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Genomic and species diversity patterns across multiple trophic levels in riverscapes

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Testing whether intra- and interspecific biodiversity facets co-vary spatially across trophic levels is of utmost importance to generalize processes driving biodiversity patterns in natural landscapes. Similar processes are expected to act on intra- and interspecific diversity, which should lead to positive co-variation between genetic and species diversity. Although this prediction has been verified within trophic levels, it has rarely been tested across multiple trophic levels. To meet this challenge, we focused on a riverine freshwater ecosystem in which we sampled intra- (genomic diversity) and interspecific (species diversity) data across three trophic levels: riparian trees, benthic macroinvertebrates and fishes. For each trophic level, we quantified α- and β-diversity at both the intra- (SNP diversity within populations of *Alnus glutinosa*, *Gammarus* sp. or *Phoxinus dragarum*) and interspecific levels (species diversity within communities). We first tested for a global spatial co-variation of diversity across trophic levels and diversity facets. We then tested whether relevant environmental parameters similarly affected each biodiversity estimate and explained potential spatial co-variation among biodiversity components. We did not evidence any spatial co-variation of biodiversity across trophic levels and diversity facets, neither for α- nor for β-diversity. We found that sites situated in the Western part of the sampling area had higher α-diversities, and that highly connected sites had lower β-diversities, which holds true for all trophic levels and diversity facets. Nonetheless, the effects of other environmental predictors were specific to each biodiversity component, likely explaining the absence of spatial co-variation among biodiversity components. Our study demonstrates that global biodiversity patterns in rivers can be hard to generalize and are rather idiosyncratic, even though a few processes might have consistent impacts on biodiversity components across trophic levels.

Keywords: *Alnus* and *Gammarus* and *Phoxinus*, biodiversity patterns, community structure and population genomics, fish and invertebrates and riparian trees, river ecosystems, species-genetic diversity correlations

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Introduction

Describing and understanding biodiversity patterns is a major objective for many ecologists and evolutionary biologists. Biodiversity describes the diversity of living forms and is traditionally decomposed into an interspecific facet that encompasses diversity observed among species, and an intraspecific facet that encompasses diversity observed within species. Studies on biodiversity patterns have historically focused on one of these facets at a time (Gaston 2000, Turner 2005, Storfer et al. 2010), and our understandings of patterns and processes for inter- and intraspecific biodiversity have emerged independently, for instance from community ecology and population genetics (Hubbell 2001, Manel et al. 2003, Vellend 2010, Charlesworth and Charlesworth 2017, Okazaki et al. 2021). Yet, these two facets of biodiversity are actually forming a single entity, as variation observed within species eventually leads to speciation over the long-term. Developing approaches to jointly understand the processes shaping these biodiversity facets may significantly improve our perception of biodiversity (Vellend and Geber 2005, Coates et al. 2018, Blanchet et al. 2022).

Conceptual and theoretical frameworks have been proposed to jointly analyze and understand patterns of intra- and interspecific diversity. These frameworks lay on the idea that these two facets of biodiversity (in particular genetic and species diversity) are shaped by four similar processes acting in parallel over ecological and evolutionary timescales (Antonovics 1976, Vellend and Geber 2005, Vellend and Orrock 2009): 1) selection, which results in differential survival and reproductive output of some genotypes or species because of biotic or abiotic interactions (Linnen and Hoekstra 2009, McPeek 2017), 2) genetic and ecological drift, that are respectively the random processes by which populations and communities will change over time in diversity or composition (Kimura 1979, Hubbell 2001, Hu et al. 2006, Vellend 2010), 3) mutation and speciation, that generate novel sources of genetic variation within populations or species variation within communities, respectively (Williams 1992, Vellend and Geber 2005) and 4) gene flow and dispersal, that are processes redistributing genotypes -and bringing new ones- within a population or species within a habitat (McPeek and Gomulkiewicz 2005, McPeek 2017). Many empirical studies have demonstrated that these processes can actually shape the two facets of biodiversity simultaneously, and may lead to positive species genetic diversity correlations (SGDCs), that are co-variations between genetic and species diversity: areas that are rich in species are also genetically rich, whereas areas that are poor in species are also genetically poor (Vellend 2005, Kahilainen et al. 2014, Lamy et al. 2017, Schmidt et al. 2022). Nonetheless, most of SGDC studies have considered a single trophic level (e.g. primary producers, Taberlet et al. 2012, Whitlock 2014, Xie et al. 2021; primary consumers, Robinson et al. 2010, Papadopoulou et al. 2011, Seymour et al. 2016; secondary consumers, Fourtune et al. 2016), whereas biodiversity is by nature multi-trophic. Applying this framework to a multi-trophic perspective would be much more realistic, and would therefore provide insightful bases for the design of integrative conservation plans, i.e. plans that simultaneously conserve all facets of biodiversity across all trophic levels. It would also reveal how the different facets of biodiversity interact across trophic levels to shape ecosystem functions.

There is a growing interest to consider biodiversity as inherently multitrophic because: 1) biodiversity patterns are too often considered trophic-level specific, 2) multi-species studies are needed to understand species interactions and energy flows and 3) an integrated food-web perspective in biodiversity patterns studies may lead to a more holistic understanding of ecosystem functioning (Altermatt et al. 2020, Lau et al. 2020, Zhang et al. 2020). Biodiversity patterns have already been considered within a multitrophic perspective. For instance, distribution patterns of hosts and parasites are often considered jointly (Mazé-Guilmo et al. 2016, Colosimo et al. 2021), as well as prey and their predators (Yang et al. 2018, Passoni et al. 2022). Similarly, biodiversity hotspots at regional and global scales are often identified through distribution of rare and iconic species from multiple trophic levels (Myers et al. 2000, Grenouillet et al. 2007, Stork and Habel 2014, Schuldt et al. 2015, Zhang et al. 2020, Blackman et al. 2022). This multitrophic framework has also been applied to understand the complex links between biodiversity and ecosystem functions, as the efficiency of these functions directly depend on the flow of energy among trophic levels (Thébault and Loreau 2006, Yang et al. 2018, Raffard et al. 2021, Timóteo et al. 2022). However, to our knowledge, very few studies have tested for patterns of spatial co-variation among multiple facets of diversity (i.e. inter- and intraspecific diversity facets) and across multiple trophic levels. As a consequence, several major questions remain unresolved. For instance, we still do not know whether the intraspecific diversity of a predator species varies with the interspecific diversity of its prey. Given that more prey species should favor niche partitioning in the predator's population (Bolnick et al. 2007, Moya-Laraño 2011), we may expect a positive co-variation between intraspecific predator diversity and interspecific prey diversity. Conversely, a highly diversified predator population should use a wider range of resources and hence favor the co-existence of multiple prey species, compared to a predator population with a low intraspecific diversity (Raffard et al. 2021). Such positive co-variation would suggest a global spatial consistency across trophic levels and diversity facets. Alternatively, this spatial co-variation (or the absence thereof) may result from common neutral processes (dispersal, drift) acting similarly (or dissimilarly) at all levels of biodiversity, although this has rarely been tested.

