Title: Multi-decadal improvements in the assessed quality of European stream invertebrate communities are inconsistently reflected in biodiversity metrics

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Abstract

Humans negatively impact terrestrial, marine, and particularly freshwater ecosystems, but metrics commonly used to summarize changes in associated biological communities (e.g., abundance or richness) often fail to reflect this degradation. To determine why, we quantified annual trends (1992–2019) in stream ecological quality (representing anthropogenic degradation) based on 1,234 invertebrate communities from 22 European countries. We then analyzed whether changes in quality were consistently reflected in changes in community abundance, biodiversity, or composition at the continent-scale, the country-scale for 14 countries with sufficient data, and within individual sites. The ecological quality of European streams improved from 1992 until the 2010s, likely owing to improved water quality and habitat conditions. However, improvements plateaued during the 2010s, suggesting persisting, intensifying, or emerging stressors. Temporal quality improvements were most related to increases in taxon richness, particularly at the continent- and country-scale, but responses were highly variable at the site-scale. We found no consistent relationship between ecological quality and community abundance, diversity, or compositional turnover. These results indicate that many community metrics may not consistently reflect degradation because communities vary in how they respond to anthropogenic impacts. Caution is therefore warranted when selecting and using such metrics

to make general inferences about anthropogenic change.

Introduction

Reports of human-driven species extinctions[1,2] and environmental degradation[3,4,5] have spurred concerns of widespread anthropogenic impacts on Earth's ecosystems, particularly in freshwaters[6]. Despite these concerns, several large-scale temporal studies of freshwater, terrestrial, and marine communities have found no evidence of systematic biodiversity loss[7–14]. These studies commonly use local-scale trends in community metrics, such as total abundance (or biomass), taxon richness (i.e., α-diversity), evenness, and temporal turnover (i.e., temporal β-diversity), to assess broad-scale biodiversity change[7,8,9,10,12,13] and infer its anthropogenic drivers[10,12,13]. However, the usefulness of these metrics is debated because the baseline data necessary to determine whether they are degrading, improving, or undergoing natural fluctuations are notoriously lacking[15,16]. Additionally, community metrics can suffer from issues of scalability in which they may respond consistently to degradation at finer spatial scales (e.g., within a region), but inconsistently when different regions, taxa, or habitats are combined in broader-scale analyses[17]. For example, ecosystem degradation can drive declines in community abundance and richness in some localities[4,18,19], whereas others may exhibit no overall change (e.g., if species gains match losses[20]) or even exhibit increases when tolerant species establish new populations[18,21]. Local-scale community metrics may therefore respond to degradation in different ways in different places, thus potentially explaining the often equivocal or contradictory results when local trends are pooled in broad-scale biodiversity studies.

Using local-scale community changes to draw broader-scale inferences about anthropogenic impacts requires first establishing whether any community metrics can consistently reflect degradation across spatial scales. Doing so requires quantifying degradation across multiple communities spanning broad geographic areas, which is challenging owing to the previously discussed lack of baseline data. Furthermore, accurately quantifying temporal trends is complicated by the need for high quality time-series data[22,23] collected from similar taxa, habitats, and sampling methodologies to ensure comparability of communities and stressors across regions[15,16,24]. A feasible solution is to use organisms commonly collected by biomonitoring programs, such as stream invertebrates[25], to relate community metrics to anthropogenic degradation. Biomonitoring programs address the issue of missing baselines by comparing sampled communities to established least-impacted or 'reference' communities, with degradation represented as the degree of deviation from reference conditions, termed 'ecological quality' (sensu the European Union Water Framework Directive; WFD[26]). Biomonitoring data on stream invertebrate communities has also been collected for decades following standardized methodologies[25], enabling robust time-series analyses and promoting comparability across space and time. Moreover, invertebrate biomonitoring indices used to summarize changes in sensitive taxa (e.g., Ephemeroptera, Plecoptera, and Trichoptera) or traits (e.g., functional feeding groups) can help indicate the environmental drivers of community change[25,27].

Here, we used stream invertebrate time series collected from 1,234 sites across 22 European countries (Fig. 1) following WFD-compliant assessment methods to: (1) quantify temporal trends (1992–2019) in ecological quality at continent, country, and site spatial scales; and (2) relate these trends to common metrics describing community abundance, biodiversity (e.g., richness), and composition, and common biomonitoring indices to indicate potential environmental drivers. Our results offer new insights into the benefits and detriments of upscaling local community changes into broader-scale inferences about anthropogenic degradation. Additionally, we provide the first European-scale assessment of long-term trends in freshwater ecological quality.

Results

Continental-scale trends in ecological quality

Ecological quality was measured using Water Framework Directive (WFD[26]) Ecological Quality Ratios (EQR) and Ecological Quality Classes (EQC). EQRs are a continuous ratio of the similarity between sampled and reference invertebrate communities, with higher values equaling higher similarity and thus less anthropogenic degradation. EQRs typically range from 0 (0% similarity) to 1 (100% similarity), although the exact range can vary by country. The EQRs are then 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 waterbody has satisfied the WFD target of achieving a 'good' or 'high' quality status, whereas EQRs are better suited for statistical analyses because they provide a more precise representation of ecological quality. Some uncertainties exist in the degree to which EQRs/EQCs represent all anthropogenic environmental changes[28]. However, they are well-established measures of general anthropogenic degradation[28] that are assumed to be comparable across countries[29].

Ecological quality (i.e., EQRs/EQCs) improved across our sites from 1992 until around the 2010s, as evidenced by significant year terms in models for both EQRs (n = 18,577, edf = 4.35, F = 82.28, P < 0.001) and EQCs (n = 18,594, edf = 3.24, F = 106.07, P < 0.001; Fig. 2). EQRs initially increased by around 0.04–0.065 standard deviations y^{-1}, with EQCs improving by about 0.035–0.05 classes y^{-1}. However, little to no change occurred after the early 2010s when

EQRs plateaued around 0.2 standard deviations above the long-term average and the EQCs at around 2.1, which is just below the target of a 'good' EQC value of 2 set by the WFD[26] (Fig. 2 and see Extended Data Fig. 1 for annual changes). 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 community metrics and biomonitoring indices

Ecological quality was moderately related to the community metrics and biomonitoring indices (based on a significant global permutation test; n = 18,572, $F_{1,18570}$ = 3,080.0, 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 increases in 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 index and the Saprobic Index which were not included because they are not calculated in all countries.

A possible caveat to these results is that, for certain countries, calculations of ecological quality incorporates some of the analyzed community metrics and biomonitoring indices, such as taxon richness and EPT richness (both of which are also correlated to one another). To test for the influence of this circularity, we removed the sites from countries that do so (around 30% of the total number) and repeated our analyses. The removals had no substantial influence on our principal results (Supplementary Figs. 2 and 3) and we therefore provide the results from the full dataset.

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 14 countries with enough data to parameterize individual models (representing 99% of the sites). The continental-scale temporal improvements in ecological quality were driven by improvements in communities from Belgium, Denmark, France, Norway, and Spain (Fig. 4 and Supplementary Tables 3 and 4). Seventy percent of the sampled communities from these countries were at the good or high-quality class in their most recent year of sampling. Modeled temporal relationships for the EQCs indicated improvements from EQC values of 3 to 2.2 in Belgium, from 2.9 to 2.2 in Denmark, from 2.4 to 1.5 in France, 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 ecological quality in the other countries, such as Ireland (EQCs remained stable around 2.8), the Netherlands (3.4), and Sweden (1.0; Fig. 4d). Based solely on trendlines, quality may be improving in Luxembourg (modeled EQCs change from 2.6 to 2.1 during 1992 through 2019), Hungary (3.1 to 2.7), Finland (1.2 to 1.0), and the UK (2.3 to 1.5), versus degrading in Germany (1.9 to 2.3) and Estonia (1.3 to 1.6; Fig. 4d). However, these patterns were non-significant (Supplementary Tables 3 and 4) with large confidence intervals (Fig. 4b, d).

