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

Authors:

Jérôme G. Prunier [1] *, Mathieu Chevalier [2], Allan Raffard [1], Géraldine Loot [3], Nicolas Poulet [4], Simon Blanchet[1,3]*

Affiliations :

[1] Centre National de la Recherche Scientifique (CNRS), Université Paul Sabatier (UPS); Station d'Ecologie Théorique et Expérimentale, UMR 5321, F-09200 Moulis, France

[2] Department of Ecology and Evolution, University of Lausanne, Biophore, CH-1015 Lausanne, Switzerland

[3] CNRS, UPS, École Nationale de Formation Agronomique (ENFA) ; UMR 5174 EDB (Laboratoire Évolution & Diversité Biologique), 118 route de Narbonne, F-31062 Toulouse cedex 4, France

[4] Pôle écohydraulique AFB-IMT, allée du Pr Camille Soula, 31400 Toulouse, France

*** Corresponding authors:**

Jérôme G. Prunier and Simon Blanchet

Station d'Ecologie Théorique et Expérimentale, UMR 5321, F-09200 Moulis, France

2 route du CNRS, 09200 Moulis

Phone: (+33)561040361

Email: jerome.prunier@gmail.com, simon.blanchet@sete.cnrs.fr

ORCIDs: Jérôme G. Prunier 0000-0003-4110-2567, Simon Blanchet 0000-0002-3843-589X

Abstract

Theory predicts that biodiversity is causally linked to key ecological functions such as biomass productivity, and that loss in functional traits both among- and within-species can reduce the efficiency of ecosystem functions. There has been ample empirical and experimental demonstration that species loss indeed reduces the efficiency of ecosystem functions, with tremendous impacts on services provided by biodiversity. Nonetheless, and despite the fact that within-species diversity is strongly altered by human activities, there have been little attempts to empirically test (i) whether intraspecific genetic diversity actually promotes productivity and stability in wild populations, and, (ii) if so, to quantify its relative importance compared to other determinants. Capitalizing on 20-year demographic surveys in wild fish populations, we show that genetic diversity does not increase mean biomass production in local populations, but strongly and consistently stabilizes biomass production over time. Genetic diversity accounts for about 20% of explained variance in biomass stability across species, an important contribution about half that of environment and demography (about 40% each). Populations having suffered from demographic bottlenecks in the recent past 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 intraspecific 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 trait complementarity among species, interspecific diversity allows ecological communities to optimally capture essential resources, transform those resources into biomass and recycle them (4–6). In species-rich communities, these ecological processes are maintained even in the face of environmental variations, thus promoting ecosystem productivity and stability over time (7–9): this is the insurance effect of species richness (10). The drastic erosion in species diversity observed worldwide (11) is hence prejudicial, as it is expected to deeply impair natural ecosystems' capacity to durably sustain human health and wellbeing (2, 3). 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 (15, 16). By promoting intraspecific phenotypic diversity (17, 18), genetic diversity may indeed favor both the occurrence of highly productive phenotypes (19) and the functional complementarity among individuals through spatial or temporal niche partitioning (6), thus fostering a more efficient exploitation of available resources over time (2, 10). Genetically-diversified populations are therefore predicted to have higher and more stable biomass production than genetically-impoverished populations, notably under fluctuating or stressful environmental conditions (15, 16). This direct relationship between genetic diversity and biomass is expected to be particularly strong in ecosystems where species diversity is naturally low, which is actually the norm in many temperate ecosystems (20). In such cases, the functioning of ecosystems probably depends more on the complementarity among genotypes than on the complementarity among species (21–23), emphasizing the importance of maintaining genetic diversity to preserve ecosystem functions and services (15).

Most studies investigating the relationship between genetic diversity and ecological functions such as biomass production are based on experimental or semi-experimental settings, where population densities and levels of genetic diversity are manipulated, while environmental conditions are controlled and maintained constant over time. However, observational studies conducted in natural settings are still

scarce and mostly concern plants (24). Although these studies offer a number of advantages, 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 (25)) and more recent -if not ongoing- ecological processes affecting individual life history traits or population demography (e.g., stressful environmental conditions (26), bottleneck events (27), or strong directional selection (28, 29)). This natural complexity cannot be fully grasped by experimental studies (24). 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 (6, 15, 16). They yet raise several difficulties. First, assessing the influence of genetic diversity on the stability of biomass production over several generations or seasonal cycles implies long-term monitoring programs of both population density and biomass production, but such data are usually difficult to collect and are still scarce. Furthermore, the relationships between genetic diversity and biomass in across-population studies may be masked by the interplay with other factors also involved in population productivity, such as population density and environmental conditions, making it difficult to disentangle their respective contributions (6, 24). This last issue may however be partly alleviated through the use of causal modeling procedures, making it possible to thoroughly confront theoretical expectations and experimental findings with the “real world” (4, 30).