In this study, our objectives were to test empirically whether inter- and intraspecific biodiversity facets spatially co-vary within and among multiple trophic levels in spatially-structured ecosystems, and, if any, to identify eco-evolutionary processes sustaining these general co-variation (or the lack of). To do so, we focused on a riverine freshwater ecosystem in which we measured species and genomic diversity, across three trophic levels, namely riparian trees, benthic

macroinvertebrates and fishes (Fig. 1). For each trophic level, we quantified species diversity (α) and uniqueness (β) based on the abundance of each taxa. We further selected a dominant and functionally relevant species within each trophic level (*Alnus glutinosa*, *Gammarus* sp. and *Phoxinus dragarum*, Fig. 1) to quantify genomic (SNPs) diversity (α) and uniqueness (β) within species. We relied on a meta-analytic approach to test our working hypothesis of a global (i.e. within and between trophic levels) positive correlation between species and genomic diversity, which should be true if common processes similarly influence species and genomic diversity in trees, macroinvertebrates and fishes (Vellend 2010, Charlesworth and Charlesworth 2017). Finally, we aimed at testing the relationships between the different diversity components and a series of environmental predictors sustaining potential ecological and evolutionary processes at work in river ecosystems. To do so, we measured eight relevant environmental parameters (river width, connectivity, oxygen and temperature, eutrophication, pH, altitude, distance from outlet and east–west gradient), and tested whether they significantly affected each biodiversity facet and whether these effects were consistent across all facets.

Material and methods

Study area and trophic chain

We sampled a total of 51 sites in the Pyrenees Mountains (southern France, Fig. 2). The Pyrenees are oriented east–west, and the altitudinal gradient therefore follows a north–south gradient, with southern sites being, –up to a certain limit, higher in altitude. To maximize environmental variation among sites while limiting the confounding altitudinal factor (Blanchet et al. 2020), we therefore focused on an east–west gradient at the foothill of Pyrenees Mountains (sites were within a 236–634 m altitudinal range, Supporting information). We focused on a tri-trophic food chain that is common in river ecosystems. It implies riparian trees, a guild of benthic macroinvertebrates (i.e. hereafter referred to as shredders) decomposing the leaves from these trees when they fall into the water, and fishes feeding on these invertebrates (Fig. 1). We sampled and described the species diversity of these three trophic levels on each site (hereafter) and we characterized the genomic diversity of a single species within each trophic level (Fig. 1). They were selected on the basis of both functional importance for the transformation and transfer of energy in these ecosystems, and abundance in the area (which eased their sampling).

For the riparian trees, we selected the common alder *Alnus glutinosa* (Betulaceae). This abundant tree species in European rivers is an important source of energy (through the organic matter delivered when leaves fall into the river in autumn), that provides shelter for many aquatic species with its bare roots, stabilizes river banks, and plays an important role for nitrogen fixation (Milner and Gloyne-Phillips 2005, Andreoli et al. 2020, Khan et al. 2022). For the shredders, we selected a crustacean species belonging to Gammarids (amphipods). Gammarids can be very abundant and are extremely efficient for decomposing the dead organic matter (including that of tree leaves, Wallace and Webster 1996, Maltby et al. 2002, Dangles and Malmqvist 2004), and hence to recycle nutrients and make them available to producers (Cummins 1974). Here, we focused on the most abundant Gammarid species in the area that we named hereafter *Gammarus* sp. as this species has not yet been officially named, although it has been shown to be phylogenetically independent from its most closely related species, *Gammarus fossarum* (Carnevali 2022, Piscart unpubl.). For the fish species, we focused on the Occitanean minnow *P. dragarum*, a Cyprinid species measuring ~ 50–90 mm as an adult and abundant in cold rivers (Denys et al. 2020). It is a gregarious and omnivorous species

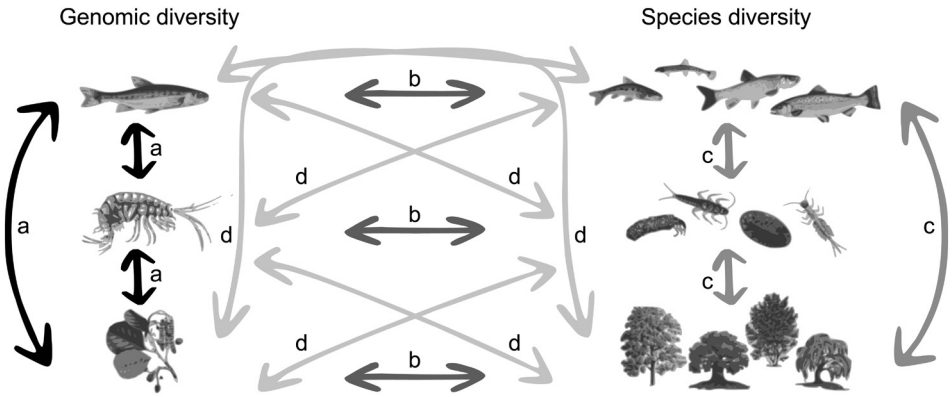

Figure 1. The six biodiversity components covered by our study. We focused on a tri-trophic food chain common in mountain rivers, from bottom to top: riparian trees, benthic macroinvertebrates and fishes. In each trophic level, we quantified two facets of biodiversity: genomic diversity, in a single target species within each trophic level (left part, from the top to the bottom: *Phoxinus dragarum*, *Gammarus* sp., *Alnus glutinosa*) and species diversity (right part). To compare biodiversity across trophic levels and diversity facets, we considered four groups of correlations (a) genomic-genomic diversity correlations (GGDCs, black arrows); (b) species-species diversity correlations (SSDCs, middle gray arrows); (c) species-genomic diversity correlations within trophic level (within-SGDCs, dark gray arrows); (d) species-genomic diversity correlation between trophic levels (between-SGDCs, light gray arrows).

