

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

3

4 **Authors:**

5 Jérôme G. Prunier ^{1*}, Mathieu Chevalier ², Allan Raffard ¹, Géraldine Loot ³, Nicolas Poulet ⁴, Simon
6 Blanchet ^{1,3*}

7

8 **Affiliations :**

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

11 ² Department of Ecology and Evolution, University of Lausanne, Biophore, CH-1015 Lausanne,
12 Switzerland

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

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

16

17 *** Corresponding authors:**

18 Jérôme G. Prunier and Simon Blanchet

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

20 2 route du CNRS, 09200 Moulis

21 Phone: (+33)561040361

22

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

24

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

26

27

28 **Abstract**

29 Theory predicts that biodiversity is causally linked to key ecological functions such as biomass
30 productivity, and that loss in functional traits both among- and within-species can reduce the efficiency of
31 ecosystem functions. There has been ample empirical and experimental demonstration that species loss
32 indeed reduces the efficiency of ecosystem functions, with tremendous impacts on services provided by
33 biodiversity. Nonetheless, and despite the fact that within-species diversity is strongly altered by human
34 activities, there have been little attempts to empirically test (i) whether intraspecific genetic diversity
35 actually promotes productivity and stability in wild populations, and, (ii) if so, to quantify its relative
36 importance compared to other determinants. Capitalizing on 20-year demographic surveys in wild fish
37 populations, we show that genetic diversity does not increase mean biomass production in local
38 populations, but strongly and consistently stabilizes biomass production over time. Genetic diversity
39 accounts for about 20% of explained variance in biomass stability across species, an important
40 contribution about half that of environment and demography (about 40% each). Populations having
41 suffered from demographic bottlenecks in the recent past harbored lower levels of genetic diversity and
42 showed less stability in biomass production over the last 20 years. Our study demonstrates that the loss of
43 intraspecific genetic diversity can destabilize biomass productivity in natural vertebrate populations in just
44 a few generations, strengthening the importance for human societies to adopt prominent environmental
45 policies to favor all facets of biodiversity.

46

47 **Introduction**

48 There is now unequivocal evidence that biodiversity sustains critical ecosystem services that benefit
49 directly to humanity, such as water filtering, pollination and biomass production (1–3). By promoting trait
50 complementarity among species, interspecific diversity allows ecological communities to optimally capture
51 essential resources, transform those resources into biomass and recycle them (4–6). In species-rich
52 communities, these ecological processes are maintained even in the face of environmental variations,
53 thus promoting ecosystem productivity and stability over time (7–9): this is the insurance effect of species
54 richness (10). The drastic erosion in species diversity observed worldwide (11) is hence prejudicial, as it is
55 expected to deeply impair natural ecosystems' capacity to durably sustain human health and wellbeing (2,
56 3). However, the loss of species is only the tip of the iceberg. In most taxa, another form of biodiversity
57 erosion is indeed silently underway: the loss of intraspecific genetic diversity (12, 13).

58 Beyond its positive influence on individual fitness and evolutionary rescue (14), intraspecific genetic
59 diversity is expected to play a role similar to species diversity in driving key ecological functions such as
60 biomass production (15, 16). By promoting intraspecific phenotypic diversity (17, 18), genetic diversity
61 may indeed favor both the occurrence of highly productive phenotypes (19) and the functional
62 complementarity among individuals through spatial or temporal niche partitioning (6), thus fostering a
63 more efficient exploitation of available resources over time (2, 10). Genetically-diversified populations are
64 therefore predicted to have higher and more stable biomass production than genetically-impooverished
65 populations, notably under fluctuating or stressful environmental conditions (15, 16). This direct
66 relationship between genetic diversity and biomass is expected to be particularly strong in ecosystems
67 where species diversity is naturally low, which is actually the norm in many temperate ecosystems (20). In
68 such cases, the functioning of ecosystems probably depends more on the complementarity among
69 genotypes than on the complementarity among species (21–23), emphasizing the importance of
70 maintaining genetic diversity to preserve ecosystem functions and services (15).

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

75 scarce and mostly concern plants (24). Although these studies offer a number of advantages, experiments
76 do not allow spanning large spatial and temporal scales or to investigate the influence of historical
77 contingencies. Local levels of genetic diversity indeed result from the interplay between long-term
78 evolutionary trajectories (e.g., localization and size of glacial refugia (25)) and more recent -if not ongoing-
79 ecological processes affecting individual life history traits or population demography (e.g., stressful
80 environmental conditions (26), bottleneck events (27), or strong directional selection (28, 29)). This natural
81 complexity cannot be fully grasped by experimental studies (24). Observational field surveys are on the
82 contrary more realistic and may provide important insights into the contribution of genetic diversity, and
83 the loss of it, to biomass production and stability in natural settings, in accordance or in disagreement with
84 theoretical expectations and experimental findings (6, 15, 16). They yet raise several difficulties. First,
85 assessing the influence of genetic diversity on the stability of biomass production over several generations
86 or seasonal cycles implies long-term monitoring programs of both population density and biomass
87 production, but such data are usually difficult to collect and are still scarce. Furthermore, the relationships
88 between genetic diversity and biomass in across-population studies may be masked by the interplay with
89 other factors also involved in population productivity, such as population density and environmental
90 conditions, making it difficult to disentangle their respective contributions (6, 24). This last issue may
91 however be partly alleviated through the use of causal modeling procedures, making it possible to
92 thoroughly confront theoretical expectations and experimental findings with the “real world” (4, 30).

93 Capitalizing on long-term demographic surveys (up to 22 years) conducted in 47 rivers from a large
94 watershed (the Garonne-Dordogne water basin, South-Western France; Figure 1), we assessed the
95 relationship between genetic diversity and biomass production (mean biomass production and temporal
96 stability in biomass production) at the population level in three parapatric freshwater fish species: the chub
97 *Squalius cephalus*, the Languedoc gudgeon *Gobio occitaniae* and the minnow *Phoxinus phoxinus*. To that
98 aim, we designed a causal model depicting all the expected causal links between biomass variables,
99 genetic diversity and several environmental and demographic predictors. Rivers are characterized by
100 strong environmental gradients that we synthesized in the form of an upstream-downstream gradient and
101 an eutrophic gradient. The former is a critical feature known to shape spatial patterns of both genetic
102 diversity and biomass in dendritic networks (31, 32), whereas the latter may act as a possible stressor that

103 can affect both population dynamics and productivity (33). As local population dynamics may also
104 influence both genetic diversity and biomass, we considered several demographic covariates: mean
105 population density, long-term stability in population density and bottleneck probability, the latter indicating
106 past changes in effective population size (34). By building this causal model, we aimed to answer the
107 following questions: do the positive relationships found experimentally between intraspecific genetic
108 diversity and biomass production/stability hold true in natural settings? If any, is the contribution of genetic
109 diversity to biomass production/stability similar across species, and comparable in magnitude to that of
110 other environmental and demographic determinants? Finally, is it possible to detect the impact of the
111 ongoing genetic erosion, i.e., the loss of intraspecific genetic diversity in response to a recent reduction in
112 population size, on biomass production and stability? This latter point remains controversial but of high
113 concern: with an estimated 6% loss of intraspecific genetic diversity in wild organisms since the industrial
114 revolution (35), the impact of human-induced genetic erosion on natural ecosystems' capacity to provide
115 critical provisioning and regulating services to humanity may actually be much more important than
116 anticipated, making it a critical conservation issue.

