Loss of genetic diversity in wild fish populations reduces biomass stability over time.

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Abstract

Biodiversity sustains key ecosystem functions, and ongoing species losses have tremendous impacts on good and services provided by biodiversity. Before species are extirpated, they yet lose intraspecific genetic diversity. The loss of intraspecific diversity has implications for the evolutionary potential of species, but may also alter ecological and ecosystem functions such as biomass productivity. However, there have been little attempts to empirically test whether intraspecific genetic diversity actually promotes productivity and stability in wild populations, and, if so, to quantify its relative importance compared to other determinants. Capitalizing on 20-year demographic surveys in wild fish meta-populations, we demonstrated that intraspecific genetic diversity did not increase mean biomass production in local populations, but strongly and consistently stabilized biomass production over time. Overall, genetic diversity accounted for about 20% of explained variance in biomass stability across species, a significant contribution that was about half that of environment and demography (40% each). Populations having suffered from past demographic bottlenecks harbored lower levels of genetic diversity and showed less stability in biomass production over the last 20 years. Our study demonstrates that the loss of genetic diversity can destabilize biomass productivity in natural vertebrate populations in just a few generations, strengthening the importance for human societies to adopt prominent environmental policies to favor all facets of biodiversity.

Introduction

There is now unequivocal evidence that biodiversity sustains critical ecosystem services that benefit directly to humanity, such as water filtering, pollination and biomass production (1–3). By promoting higher complementarity among species (4, 5), interspecific diversity allows ecological communities to optimally capture essential resources, transform those resources into biomass and recycle them. In species-rich communities, these ecological processes are maintained even in face of environmental variations, thus promoting ecosystem productivity and stability over time (6–10). The drastic erosion in species diversity observed worldwide is hence prejudicial, as it is expected to deeply impair natural ecosystems' capacity to durably sustain human health and wellbeing (2, 3, 11). However, the loss of species is only the tip of the iceberg. In most taxa, another form of biodiversity erosion is indeed silently underway: the loss of intraspecific genetic diversity (12, 13).

Beyond its positive influence on individual fitness and evolutionary rescue (14), intraspecific genetic diversity is expected to play a role similar to species diversity in driving key ecological functions such as biomass production (1). Assuming that genetic variation promotes intraspecific phenotypic variation and thus complementarity among individuals (15), genetically-diversified populations are predicted to have higher and more stable biomass yields than genetically impoverished populations, notably under stressful environmental conditions (16, 17). This direct relationship between genetic diversity and biomass production is expected to be particularly strong in ecosystems where species diversity is naturally low, which is actually the norm in many temperate ecosystems (18). Indeed, the functioning of such ecosystems probably depends more on complementarity among genotypes than on complementarity among species (19–21), emphasizing the importance of maintaining genetic diversity to preserve ecosystem functions and services (16).

However, most studies investigating the relationship between genetic diversity and ecological functions such as biomass production are based on experimental or semi-experimental designs, where population densities and levels of genetic diversity are manipulated, and environmental conditions are controlled and maintained constant over time (22). Contrary to field surveys, and although they offer a number of advantages (16, 22), experiments do not allow spanning large spatial and temporal scales or to investigate the influence of historical contingencies. Local levels of genetic diversity indeed result from the

interplay between long-term evolutionary trajectories (e.g., localization and size of glacial refugia (23)) and more recent (if not ongoing) ecological processes affecting individual life history traits (e.g., stressful environmental conditions (24)) or population demography (e.g., bottleneck events (25)). This natural complexity cannot be fully grasped from experimental studies (26). Observational field surveys are on the contrary more realistic and may provide important insights into the contribution of genetic diversity, and the loss of it, to biomass production and stability in natural settings, in accordance or in disagreement with theoretical expectations and experimental findings (16, 27, 28). They yet raise several difficulties. First, assessing the influence of genetic diversity on the stability of biomass production over several generations or over several seasonal cycles implies long-term monitoring programs of both population density and biomass production, but such data are still scarce or difficult to collect in many situations. Furthermore, genetic diversity may be correlated with variables that are also involved in biomass production, such as population density and environmental heterogeneity, making it difficult to disentangle their respective contributions (16). This last issue may however be partly alleviated through the use of causal modeling procedures (29), making it possible to thoroughly confront theoretical expectations and experimental findings with the “real world” (30, 31).

Capitalizing on long-term demographic surveys (up to 22 years) conducted in 47 rivers from a large watershed (the Garonne-Dordogne water basin, South-Western France; Figure 1), we assessed the relationship between genetic diversity and biomass yields (mean biomass production and temporal stability in biomass production) at the population level in three parapatric freshwater fish species. To that aim, we designed a causal model depicting all the expected causal links between biomass variables, genetic diversity and several environmental and demographic predictors. Rivers are characterized by strong environmental gradients that we synthetized in the form of an upstream-downstream gradient and a eutrophic gradient. The former is a critical feature known to shape both spatial patterns of genetic diversity and biomass yields in dendritic networks (32, 33) whereas the latter may act as a possible stressor and affect both population dynamics and productivity (34). As local population dynamics may also influence both genetic diversity and biomass yields, we considered several demographic covariates: mean population density, long-term stability in population density as well as bottleneck probability, the latter indicating past changes in population size (35). By investigating this causal model, we answered the

following questions: do the positive relationships between genetic variation and biomass production and stability hold in natural settings? If any, is the contribution of genetic variation to biomass production/stability similar across species, and comparable in magnitude to that of other environmental and demographic determinants? Finally, and most importantly, is it possible to detect the impact of the ongoing genetic erosion, e.g., the loss of genetic diversity in response to a recent reduction in population size, on biomass production and stability? This latter point remains controversial but of high concern: with an estimated 6% loss of intraspecific genetic diversity in wild organisms since the industrial revolution (36), the impact of human-induced genetic erosion on natural ecosystems' capacity to provide critical provisioning and regulating services to humanity may actually be much more important than anticipated, making it a critical conservation issue.