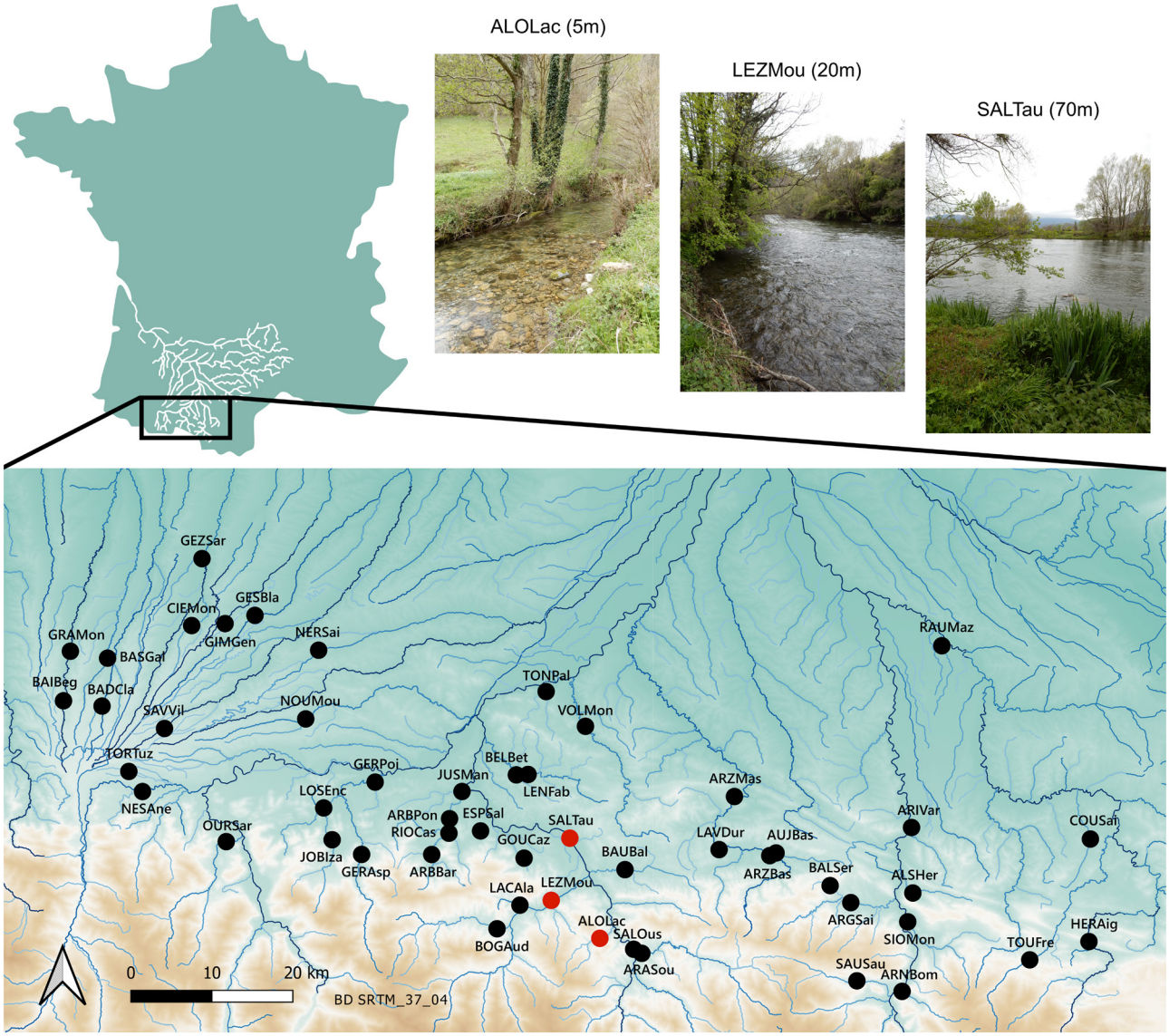

Figure 2. Distribution of the 51 sampling sites (black dots) along the east–west gradient at the foothill of the Pyrenees Mountains. A six-letter code represents each site, the three first letters indicate the river name and the three last letters refer to the closest city (or village). The width of the river is indicated in brackets for three sites (red dots).

feeding on algae, plant debris, invertebrates such as mollusks, crustaceans (including Gammarids), insects (including their larvae) and occasionally the eggs of other fishes (Raffard et al. 2020). It is an important predator in these ecosystems that strongly impacts invertebrate community structure and ecosystem functioning (Bertrand and Gido 2007, Miró et al. 2018, Raffard et al. 2021).

Sampling

In each site, we collected data on the composition and abundance of species within each trophic level, and we sampled up to 32 individuals of each of the three target species. Riparian tree species diversity was characterized at a single occasion (July–August 2021) because of the sessile character of trees, whereas fish and invertebrate species diversity were characterized over two occasions (June and November 2020 for invertebrates and summers 2020 and 2021 for fishes) to allow a precise estimate of the occurrence and abundance of species despite the movement of individuals.

For fishes, we performed electrofishing using a single-pass approach (Bateman et al. 2005, Hanks et al. 2018) over a mean area of ~ 469.9 m^2 (±174 m^2) in summers 2020 and 2021 (from mid-July to mid-August, during the low-flow period) on each site. We collected all specimens using nets, and then we anesthetized, identified and counted each of them to the species level. Fish species richness varied from 1 to 11 (mean = 4.235 ± 1.472 [SD], Supporting information). Abundances of each fish species were estimated as the number of individuals per m^2, and we averaged densities over

the two sampling years to get a single estimate per species and per site. During the 2020 electric-fishing session, we further collected a small piece of pelvic fin for up to 32 individuals of *P. dragarum* (range: 30–32, Supporting information) that we individually stored in a 1.5 ml tube with 96% ethanol for later DNA extractions.

To quantify the invertebrate communities involved in leaf degradation, we used experimental and standardized devices. In each site, we placed one natural coconut brush and one litter bag in four micro-habitats (close to or within root system of *A. glutinosa*) along the river bank (the same as for the electrofishing) in July and November 2020. Senescent leaves were collected during fall 2019 in each site from five *Alnus* trees and dried. Four grams were placed in bags made from two 15 × 11 cm pieces of wire mesh (mesh size = 0.8 cm) and closed with staples and iron wire to allow invertebrates to colonize the litter bag and to consume the leaves from their site. Coco brushes were 15 cm long and 5.5 cm large, and the length of the bristles was 7.5 cm. After ~ 10 days and ~ 1.5 months of colonization for litter bags and coco-brushes respectively, we removed each device from the river and brought them back to the laboratory. Invertebrates were stored in alcohol until their taxonomic assignment to the family level using a determination key (Tachet et al. 2010). The number of families per site varied from 15 to 42 (mean = 27.275 ± 4.579 [SD], Supporting information). We assumed that the family richness was a good proxy for the species richness. In November 2020, the sorting was done up the genus level and we found a strong positive correlation between the number of families and the number of genus at the site level (Pearson's r = 0.972, n = 147, $p < 0.001$, Supporting information). The abundance of each family was estimated as the cumulative number of individuals from the four coco brushes and the four litter bags, and we averaged the abundances over the two sampling months to get a single estimate per family and per site. In February 2020, we collected up to 32 specimens of *Gammarus* sp. in alder roots (range: 19–32 individuals. Notice that, in some sites, the *Gammarus* species found is different from our target, then reported as absent in our dataset, Supporting information) and we stored each of them into a 1.5 ml tube containing 96% ethanol for later DNA extractions.