117

118 **Materials and Methods**

119 **Study area and biological models**

120 The study was carried out in the Garonne-Dordogne river basin (South-Western France; Figure 1). We
121 selected 47 river sections evenly scattered across the whole basin to reflect the environmental variability
122 existing along the upstream–downstream gradient. All these sites are yearly monitored by the French
123 Agency for Biodiversity (AFB) since 1989 (36). Fish communities in this river basin are generally poorly
124 diverse (3 to 15 species in general (37)) and we focused on three of the most common species (38): the
125 Eurasian minnow *Phoxinus phoxinus*, the Languedoc gudgeon *Gobio occitaniae* and the chub *Squalius*
126 *cephalus*. These cypriniform fish species vary in their mean body length (minnows: 80–90 mm; gudgeons:
127 120–150 mm; chubs: 300–500 mm; (39)). They are all generalist species mainly feeding on invertebrates
128 (although chubs can also predate on small-bodied fish) but occupy different habitats (38): chubs are
129 primarily found in downstream sections at relatively low densities (~ 0.01 ind.m⁻²), minnows are primarily
130 found in upstream sections at relatively high densities (~ 0.10 ind.m⁻²), whereas gudgeons are found all
131 along the river basin in various habitats and at relatively high densities (~ 0.08 ind.m⁻²; (39, 40)).

132 **Demographic and biomass data**

133 Demographic and biomass data were extracted from the AFB databases (41). We only retained sites
134 monitored for 10 to 22 years (mean = 15.02) with a constant sampling effort. For each species, site and
135 year of survey, we collected the local fish density (number of individuals per m²) and the local fish
136 biomass, expressed in g.m⁻². For each species and each site, we computed the local population density
137 and the local biomass production as the mean of density and biomass values over years. Metrics of
138 density stability and biomass stability were both computed as the inverse of the squared coefficient of
139 variation of density (respectively, biomass) over years, following (42). All variables related to density
140 (population density and density stability) and biomass (biomass production and biomass stability) were
141 log-transformed before analyses to meet normality assumptions.

142 **Genetic data**

143 The 47 river stations were sampled once in 2014 with up to 30 adults from each species caught by
144 electrofishing, resulting in a set of 35, 37 and 21 sampled populations in minnows, gudgeons and chubs,

145 respectively. On the field, a small piece of pelvic fin was collected from each individual and was preserved
146 in 70% ethanol, before releasing fish in situ. Genomic DNA was extracted using a salt-extraction protocol
147 (43) and used to obtain, for each species, population-based allelic frequencies following a paired-end,
148 pool-seq procedure (44), as detailed in Appendix S2a. Read assembly, SNP calling and filtering (see
149 Appendix S2b for details) generated a total of 1244 SNPs in minnows, 1892 SNPs in gudgeons and 1847
150 SNPs in chubs. Genomic data were further completed with microsatellite genotypes (Appendix S1), with
151 17, 13 and 16 loci in minnows, gudgeons and chubs, respectively.

152 For each species and site, we computed a total of six metrics of genetic diversity. First, we used SNPs
153 allelic frequencies to compute two metrics in R (45): the expected level of heterozygosity across SNPs loci
154 (sHe) and the observed level of SNP polymorphism (sPo), computed as the number of non-fixed loci ($0 <$
155 $\text{allelic frequency} < 1$) divided by the total number of loci with non-missing data in a given population. We
156 then used microsatellite data to compute four additional metrics using the softwares GENETIX 4.3 (46)
157 and ADZE 1.0 (47): the expected (μHe) and observed (μHo) levels of heterozygosity across microsatellite
158 loci, the mean number of alleles per locus (μNam) and the standardized allelic richness (μAR) based on a
159 standardized sample size of 20.

160 To capture overall trends in species-specific patterns of genetic diversity and smooth possible
161 particularities of each metric (48), the six metrics of genetic diversity were compiled using a principal
162 component analysis (PCA). Only the first component was retained in each species, respectively
163 accounting for 75.7, 68.8 and 86 % of variance in genetic data in minnows, gudgeons and chubs,
164 respectively. In general, all variables equally contributed to the retained components, which were thus
165 considered as species-specific synthetic predictors for genetic diversity, with genetically impoverished
166 populations on the one hand (negative coordinates) and genetically diversified populations on the other
167 hand (positive coordinates; Appendix S6a). This synthetic predictor was highly correlated with mean allelic
168 richness in each species ($r > 0.9$).

169 As genetic data could not be collected over years, we also computed the M-ratio (34) to determine
170 whether sampled populations experienced recent demographic bottlenecks. The M-ratio is the ratio
171 between the number of observed alleles at a microsatellite locus and the allelic range of that locus, the
172 latter being supposed to decrease slower than the number of alleles during a demographic collapse. This

173 index ranges from 0 to 1: empirical M-ratio values lower than a critical value of 0.68 indicate significant
174 bottleneck (34). For each populations and each species, the M-ratio was computed for each microsatellite
175 locus and then averaged over loci following (49). We used $1-(M\text{-ratio})$ as a proxy for demographic
176 bottleneck probability.

177 **Environmental data**

178 Each site was described using 17 environmental variables susceptible to affect demography, biomass
179 and genetic diversity of fish populations. From the French Theoretical Hydrological Network (50), we
180 extracted seven variables related to river topography: distance from the mouth (in m), distance from the
181 source (in m), river width (in m), slope (in degrees), altitude (in m) and mean annual water flow (in $m^3.s^{-1}$).
182 Additionally, we computed the betweenness centrality index as a measure of local connectivity along
183 the dendritic network (ComplexNetGIS toolbox in ARCGIS; (51)). Nine other variables were related to
184 water quality and were obtained from the database of the Water Information System of the Adour Garonne
185 basin (<http://adour-garonne.eaufrance.fr>): Temperature (in °C), dissolved oxygen concentration (in $mg.L^{-1}$),
186 oxygen saturation (in %), concentrations (in $mg.L^{-1}$) in nitrogen compounds (total nitrogen N, ammonium
187 NH_4^+ , nitrates NO_3^- and nitrites NO_2^-) and concentrations in phosphorus compounds (total phosphorus P
188 and phosphate PO_4^{3-}). Only data from years 2012 to 2015 and from June to August were selected and
189 averaged over months and years. Older data, although incomplete, suggested that water quality remained
190 relatively stable over the considered period (Appendix S3). Except for a few sites that might be subject to
191 local water pollution resulting from phosphorus inputs, all sites showed good to very good water quality
192 according to the French implementation of the European Water Framework Directive 2000/60/EC
193 (Appendix S4). Using a database from the AFB (52), we further computed a quantitative index of
194 anthropogenic river alteration (ANTH) to describe observed hydrological, morphological and thermic
195 alterations resulting from human activities such as damming, channelization or urbanization (see Appendix
196 S5 for details and computation). This index theoretically ranges from 0 (no identified anthropogenic
197 alteration) to 1 (maximum alteration) but did not exceed 0.525 in our dataset, with a mean of 0.275.
198 Environmental variables were log-transformed to meet normality assumption when required.