Materials and Methods

Study area and biological models

The study was carried out in the Garonne-Dordogne river basin (South-Western France; Figure 1). We selected 47 river sections evenly scattered across the whole basin to reflect the environmental variability existing along the upstream–downstream gradient. All these sites are yearly monitored by the French Agency for Biodiversity (AFB) since 1989 (50). Fish communities in this river basin are generally poorly diverse (3 to 15 species in general) and we focused on three of the most common species (51): the Eurasian minnow *Phoxinus phoxinus*, the Languedoc gudgeon *Gobio occitaniae* and the chub *Squalius cephalus*. These cypriniform fish species vary in their mean body length (minnows: 80–90 mm; gudgeons: 120–150 mm; chubs: 300–500 mm; (52)). They are all generalist species mainly feeding on invertebrates (although chubs can also predate on small-bodied fish) but occupy different habitats (51): chubs are primarily found in downstream sections at relatively low densities (~0.01 ind.m-2), minnows are primarily found in upstream sections at relatively high densities (~0.10 ind.m-2), whereas gudgeons are found all along the river basin in various habitats and at relatively high densities (~0.08 ind.m-2; (42, 52)).

Demographic and biomass data

Demographic and biomass data were extracted from the AFB databases (53). We only retained sites monitored for 10 to 22 years (mean = 15.02) with a constant sampling effort. For each species, site and year of survey, we collected the local fish density (number of individuals per m^2) and the local fish biomass, expressed in g.m-2. For each species and each site, we computed the local population density and the local biomass production as the mean of density and biomass values over years. Metrics of density stability and biomass stability were both computed as the inverse of the squared coefficient of variation of density (respectively, biomass) over years, following (54). All variables related to density (population density and density stability) and biomass (biomass production and biomass stability) were log-transformed before analyses to meet normality assumptions.

Genetic data

The 47 river stations were sampled once in 2014 with up to 30 adults from each species caught by electrofishing, resulting in a set of 35, 37 and 21 sampled populations in minnows, gudgeons and chubs, respectively. On the field, a small piece of pelvic fin was collected from each individual and was preserved in 70% ethanol, before releasing fish in situ. Genomic DNA was extracted using a salt-extraction protocol (55) and used to obtain, for each species, population-based allelic frequencies following a paired-end, pool-seq procedure (56), as detailed in Appendix S3a. Read assembly, SNP calling and filtering (see Appendix S3b for details) generated a total of 1244 SNPs in minnows, 1892 SNPs in gudgeons and 1847 SNPs in chubs. Genomic data were further completed with microsatellite genotypes from individuals sampled in 2011 (Appendix S2), with 17, 13 and 16 loci in minnows, gudgeons and chubs, respectively.

For each species and site, we computed a total of six metrics of genetic diversity. First, we used SNPs allelic frequencies to compute two metrics in R (57): the expected level of heterozygosity across SNPs loci (sHe) and the observed level of SNP polymorphism (sPo), computed as the number of non-fixed loci ($0 <$ allelic frequency < 1) divided by the total number of loci with non-missing data in a given population. We then used microsatellite data to compute four additional metrics using the softwares GENETIX 4.3 (58) and ADZE 1.0 (59): the expected (µHe) and observed (µHo) levels of heterozygosity across microsatellite

loci, the mean number of alleles per locus (µNam) and the standardized allelic richness (µAR) based on a standardized sample size of 20.

To capture overall trends in species-specific patterns of genetic diversity and smooth possible particularities of each metric (60), the six metrics of genetic diversity were compiled using a principal component analysis (PCA). Only the first component was retained in each species, respectively accounting for 75.7, 68.8 and 86 % of variance in genetic data in minnows, gudgeons and chubs, respectively. In general, all variables equally contributed to the retained components, which were thus considered as species-specific synthetic predictors for genetic diversity, with genetically impoverished populations on the one hand (negative coordinates) and genetically diversified populations on the other hand (positive coordinates; Appendix S7a).

As genetic data could not be collected over years, we also computed the M-ratio (35) to determine whether sampled populations experienced recent demographic bottlenecks. The M-ratio is the ratio between the number of observed alleles at a microsatellite locus and the allelic range of that locus, the latter being supposed to decrease slower than the number of alleles during a demographic collapse. This index ranges from 0 to 1: empirical M-ratio values lower than a critical value of 0.68 indicate significant bottleneck (35). For each populations and each species, the M-ratio was computed for each microsatellite locus and then averaged over loci following (61; Appendix S1). We used the one minus the M-ratio as a proxy for demographic bottleneck probability.

Environmental data

Each site was described using 17 environmental variables susceptible to affect demography, biomass yields and genetic diversity of fish populations. From the French Theoretical Hydrological Network (62), we extracted seven variables related to river topography: distance from the mouth (in m), distance from the source (in m), river width (in m), slope (in degrees), altitude (in m) and mean annual water flow (in m3.s-1). Additionally, we computed the betweenness centrality index as a measure of local connectivity along the dendritic network (ComplexNetGIS toolbox in ARCGIS; (63)). Nine other variables were related to water quality and were obtained from the database of the Water Information System of the Adour Garonne basin (http://adour-garonne.eaufrance.fr): Temperature (in °C), dissolved oxygen concentration

(in mg.L-1) and oxygen saturation (in %), as well as the concentrations (in mg.L-1) in nitrogen compounds (total nitrogen N, ammonium NH4+, nitrates NO3- and nitrites NO2-) and in phosphorus compounds (total phosphorus P and phosphate PO43-). Only data from years 2012 to 2015 and from June to August were selected and averaged over months and years. Older data, although incomplete, suggested that water quality remained relatively stable over the considered period (Appendix S4). Except for a few sites that might be subject to local water pollution resulting from phosphorus inputs, all sites showed good to very good water quality according to the French implementation of the European Water Framework Directive 2000/60/EC (Appendix S5). Additionally, we computed a quantitative index of anthropogenic river alteration (ANTH) using a database from the AFB (64), which notably describes observed hydrological, morphological and thermic alterations resulting from human activities such as damming, channelization or urbanization (see Appendix S6 for details and computation). This index theoretically ranges from 0 (no identified anthropogenic alteration) to 1 (maximum alteration) but did not exceed 0.525 in our dataset, with a mean of 0.275. Environmental variables were log-transformed to meet normality assumption when required.

The 17 environmental variables were synthetized using a PCA (Figure 5; Appendix S7b). The two first components were retained, accounting for 58.5 % of the total variance in environmental variables. The first component (37.2% of variance) stood for the upstream-downstream gradient, with altitude and slope on the one hand (upstream stations with negative coordinates) and distance from the source, betweenness, temperature, river width and flow regime on the other hand (downstream stations with positive coordinates). The second component (21.3% of variance) stood for an eutrophic gradient, with dissolved oxygen, oxygen saturation and distance from the river mouth on the one hand (nutrient-impoverished and highly oxygenated river stations with negative coordinates) and total phosphorus, total nitrogen, nitrates and nitrites on the other hand (nutrient-rich and poorly oxygenated stations with positive coordinates). Ammonium and phosphate concentrations, as well as anthropogenic river alteration, did not contribute substantially to any of the retained components.

