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Ecological but Not Biological Traits of European Riverine Invertebrates Respond Consistently to Anthropogenic Impacts

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ABSTRACT

Aim: To determine which riverine invertebrate traits respond consistently to anthropogenic impacts across multiple biogeographic regions.

Location: Europe.

Time Period: 1981–2021.

Major Taxa Studied: Riverine invertebrates.

Methods: We compiled a database of riverine invertebrate community time series for 673 sites across six European countries spanning six freshwater ecoregions. We compared trait responses to anthropogenic impacts (quantified as changes in 'ecological quality') among regions for seven 'ecological' traits, which reflect habitat preferences, and nine 'biological' traits (e.g., morphology or life history), which represent taxon-specific attributes that can influence ecosystem processes.

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Results: Four ecological traits (current, microhabitat, salinity and trophic preferences) and one biological trait (dispersal mode) responded consistently across regions. These responses were primarily driven by spatial differences among poorer to better quality sites. Responses to temporal changes in quality were comparable but less pronounced.

Main Conclusions: Consistent responses to anthropogenic impacts across multiple ecological traits indicate these traits may improve broader scale measurements, comparisons and predictions of community responses. However, we could not use ecological traits to identify the actions of specific stressors because multiple traits always responded as a group. Inconsistent responses across almost all biological traits indicated that these traits may be less predictive of impacts across regions. Predictions of how biological traits, and associated ecosystem processes, respond to anthropogenic impacts may be most effective at regional scales where responses are more consistent.

1 | Introduction

Efforts to curtail human-driven changes in ecological communities benefit from comparing community responses to anthropogenic impacts across broad spatial scales. Such comparisons can determine whether humans are driving consistent declines or increases in certain taxa, which can help to predict future change (McGinty et al. 2021), develop biomonitoring indices (Vandewalle et al. 2010) and identify effective management actions (Manfrin et al. 2019). Trait-based approaches facilitate these comparisons by characterising communities using measurable characteristics of present taxa, such as the primary morphological attributes or habitat preferences of the community, rather than taxonomic identity. Using traits facilitates broad-scale comparisons because taxonomically different communities can be compared using the same set of traits (McGill et al. 2006). Ideally, once consistent changes in trait composition (hereafter 'trait responses') across communities are identified, then generalisable predictions can be developed regarding how different communities respond to the same anthropogenic impacts. Such predictions assume that the same driver will select for the same traits (Southwood 1977; Verberk, van Noordwijk, and Hildrew 2013) because these traits promote survival and reproduction in impacted habitats. Identifying consistent trait responses also facilitates predicting the consequences of community change for ecosystem stability and functioning, which are influenced by trait composition (Lavorel and Garnier 2002).

Despite the potential comparative and predictive benefits of trait-based approaches, understanding of the consistency and thus predictability of trait responses to anthropogenic impacts across biogeographic regions remains incomplete. For example, some studies have identified broad-scale commonalities in trait responses to anthropogenic impacts, such as shifts to smaller-bodied birds (Richards, Cooke, and Bates 2021) and mammals (McCain and King 2014). However, many other studies show no consistent broad-scale trait responses, such as in fishes (Brumm, Infante, and Cooper 2023), reptiles (Doherty et al. 2020), freshwater invertebrates (Hamilton et al. 2020; Statzner and Bêche 2010) and terrestrial invertebrates (Bartomeus et al. 2018; Tordoff et al. 2022). This variability may reflect limitations in analysed traits. Certain traits, such as body size (Poff et al. 2006; Wilkes et al. 2020), are more plastic (i.e., unconstrained by phylogeny) and so may respond inconsistently because of their stronger adaptability to changes in local environmental conditions. Additionally, some trait responses may be constrained by genetic and physiological linkages to other traits (e.g., one gene or physiological process controls multiple traits; Smith 2016), by trait trade-offs (e.g., greater investment in one trait is linked to lower investment in another) or by shared environmental and evolutionary constraints (Poff et al. 2006; Verberk, van Noordwijk, and Hildrew 2013). Such linkages can prevent traits from responding to anthropogenic impacts if their linked traits do not also respond (Pilière et al. 2016). In summary, although some traits may respond consistently across regions and so can inform broad-scale predictions, others may not, necessitating distinguishing which types of traits belong to which group.

Of particular importance is the need to evaluate the consistency of ecological versus biological trait responses. An 'ecological trait' *sensu* Usseglio-Polatera et al. (2000) is any measure describing a species' environmental requirements or habitat preferences, such as categorising different species into those that inhabit grasslands versus forests. 'Biological traits' *sensu* Usseglio-Polatera et al. (2000) are measures representing inherent taxon-specific attributes (e.g., body size, life history or feeding morphology), which can have clearer links to ecosystem processes (Verberk, van Noordwijk, and Hildrew 2013), such as feeding traits influencing energy transfer (Hébert, Beisner, and Maranger 2017). Both ecological and biological traits are often hypothesised to respond consistently to anthropogenic impacts (Statzner and Bêche 2010; Doherty et al. 2020), given that they reflect preferences for and adaptations to prevailing environmental conditions, respectively. However, differences in how these two trait groups are measured could influence their response consistency. Ecological trait values are estimated from taxon distributions across broad environmental gradients, meaning these traits may be more likely to respond in the same way to environmental changes across regions (Soberón 2007). In contrast, biological traits are directly measured from taxon characteristics, which are more influenced by local-scale abiotic and biotic interactions, such as predation and competition, potentially resulting in more spatially variable responses (Rosado et al. 2016; Soberón 2007). If so, this could hinder broad-scale, trait-based predictions of changes in ecosystem processes, which typically focus on changes in biological traits. Investigating the spatial consistency of ecological versus biological trait responses is therefore important both for determining which traits are the most broadly predictive, and for informing how to scale up these predictions to their ecosystem-level consequences.

