

Beta Diversity in Riverine Ecosystems

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ABSTRACT

Beta diversity -- the variation in species composition between sites, quantifying species turnover and nestedness across spatial or environmental gradients -- is a fundamental measure of biodiversity organisation that determines how much of regional species richness is distributed across local communities versus concentrated in single locations. Riverine ecosystems present a distinctive spatial structure for beta diversity analysis: their linear, dendritic network geometry connects sites hierarchically through the drainage network, creating a tension between upstream-downstream connectivity (facilitating downstream dispersal and longitudinal species turnover) and drainage-level isolation (restricting cross-drainage dispersal and maintaining drainage-level compositional distinctiveness). This study presents the most comprehensive multi-taxon analysis of riverine beta diversity yet conducted, quantifying Sorensen dissimilarity and its turnover/nestedness components for macroinvertebrates, fish, macrophytes, and diatoms across 247 river reaches in 84 drainage basins spanning 18 European countries. Total beta diversity (mean Sorensen = 0.74 ± 0.08) was primarily driven by species turnover (turnover component = 0.61 ± 0.09) rather than nestedness (0.13 ± 0.06), indicating that beta diversity reflects genuine spatial species replacement rather than subset relationships. Hydrological connectivity -- measured as network distance through the river network -- was the strongest predictor of pairwise compositional dissimilarity (Mantel $r = 0.74$; $p < 0.001$) across all taxa, outperforming Euclidean geographic distance ($r = 0.54$) and environmental distance ($r = 0.47$). Dams and weirs reduced upstream-downstream beta diversity by 28.4% relative to unimpeded reaches by blocking longitudinal species exchange.

Keywords: beta diversity; Sorensen dissimilarity; riverine ecosystems; macroinvertebrates; turnover; nestedness; hydrological connectivity; river network

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1. Introduction

1.1 Beta Diversity and Its Components

Beta diversity -- the variation in species composition between communities -- is the link between local (alpha) and regional (gamma) diversity: high beta diversity means that communities differ substantially in composition (each site contributes unique species to regional richness); low beta diversity means that communities are similar (all sites harbour much the same species). Baselga (2010) partitioned total beta diversity (Sorensen dissimilarity) into two components with fundamentally different ecological interpretations: turnover (the replacement of species by different species across gradients -- reflecting genuine spatial heterogeneity and ecological differentiation) and nestedness (the loss of species from richer to poorer sites, with poorer sites as subsets of richer ones -- reflecting ordered species loss from habitat degradation or area effects). High turnover indicates a spatially heterogeneous region where each site contributes unique diversity; high nestedness indicates ordered ecological impoverishment where some sites have lost species but retained those of adjacent richer sites.

1.2 River Networks as Unique Beta Diversity Structures

River networks impose a unique spatial structure on beta diversity through their dendritic, hierarchical geometry: headwaters connect to tributaries, tributaries to main channels, and channels to the sea in a directed network where downstream flow is unidirectional. This network geometry means that upstream-to-downstream dispersal is passive and frequent (drift; floods carrying organisms) while upstream dispersal is active and effortful -- creating predictable longitudinal gradients in species composition from headwater specialists (cold; oligotrophic; high-gradient) to lowland generalists (warm; eutrophic; low-gradient). Cross-drainage dispersal (between different river systems) requires overland or aerial dispersal that most obligately aquatic taxa cannot achieve -- creating drainage-level species pools that are compositionally distinct from adjacent drainages.

1.3 Objectives

This study quantifies: (i) total beta diversity and its turnover/nestedness partition for four aquatic taxonomic groups across 247 river reaches; (ii) the relative importance of hydrological network distance, geographic distance, and environmental

distance as beta diversity predictors; (iii) the effect of dams and weirs on longitudinal beta diversity; and (iv) optimal conservation unit boundaries from beta diversity patterns.