Statistical analyses

For each species, genetic diversity and all variables related to environment (upstream-downstream gradient and eutrophic gradient), demography (population density, density stability and bottleneck probability) and biomass yields (biomass production and biomass stability) were standardized to z-scores. Our objective was to investigate how genetic diversity might influence biomass production and stability in each species, while accounting for the direct and indirect influence of demography and environment (31, 65). To that aim, we designed a full causal model describing the expected direct and indirect links among all variables (Appendix S8). We hypothesized that genetic diversity would directly promote biomass production and biomass stability, either in an additive way, or in interaction with environmental variables. Interactions were simply computed as the cross-product of genetic diversity with each environmental variable (66). All other paths were used to control for the possible direct and indirect influence of other variables. We notably hypothesized that population density and density stability would respectively affect biomass production and biomass stability, both directly (biomass varying in proportion to density) and indirectly, through pathways involving genetic diversity (low densities or low stability favoring genetic drift (67)). Density stability was also expected to indirectly affect genetic diversity through demographic bottlenecks: in the event of recent demographic collapse (in the 20 years preceding genetic sampling), density stability should correlate negatively with the bottleneck probability, which is in turn expected to decrease genetic diversity. Finally, we hypothesized that the environmental characteristics of river stations (upstream-downstream gradient, eutrophic gradient and the corresponding first-order interaction computed as their cross-product) would affect variations in biomass yields both directly (for instance through higher intraspecific competition in harsh conditions) and indirectly, through pathways involving genetic diversity (promoted for instance by higher proximity to glacial refugees or higher local connectivity; (32)) and/or population dynamics (eutrophic conditions for instance leading to an increase in fish mortality or oligotrophic conditions leading to an increase in competition for resources).

We then used a causal modeling procedure to infer actual causal relationships among variables. Specifically, we used path analyses (29) with maximum likelihood estimation and ‘Huber-White’ robust standard errors to assess, in each species, the validity of the full model and to simplify it when needed. Model simplification was performed by removing non-significant paths one at a time, provided that cross-

products were always associated with their additive terms (68) and that removal led to an increase in the relative fit of the model (i.e., a decrease in AIC score (69)). Simplification was stopped as soon as the model reached a satisfactory absolute fit. Following Hu and Bentler (70), a model absolute fit was considered as satisfactory when the standardized root mean square residual (SRMR) and the Comparative Fit Index (CFI) were lower than ≤ 0.09 and higher than ≥ 0.96, respectively. Additionally, we checked that the p-value associated with the model χ^2 statistic, a classical fit index measuring the magnitude of discrepancy between the sample and the fitted covariance matrices (70), was non-significant ($p > 0.05$). To avoid model overfitting, we proceeded in two stages. In each species, we first considered a subset of the full causal model excluding biomass variables and all related links, and performed model simplification to get estimates for all important direct and indirect relationships among environmental gradients, demographic variations and genetic diversity. Retained path coefficients, set to their mean estimate, were subsequently considered as fixed parameters within the full causal model and a second set of model simplification was performed to get estimates for all important direct and indirect relationships pointing towards biomass variables. All path analyses were run using the R function lavaan (package lavaan; (71)).

For each response variable, we (a) computed the amount of variance (R^2) explained by the retained model in each species. To assess the relative contribution of genetic diversity, demography and environment to the variance in biomass variables, we computing R^2 from further simplified models with (b) all variables related to density being discarded (amount of variance explained by both environment and genetic diversity), then (c) with all variables related to genetic diversity (genetic diversity and associated cross-products) being discarded (amount of variance explained by environment only). The relative contributions of demography and genetic diversity to the variance in biomass variables were respectively obtained by subtracting R^2 of (b) from R^2 of (a) and by subtracting R^2 of (c) from R^2 of (b). We finally averaged these contributions across species and build 100% stacked barplots to illustrate the overall contribution of genetic diversity, demography and environment to the total explained variance in each biomass variable.

Results

Contrary to our predictions, we did not find evidence that genetic variation was related to mean biomass production at the local scale (Figure 2 and Figure 3A). However, we demonstrated that, in the three considered species, local populations with higher levels of genetic diversity displayed less variability in biomass production over time than genetically impoverished populations, sustaining the idea that intraspecific genetic diversity stabilizes biomass production over time. In the chub *Squalius cephalus* (Figure 2A), biomass stability increased with genetic diversity, particularly in the most eutrophic (i.e. stressful) habitats (Figure 4A). In the Languedoc gudgeon *Gobio occitaniae* (Figure 2B), biomass stability similarly increased with increasing levels of genetic diversity and in the most upstream habitats, but decreased with eutrophication (Figure 4B). In the minnow *Phoxinus phoxinus* (Figure 2C), the retained interaction between the upstream-downstream gradient and genetic diversity actually stemmed from an uneven distribution of populations within the parameter space, with no genetically impoverished populations in the downstream part of the basin (Figure 4C). As a result, biomass stability actually increased both upstreamward and with increasing levels of genetic diversity, as observed in the Languedoc gudgeon. These striking findings were supported by robust simplified causal models that correctly represented observed data in each species (satisfactory absolute fit indices after model simplification; Tables 1 and 2; see Appendix S9 for detailed results).

The relative contribution of genetic diversity to the overall explained variance in biomass stability across species was of 21.7%, a non-negligible value, although about twice lower than that of environmentally- and demographically-related variables (37.7% and 40.6% respectively; Figure 3B). These contributions were yet highly species-dependent. Genetic diversity accounted for 23% of the total variance in biomass stability in chubs, a contribution twice higher than that of demography (11.3%) and much higher than that of environment (2.6%). In gudgeons, the contribution of genetic diversity was comparable to that of demography (11.2%) but lower than that of the environment (50.1%). It was the lowest in minnows (5%), environment and demography accounting for 15.2% and 49.5% of variance in biomass stability, respectively.

