Title: Multi-decadal improvements in the ecological quality of European rivers are not consistently reflected in biodiversity metrics

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Abstract

Humans impact terrestrial, marine, and freshwater ecosystems, yet many broad-scale studies have found no systematic, negative biodiversity changes (e.g., decreasing abundance or taxon richness). Here, we show that mixed biodiversity responses may arise because community metrics exhibit variable responses to anthropogenic impacts across broad spatial scales. We first quantified temporal trends in anthropogenic impacts for 1,365 riverine invertebrate communities from 23 European countries, based on similarity to least-impacted reference communities. Reference comparisons provide necessary, but often missing, baselines for evaluating whether communities are negatively impacted or have improved (less or more similar, respectively). We then determined whether changing impacts were consistently reflected in metrics of community abundance, taxon richness, evenness, and composition. Invertebrate communities improved, i.e., became more similar to reference conditions, from 1992 until the 2010s, after which improvements plateaued. Improvements were generally reflected by higher taxon richness, providing evidence that certain community metrics can broadly indicate anthropogenic impacts. However, richness responses were highly variable among sites, and we found no consistent responses in community abundance, evenness, or composition. These findings suggest that, without sufficient data and careful metric selection, many common community metrics cannot reliably reflect anthropogenic impacts, helping explain the prevalence of mixed biodiversity trends.

Introduction

Reports of human-driven species extinctions[1,2] and environmental change[3–5] indicate widespread degradation of Earth's ecosystems, particularly freshwaters[6]. However, a growing number of continental- and global-scale temporal studies of freshwater, terrestrial, and marine communities have found no evidence of systematic, negative biodiversity changes[7–15], instead reporting a mixture of negative, positive, and neutral changes. Such studies typically infer that negative biodiversity changes (often defined as declining abundance or taxon richness) indicate anthropogenic degradation[8,16,17], whereas positive changes indicate improving environmental quality[13,18,19]. Studies finding mixed biodiversity changes therefore suggest a balance of degradation, improvement, and no change[7,9,11,12]. These studies have spurred debate about whether anthropogenic impacts are truly mixed[20], and the role methodological issues play in producing mixed biodiversity trends, including issues of poor data quality, quantity, and representativeness[21–23].

One unaddressed explanation for the prevalence of mixed biodiversity trends is that common metrics used to summarize community change, such as abundance or taxon richness, cannot reliably indicate anthropogenic impacts. This unreliability may occur because different stressors can have contrasting effects, species have varying tolerances to different stressors, and communities have different historical and environmental contexts that influence their response[25]. For example, anthropogenic impacts may drive declines in community abundance or richness in some localities[4,17,26], whereas others may exhibit no overall change if gains match losses[27], or may even exhibit increases when tolerant species proliferate[26,28]. Consequently, the mixed biodiversity trends found by many studies may be a result of variable community responses to anthropogenic impacts. An additional complication is that most biodiversity studies lack the pre-disturbance baseline data needed to contextualize observed trends. Without baselines, it is difficult to determine whether biodiversity changes result from anthropogenic impacts, or from natural fluctuations[21,22], changing baselines, or as a statistical artifact of the period chosen for analysis[29].

To better understand what broad-scale studies of local biodiversity trends can and cannot tell us, we must determine whether any aspect of biodiversity can consistently reflect anthropogenic impacts across broad spatial scales. Doing so involves first quantifying the degree of impact across numerous communities, which requires comparisons to unimpacted conditions. Next, variability in impact should be related to variability in common biodiversity metrics that summarize communities, such as abundance, taxon richness, evenness, and temporal turnover, to determine whether any relationships are consistent across finer (e.g., within sites and regions) to broader (e.g., continental) spatial scales. Ideally, such analyses would use high quality time-series data collected from similar taxa and habitats using similar sampling methodologies to ensure comparability[21,22,30].

While no dataset can perfectly fulfill these requirements, a feasible solution is to use organisms commonly collected by biomonitoring programs, such as riverine invertebrates[31]. Biomonitoring programs can compensate for missing historical baselines by replacing them with modeled or collected data from other minimally or least-impacted ‘reference’ communities. The degree of impact is then quantified using an index of the similarity between sampled versus reference communities, which we hereafter refer to as ‘ecological quality’. Ecological quality indices provide what many biodiversity studies are typically missing, specifically a consistent measure of how communities have changed compared to reference conditions, with greater deviation indicating more severe anthropogenic impacts regardless of differences in stressors or community contexts. This index can then be related to common community metrics to identify any consistent associations. Moreover, established biomonitoring indices summarizing components of community composition, such as the occurrence of sensitive taxa[31,32], provide support for environmental changes inferred from changes in ecological quality. Lastly, riverine invertebrates have been sampled for decades worldwide following standardized methodologies[31], enabling robust time-series analyses and ensuring the same taxa from the same habitats are compared.

Here, we used riverine invertebrate biomonitoring data from 1,365 sites across 23 European countries (Fig. 1) to fill the knowledge gaps outlined above. First, to characterize changes in anthropogenic impacts, we quantified temporal trends (1992–2019) in ecological quality at continent, country, and site spatial scales. These analyses determine how communities have changed relative to baseline conditions, and provide a European-scale assessment of long-term trends in ecological quality. Second, to identify community metrics that consistently reflect anthropogenic impacts, we related ecological quality to common metrics summarizing community abundance, biodiversity (e.g., richness), and composition, and to common biomonitoring indices that reflect the occurrence of sensitive taxa.

Results

Continental-scale trends in ecological quality

Ecological quality was measured using Ecological Quality Ratios (EQR) and Ecological Quality Classes (EQC), as defined by the European Union Water Framework Directive (WFD[33]). EQRs are a continuous ratio of the similarity between sampled and least-impacted reference invertebrate communities. EQRs range from 0 (0% similarity) to 1 (100% similarity) and the values within this range are allocated into one of five numeric EQCs of 1 (High), 2 (Good), 3 (Moderate), 4 (Poor), or 5 (Bad) based on country-specific classification systems (detailed in Supplementary Table 1). EQCs are used to determine whether a given invertebrate community has satisfied the WFD target of achieving a ‘good’ or ‘high’ ecological quality status, whereas EQRs are better suited for statistical analyses because they provide a more precise representation of community similarity to the references. Some uncertainties exist in the degree to which EQRs/EQCs represent all anthropogenic environmental changes[34]. However, they are well-established measures of general impact[34] that are assumed to be comparable across countries[35].

Based on generalized additive mixed models (GAMMs), ecological quality (represented as both EQRs and EQCs) improved across our sites from 1992 until around the 2010s, evidenced by significant smoothed year terms in models for both EQRs (Wald test, n = 19,660, effective degrees of freedom (e.d.f.) = 5.06, F = 69.00, P < 0.001) and EQCs (Wald test, n = 19,697, e.d.f. = 3.98, F = 86.80, P < 0.001; Fig. 2). EQRs initially improved by around 0.006–0.013 y^{-1}, with EQCs improving by about 0.035–0.05 classes y^{-1} (Extended Data Fig. 1). However, little to no change occurred after the early 2010s when EQRs plateaued around 0.7 and EQCs plateaued around 2.2, which is just below the target of a ‘good’ EQC value of 2 set by the WFD[33] (Fig. 2). These trends were robust to the inclusion or exclusion of individual countries, despite differences in time series length among countries (Supplementary Table 2 and Supplementary Fig. 1).

Continental-scale metrics and indices

Ecological quality was moderately related to the community metrics and biomonitoring indices (based on a significant global permutation test; n = 19,654, $F_{1,19653}$ = 3,214.7, R^2 = 0.14, P = 0.001). Specifically, improvements in ecological quality from 1992 through the 2000s were most associated with increases in taxon richness, Shannon diversity, and the Ephemeroptera, Plecoptera, and Trichoptera (EPT) indices (Fig. 3), with increased EPT indicating improved water quality and habitat conditions (see Extended Data Table 1). Other community metrics and biomonitoring indices exhibited weaker or no relationships (Fig. 3), excluding the Average Score Per Taxon (ASPT) index and the Saprobic Index, which were not included because not all countries use them.

A caveat to these results is that certain countries calculate ecological quality using multiple metrics and indices, which can partly incorporate those we analyzed, particularly taxon richness, Shannon diversity, EPT richness, and the ASPT index (used in around 20–40% of sites; detailed in Supplementary Table 1). This results in a potential problem of circularity, although ecological quality can change even if some of its composite metrics do not (or vice versa) because multiple metrics/indices are typically used. To test for the influence of this circularity, we removed sites that use potentially circular metrics/indices and repeated our analyses. The removal did not substantially influence our results (Supplementary Figs. 2 and 3).