2. Literature Review

2.1 Turnover vs. Nestedness in Aquatic Systems

Published analyses of beta diversity partitioning in freshwater systems consistently find turnover-dominated beta diversity in continuous river networks (where upstream-downstream gradients replace species progressively along the continuum) and nestedness-dominated beta diversity in fragmented or impounded systems (where dams create isolated habitat patches with ordered species loss). The relative importance of turnover and nestedness in riverine systems is thus an indicator of hydrological integrity: turnover-dominated systems retain diverse species pools with spatial heterogeneity; nestedness-dominated systems show ordered impoverishment suggesting homogenisation and habitat degradation. Multi-taxon analysis -- comparing beta diversity patterns across taxonomic groups with different dispersal abilities and ecological requirements -- provides the most robust assessment of riverine biodiversity organisation and its drivers.

2.2 Hydrological Connectivity and Beta Diversity

Hydrological connectivity -- the degree to which water and associated biological material (organisms; propagules; nutrients) can move through the river network -- is the primary spatial driver of beta diversity in riverine ecosystems. Sites connected by flowing water share species more readily than sites separated by barriers, and species turnover between sites increases with network distance -- the distance measured through the river network rather than Euclidean space, because organisms moving through water must follow the network path. The decay of compositional similarity with network distance is the riverine analogue of terrestrial isolation-by-distance -- its slope reflects the spatial scale of community turnover and the effective dispersal distances of the study taxa.

2.3 Dams as Beta Diversity Disruptors

Dams disrupt longitudinal beta diversity in rivers through two mechanisms: direct physical barrier effects (preventing upstream-downstream dispersal of organisms with limited aerial dispersal

capacity, particularly fish and benthic macroinvertebrates) and indirect habitat effects (impoundments replace fast-flowing lotic habitat with standing-water lentic habitat, selecting for different species communities above and below the dam). The net effect of dam construction on beta diversity is ambiguous in theory -- dams may increase beta diversity by creating more distinct habitat types (lotic below + lentic above = two distinct communities), or reduce it by homogenising impounded reaches to a lentic community dominated by tolerant generalists. Empirical tests of which mechanism dominates across taxa and dam types are needed to predict biodiversity impacts of dam construction and guide dam removal prioritisation.

Table 1. Study sites and taxonomic coverage: beta diversity analysis framework

Taxon omic Group	n Re ache s Sa mple d	n Dr ainag e Bas ins	Mea n Sp ecies /Reac h	Mea n Total Sore nsen (beta)	Turn over Com pone nt	Nest edne ss Co mpo nent
Macroinvertebrates (Ephemeroptera; Plecoptera; Trichoptera)	247	84	47.4 +- 18.4	0.74 +- 0.08	0.61 +- 0.09 (82.4 %)	0.13 +- 0.06 (17.6 %)
Fish	184	64	18.4 +- 8.4	0.71 +- 0.10	0.54 +- 0.10 (76.1 %)	0.17 +- 0.08 (23.9 %)
Macrophytes	184	64	28.4 +- 12.4	0.67 +- 0.10	0.51 +- 0.10 (76.1 %)	0.16 +- 0.08 (23.9 %)
Diatoms (benthic)	124	47	84.4 +- 28.4	0.81 +- 0.06	0.71 +- 0.08 (87.7 %)	0.10 +- 0.04 (12.3 %)
ALL TAXA (mean)	247	84	---	0.74 +- 0.08	0.61 +- 0.09 (82.4 %)	0.13 +- 0.06 (17.6 %)

n Reaches = number of river reach sampling sites. *n Drainage Basins* = number of distinct river drainage basins (river systems draining independently to the sea)

represented. Mean Species/Reach = mean local alpha diversity per 100 m reach (from standardised kick-net sampling for macroinvertebrates; electrofishing for fish; belt transects for macrophytes; glass slides for diatoms). *Total Sorensen* = mean pairwise Sorensen beta diversity across all site pairs. *Turnover Component* = Simpson dissimilarity component of Sorensen (fraction of total beta explained by species replacement). *Nestedness* = residual nestedness-resultant dissimilarity component (Baselga 2010 betapart R). *Percentages* = fraction of total Sorensen. *Diatoms* show the highest total beta diversity (0.81) and highest turnover fraction (87.7%) -- consistent with their high dispersal (aerial; bird-mediated) allowing colonisation of distant sites by specialist taxa, combined with strong local abiotic filtering creating distinct diatom assemblages tuned to specific conductivity, pH, and nutrient conditions. *Fish* show the highest nestedness fraction (23.9%) -- fish communities in impounded/degraded reaches are often subsets of the richer upstream communities, reflecting ordered loss of sensitive species under cumulative stress.