199 The 17 environmental variables were synthetized using a PCA (Figure 5; Appendix S6b). The two first
200 components were retained, accounting for 58.5 % of the total variance in environmental variables. The

201 first component (37.2% of variance) stood for the upstream-downstream gradient, with altitude and slope
202 on the one hand (upstream stations with negative coordinates) and distance from the source,
203 betweenness, temperature, river width and flow regime on the other hand (downstream stations with
204 positive coordinates). The second component (21.3% of variance) stood for an eutrophic gradient, with
205 dissolved oxygen, oxygen saturation and distance from the river mouth on the one hand (nutrient-
206 impoverished and highly oxygenated river stations with negative coordinates) and total phosphorus, total
207 nitrogen, nitrates and nitrites on the other hand (nutrient-rich and poorly oxygenated stations with positive
208 coordinates). Ammonium and phosphate concentrations, as well as anthropogenic river alteration, did not
209 contribute substantially to any of the retained components.

210 **Statistical analyses**

211 For each species, genetic diversity and all variables related to environment (upstream-downstream
212 gradient and eutrophic gradient), demography (population density, density stability and bottleneck
213 probability) and biomass (biomass production and biomass stability) were standardized to z-scores. Our
214 objective was to investigate how genetic diversity might influence biomass production and stability in each
215 species, while accounting for the direct and indirect effects of demography and environment (30, 53). To
216 that aim, we designed a full causal model describing the expected direct and indirect links among all
217 variables (Appendix S7). We hypothesized that genetic diversity would directly promote biomass
218 production and biomass stability, either in an additive way, or in interaction with environmental variables.
219 Interactions were computed as the cross-product of genetic diversity with each environmental variable
220 (54). All other paths were used to control for the possible direct and indirect influence of other variables.
221 We notably hypothesized that mean population density and density stability would respectively affect
222 biomass production and biomass stability, both directly (biomass varying in proportion to density) and
223 indirectly, through pathways involving genetic diversity (low densities or low stability favoring genetic drift
224 (55)). Density stability was also expected to indirectly affect genetic diversity through demographic
225 bottlenecks: in the event of recent demographic collapse (in the 20 years preceding genetic sampling),
226 density stability should correlate negatively with the bottleneck probability, which is in turn expected to
227 decrease genetic diversity. Finally, we hypothesized that the environmental characteristics of river stations
228 (upstream-downstream gradient, eutrophic gradient and the corresponding first-order interaction

229 computed as their cross-product) would affect variations in biomass both directly (for instance through
230 higher intraspecific competition in harsh conditions) and indirectly, through pathways involving genetic
231 diversity (promoted for instance by higher proximity to glacial refugees or higher local connectivity (31))
232 and/or population dynamics (eutrophic conditions for instance leading to an increase in fish mortality or
233 oligotrophic conditions leading to an increase in competition for resources).

234 We then used a causal modeling procedure to infer actual causal relationships among variables.
235 Specifically, we used path analyses (56) with maximum likelihood estimation and 'Huber-White' robust
236 standard errors to assess, in each species, the validity of the full model and to simplify it when needed.
237 Model simplification was performed by removing non-significant paths one at a time, provided that cross-
238 products were always associated with their additive terms (57) and that removal led to an increase in the
239 relative fit of the model (i.e., a decrease in AIC score (58)). Simplification was stopped as soon as the
240 model reached a satisfactory absolute fit. Following Hu and Bentler (59), a model absolute fit was
241 considered as satisfactory when the standardized root mean square residual (SRMR) and the
242 Comparative Fit Index (CFI) were lower than ≤ 0.09 and higher than ≥ 0.96 , respectively. Additionally, we
243 checked that the p-value associated with the model χ^2 statistic, a classical fit index measuring the
244 magnitude of discrepancy between the sample and the fitted covariance matrices (59), was non-significant
245 ($p > 0.05$). To avoid model overfitting, we proceeded in two stages. In each species, we first considered a
246 subset of the full causal model excluding biomass variables and all related links, and performed model
247 simplification to get estimates for all important direct and indirect relationships among environmental
248 gradients, demographic variations and genetic diversity. Retained path coefficients, set to their mean
249 estimate, were subsequently considered as fixed parameters within the full causal model and a second set
250 of model simplification was performed to get estimates for all important direct and indirect relationships
251 pointing towards biomass variables. All path analyses were run using the R function lavaan (60).

252 For each response variable, we (a) computed the amount of variance (R^2) explained by the retained
253 model in each species. To assess the relative contribution of genetic diversity, demography and
254 environment to the variance in biomass variables, we computing R^2 from further simplified models with (b)
255 all variables related to density being discarded (amount of variance explained by both environment and
256 genetic diversity), then (c) with all variables related to genetic diversity (genetic diversity and associated

257 cross-products) being discarded (amount of variance explained by environment only). The relative
258 contributions of demography and genetic diversity to the variance in biomass variables were respectively
259 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
260 averaged these contributions across species and build 100% stacked barplots to illustrate the overall
261 contribution of genetic diversity, demography and environment to the total explained variance in each
262 biomass variable.

263 **Results**

264 Contrary to our predictions, we did not find evidence that genetic diversity is related to mean biomass
265 production at the local scale (Figure 2 and Figure 3B). We however demonstrate that, in the three
266 considered species, populations with higher levels of genetic diversity display higher biomass stability over
267 time than genetically-impovertished populations, sustaining the idea that intraspecific genetic diversity
268 stabilizes biomass production (Figure 2 and Figure 3C). The relative contribution of genetic diversity to the
269 overall explained variance in biomass stability across species was of 21.7%, a significant value about half
270 that of environmentally- and demographically-related variables (37.7% and 40.6% respectively; Figure
271 3C). This striking finding is supported by robust simplified causal models that correctly represent observed
272 data in each species (satisfactory absolute fit indices after model simplification; Tables 1 and 2; see
273 Appendix S8 for detailed results).

274 The contribution of genetic diversity to biomass stability was yet both species- and context-dependent.
275 It was the highest in the chub, genetic diversity accounting for 23% of the total variance in biomass
276 stability, a contribution twice higher than that of demography (11.3%) and much higher than that of
277 environment (2.6%). The retained interaction between the eutrophic gradient and genetic diversity in this
278 species, though marginally significant (probably because of a low sample size; $n = 21$, $\beta = 0.292$, $p =$
279 0.085 ; $\Delta AIC = +0.55$ when removed from the model) indicates that biomass stability increases with genetic
280 diversity, though mainly in the most eutrophic (i.e. stressful) habitats (Figure 2A and 4A). In the
281 Languedoc gudgeon, the contribution of genetic diversity to biomass stability (11.2%) was comparable to
282 that of demography (12.1%) but lower than that of the environment (50.1%). In this species, biomass
283 stability increases with increasing levels of genetic diversity ($n = 37$, $\beta = 0.198$, $p = 0.006$). It also
284 increases upstreamward but decreases with eutrophication. The contribution of genetic diversity to
285 biomass stability was the lowest in the minnow (5%), environment and demography accounting for 15.2%
286 and 49.5% of variance in biomass stability, respectively. The retained interaction between the upstream-
287 downstream gradient and genetic diversity ($n = 35$, $\beta = -0.188$, $p = 0.023$) is characterized by an uneven
288 distribution of populations within the parameter space, with no genetically impoverished populations in the
289 downstream part of the basin (Figure 4B). As a result, biomass stability in minnows actually slightly

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

292 These idiosyncrasies in the contribution of intraspecific diversity to biomass stability may be related to
293 the evolutionary history of each species within the basin, as indicated by the systematic negative
294 relationships between bottleneck probability and genetic diversity in all three species (Figure 2 and Figure
295 3A). In minnows, the species with the lowest contribution of genetic diversity to biomass stability,
296 monitored populations showed high levels of genetic diversity (e.g., 5.9 ± 0.8 alleles per microsatellite
297 locus on average) and only 5.7% of them experienced a significant bottleneck. On the contrary, low levels
298 of genetic diversity (3.6 ± 0.6 alleles per locus) and a high proportion of populations having experienced a
299 significant bottleneck (85.7%) indicate that chubs, the species with the highest genetic contribution to
300 biomass stability, suffered from strong genetic erosion in the past. Finally, only in gudgeon populations did
301 we find a significant negative link between population stability (as measured over about 20 years) and
302 bottleneck probability (Figure 2B). Together with a moderate proportion of populations having experienced
303 a significant bottleneck (29.7%) and high levels of genetic diversity (as high as in minnows; 5.6 ± 0.7
304 alleles per locus; $F_{(1,70)} = 2.35$, $p = 0.13$), these results reveal signs of incipient genetic erosion in
305 gudgeons.