To examine the spatial consistency of ecological versus biological trait responses, we used riverine invertebrate community time series from 673 sites across six European countries spanning six freshwater ecoregions (Figure 1). These communities have been sampled across Europe for decades because

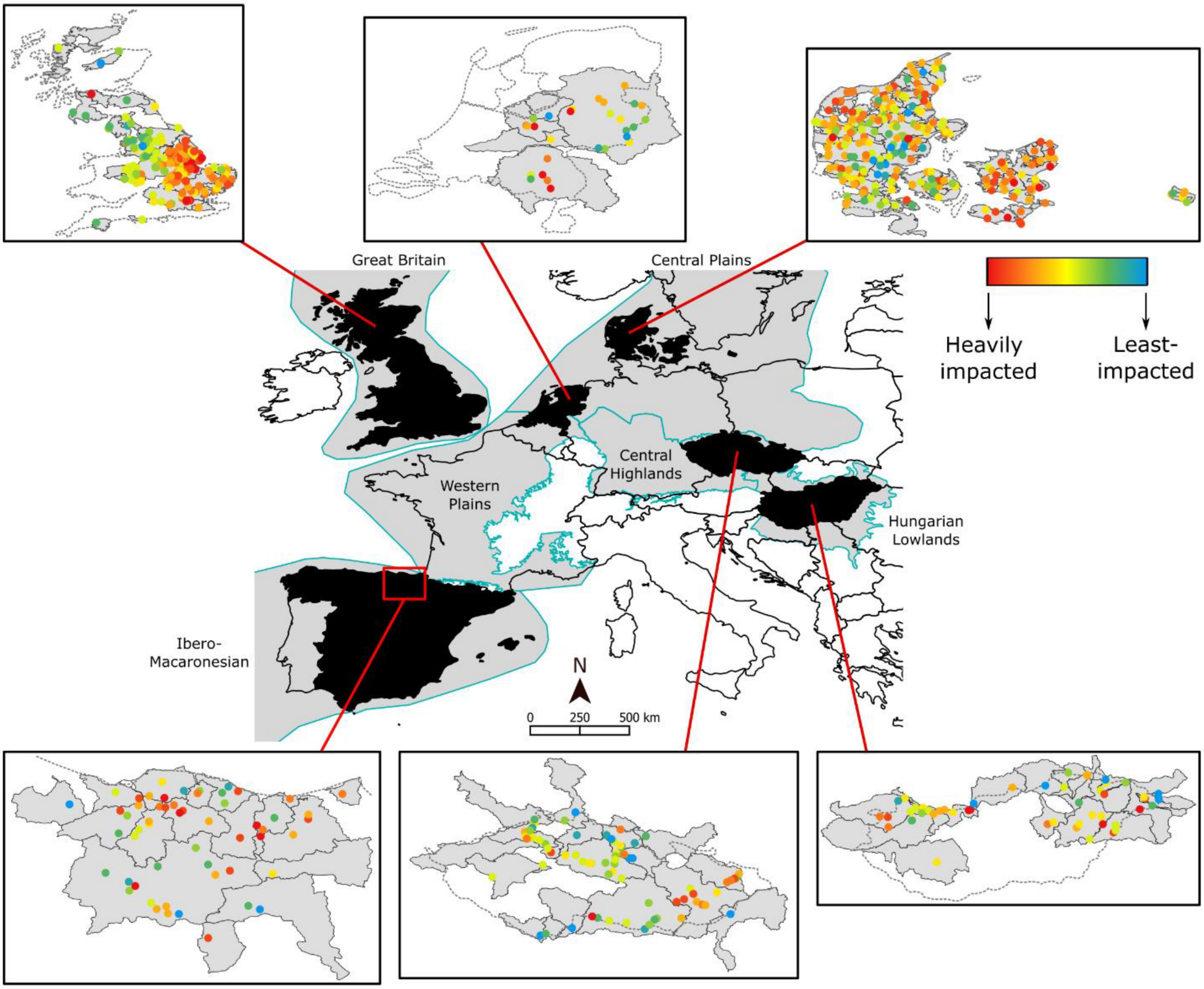

FIGURE 1 | Spatial distribution of our 673 sampling sites across six countries (black shaded areas and grey dashed outlines in the insets), six ecoregions (grey shaded map areas with blue borders; based on Illies 1978) and 185 catchments in Europe (grey shaded areas of the insets). River sites span a gradient of heavily impacted to least-impacted conditions based on the ecological quality of the invertebrate community (see *Methods* for how ecological quality was quantified).

their constituent taxa are indicators of river health owing to their taxon-specific sensitivities to stressors that degrade water and habitat quality (Metcalfe 1989), such as organic pollution (Paisley, Trigg, and Walley 2014). Trait values for these organisms are also publicly available (Schmidt-Kloiber and Hering 2015). Riverine invertebrates therefore provide a useful study system for investigating trait response consistency to anthropogenic impacts across a broad geographic area. Additionally, given their widespread use in ecological health assessments, identifying consistent invertebrate trait responses could reveal broadly applicable, trait-based indicators of ecosystem degradation.

Our aim was to compare the within and across ecoregional consistency of responses in seven ecological and nine biological traits (Table 1) to spatiotemporal variation in anthropogenic impacts. We measured the degree of impact as the ratio of observed community metrics to those in least-impacted reference conditions (termed 'ecological quality'; see Section 2). Ecological quality integrates the impacts of multiple common freshwater stressors and enables comparable estimation of impact across countries. We predicted that ecological traits would respond more consistently to anthropogenic impacts than biological traits because the former reflect environmental preferences and so are more likely to change with environmental conditions.

2 | Methods

2.1 | Taxonomic Composition

We used time-series data from Welti et al. (2024) describing riverine invertebrate community composition for multiple European freshwater ecoregions, with additional data for Czechia collected via data requests to ecologists and environmental managers. Our data requirements were as follows: (i) sampling sites within each region encompass a gradient from heavily impacted to least-impacted conditions; (ii) taxa were identified to a mixed

TABLE 1 | Descriptions and sources for seven ecological and nine biological traits selected based on Dolédec, Statzner, and Bournard (1999), Dolédec and Statzner (2008), Mondy and Usseglio-Polatera (2014) and Berger et al. (2018). 'Coverage' lists the per cent of taxa with available trait values with no gap filling and the per cent with trait values after gap filling (also see Data S2).