These idiosyncrasies in the contribution of intraspecific diversity to biomass stability may be related to the evolutionary history of each species within the basin, as indicated by the systematic negative

relationships between bottleneck probability and genetic diversity in all three species (Figure 2). In minnows, the species with the lowest contribution, monitored populations showed high levels of genetic variation (e.g., 5.9 ± 0.8 alleles per microsatellite locus on average) and only 5.7% of them experienced a significant bottleneck (Fig. 3C-D). On the contrary, low levels of genetic variation (3.6 ± 0.6 alleles per locus) and a high proportion of populations having experienced a significant bottleneck (up to 85.7%) indicate that chubs, the species with the highest genetic contribution to biomass stability, suffered from strong genetic erosion in the past. Finally, only in gudgeon populations did we find a significant negative link between population stability (as measured over about 20 years) and bottleneck probability (Figure 2B). Together with a moderate proportion of populations having experienced a significant bottleneck (29.7%) and high levels of genetic diversity (as high as in minnows; 5.6 ± 0.7 alleles per locus), these results reveal signs of incipient genetic erosion in gudgeons.

In addition to revealing the consistent contribution of genetic diversity, or the loss of it, to biomass stability, our modeling framework allowed identifying other recurrent and theoretically-grounded relationships between variables. As expected, biomass yields were always positively linked to their demographic counterparts (i.e., biomass production and biomass stability were positively related to population density and population stability, respectively; Figure 2), explaining from 45.7% to 85.5 % of the variance in biomass production (Figure 3A) and from 11.4% to 49.5% of variance in biomass stability (Figure 3B). Similarly, we found a systematic downstream increase in genetic diversity, although this pattern only held true in oligotrophic stations in the case of minnows (Figure 4D). In gudgeons, genetic diversity was also positively influenced by the eutrophic gradient. We finally identified several significant paths linking environment variables to population dynamics and biomass yields. For instance, population density was found to increase downstreamward in chubs but upstreamward in gudgeons. Density stability and biomass production were found to decrease downstreamward and biomass stability to decrease with eutrophication in both minnows and gudgeons (Figure 2). All these expected findings confirm that causal models were biologically sound and robust for all species.

Discussion

By promoting phenotypic diversity (15), intraspecific genetic diversity is expected to favor niche complementarity and facilitative interactions among individuals. It may therefore reduce intra- but also interspecific competition and allow a more efficient exploitation of available resources (10, 16, 28). This positive influence of genetic diversity on ecological properties of populations, but also of communities and ecosystems (37), is expected to be particularly important in harsh or unpredictable environmental conditions (22). Many experimental studies demonstrated such benefits of genetic diversity under controlled or semi-controlled conditions (see (28) for a review) , but observational studies conducted in natural settings are still scarce and only concern plants (26, 38). Capitalizing on long-term surveys, we here report systematic positive relationships between intraspecific genetic diversity and temporal stability in the biomass production of wild populations of freshwater fish species. These findings provide the first evidence that the relationship between intraspecific genetic diversity and biomass yields holds true in natural ecosystems.

Overall, intraspecific genetic diversity accounted for more than 20% of the explained variance in biomass stability across species. Although this contribution was about twice lower than that of other predictors, it indicates that intraspecific diversity is actually a substantial driver of stability in fish biomass production, somehow as important as other determinants such as environment and demography. It thus plays a role similar to that of interspecific diversity: species richness has been shown to buffer natural fish biomass production from environmental variations (31) but our findings suggest that both facets of biodiversity may actually contribute to biomass stability in the wild (16, 22). Interestingly, we did not identify any relationship between genetic diversity and mean biomass production over years, although our models explained about 60% of variance in chubs, and up to 95% in gudgeons and minnows: biomass production was here mainly explained by demography and, particularly in gudgeons, by environmental variation. With only biomass stability being identified as driven by intraspecific genetic diversity, our study highlights the usefulness of long-term field surveys when investigating the determinants of ecological dynamics in natural settings (39). The contribution of genetic diversity to the variance in biomass stability was yet highly species-dependent, which seems to be partly explained by the evolutionary trajectory of each species, and notably by the severity of past genetic erosion. The genetic contribution was indeed the

highest for the species that suffered from the strongest and widespread past genetic erosion (the chub), intermediate for the species showing signs of incipient erosion (the Languedoc gudgeon) and the lowest for the species that did not suffer from past erosion (the minnow). Although these results would deserve further investigation (for instance with studies focusing on other species/taxa or other ecosystems), they strongly suggest that the contemporary loss of genetic diversity observed worldwide (36) may impact ecological functions in the same way as the loss of species (8), with possible critical consequences in terms of ecosystem functioning and provision of services (37).

A major difficulty when investigating biodiversity-functions relationships in the wild is to control for the direct and indirect effects of factors (other than biodiversity) that can affect ecosystem functions. This is notably the case in spatially-structured landscapes such as rivers in which both spatial patterns of genetic diversity and biomass yields are expected to depend on co-varying environmental factors along an upstream-downstream gradient (32, 40, 41). This gradient is for instance known to shape evolutionary processes such as downstream-biased gene flow and upstream-biased genetic drift, generating patterns of downstream increase in genetic diversity (32). We accordingly detected a classical downstream increase in genetic diversity in all three species, indicating that the river network topology also indirectly contributed to a downstream increase in biomass stability. The upstream-downstream gradient might also affect ecological processes such as foraging success, recruitment and competition, in turn causing spatial variations in population dynamics and biomass yields (42, 43). In minnows and gudgeons for instance, two species whose biological requirements are respectively fulfilled in the upstream and the intermediate parts of the studied basin (42), the upstream-downstream gradient was responsible for a downstream decrease in both biomass production and biomass stability, either directly or indirectly, through demography.

Fish species may also react differently to eutrophication levels. Associated with hypoxia and possible exposure to sub-lethal concentrations of pollutants, eutrophication has indeed been shown to affect individual behavior and physiology in different freshwater species, in turn impacting key-ecological processes such as recruitment (44, 45). We for instance demonstrated that eutrophication indirectly influenced biomass stability through a decrease in density stability in the two most sensitive fish species (minnows and gudgeons). In chubs, a species that can tolerate degraded water quality (46), the positive relationship between genetic diversity and biomass stability was particularly pronounced in the most

eutrophic habitats (Figure 3B). In accordance with empirical findings showing that among-individual functional complementarity promoted by genetic and phenotypic variation is of greater importance under more stressful than under benign conditions (22), this result suggests that genetic diversity may locally contribute to higher individual tolerance and benefit to populations by buffering the possible negative aftermaths of eutrophication or other anthropogenic stressors.