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 production (mean biomass production and temporal stability in biomass production) at the population level in three parapatric freshwater fish species: the chub *Squalius cephalus*, the Languedoc gudgeon *Gobio occitaniae* and the minnow *Phoxinus phoxinus*. 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 an eutrophic gradient. The former is a critical feature known to shape spatial patterns of both genetic diversity and biomass in dendritic networks (31, 32), whereas the latter may act as a possible stressor that

can affect both population dynamics and productivity (33). As local population dynamics may also influence both genetic diversity and biomass, we considered several demographic covariates: mean population density, long-term stability in population density and bottleneck probability, the latter indicating past changes in effective population size (34). By building this causal model, we aimed to answer the following questions: do the positive relationships found experimentally between intraspecific genetic diversity and biomass production/stability hold true in natural settings? If any, is the contribution of genetic diversity to biomass production/stability similar across species, and comparable in magnitude to that of other environmental and demographic determinants? Finally, is it possible to detect the impact of the ongoing genetic erosion, i.e., the loss of intraspecific 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 (35), 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 (36). Fish communities in this river basin are generally poorly diverse (3 to 15 species in general (37)) and we focused on three of the most common species (38): 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; (39)). They are all generalist species mainly feeding on invertebrates (although chubs can also predate on small-bodied fish) but occupy different habitats (38): 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; (39, 40)).

Demographic and biomass data

Demographic and biomass data were extracted from the AFB databases (41). 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 (42). 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 (43) and used to obtain, for each species, population-based allelic frequencies following a paired-end, pool-seq procedure (44), as detailed in Appendix S2a. Read assembly, SNP calling and filtering (see Appendix S2b 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 (Appendix S1), 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 (45): 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 (46) and ADZE 1.0 (47): 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 (48), 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 S6a). This synthetic predictor was highly correlated with mean allelic richness in each species ($r > 0.9$).

As genetic data could not be collected over years, we also computed the M-ratio (34) 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 (34). For each populations and each species, the M-ratio was computed for each microsatellite locus and then averaged over loci following (49). We used 1-(M-ratio) as a proxy for demographic bottleneck probability.

Environmental data

Each site was described using 17 environmental variables susceptible to affect demography, biomass and genetic diversity of fish populations. From the French Theoretical Hydrological Network (50), 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; (51)). 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 $mg.L^{-1}$), oxygen saturation (in %), concentrations (in $mg.L^{-1}$) in nitrogen compounds (total nitrogen N, ammonium NH^{4}+, nitrates NO^{3-} and nitrites NO^{2-}) and concentrations in phosphorus compounds (total phosphorus P and phosphate PO_4^{3-}). 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 S3). 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 S4). Using a database from the AFB (52), we further computed a quantitative index of anthropogenic river alteration (ANTH) to describe observed hydrological, morphological and thermic alterations resulting from human activities such as damming, channelization or urbanization (see Appendix S5 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 S6b). 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 (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 effects of demography and environment (30, 53). To that aim, we designed a full causal model describing the expected direct and indirect links among all variables (Appendix S7). 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 computed as the cross-product of genetic diversity with each environmental variable (54). All other paths were used to control for the possible direct and indirect influence of other variables. We notably hypothesized that mean 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 (55)). 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 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 (31)) 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 (56) 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 (57) and that removal led to an increase in the relative fit of the model (i.e., a decrease in AIC score (58)). Simplification was stopped as soon as the model reached a satisfactory absolute fit. Following Hu and Bentler (59), 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 (59), 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 (60).

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 diversity is related to mean biomass production at the local scale (Figure 2 and Figure 3B). We however demonstrate that, in the three considered species, populations with higher levels of genetic diversity display higher biomass stability over time than genetically-impoverished populations, sustaining the idea that intraspecific genetic diversity stabilizes biomass production (Figure 2 and Figure 3C). The relative contribution of genetic diversity to the overall explained variance in biomass stability across species was of 21.7%, a significant value about half that of environmentally- and demographically-related variables (37.7% and 40.6% respectively; Figure 3C). This striking finding is supported by robust simplified causal models that correctly represent observed data in each species (satisfactory absolute fit indices after model simplification; Tables 1 and 2; see Appendix S8 for detailed results).