Country-scale trends in ecological quality

We quantified country-scale temporal changes in ecological quality and its relationships to the community metrics and biomonitoring indices for 15 countries with adequate data to parameterize individual models, which represented 99% of the sites. The continental-scale temporal improvements in ecological quality were driven by improvements in communities from Belgium, Denmark, France, Hungary, Norway, and Spain (Fig. 4 and Supplementary Tables 3 and 4). Between 40–85% of the sampled communities from these countries were at good or high EQCs in their most recent year of sampling. Modeled temporal relationships for the EQC values indicated improvements from 3 to 2.2 in Belgium, from 2.9 to 2.2 in Denmark, from 2.4 to 1.5 in France, from 3.1 to 2.7 in Hungary, from 3.3 to 2.6 in Norway, and from 3.8 to 2.2 in Spain (Fig. 4c). Conversely, we found no statistical evidence of improvements in the other countries, such as Czechia (EQCs remained stable around 3.2), Ireland (2.8), Lithuania (2.3), the Netherlands (3.5), and Sweden (1.0; Fig. 4d). Based solely on trendlines, ecological quality may be improving in Luxembourg (modeled EQCs change from 2.6 to 2.1 during 1992 through 2019), Finland (1.2 to 1.0), and the UK (2.3 to 1.6), versus degrading in Germany (2.0 to 2.1; Fig. 4d). However, these patterns were non-significant (Supplementary Tables 3 and 4) with large confidence intervals.

Country-scale metrics and indices

Taxon richness and Shannon diversity were the community metrics that exhibited the strongest relationships to changes in ecological quality in most countries (Fig. 5 and Extended Data Fig. 2), aligning with the continental-scale patterns, but trends varied spatially. For example, richness exhibited less change in relation to ecological quality in Germany (Fig. 5c), Denmark (Fig. 5d), and particularly the Netherlands (Fig. 5i) compared to the other countries, with similarly weaker relationships for Shannon diversity in Denmark (Fig. 5d), France (Fig. 5f), and the Netherlands (Fig. 5i). Additionally, the degree to which the community metrics were related to ecological quality varied widely among countries, from ecological quality explaining almost 30% of the total variation in metrics/indices in some countries (e.g., Lithuania; Fig. 5h) down to less than 10% in others (e.g., Sweden; Fig. 5j). These spatial differences indicate that the community metrics varied more in relation to ecological quality in some regions (those with more explained variation) versus less in others.

Ecological quality was always positively related to biomonitoring indices of water/habitat quality in all countries, specifically EPT richness and the ASPT index in countries that use this index. Relationships to other indices were country-specific (see Supplementary Figs. 4–7 for statistics). For example, in Czechia (Fig. 5b), Denmark (Fig. 5d), Spain (Fig. 5e), and the Netherlands (Fig. 5i), years with better ecological quality were more strongly associated with a lower proportion of taxa with preferences for littoral habitats compared to other countries, which could indicate a stronger influence of flow alteration in these regions (see Extended Data Table 1). Similarly, ecological quality was more strongly associated with the Community Temperature Index and the Saprobic Index in Germany (Fig. 5c) and the Netherlands (Fig. 5i), which may indicate a stronger influence of warming and organic pollution.

Site-scale ecological quality, metrics, and indices

Site-scale ecological quality trends were often positive (Fig. 6; 37% with positive slopes and confidence intervals that did not overlap 0), aligning with the general improvements shown in our other analyses. However, 57% of sites exhibited no strong evidence for change, indicating substantial site-scale variability in whether ecological quality was changing. The ecological quality of 6% of all sites also tended to decrease over time, which encompassed sites in 17 of the total 23 countries.

Site-scale temporal changes in ecological quality exhibited the strongest relationships to changes in taxon richness (Fig. 6a) followed by Shannon diversity (Fig. 6b), with weaker to no relationships to all other community metrics (Fig. 6). However, even the more consistent relationships varied widely among sites, as evidenced by generally low R^2 values. For example, 24% of sites exhibited the same direction of change in both richness and ecological quality (here ‘change’ means a slope value whose confidence intervals do not overlap 0), but 31% exhibited no change in richness when ecological quality changed or vice versa, and 2% exhibited opposing changes (Fig. 6a and Extended Data Table 2). This variability was more pronounced in community metrics with weaker relationships to ecological quality and lower R^2 values, such as Shannon diversity for which only 11% of sites exhibited matching relationships and 43% exhibited no match, i.e., either Shannon diversity did not change when ecological quality did or vice versa (Fig. 6b). Of the biomonitoring indices, ecological quality primarily exhibited positive relationships to the EPT and ASPT indices and particularly to EPT richness (see Extended Data Fig. 3).

Discussion

Our results have important implications for upscaling local biodiversity trends into broader inferences about anthropogenic impacts, and for monitoring and analyzing biodiversity change. Many studies report various changes in animal and plant biodiversity and use these changes to infer likely drivers. For example, several studies report positive changes in European freshwater[11–13,18,32] and marine biodiversity[11,19], and suggest these trends reflect improvements in water and habitat quality. However, questions remain about potential issues with making such linkages, including problems in analyzing sporadic biodiversity time series with missing baselines[21,22], variable community responses, and the quality and representativeness of the underlying datasets (for example, ref. 36). Our findings help to resolve these questions using European riverine invertebrates as a case study. We found that ecological quality generally increased from the 1990s to 2010s, as did the number of sensitive taxa, indicating reduced anthropogenic impacts, albeit the required ‘good’ ecological status has not yet been achieved on average. Better ecological quality likely occurred owing to European policies introduced in the

1990s and 2000s to reduce pollution, such as through improved wastewater treatment[37]. Increases in ecological quality then plateaued after the 2010s. Further research is needed to determine why improvements stalled[18], but likely candidates include unaddressed stressors, such as diffuse pollution and physical habitat modification[38,39], intensifying stressors such as climate change[40], and emerging stressors such as new pesticides, pharmaceuticals, and other substances[41,42]. Regardless of the specific drivers, the general improvements we found in ecological quality match positive changes in European freshwater biodiversity reported by other studies during the same period[11,12]. This match illustrates that, despite different stressors and stressor effects, biodiversity can exhibit consistent responses to anthropogenic impacts across broader spatial scales.

Improvements in ecological quality exhibited the strongest relationships to increases in taxon richness across all spatial scales, suggesting that richness could be a reliable broad-scale indicator of anthropogenic impacts. Richness is commonly used in biodiversity and biomonitoring assessments for a range of taxonomic groups partly owing to the comparative ease of data collection and metric calculation[43,44]. However, its usefulness is debated because it requires a harmonized taxa list across regions, it does not reflect compositional changes, its response depends on the spatial scale of study, and the baseline data to contextualize how and why richness has changed is generally lacking[21–23,27,45]. Despite these limitations, our results indicate that richness can provide meaningful insights into general patterns of anthropogenic impacts (other studies have found similar results[4]). This relationship likely occurred in our dataset because better river conditions can increase richness by increasing habitat quality, quantity, and heterogeneity[46,47] and by increasing the presence of pollution-sensitive species[31,32]. This association may apply beyond riverine invertebrates given that taxon richness is often positively related to habitat quality for a variety of taxonomic groups[4,48,49]. Studies that identified mixed changes in local richness across large geographic areas, including in plants, fishes, birds, mammals, and terrestrial insects[7–9,26,50,51], may therefore be correct when inferring a similar mixture of negative impacts, improvement, and no change. These studies still, however, suffer from issues of representativeness. For example, sampling an equal mixture of degrading and improving sites will undoubtedly produce mixed responses, but this does not mean the sampled sites represent the state of anthropogenic impacts across the globe. Similarly, data is often missing for certain continental regions, such as the Mediterranean in our dataset, and from outside North America, Europe, or Oceania[21,22]. These limitations mean that further work is required to evaluate the degree of anthropogenic impact, and the usefulness of richness as a broad-scale indicator, across different major biogeographic regions.

While richness was broadly positively related to ecological quality, this relationship was highly variable among countries and at the site-scale, with most sites exhibiting no response or even negative relationships. No change in richness as ecological quality changes could occur at sites where taxa losses are balanced by gains[27]. Alternatively, richness may change even when ecological quality does not due to natural population declines and colonization processes[20,27] or human-driven species introductions and range expansions[26]. We also observed some opposing relationships. For example, sometimes worsening impacts were associated with higher richness, which can occur when tolerant species and non-natives establish[52], or sometimes improvement was associated with lower richness, which may occur if declines in tolerant taxa outweigh gains in sensitive species[28]. This response variability highlights that richness may be a reliable indicator of impact across broader spatial scales, but this requires a large quantity of data to control for high spatial heterogeneity in responses among sampling sites[23]. Smaller-scale studies or those with less data may therefore find richness to be an inconsistent indicator of anthropogenic impacts[8,27,53]. Furthermore, the high spatial variability we found in richness responses suggests that studies may not be able to decompose broader-scale richness trends into finer-scale categories, such as by different regions, taxonomic groups, or habitat types[7,11,50], and assume that richness responds similarly to anthropogenic impacts across categories[54,55]. Accounting for variability in richness responses may be best accomplished through multimetric approaches that combine changes in two or more metrics, such as richness and a composition metric. This approach better captures changes in different aspects of each community, which may more reliably reflect anthropogenic impacts and provide more consistent information for management and conservation[56].