					Coverage	
Trait group	**Trait**	**Values**	**Modalities**	**Source**	**No gap filling**	**Gap filled**
Ecological	Current preference[a]	0, 1	Limnobiont[c], limnophil, limno- to rheophil, rheo- to limnophil, rheophil, rheobiont[c], indifferent	Schmidt-Kloiber and Hering (2015)	80%	96%
	Microhabitat preference	0–10	Argyllal (silt/loam/clay), pelal (mud), psammal (sand), akal (0.2–2 cm grain size), lithal (> 2 cm grain size), phytal (algae/mosses/macrophytes), POM (particulate organic matter), other	Schmidt-Kloiber and Hering (2015)	75%	97%
	pH preference	0–3	< 4, > 4–4.5, > 4.5–5, > 5–5.5, > 5.5–6, > 6	Tachet et al. (2010)	46%	94%
	Salinity preference	0–3	Lower salinity, higher salinity	Tachet et al. (2010)	48%	96%
	Stream zone preference[b]	0–10	Eucrenal, hypocrenal, epirhithral, metarhithral, hyporhithral, epipotamal, metapotamal, hypopotamal, littoral	Schmidt-Kloiber and Hering (2015)	67%	95%
	Temperature preference	0–3	Psychrophilic, thermophilic, eurythermic	Tachet et al. (2010)	47%	96%
	Trophic preference	0–3	Oligotrophic, mesotrophic, eutrophic	Tachet et al. (2010)	47%	96%
Biological	Body size	0–3	≤ 0.25, > 0.25–0.5, > 0.5–1, > 1–2, > 2–4, > 4–8, > 8 cm	Tachet et al. (2010)	61%	97%
	Dispersal mode	0–3	Aquatic passive, aquatic active, aerial passive, aerial active	Tachet et al. (2010)	61%	96%
	Feeding type	0–10	Grazers/scrapers, miners, xylophagous[c], shredders, gatherers/collectors, active filter feeders, passive filter feeders, predators, parasites[c], other	Schmidt-Kloiber and Hering (2015)	91%	98%
	Life duration	0–3	< 1 year, > 1 year	Tachet et al. (2010)	60%	96%
	Locomotion	0–10	Swimming/skating, swimming/diving, burrowing/boring, sprawling/walking, sessile, other	Schmidt-Kloiber and Hering (2015)	74%	96%
	Reproduction	0–3	Ovoviviparity, isolated eggs (free), isolated eggs (cemented), clutches (cemented or fixed), clutches (free), clutches (vegetation)[c], clutches (terrestrial), asexual	Tachet et al. (2010)	47%	95%
	Reproductive cycles per year	0–3	< 1, 1, > 1	Tachet et al. (2010)	61%	96%
	Resistance forms	0–3	Eggs/gemmule/statoblasts, cocoons, housings against desiccation[c], diapause/dormancy, none	Tachet et al. (2010)	46%	92%
	Respiration	0–3	Tegument, gill, plastron, spiracle, hydrostatic vesicle[c]	Tachet et al. (2010)	48%	96%

[a] Ordered from slower to faster currents.

[b] Ordered longitudinally from upstream (crenal) to intermediate (rhithral) to downstream (potamal) zones.

[c] Modalities excluded from analyses because they are not present in all countries.

resolution, generally a combination of families, genera and species, which is the best quality data typically available for riverine invertebrates; (iii) samples were collected during spring (March–May), which was the most frequent sampling period and thus was selected to control for seasonality; (iv) all samples within a time series were collected using the same method; and (v) taxon abundances were recorded, enabling using abundance-weighted trait values.

Data meeting our criteria were available from Czechia ($n=72$; 2000–2021), Denmark ($n=248$; 1992–2019), Hungary ($n=49$; 2001–2019), the Netherlands ($n=28$; 1981–2019), Spain ($n=55$; 1993–2019) and the United Kingdom ($n=221$; 1994–2019). Sampling sites encompassed a range of river sizes (Strahler orders 1–10; mean ± SD of 4.9 ± 1.4) and six European freshwater ecoregions (Figure 1). Sampling methods for each country are detailed in Supporting Information S1. Most taxa were identified to the family, genus or species level, with some classified to intermediate (e.g., subfamily) or higher levels (e.g., Oligochaeta at subclass); the identification level can also vary among countries because of differences in national policy and practice (Birk et al. 2012). The abundance of each taxon in each site and year was converted to relative abundance and square-root transformed (i.e., the Hellinger transformation; Legendre and Gallagher 2001) both to standardise abundance units across the datasets and to down-weight the influence of highly abundant species, thus focusing on differences in taxonomic composition.

2.2 | Trait Composition

We used seven ecological traits and nine biological traits to represent invertebrate communities, which were selected based on previous research (Table 1). Trait values were obtained from Schmidt-Kloiber and Hering (2015) and Tachet et al. (2010). These values reflect how strongly a taxon expresses separate categories or 'modalities' within each trait (termed 'affinity'), such as the affinity for shredding, grazing, scraping and predator modalities within the feeding type trait. A taxon can have affinities for multiple modalities and affinities are binary (0/1) or fuzzy-coded (integers ranging from 0 to 3, 0 to 5 or 0 to 10), with higher values representing higher affinities.

We analysed 81 trait modalities, with seven excluded because they were lacking in some countries, precluding analysis of response consistency (denoted in Table 1). Modality values were available for 46%–91% of taxa at their level of identification, depending on the trait, with many missing values reflecting missing species-level trait information, particularly from Tachet et al. (2010). We filled missing values using a standard gap-filling approach for invertebrates whereby trait values from higher taxonomic levels are assigned to lower taxa (Kunz et al. 2022). We supplemented this with a trait averaging approach whereby, if values from a higher level were also missing, we used the average value across other related taxa, which produces similar trait–environment relationships to higher-level trait values (Kunz et al. 2022). For example, if a modality value was missing for a species, we assigned the genus value or, where this was missing, the average of all species with trait information within the genus. If both species- and genus-level information was missing, we assigned the family-level value or, where this was missing, the average value of all taxa with trait information within the family. This gap-filling procedure provided values for 94%–98% of all taxa (Data S2 lists the trait value assignment levels). To test for potential biases introduced by trait averaging, we analysed datasets with and without averaging and compared the results.

Trait values were converted to proportions to enable binary and fuzzy-coded traits to be combined in the same dataset. We then calculated the trait composition for each site and year on the basis of the affinity value of each trait modality, weighted by the Hellinger-transformed abundance of each taxon, using Lavorel et al.'s (2008) formula:

$$\mathrm{CWM} = \sum_{i=1}^{n} p_i \times \mathrm{trait}_i$$

where CWM is the 'community-weighted mean' for a given trait modality, p_i is the Hellinger-transformed abundance of taxon i and trait_i is the affinity value for taxon i.

2.3 | Anthropogenic Impacts

We represented changes in anthropogenic impacts across sites and years using ecological quality as represented by the ecological quality ratio (EQR), which reflects integrated community responses to multiple stressors, such as organic pollutants and general environmental degradation (Birk et al. 2012; Jones et al. 2023). Country-specific EQRs are calculated following European Union Water Framework Directive compliant methods (listed in Supporting Information S1). Methods differ among countries, but all compare observed community metrics (e.g., taxon richness and/or the presence of sensitive taxa) to the same metrics from least-impacted reference communities. The EQR is the observed:reference metric ratio, which ranges from close to 0 to >1, with lower values indicating greater deviation from reference conditions and thus greater impacts. EQRs in some countries are calculated using traits that are established regional indicators of anthropogenic impacts. Specifically, Hungary uses some current preference modalities, Czechia uses some feeding type and microhabitat preference modalities, and both Czechia and Hungary use some stream zone preference modalities (Supporting Information S1). We therefore already know these traits will respond to anthropogenic impacts in these respective regions. Furthermore, the metrics used in EQR calculations are often tuned to detect community responses to organic pollutants. The trophic preference trait (Table 1), which relates to nutrient status, is thus likely to respond to nutrient-driven variation in ecological quality. Despite these known or expected trait responses, it is still important to determine their consistency at broader spatial scales.