For trees, we identified riparian species on a transect of ~ 200 m (the same transect as for fishes and invertebrates) along both river banks, using PlantNet (https://identify.plantnet.org) and the 'Flore complète illustrée en couleurs de France, Suisse et Belgique' (Bonnier and de Layens 1913) in Summer 2021. Because our aim was to identify and count trees that contributed significantly to the leaf incomes in the river bed, we considered only those trees with trunks larger than 2 cm in diameter, less than a meter from the river bank, and/or with at least one branch overhanging the river. Tree species richness varied from 7 to 20 (mean = 14.412 ± 2.669 [SD], Supporting information). Leaves from *A. glutinosa* were sampled in May 2020, when the young leaves have just emerged to limit phenolic and flavonoid compounds. We collected three leaves from up to 32 trees (range 3–32, Supporting information) evenly spread along a 200 m river stretch, and stored them in zipper storage bags with 300 g of silica beads for later DNA extractions. As *A. glutinosa* usually produces multiple stems along a river stretch, it may be difficult on the field to determine whether two trunks belong or not to the same individual. When there were less than 32 stems in the site, we collected leaves from all stems composing the population, assuming that a low genomic diversity due to double sampling of the same individual is representative of the site diversity. When there were more than 32 stems, we collected leaves from one stem every two or three stems (depending on stem density) to obtain 32 samples evenly distributed along the 200 m transect.

Environmental parameters

Eight environmental parameters were described on each site. They were chosen because they have previously been found (or are expected) to shape biodiversity patterns in rivers (Altermatt 2013, Fourtune et al. 2016).

1) Width of the river bed in each site was averaged from five measurements taken over each 200 m river stretch. Narrower sites should be less diverse (Altermatt 2013, Fourtune et al. 2016).
2) Connectivity to all other sites was calculated as the 'closeness centrality' (i.e. the inverse of the sum of the distances of a node to all other nodes along the shortest paths possible, Newman 2010) using QGIS and the 'RiverDist' R package (www.r-project.org, Tyers and Tyers 2017). The higher the centrality, the higher the connectivity of one site to all other sites. Less connected sites should be less diverse.
3) Oxygen and temperature, two major natural parameters in rivers, were measured in summers 2020 and 2021 on each site using a multi-parameter probe (Aqua TROLL 500, in-situ Inc.), and values were averaged over periods to get a single estimate per parameter and per site. A principal component analysis (PCA, Supporting information) combining three parameters of interest (oxygen concentration in mg l^{-1}, percentage saturation and water temperature) was performed, and coordinates of each site on the first axis (55.55% of the total variance) were used as a synthetic variable. Positive coordinates represented colder sites with high concentrations in oxygen.
4) Eutrophication, a major anthropogenic parameter in rivers, was estimated at each site based on the concentration in $NO_3^- + NO_2^-$, NH_4^+ and PO_4^{3-}, as well as local specific conductivity values. Specific conductivity (µS cm^{-1}) was measured using the same multiparameter probe as above. $NO_3^- + NO_2^-$, NH_4^+ and PO_4^{3-} concentrations were estimated during summers 2020 and 2021 from a filtered water volume (100 ml) using the Alpkem Flow Solution Iv Autoanalyzer (OI analytical). Chemical analyses were externalized to Laboratoire Ecologie Fonctionnelle et Environnement (University Paul Sabatier, Toulouse, France) and were performed according to standardized

protocols. A PCA combining the four above-mentioned parameters was performed, and coordinates of each site on the first axis (37.82% of the total variance) were used as a synthetic variable. Positive coordinates represented sites with both high concentrations in $NO_3^- + NO_2^-$, and high specific conductivity (Supporting information).

5) pH of each site was measured using the same multiparameter probe and was estimated during summers 2020 and 2021.Values were averaged over periods to get a single estimate per parameter and per site. pH influences the availability of ions for living organisms; acidic waters are indicative of anthropized environments.
6) Altitude, distance from outlet and east–west gradient were estimated for each site using QGIS. Sites in altitude and/or far from the outlet should be more isolated and consequently less diverse (Altermatt 2013, Fourtune et al. 2016). The east–west gradient potentially indicates the presence of multiple past glacial refugees along the Pyrenees chain (Delmas et al. 2008), and/or a more stable climate over geological time close to the Atlantic Ocean (i.e. in the western part of our sampling area, Fig. 2).

Multicollinearity among these eight environmental parameters was tested using the VIF function in R package 'regclass' (www.r-project.org, Section: Diversity-environment correlations). We did not find strong collinearity among parameters as VIF values ranged from 1.389 to 2.915, below the typical threshold of 10 (Zuur et al. 2009). Moreover, Pearson's correlations between parameters were weak, below the 0.7 threshold advised by Dormann et al. 2013 (Supporting information).

DNA extractions and SNP genotyping

DNA from *A. glutinosa* was extracted using the DNeasy 96 Plant Kit (QIAGEN) from 12 dry chips (4 mm in diameter) sampled from each leaf. For *Gammarus* sp., DNA was extracted using the DNeasy Blood and tissue kit (QIAGEN) from the head of each individual by slightly modifying the initial protocol (overnight lysis). For *P. dragarum*, DNA was extracted using a salt-extraction protocol directly from finclips (Aljanabi and Martinez 1997). For the three species, DNA concentrations were measured using Qubit ver. 3.0 fluorometer (Life Technologies).

Sequencing was performed based on pools of DNA ('pool-seq' approach, (Schlötterer et al. 2014, Abrams et al. 2021) from each population and each species. Individual DNA samples were therefore combined to produce a single pool of DNA per population (and per species), with equimolar contributions from each individual. The number of individuals in each pool corresponds to the number of individuals sampled in each population (Supporting information). It is noteworthy that 32 individuals were sampled for most species and most sites; when less than 32 individuals were sampled (despite important and standardized sampling efforts), we expected genomic α-diversity of these populations to be comparatively lower. Nonetheless, we did not correct for the number of individuals in pools, assuming that a small sample size actually represents the small size (low abundance) of the population. We externalized library preparation and pool-sequencing to LGC Genomics, Biosearch Technologies (Berlin, Germany). To infer genomic diversity in our populational pool, we followed LGC recommendations for restriction enzyme choice and sequencing methods to maximize loci yield in each species. Normalized genotyping-by-sequencing (nGBS) was used for *P. dragarum* (single digest protocol with MsII) whereas double-digest restriction-site associated DNA (ddRAD-seq) was used for *A. Glutinosa* and *Gammarus* sp. (respectively, PstI/MseI and Pst/HindIII enzymes). Our 128 pools (52 pools in *A. glutinosa*, 32 pools in *Gammarus* sp. and 44 pools in *P. dragarum*, Supporting information) were then sequenced on an Illumina NovaSeq (2 × 150 pb). Resulted short reads were subsequently processed for SNP identification.