In line with both theoretical expectations and collective experimental evidence (22), we found strong evidence that "real world" genetic diversity directly promotes temporal stability in biomass production, particularly under the most stressful conditions. Similarly to what was demonstrated in natural settings at the interspecific level (8), we showed that genetic diversity was somehow as important as other predictors such as environment and demography to sustain biomass production over time. Given both the abundance and the importance of studied species within trophic chains, we suggest that genetic diversity might also indirectly promote community and ecosystem stability (28, 37), although deciphering these relationships lied beyond the scope of our study. Future studies are now needed to confirm the significance of these results in other taxa and to disentangle the relative contribution of intra- and interspecific diversity in explaining biomass yields in the wild (21), notably in temperate ecosystems where species diversity is naturally low. We yet also demonstrated that genetic erosion may jeopardize these direct benefits in just a few generations. Considering the dramatic erosion of biodiversity worldwide and the associated risks for the functioning and productivity of ecosystems (36, 47), our study adds to the growing body of knowledge and stress the need for human societies to adopt prominent environmental policies favoring all facets of biodiversity (48, 49).

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Figures and Tables

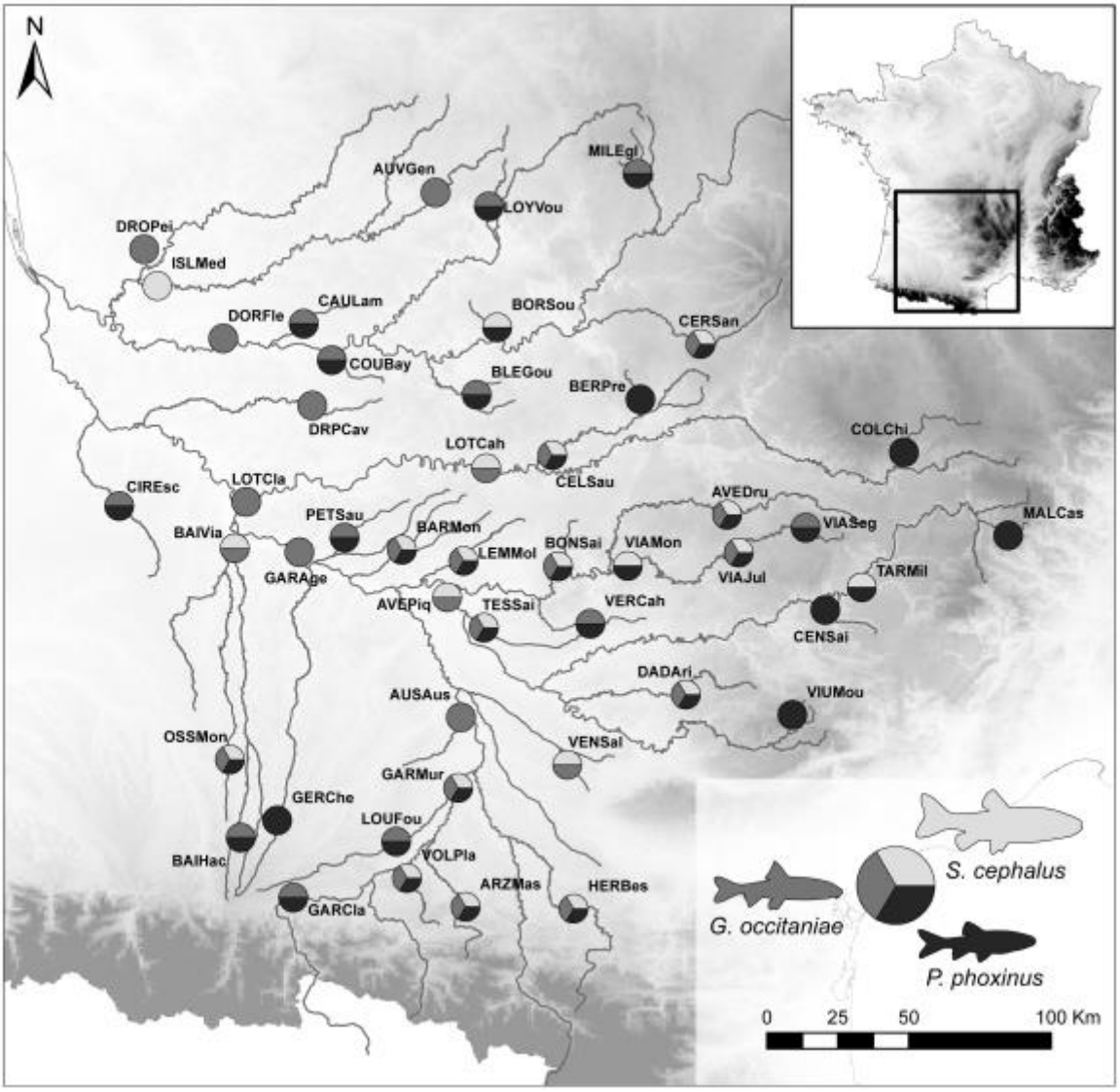
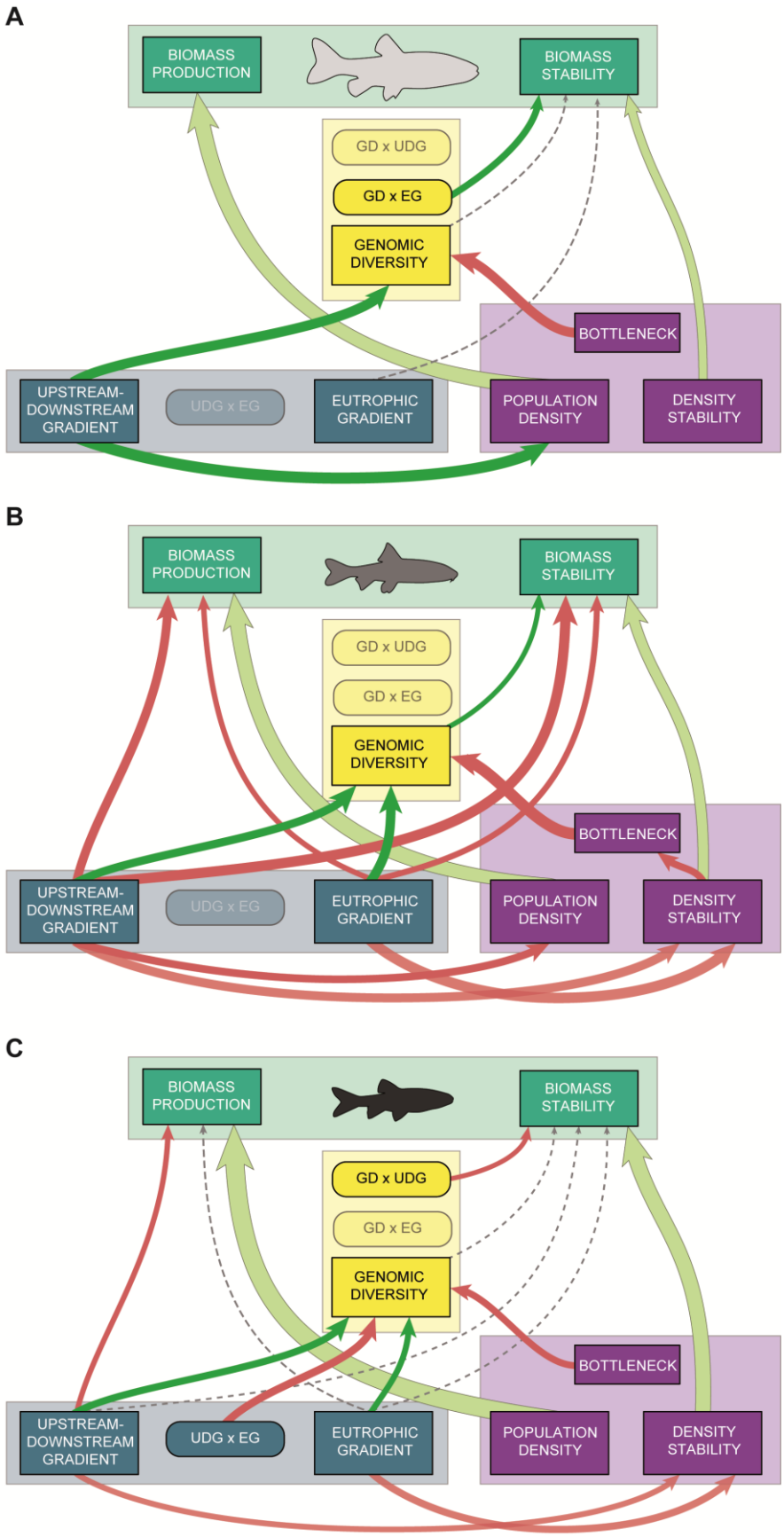


