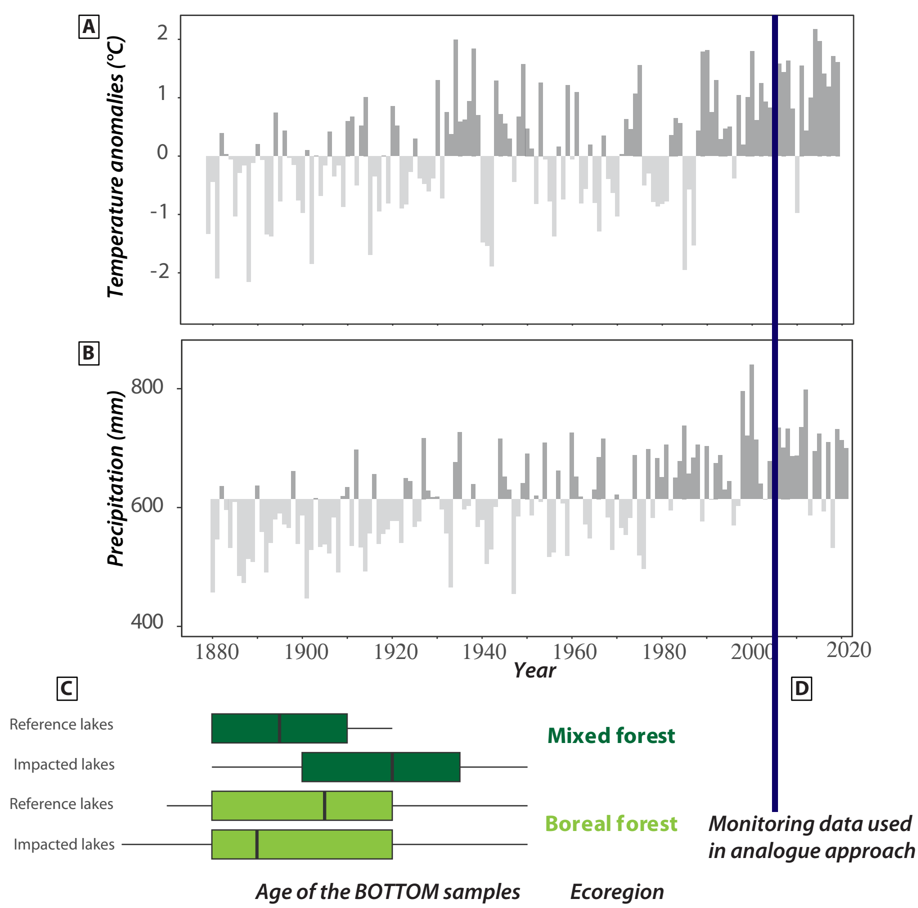


**Fig. 1.** Variation in mean annual temperature (A) and precipitation (B) between 1880 and 2020 (Swedish Meteorological and Hydrological Institute; https://smhi.se). Boxplots show the age of the BOTTOM samples for each pressure group within each ecoregion. Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions. Statistical tests revealed no significant difference between these categories (Kruskal-Wallis test, $p$-value >0.05). The purple bar at 2006 indicates the monitoring data year used to establish reference conditions through the spatial approach.

## 3. Results

The climate, defined by temperature patterns and precipitation regime, in Sweden around the periods used as references in paleolimnological approaches (at *ca.* 1900) was significantly different compared to 2006 (i.e., the year used for spatial analogue calibration; Johnson and Goedkoop, 2007), reflecting broader patterns of climate change over the 20th century. During the period represented by BOTTOM samples (at *ca.* 1900), Sweden experienced colder average temperatures and drier conditions (Fig. 1). By contrast, the year 2006 had a notably warmer climate and wetter conditions, underscoring the long-term warming trend noticeable in Sweden. A similar pattern can also be observed when comparing these two periods to the current climate (Fig. 1).