Country-scale community metrics and biomonitoring indices

Taxon richness and Shannon diversity were the community metrics that exhibited the strongest relationships to changes in ecological quality in most countries (see 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.

5b), Denmark (Fig. 5c), and the Netherlands (Fig. 5h) compared to the other countries, with similarly weaker relationships for Shannon diversity in Denmark (Fig. 5c), France (Fig. 5e), and the Netherlands (Fig. 5h).

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 for which ASPT is calculated. Relationships to other indices were country-specific (see Supplementary Figs. 4–7 for statistics). For example, in Denmark (Fig. 5c), Spain (Fig. 5d), and the Netherlands (Fig. 5h), 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 (see Extended Data Table 1). Similarly, ecological quality was more strongly associated with the Community Temperature Index in the Netherlands (Fig. 5h), which may indicate a stronger influence of warming, and the Saprobic Index in Germany (Fig. 5b) and the Netherlands (Fig. 5h), which may indicate a stronger influence of organic pollution.

Site-scale trends in ecological quality, community metrics, and biomonitoring indices

Site-scale quality trends were often positive (Fig. 6; 40% with positive slopes that did not overlap 0), aligning with the general improvements shown in our other analyses. However, 55% of sites exhibited no strong evidence for change, indicating substantial site-scale variability in whether quality was changing. The ecological quality of 5% of all sites also tended to decrease through time, which encompassed sites in 15 (of 22) 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; note that all relationships are significant owing to the quantity of data). However, even the more consistent relationships varied widely among sites, as evidenced by generally low R^2 values. For example, 26% of sites exhibited the same direction of change in both richness and quality (here ‘change’ means a slope value whose confidence intervals do not overlap 0), but 30% exhibited no change in richness when quality changed or vice versa, and 2% exhibited opposing changes (Fig. 6a). 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 45% exhibited no response, i.e., either Shannon diversity did not change when 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 provide the first assessment of long-term changes in the ecological quality of stream invertebrate communities at the European scale. Ecological quality has generally improved albeit on average the required ‘good’ ecological status has still not yet been achieved. Freshwaters are among the ecosystems most strongly affected by anthropogenic degradation[30] and European rivers have been particularly impacted owing to a long history of urban and industrial development, poor municipal wastewater treatment, and hydromorphological alterations[31,32,33]. To address these impacts, various policies were introduced during the 1970s through 2000s to improve water quality for public health, to protect fisheries, to mitigate nutrient pollution, and to recover degraded habitats (e.g., via wastewater treatment[31,32]). The partial improvements we found in ecological quality during the 1990s through 2000s likely reflect the beneficial effects of these protective legislative efforts, particularly given their association to increased taxon richness and biomonitoring indices reflecting enhanced water quality and habitat conditions.

Despite policies to address freshwater degradation, we found that most sites never improved and of those that did their improvements plateaued after the early 2010s, indicating that extensive efforts are still needed to address stressors restricting recovery. Wastewater and point-source pollutants are likely targets, but focusing solely on these stressors may only produce initial improvements that then taper off[34] (as observed here) because other important stressors remain unaddressed, such as diffuse pollution from agricultural runoff and physical habitat modification[32,35]. Many stressors are also intensifying, such as climate change[36], salinization[37], microplastics[38], and invasive species[35], while others are emerging, such as newly developed and ecologically harmful pesticides and pharmaceuticals[39,40]. Efforts to address multiple stressors may therefore be required for recovery to progress. Management efforts also need to be better adapted to differences in local stressor types, their intensities, and interactions. For example, ecological quality in regions that exhibited no improvement, specifically in Germany and the Netherlands, may be constrained by organic pollution (as indicated by the association to the Saprobic Index in these regions). Waterbodies in these countries may therefore experience higher nutrient inputs, with diffuse agricultural pollution being an important driver[41,42], which may require more targeted or intensive management to control. Plateauing improvements may also be caused by a decline in the number of ecosystems that are capable of further recovery, such as ecosystems that are permanently damaged (e.g., persistent pollutants[43] or extirpated species[44]) or that are already in good or better condition (e.g., consistently high quality sites in Sweden). In summary, research is required to determine the specific reasons why many European stream communities have generally failed to improve, if further recovery is even possible, and how to resume the recovery process.

Improvements in ecological quality exhibited the strongest relationships to increases in taxon richness across all spatial scales, suggesting that richness could be a broad-scale indicator of anthropogenic degradation. Richness is commonly used in biodiversity and biomonitoring assessments for a range of biotic groups partly owing to the comparative ease of data collection and metric calculation[45,46]. However, its usefulness can be limited by its inability to reflect compositional changes, because its response depends on the spatial scale of study, and the baseline data to contextualize observed changes is notoriously lacking[15,16,20,47]. Despite these limitations, our results suggest that richness trends may provide meaningful insights into general patterns of anthropogenic degradation across broad spatial scales (similar results have been reported elsewhere[4]). This relationship likely occurred in our dataset because better stream conditions can increase richness by increasing habitat quality, quantity, and heterogeneity[48,49] and by increasing the presence of pollution-sensitive species[25]. This association may apply beyond stream invertebrates given that taxon richness is often positively related to habitat quality in other taxonomic groups[4,50,51]. Studies that have identified contrasting local-scale changes in the richness of other taxa across large geographic areas (e.g., plants, fishes, birds, mammals, and terrestrial insects[7–10,18]) may therefore similarly indicate no general pattern of anthropogenic degradation. These studies (including this study) still suffer from different sampling biases, such as having little to no data from outside North America, Europe, or Oceania[15,16]. Further work is therefore required to evaluate the usefulness of richness as a broad-scale indicator of degradation across different major biogeographic regions.

While richness was broadly related to ecological quality, this relationship was highly variable at the site-scale, with more sites exhibiting no response or opposing responses between richness and quality. No change in richness as ecological quality changes could occur at sites where taxa losses are balanced by gains[20]. Alternatively, richness may change even when quality does not due to natural extinction and immigration processes[20] or human-driven species introductions and range expansions[18]. We also observed some opposing relationships. For example, sometimes degradation was associated with higher richness, which can occur when degradation facilitates non-native establishment[52], or sometimes improvement was associated with lower richness, which may occur when losses of tolerant taxa outweigh gains in sensitive taxa[21]. The spatial variability we observed highlights that richness may be a sufficient indicator of general degradation at broader spatial scales, but this is not necessarily true at finer scales. Consequently, studies may not be able to break down broader-scale richness trends into finer-scale categories, such as by regions or habitat types[7,10,12], and assume that richness responds in the same way to degradation across categories[17]. Accounting for variability in richness responses may be best accomplished through multimetric approaches that combine changes in two or more metrics (e.g., richness and a composition metric). This approach captures how different aspects of each biotic community are responding and may therefore more reliably reflect degradation at both broader and finer spatial scales, thus better informing management and conservation efforts[53].