Most community metrics, specifically Shannon diversity, abundance, evenness, and temporal turnover, exhibited little to no general relationship to ecological quality. This result shows how changes in anthropogenic impacts can fail to translate to consistent changes in many common community metrics across broader spatial scales, which may partly explain why broad-scale biodiversity studies often find a mixture of trends. Such inconsistency may be more pronounced for metrics compared across communities from different taxonomic groups or habitat types[7–12], given the high variability we found even within approximately the same system, i.e., invertebrates sampled from the river bottom following similar methodologies. Community metrics other than those we examined may provide more consistent insight into anthropogenic change, such as observed:expected richness[57], genetic diversity, functional diversity, or trait composition[58–60]. However, responses in these types of metrics can be similarly variable across communities[10,18]. Alternatively, measuring the ‘quality’ of a community in a different way, for example using ecosystem functionality, could produce more consistent responses in community metrics that best reflect relevant functions, such as abundance/biomass[17] or evenness[61]. Using biodiversity to infer anthropogenic impacts therefore requires careful consideration of which community metrics are the best indicators for the habitat types and taxa in question and what is the most suitable way to measure impact. The answers to these questions will also undoubtedly change depending on whether the study is broad in scale and so requires general indicators versus focusing on finer-scale changes in particular regions or ecosystems[62].

Our analyses have two principal limitations that we cannot address. Although our results are supported by a robust dataset and match other reported conclusions about improvements in European freshwater communities[13,32,38], they are limited first by the spatial coverage of our sites and second by the temporal duration of monitoring. Spatially, our analyses are restricted to only river sites for which we could obtain data that met our criteria. Consequently, ecological quality trends informed by more spatially extensive datasets may reliably reflect country-scale changes (e.g., Denmark or France), but trends informed by less extensive datasets (e.g., Ireland or Norway) may not reflect the overall status of rivers in the region. Temporally, our analyses were restricted to starting in the early 1990s because reliable monitoring data across different countries was only available during this period. Our results therefore reflect how communities have changed during the last 30 years, but cannot reflect the full extent of change compared to historical, pre-disturbance baselines.

With the above caveats in mind, our findings show that some community metrics, specifically richness, can consistently indicate anthropogenic impacts across broad spatial scales. However, variability in community responses means that such inferences must be made carefully, ensuring comparison of similar taxa and habitats and with an appropriate amount of data. Additionally, we found many commonly used community metrics cannot consistently indicate anthropogenic impacts. Acknowledging and incorporating this variability into biodiversity analyses and monitoring programs is essential for identifying impacted communities and for better protecting biodiversity in an era of global change.

Methods

Riverine invertebrate data

We collated annual data on invertebrate community composition that was consistently collected from 1,365 river sampling locations across 23 European countries. These data primarily come from Haase et al. 2023[18], although additional data for Czechia and Lithuania was provided via requests to ecologists and environmental managers. An advantage of this European-scale analysis is that all invertebrate biomonitoring and index calculation is performed in compliance with the European Union Water Framework Directive (WFD), ensuring comparability among regions. Across all countries, the included rivers encompass a wide range of river sizes (Strahler order mean ± SD of 4.5 ± 1.9, range 1–10), catchment sizes, and severity in anthropogenic impacts, from more pristine to heavily impacted ecosystems (Fig. 1). The time series ranged between 1992 and 2019 and each consisted of at least seven years of data. Sampling was always conducted at the same river sites, during the same seasons (any three consecutive months), and using the same methods across years. Invertebrates were generally collected following WFD-compliant methods across countries, i.e., primarily multi-habitat kick-net samples collected from the river bottom. Taxa were identified to family, genus, or species level, although some were classified to intermediate (e.g., Chironominae at subfamily) or higher levels (e.g., Oligochaeta at subclass), with Chironomidae and Gammaridae typically the most abundant taxa across countries. The mean starting year for the time series was 1999, the mean end year was 2017, with a mean of 15 sampling years per site and a mean total time series length of 18 years (see Supplementary Table 2 for further time series details).

Ecological quality

The WFD is the principal piece of European protective water legislation that aims for all freshwaters to reach a 'good' or 'high' ecological status[33]. The ecological status of a river is quantified using multiple environmental parameters and taxonomic groups, but here we focused specifically on status measured using the ecological quality of the invertebrate community. We used WFD-compliant methods to calculate Ecological Quality Ratios (EQRs) and Ecological Quality Classes (EQCs). EQRs and EQCs were calculated by our co-authors using country-specific metrics/indices for the invertebrate data they provided (country-specific methods detailed in Supplementary Table 1). We used the EQCs as a policy-relevant indication of the status of a community, whereas we used the EQRs in most statistical analyses because they are continuous rather than discrete and thus represent ecological quality more precisely.

Common community metrics

We calculated six community metrics for each river site and year: (i) abundance (number of individuals); (ii) taxon richness (number of taxa); (iii) evenness measured using Pielou's index[63]; (iv) diversity measured using the Shannon index[64]; and (v/vi) temporal turnover measured as the % difference in the proportional abundance of each taxon between consecutive years[8] and between each year and the first year[27] based on the Sørensen index. We chose these metrics because all are commonly used (or advocated for use) in biodiversity analyses and biomonitoring. Using multiple metrics also allowed us to examine the link between ecological quality and different aspects of the invertebrate community.

Biomonitoring indices of water and habitat conditions

We calculated eight invertebrate biomonitoring indices that can indicate changes in water quality and habitat conditions (detailed in Extended Data Table 1). Three indices respectively reflect the (i–iii) abundance, richness, and proportion (% of the community) of Ephemeroptera, Plecoptera, and Trichoptera (EPT), which encompass species that are often the most sensitive to anthropogenic impacts. Higher EPT values indicate the community contains more sensitive taxa. Two additional indices, (iv) the Average Score Per Taxon (ASPT) index and (v) the Saprobic Index, reflect expert assessments of taxon-specific tolerances to anthropogenic impacts, usually chemical or organic pollution. Higher values of the former and lower values of the latter indicate the community contains more pollution-sensitive taxa. Lastly, we included (vi) the Community Temperature Index, which reflects preferences for wider versus narrower temperature ranges[65]; (vii) the proportion (%) of littoral taxa, which can reflect community responses to flow alteration; and (viii) the Rhithron feeding type index, which reflects changes in the proportional abundance of different feeding guilds based on the assumption that certain guilds dominate in more impacted rivers. All indices are commonly used in European river biomonitoring[66], except for the Community Temperature Index which we included as an indicator of climate warming despite such indicators not yet being commonly used.

Statistical analyses

We split our analyses into three parts: (1) a continental-scale analysis that examined overall temporal ecological quality trends and their relationships to the metrics/indices across countries; and (2) a country-scale and (3) a site-scale analysis that examined variability in these trends and relationships at finer spatial scales. All analyses were performed in R version 4.2.0[67].

To quantify continental-scale changes in ecological quality, we modeled temporal trends in EQCs and EQRs across countries using GAMMs, which enable modeling non-linear trends through time. The response variable for these models was the EQC or EQR for each site and year. The predictor variables included a smoothed term for year modeled using thin-plate regression splines and a basis dimension of $k = 10$, which we confirmed via comparisons to the e.d.f. and based on whether the relationship changed when the basis dimension was increased. We also included a random slope and intercept term for country to help control for differences among countries in sampling methods and effort, and random intercept terms for sampling year and sampling month to control for non-independence among samples collected from the same years and months. Additionally, we included a first-order autoregressive structure to control for temporal autocorrelation in samples collected from the same site in consecutive years. We found no strong evidence for spatial autocorrelation (Supplementary Figs. 8 and 9). Significance ($P < 0.05$) of the smoothed year term in the finalized models was assessed with Wald tests.

To delineate continental-scale relationships between ecological quality and the community metrics and biomonitoring indices, we combined redundancy analysis (RDA) with GAMMs. We used the RDA to identify which metrics/indices were most related to changes in ecological quality and then used GAMMs to quantify the shape and strength of these relationships. The RDA modeled similarities (based on Euclidean distance) in the community metrics and biomonitoring indices across all sites and years in relation to the EQRs (excluding the ASPT and Saprobic Index which are not calculated in all countries). Abundance was $\log_{10}$-transformed and all metrics were converted to *z*-scores prior to analysis (i.e., centered to their country-specific means and standard deviations) to enable comparison of metrics with different country-specific units or ranges, such as abundance. We identified the variables most related to ecological quality based on their loadings onto RDA axis 1, i.e., the dimension representing changes in the EQRs. Relationships between EQRs and metrics with the highest loadings were then confirmed using GAMMs that included the same random effects and other control variables as the continental-scale models.

To quantify country-scale temporal change in ecological quality and its relationships to the community metrics and biomonitoring indices, we analyzed the data for 15 separate countries that had samples from at least ten sites (comprising 99% of our dataset), thus providing enough information to parameterize models for each country. We modeled temporal trends in EQCs and EQRs within each country using GAMMs following the methods used in the continental-scale analysis. We also conducted 15 RDAs that related all applicable metrics/indices for each country to their respective EQRs and used GAMMs to further examine these relationships.