The contribution of genetic diversity to biomass stability was yet both species- and context-dependent. It was the highest in the chub, genetic diversity accounting for 23% of the total variance in biomass stability, a contribution twice higher than that of demography (11.3%) and much higher than that of environment (2.6%). The retained interaction between the eutrophic gradient and genetic diversity in this species, though marginally significant (probably because of a low sample size; $n = 21$, $\beta = 0.292$, $p = 0.085$; $\Delta AIC = +0.55$ when removed from the model) indicates that biomass stability increases with genetic diversity, though mainly in the most eutrophic (i.e. stressful) habitats (Figure 2A and 4A). In the Languedoc gudgeon, the contribution of genetic diversity to biomass stability (11.2%) was comparable to that of demography (12.1%) but lower than that of the environment (50.1%). In this species, biomass stability increases with increasing levels of genetic diversity ($n = 37$, $\beta = 0.198$, $p = 0.006$). It also increases upstreamward but decreases with eutrophication. The contribution of genetic diversity to biomass stability was the lowest in the minnow (5%), environment and demography accounting for 15.2% and 49.5% of variance in biomass stability, respectively. The retained interaction between the upstream-downstream gradient and genetic diversity ($n = 35$, $\beta = -0.188$, $p = 0.023$) is characterized by an uneven distribution of populations within the parameter space, with no genetically impoverished populations in the downstream part of the basin (Figure 4B). As a result, biomass stability in minnows actually slightly

increases both upstreamward and with increasing levels of genetic diversity, as observed in the Languedoc gudgeon.

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 and Figure 3A). In minnows, the species with the lowest contribution of genetic diversity to biomass stability, monitored populations showed high levels of genetic diversity (e.g., 5.9 ± 0.8 alleles per microsatellite locus on average) and only 5.7% of them experienced a significant bottleneck. On the contrary, low levels of genetic diversity (3.6 ± 0.6 alleles per locus) and a high proportion of populations having experienced a significant bottleneck (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; $F_{(1,70)} = 2.35$, $p = 0.13$), 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 indicating that our simplified causal models were biologically sound (see Appendices S9 and S10 for graphical outputs and related discussion). As expected, biomass production and biomass stability were always positively linked to their demographic counterparts (i.e., population density and population stability, respectively; Figure 2), explaining from 11.4% to 85.5 % of the variance in biomass variables (Figure 3B-C). Similarly, we found a systematic downstream increase in genetic diversity, although this pattern only held true in oligotrophic conditions in the case of minnows (Appendix S10). We finally identified several significant paths linking environment gradients to population dynamics and biomass variables. 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).

Discussion

Capitalizing on long-term demographic surveys, we report systematic positive relationships between intraspecific genetic diversity and temporal stability in biomass production in three freshwater fish species. These positive relationships indicate a buffering effect of genetic diversity, genetically-impoverished populations being less efficient in maintaining stable biomass production over time than genetically-diversified populations (10). By favoring the occurrence of highly productive phenotypes and/or a higher functional complementarity among phenotypes, higher genetic diversity likely allows populations to maintain an efficient exploitation of available resources in the face of natural environmental fluctuations, insuring a stable production of biomass (2, 6, 10). Interestingly, and contrary to our expectations, this buffering effect of genetic diversity did not come with a performance-enhancing effect (10): genetically-diversified populations did not tend to show higher mean biomass production than genetically-impoverished populations. In minnows and gudgeons for instance, mean biomass production was almost exclusively driven by demography and the environment ($R^2 > 95\%$), suggesting that, in these species, the effect of genetic diversity, if any, might be too tenuous to be tractable when compared to the effect of other determinants. Mean biomass production might also be driven by factors that we did not consider in our study, such as interspecific interactions at the community-level (61) or terrestrial subsidies at the ecosystem level (62), possibly accounting for the 40% of unexplained variance in chubs. Nevertheless, our study provides one of the first evidence that “real world” genetic diversity can directly promote temporal stability in biomass production in wild organisms, in line with both theoretical expectations and experimental evidence (15, 16)

Overall, intraspecific genetic diversity accounted for more than 20% of the explained variance in biomass stability across species, a contribution about half that of other predictors such as environmental variation and demography. Our findings not only indicate that the relationship between intraspecific diversity and biomass holds true in natural ecosystems, but also that this relationship can be substantial and comparable to the effects of other undisputable determinants of productivity, as recently shown for interspecific diversity (7). While species richness can buffer natural fish biomass production against environmental variations (30), we argue that both intra- and interspecific facets of biodiversity may actually contribute to biomass stability in the wild (15, 16).