Overall, there was a good correlation between present-day monitoring results and sediment-based (TOP contemporary layer) BQI values ($R^2 = 0.55$; $p < 0.001$; Fig. 2), indicating consistency in ecological assessments based on both approaches. However, the slope of the regression line was 1.37 (Fig. 2) and the observed deviation from the theoretical 1:1 line indicated some variability, potentially related to the predominance of individual chironomid taxa (Fig. 3A). Among the predominant taxa, *Tanytarsus lugens*-type was the most widespread, occurring in high abundances at all sampling sites (Fig. 3B), and *Sergentia coracina*-type, also notably prevalent, was found in high abundances in 80 % of the lakes (Fig. 3B). Importantly, these two predominant taxa shared a tolerance coefficient of 3 (Table 2), indicating a moderate tolerance to eutrophic conditions and low oxygen levels. As a result, their presence in most or all lakes tended to lower sediment-based BQI scores at the upper end of the monitoring BQI gradient, and, conversely, higher sediment-based BQI scores where monitoring-based BQI is otherwise low due to their absence in contemporary observations.

We applied the developed model linking sediment-based and monitoring BQI data (Fig. 2) to infer reference conditions using chironomid assemblages preserved in sediment layers dated to *ca.* 1900 (BOTTOM samples). The inferred BQI reference values from sediment-based data were only slightly higher on average (2.70 and 3.05 for mixed forest and the boreal forest ecoregions, respectively) than the monitoring-based benchmarks of 2.68 for the mixed forest and 3.00 for the boreal forest ecoregions (Table 1 and Fig. 4). However, since the inferences were lake-specific, substantial variation was observed within both ecoregions.

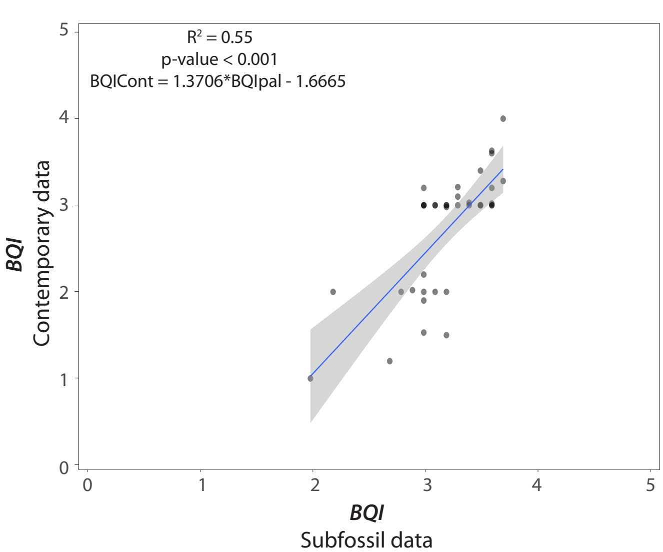


**Fig. 2.** Relationship between Benthic Quality Index (BQI) calculated using contemporary data (https://miljodata.slu.se/mvm/) and subfossil chironomids in 37 Swedish lakes. Statistical test showed a strong positive correlation between the two variables.

Reference BQI values ranged from 0.83 to 3.34 in the mixed forest ecoregion and from 2.44 to 3.53 in the boreal forest ecoregion (Table 1 and Fig. 4), highlighting the influence of local and regional conditions on the taxonomic composition of chironomid assemblages and BQI values.

We found moderate agreement between EQR values for the spatial and sediment-basesd approaches, with a strong, positive, and statistically significant correlation observed in the mixed forest ecoregion ($r = 0.57$, $p < 0.01$; Fig. 5A), whereas no significant association was found for the boreal forest ecoregion ($p = 0.21$; Fig. 5B). Furthermore, the dispersion of EQR values was much greater when using sediment-based reference values, as this method is site-specific (as visible in the boxplots displayed in Fig. 5). As a result, the EQR values and their classification with ecoregion-specific class boundaries did not differ markedly between approaches (Kruskal-Wallis test; $p > 0.05$; Fig. 6). Nonetheless, a lower proportion of EQR >1 was observed when using sediment-based reference conditions (41 % of the observed data with EQR >1) compared to the spatial analogue method in the mixed forest ecoregion (53 % of the observed data with EQR >1; Fig. 6A). Additionally, the distribution of EQR values across different class boundaries appeared more gradual in the boreal forest ecoregion with the paleolimnological approach (Fig. 6B), suggesting a more continuous and nuanced assessment of ecological quality in this ecoregion.