Data processing was performed according to De Kort et al. (2018), except that sequence alignment was performed on reference genomes. Genome of *A. glutinosa* was already available in NCBI (0.621 Gb, Griesmann et al. 2018). For *Gammarus* sp. and *P. dragarum*, we built reference genomes from Illumina short-read sequencing and PacBio long read sequencing respectively. This resulted in two reference genomes (respectively 3.916 and 0.968 Gb, Supporting information). SNP calling was performed following De Kort et al. (2018) methodology: 1) raw *fastq* files were filtered using *trimmomatic* function (Bolger et al. 2014) and *clone_filter* function (from stacks, Catchen et al. 2013) to remove low quality scores reads and PCR duplicates; 2) reference genomes (in *fasta* format) were then indexed; 3) filtered *fastq* files were then aligned to indexed reference genomes using the *mem* function in bwa; 4) aligned *SAM* files were converted into *BAM* format and filtered for unpaired and badly/non-mapped reads; 5) all indexed and filtered *BAM* files were then assembled in a single *mpileup* file and 6) SNP allelic frequencies were finally obtained using Popoolation2 (Kofler et al. 2011, De Kort et al. 2018 for detailed functions of each step). We only conserved bi-allelic SNPs and removed low variability SNPs in allelic frequency (FreqMax – FreqMin < 0.05). In order to allow calculation of similar estimates for genomic and species diversity (hereafter), we transformed the allelic frequency table into an allele count table by multiplying each allelic frequency by the number of individuals from each pool.

Statistical analysis

Estimation of α- and β-diversity estimates

The same α- and β- diversity estimates were calculated for both species and genomic diversity to ease comparisons (Supporting information). Species and genomic α-diversity were measured using the Shannon entropy from the 'hillR' R package (www.r-project.org, Chao et al. 2014). The Shannon entropy is a metric of evenness that takes into account the distribution of (allele or species) abundances in the site (Gaggiotti et al. 2018). Species and genomic β-diversity

were quantified as the average of the pairwise (between sites) Bray–Curtis dissimilarity estimates using the 'betapart' R package (www.r-project.org, Baselga et al. 2018). The pairwise Bray–Curtis dissimilarity metric quantifies the dissimilarity between the composition of two different sites based on abundance data. It ranges from 0 to 1, 0 indicates that the two sites share all the species and 1 indicates that the two sites have no common species. We averaged the pairwise estimates across sites to quantify the 'uniqueness' of a site (i.e. the extent to which a site is dissimilar from all other sites, Paz-Vinas et al. 2015).

Spatial co-variation among α- and β-diversity estimates across species

Pearson's correlation coefficients (r) were used to assess the strength of pairwise associations between genomic diversity and species diversity, both within and between trophic levels, and for both α- and β-diversity estimates. We tested the global correlation (mean of the α- or β-correlation values) for four types of correlations: genomic–genomic diversity correlations (three estimates, GGDCs), species–species diversity correlations (three estimates, SSDCs), species–genomic diversity correlations within trophic levels (three estimates, within-SGDCs) and species–genomic diversity correlations between trophic levels (six estimates, between-SGDCs, Fig. 1). A standardized effect size (SES) of each correlation coefficient was calculated using the Fisher's *Z* transformation (*Zr*, Rosenberg 2000, Nakagawa and Cuthill 2007). We finally calculated the mean *Zr* and associated 95% confidence intervals CI (for α- and β-diversity separately) for the global correlation and for the four types of correlations (Fig. 1).

Drivers of α- and β-diversity across biodiversity facets and trophic levels

To infer the links between biodiversity and environmental predictors, we ran a linear model for each diversity facet and each trophic level separately (i.e. six models for each α- and β-diversity). In these models, the corresponding diversity facet was the dependent variable and the eight environmental parameters (width, connectivity, oxygen and temperature, eutrophication, pH, altitude, distance from outlet and east–west gradient) were the predictors. From each model, we retrieved the *t*-values associated with each environmental predictor as an estimate of its effect size on the corresponding diversity facet. *t*-values were transformed into standardized effect sizes (SES, Fisher's *Z*, *Zr*, Rosenberg 2000) and associated asymptotic variances (*vZ*) were calculated (Rosenberg 2000).

We then used these SES to test whether the effects of each environmental predictor were consistent among diversity facets and across trophic levels. To do so, we estimated, for each environmental predictor independently, the mean SES (and associated 95% CI) across all diversity facets and all trophic levels using intercept-only linear models, with SES (six estimates for α- and β-diversity components, respectively) as the dependent variables and variance *vZ* as a weighting parameter. If effects of a predictor are consistent across diversity facets and across trophic levels, its mean SES (that is, the model intercept) should be significantly different from zero (either positively or negatively).

Results

Spatial co-variation among diversity estimates across species

Patterns of α-diversity

For α-diversity, the mean *Zr* was not significantly different from zero ($Zr_{All} = -0.024$, 95% CI [−0.123, 0.074], Fig. 3a, Supporting information), suggesting no global spatial co-variation among biodiversity facets across trophic levels. When these co-variations were measured for each type of correlation independently (Fig. 1a–d), we found a trend toward a negative *Zr* for genomic–genomic diversity correlations (GGDCs, mean $Zr_{SSDCs} = -0.238$, 95% CI [−0.626, 0.151] while other co-variations showed the opposite (positive) trend. However, none of the mean *Zr* was significantly different from zero, confirming the general absence of global co-variation (Fig. 3a).

Patterns of β-diversity

For β-diversity, the mean *Zr* was not significantly different from zero (mean $Zr_{All} = 0.040$, 95% CI [−0.060, 0.137], Fig. 3b), indicating that there was no general spatial pattern of β-diversity among biodiversity facets and across trophic levels. When co-variation was estimated for each type of correlation independently (Fig. 1a–d), we found a negative and significant *Zr* for the genomic–genomic diversity correlations (GGDCs, mean $Zr_{GGDCs} = -0.184$, 95% CI [−0.193, −0.176]), suggesting that genomic uniqueness was inversely related among trophic levels (Fig. 3b). co-variations for other types of correlations were not significant.

Drivers of biodiversity across diversity facets and trophic levels

Environmental predictors of α-diversity

The intercept-only model showed that none of the environmental parameters but east–west gradient was a significant and consistent predictor for species and genomic α-diversity (Fig. 4a). The east–west gradient had a global, significant and negative influence on α-diversity ($Zr_{east–west\ gradient} = -0.146$, 95% CI [−0.278, −0.013], Fig. 4a); the most eastern sites harbored lower genomic and species diversity than the most western sites, irrespectively of the trophic level. The general absence of correlation between environmental predictors and α-diversity suggests that each α-diversity estimate was differently explained by a unique set of predictors (Supporting information), except for east–west gradient.