To quantify the site-scale relationships between ecological quality and the community metrics and biomonitoring indices, we calculated the slopes of temporal change in the EQRs and metrics/indices for each site. Slopes were calculated using robust regressions[68] to downweight the importance of data from the first and last years, which can strongly influence slope estimates in time series analyses[21,29]. We then related the EQR slopes to the associated slopes for each community metric and biomonitoring index at each site using linear mixed models. These models included a random slope and intercept term for each country and the contribution of each site was weighted by the $\log_{10}$-transformed inverse of the summed squared standard errors of its slope estimates to ensure that slopes with more error contributed less to modeled relationships.

Data availability

All community metrics, biomonitoring indices, and ecological quality data needed to reproduce our analyses are publicly available from Figshare at https://doi.org/10.6084/m9.figshare.24486769

Code availability

All code used for our analyses is available upon request.

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Author Contributions Statement

JSS and PH conceived the study. EARW cleaned the data and JSS performed the analyses. JSS and PH wrote the majority of the manuscript. FA, MA-C, JA, NJB, LiB, JB, LuB, NB, MC-A, ZC, EdE, AD, GD, TEE, VE, MJF, MFe, MFl, MAEF, RF, PLMG, JH, DH, K-LH, SCJ, RKJ, LK, BK, LL, AL, PL, AWL, BGM, TM, DO, RP, VP, PP, FP, MP, JJR, RBS, AS-K, AlS, AgS, MS, RS, HT, VT, IT, RV, GáV, GaV, RCMV, and SV provided invertebrate data or contributed to calculating ecological quality values for their respective countries, and all edited the manuscript.

Competing Interests Statement

Alberto Scotti is affiliated with APEM Ltd., which is an environmental consultancy company, although they provided no funding for this study. No other authors have competing interests.

Figure Legends/Captions

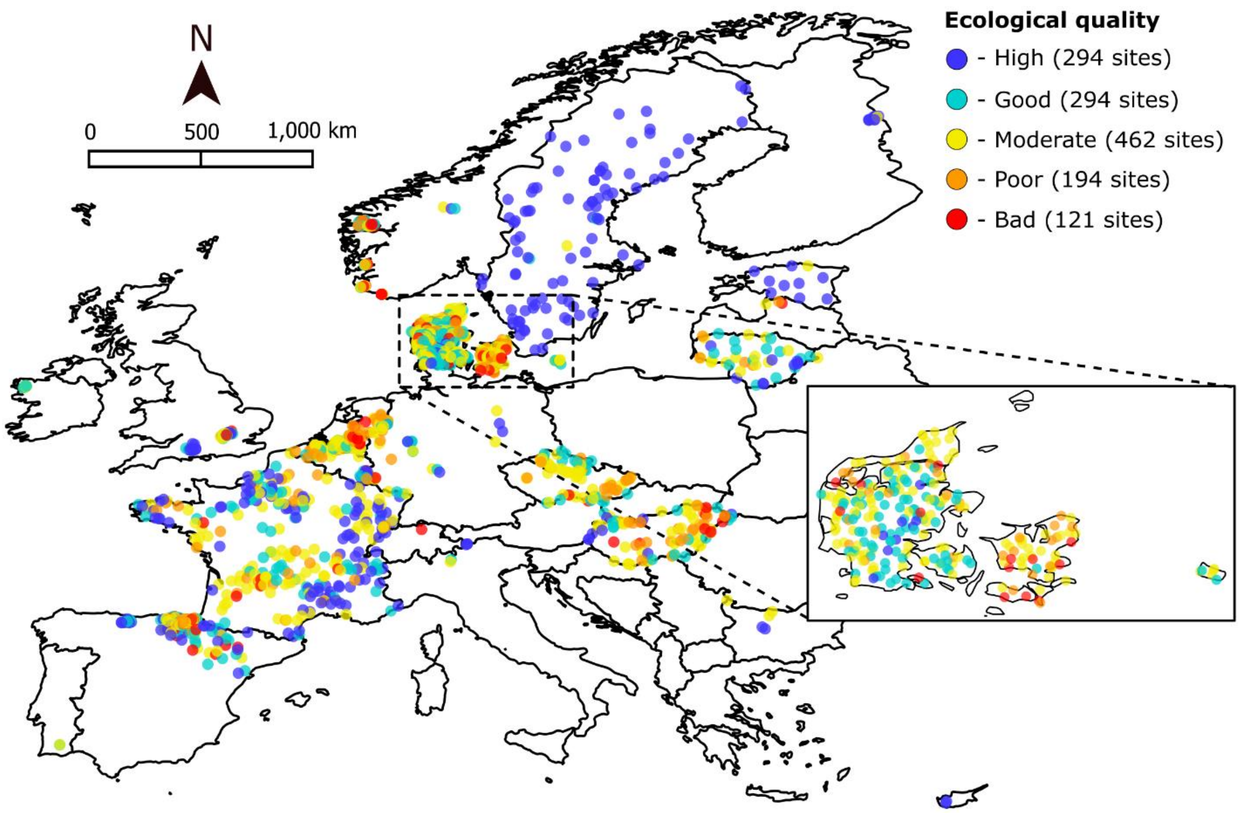


Fig. 1: Locations and ecological quality of 1,365 river sites across Europe. Site colors indicate biomonitoring assessments of the ecological quality of the invertebrate community in the first year of sampling (calculated as the Ecological Quality Class, EQC; see *Methods*). The EQCs of some densely clustered sites are hidden, as illustrated for Denmark. © EuroGeographics for the administrative boundaries[24].

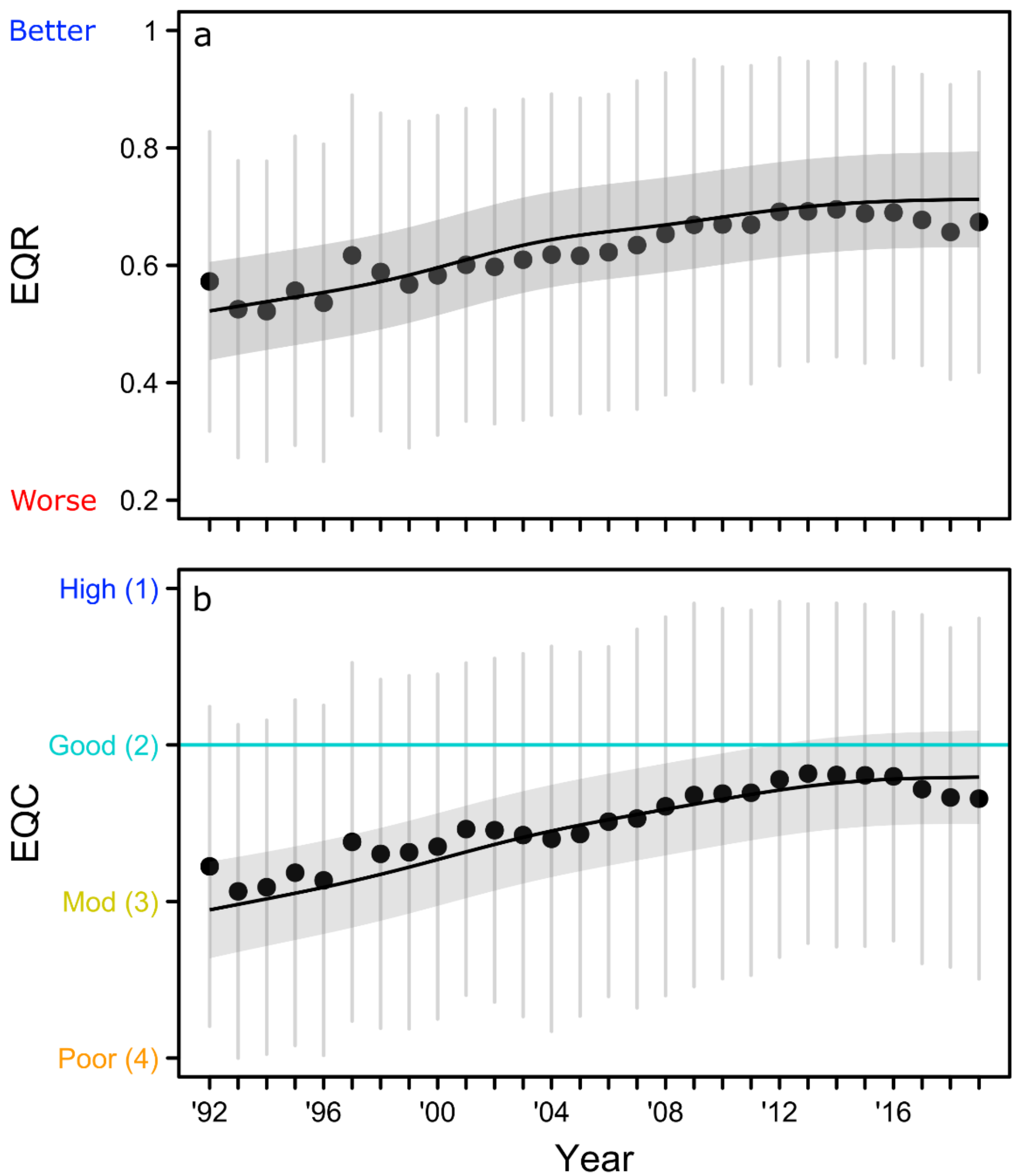


Fig. 2: Continental-scale trends in ecological quality. Trends in **a**, EQRs (n = 19,660) and **b**, EQCs ('Mod' = moderate; n = 19,697) across 1,365 European riverine invertebrate communities during 1992–2019. Black points and grey vertical lines respectively indicate the annual means and standard deviations. Fitted relationships (black line) and 95% confidence intervals (grey background) were based on generalized additive mixed model output. The European Union Water Framework Directive target of a 'good' EQC is indicated by a light blue line in **b**. The 'bad' EQC (class 5) is not plotted.