## 4. Discussion

Assessments based on both spatial analogues and paleolimnological reconstructions yielded broadly comparable results and ecological classifications. The most notable differences were observed across a range of sediment-based reference conditions rather than a single value per ecoregion for the spatial approach (i.e., being similar for all lakes in the same ecoregion), underscoring the inherent advantage of using paleolimnological data to establish lake-specific baseline conditions. Our findings also indicated that sediment-based inferences of reference conditions were stricter and reduced the frequency of cases where EQR values exceeded 1, an indication that reference conditions may be underestimated relative to the present-day state, thereby enabling more accurate and meaningful ecological assessments (Hawkins et al., 2010). Indeed, EQR values greater than 1 may typically reflect inadequately defined reference conditions and/or high uncertainty in reference conditions, often arising from the limitations of spatial analogues that overlook fine-scale typological differences due to overly broad ecosystem typologies. While reporting EQR values greater than 1 is not, in itself, a major issue for ecological classification, it can inadvertently hinder the early detection of changes in ecological status, as the increased distance to the nearest class boundaries reduces sensitivity to early-stage degradation. In contrast, paleolimnological reconstructions provide a more precise, site-specific historical context, supporting finer-scale ecological management and more effectively tailored restoration strategies for individual lakes (Battarbee and Bennion, 2011; Bennion et al., 2011; Saulnier-Talbot, 2016). Establishing reference conditions using paleolimnological approaches could, therefore, serve as a relevant complementary approach in areas where spatial analogues might fail to capture the full diversity of ecosystems (such as in the mixed forest ecoregion). Paleolimnology provides a more realistic, undisturbed baseline, representing the "ideal" restoration target. However, given more than a century of ongoing climate change and associated shift in biological communities (Belle and Johnson, 2024), fully restoring lakes to their historical state may no longer be feasible. In this context, paleo-based baselines should serve as the ultimate reference for understanding the full impact of climate change and guiding long-term restoration goals.

The comparison between the periods used for sediment-based inferences (at *ca.* 1900) and spatial analogue (in 2006) was also complicated by differing climatic conditions (Schimanke et al., 2022) and human impacts, making an assessment of the performance of the two