The buffering effect of intraspecific diversity was both species- and context-dependent, illustrating the complexity of natural systems and the importance of moving from experimentally-based to empirically-based studies to better understand relationships between biodiversity and ecological functions (2, 4, 24). Indeed, contrary to the additive effect of genetic diversity reported for gudgeons and minnows, the positive relationship between genetic diversity and biomass stability in chubs, a species known to tolerate degraded water quality (63), was only expressed under the most eutrophic conditions. Associated with hypoxia and possible exposure to sub-lethal concentrations of pollutants, eutrophication has been shown to adversely affect individual behavior and physiology as well as population dynamics in different freshwater species (64, 65). High levels of genetic diversity in these stressful conditions may favor the occurrence of well adapted and more productive phenotypes in this species, thus locally buffering the negative aftermaths of eutrophication (6). Although deciphering the actual mechanisms underlying the ecological effects of genetic diversity would require gathering detailed functional trait data in each species, this context-dependent buffering effect of genetic diversity in chubs further highlights the importance for populations to benefit from high levels of genetic diversity, especially in a rapidly changing world with ever-increasing anthropogenic pressures (35, 66).

Among-species differences in the contribution of genetic diversity to the variance in biomass stability may be partly explained by the recent evolutionary trajectory of each species (2), and notably by the severity of past –yet recent– genetic erosion through demographic bottlenecks (67). The contribution of genetic diversity to biomass stability was indeed the highest for the species that suffered from the strongest and widespread past genetic erosion (the chub), the lowest for the species spared from genetic erosion (the minnow), and intermediate for the species undergoing genetic erosion (the Languedoc gudgeon). These findings provide one of the first non-experimental evidence that contemporary evolutionary processes such as genetic erosion due to random drift can shape ecological dynamics in natural settings (24), hence leady to tight “evo-to-eco” relationships. These “real world” eco-evolutionary dynamics have important implications in terms of conservation. Since the loss of genetic diversity always precede the loss of species (12), our results indeed suggest that genetic erosion (a very common observation in wild species impacted by environmental changes and human activities (68, 69)) may adversely affect key-ecological functions long before the first species of a community becomes extirpated.

Perhaps most importantly, these negative effects may occur from the very first signs of genetic erosion and therefore even in species that would be considered as having a good conservation status based on conventional measures of intraspecific diversity such as allelic richness or expected heterozygosity (70). This is perfectly exemplified in the case of the Languedoc gudgeon, a species that display high levels of genetic diversity (as high as in minnows) but in which almost a third of monitored populations actually exhibit signs of ongoing genetic erosion when considering dedicated metrics such as the M-ratio (34) (see Material and Methods for details). We therefore suspect that the loss of intraspecific diversity observed worldwide (35) is actually responsible for a considerable alteration of many ecological processes in nature, but that these adverse effects might have been underestimated.

To conclude, we found strong evidence that “real world” genetic diversity directly promotes temporal stability in biomass production in the three considered freshwater fish species. Future studies are now needed to confirm the significance of these results in other taxa and other ecosystems and to disentangle the relative contribution of intra- and interspecific diversity in explaining biomass production in the wild (23), notably in temperate ecosystems where species diversity is naturally low. Our findings yet also strongly suggest that the impact of human-induced genetic erosion on natural ecosystems’ capacity to provide critical provisioning and regulating services to humanity is probably much more important than anticipated, making it a critical conservation issue and stressing the need for human societies to adopt prominent environmental policies favoring all facets of biodiversity (71, 72).