Most community metrics (Shannon diversity, abundance, evenness, and temporal turnover) exhibited little to no general relationship to ecological quality. This result shows how anthropogenic impacts can fail to translate to consistent changes in many common community metrics across broader spatial scales. Such inconsistency may be more pronounced for metrics compared across communities from different taxonomic groups or habitat types[7–9,11–13], given the high variability we found even within approximately the same system (i.e., invertebrates sampled from the stream bottom following similar methodologies). Community metrics other than those we examined may provide more consistent insight into anthropogenic change, such as genetic diversity, functional diversity, or trait composition[54–56]. However, responses in these types of metrics can be similarly variable across communities[11]. 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[19] or evenness[57]. Using community metrics to infer anthropogenic impacts therefore requires careful consideration of which metrics are the best indicators for the habitat types and taxa in question and what is the most suitable way to measure degradation. 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[58].

Our analyses have two principal limitations that we cannot address. First, although our results are supported by a robust dataset and match other reported conclusions about improvements in European freshwater communities[14,32], they are limited by the extent and duration of monitoring. For example, quality trends informed by more spatiotemporally extensive datasets are likely broadly representative of country-scale changes (e.g., Denmark and France), whereas trends informed by less spatially extensive datasets may be less robust (e.g., Ireland and Norway). Likewise, the limited duration of most monitoring programs means that we calculated ecological quality using reference ecosystems, which may not reflect the full level of anthropogenic impact compared to true historical baselines. Second, the biomonitoring indices we used are indirect measurements that only permit inferences of the likely environmental drivers of observed community changes. A similar issue applies to WFD methods of quantifying ecological quality via comparisons to reference ecosystems, which provides a general overview of anthropogenic impacts but can fail to identify all relevant stressors[28]. General indicators are sufficient to inform policy and legislative requirements, but identifying and addressing specific freshwater stressors can require more detailed investigations of multiple taxonomic groups (e.g., fishes, macrophytes, algae, plankton, etc.) and expanded environmental monitoring. Regardless of these caveats, our results show that many commonly used community metrics cannot consistently indicate anthropogenic impacts. Acknowledging and incorporating this variability into scientific analyses and monitoring programs is essential for identifying impacted communities and for protecting biodiversity in an era of global change.

Methods

Stream invertebrate data

We collated annual data on stream invertebrate community composition at 1,234 sites across 22 European countries via data requests to ecologists and environmental managers. The included waterbodies encompass a wide range of 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 eight years of data, with sampling conducted during the same seasons (any three consecutive months) and using the same methods within sites through time. Invertebrates were generally collected following Water Framework Directive (WFD) compliant methods across countries, i.e., primarily multi-habitat kick-net samples collected from the stream bottom. Taxa were identified to the family-, genus-, or species-level, although some were classified to intermediate (e.g., Chironominae at subfamily) or higher levels (e.g., Oligochaeta at subclass). 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 waterbodies to reach a status of 'good' or 'high' ecological quality[26]. The ecological quality of a waterbody is quantified using multiple environmental parameters and taxonomic groups, but here we focused specifically on ecological quality measured using the invertebrate community. Our co-authors used WFD-compliant methods to calculate the Ecological Quality Ratios (EQR) and Ecological Quality Classes (EQC) for their respective countries because each country uses different biomonitoring indices to represent ecological quality (detailed in Supplementary Table 1). We used the EQCs as a policy-relevant indication of quality, 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 site and year: (i) abundance (number of individuals per sample); (ii) taxon richness (number of taxa per sample); (iii) evenness measured using Pielou's index[59]; (iv) diversity measured using the Shannon index[60]; 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[20]. We chose these metrics because all are commonly used (or advocated for use) in biodiversity and biomonitoring. Using multiple metrics also allowed us to examine the link between ecological quality and different aspects of the invertebrate community.

Biomonitoring indices reflecting water quality and habitat conditions

We calculated eight invertebrate biomonitoring indices that can indicate changes in stream water quality and habitat conditions: the (i–iii) abundance, richness, and proportion (% of the community) of Ephemeroptera, Plecoptera, and Trichoptera (EPT); (iv) the Average Score Per Taxon (ASPT) index; (v) the Community Temperature Index; (vi) the proportion (%) of littoral taxa; (vii) the Saprobic Index; and (viii) the Rhithron feeding type index (described and referenced in Extended Data Table 1). These indices are based on observed associations between stream invertebrates and environmental conditions, such as which taxa vary along a gradient of organic enrichment, or from relationships between invertebrate traits and different anthropogenic stressors. All indices are commonly used in Europe in the biomonitoring of anthropogenic degradation in stream ecosystems[27], except for the Community Temperature Index which we included as an indicator of climate warming despite such indicators not yet being commonly used in European waterbody assessments.

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.

To quantify continental-scale changes in ecological quality, we modeled temporal trends in EQCs and EQRs across countries using generalized additive mixed models (GAMMs), which enable modeling of non-linear trends through time. The response variable for these models was the EQC or EQR for each site and year. The EQRs were also transformed to *z*-scores (i.e., centered to their country-specific means and standard deviations) so that the different EQR ranges could be compared across countries. The predictor variables included a continuous fixed term for year and different random effects to control for differences in the effect of year across countries and to control for pseudo-replication among sites sampled from the same country, year, and season. These random effects included a random slope and intercept term for country, a random intercept term for sampling year, and a random intercept term for sampling month. We also 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 fixed 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 the metrics/indices that 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 this analysis. 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 modeled using GAMMs.

To quantify country-scale temporal change in ecological quality and its relationships to the community metrics and biomonitoring indices, we analyzed the data for 14 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 (excluding the country-level random effects). We also conducted 14 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 also calculated the slopes of temporal change in the EQRs and metrics/indices for each site. Slopes were calculated using robust regressions[61] to downweight the importance of data from the first and last years, which can be highly influential on slope estimations in time series analyses[15,22]. 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.

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Contributions

JSS and PH conceived the study. EARW cleaned the data and JSS performed the analyses. JSS and PH wrote the majority of the manuscript with contributions from all authors. All authors (excepting NúB, DH, JH, and SCJ) provided stream invertebrate data and contributed to calculating ecological quality values for their respective countries.