EQRs were unavailable for the United Kingdom, so we quantified ecological quality using the Whalley Hawkes Paisley Trigg Average Score Per Taxon index (hereafter '$\mathrm{ASPT}_{\mathrm{WHPT}}$'), which is an element of, and positively related to, the UK EQR (Paisley, Trigg, and Walley 2014; Sinclair et al. 2024). ASPT$_{\mathrm{WHPT}}$ is calculated by scoring all taxa in a sample from −1.6 to 13 based on their sensitivity to organic pollution and then averaging these scores. Higher scores are assigned to taxa sensitive to organic pollution, thus higher ASPT$_{\mathrm{WHPT}}$ values indicate less polluted communities.

Based on calculated EQR or ASPT$_{\mathrm{WHPT}}$ values, our sites encompassed a wide gradient of severity in anthropogenic impacts in Czechia (EQRs ranging from 0.08–to 0.8; mean ± SD of 0.46 ± 0.15), Denmark (0–1.25; 0.55 ± 0.24), Hungary (0–0.97; 0.53 ± 0.21), the Netherlands (0.04–0.89; 0.44 ± 0.2), Spain (0.015–1.22; 0.47 ± 0.23) and the United Kingdom (ASPT$_{\mathrm{WHPT}}$ of 2.54–9.8; 5.66 ± 1.12).

2.4 | Statistical Analyses

To relate taxonomic and trait composition to ecological quality in each country, we used redundancy analyses (RDAs) performed via the *vegan* package in R (Oksanen et al. 2022; R Core Team 2023). The response variables were taxonomic or trait composition in each site and year, and the predictor variable was the EQR or ASPT$_{\mathrm{WHPT}}$. Because multiple sites and years were included, we evaluated whether the trait RDA results were driven by spatial differences among sites or changes through time within each site. To do so, we decomposed ecological quality into its spatial and temporal components and conducted variation partitioning to evaluate their relative contributions using the *varpart* function in *vegan*. We quantified the spatial component as the average ecological quality for each site across years (i.e., differences among sites), and the temporal component as the difference between ecological quality in each year and the site average (i.e., site-specific change over time). We down-weighted the influence of traits with more modalities or higher correlations to other traits using weights calculated via the *gawdis* function from the *gawdis* package (de Bello et al. 2021), which ensured the uniform contribution of all traits.

To identify trait modalities that consistently responded to anthropogenic impacts, we identified modalities that always increased or decreased in relation to increases in ecological quality on the basis of their loadings on the first RDA axis, which represented changes in ecological quality in each country. We then identified trait modalities that always exhibited greater variation than expected by chance. To do so, we constructed null distributions of the RDAs by shuffling the community-weighted trait composition data for each country 1000 times to break any relationships to ecological quality. We then repeated each trait RDA using the shuffled compositions and extracted the loadings for each modality on the first axis. Modalities with loadings > 95% of the null distribution values in every country were considered ‘consistent’ because they always varied more than expected by chance in relation to ecological quality. To avoid being too stringent with this 95% rule, we also report trait modalities meeting the 95% criterion in five countries and a 90% criterion in the sixth.

To quantify effect sizes for traits identified to respond consistently, and to account for more complex spatial and temporal relationships, we related the values for each consistent trait modality, pooled across countries, to ecological quality using generalised additive mixed models (GAMMs) performed using the *mgcv* package (Wood 2017). The modelled response variable for these models was the CWM affinity value for the relevant trait modality in all sites and years. Predictor variables included a smoothed fixed term for ecological quality, which was transformed to country-specific *z*-scores by subtracting the mean and dividing by the standard deviation in each country. To control for spatial relationships, we included unsmoothed fixed terms for latitude and longitude, and a random intercept term for country. We also controlled for spatial autocorrelation using unsmoothed fixed terms of Moran's Eigenvector Maps calculated using principal coordinates of neighbour matrices (Dray et al. 2012). To control for temporal relationships, we included a random intercept term for sampling year, and a first-order autoregressive structure to model temporal autocorrelation within successive samples from the same site. GAMMs used a beta (logit link) or Gaussian (identity link) distribution depending on which produced the best model fit. The smoothed ecological quality predictor used thin-plate regression splines and a basis dimension of $k = 10$, which we confirmed via comparison with the effective degrees of freedom and based on whether relationships changed when the basis dimension was increased. Significance ($p < 0.05$) of the relationship between a trait modality and ecological quality was determined using Wald tests.

Additionally, we quantified the effect sizes of the average affinity value across all consistently responding traits within each country to determine whether the same degree of overall trait change occurred among countries, and to compliment the GAMMs that examined individual modality responses. We first split modalities into two groups: those that were consistently (1) positively or (2) negatively related to ecological quality. We then averaged the CWM affinity values across the modalities in each group for each site and year, then related these averages to a smoothed fixed term for ecological quality separately for each country using GAMMs. These analyses determined how the average affinity of the consistent trait modalities changed with ecological quality across all communities in each country. GAMMs included the same control variables and distributions as the all-country GAMMs, excepting country-specific random effects or transformations.

3 | Results

3.1 | Taxonomic Composition

Ecological quality explained between 5.6% (Hungary) and 15.3% (Spain) of taxonomic variability across countries (Figure 2). Such low overall explained variance is not unexpected (Møller and Jennions 2002) given we related a single predictor to changes in 62–273 taxa across large geographic areas. Sites and years with better ecological quality were characterised by more: (i) Baetidae (mayflies), specifically *Baetis* sp.; (ii) Gammaridae (amphipods), such as *Gammarus* sp.; (iii) Simuliidae (blackflies), such as *Simulium* sp.; (iv) Elmidae (riffle beetles), such as *Elmis* sp.; and (v) *Hydropsyche* sp. (caddisflies; Figure 2). Conversely, sites and years with poorer ecological quality were characterised by: (i) Asellidae (isopods), specifically *Asellus* sp.; (ii) Oligochaeta (worms), including Naididae; and (iii) Chironomidae (non-biting midges), including Orthocladiinae (Figure 2).