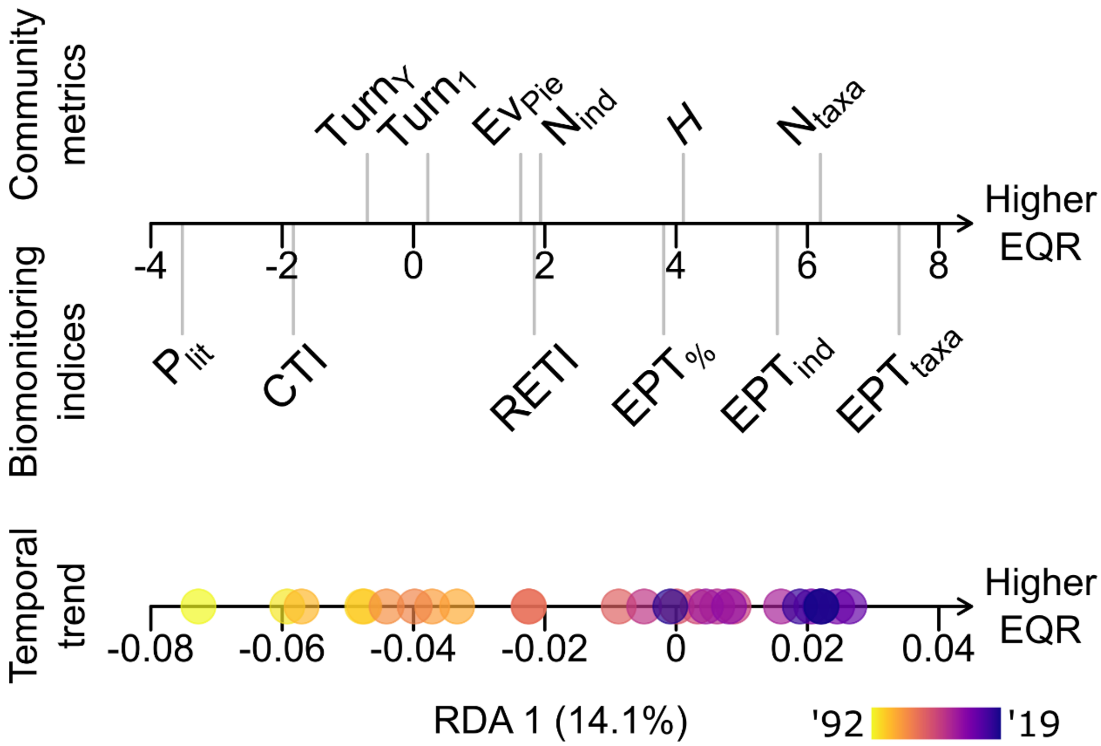


Fig. 3: Continental-scale links between ecological quality, community metrics, and biomonitoring indices. RDA of the continental-scale relationship between EQRs (black arrows) and the community metrics and biomonitoring indices (upper arrow); temporal trends in metrics/indices are also shown during 1992–2019 (lower arrow). Metrics/indices with higher or lower scores on RDA axis 1 indicate stronger relationships to ecological quality, with 0 indicating no relationship. The community metrics comprise abundance (N_{ind}), richness (N_{taxa}), evenness (Ev_{Pie}), Shannon diversity (*H*), and temporal turnover between consecutive years ($Turn_Y$) and compared to the first year ($Turn_1$). The biomonitoring indices comprise the total abundance (EPT_{ind}), and proportion ($EPT_{\%}$) and richness (EPT_{taxa}) of EPT, in addition to the Community Temperature Index (CTI), the proportion of littoral taxa (P_{lit}), and the Rhithron feeding type index (RETI; see Extended Data Table 1). Temporal trends are visualized as the centroid position of all sites in each year and are colored from earlier (yellow) to later (purple) years.

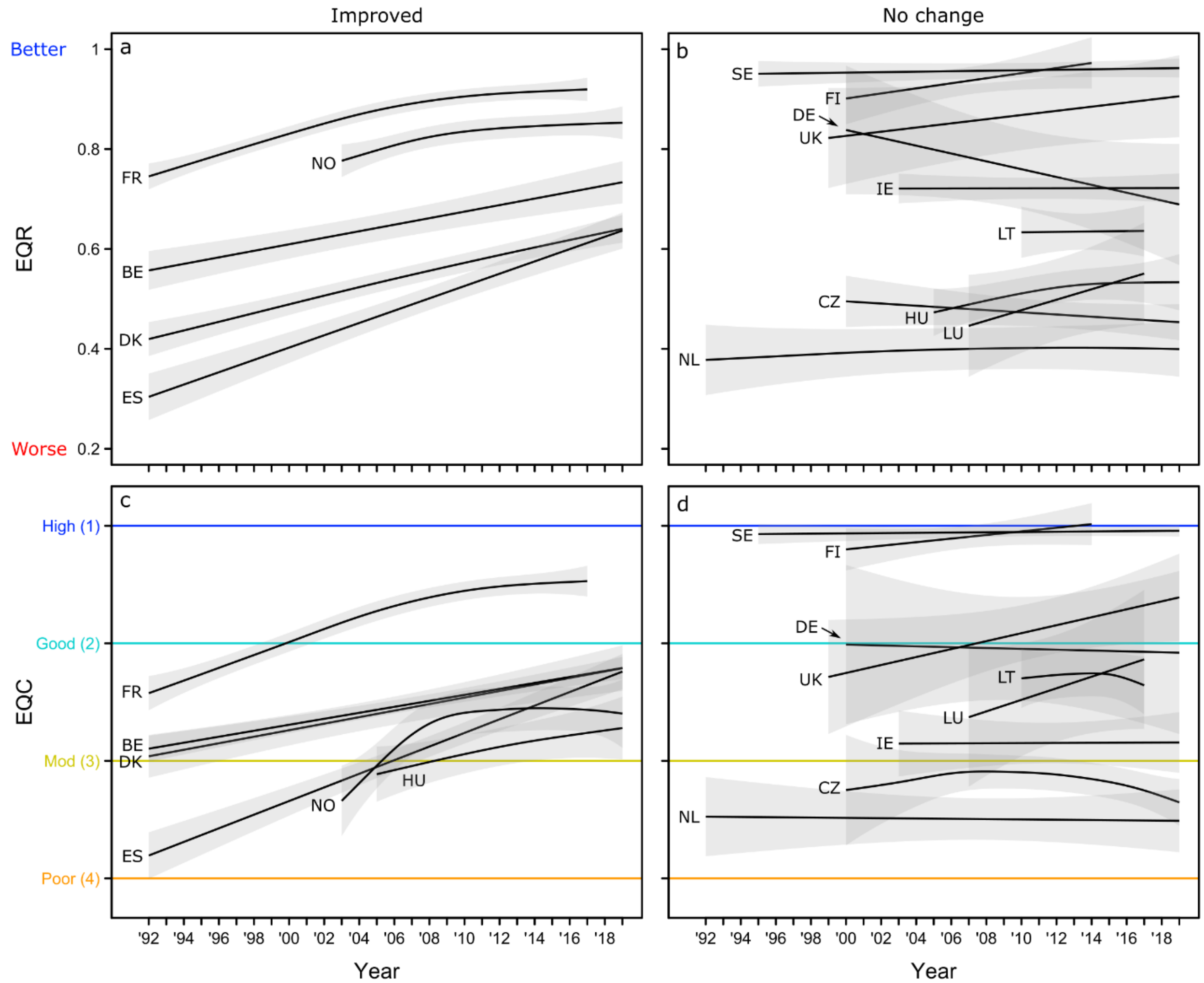


Fig. 4: Country-scale trends in ecological quality. Temporal changes in **a, b** EQRs and **c, d** EQCs across European riverine invertebrate communities from 15 countries during 1992–2019. Fitted relationships (solid lines) and 95% confidence intervals (grey backgrounds) are based on GAMM outputs for Belgium (BE), Czechia (CZ), Denmark (DK), Finland (FI), France (FR), Germany (DE), Hungary (HU), Ireland (IE), Lithuania (LT), Luxembourg (LU), the Netherlands, (NL), Norway (NO), Spain (ES), Sweden (SE), and the UK. Countries in **a, c** have statistical evidence for improvements over time, whereas those in **b, d** have no evidence for change. EQC categories (**c, d**) are illustrated using colored lines for 'high' (dark blue), 'good' (light blue), 'moderate' (yellow), and 'poor' (orange) classes. The 'bad' EQC (class 5) is not plotted.