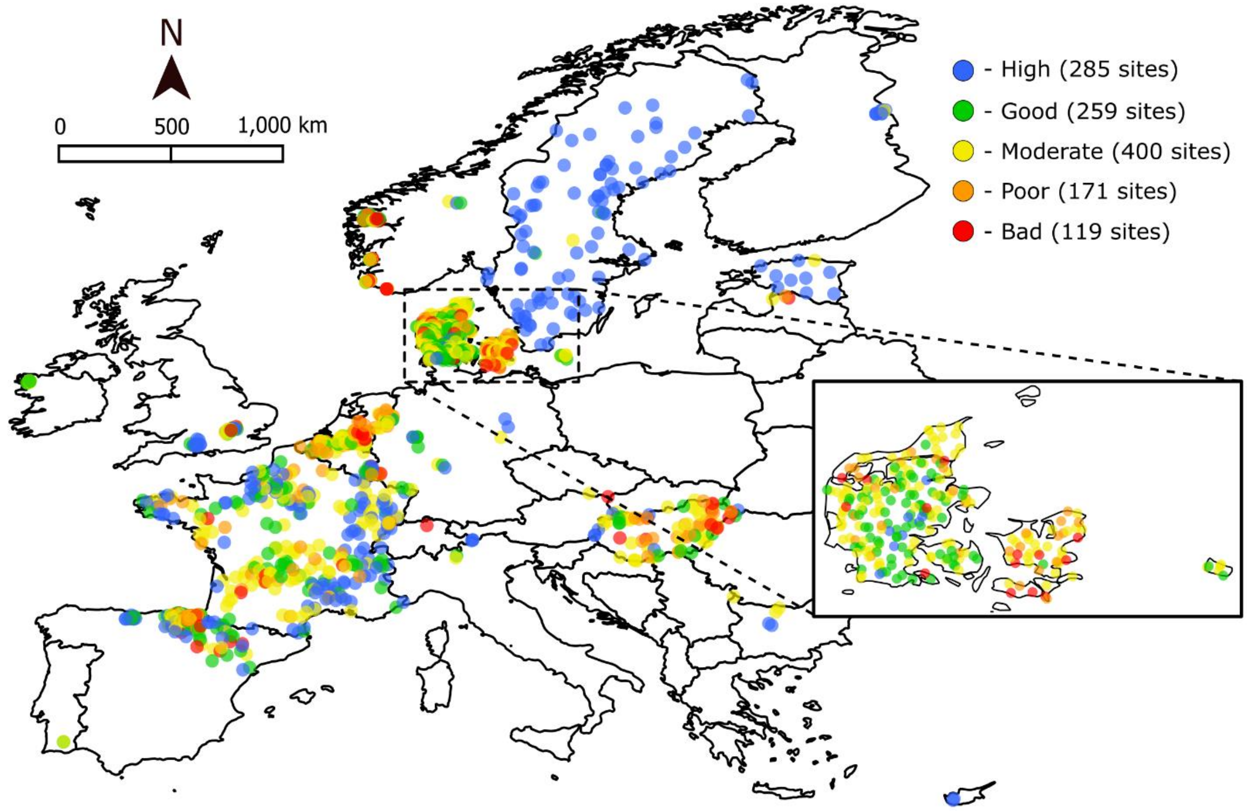


Fig. 1: Locations and ecological quality of 1,234 stream sampling sites across Europe. Sites are colored using biomonitoring assessments of stream ecological quality (calculated as the Ecological Quality Class, EQC; see *Methods*) based on the invertebrate community in the first year of sampling. The EQC of some sites in denser clusters is hidden, as illustrated for Denmark.

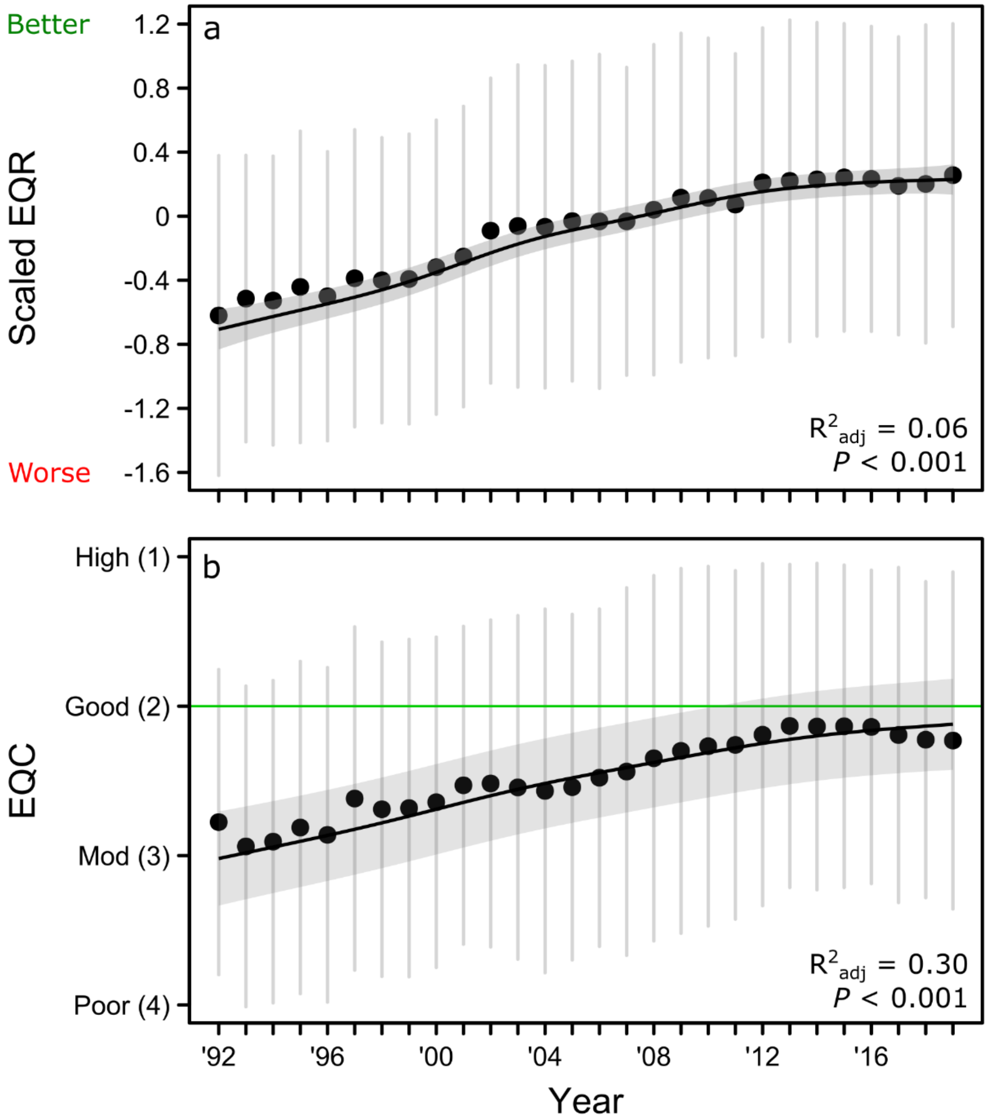


Fig. 2: Continental-scale trends in ecological quality. Trends in (**a**) Ecological Quality Ratios (EQRs; scaled to country-specific means and standard deviations) and (**b**) Ecological Quality Classes (EQCs; ‘Mod’ = moderate) across 1,234 sampled European stream sites during 1992–2019. Black points and gray vertical lines respectively indicate the annual means and standard deviations. Fitted relationships (black line) and confidence intervals (gray background) were based on generalized additive mixed model output. The European Union Water Framework Directive target of a ‘good’ EQC is indicated by a green line in (**b**). The ‘bad’ EQC (class 5) is not plotted.