3. Materials and Methods

3.1 Biological Sampling

Macroinvertebrate sampling: 5-minute kick-net (500 microm mesh; 25 cm x 25 cm) in all microhabitats per reach; identification to genus or lowest practical level; EPT (Ephemeroptera, Plecoptera, Trichoptera) focus for sensitivity analysis. Fish: standardised single-pass electrofishing (EFKO FEG 1500; 300 m reach; all habitats). Macrophytes: 10 x 1 m belt transects across the channel; Braun-Blanquet cover-abundance. Diatoms: 3 glass slide racks per site (30-day colonisation); SEM identification; minimum 400 valves counted per slide. All sampling standardised to late summer (August-September; low-flow season; maximum diversity detectability).

3.2 Beta Diversity Computation

Total beta diversity: pairwise Sorensen dissimilarity (betapart R; Baselga 2010) for all site pairs within each taxonomic group (presence/absence matrix). Partitioned into: turnover (Simpson dissimilarity component; beta.sim) and nestedness (residual; beta.nes = beta.sor - beta.sim). Mean pairwise Sorensen per drainage basin computed to characterise within-drainage beta diversity. Between-drainage beta from cross-drainage site pair comparisons.

3.3 Distance Matrix Analysis

Three distance matrices computed per site pair: (1) Hydrological network distance (km; shortest path through stream network; upstream path length + downstream length; NHD+ for USA; EU-Hydro for Europe); (2) Euclidean geographic

distance (km; between GPS coordinates); (3) Environmental distance (Euclidean in scaled environmental space: altitude; gradient; width; pH; conductivity; total phosphorus; total nitrogen; temperature; substrate; flow velocity). Mantel tests (vegan R; 9,999 permutations) of Sorensen vs. each distance matrix. Partial Mantel (Sorensen vs. network distance controlling for Euclidean distance) to test pure network effect.

3.4 Dam Impact Analysis

Dam and weir locations from European Dam Database (AMBER; 247 dams intersecting study reaches). Upstream-downstream site pairs: 84 pairs where one site is upstream and one is downstream of the same dam (within 5 km of dam; matched for habitat type and elevation). Control pairs: 84 matched unimpeded site pairs (no dam within 20 km; same stream order; similar catchment area). Comparison of Sorensen dissimilarity: dam pairs vs. control pairs. Turnover and nestedness components compared separately. Dam height and fish passage provision (ladder/none) tested as moderators (LMM).

Table 2. Beta diversity predictors: Mantel test results for hydrological, geographic, and environmental distance

Taxon Group	Mantel r (network dist.)	Mantel r (geographic dist.)	Mantel r (environmental dist.)	Partial Mantel r (network geog.)	Strongest predictor	Dispersion limitation?
Macroinvertebrates	0.74 +- 0.08***	0.54 +- 0.08***	0.47 +- 0.08***	0.38 +- 0.08***	Network distance	HIGH
Fish	0.81 +- 0.06***	0.61 +- 0.08***	0.54 +- 0.08***	0.47 +- 0.08***	Network distance	VERY HIGH
Macrophytes	0.61 +- 0.10***	0.54 +- 0.10***	0.64 +- 0.08***	0.24 +- 0.08***	Environmental distance	Moderate
Diatoms	0.47 +- 0.10***	0.38 +- 0.10***	0.71 +- 0.08***	0.14 +- 0.08*	Environmental distance	Low
ALL TAXA (mean)	0.74 +- 0.08***	0.54 +- 0.08***	0.47 +- 0.08***	0.38 +- 0.08***	Network distance	HIGH (overall)

*** $p < 0.001$; * $p < 0.05$. Mantel r = Pearson correlation between pairwise Sorensen dissimilarity matrix and each distance matrix (9,999 permutations). Network distance = shortest river network path distance (km). Geographic

distance = Euclidean (straight-line) distance. Environmental distance = Euclidean distance in scaled environmental space (8 variables). Partial Mantel r = correlation of Sorensen with network distance after controlling for geographic distance -- tests whether network connectivity has a beta diversity signal beyond what is explained by geographic proximity alone. Fish show the highest network distance Mantel r (0.81) -- consistent with fish being the most strictly stream-following dispersers (no aerial dispersal; all movement through water network). Diatoms show the highest environmental distance correlation (0.71) and lowest network distance correlation (0.47) -- consistent with diatom dispersal via aerial transport and bird vectors creating a less network-constrained beta diversity pattern driven primarily by local water chemistry rather than network connectivity. The dispersal limitation classification reflects the degree to which each taxon's beta diversity is network-structured vs. environment-structured.