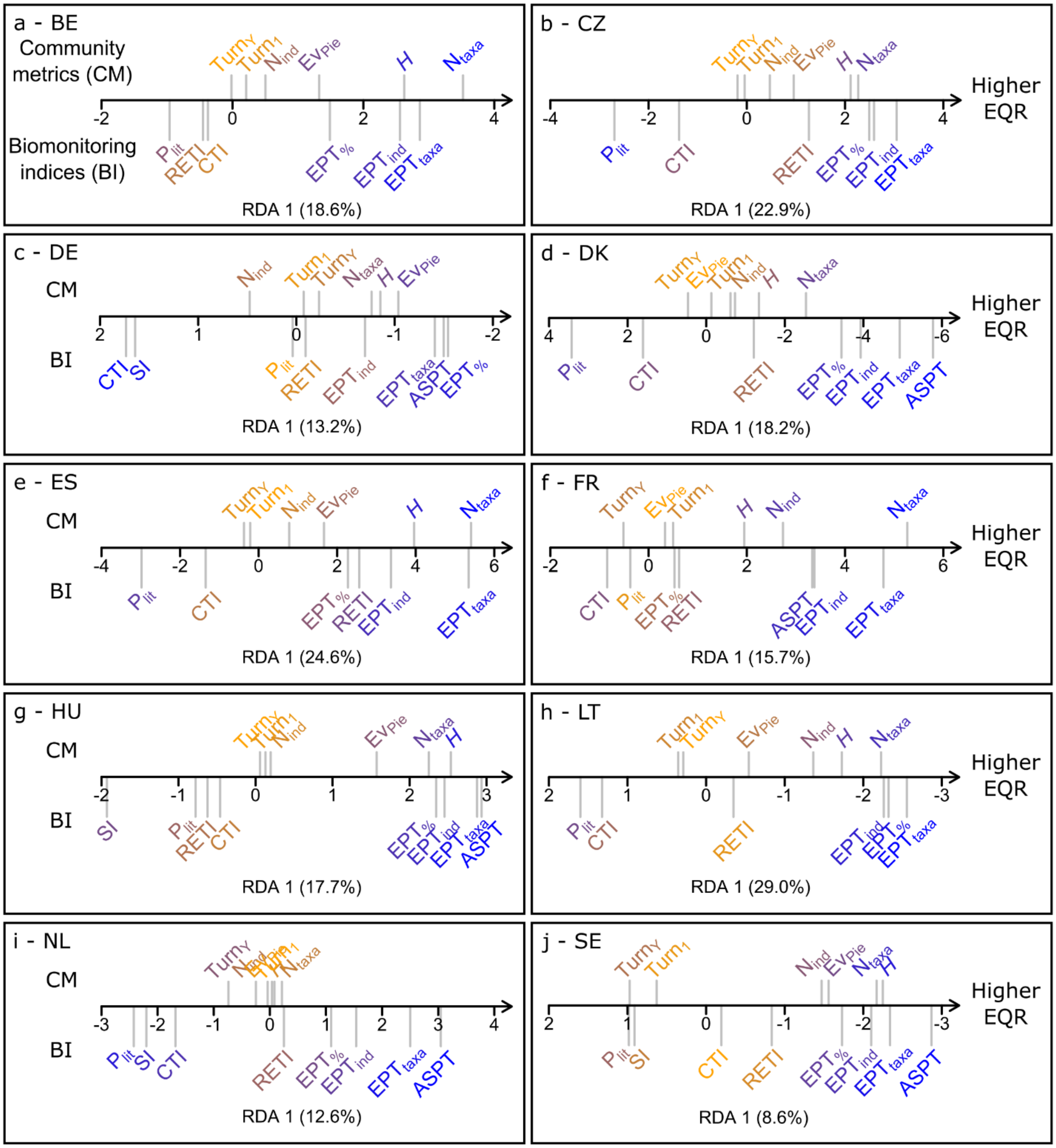


Fig. 5: Country-scale links between ecological quality, community metrics, and biomonitoring indices. RDA of the relationship between EQRs (black arrows) and community metrics and biomonitoring indices for **a**, BE, **b**, CZ, **c**, DE, **d**, DK, **e**, ES, **f**, FR, **g**, HU, **h**, LT, **I**, NL, and **j**, SE. Only the ten countries with the most comprehensive datasets are plotted (see Extended Data Fig. 2 for the other countries). The community metrics comprise N_{ind}, N_{taxa}, Ev_{Pie},

H, Turn_{Y} and Turn_{1}. The biomonitoring indices comprise EPT_{ind}, $\mathrm{EPT}_{\%}$, EPT_{taxa}, CTI, P_{lit} and RETI, in addition to the Average Score Per Taxon (ASPT) index and the Saprobic Index (SI; see Extended Data Table 1). Metrics and indices are colored from orange to blue based on their respective weaker to stronger relationships to ecological quality, quantified based on their loadings on RDA axis 1.

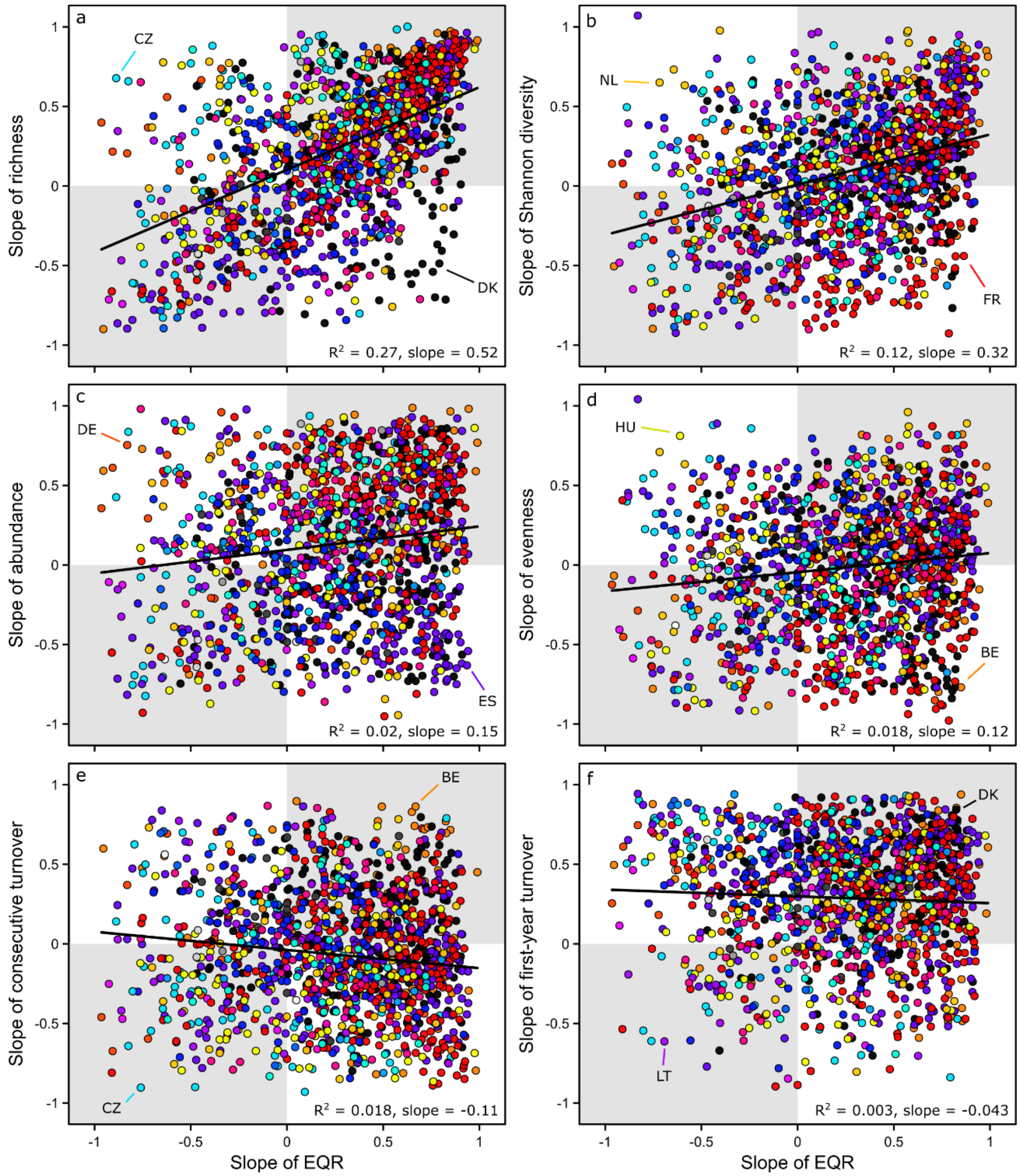


Fig. 6: Site-scale links between ecological quality and community metrics. Relationships between the EQR slopes at each site and the slopes of **a**, taxon richness, **b**, Shannon diversity, **c**, abundance, **d**, evenness, **e**, temporal turnover between consecutive years, and **f**, temporal turnover between each year and the first year. Sites with matching ecological quality and metric trends are in the grey shaded areas, whereas opposing relationships are in the white areas. Sites

are colored by country, and some example countries with sites that exhibit strong opposing relationships to the overall trend are indicated with arrows (BE: Belgium; CZ: Czechia; DE: Germany; DK: Denmark; ES: Spain; FR: France; HU: Hungary; LT: Lithuania; NL: the Netherlands). Best-fit lines (black), R^2 values, and estimated slopes are based on the associated linear mixed models.