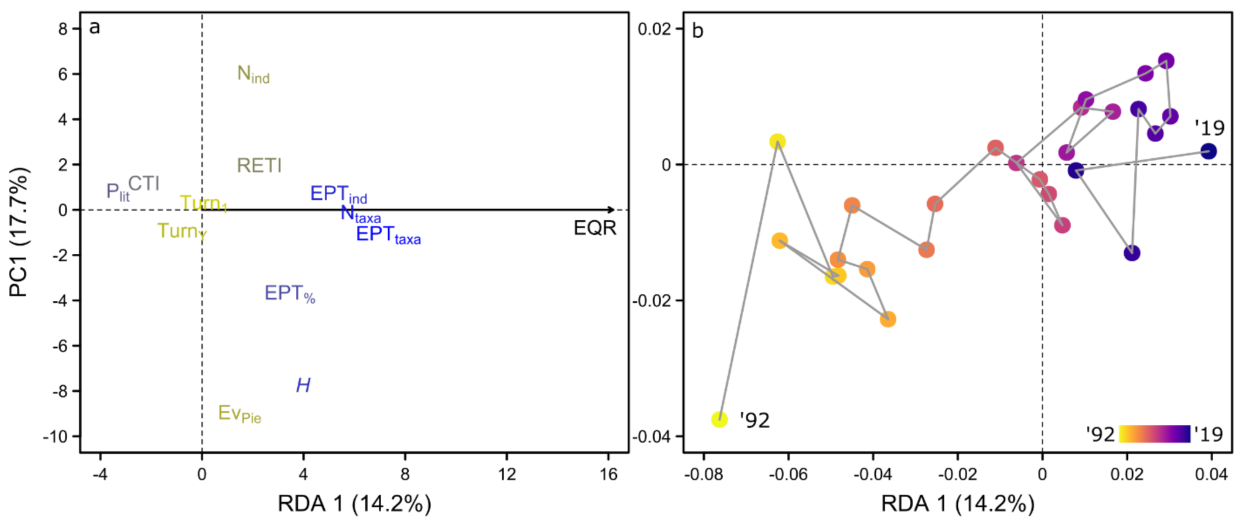
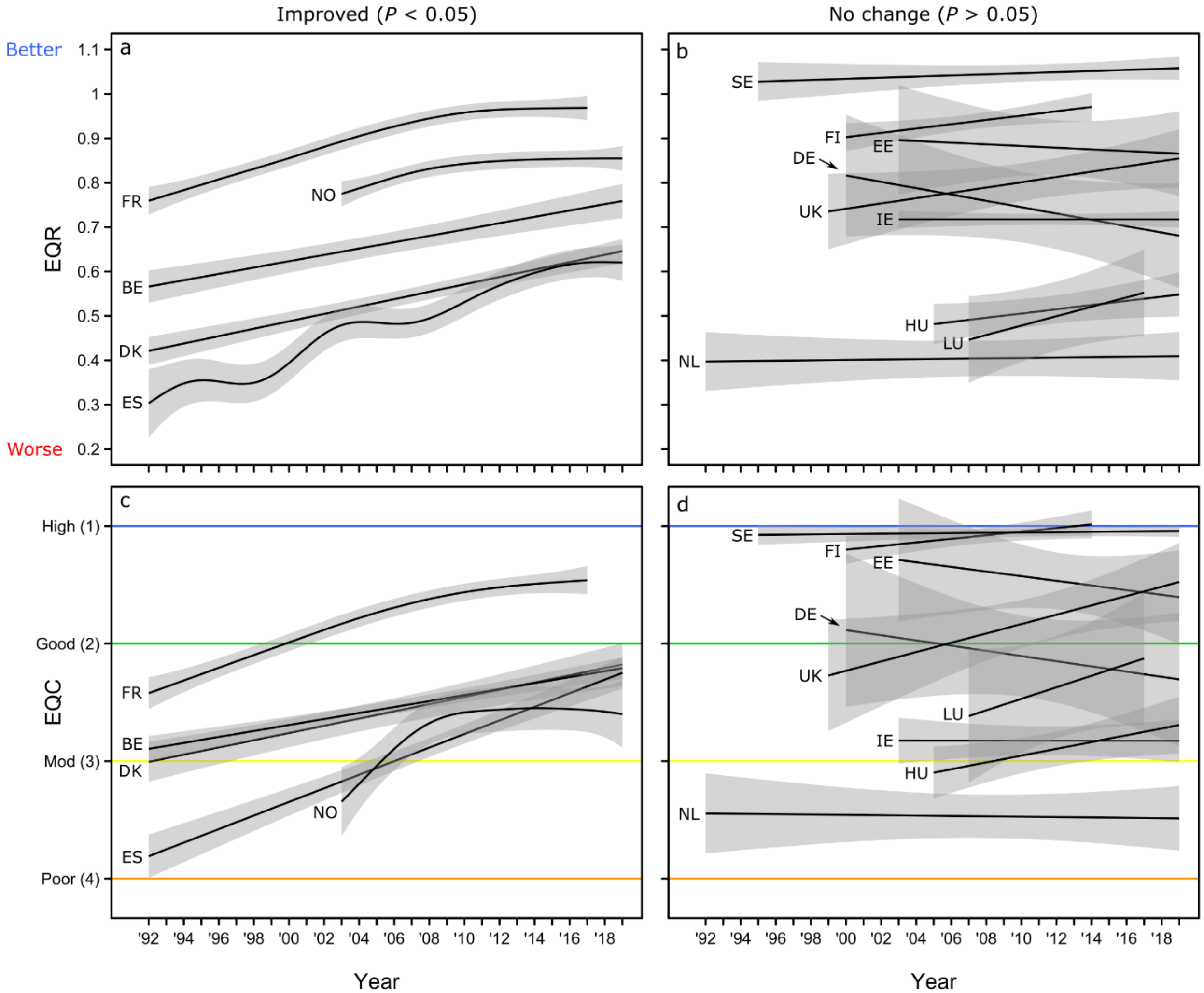


Fig. 3: Continental-scale links between ecological quality, community metrics, and biomonitoring indices. Redundancy analysis (RDA) of the continental-scale relationship between (**a**) Ecological Quality Ratios ('EQR'; black arrow) and the community metrics and biomonitoring indices, and (**b**) temporal trends in metrics/indices during 1992–2019. 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; see Extended Data Table 1). Metrics and indices are colored from yellow to blue based on their loadings on RDA axis 1, the only axis reflecting relationships with the EQRs (blues indicate stronger relationships to quality). Temporal trends are visualized in (**b**) with year positions calculated as the centroid of all sites in each year.



671 **Fig. 4: Country-scale trends in ecological quality.** Temporal changes in (**a, b**) Ecological
672 Quality Ratios (EQRs) and (**c, d**) Ecological Quality Classes (EQCs) across European stream
673 communities from 14 countries during 1992–2019. Fitted relationships (solid lines) and
674 confidence intervals (gray backgrounds) are based on generalized additive mixed models for
675 Belgium (BE), Denmark (DK), Estonia (EE), Finland (FI), France (FR), Germany (DE),
676 Hungary (HU), Ireland (IE), Luxembourg (LU), the Netherlands, (NL), Norway (NO), Spain
677 (ES), Sweden (SE), and the UK. Countries in (**a, c**) have statistical evidence for quality
678 improvements through time (*P* < 0.05), whereas those in (**b, d**) have no evidence for change (*P* >
679 0.05). EQC categories (**c, d**) are illustrated using colored lines following the Water Framework

Directive colour codes for High (blue), Good (green), Moderate (‘Mod’; yellow), and Poor (orange) classes; the Bad class is not plotted.