Environmental predictors of β-diversity

The intercept-only model showed that connectivity was a significant and consistent predictor for species and genomic β-diversity (Fig. 4b). The connectivity of the sampling site

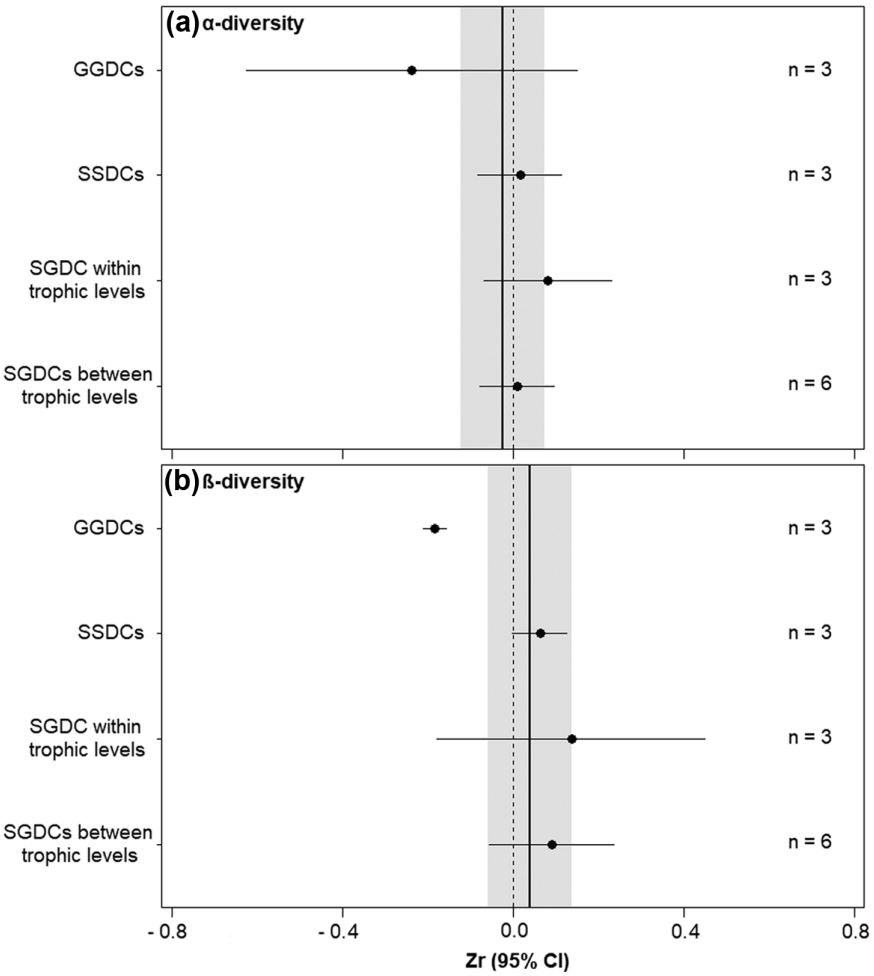

Figure 3. Forest plot of correlation strength depending on the type of correlation considered. *Zr* is a standardized correlation coefficient based on (a) Shannon entropy (α-diversity) and (b) Bray–Curtis dissimilarity uniqueness (β-diversity). The dashed vertical line stands for the absence of correlation ($Zr = 0$). On each panel, the bold vertical line refers to the general arithmetic mean of all correlations confounded and the shaded area indicates 95% confidence interval. We considered four types of correlations: 1) genomic–genomic diversity correlations (GGDCs); 2) species–genomic diversity correlations within trophic level (SGDCs within trophic levels); 3) species–species diversity correlations (SSDCs); 4) species–genomic diversity correlation between trophic levels (SGDCs between trophic levels, cf. Fig. 1. for visualization).

had a global, significant and negative influence on β-diversity (mean $Zr_{Connectivity} = -0.073$, 95% CI [−0.140, −0.007], Fig. 4b), suggesting that genomic and species uniqueness were higher for poorly-connected sites, whatever the trophic level. As for α-diversity, each β-diversity estimate was thus differently explained by a unique set of predictors (Supporting information), except for connectivity.

Discussion

Contrary to theoretical expectations, we demonstrate that, in our system, there was no global spatial co-variation among biodiversity facets (species and genomic diversity facets) and across trophic levels (riparian trees, benthic macroinvertebrates and fishes), neither for α-diversity nor for β-diversity. We only found that genomic β-diversity estimates negatively covaried (although weakly) among the three target species, i.e. when a species was genomically unique in a site, the other(s) species tended to be more ordinary genomically. This absence of spatial co-variation among biodiversity components was coherent with the observation that most of the environmental predictors we considered did not consistently impact all biodiversity components. Rather, most environmental parameters were associated with each biodiversity component idiosyncratically. However, two environmental parameters (east–west gradient for α-diversity and connectivity for β-diversity) altered all biodiversity components consistently, although the sizes of these common effects were not strong enough to generate global spatial co-variation among biodiversity components.

In general, there was no spatial co-variation between species and genomic diversity, neither within nor across trophic levels. Positive species-genetic diversity correlations have