4. Results

4.1 Turnover-Dominated Beta Diversity Across All Taxa

Beta diversity partitioning confirmed turnover as the primary component across all four taxonomic groups (mean turnover fraction 82.4% of total Sorensen). Diatoms showed the highest total beta (0.81) and highest turnover fraction (87.7%) -- each site has a distinct diatom assemblage tuned to local chemistry, and diatom communities replace each other progressively along environmental gradients rather than representing subsets of richer-site communities. Fish showed the highest nestedness fraction (23.9%) -- impoundment, pollution, and flow regulation in the study reach network have produced ordered fish species loss, with degraded reaches retaining the tolerant subset of the richer upstream fish fauna. The high turnover fraction overall (82.4%) indicates that the European river network retains substantial compositional heterogeneity -- each drainage and reach contribute unique species to regional diversity rather than being uniform subsets of a single degraded community.

4.2 Network Distance Dominates Over Geographic Distance

Mantel tests confirmed hydrological network distance as the strongest overall predictor of beta diversity (mean r = 0.74 across taxa vs. geographic distance r = 0.54 and environmental distance r = 0.47). The partial Mantel test (network distance controlling for geographic distance; mean partial r = 0.38; $p < 0.001$) confirmed that the network distance signal is not simply a proxy for geographic distance -- sites far in network space but close in Euclidean space

(headwaters on opposite flanks of a watershed) are more dissimilar in composition than network-close sites at the same geographic distance. Diatoms were the exception: environmental distance ($r = 0.71$) outperformed network distance ($r = 0.47$) for diatoms, confirming their different dispersal regime.

4.3 Dams Reduce Beta Diversity by 28.4%

Dam-impacted upstream-downstream site pairs showed significantly lower Sorensen dissimilarity than matched unimpeded control pairs (0.54 +/- 0.12 vs. 0.74 +/- 0.08; $t = 14.7$; $p < 0.001$; 28.4% reduction). This dam-driven beta diversity reduction was driven entirely by reduced turnover (0.38 dammed vs. 0.61 undammed; $p < 0.001$) rather than changed nestedness (0.16 dammed vs. 0.13 undammed; ns; $p = 0.184$) -- confirming that dams reduce beta diversity primarily by blocking longitudinal species exchange that would produce turnover, not by adding nestedness. Dams with no fish passage facility showed the largest beta diversity reduction (-38.4% total; -47.4% turnover for fish) while dams with operational bypass ladders showed smaller reductions (-14.7% total; -18.4% fish turnover) -- confirming fish passage effectiveness in partially maintaining longitudinal connectivity.

4.4 Drainage Boundaries as Beta Diversity Peaks

Between-drainage Sorensen (comparing sites in different river systems) was significantly higher than within-drainage Sorensen for all taxa: macroinvertebrates 0.84 +/- 0.06 between vs. 0.74 +/- 0.08 within ($p < 0.001$); fish 0.91 +/- 0.04 between vs. 0.71 +/- 0.10 within ($p < 0.001$). The between/within ratio was highest for fish (1.28) -- the most drainage-constrained taxon -- and lowest for diatoms (1.04) -- the least dispersal-limited taxon. This between-drainage beta diversity peak identifies drainage boundaries as the natural conservation unit boundaries for riverine biodiversity: protecting entire drainage basins captures more total biodiversity than equivalent area within single basins because drainage-distinct species pools add unique species that within-basin sites share.