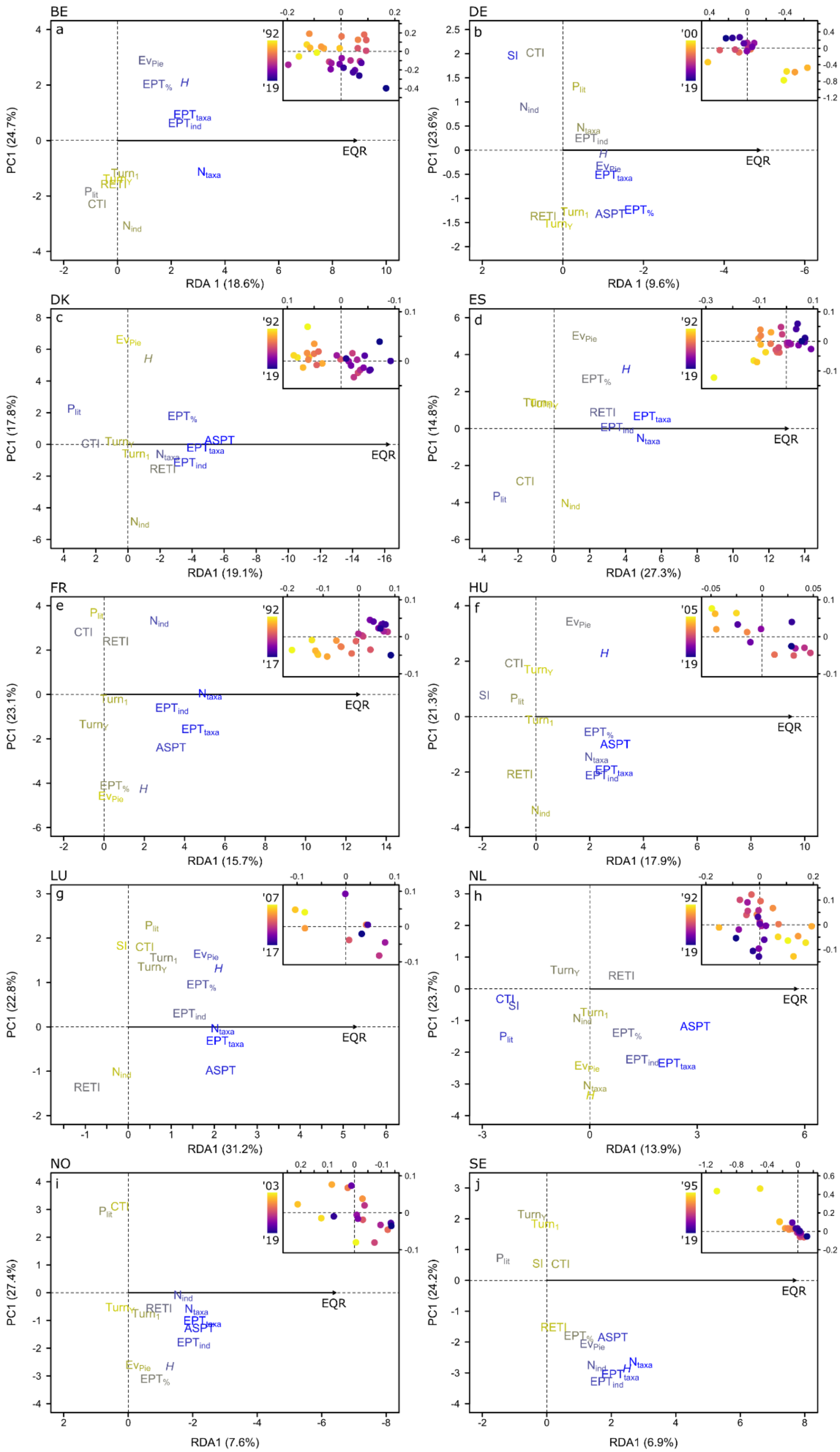

BE
a
PC1 (24.7%)
RDA 1 (18.6%)
EQR
DE
b
PC1 (23.6%)
RDA 1 (9.6%)
EQR
DK
c
PC1 (17.8%)
RDA1 (19.1%)
EQR
ES
d
PC1 (14.8%)
RDA1 (27.3%)
EQR
FR
e
PC1 (23.1%)
RDA1 (15.7%)
EQR
HU
f
PC1 (21.3%)
RDA1 (17.9%)
EQR
LU
g
PC1 (22.8%)
RDA1 (31.2%)
EQR
NL
h
PC1 (23.7%)
RDA1 (13.9%)
EQR
NO
i
PC1 (27.4%)
RDA1 (7.6%)
EQR
SE
j
PC1 (24.2%)
RDA1 (6.9%)
EQR

Fig. 5: Country-scale links between ecological quality, community metrics, and biomonitoring indices. Redundancy analyses (RDA) of the relationship between Ecological Quality Ratios (EQRs; black arrows) and community metrics and biomonitoring indices for (**a**) Belgium (BE), (**b**) Germany (DE), (**c**) Denmark (DK), (**d**) Spain (ES), (**e**) France (FR), (**f**) Hungary (HU), (**g**) Luxembourg (LU), (**h**) the Netherlands (NL), (**i**) Norway (NO), and (**j**) Sweden (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 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 Average Score Per Taxon (ASPT) index, the Community Temperature Index (CTI), the proportion of littoral taxa (P_{lit}), the Saprobic Index (SI), and the Rhithron feeding type index (RETI; see Extended Data Table 1). Metrics and indices are colored from yellow to blue based on their loadings on RDA axis 1, the only axis reflecting relationships with the EQRs (blues indicate stronger relationships to quality). Temporal trends are visualized in the top right corner of each panel, with year positions calculated as the centroid of all sites in each year.