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Figures and Tables

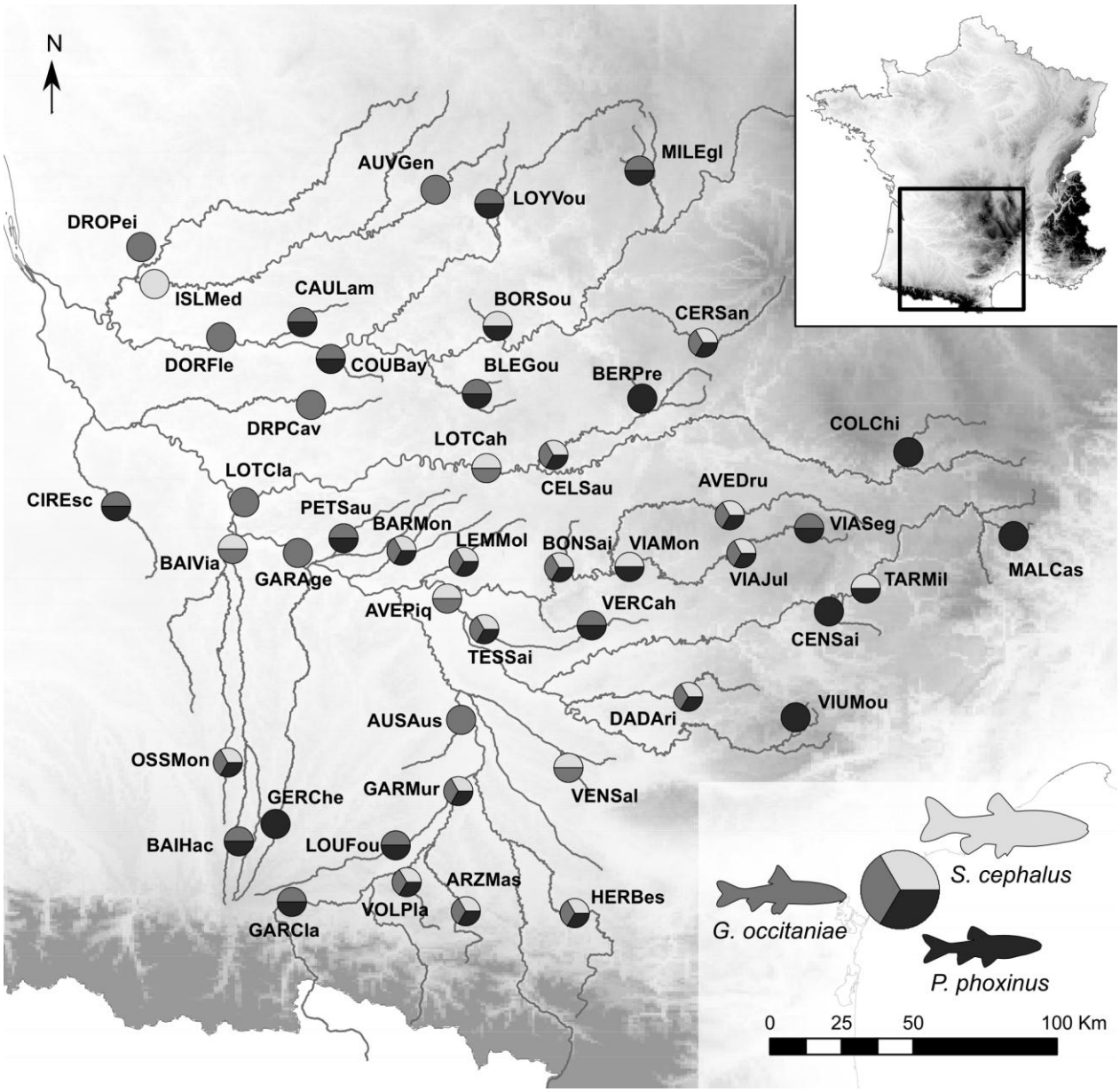
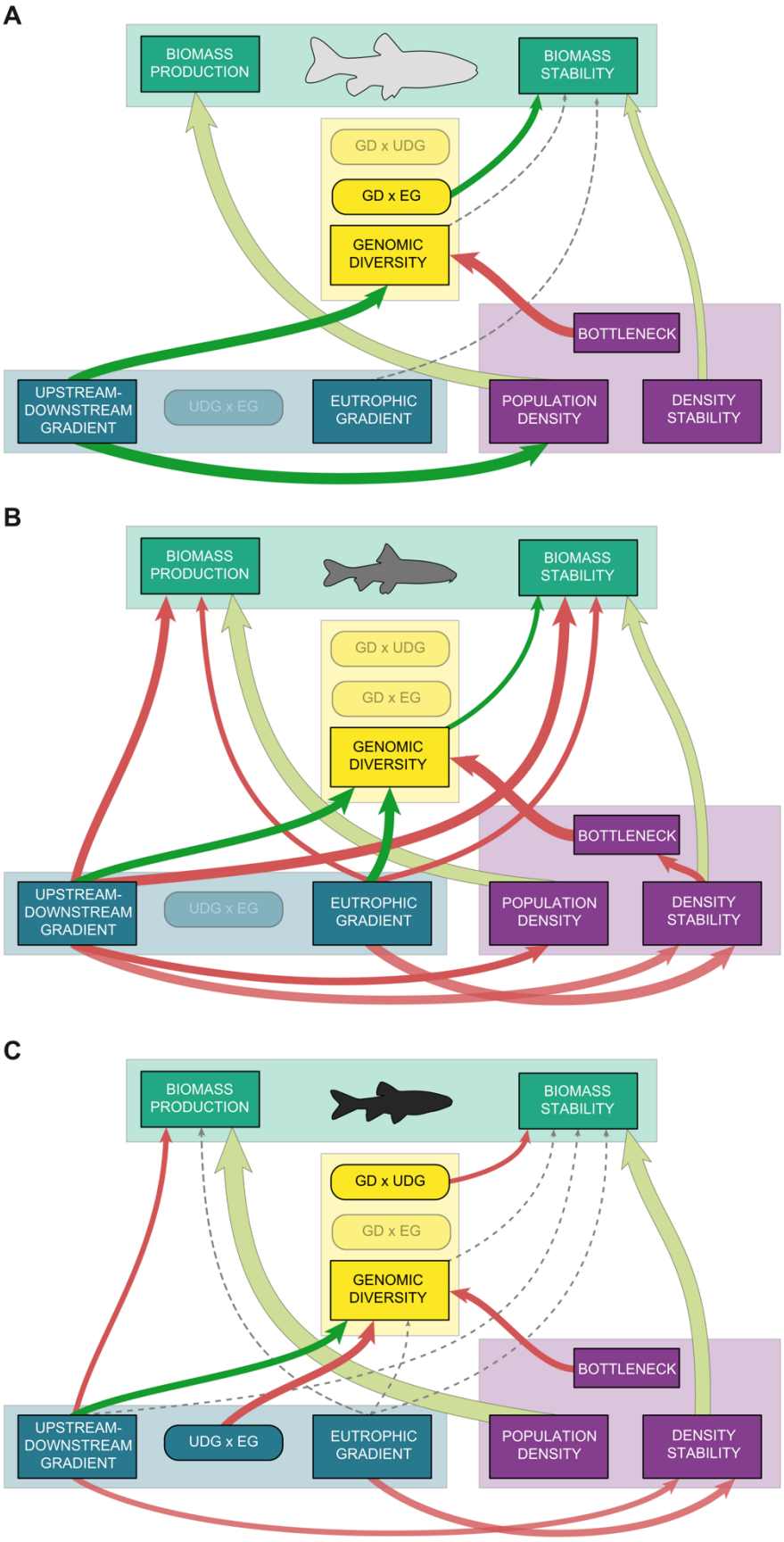