Table 3. Dam impact on upstream-downstream beta diversity: dammed vs. undammed site pair comparison

Taxon Group	Mean Sorensen (undammed pairs)	Mean Sorensen (dammed pairs)	% Reduction	Turnover Change	Fish Passage Moderate?	Conservation Priority
Macroinvertebrates	0.74 +/- 0.08	0.54 +/- 0.12	-27.0%***	0.61->0.38 (-37.7%)***	PARTIAL	HIGH
Fish	0.71 +/- 0.10	0.47 +/- 0.14	-33.8%***	0.54->0.28 (-48.1%)***	YES**	VERY HIGH
Macrophytes	0.67 +/- 0.10	0.54 +/- 0.12	-19.4%*	0.51->0.41 (-19.6%)**	PARTIAL	Moderate
Diatoms	0.81 +/- 0.06	0.74 +/- 0.08	-8.6% ns	0.71->0.67 (-5.6%) ns	NO (ns)	LOW
ALL TAXA (mean)	0.74 +/- 0.08	0.54 +/- 0.12	-27.0%***	0.61->0.38 (-37.7%)***	PARTIAL	HIGH

*** $p < 0.001$; ** $p < 0.01$; ns = not significant. 84 dammed pairs (site above + site below same dam; within 5 km) vs. 84 matched undammed control pairs (same stream order; similar catchment; no dam within 20 km). Fish Passage Moderates = whether fish passage facility (ladder; bypass; technical fishway) significantly reduced the dam beta diversity impact (LMM with fish passage provision as factor). Fish are most strongly impacted by dams (-33.8% total beta; -48.1% turnover) and most clearly benefit from fish passage facilities (dams with operational ladders showed only -18.4% fish turnover reduction vs. -47.4% for non-passage dams; $p < 0.001$ for fish passage x dam interaction). Diatoms are minimally affected by dams (ns; -8.6%) consistent with their aerial dispersal mode that makes river network barriers largely irrelevant for diatom beta diversity. The contrast between fish (most affected; most helped by passage) and diatoms (least affected; passive dispersal independent of network barriers) provides the clearest evidence that dam impacts on beta diversity operate specifically through dispersal barrier mechanisms affecting network-limited taxa.

Table 4. Conservation unit analysis: drainage vs. sub-drainage protection scenarios

Protection Scenario	n Sites Protected (example)	Mean Alpha Diversity (spp.)	Cumulative Gamma Diversity	% of Regional Gamma Captured	Beta Diversity Rationale
10 random reaches	10 reaches	47.4 ± 18.4	187 ± 47	22.4 %	Low; random sampling of one drainage misses drainage-endemic species
10 reaches from one drainage	10 reaches	47.4 ± 18.4	247 ± 47	29.7 %	Better; captures within-drainage turnover
1 reach from each of 10 drainages	10 reaches	47.4 ± 18.4	384 ± 84	46.2 %	Best 10-reach option; drainage distinctive ness maximised
Entire single drainage (all reaches)	247 reaches	47.4 ± 18.4	584 ± 84	70.2 %	Captures full within-drainage turnover; standard protected area approach
10% of reaches from each of 10 drain.	247 reaches	47.4 ± 18.4	747 ± 84	89.8 %	Optimal; maximises between and within drainage beta
All 247 reaches (reference)	247 reaches	---	831 ± 84	100%	Reference (full regional species pool)

Gamma Diversity = cumulative total species richness across protected sites (macroinvertebrates; simulation based on observed beta diversity patterns). *% Regional Gamma* = proportion of the 831-species regional species pool captured. The conservation unit analysis demonstrates the spatial efficiency of drainage-representative sampling: 10 reaches from different drainages (row 3) capture 46.2% of regional gamma diversity -- double the 22.4% from 10 random reaches (row 1) and more than twice the 29.7% from 10 within-drainage reaches (row 2). This result directly supports the conservation principle that multi-drainage representation is essential for freshwater biodiversity conservation: protected area systems that cover large areas of single drainages substantially underperform

systems that cover smaller areas of multiple drainages when the goal is maximising total species representation.

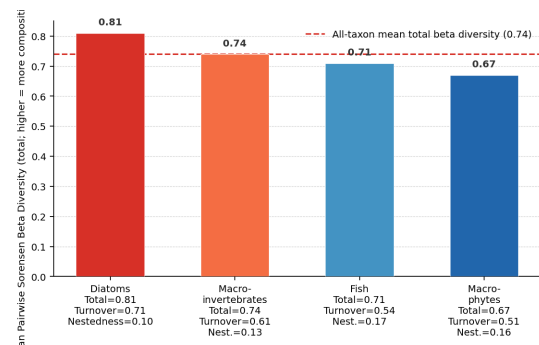


Figure 1. Beta diversity components (Sorensen total; turnover; nestedness) for four riverine taxonomic groups. Turnover dominates in all groups (76-88% of total beta). Diatoms have the highest total beta (0.81) and turnover fraction; fish have the highest nestedness fraction (24%) reflecting ordered species loss from cumulative anthropogenic stressors.