Figure 1. Geographic situation of the Garonne-Dordogne river basin in South-Western France and localization of the 47 unique river stations, with pie charts indicating species (co-)occurrence within each station. The black arrow indicates the location of the river mouth. Background is a shaded relief map.


A
BIOMASS PRODUCTION
BIOMASS STABILITY
GD x UDG
GD x EG
GENOMIC DIVERSITY
BOTTLENECK
UPSTREAM-DOWNSTREAM GRADIENT
UDG x EG
EUTROPHIC GRADIENT
POPULATION DENSITY
DENSITY STABILITY
B
BIOMASS PRODUCTION
BIOMASS STABILITY
GD x UDG
GD x EG
GENOMIC DIVERSITY
BOTTLENECK
UPSTREAM-DOWNSTREAM GRADIENT
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EUTROPHIC GRADIENT
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BIOMASS PRODUCTION
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EUTROPHIC GRADIENT
POPULATION DENSITY
DENSITY STABILITY

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Figure 2. Simplified causal graphs depicting retained links among environmental (blue rectangles), demographic (purple rectangles), genetic (yellow rectangles) and biomass variables (green rectangles) in chubs (A), gudgeons (B) and minnows (C). First-order interactions are represented by rounded rectangles (washed-out when not involved in any causal link). Red and green arrows represent negative and positive significant paths, respectively, with the width of arrows proportional to the absolute value of the corresponding path coefficient. Washed-out green arrows stand for direct positive links between density and biomass variables. Dashed grey arrows represent non-significant paths. Covariations and paths removed during the simplification procedure are not displayed, for the sake of clarity.