306 In addition to revealing the consistent contribution of genetic diversity, or the loss of it, to biomass
307 stability, our modeling framework allowed identifying other recurrent and theoretically-grounded
308 relationships between variables indicating that our simplified causal models were biologically sound (see
309 Appendices S9 and S10 for graphical outputs and related discussion). As expected, biomass production
310 and biomass stability were always positively linked to their demographic counterparts (i.e., population
311 density and population stability, respectively; Figure 2), explaining from 11.4% to 85.5 % of the variance in
312 biomass variables (Figure 3B-C). Similarly, we found a systematic downstream increase in genetic
313 diversity, although this pattern only held true in oligotrophic conditions in the case of minnows (Appendix
314 S10). We finally identified several significant paths linking environment gradients to population dynamics
315 and biomass variables. For instance, population density was found to increase downstreamward in chubs
316 but upstreamward in gudgeons. Density stability and biomass production were found to decrease

317 downstreamward and biomass stability to decrease with eutrophication in both minnows and gudgeons
318 (Figure 2).

319 **Discussion**

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

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

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

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

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

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

393

394 **Acknowledgments**

395 We warmly thank all the colleagues and students who helped with field sampling. We are also grateful to
396 J. Côte and J. Canal for respectively providing insightful details and explanations about the AFB database
397 and about the ecological state of studied rivers in regard of the French implementation of the European
398 Water Framework Directive 2000/60/EC. This work has been financially supported by grants to SB from
399 the Agence Française pour la Biodiversité (AFB).

400

401 **References**

- 402 1. B. Worm, *et al.*, Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science* **314**, 787–790
403 (2006).
- 404 2. B. J. Cardinale, *et al.*, Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67 (2012).
- 405 3. G. M. Mace, K. Norris, A. H. Fitter, Biodiversity and ecosystem services: a multilayered relationship.
406 **27**, 8 (2012).
- 407 4. L. De Meester, *et al.*, Analysing eco-evolutionary dynamics—The challenging complexity of the real
408 world. *Functional Ecology* **33**, 43–59 (2019).
- 409 5. A. Hector, The Effect of Diversity on Productivity: Detecting the Role of Species Complementarity.
410 *Oikos* **82**, 597 (1998).
- 411 6. M. Loreau, Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3–17
412 (2000).
- 413 7. J. E. Duffy, C. M. Godwin, B. J. Cardinale, Biodiversity effects in the wild are common and as strong
414 as key drivers of productivity. *Nature* **549**, 261–264 (2017).
- 415 8. K. Gross, *et al.*, Species Richness and the Temporal Stability of Biomass Production: A New
416 Analysis of Recent Biodiversity Experiments. *The American Naturalist* **183**, 1–12 (2014).
- 417 9. D. U. Hooper, *et al.*, Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current
418 Knowledge. *Ecological Monographs* **75**, 3–35 (2005).
- 419 10. S. Yachi, M. Loreau, Biodiversity and ecosystem productivity in a fluctuating environment: The
420 insurance hypothesis. *Proceedings of the National Academy of Sciences* **96**, 1463–1468 (1999).
- 421 11. A. D. Barnosky, *et al.*, Has the Earth’s sixth mass extinction already arrived? *Nature* **471**, 51–57
422 (2011).
- 423 12. D. Spielman, B. W. Brook, R. Frankham, Most species are not driven to extinction before genetic
424 factors impact them. *Proceedings of the National Academy of Sciences* **101**, 15261–15264 (2004).
- 425 13. R. Frankham, Genetics and extinction. *Biological Conservation* **126**, 131–140 (2005).
- 426 14. D. H. Reed, R. Frankham, Correlation between fitness and genetic diversity. *Conservation Biology*
427 **17**, 230–237 (2003).

- 428 15. A. R. Hughes, B. D. Inouye, M. T. J. Johnson, N. Underwood, M. Vellend, Ecological consequences
429 of genetic diversity. *Ecology Letters* **11**, 609–623 (2008).
- 430 16. A. Forsman, L. Wennersten, Inter-individual variation promotes ecological success of populations
431 and species: evidence from experimental and comparative studies. *Ecography* **39**, 630–648 (2016).
- 432 17. S. M. Evans, E. A. Sinclair, A. G. B. Poore, K. F. Bain, A. Vergés, Genotypic richness predicts
433 phenotypic variation in an endangered clonal plant. *PeerJ* **4**, e1633 (2016).
- 434 18. D. I. Bolnick, *et al.*, Why intraspecific trait variation matters in community ecology. *Trends in Ecology*
435 *& Evolution* **26**, 183–192 (2011).
- 436 19. D. Tilman, C. L. Lehman, K. T. Thomson, Plant diversity and ecosystem productivity: Theoretical
437 considerations. *Proceedings of the National Academy of Sciences* **94**, 1857–1861 (1997).
- 438 20. D. M. Olson, *et al.*, Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience* **51**,
439 933 (2001).
- 440 21. T. B. H. Reusch, A. Ehlers, A. Hammerli, B. Worm, Ecosystem recovery after climatic extremes
441 enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences* **102**, 2826–2831
442 (2005).
- 443 22. A. Siefert, *et al.*, A global meta-analysis of the relative extent of intraspecific trait variation in plant
444 communities. *Ecol Lett* **18**, 1406–1419 (2015).
- 445 23. M. Vellend, M. A. Geber, Connections between species diversity and genetic diversity. *Ecology*
446 *Letters* **8**, 767–781 (2005).
- 447 24. A. P. Hendry, A critique for eco-evolutionary dynamics. *Functional Ecology* **33**, 84–94 (2019).
- 448 25. R. J. Petit, Glacial Refugia: Hotspots But Not Melting Pots of Genetic Diversity. *Science* **300**, 1563–
449 1565 (2003).
- 450 26. E. Bestion, *et al.*, Altered trophic interactions in warming climates: consequences for predator diet
451 breadth and fitness. *Proc. R. Soc. B* **286**, 20192227 (2019).
- 452 27. M. Jangjoo, S. F. Matter, J. Roland, N. Keyghobadi, Connectivity rescues genetic diversity after a
453 demographic bottleneck in a butterfly population network. *Proceedings of the National Academy of*
454 *Sciences* **113**, 10914–10919 (2016).