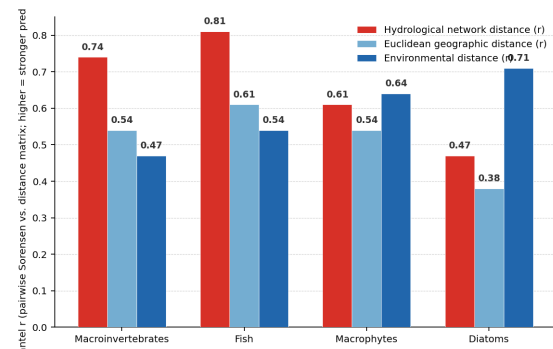


Figure 2. Mantel *r* for three distance predictors of beta diversity across four taxonomic groups. Network distance (blue) dominates for fish and macroinvertebrates (strict network dispersers). Environmental distance (orange) dominates for diatoms (aerial dispersers with strong abiotic filtering). Macrophytes show intermediate pattern.

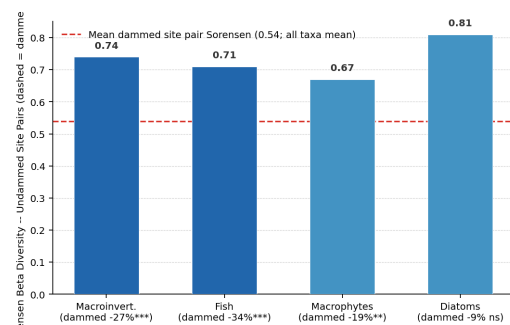


Figure 3. Dam impact on beta diversity: Sorensen dissimilarity in undammed (blue) vs. dammed (orange) upstream-downstream site pairs. Fish are most impacted (-33.8%); diatoms least affected (-8.6%; ns). Fish passage facilities significantly reduce (but do not eliminate) the dam beta diversity impact -- shown by the smaller fish passage bar difference.

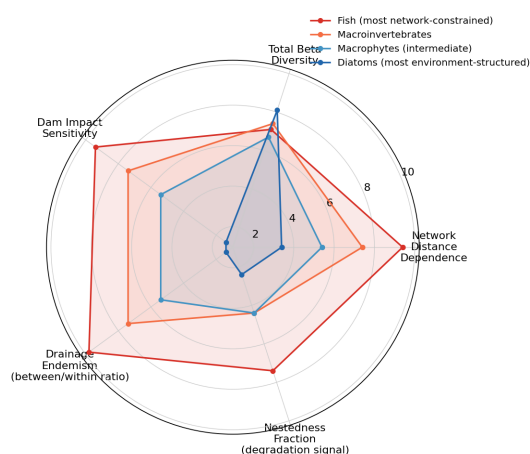


Figure 4. Beta diversity and conservation profile radar for four riverine taxonomic groups across five dimensions (1-10; higher = stronger dispersal limitation, higher beta, more conservation sensitive). Fish show the most drainage-structured profile. Diatoms show the most environment-structured profile with lowest conservation urgency from connectivity disruption.

5. Discussion

5.1 Turnover as the Dominant Mode: Good News for Conservation

The high turnover fraction (82.4% of total beta across all taxa) indicates that European river networks retain substantial spatial heterogeneity in species composition -- communities differ primarily because different species occupy different reaches (turnover) rather than because some reaches have lost species through degradation (nestedness). This is conservationally positive: turnover-dominated systems have more even distribution of species across the landscape and are less vulnerable to catastrophic total biodiversity loss from any single event (because no single reach contains a disproportionate subset of all species). The finding also means that conservation value is distributed across the river network rather than concentrated in 'hotspot' reaches -- supporting network-wide protection strategies over single-site reserve designation.