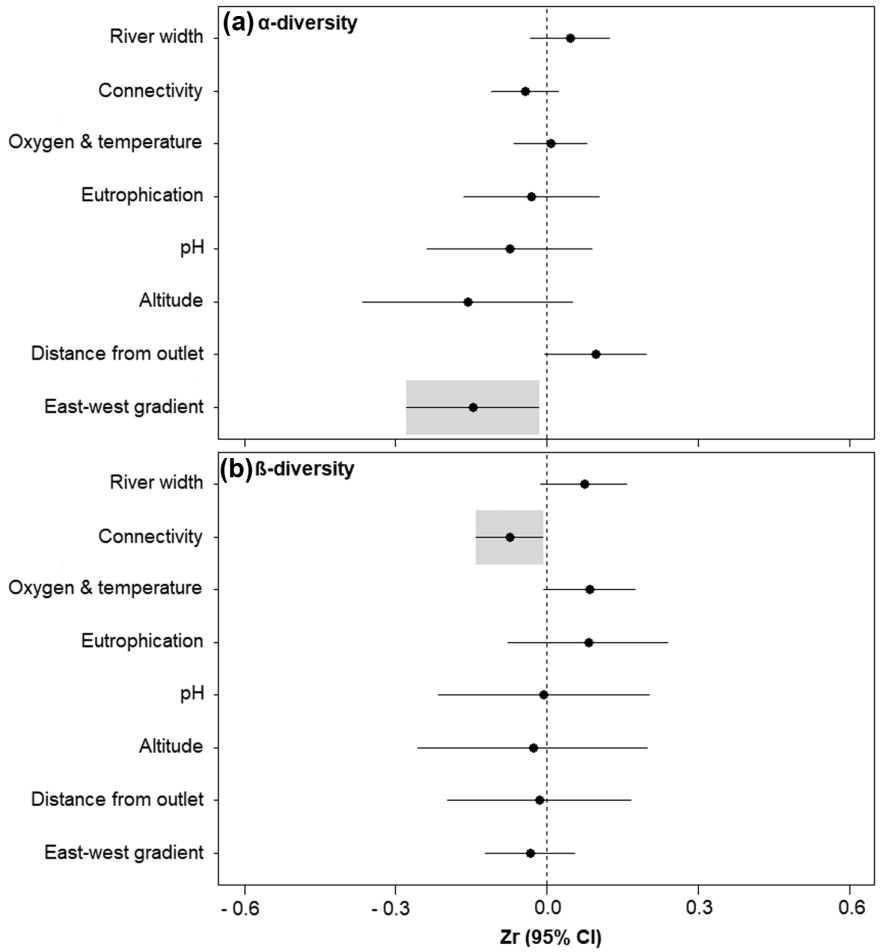

Figure 4. Values of correlation strength between environmental parameters and biological diversities. *Zr* are standardized correlation coefficients based on (a) Shannon entropy (α-diversity) and (b) Bray–Curtis dissimilarity uniqueness (β-diversity). The dashed vertical line stands for the absence of correlation ($Zr = 0$). On each panel, the shaded area indicates 95% CI of the significant correlation.

already been reported within trophic levels in several taxonomic groups (Vellend et al. 2014, Xie et al. 2021), which we did not find here. For instance, positive species–genetic diversity correlations have been found in mountain riparian forest (Wei and Jiang 2012), in freshwater invertebrates (Watanabe and Monaghan 2017) and in freshwater fishes (Fourtune et al. 2016). In particular, in the same river drainage as our study, Fourtune et al. (2016) found moderate (but significant) positive correlations between fish species richness and allelic richness measured in four freshwater fishes (including *P. dragarum*). This is surprising that, within the same river drainage and the same biological system (fish, Supporting information), our results differ from those of Fourtune et al. (2016). A likely explanation is that, contrary to most studies focusing on river systems, including that of Fourtune et al. (2016), we focused on the headwaters in a relatively narrow range of altitudes, rather than on the classical upstream–downstream gradient. On the one hand, we obviously missed the most downstream sites and therefore restrained the environmental and biological variation that naturally exist on this type of ecosystem (Blanchet et al. 2020). We would probably have obtained stronger overall spatial covariation if we had considered the entire upstream–downstream gradient (that is orientated north-west/south-east, Fig. 1), at least in fishes as observed in Fourtune et al. (2016). However, we retained substantial variation in our dataset, with for instance mean summer temperatures ranging from 11.29 to 17.38°C, river width ranging from 1.30 to 22 m (Supporting information), and the number of species ranging from 7 to 20, 15 to 42 and 1 to 11 for riparian tree species, benthic macroinvertebrates and fishes respectively (Supporting information). On the other hand, this design provides a powerful way to limit collinearity among spatial parameters (altitude, distance from the mouth) and environmental/physical parameters (water temperature, river width, conductivity, etc…), which can be highly problematic to statistically tease apart causal relationships (Prunier et al. 2015, Blanchet et al. 2020). As an alternative, yet non-exclusive, explanation for the general lack of co-variation between species and genomic diversity, we can speculate that the choice of the target species for estimating genomic diversity modulates the strength of the co-variation (Taberlet et al. 2012, Laroche et al. 2015, Fourtune et al.

2016). For instance, species abundance or species characteristics such as the mutation-to-gene flow ratio modulate the strength of SGDCs (within trophic levels, Vellend 2005, Laroche et al. 2015). Hence, although here we focused on the most abundant species within each trophic level (SGDCs are expected to be the stronger when the target species is highly abundant, Vellend 2005), we cannot rule out the possibility that having focused on rarest species with different traits (notably in term of dispersal or competitive ability) would have altered our findings. The absence of species-genetic diversity correlations is nonetheless coherent with recent meta-analyses (Taberlet et al. 2012, Kahilainen et al. 2014, Vellend et al. 2014, Xie et al. 2021) highlighting that the strength of correlations between species and genetic diversity is actually heterogeneous, explaining why a non-negligible proportion of published correlations are non-significant. Overall, our results and those from Fourtune et al. (2016) in the same river drainage suggest that the spatial scale of observation may actually change conclusions regarding the strength and form of species–genetic diversity correlations.

Most of the eight environmental parameters did not consistently impact biodiversity components. This result is coherent with the absence of global spatial co-variation among biodiversity components, and suggests that idiosyncratic processes are shaping biodiversity patterns in this ecosystem. Indeed, each biodiversity component tends to show a unique response to each environmental parameter, even within the same biodiversity facet (Supporting information). For instance, eutrophication exhibited contrasted effects on α- and β-diversity estimates. For α-diversity, we identified that eutrophication had 1) a negative relationship with *Gammarus* sp. genomic diversity, 2) no relationship with *A. glutinosa* genomic diversity, riparian trees and macroinvertebrates species diversity and 3) a positive relationship with *P. dragarum* genomic diversity and fish species diversity (Supporting information). Similarly, the distance from the outlet had contrasted effects on α- and β-diversity estimates. For β-diversity, we identified that distance from the outlet had 1) a negative relationship with fish species uniqueness, 2) no relationship with *A. glutinosa* genomic uniqueness and 3) a positive relationship with macroinvertebrates species uniqueness (Supporting information). These inconsistent relationships between environmental predictors and biodiversity components unlikely results from a lack of environmental heterogeneity within our sampling area (Supporting information), and rather suggests that each facet within each trophic level reacts differently to local conditions. Processes associated with these environmental parameters (both neutral and non-neutral processes) therefore have different effects on the various biodiversity facets and trophic levels, which might limit the emergence of global spatial patterns of biodiversity.

Nonetheless, we found coherent relationships between two environmental predictors and all the biodiversity components, i.e. the east–west gradient for α-diversity and connectivity for β-diversity. Indeed, all α-diversity estimates were significantly and negatively associated with the east–west gradient, which indicates that biological diversity was higher in the western part of the network, i.e. closer to the Atlantic Ocean. This can suggest the presence of an ancient glacial refuge in the western part of the network from which individuals colonized to the east. This hypothesis is coherent with the traces of an ancient glacier at the east of the Pyrenees in the Quaternary period (Calvet et al. 2011). Alternatively, yet not exclusively, the oceanic influence in the west may stabilize climate over geological time, hence limiting population size variation in this area and favoring biological diversity (Sandel et al. 2011, De Kort et al. 2021). All β-diversity estimates were significantly and negatively associated with connectivity, which suggests that highly unique areas (both in terms of genomic and species composition) are found in poorly connected sites. This was expected given the dendritic structure of river networks (Altermatt 2013, Carrara et al. 2014, Vitorino Júnior et al. 2016). Upstream sites are supposed to be isolated from each other, hence favoring the effect of ecological and genetic drift and the differentiation of populations and communities (Carrara et al. 2014, Paz-Vinas and Blanchet 2015). Nonetheless, although coherent in their direction, the global effect sizes associated with these two environmental predictors were weak ($Zr < 0.20$) and were unlikely to be strong enough to generate significant patterns of co-variation across trophic levels and biodiversity facets. It is likely that the idiosyncratic effects discussed above (Supporting information) are blurring the past imprints of the east–west gradient and connectivity.