Figure 1. Geographic situation of the Garonne-Dordogne river basin in South-Western France and localization of the 47 unique river stations, with pie charts indicating species (co-)occurrence within each station. The black arrow indicates the location of the river mouth. Background is a shaded relief 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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GENOMIC DIVERSITY
BOTTLENECK
UPSTREAM-DOWNSTREAM GRADIENT
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EUTROPHIC GRADIENT
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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 ($\alpha \geq 0.1$). Covariations and paths removed during the simplification procedure are not displayed, for the sake of clarity.

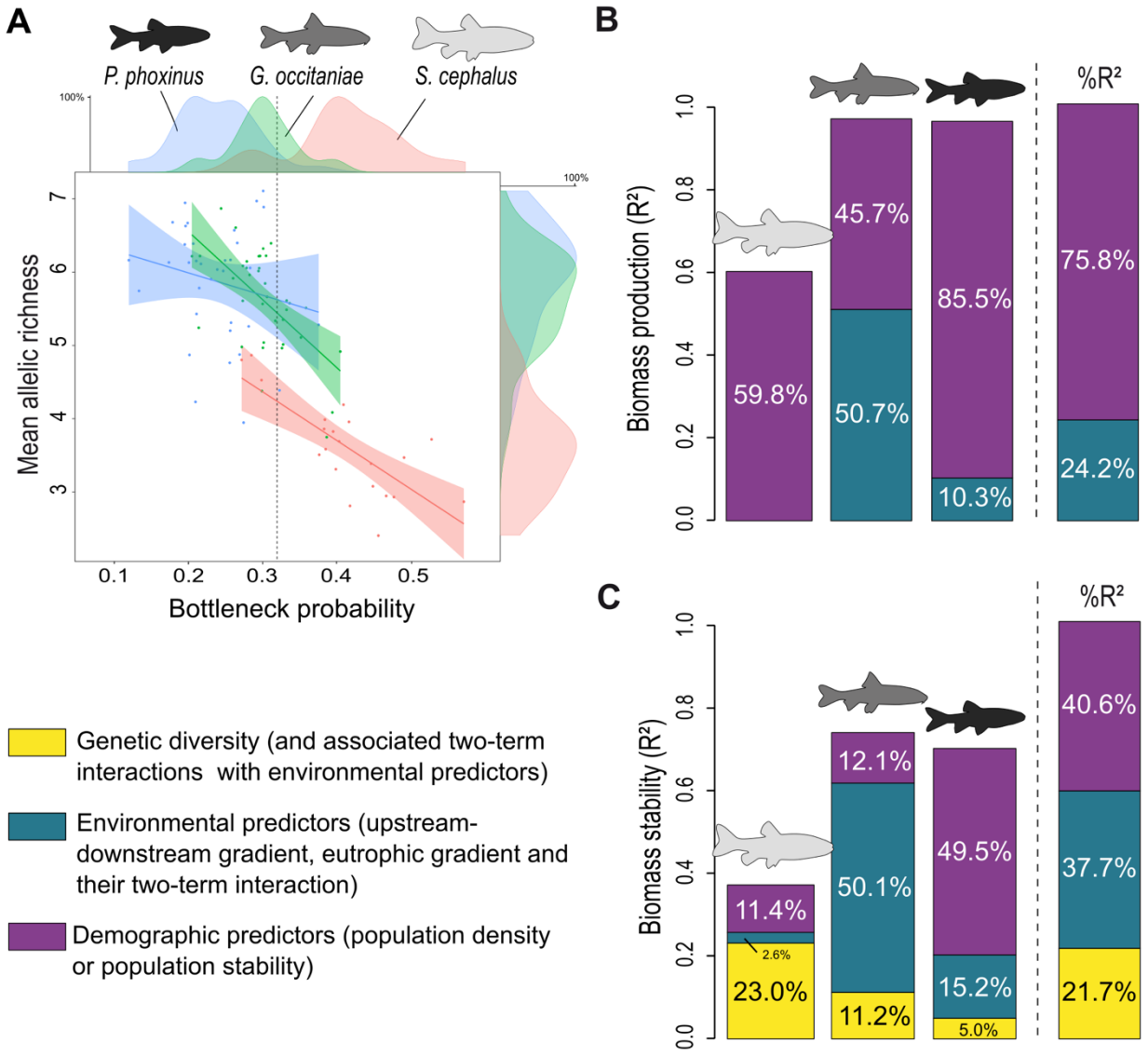

Figure 3. Panel A: Linear relationships between bottleneck probability and mean allelic richness (main plot) and kernel density estimates of bottleneck probabilities (top marginal plot) and of mean allelic richness data (right marginal plot) in each species. The vertical dashed line indicates the threshold above which populations are supposed to have experienced a significant bottleneck (probability > 0.32). Panel B and C: 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 (b) and temporal stability in biomass production (c) in

each species. The average contributions of each predictor to the explained variance in biomass variables across species is shown in the form of 100% stacked barplots (%R^2). Colors are the same as in Figure 2.