Extended Data Table Legends/Captions

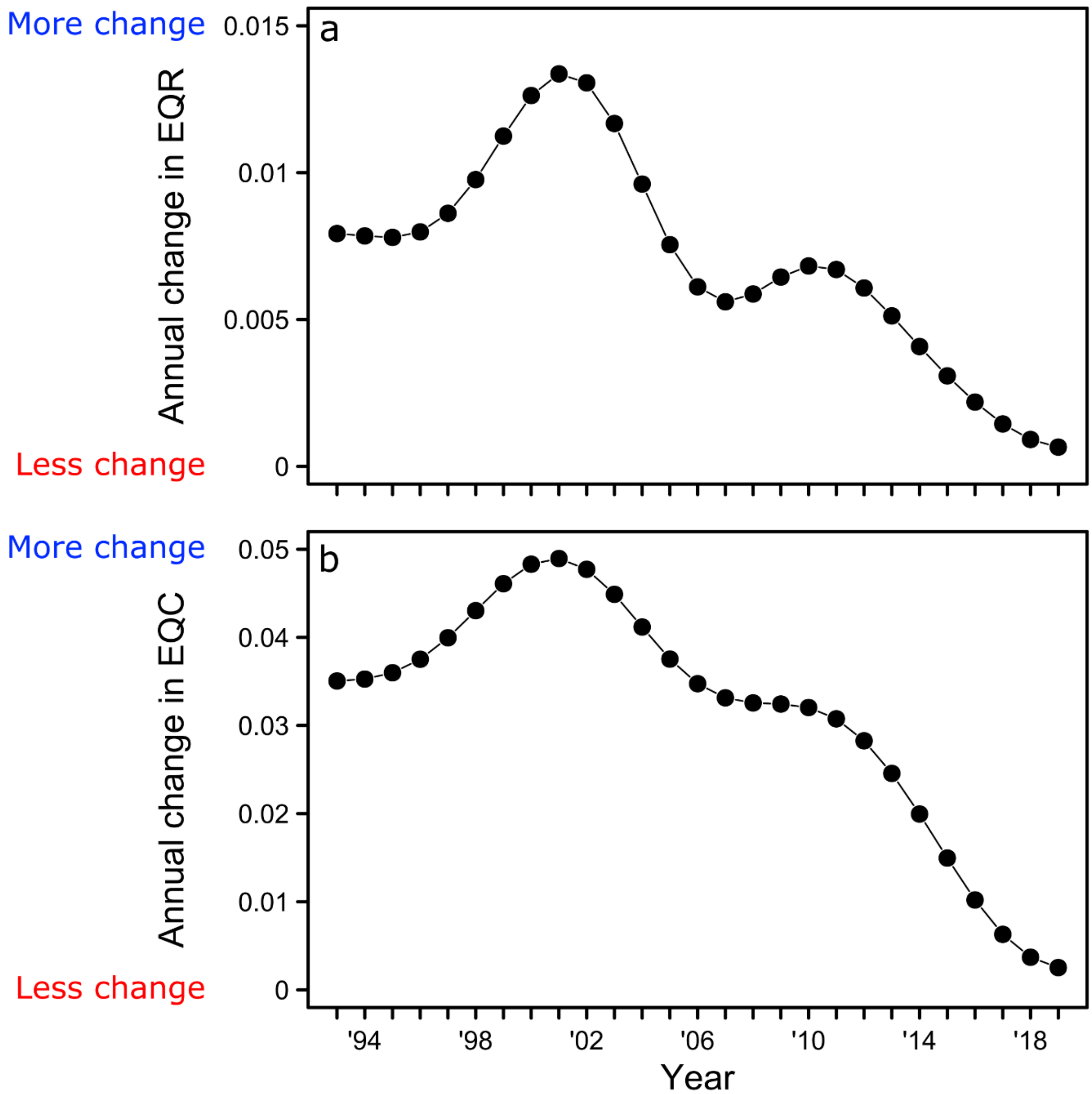
Metrics	Abbreviation	Meaning	Specific stressors	Number of countries
Ephemeroptera, Plecoptera, and Trichoptera	EPT	The abundance, richness, and proportion of EPT taxa[65]. Higher values indicate more EPT taxa, which tend to occur in less-impacted rivers.	–	23
Average Score Per Taxon	ASPT	Average of pollution-tolerance scores for present taxa (also weighted by abundance in the UK). Higher values indicate communities comprising taxa associated with less-impacted rivers.	–	14
Saprobic Index	SI	Abundance-weighted index of taxon-specific saprobic values. Higher values indicate communities comprised of taxa that tend to occur in enriched rivers.	Organic pollution[65]	8
Community Temperature Index	CTI	Abundance-weighted average of taxon-specific preferences for temperature variability. Higher values indicate communities characterized by taxa with warmer and wider temperature preferences.	Warming[64]	23
Proportion of littoral taxa	P_{Lit}	Proportion of the invertebrate community comprising taxa with any affinity for littoral habitats (based on the stream zonation trait from www.freshwaterecology.info). Higher values indicate more littoral taxa, which tend to prefer slower currents.	Flow alteration[65]	23
Rhithron feeding type index	RETI	Proportion of feeding types associated with more upstream habitats, specifically grazers, shredders, or taxa that feed on woody debris[65]. Higher values indicate communities comprised of taxa that tend to prefer less-impacted rivers.	–	23

Extended Data Table 1: List and description of invertebrate biomonitoring indices. These indices were used to determine whether changes in ecological quality corresponded to shifts in sensitive versus tolerant invertebrates, which provides supporting evidence that ecological quality reflects general anthropogenic impacts on river water and habitat quality. Some indices can also indicate the effects of specific stressors. We also list the number of countries for which each index was calculated out of 23 total in our dataset. References for the ASPT indices are provided in Supplementary Table 1.

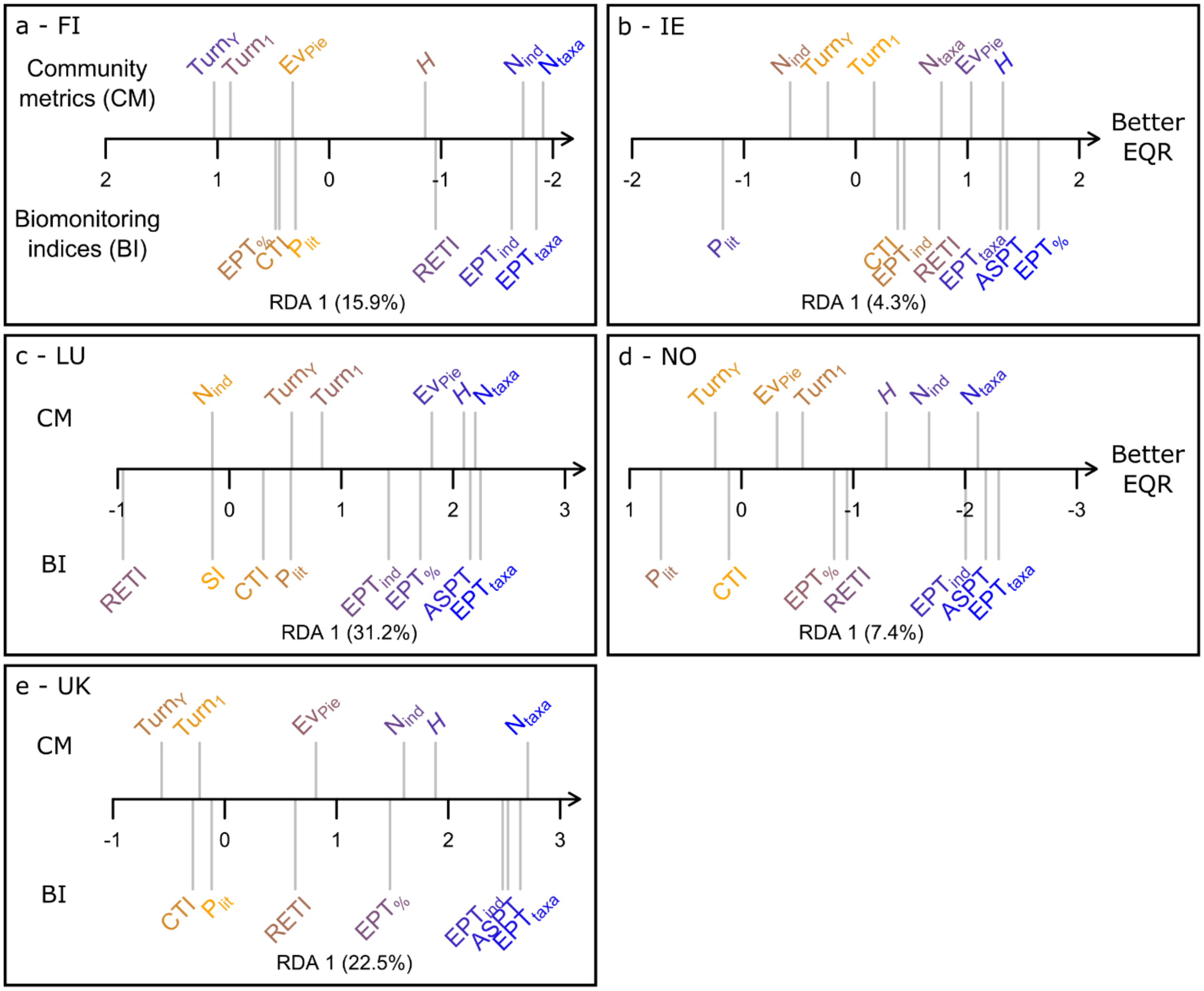
Metric	Matching	No match	Opposing
Abundance	13%	40%	6%
Evenness	6%	45%	6%
Richness	24%	31%	2%
Shannon diversity	11%	43%	3%
Turnover (consecutive)	7%	45%	4%
Turnover (first-year)	4%	43%	18%