- 455 28. D. W. Coltman, *et al.*, Undesirable evolutionary consequences of trophy hunting. *Nature* **426**, 655–
456 658 (2003).
- 457 29. E. P. Palkovacs, M. M. Moritsch, G. M. Contolini, F. Pelletier, Ecology of harvest-driven trait changes
458 and implications for ecosystem management. *Front Ecol Environ* **16**, 20–28 (2018).
- 459 30. J. E. Duffy, J. S. Lefcheck, R. D. Stuart-Smith, S. A. Navarrete, G. J. Edgar, Biodiversity enhances
460 reef fish biomass and resistance to climate change. *Proceedings of the National Academy of*
461 *Sciences* **113**, 6230–6235 (2016).
- 462 31. I. Paz-Vinas, G. Loot, V. M. Stevens, S. Blanchet, Evolutionary processes driving spatial patterns of
463 intraspecific genetic diversity in river ecosystems. *Molecular Ecology* **24**, 4586–4604 (2015).
- 464 32. P. M. Kiffney, C. M. Greene, J. E. Hall, J. R. Davies, Tributary streams create spatial discontinuities
465 in habitat, biological productivity, and diversity in mainstem rivers. *Can. J. Fish. Aquat. Sci.* **63**,
466 2518–2530 (2006).
- 467 33. V. H. Smith, G. D. Tilman, J. C. Nekola, Eutrophication: impacts of excess nutrient inputs on
468 freshwater, marine, and terrestrial ecosystems. *Environmental Pollution* **100**, 179–196 (1999).
- 469 34. J. C. Garza, E. G. Williamson, Detection of reduction in population size using data from
470 microsatellite loci. *Molecular Ecology* **10**, 305–318 (2001).
- 471 35. D. M. Leigh, A. P. Hendry, E. Vázquez-Domínguez, V. L. Friesen, Estimated six per cent loss of
472 genetic variation in wild populations since the industrial revolution. *Evol Appl*, eva.12810 (2019).
- 473 36. N. Poulet, L. Beaulaton, S. Dembski, Time trends in fish populations in metropolitan France: insights
474 from national monitoring data. *Journal of Fish Biology* **79**, 1436–1452 (2011).
- 475 37. S. Blanchet, M. R. Helmus, S. Brosse, G. Grenouillet, Regional vs local drivers of phylogenetic and
476 species diversity in stream fish communities. *Freshw Biol* **59**, 450–462 (2014).
- 477 38. L. Fournet, I. Paz-Vinas, G. Loot, J. G. Prunier, S. Blanchet, Lessons from the fish: a multi-species
478 analysis reveals common processes underlying similar species-genetic diversity correlations.
479 *Freshwater Biology* **61**, 1830–1845 (2016).
- 480 39. P. Keith, H. Persat, E. Feunteun, B. Adam, M. Geniez, *Les Poissons d'eau douce de France*,
481 Muséum National d'Histoire Naturelle and Publications Biotope (2011).

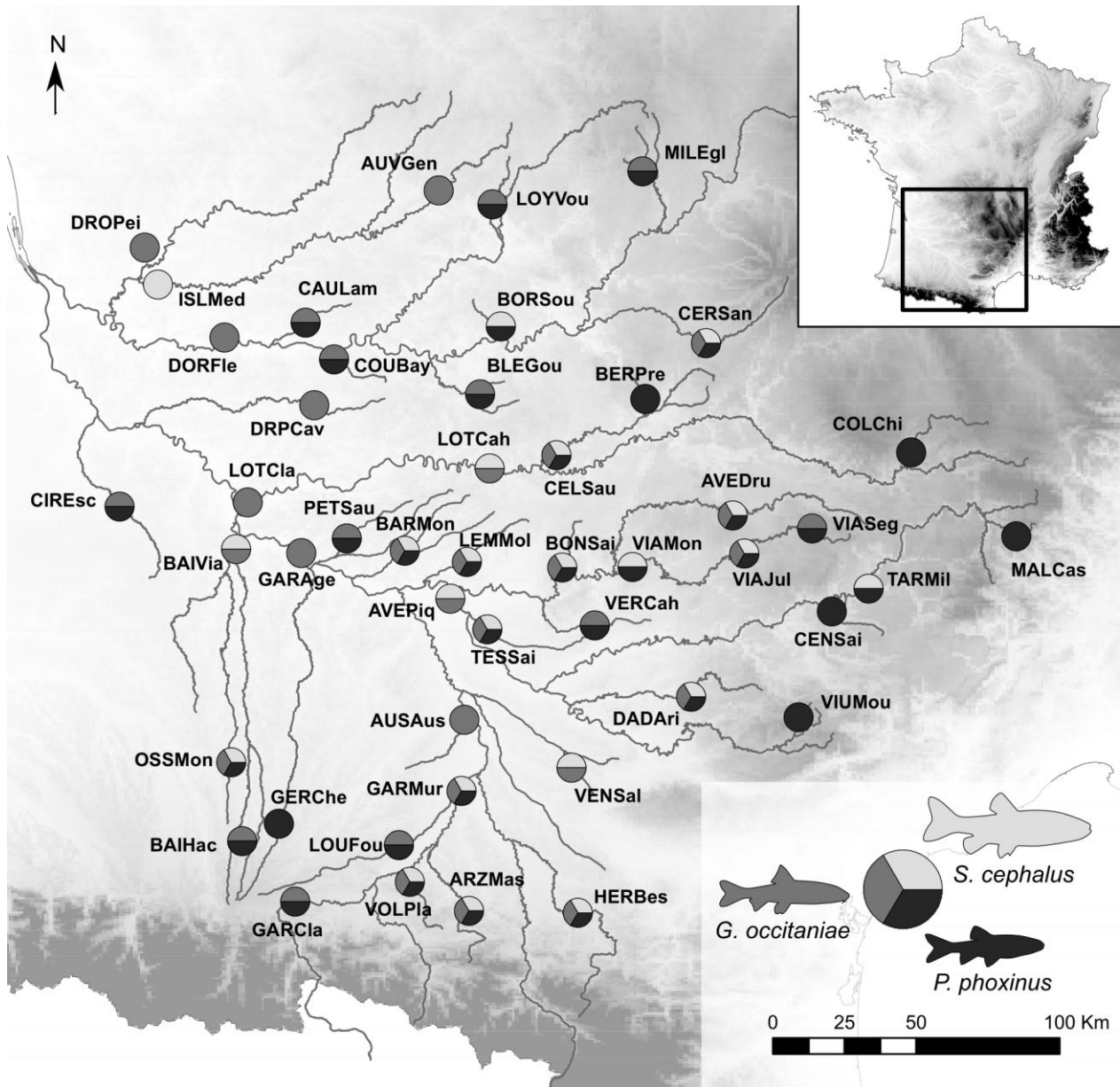
- 482 40. L. Buisson, L. Blanc, G. Grenouillet, Modelling stream fish species distribution in a river network: the
483 relative effects of temperature versus physical factors. *Ecol Freshwater Fish* **17**, 244–257 (2008).
- 484 41. M. Chevalier, L. Comte, P. Laffaille, G. Grenouillet, Interactions between species attributes explain
485 population dynamics in stream fishes under changing climate. *Ecosphere* **9**, e02061 (2018).
- 486 42. B. Haegeman, *et al.*, “Resilience, invariability, and ecological stability across levels of organization”
487 (Ecology, 2016) <https://doi.org/10.1101/085852> (April 25, 2019).
- 488 43. S. M. Aljanabi, I. Martinez, Universal and rapid salt-extraction of high quality genomic DNA for PCR-
489 based techniques. *Nucleic acids research* **25**, 4692–4693 (1997).
- 490 44. A. Futschik, C. Schlotterer, The Next Generation of Molecular Markers From Massively Parallel
491 Sequencing of Pooled DNA Samples. *Genetics* **186**, 207–218 (2010).
- 492 45. R Development Core Team, *R: A Language and Environment for Statistical Computing*, R
493 *Foundation for Statistical Computing* (2014).
- 494 46. K. Belkhir, P. Borsa, L. Chikhi, N. Raufaste, F. Bonhomme, *GENETIX 4.03, logiciel sous*
495 *Windows™ pour la génétique des populations. Laboratoire Génome, Populations, Interactions*
496 *CNRS UMR 5000, Université de Montpellier II, Montpellier (France)*. (2004).
- 497 47. Z. A. Szpiech, M. Jakobsson, N. A. Rosenberg, ADZE: A rarefaction approach for counting alleles
498 private to combinations of populations. *Bioinformatics* **24**, 2498–2504 (2008).
- 499 48. A. R. Hughes, J. J. Stachowicz, Ecological impacts of genotypic diversity in the clonal seagrass
500 *Zostera marina*. *Ecology* **90**, 1412–1419 (2009).
- 501 49. E. Mathieu-Bégné, G. Loot, M. Chevalier, I. Paz-Vinas, S. Blanchet, Demographic and genetic
502 collapses in spatially structured populations: insights from a long-term survey in wild fish
503 metapopulations. *Oikos* **128**, 196–207 (2019).
- 504 50. H. Pella, J. Lejot, N. Lamouroux, T. Snelder, Le réseau hydrographique théorique (RHT) français et
505 ses attributs environnementaux. *Géomorphologie : relief, processus, environnement* **3** (2012).
- 506 51. S. Caschili, “ComplexNetGIS: a tool for the analysis of complex spatial networks” in *Informatica e*
507 *Pianificazione Urbana e Territoriale*, G. Las Casas, P. Potrandolfi, B. Murgante, Eds. (Melfi, 2010),
508 pp. 233–242.