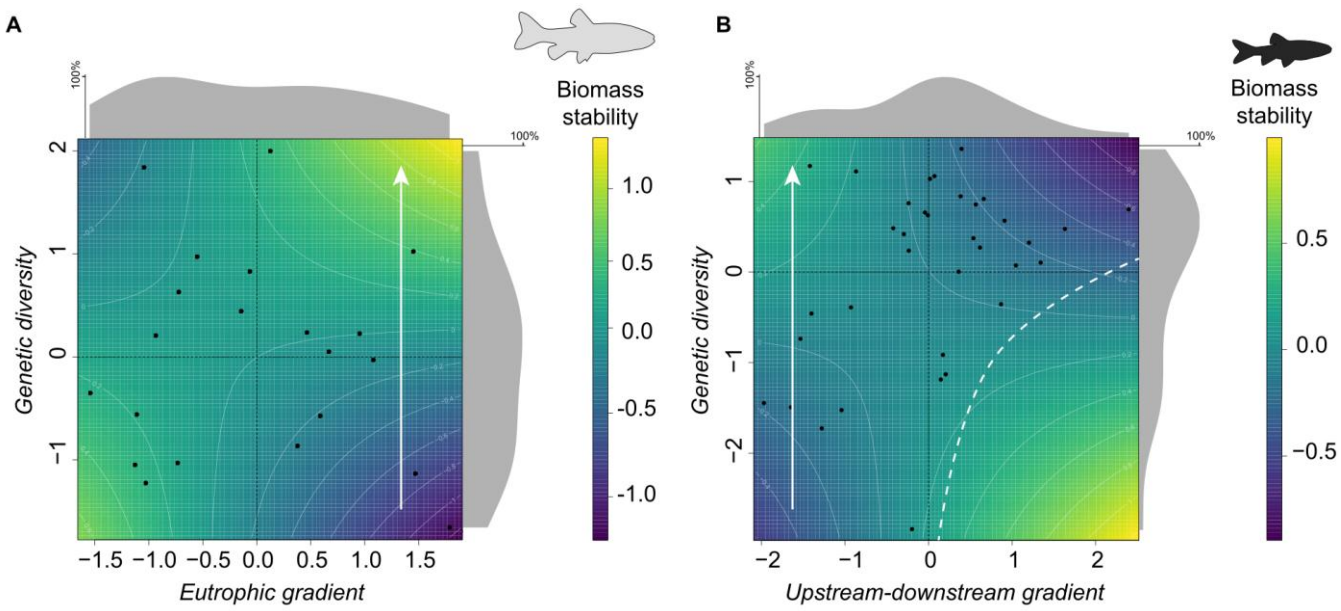

Figure 4. Continuous representations of first-order interactions associated with biomass stability in final simplified models in chubs (A) and minnows (B). Predicted values of biomass stability were computed across all possible values of the two corresponding additive terms and plotted as a colored surface 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 B. White arrows indicate noticeable trends. Biomass stability increased with genetic diversity in both species but mostly in eutrophic habitats in chubs (A) and in upstream populations in minnows (B).

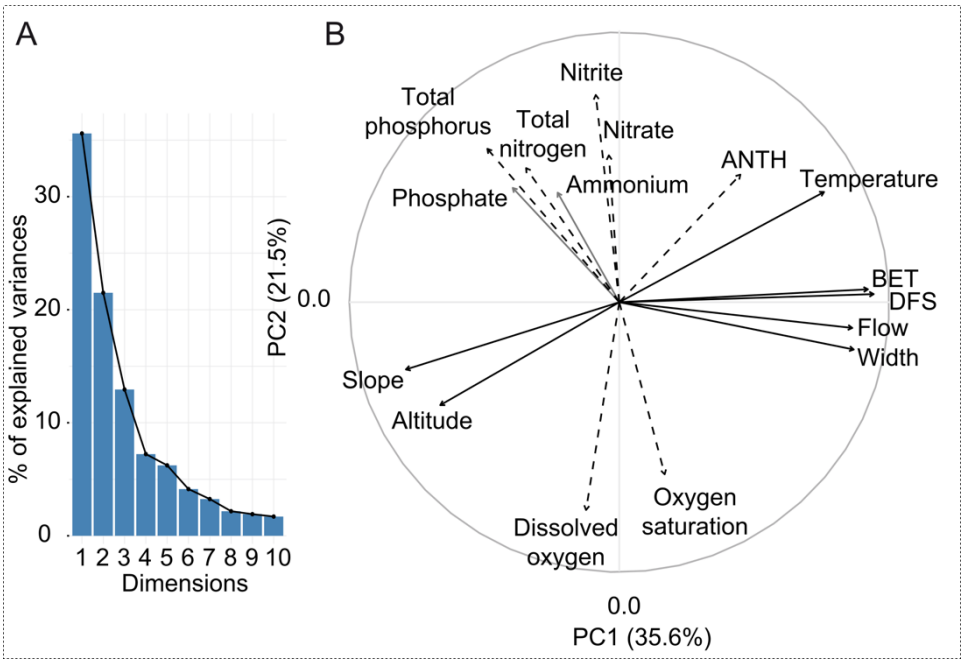

Figure 5. Characteristics of the two first principal components based on environmental data. Panel A: Eigenvalues corresponding to the amount of the variation explained by each principal component. Panel B: Visualization of the two first principal components (PC), with PC1 standing for the upstream-downstream 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). See Appendix S8 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; ***: $p < 0.01$; **: $p < 0.05$; *: $p < 0.1$.

		S. cephalus	*G. occitaniae*	*P. Phoxinus*
Model fit indices	χ^2 p-value	0.908	0.872	0.986
	CFI	1	1	1
	SRMR	0.037	0.081	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		/	/	-0.350 ***
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		/	-0.500 ***	-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	0.830	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 ***	-0.220 ***
Eutrophic gradient → Biomass production		/	-0.221 ***	-0.071
	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