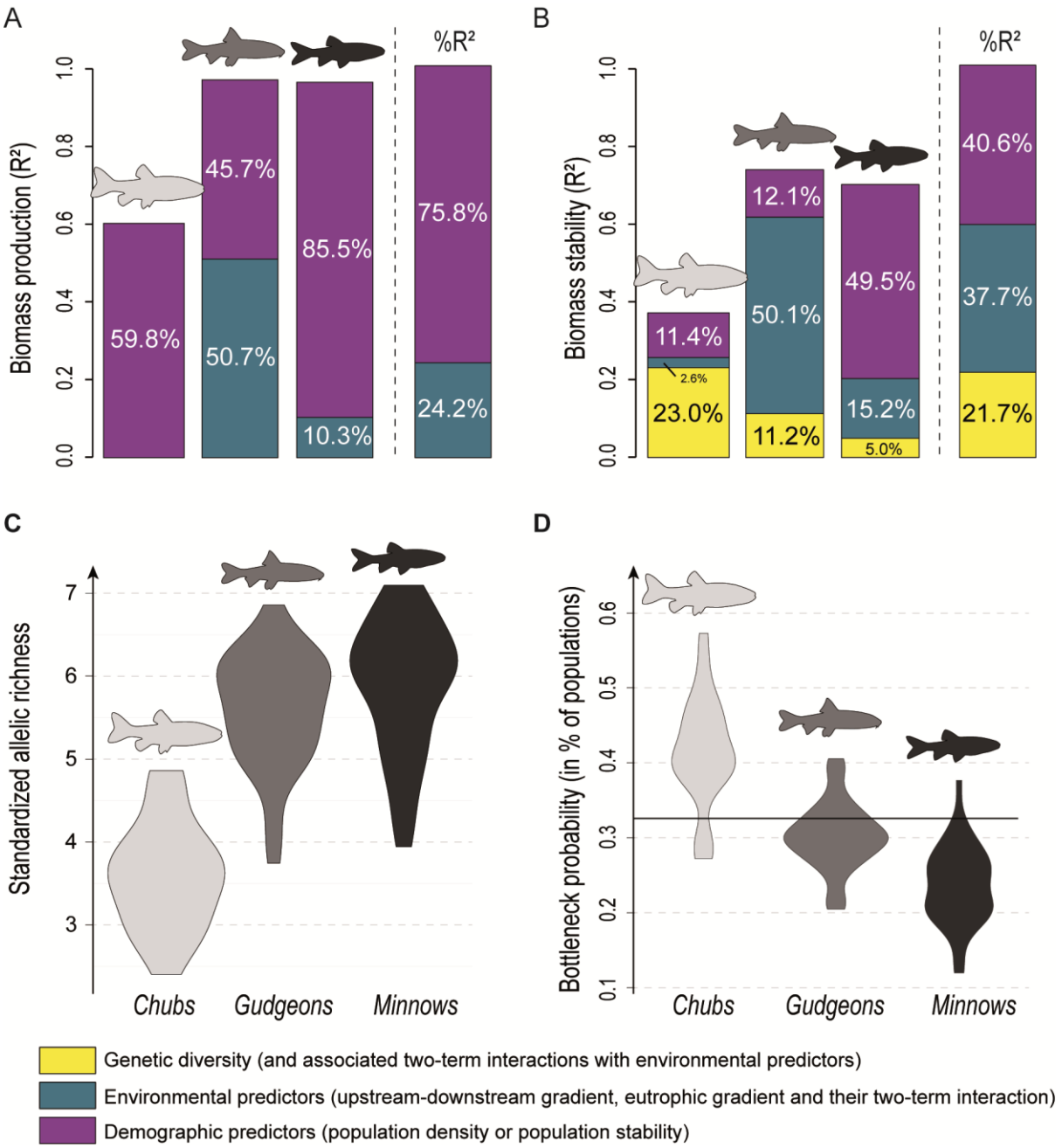

Figure 3. Upper panels: Contributions of demographic variables (mean density and density stability), environmental gradients (upstream-downstream gradient and eutrophic gradient) and genetic diversity (genetic diversity and associated interactions) to biomass production (A) and temporal stability in biomass production (B) in each species. The average contributions of each predictor to the explained variance in biomass yields across species is shown in the form of 100% stacked barplots (%R²). Colors are the same as in Figure 2. Lower panels: Distribution of levels of genetic diversity (C; here, microsatellite standardized

allelic richness) and bottleneck probability (D) as measured at the population-level in each species. The horizontal black line in D indicates the threshold above which populations are supposed to have experienced recent and severe bottleneck (M-ratio < 0.68).

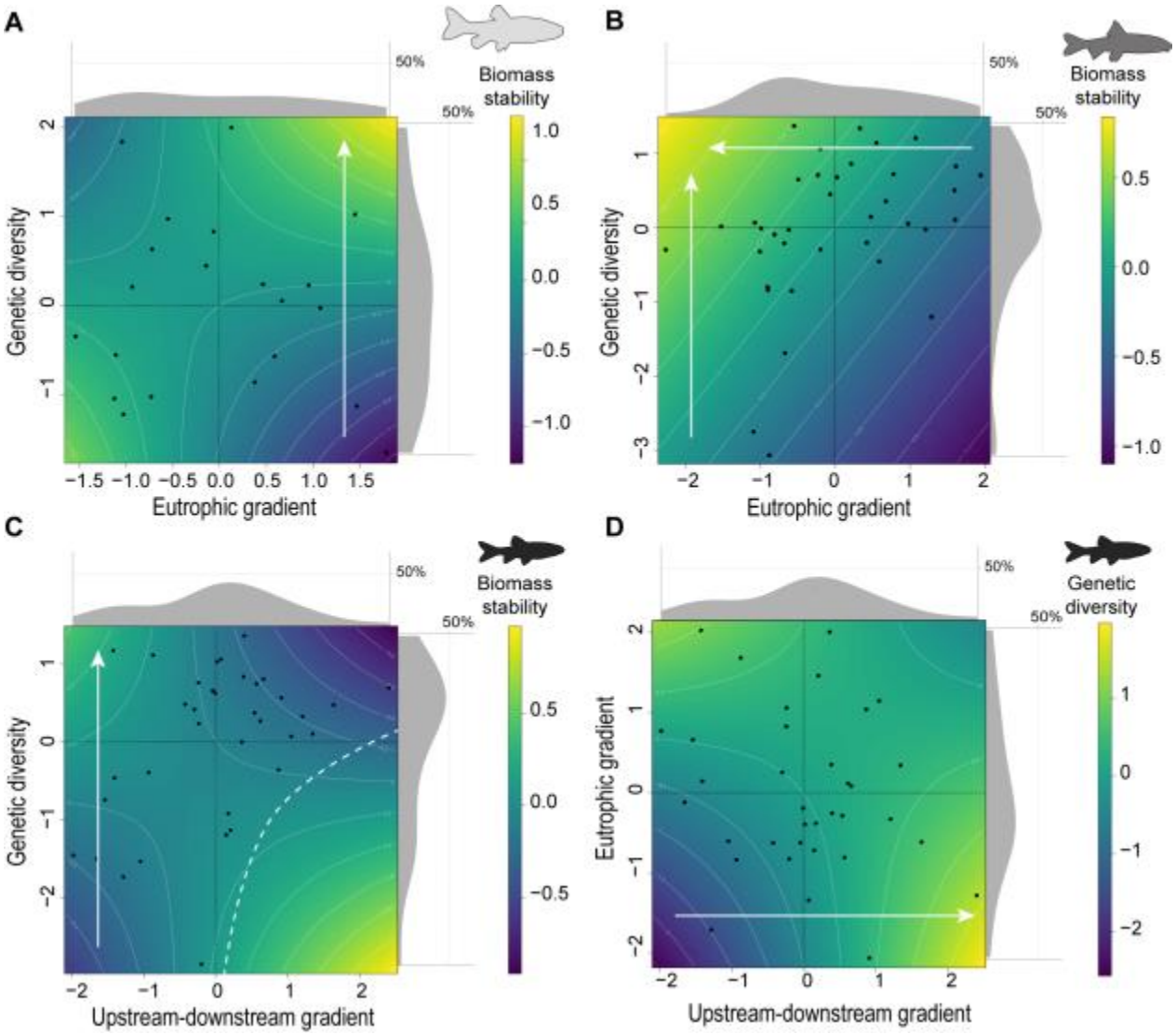

Figure 4. Continuous representations of additive relationships or first-order interactions associated with biomass stability (A to C) and genetic diversity (D) in final simplified models in chubs (A), gudgeons (B) and minnows (C and D). Predicted values of biomass stability and genetic diversity were computed across all possible values of the two corresponding additive terms and plotted as a colored surface with contours. Horizontal and vertical black dashed lines indicate additive trends (i.e., the predicted relationship between the response and a given predictor when the other predictor is set to zero). Black dots, standing for observed data, and lateral shaded surfaces, standing for kernel density estimates of data points along each additive variable, allow visualizing the occupied parameter space. The white dashed line delimits an empty space in panel C. White arrows indicate noticeable trends. Biomass stability increased with genetic

diversity in all species (A-C) but mostly in eutrophic habitats in chubs (A) and in upstream populations in minnows (C). Biomass stability also decreased with eutrophication in gudgeons (B). Minnows showed a classical downstream increase in genetic diversity, but under the less eutrophic conditions only (D).