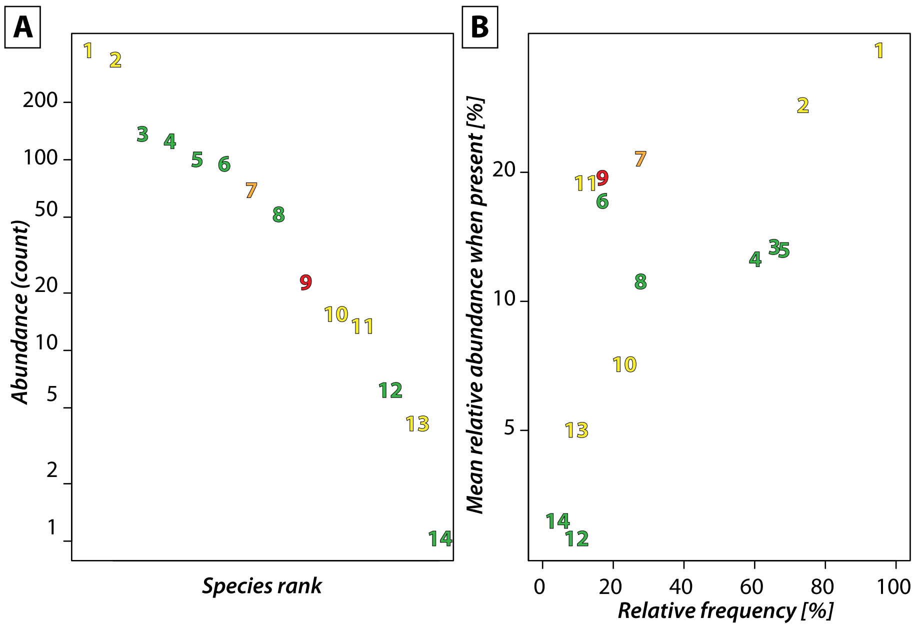


**Fig. 3.** **(A)** Whittaker plot showing the total number of head capsules counted per indicator taxa in all lakes plotted in descending order against rank. **(B)** Relationship between the occurrence of the indicator taxa and their mean relative abundance when present. Numbers correspond to: 1 = *Tanytarsus lugens*-type; 2 = *Sergentia coracina*-type; 3 = *Heterotanytarsus*; 4 = *Micropsectra insignilobus*-type; 5 = *Heterotrissocladius marcidus*-type; 6 = *Heterotrissocladius maeaeri*-type 1; 7 = *Chironomus anthracinus*-type; 8 = *Heterotrissocladius maeaeri*-type 2; 9 = *Chironomus plumosus*-type; 10 = *Tanytarsus lactescens*-type; 11 = *Stictochironomus rosenschoeldi*-type; 12 = *Heterotrissocladius grimshawi*-type; 13 = *Tanytarsus pallidicornis*-type; and 14 = *Paracladopelma*. Colours refer to their coefficients in the BQI (see also Table 2): with green = 4; yellow = 3, orange = 2 and red = 1.

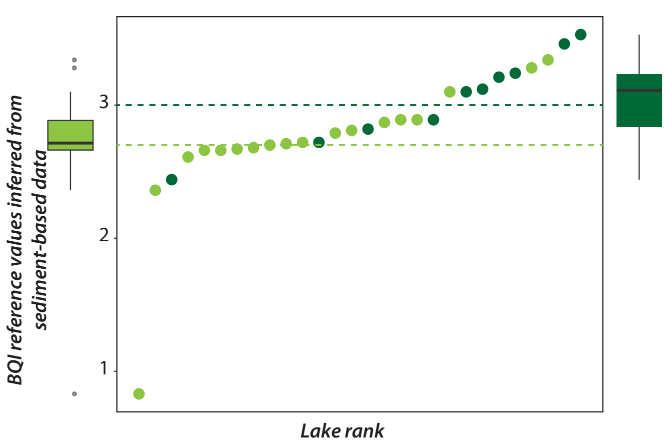


**Fig. 4.** Benthic Quality Index (BQI) reference values calculated using the subfossil chironomid assemblages from the BOTTOM sediment samples in the different ecoregions plotted in ascending order according to their rank. The dashed lines represent the reference BQI values from the spatial analogue approach used in the different ecoregions. On the y-axis, boxplots show the BQI reference values calculated using the paleolimnological approach. Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions.

approaches precarious. Overall, sediment-based reference values taken around 1900 tend to be slightly higher than the ones established in 2006 using spatial analogue techniques. This observation is consistent with the concept of shifting baselines and the impact of climate change on lake ecological status (Free et al., 2024). Chironomid assemblages, especially in northern regions of Swedens predominated by cold-water stenotherm taxa, are particularly sensitive to changes in water temperature (Luoto, 2009; Heiri et al., 2011). Furthermore, these cold-water stenotherm taxa show the highest tolerance scores in the BQI calculation (Wiederholm, 1980; Johnson and Goedkoop, 2007), and thus typically show positive co-tolerance (as conceptualized by Vinebrooke et al., 2004) to temperature and eutrophication (e.g., cold stenotherm species also being indicators of oligotrophic conditions, and *vice versa*). In this context, warming and eutrophication may lead to similar effects on BQI, corresponding to a decrease in BQI values caused by lower development of cold-water oligotrophic taxa and higher abundances of warm-water and eutrophic taxa (Belle et al., 2024). Furthermore, the observed difference between sediment- and spatial-based values could reflect some levels of human impact (other than climate change) on the reference lakes. In Sweden, reference sites are typically selected using criteria that allow for an “acceptable” level of human pressure on lake ecosystems (e.g., less than 10 % agricultural land use in the catchment area of Swedish reference sites; Johnson and Goedkoop, 2007). While spatial analogue-based baselines partially account for climate change and may provide more practical and achievable management targets for assessing human pressures beyond climate, the challenge of determining the “acceptable” level of human impact on reference sites remains unresolved and this uncertainty could hinder effective management and assessment.