Despite the fact that we did not detect any global spatial co-variation between species and genomic diversity across multiple trophic levels in a complex riverscape, our findings have both practical and theoretical implications. First, the absence of an overall link between all biodiversity components implies that biodiversity hotspots should not be generalized spatially de facto (Westgate et al. 2014). This suggests that, if we are to conserve all components of biodiversity in this area, trophic- and facet-specific conservation areas should be designed to avoid conflicting strategies and undesirable effects of preserving only a few areas, targeted toward one of the facets or one of the trophic levels (Kahilainen et al. 2014). For instance, given the absence of SGDC both within and between trophic levels, genetic diversity of common species should not be used in this area as surrogate for species diversity, from the same or from different trophic levels, in conservation plans (Westgate et al. 2014). Potentially conflicting issues are even more prominent for genomic β-diversity as we found a negative co-variation among the three species we investigated. This indicates that biodiversity hotspots areas of uniqueness are inversely correlated in each species. Consequently, simple strategies such as environmental clustering strategies (for instance, prioritizing the conservation of highly heterogeneous sites) might not be appropriate to conserve all biodiversity components. Other strategies such as systematic conservation planning or the maximization of complementary richness are probably more relevant, in a multitrophic context, to take into account the low consistency in biodiversity patterns (Arponen et al. 2008, Paz-Vinas et al. 2018). Second, both inter- and intraspecific

diversity facets are known to affect the structure of communities and the functioning of ecosystems (Hooper et al. 2005, Crutsinger et al. 2009, Cardinale et al. 2012, Des Roches et al. 2018, Raffard et al. 2019), and multitrophic approaches are required to understand the context-dependency of biodiversity–ecosystem functioning relationships (Eisenhauer et al. 2019). Here, the absence of co-variation between the multiple facets of diversity and across trophic levels within a common landscape reinforces the idea of using integrative measures of diversity – i.e. taking into account several facets of diversity and several trophic levels – to predict the global functioning of ecosystems (Eduardo 2016, Moi et al. 2021). However, it is still useful to keep simple estimates of diversity (to keep apart the different trophic levels and diversity facets in the analyses) to reveal the implications of current changes in biodiversity for ecosystem functioning. For instance, a better understanding of trophic complementarity (i.e. the originality of a species for ecosystem functioning in a multispecies context, Poisot et al. 2013) requires separate analysis of each trophic level. Our study shows that hotspots of different components of biodiversity are scattered in river landscapes. This reinforces the idea that both multitrophic and multifaceted approaches are relevant, and complementary, to build integrated conservation plans and to better understand the link between all biodiversity components of an ecosystem and its functioning and dynamics.

To conclude, we provide an empirical test of the spatial co-variation between inter- and intraspecific biodiversity facets across multiple trophic levels, and our findings reinforce the idea that explicit multitrophic approaches are required to get a more holistic vision of biodiversity patterns. Our work suggests that spatial co-variation of biodiversity across diversity facets and across trophic levels is not a general rule, probably because most environmental parameters do not consistently affect all biodiversity components. The east–west positioning of the sampling sites along the Pyrenean mountain chain influences consistently all estimates of α-diversity and site connectivity influences consistently all estimates β-diversity, but the common effects of these two drivers were not strong enough to generate coherent patterns of biodiversity.

This multitrophic perspective of biodiversity patterns raises many additional challenging questions that should be considered in the future. For instance, what is the role of inter- and intraspecific diversity in shaping the functioning of such complex ecosystems? Is it possible that different diversity facets have different impacts on ecosystem functioning within trophic levels? Moreover, we did not incorporate realized trophic interactions (among and within trophic levels), and more generally interactions between organisms in our multi-trophic analyses, which we believe would be an important step forward in future SGDCs studies. Trophic interactions can be quantified using stable isotope analyses and/or gut content analyses for instance, and we can expect that the strength and sign of SGDCs may vary according to the strength of the trophic interaction for instance. Moreover, trophic interactions change over space and time (Chesson 2000), which was not considered in our study. Future works should further explore the strength of inter- and intraspecific interactions to draw more precise conclusions about the role of biotic interactions in modulating biodiversity patterns across trophic levels. Finally, it is possible that spatial co-variation between genomic and species diversity might be revealed more precisely by shifting from a 'single target species' approach (genomic diversity is inferred from a single species) to a 'multiple target species' approach (genomic diversity is inferred from a several species). This could be done for instance by 1) estimating spatial covariation between species diversity and the average genomic diversity of several species within the community, and/or 2) estimating genomic diversity jointly from all species within the focal community by sequencing genes that are phylogenetically conserved across species (Blanchet et al. 2022).To answer these questions (and others), we encourage scientists to integrate multiple trophic levels and multiple facets of biodiversity to future empirical and theoretical studies to better understand the spatial distribution of biodiversity, the underlying processes that shape biodiversity on Earth, and their consequences on ecosystem functioning.

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Author contributions

Laura Fargeot: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Project administration (lead); Software (equal); Supervision (equal); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Camille Poesy**: Investigation (lead); Methodology (equal); Project administration (supporting); Supervision (equal); Validation (equal). **Maxim Lefort**: Data curation (supporting); Investigation (lead); Methodology (supporting); Project administration (supporting); Supervision (equal). **Jérôme G. Prunier**: Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Resources (equal); Software (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Madoka Krick**: Investigation (equal); Methodology (supporting). **Charlotte Veyssière**: Investigation (equal); Methodology (supporting). **Murielle Richard**: Investigation (supporting); Methodology (supporting); Writing – review and editing (equal). **Chiara Mercier**: Investigation (equal). **Morgan Sautreuil**: Investigation (equal). **Natan Huberson**: Investigation (equal). **Nadia Langford**: Investigation (equal). **Delphine Legrand**: Validation (equal); Visualization (supporting); Writing – review and editing (equal). **Géraldine Loot**: Investigation (supporting); Validation (equal); Visualization (supporting); Writing – review and editing (supporting). **Simon Blanchet**: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead);

Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Software (supporting); Supervision (lead); Validation (equal); Visualization (lead); Writing – original draft (supporting); Writing – review and editing (lead).

Data availability statement

Data are available from Figshare: https://doi.org/10.6084/m9.figshare.21961358.v1 (Fargeot et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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