- 509 52. D. Pont, O. Delaigue, J. Belliard, A. Marzin, M. Logez, “Programme IPR+ : révision de l’indice
510 poisson rivière pour l’application de la DCE - version V.2.0 de l’indicateur.” (IRSTEA-ONEMA, 2013).
- 511 53. J. Oehri, B. Schmid, G. Schaepman-Strub, P. A. Niklaus, Biodiversity promotes primary productivity
512 and growing season lengthening at the landscape scale. *Proceedings of the National Academy of*
513 *Sciences* **114**, 10160–10165 (2017).
- 514 54. L. S. Aiken, S. G. West, R. R. Reno, *Multiple regression: Testing and interpreting interactions*
515 (SAGE Publications, 1991).
- 516 55. F. W. Allendorf, Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology* **5**, 181–190
517 (1986).
- 518 56. J. B. Grace, *Structural equation modelling and natural systems*. (Cambridge University Press, 2006).
- 519 57. J. M. Batista-Foguet, G. Coenders, W. E. Saris, J. Bisbe, Simultaneous Estimation of Indirect and
520 Interaction Effects using Structural Equation Models. *Metodološki zvezki* **1**, 163–184 (2004).
- 521 58. K. P. Burnham, D. R. Anderson, *Model selection and multimodel inference: a practical information-*
522 *theoretic approach*, 2nd ed (Springer, 2002).
- 523 59. L. Hu, P. M. Bentler, Cutoff criteria for fit indexes in covariance structure analysis: Conventional
524 criteria versus new alternatives. *Structural Equation Modeling: A Multidisciplinary Journal* **6**, 1–55
525 (1999).
- 526 60. Y. Rosseel, **lavaan** : An R Package for Structural Equation Modeling. *Journal of Statistical Software*
527 **48** (2012).
- 528 61. A. Raffard, F. Santoul, J. Cucherousset, S. Blanchet, The community and ecosystem consequences
529 of intraspecific diversity: a meta-analysis: The ecological effects of intraspecific diversity. *Biological*
530 *Reviews* doi: **10.1111/brv.12472** (2019).
- 531 62. S. Nakano, M. Murakami, Reciprocal subsidies: Dynamic interdependence between terrestrial and
532 aquatic food webs. *Proceedings of the National Academy of Sciences* **98**, 166–170 (2001).
- 533 63. C. Liu, Y. Chen, J. R. Britton, Influences of environmental and chemical parameters on the spatial
534 growth patterns of four riverine cyprinid fishes. *Knowl. Manag. Aquat. Ecosyst.*, 12 (2015).
- 535 64. S. M. Adams, *et al.*, The use of bioindicators for assessing the effects of pollutant stress on fish.
536 *Marine Environmental Research* **28**, 459–464 (1989).

- 537 65. M. S. Pollock, L. M. J. Clarke, M. G. Dubé, The effects of hypoxia on fishes: from ecological
538 relevance to physiological effects. *Environ. Rev.* **15**, 1–14 (2007).
- 539 66. A. Miraldo, *et al.*, An Anthropocene map of genetic diversity. *Science* **353**, 1532–1535 (2016).
- 540 67. M. Nei, T. Maruyama, R. Chakraborty, The Bottleneck Effect and Genetic Variability in Populations.
541 *Evolution* **29**, 1 (1975).
- 542 68. M. L. Pinsky, S. R. Palumbi, Meta-analysis reveals lower genetic diversity in overfished populations.
543 *Molecular Ecology* **23**, 29–39 (2014).
- 544 69. O. Honnay, H. Jacquemyn, Susceptibility of Common and Rare Plant Species to the Genetic
545 Consequences of Habitat Fragmentation. *Conservation Biology* **21**, 823–831 (2007).
- 546 70. I. Paz-Vinas, *et al.*, Systematic conservation planning for intraspecific genetic diversity. *Proceedings*
547 *of the Royal Society B: Biological Sciences* **285**, 20172746 (2018).
- 548 71. W. J. Ripple, *et al.*, World Scientists' Warning to Humanity: A Second Notice. *BioScience* **67**, 1026–
549 1028 (2017).
- 550 72. O. Rey, *et al.*, Linking epigenetics and biological conservation: Toward a *conservation epigenetics*
551 perspective. *Funct Ecol*, 1365-2435.13429 (2019).
- 552