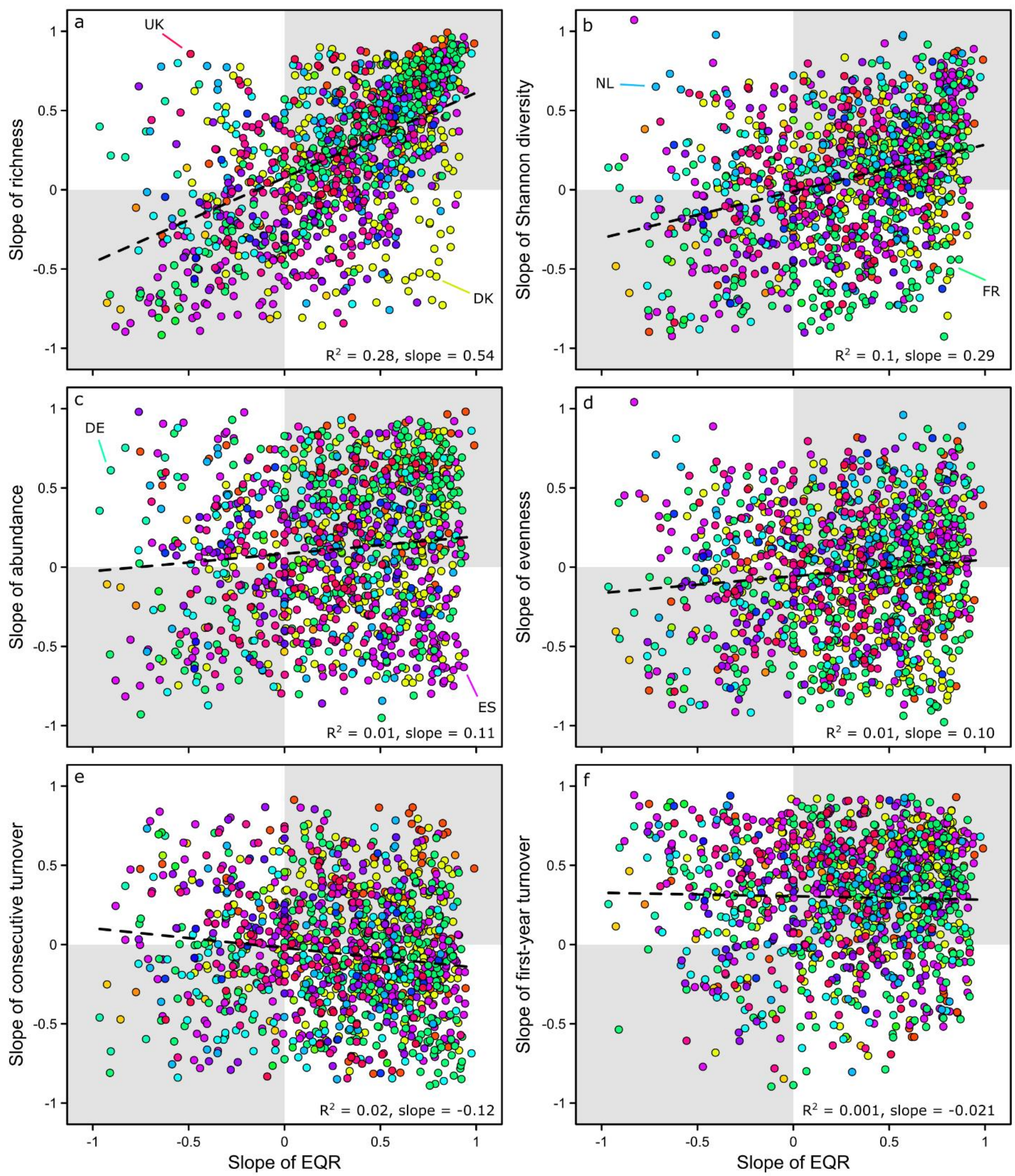


Fig. 6: Site-scale links between ecological quality and community metrics. Relationships between the slopes of the Ecological Quality Ratio (EQR) at each site and the slopes of (**a**) taxon richness, (**b**) Shannon diversity, (**c**) abundance, (**d**) evenness, (**e**) temporal turnover between

consecutive years, and (**f**) temporal turnover between each year and the first year. Sites with matching quality and metric trends are in the gray shaded areas, whereas opposing relationships are in the white areas. Sites are colored by country, and some example countries that exhibit strong opposing changes are indicated with arrows (DE: Germany; DK: Denmark; ES: Spain; FR: France; NL: Netherlands; UK: United Kingdom).

Extended Data

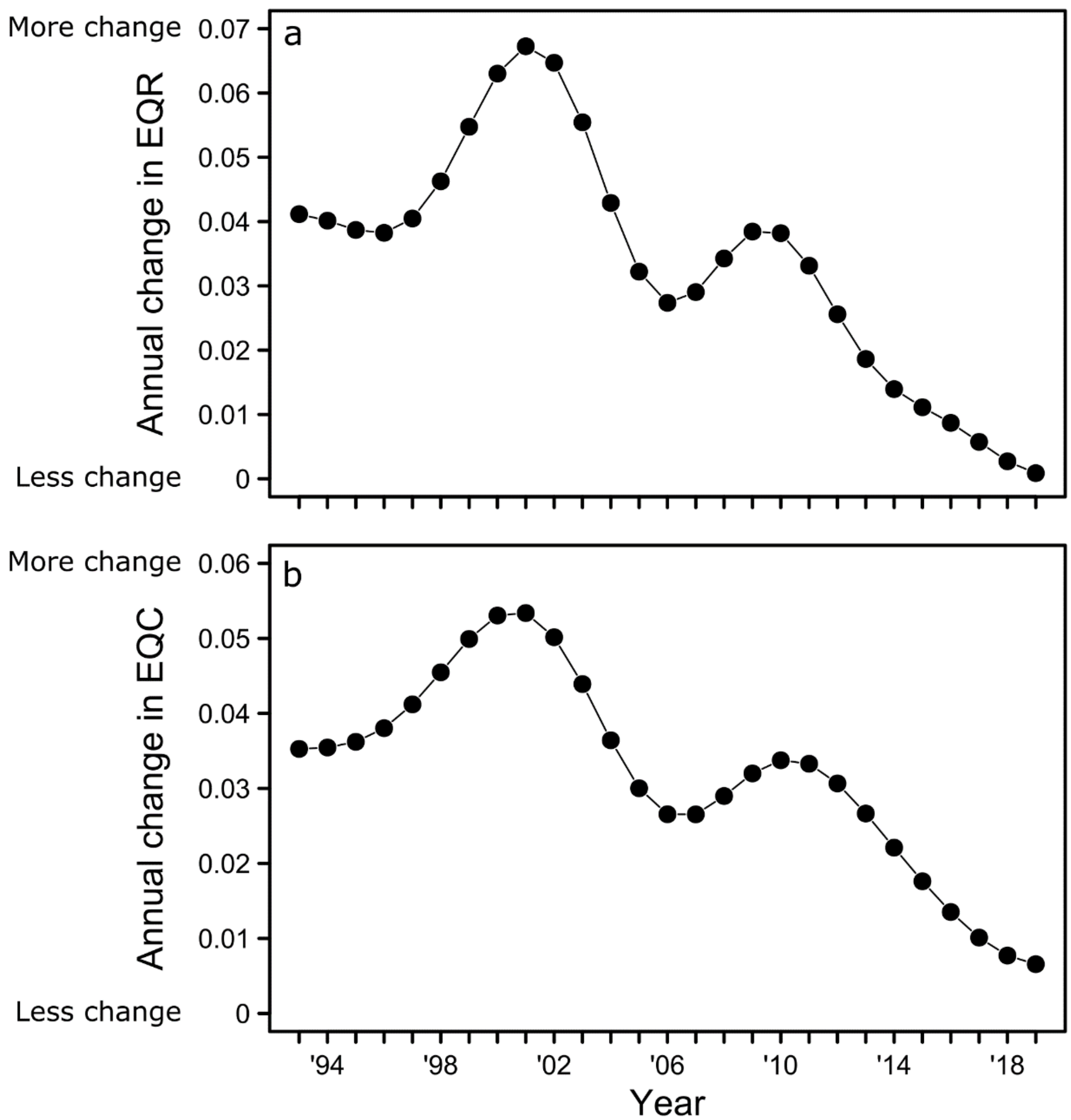
Extended Data Table 1: List and description of stream invertebrate biomonitoring indices. These indices were used to indicate anthropogenic degradation in river water/habitat quality and potentially the effects of specific stressors. We also list the number of countries for which each index was calculated out of 22 total in our dataset. References for the ASPT indices are provided in Supplementary Table 1.

Metrics	Abbreviation	Meaning	Specific stressors	Number of countries
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[27]	22
Saprobic Index	SI	Abundance-weighted index of taxon-specific saprobic values. Higher values indicate communities comprised of taxa that tend to occur in enriched waterbodies.	Organic pollution[27]	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[62]	22
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-degraded waterbodies.	–	14