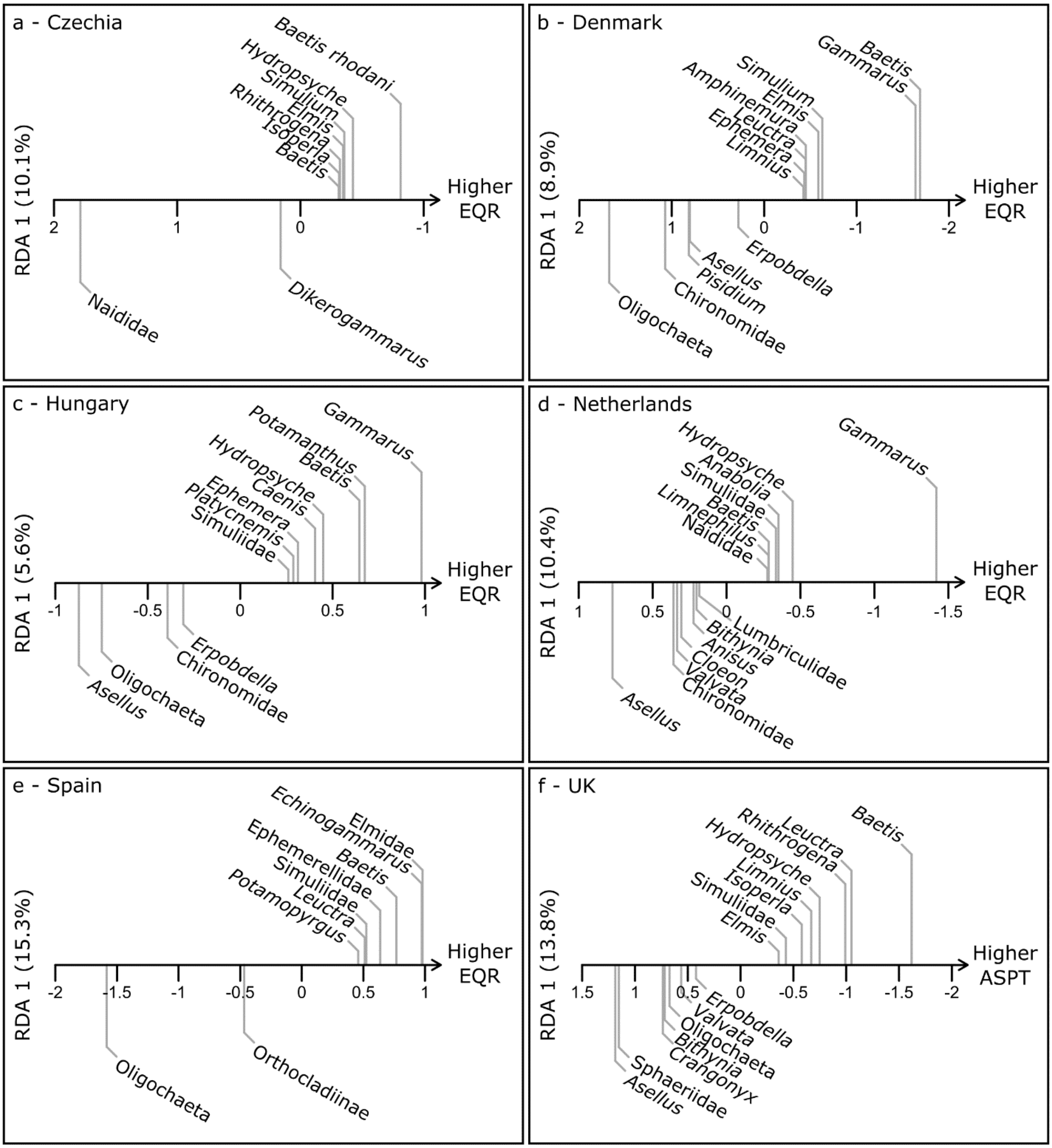

FIGURE 2 | Invertebrate taxonomic composition in relation to ecological quality (EQR or $\mathrm{ASPT}_{\mathrm{WHPT}}$) in (a) Czechia, (b) Denmark, (c) Hungary, (d) the Netherlands, (e) Spain and (f) the United Kingdom based on redundancy analysis (RDA). Taxa that exhibited little variation in relation to ecological quality (i.e., those close to 0) are not shown. Note the changing positive and negative directions of the *x*-axis, which are RDA axis scores and so the sign is irrelevant when comparing the relation to ecological quality across countries.

3.2 | Trait Composition

Ecological quality explained more variability in traits than in taxa in every country, ranging from 6.4% in Hungary to 42.0% in the United Kingdom (Figure 3 and Supporting Information S2). Variation partitioning indicated that these compositional patterns were primarily driven by differences in ecological quality among sites, which represented 83%–96% of explained trait variation in each country, with a comparatively minor effect of site-specific temporal changes in ecological quality (4%–17%).

3.3 | Modalities Across Countries

Five traits consistently responded to both spatial and temporal changes in ecological quality across all countries, based on directionality within the RDAs and differences from the null distributions (Figure 3 and Supporting Information S3 and S4). Specifically, modalities within one biological trait (dispersal mode) and four ecological traits (current, microhabitat, salinity and trophic preferences) responded consistently. Based on GAMMs for all sites and years, as ecological quality improved from its minimum to maximum values, the proportion of taxa

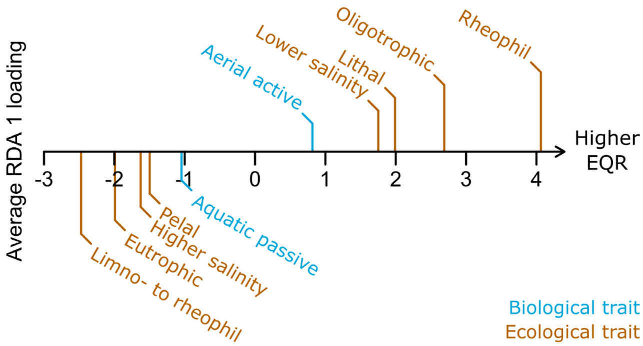

FIGURE 3 | Average invertebrate trait composition across countries in relation to ecological quality (EQR or $\text{ASPT}_{\text{WHPT}}$ in the United Kingdom) based on redundancy analysis (RDA). Average variance explained was 21.4%. Only consistently responding ecological (brown) and biological (blue) traits are shown. Trait scores on RDA 1 reflect the degree to which each trait modality varied in relation to ecological quality. Scores were calculated as the absolute score of each modality on RDA 1 from the country-specific RDAs (Supporting Information S4), which were then averaged across countries. Negative and positive signs are only used to illustrate which modality affinities were always lower or higher, respectively, in better quality communities.