Our study confirmed that using subfossil chironomids from paleolimnological approaches to infer BQI values in lakes is generally reliable, matching well previous studies showing good agreement between sediment-based and contemporary values (Jyväsjärvi et al., 2010). However, small deviations were observed, which we attributed primarily to the high occurrence of subfossil head capsules of common taxa in lake sediments, reducing the discrimination potential of these indicator species and skewing BQI inferences. For example, subfossil head capsules of *Tanytarsus lugens*-type are commonly found in sediments of Swedish lakes (Larocque et al., 2001) and were found in all of our study sites. Since this morphotype has a quality score of 3 in the BQI formula (Johnson and Goedkoop, 2007), it contributes to a lower BQI than would otherwise be observed if the taxon was absent from the monitoring data, and *vice versa*. As a result, this morphotype is likely not a reliable indicator taxon in paleolimnological studies, as it appears across lakes showing a broad range of ecological qualities. Furthermore, small discrepancies between the chironomid taxonomic composition from monitoring (samples collected from profundal zones) and subfossil data

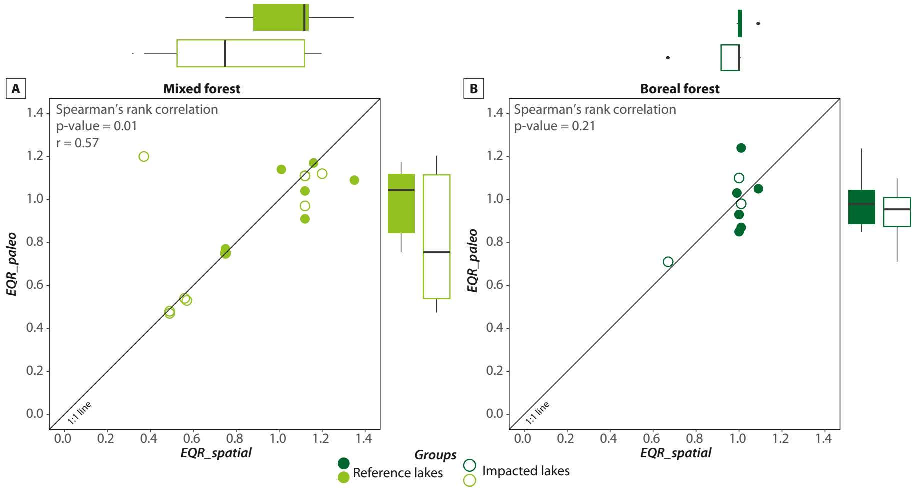


**Fig. 5.** Relationships between the ecological quality ratios calculated using spatial (EQR_spatial) and paleolimnological techniques (EQR_paleo) of the lakes in the two ecoregions (mixed forest in panel **A** and boreal forest in panel **B**). Closed circles and boxplots represent reference lakes, and open circles and boxplots represent impacted sites. Colours refer to the mixed forest (light green) and boreal forest (dark green) ecoregions.

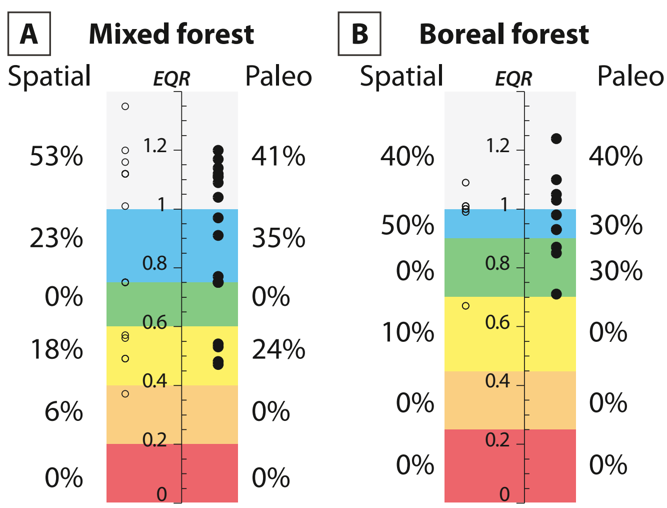


**Fig. 6.** Comparisons of the classifications of the ecological quality ratios calculated using spatial (EQR_spatial; open circles) and paleolimnological techniques (EQR_paleo; closed circles) in the two ecoregions (mixed forest in panel **A** and boreal forest in panel **B**). Percentages of total data observed within each class are also reported for each technique and ecoregion. Class boundaries are reported in Table 3. The ecological classes are represented as: Above 1 (grey), High (blue), Good (green), Moderate (yellow), Poor (orange), and Bad (red).