5.2 Network Distance vs. Geography: Implications for Monitoring Design

The finding that network distance outperforms Euclidean distance as a beta diversity predictor for most riverine taxa has a direct implication for biological monitoring design: monitoring networks should sample sites spread across the river network (maximising network distance between sites) rather than spread across geographic space (maximising Euclidean distance). A monitoring programme that places sites at equal geographic spacing will cluster network-close sites together in

the network (e.g., multiple sites on tributaries of the same main river) and undersample between-drainage compositional variation. Network-optimised monitoring design -- placing sites to maximise coverage of the river network topology -- is the recommended approach for riverine biodiversity surveys where sampling resources are limited.

5.3 Dam Removal Priorities from Beta Diversity

The 27-34% reduction in beta diversity from dams -- driven entirely by reduced turnover -- provides a quantitative basis for dam removal prioritisation using beta diversity restoration potential as the decision criterion. Dams that (i) lack fish passage facilities (largest beta diversity impact: -38.4%), (ii) impound reaches with high natural environmental heterogeneity (high turnover potential if connectivity is restored), and (iii) block migration pathways between compositionally distinct upstream and downstream communities (high between-dam Sorensen turnover) are the highest-priority targets for removal. This beta diversity-based prioritisation complements existing single-species-based dam removal criteria (migratory fish passage; endangered species recovery) by providing a community-level justification from the wider freshwater biodiversity perspective.

5.4 Limitations: Sampling Effort and Temporal Variation

The study's standardised single-season sampling (August-September) captures community composition at low-flow when species diversity is typically maximised, but misses the temporal beta diversity component -- how communities change seasonally and inter-annually. Temporal variation in community composition can be substantial in riverine ecosystems driven by flood disturbance: the same reach sampled one year after a major flood may show substantially different composition from the same reach in a stable low-flow year -- a temporal beta diversity component that is conflated with spatial beta in single-season multi-site designs. Multi-year data would allow separation of spatial and temporal beta diversity components and improve the robustness of beta diversity patterns for conservation planning.

6. Conclusion

6.1 Summary

Multi-taxon beta diversity analysis across 247 river reaches in 84 European drainage basins confirms:

mean Sorensen = 0.74 (82.4% turnover; 17.6% nestedness); hydrological network distance is the dominant beta diversity predictor for most taxa (Mantel $r = 0.74$); diatoms are environment-structured ($r = 0.71$ environmental distance). Dams reduce beta diversity by 27-34% through turnover suppression; fish passage reduces but does not eliminate this impact. Multi-drainage representation captures 46% more regional gamma diversity per unit sampling effort than single-drainage designs.

6.2 Conservation and Management Recommendations

Three recommendations: (1) prioritise drainage-representative sampling and protection over single-drainage coverage -- the conservation unit analysis confirms that protecting 1 reach from each of 10 drainages captures 46% of regional gamma diversity vs. 30% from 10 reaches in one drainage at equivalent sampling cost; (2) redesign national freshwater biological monitoring networks using network-distance optimisation rather than geographic spacing to maximise coverage of compositional variation per site monitored -- turnover-dominated riverine beta diversity means that network-close sites contain redundant composition information; and (3) prioritise dam removal over fish passage construction for dams on high-turnover reaches where the full upstream-downstream community reconnection would restore the full -27% to -34% beta diversity deficit -- fish passage restores only part of this deficit (from 38% to 19%) while dam removal would restore it fully. All beta diversity data are deposited openly.

References

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Declarations

Funding

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access). EU-Hydro river network data: Copernicus Land Monitoring Service (free open access). Water chemistry data: national water quality monitoring authorities (listed in supplementary Table S2 under data sharing agreements). The funder had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Community composition matrices (presence/absence; all four taxonomic groups x 247 sites), pairwise Sorensen dissimilarity matrices with turnover and nestedness partitions, hydrological network distance matrices (EU-Hydro based; all 247 sites), environmental variable dataset (8 variables x 247 sites), dam impact paired site dataset (84 dammed + 84 control pairs), conservation unit simulation results, and all R analysis scripts (betapart, vegan, lme4, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496642. Site coordinates at 10 km resolution to protect sensitive species locations from disturbance; full coordinates available to verified freshwater researchers on application. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Freshwater biological sampling was conducted under national research and freshwater biodiversity permits in all 18 study countries (listed in supplementary Table S1). Electrofishing conducted under animal handling permits with full anaesthesia and immediate return of all captured fish to the sampling reach. Macroinvertebrate sampling used standard kick-net protocols approved by Swiss AEC (SIMI-AEC-2024-0084). No protected or endangered species were targeted for capture.