with an affinity for active aerial dispersal increased by +0.15 (from 0.11 to 0.26; $R^2_{\text{adj}} = 0.54$, $p < 0.001$; Figure 4a). Similarly, better ecological quality was related to increased affinities for faster currents (i.e., rheophils in Table 1; +0.39; $R^2_{\text{adj}} = 0.51$, $p < 0.001$; Figure 4b), coarser substrates (i.e., lithal microhabitat preferences; +0.19; $R^2_{\text{adj}} = 0.62$, $p < 0.001$; Figure 4c), lower salinities (+0.11; $R^2_{\text{adj}} = 0.60$, $p < 0.001$; Figure 4d) and oligotrophic conditions (+0.18; $R^2_{\text{adj}} = 0.63$, $p < 0.001$; Figure 4e). Conversely, poorer ecological quality was related to increases in the proportion of taxa with an affinity for aquatic passive dispersal (+0.21; $R^2_{\text{adj}} = 0.49$, $p < 0.001$; Figure 4a) and preferences for slower currents (i.e., limno- to rheophils; +0.25; $R^2_{\text{adj}} = 0.53$, $p < 0.001$; Figure 4b), organic, finer or muddier substrates (i.e., pelal microhabitat preferences; +0.15; $R^2_{\text{adj}} = 0.41$, $p < 0.001$; Figure 4c), higher salinities (+0.11; $R^2_{\text{adj}} = 0.60$, $p < 0.001$; Figure 4d) and eutrophic conditions (+0.17; $R^2_{\text{adj}} = 0.55$, $p < 0.001$; Figure 4e).

The consistent ecological trait responses were unchanged when trait averaging was not used. However, in Spain, the dispersal modality responses reversed (Supporting Information S5), likely because the Oligochaeta—a common taxon associated with poor water quality in Spain (Figure 2e)—lack dispersal trait values. Using the average value across families, all of which have an affinity for aquatic passive dispersal, enabled detection of a shift in the dispersal trait.

3.4 | Modalities Within Countries

Effect sizes of the change in the average affinity value of the consistent trait modalities were similar among countries. Based on country-specific GAMMs, as ecological quality improved from its minimum to maximum values, the average affinity of modalities consistently positively related to ecological quality increased from 0.26 ± 0.03 (mean ± SD of the predicted values across countries) to 0.45 ± 0.08 (Figure 5; see Supporting Information S6 for model coefficients). Conversely, the average affinity of consistently negatively related modalities decreased from 0.36 ± 0.02 to 0.18 ± 0.05 (Figure 5). The narrow standard deviations of these results indicate highly consistent, cross-country changes in affinity values in relation to ecological quality.

4 | Discussion

4.1 | Consistent Trait Responses

Anthropogenic impacts in European rivers were consistently reflected by changes in four invertebrate ecological traits, specifically current, microhabitat, salinity and trophic preferences, and only one biological trait, specifically dispersal mode. Ecological traits (i.e., habitat preferences) may thus be the most useful for making broad-scale predictions about community responses to anthropogenic impacts, helping to improve the predictive capabilities of community-level research (McGill et al. 2006; Suding et al. 2008). The predictive value of ecological traits is already recognised in certain fields, such as freshwater biomonitoring where ecological traits are key tools for assessing community responses to anthropogenic impacts, including organic pollution (Paisley, Trigg, and Walley 2014) and flow alteration (Laini et al. 2022). However, these traits can be excluded from many studies due to: (i) a lack of data on habitat preferences (Cano-Barbacil, Radinger, and García-Berthou 2020; Etard, Morrill, and Newbold 2020); (ii) a focus on biological traits owing to their clearer linkage to ecosystem functions (Lavorel and Garnier 2002; Martini et al. 2021); or (iii) not considering ecological traits as 'traits' because they are not inherent taxon attributes (Verberk, van Noordwijk, and Hildrew 2013). The latter two reasons are debatable because habitat preferences can be proxies for physiological tolerances (Horrigan et al. 2007; Kimball et al. 2017), which most researchers consider to be traits (Dawson et al. 2021), and habitat-related traits can elicit trade-offs with other traits that affect ecosystem functions (e.g., growth rates; Loehle 1998). Thus, depending on the research question, including or at least separately examining ecological traits in large-scale community research could improve comparability and predictive power.

From a practical perspective, the consistently responding traits we identified could help achieve a principal aim of applied freshwater ecology to detect, measure and compare ecological degradation (Martini et al. 2021; Menezes, Baird, and Soares 2010). Riverine invertebrates are common indicators of ecosystem health. However, comparisons of country-specific assessments can be hampered by the use of different methodologies (see Supporting Information S1), which can result in differing assessment outcomes for comparable communities (Birk et al. 2012; Santos et al. 2021). For example, many countries use indices that incorporate trait information, but the traits included typically vary among countries (Birk et al. 2012). Indices can be intercalibrated across countries to minimise issues caused by methodological differences (Bennett et al. 2011), but intercalibration can be incomplete in certain regions or impossible where methods differ too widely (Birk et al. 2013; Santos et al. 2021). These problems could be resolved by developing indices that use the same set of consistently responding traits across countries. Deriving assessment indices solely from traits would reduce methodological complexity and facilitate comparisons among countries. Purely