Extended Data Table 2: Site-scale variability in the relationship between ecological quality and community metrics. Proportion of sites (out of 1,365) that match the overall relationship between the slope of a given community metric and the slope of the Ecological Quality Ratio (EQR), compared to those that exhibit no matching relationship (either the metric changes when ecological quality does not or vice versa), or opposing responses. For example, the overall relationship between the slopes of richness and the EQRs is positive (Fig. 6a) and 24% of sites match this trend. Similarly, the overall relationship between the slopes of consecutive turnover and the EQRs is negative, specifically turnover tends to decline as ecological quality improves (Fig. 6e), and 7% of sites match this relationship. Note that ‘change’ in a given metric or the EQRs is determined as a slope value whose confidence intervals do not overlap 0.

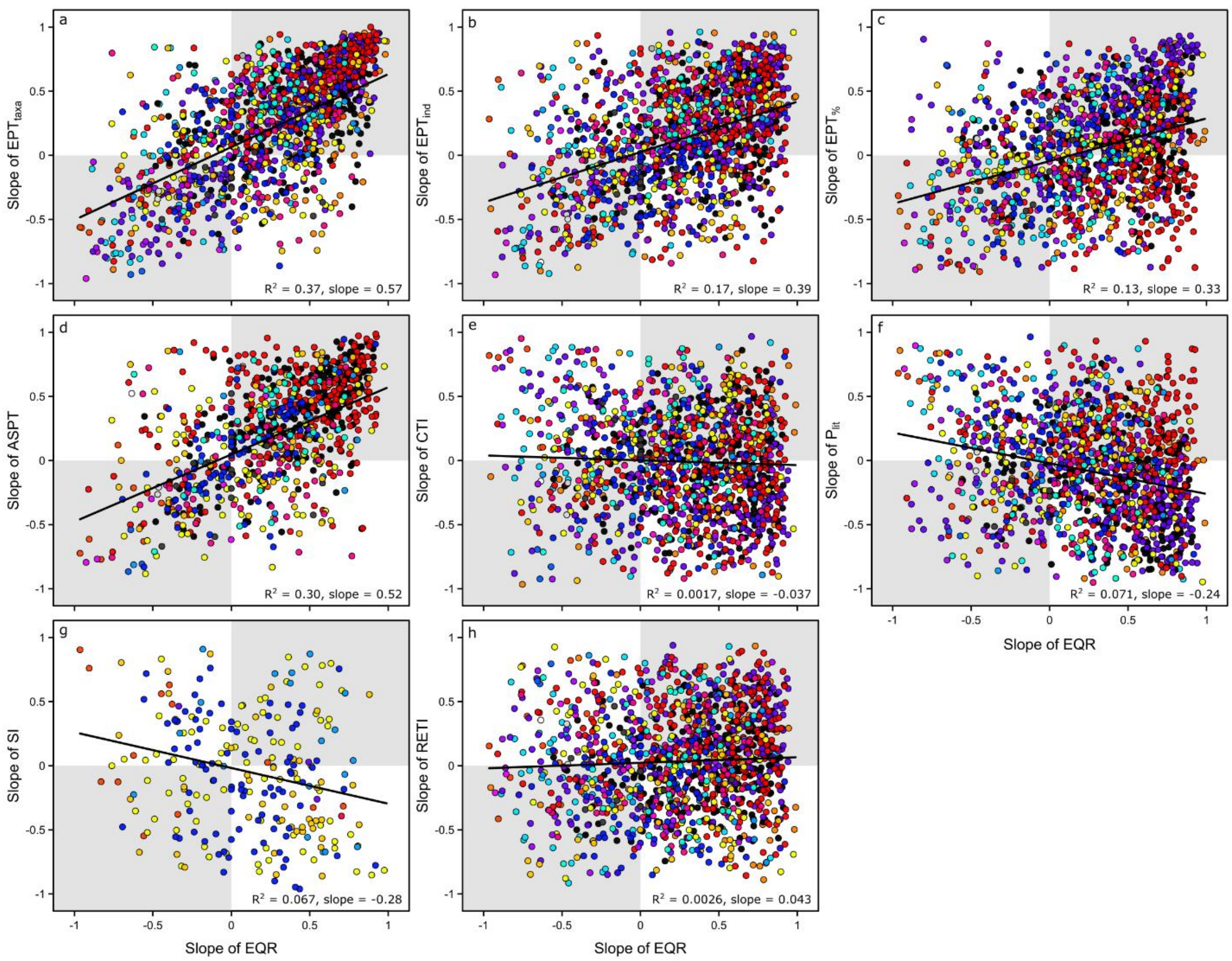
Extended Data Figure Legends/Captions



Extended Data Fig. 1: Year-to-year changes in ecological quality. Differences in the predicted (**a**) EQRs and (**b**) EQCs between each year and the previous year during 1993–2019. For example, the 1993 values are the absolute differences in the predicted EQRs/EQCs between 1992 and 1993. Thus, values closer to 0 indicate less change between successive years. Predicted values for the EQRs and EQCs were obtained from their respective generalized additive mixed models (i.e., the fitted relationships in Fig. 2).



Extended Data Fig. 2: Country-scale links between ecological quality, community metrics, and biomonitoring indices. Redundancy Analyses (RDAs) of the relationship between the Ecological Quality Ratios (EQRs; black arrows) and the community metrics and biomonitoring indices for (**a**) Finland (FI), (**b**) Ireland (IE), (**c**) Luxembourg (LU), (**d**) Norway (NO), and (**e**) the United Kingdom (UK). The community metrics comprise abundance (N_{ind}), richness (N_{taxa}), evenness (Ev_{Pie}), Shannon diversity (*H*), and temporal turnover between consecutive years ($Turn_{Y}$) and compared to the first year ($Turn_{1}$). The biomonitoring indices comprise the total abundance (EPT_{ind}), proportion ($EPT_{\%}$), and richness (EPT_{taxa}) of Ephemeroptera, Plecoptera, and Trichoptera, in addition to the Community Temperature Index (CTI), the proportion of littoral taxa (P_{lit}), and the Rhithron feeding type index (RETI; all indices are described in the *Methods* and Extended Data Table 1). Metrics and indices are colored from orange to blue based on their loadings on RDA axis 1, with blues indicating stronger relationships to ecological quality.



Extended Data Fig. 3: Site-scale links between ecological quality and biomonitoring indices. Relationship between the temporal slope of the Ecological Quality Ratio (EQR) at each site and the slope of (**a**) the richness of Ephemeroptera, Plecoptera, and Trichoptera (EPT_{taxa}), (**b**) EPT abundance (EPT_{ind}), (**c**) the proportion of EPT taxa ($EPT_{\%}$), (**d**) the Average Score Per Taxon (ASPT) index, (**e**) the Community Temperature Index (CTI), (**f**) the proportion of littoral taxa

(P_{lit}), (**g**) the Saprobic Index (SI), and (**h**) the Rhithron feeding type index (RETI). Sites are colored by country and sites with matching ecological quality and biodiversity trends are in the gray shaded areas, whereas opposing relationships are in the white areas.

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