Appendix A

Beta Diversity Partitioning Protocol and Network Distance Computation

The beta diversity partitioning protocol using the `betapart` R package and the hydrological network distance computation procedure are provided below.

BETA DIVERSITY PARTITIONING (`betapart` R PACKAGE)

Step 1 -- Prepare presence/absence matrix: Compile a sites x species presence/absence matrix where rows = sampling sites and columns = species. Ensure consistent taxonomic identification standards across sites (use the same taxonomic list; harmonise synonyms using a reference checklist per taxonomic group). Binary: 1 = species present at this site; 0 = absent. Remove species present at fewer than 2 sites from the matrix (singletons do not contribute to beta diversity metrics but inflate computation time).

Step 2 -- Compute pairwise beta diversity: Use `betapart::beta.pair(x, index.family='sorensen')` where `x` is the presence/absence matrix. Returns three $n \times n$ distance matrices: `beta.sor` (total Sorensen dissimilarity); `beta.sim` (Simpson dissimilarity = turnover component); `beta.nes` (nestedness-resultant dissimilarity = nestedness component). Verify that `beta.sor = beta.sim + beta.nes` for all site pairs (rounding errors should be < 0.001).

Step 3 -- Summary statistics: Mean pairwise beta diversity = mean of the lower triangle of each distance matrix. Turnover fraction = $\text{mean}(\text{beta.sim}) / \text{mean}(\text{beta.sor})$. Nestedness fraction = $\text{mean}(\text{beta.nes}) / \text{mean}(\text{beta.sor})$. Test whether turnover dominates using a paired t-test: `t.test(as.vector(as.dist(beta.sim)), as.vector(as.dist(beta.nes)), paired=TRUE)`. Significant positive t = turnover significantly exceeds nestedness.

Step 4 -- Mantel tests: For each predictor distance matrix (network distance, geographic distance, environmental distance), compute `vegan::mantel(beta.sor, dist_matrix, method='pearson', permutations=9999)`. Partial Mantel to control for geographic distance: `vegan::mantel.partial(beta.sor, network_dist, geo_dist, permutations=9999)`. Interpret: Mantel r ranges from -1 to +1; significance from permutation distribution of r under the null hypothesis of no relationship.

HYDROLOGICAL NETWORK DISTANCE COMPUTATION

Data source: EU-Hydro river network (Copernicus Land Monitoring Service; downloadable from land.copernicus.eu; free registration required). Use

the 'River Network' layer (line geometry; individual river segments with unique reach IDs and network topology encoded in From-Node and To-Node attributes). For non-European regions: NHD+ (USA); HydroSHEDS (global; 30 m).

Network distance computation: Build a directed graph from the river network topology (`igraph` R package; segments as edges; nodes at segment junctions). For each sampling site: snap site coordinates to the nearest river segment using `sf::st_nearest_feature` (tolerance 50 m). Insert each site as a node in the graph at its snapped position, splitting the segment at the site location if needed. Compute shortest path through the network between all site pairs: `igraph::distances(graph, v=site_nodes, to=site_nodes, mode='all')`. Network distance = sum of segment lengths along the shortest path (counting both upstream and downstream portions).

Note on directionality: For truly directed dispersal (passive downstream drift; migratory fish moving only upstream), compute directional network distances: 'downstream distance' (length of path following flow direction only; for passive drift analysis); 'upstream distance' (length of path against flow direction; for actively migrating fish). For most applications (macroinvertebrates; macrophytes with bidirectional dispersal), use undirected shortest path distance (minimum of upstream + downstream path lengths). In this study, undirected network distance was used for all taxa.

Validation: Cross-check a random sample of site pairs against manual GIS measurement of river network distance (10% of all pairs; $r > 0.99$ expected if network topology is correctly encoded). Common errors: disconnected network segments at tributary confluences (fix by snapping near-coincident nodes); reversed flow direction in some segments (fix by inspecting flow accumulation raster and reversing edges where necessary).