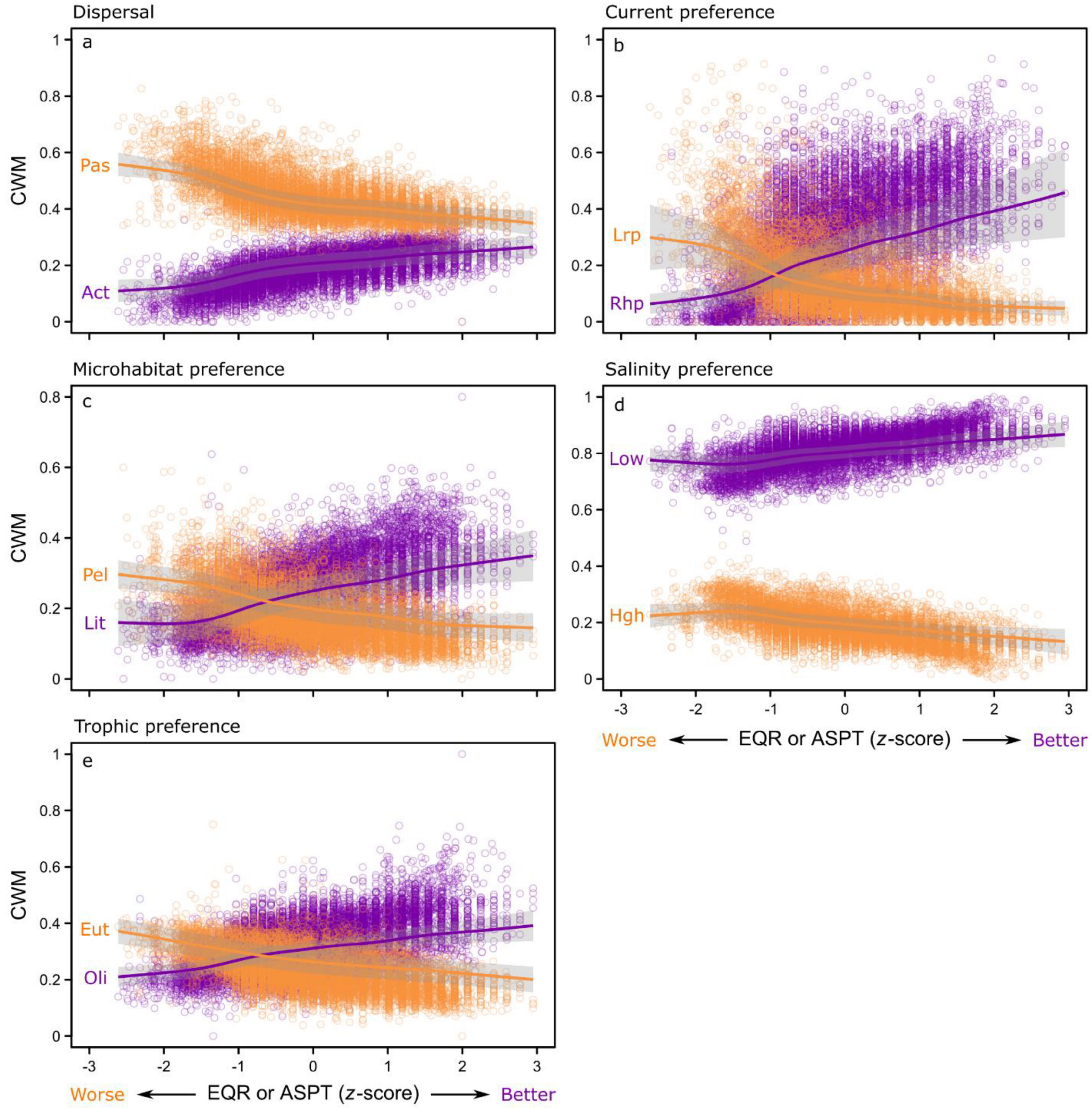

FIGURE 4 | Relationships between community-weighted mean (CWM) trait affinities and ecological quality (EQR or ASPT$_{\mathrm{WHPT}}$) across countries for trait modalities that were consistently higher (purple) or lower (orange) in better quality communities. Best-fit lines and 95% confidence intervals were derived from the respective generalised additive mixed models. Modalities encompass one biological trait: (a) dispersal mode ('Act' = aerial active; 'Pas' = aquatic passive); and four ecological traits: (b) current preference ('Rhp' = rheophil; 'Lrp' = limno- to rheophil), (c) microhabitat preference ('Lit' = lithal; 'Pel' = pelal), (d) salinity preference ('Low' = lower; 'Hgh' = higher) and (e) trophic preference ('Oli' = oligotrophic; 'Eut' = eutrophic). Note the change in the scale of the *y*-axis in panel (c).

trait-based assessment indices have already been applied at broader spatial scales in other taxa (e.g., the pan-European fish index; Pont, Hugueny, and Rogers 2007), which, combined with the consistent trait responses we identified, suggests a similar approach may be effective in riverine invertebrates.

4.2 | Potentially Linked Trait Responses

Although the five consistently responding traits we identified may facilitate comparison and prediction of community responses to anthropogenic impacts, their concurrent changes prevented us from ascribing responses to specific freshwater stressors. Changes in current, microhabitat, salinity and trophic preference trait modalities may each represent the ecological impacts of associated stressors common to European rivers, respectively flow alteration due to water resource use (Carlisle, Nelson, and Eng 2014), elevated fine sediment levels (Chará-Serna et al. 2015), salinisation (Cañedo-Argüelles et al. 2016) and increased nutrient concentrations (Wassen et al. 2022). However, we lack the environmental data needed to confirm these relationships, and responses in some traits may not be driven by an associated stressor but rather by trait linkages (Jones et al. 2023). For example, taxa sensitive to