likely result from erosion of taxa from shallower areas and head capsules being redeposited in the profundal (i.e., coring site, van Hardenbroek et al., 2011). However, all studied lakes were selected to be similar in depth and size, and therefore, differences related to erosion are likely negligible. The modelling approach developed in this study may, however, not be suitable for lakes with markedly different morphometry and erosion dynamics, where sediment mixing and remobilization could weaken the relationship between contemporary and sediment-based BQI.

The effects of climate change on ecological baselines are anticipated to blur the distinction between natural variability, climate effects, and anthropogenic impacts, challenging the accuracy of traditional assessment frameworks. As a result, there is a growing risk that ecological assessments may no longer reflect true anthropogenic impacts but rather include natural responses due to a climate-induced shifting baselines. Therefore, there is an urgent need to better understand and quantify the net effects of climate change on lakes and on the tools used to evaluate their ecological status. Without such adaptations, ecological assessments risk underestimating or misclassifying the true condition of aquatic ecosystems in a warming world (Free et al., 2024). Finally, reference conditions have traditionally been defined using a static framework, established once and seldom revised (Dodds et al., 2006; Poikane et al., 2010, 2016). While this approach has provided a standardized basis for comparison, it generally excludes the influence of long-term climate change, assuming that the environmental conditions under which reference states were defined remain relatively stable over time (Deeds et al., 2022). One alternative approach could be the development of "adaptive reference conditions", dynamic baselines that can be periodically updated to reflect current and projected climatic trends (Johnson et al., 2010; Hiers et al., 2012). Alternatively, reference conditions might incorporate scenario-based models, using climate projections to infer future lake conditions and assess how indicators such as species composition or nutrient levels may change under different warming pathways. Ultimately, integrating climate fluctuations into the reference condition concept is critical to maintaining the relevance and accuracy of ecological assessments, helping to differentiate between shifts caused by climate versus those driven by human pressures (Free et al., 2024). This paradigm shift in defining reference conditions (static *vs.* adaptive framework) should allow us to better adapt lake management interventions to different climate scenarios. This is particularly important in the context of global warming, where traditional reference conditions, even though based on relatively recent data, may no longer represent truly undisturbed states. By extending our ecological perspective further into the past, paleolimnology supports the development of more accurate and appropriate baselines for assessing ecological status and guiding long-term lake management strategies.

## 5. Conclusion

Sediment-based baselines should be considered as the ultimate reference for understanding the full extent of climate change impacts and for guiding long-term restoration goals. However, given ongoing climate change, fully restoring lakes to their historical state may no longer be realistic, and spatial analogue-based baselines may offer more practical and attainable management targets for assessing human pressures beyond climate factors. The differences observed between these two approaches underscore the challenges posed by shifting baselines, where climate change impacts are increasingly intertwined with human activities. In light of these complexities, we propose that paleolimnological data should complement current monitoring efforts, particularly in regions where spatial analogues may not fully capture local conditions. This combination will help to more comprehensively assess the effects of climate change on lake ecological status and biodiversity dynamics. Ultimately, integrating climate effects into ecological assessments is essential for accurately tracking lake ecological quality in an increasingly warming world.

## CRediT authorship contribution statement

**Simon Belle:** Writing – original draft, Visualization, Funding acquisition, Formal analysis, Conceptualization. **Richard K. Johnson:** Writing – review & editing, Data curation. **Gary Free:** Writing – review & editing. **Jens Folster:** Writing – review & editing, Data curation. **Brian Huser:** Writing – review & editing, Investigation, Funding acquisition. **Sandra Mingarelli:** Writing – review & editing.

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## Declaration of competing interest

The authors declare that they have no competing interests.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.128077.

## Data availability

Data will be made available on request.

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