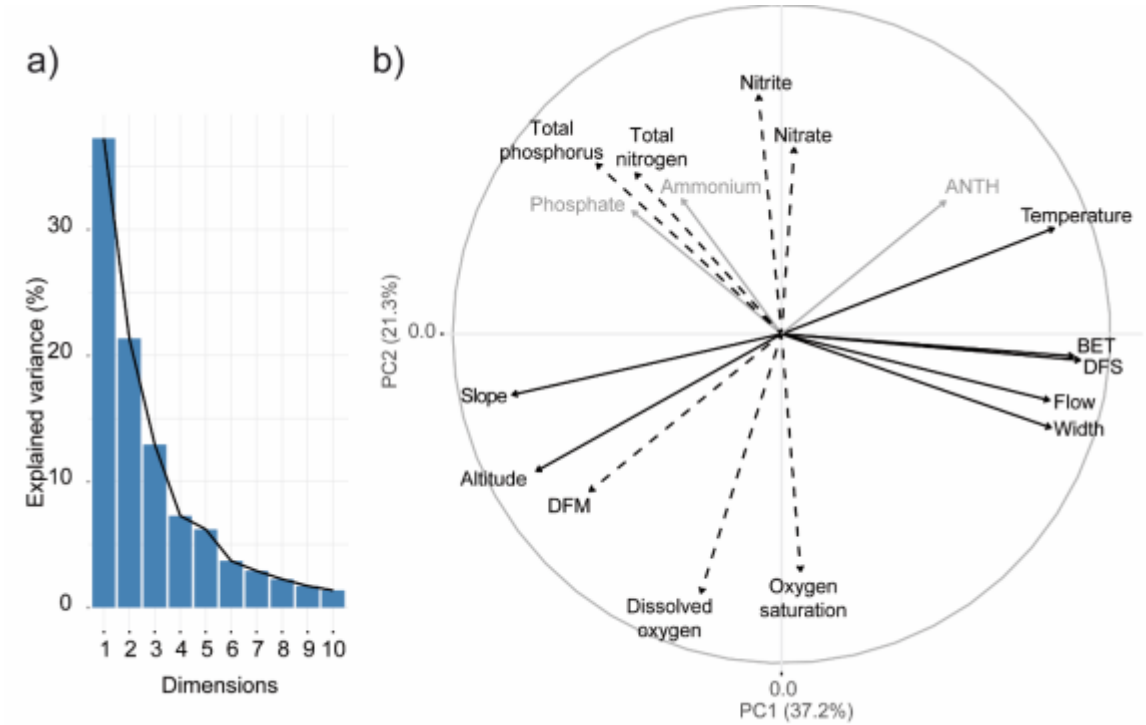

Figure 5. Characteristics of the two first principal components based on environmental data. a) Eigenvalues corresponding to the amount of the variation explained by each principal component. b) Visualization of the two first principal components (PC), with PC1 standing for the upstream-downstream gradient and PC2 standing for the eutrophic gradient. Percentage of variance explained by each component is also indicated. BET: Betweenness; DFM: Distance from the river mouth; DFS: Distance from the source; ANTH: anthropogenic river alteration. Solid black arrows: variables with a significant contribution to PC1; dashed black arrows: variables with a significant contribution to PC2; grey arrows: variables that did not contribute to any of the two first components.

Table 1. Main results from the first set of causal models, excluding biomass variables. For each species, the table provides absolute fit indices (CFI, SRMR and p-value; see text for details), amounts of explained variance (R^2) in response variables (indicated with an arrow) and estimates of path coefficients (indicated by arrows). Significant path coefficients threshold are in bold (see Appendix S9 for a table with 95% confidence intervals). Slashes indicate links that were discarded in the course of model simplification. Only links retained in at least one species are shown. UDG: upstream-downstream gradient; EG: Eutrophic gradient.

		S. cephalus	*G. occitaniae*	*P. Phoxinus*
Model fit indices	χ^2 p-value	0.908	0.638	0.986
	CFI	1	1	1
	SRMR	0.037	0.075	0.017
Upstream-downstream gradient	→ Genetic diversity	**0.469**	**0.372**	**0.311**
Eutrophic gradient	→ Genetic diversity	/	**0.444**	0.249
UDG x EG	→ Genetic diversity	/	/	**-0.35**
Bottleneck	→ Genetic diversity	**-0.451**	**-0.555**	-0.296
	R^2	0.548	0.548	0.353
Density stability	→ Bottleneck	/	**-0.309**	/
	R^2	/	0.095	/
Upstream-downstream gradient	→ Mean density	**0.544**	**-0.372**	/
	R^2	0.296	0.272	/
Upstream-downstream gradient	→ Density stability	/	**-0.415**	-0.241
Eutrophic gradient	→ Density stability	/	**-0.5**	**-0.319**
	R^2	/	0.371	0.129

Table 2. Main results from the second set of causal models including biomass variables, with estimates from the first set of causal models being fixed. GD: Genetic diversity. See table 1 for complete legend.

		S. cephalus	*G. occitaniae*	*P. Phoxinus*
Model fit indices	χ^2 p-value	0.83	0.957	0.119
	CFI	1	1	0.961
	SRMR	0.067	0.079	0.084
Mean density	→ Biomass production	**0.733**	**0.737**	**0.932**
Upstream-downstream gradient	→ Biomass production	/	**-0.406**	-0.296
Eutrophic gradient	→ Biomass production	/	**-0.221**	-0.22
	R^2	0.598	0.909	0.959
Density stability	→ Biomass stability	**0.393**	**0.509**	**0.754**
Upstream-downstream gradient	→ Biomass stability	/	**-0.486**	-0.114
Eutrophic gradient	→ Biomass stability	-0.096	**-0.253**	**-0.158**
Genetic diversity	→ Biomass stability	0.134	**0.198**	-0.079
GD x UDG	→ Biomass stability	/	/	**-0.188**
GD x EG	→ Biomass stability	**0.292**	/	/
	R^2	0.363	0.738	0.705