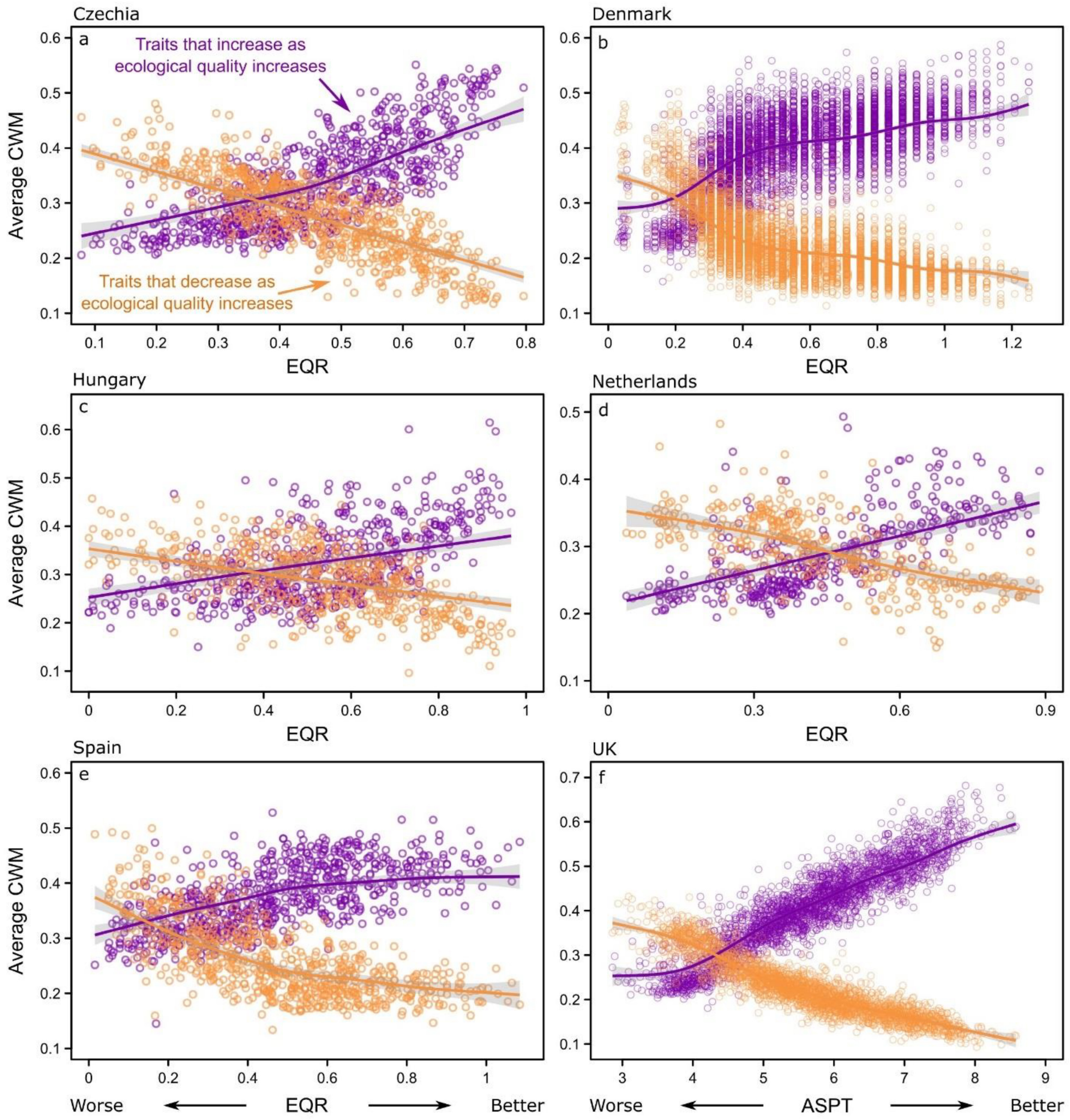

FIGURE 5 | Relationships between the average community-weighted mean (CWM) affinities of trait modalities whose values consistently increase (purple) or decrease (orange) as ecological quality increases (based on EQR or ASPT$_{\text{WHPT}}$) in (a) Czechia, (b) Denmark, (c) Hungary, (d) the Netherlands, (e) Spain and (f) the United Kingdom. Best-fit lines and 95% confidence intervals were derived from generalised additive mixed models for each country (Supporting Information S6). Modalities that we found consistently increased as ecological quality increased include aerial active dispersal and rheophil, lithal, lower salinity and oligotrophic preferences. Consistently decreasing modalities included aquatic passive dispersal and slower current, finer substrate, higher salinity and eutrophic preferences. Note the changing scale of the *y*-axis.

elevated nutrient concentrations are also somewhat sensitive to higher salinity, evidenced by moderate correlations among some trophic and salinity preference modalities (Data S1). Consequently, even if salinity is unchanged, elevated nutrients could drive declines in both nutrient-sensitive and salinity-sensitive taxa, meaning we cannot assume that different trait responses are driven by different stressors. Even the consistent response in the biological dispersal mode trait could result from trait linkages. For example, invertebrates with preferences for coarser substrates can also be aerial active dispersers that oviposit on rocks (e.g., the mayfly *Rhithrogena* sp.). Such correlations among ecological and biological traits were not strong (r among modalities was always < 0.5; Data S1), but these potential linkages cannot be ignored and could be particularly difficult to disentangle in specific taxonomic groups with stronger inter-trait relationships.

4.3 | Inconsistent Trait Responses

We identified high regional variation in the degree to which traits responded to anthropogenic impacts, with ecological quality explaining as little as 6% up to 42% of total differences in trait composition. This regional variability could be driven by both methodological and ecological differences among regions. For example, Hungary and the Netherlands exhibited the lowest explained variation and had the fewest sites, raising the question of whether more data may have improved these relationships. Additionally, some countries calculate ecological quality using metrics that prioritise the detection of organic pollution (Birk et al. 2012). If communities are impacted by other stressors that are not well-reflected by ecological quality indices (e.g., hydromorphological alteration; Laini et al. 2022); then, traits may change when ecological quality indices do not, producing weaker relationships. However, these possibilities do not fully explain our results, given that some countries with fewer sites still exhibited strong relationships (e.g., Spain), as did countries that prioritise detecting organic pollution (e.g., Denmark; Skriver, Friberg, and Kirkegaard 2000). An alternative ecological explanation is that the strength of trait responses to anthropogenic impacts simply varies among regions. This spatial variability could be driven by different factors, including climate (e.g., trait response strength can differ between warmer and colder regions; Murray, Nowakowski, and Frishkoff 2021), or due to the extirpation of sensitive species from some regional species pools (Heino 2013). Trait-based predictions of community responses to anthropogenic impacts may thus be less accurate in regions that exhibit weaker responses.

Inconsistent responses for almost all biological traits matched our expectation that these traits would respond less consistently than ecological traits. This response variability is unlikely to reflect regional differences in stressor types and intensities because the consistent ecological trait responses suggested similar anthropogenic impacts affected all communities. High spatial variability in biological trait responses could hamper extrapolation of community-level trait predictions to their ecosystem-level consequences. Biological traits typically have clearer links to key ecosystem processes than ecological traits, such as feeding traits affecting organic matter processing and energy transfer (Thompson et al. 2020; Vandewalle et al. 2010), or life-history traits affecting growth rates and thus community recovery from disturbance (Salguero-Gómez et al. 2016; Winemiller et al. 2015). However, if these traits respond inconsistently to anthropogenic impacts across regions, as we found here, then making broad-scale predictions of changes in associated ecosystem processes requires prior knowledge of which biological traits will respond in each region. Obtaining such regionally contextual knowledge is difficult for broad-scale studies, potentially limiting ecosystem-level predictions to individual regions or habitat types in which biological trait responses are more consistent.

4.4 | Limitations

Our analyses have two principal limitations. First, all taxa have a single value for each trait modality derived from expert opinions, which could influence the consistency of some trait responses if the value is inaccurate, missing or more variable than represented by fuzzy coding. This limitation will diminish through efforts to fill incomplete trait information and to measure inter-regional and intraspecific trait variability. Second, although our dataset covers six freshwater ecoregions across much of Europe, we lacked data from certain areas, including many Nordic and Mediterranean regions. Further research is therefore required to determine how the consistently responding traits we identified respond to anthropogenic impacts in other regions.

4.5 | Broader Implications

We found that primarily ecological traits consistently characterised invertebrate community responses to anthropogenic impacts, likely because these traits are closely linked to common stressors affecting water quality and wider habitat conditions. These findings match conclusions from other terrestrial and aquatic research showing that the traits most closely linked to anthropogenic habitat alteration can be the most useful for making broad-scale comparisons, and for predicting future responses. Examples of such research include vertical habitat position in frogs responding to deforestation (Murray, Nowakowski, and Frishkoff 2021), fish with narrower thermal envelopes being more vulnerable to climate warming (Jarić et al. 2019), and birds with narrower habitat breadths being more vulnerable to habitat alteration (Richards, Cooke, and Bates 2021). Even consistent responses in some biological traits could be driven by their relationships to ecological traits, such as our results suggesting a link between the biological dispersal mode trait and several ecological traits. Ongoing global change requires approaches that enable measuring, comparing and predicting responses of different communities to anthropogenic impacts, and our work suggests that a stronger focus on ecological traits could move us closer towards this goal.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code needed to reproduce our trait analyses are publicly available at https://doi.org/10.6084/m9.figshare.25266322. As approved by the EiCs at GEB, taxonomic data for Czechia are only available via direct request to Petr Pařil (paril@sci.muni.cz).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.