553 **Figures and Tables**

554

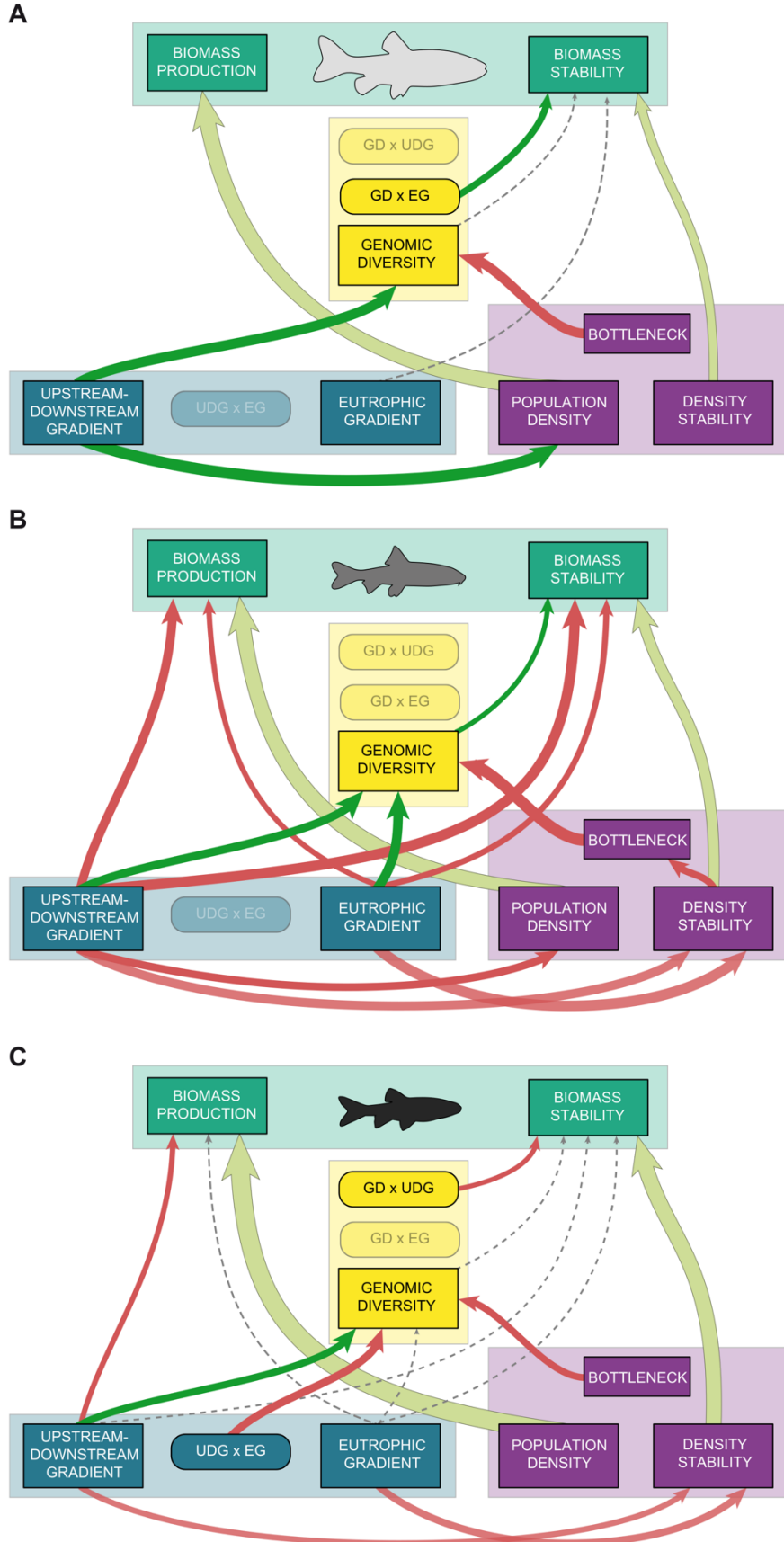


555

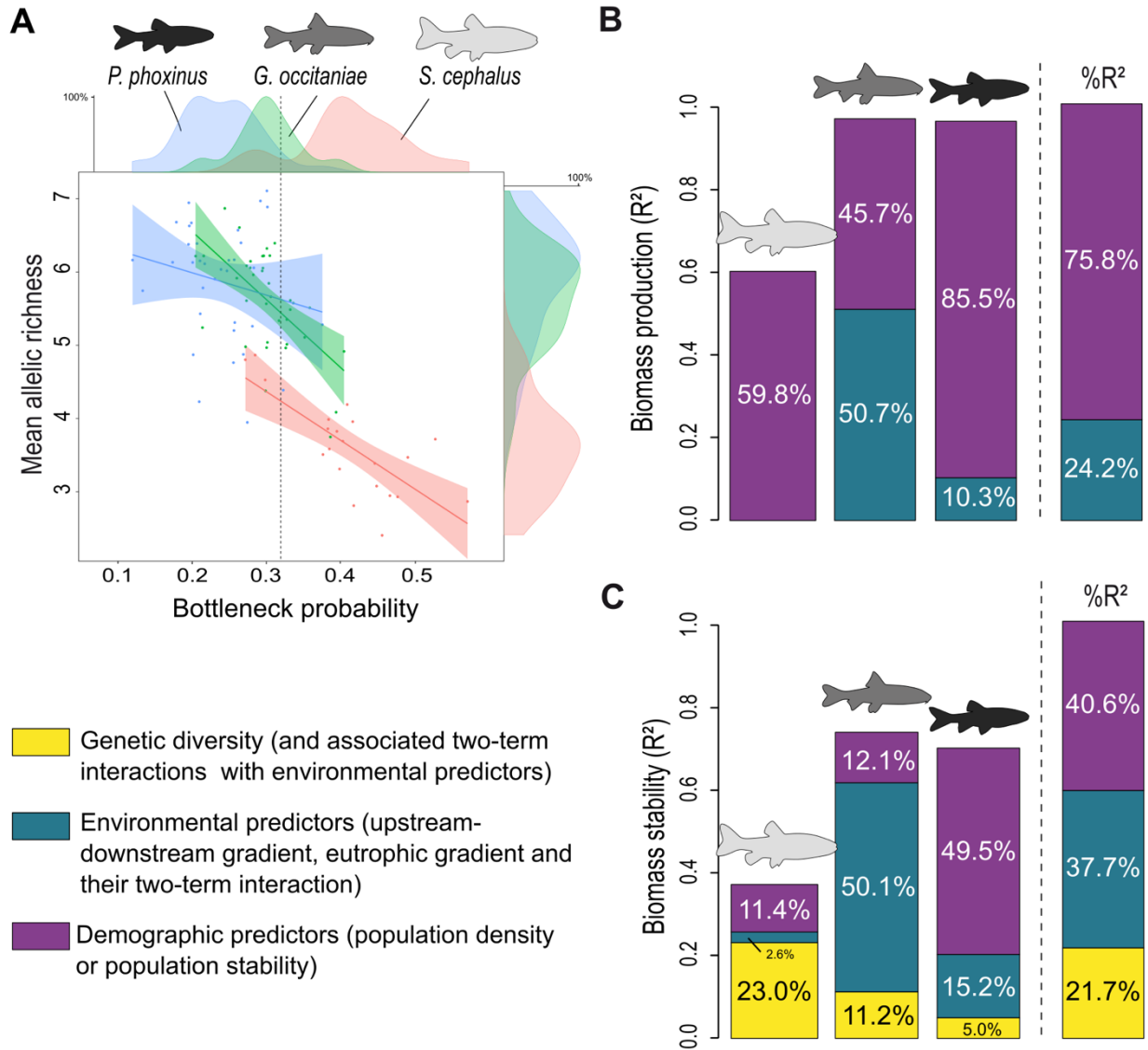
556 **Figure 1.** Geographic situation of the Garonne-Dordogne river basin in South-Western France and
557 localization of the 47 unique river stations, with pie charts indicating species (co-)occurrence within each
558 station. The black arrow indicates the location of the river mouth. Background is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

559

560



562 **Figure 2.** Simplified causal graphs depicting retained links among environmental (blue rectangles),
563 demographic (purple rectangles), genetic (yellow rectangles) and biomass variables (green rectangles) in
564 chubs (A), gudgeons (B) and minnows (C). First-order interactions are represented by rounded rectangles
565 (washed-out when not involved in any causal link). Red and green arrows represent negative and positive
566 significant paths, respectively, with the width of arrows proportional to the absolute value of the
567 corresponding path coefficient. Washed-out green arrows stand for direct positive links between density
568 and biomass variables. Dashed grey arrows represent non-significant paths ($\alpha \geq 0.1$). Covariations and
569 paths removed during the simplification procedure are not displayed, for the sake of clarity.
570
571