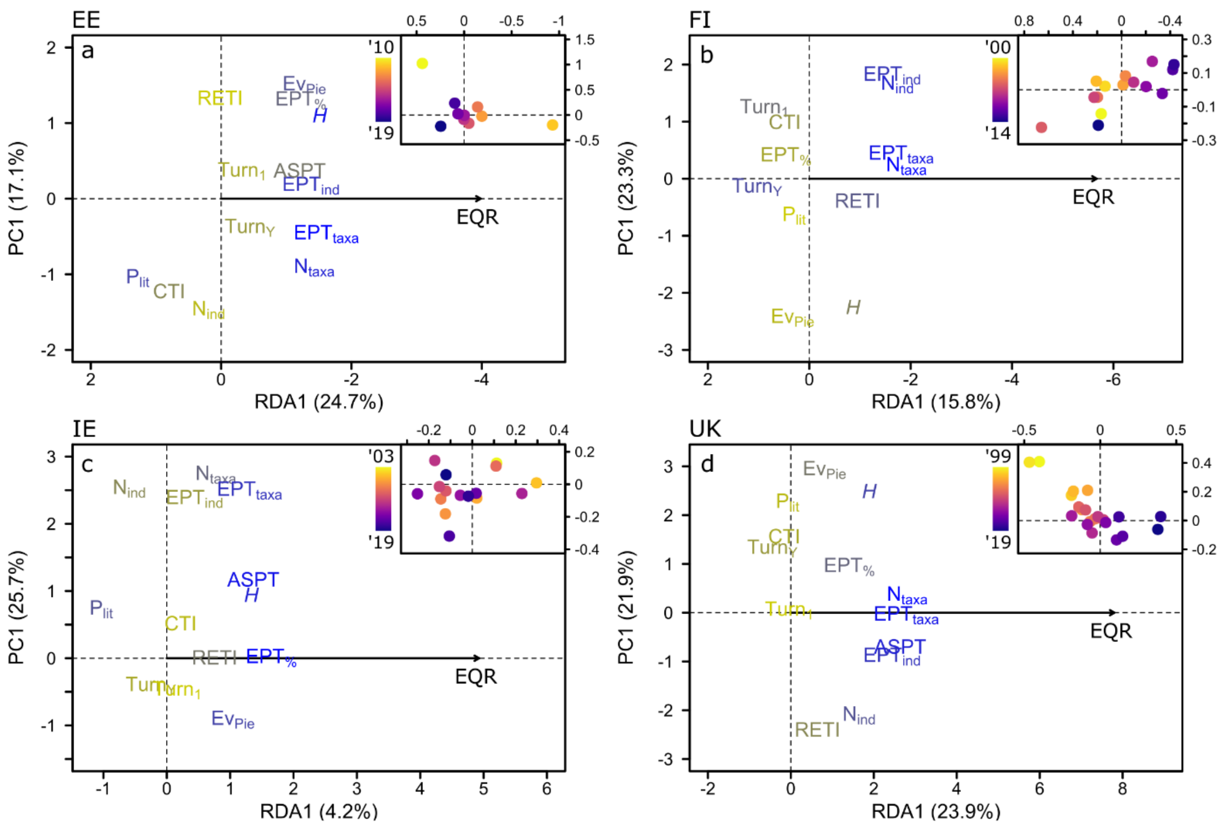
Ephemeroptera, Plecoptera, and Trichoptera	EPT	The abundance, richness, and proportion of EPT taxa[27]. Higher values indicate more EPT taxa, which tend to occur in less-degraded waterbodies.	–	22
Rhithron feeding type index	RETI	Proportion of feeding types associated with more upstream habitats, specifically grazers, shredders, or taxa that feed on woody debris[27]. Higher values indicate communities comprised of taxa that tend to prefer less-degraded waterbodies.	–	22

Extended Data Table 2: Site-scale variability in the relationship between ecological quality and community metrics. Proportion of sites (out of 1,234) 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 response (either the metric changes when 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 26% of sites match this trend. Conversely, the overall relationship between the slopes of consecutive turnover and the EQRs is negative (i.e., turnover tends to decline as 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.

Metric	Matching	No change	Opposing
Abundance	14%	40%	6%
Evenness	6%	47%	6%
Richness	26%	30%	2%
Shannon diversity	11%	45%	3%
Turnover (consecutive)	7%	47%	4%
Turnover (first-year)	4%	43%	20%

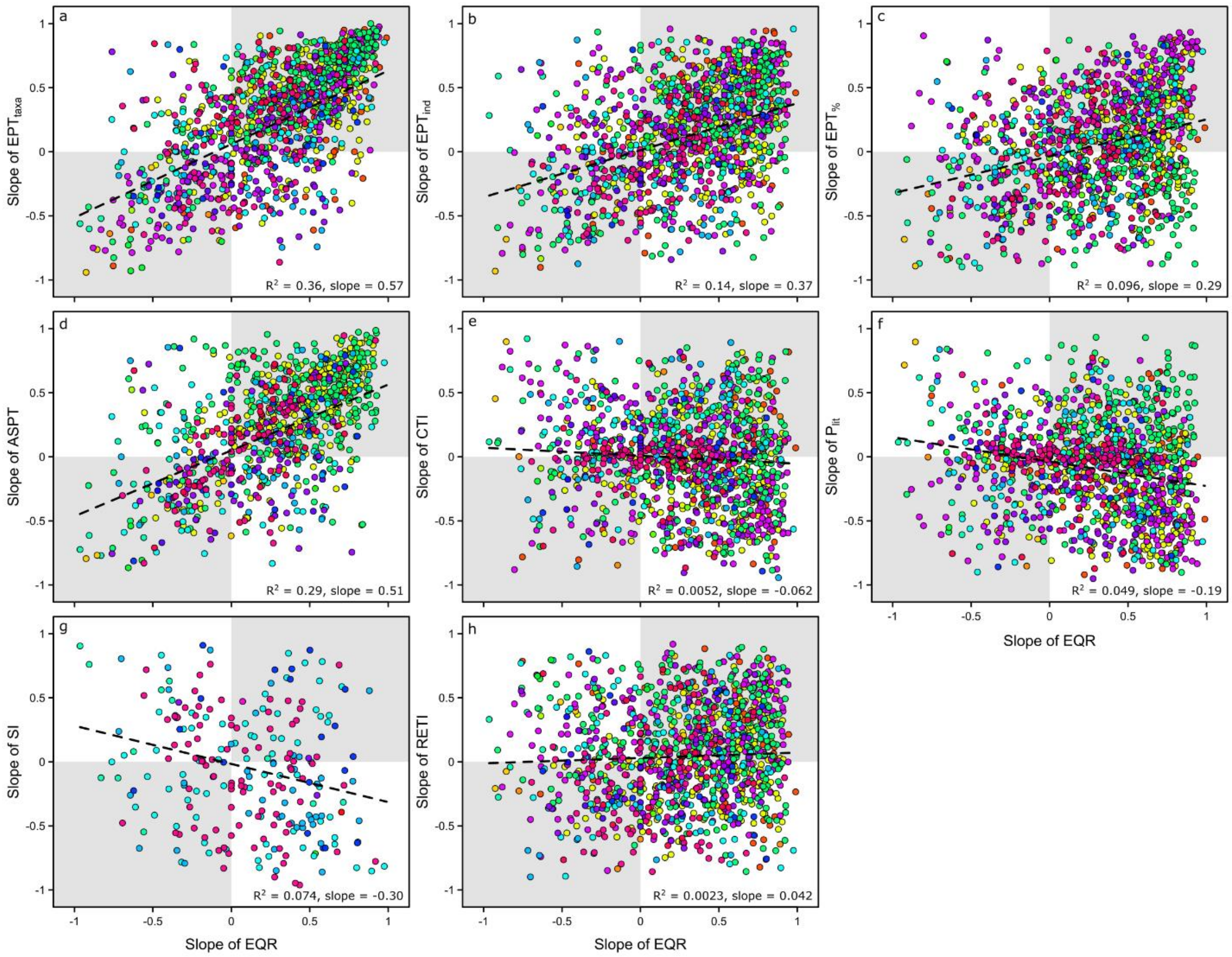


Extended Data Fig. 1: Year-to-year changes in ecological quality. Differences in the predicted (**a**) EQRs and (**b**) EQCs between each year and the previous year during 1992–2019. For example, the 1993 values are the absolute differences in the predicted EQRs/EQCs between 1992 and 1993. Thus, values 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**) Estonia (EE), (**b**) Finland (FI), (**c**) Ireland (IE), and (**d**) 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 yellow to blue based on their loadings onto RDA axis 1; the only axis reflecting relationships to the EQRs (blues indicate stronger relationships to quality).

Temporal trends are visualized in the top right corner of each panel, with year positions calculated as the centroid of all sites in each year.



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 quality and biodiversity trends are in the gray shaded areas, whereas opposing relationships are in the white areas.