Intraspecific diversity loss in a predator species alters prey community structure and ecosystem functions

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Abstract

Loss in intraspecific diversity can alter ecosystem functions, but the underlying mechanisms are still elusive, and intraspecific biodiversity-ecosystem function relationships (iBEFs) have been restrained to primary producers. Here, we manipulated genetic and functional richness of a fish consumer (*Phoxinus phoxinus*), to test whether iBEFs exist in consumer species, and whether they are more likely sustained by genetic or functional richness. We found that both genotypic and functional richness affected ecosystem functioning, either independently or in interaction. Loss in genotypic richness reduced benthic invertebrate diversity consistently across functional richness treatments, whereas it reduced zooplankton diversity only when functional richness was high. Finally, both losses in genotypic and functional richness altered essential functions (e.g. decomposition) through trophic cascades. We concluded that iBEFs lead to substantial top-down effects on entire food chains. The loss of genotypic richness was similarly prejudicial than the loss of functional richness, probably because it sustains "cryptic" functional diversity.

42 **Introduction**

43 Human disturbances associated with global change are increasingly altering
44 worldwide patterns of species diversity, as well the functions and services provided by
45 ecosystems (Parmesan 2006; Naeem *et al.* 2009; Isbell *et al.* 2017). Nonetheless changes
46 observed at the species and ecosystem levels are always preceded by changes in phenotypic
47 and genotypic composition within plant and animal populations (Clements & Ozgul 2016;
48 Clements *et al.* 2017; Baruah *et al.* 2019). Accordingly, extremely rapid changes in
49 intraspecific diversity are currently occurring worldwide (Darimont *et al.* 2009; Mimura *et al.*
50 2016; Miraldo *et al.* 2016; Leigh *et al.* 2019). Changes in intraspecific diversity can affect
51 species turnover and composition (Vellend 2005; Vellend & Geber 2005), as well as
52 ecosystem functioning (Des Roches *et al.* 2018; Raffard *et al.* 2019c). For instance, the loss of
53 genotypes within primary producers can reduce ecosystem process rates and species diversity
54 (Crutsinger *et al.* 2006; Johnson *et al.* 2006; Fridley & Grime 2010), suggesting the existence
55 of biodiversity-ecosystem functioning relationships at the intraspecific level (iBEFs, Hughes
56 *et al.* 2008; Koricheva & Hayes 2018; Raffard *et al.* 2019c), in addition to the more widely
57 studied BEFs at the interspecific level.

58 The relationships between intraspecific diversity and ecosystem functioning are
59 challenging to study and this is primarily because of the confusion between genetic and
60 functional trait diversity. iBEF studies have initially manipulated genotypic richness within
61 experimental populations (e.g. Crutsinger *et al.* 2006; Hughes & Stachowicz 2009; Abbott *et*
62 *al.* 2017). Genetic variability is expected to encapsulate a large proportion of trait variability,
63 and thus higher genotypic richness should maintain higher functional diversity (Hughes et al.
64 2008). Although this approach allows deciphering the general effects of intraspecific diversity
65 on ecosystem functioning, it does not provide mechanisms. As a consequence, parallel studies
66 have directly manipulated functional trait richness within populations, which enabled to

67 determine a direct mechanistic linkage between functional richness and community structure
68 and ecosystem functioning (Violle *et al.* 2007; Matthews *et al.* 2011). For instance, individual
69 body mass (and traits covarying with body mass) has strong ecological effects because of the
70 associated functional differences and resource use complementarity among individuals
71 (Woodward *et al.* 2005; Hildrew *et al.* 2007; Rudolf *et al.* 2014; Harmon *et al.* 2009; Rudolf
72 & Rasmussen 2013a). Focusing on specific traits, such as body mass, might conversely blur
73 the ecological effects of "cryptic" trait variation (i.e. unmeasured functional traits) that is
74 likely supported by genotypic richness. We therefore argue that manipulating simultaneously
75 genotypic richness and the diversity of key functional traits such as body mass should allow
76 assessing whether cryptic trait diversity is ecologically important, and a better mechanistic
77 understanding of iBEFs.