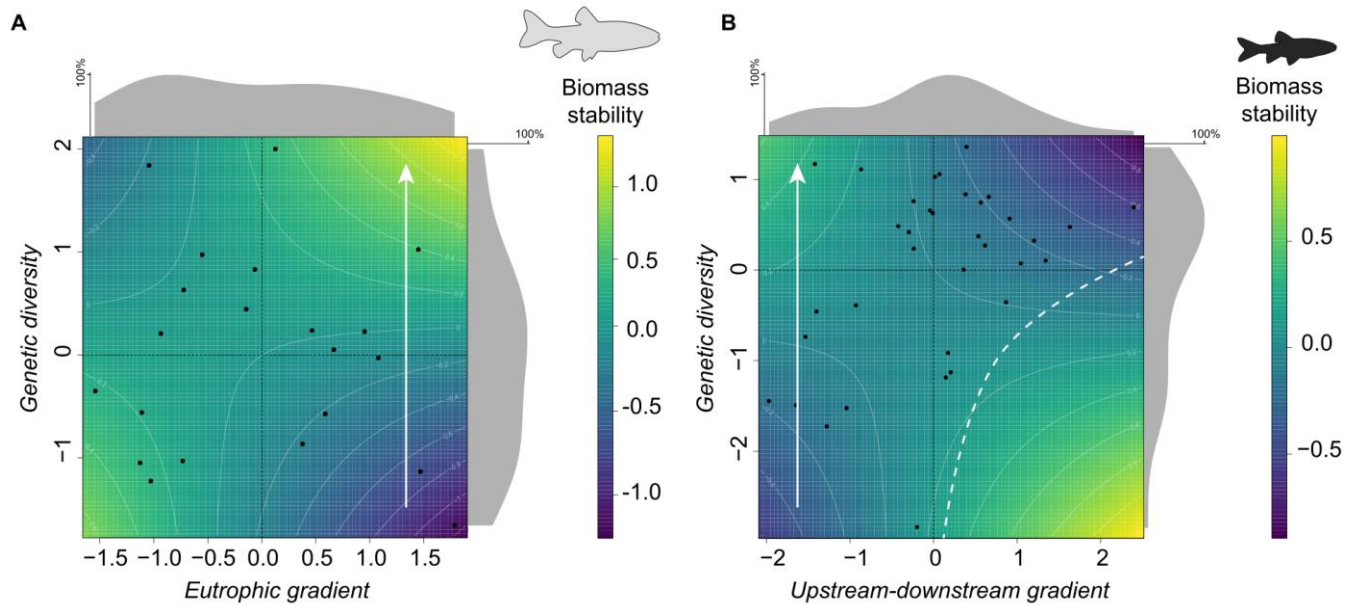


572

573

574 **Figure 3.** Panel A: Linear relationships between bottleneck probability and mean allelic richness (main
 575 plot) and kernel density estimates of bottleneck probabilities (top marginal plot) and of mean allelic
 576 richness data (right marginal plot) in each species. The vertical dashed line indicates the threshold above
 577 which populations are supposed to have experienced a significant bottleneck (probability > 0.32). Panel B
 578 and C: Contributions of demographic variables (mean density and density stability), environmental
 579 gradients (upstream-downstream gradient and eutrophic gradient) and genetic diversity (genetic diversity
 580 and associated interactions) to biomass production (b) and temporal stability in biomass production (c) in

581 each species. The average contributions of each predictor to the explained variance in biomass variables
582 across species is shown in the form of 100% stacked barplots (%R²). Colors are the same as in Figure 2.



583

584

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

595

596
597
598
599
600
601
602
603
604
605
606
607
608
609
610
611
612
613
614
615
616
617
618
619

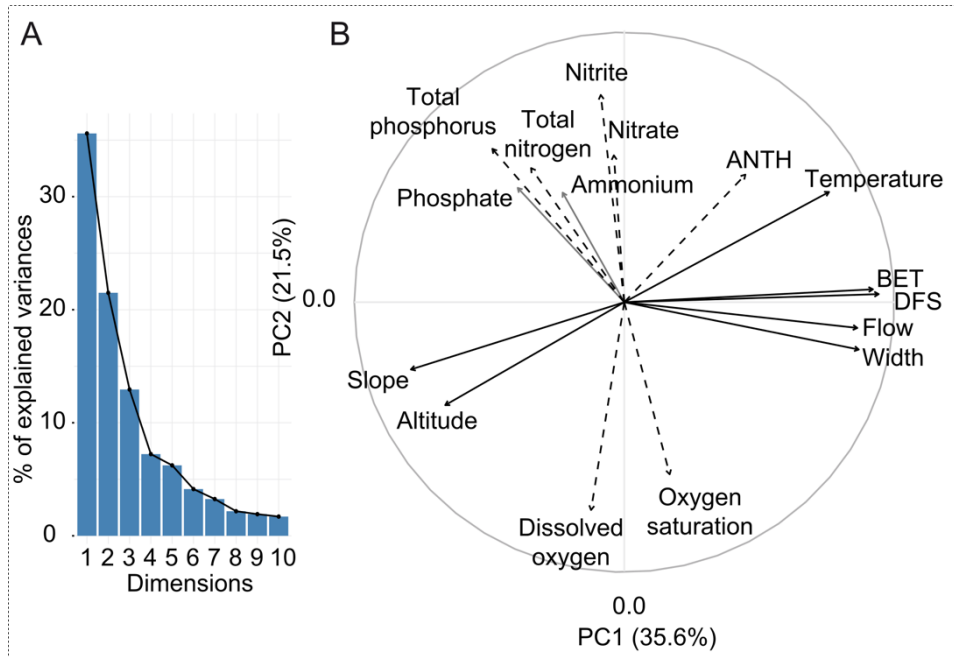


Figure 5. Characteristics of the two first principal components based on environmental data. Panel A: Eigenvalues corresponding to the amount of the variation explained by each principal component. Panel B: Visualization of the two first principal components (PC), with PC1 standing for the upstream-downstream 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.

620 **Table 1.** Main results from the first set of causal models, excluding biomass variables. For each species,
 621 the table provides absolute fit indices (CFI, SRMR and p-value; see text for details), amounts of explained
 622 variance (R^2) in response variables (indicated with an arrow) and estimates of path coefficients (indicated
 623 by arrows). See Appendix S8 for a table with 95% confidence intervals. Slashes indicate links that were
 624 discarded in the course of model simplification. Only links retained in at least one species are shown.
 625 UDG: upstream-downstream gradient; EG: Eutrophic gradient; ***: $p < 0.01$; **: $p < 0.05$; *: $p < 0.1$.

626

| | | <i>S. cephalus</i> | <i>G. occitaniae</i> | <i>P. Phoxinus</i> |
|--------------------------------------------------|------------------|--------------------|----------------------|--------------------|
| | χ^2 p-value | 0.908 | 0.872 | 0.986 |
| Model fit indices | 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 |

627

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

630

| | | <i>S. cephalus</i> | <i>G. occitaniae</i> | <i>P. Phoxinus</i> |
|---------------------------------------------------|------------------|--------------------|----------------------|--------------------|
| | χ^2 p-value | 0.830 | 0.957 | 0.119 |
| Model fit indices | 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 |

631