78 The ecological effects of biodiversity changes are particularly strong when the later
79 occur at high trophic levels such as secondary consumers or predators. Changes in the
80 diversity and abundance of predatory species can trigger important effects in functions
81 supported by lower trophic levels, especially in regulating the abundance of the lower trophic
82 levels and indirectly ecosystem functioning, such as biomass production (Shurin *et al.* 2002;
83 Barnes *et al.* 2018). High predator species richness can sometimes favour resource use
84 complementarity and decrease prey abundance (Cardinale *et al.* 2006; Griffin *et al.* 2013). In
85 some cases, however, increasing predator richness increases prey abundance through
86 mechanisms such as predator interference (Sih *et al.* 1998; O'Connor & Bruno 2009), and can
87 modify multiple ecosystem functions along food webs (Antiqueira *et al.* 2018; Barnes *et al.*
88 2018). These mechanisms have all been investigated at the interspecific level, but they may
89 also apply *within* a predatory species (intraspecific diversity), and we can expect relationships
90 –either positive or negative- between predator intraspecific diversity and the structure of prey
91 communities, that could subsequently cascade down essential ecosystem functions such as

92 decomposition rate or primary production (Duffy, 2002; Bruno & O'Connor, 2005).
93 However, it is still difficult to forecast how loss in intraspecific diversity in predatory (and
94 consumer) species could affect ecosystem functioning, because iBEFs studies have primarily
95 focused on primary producers (Koricheva & Hayes 2018; Raffard *et al.* 2019c). This is
96 despite the fact that human activities strongly affect predator and consumer populations, for
97 instance through harvest or fisheries activities, which may alter ecosystem functioning
98 through intraspecific changes in traits and genotypes (Hauser *et al.* 2002; Estes *et al.* 2011;
99 Palkovacs *et al.* 2012, 2018).

100 In this study, we investigated whether a loss in genotypic and functional diversity
101 within a consumer species at the top of a three-level trophic chain could mediate top-down
102 effects on key ecosystem functions. In a nine-months mesocosm experiment, we
103 simultaneously manipulated *genotypic richness* (number of genetic entities) and the *functional*
104 *richness* (variance in individuals body mass) of experimental populations of a freshwater fish,
105 the European minnow (*Phoxinus phoxinus*); a common and abundant species with important
106 ecosystems effects (Miró *et al.* 2018; Raffard *et al.* 2019b). We predicted that increased
107 functional richness should affect ecological functions; if functional richness captures the
108 entire functional differences among genotypes, then increasing genotypic richness should not
109 impact ecological functions further (Fig. 1a). At the opposite, if functional richness does not
110 capture all the functional differences among genotypes, then increasing genotypic richness
111 should increase functional diversity and affect ecological functions (Fig. 1b). The ecological
112 effects of genotypic and functional richness might display different shape following different
113 predictions based on possible "additive", "enhancing" or "compensatory" effects (Fig. 1), to
114 which we compared our experimental findings. Finally, we identified the mechanistic bases of
115 the ecological effects of genotypic and functional richness. We specifically tested whether the
116 loss in genotypic and functional richness affected directly populations' biomass production

117 and community structure, and indirectly ecosystem functioning mediated by changes in
118 community structure of benthic and pelagic food web.

119

120 **Material and methods**

121 *Model species*

122 The European minnow (*P. phoxinus*) is a common species occurring across Western Europe,
123 living in relatively cold water (summer water temperature generally lower than 24°C)
124 including mountains lakes, small rivers at intermediate altitude and mountain streams (Keith
125 *et al.* 2011). It is a small-bodied cyprinid fish species (<12 cm long, 4-8 cm long as an adult
126 in general) playing the role of secondary consumer in most ecosystems (Raffard *et al.* 2020),
127 with a generalist diet composed of small invertebrates, algae or zooplankton (Frost 1943;
128 Collin & Fumagalli 2011). Populations of European minnows differed in their genetic and
129 phenotypic richness (Fourtune *et al.* 2018), and previous works revealed that genetically and
130 phenotypically unique populations differently affect prey community abundance and
131 ecosystem functions (Raffard *et al.* 2019b).

132 We selected ten populations from a large river basin in southern France (the Garonne
133 catchment) based on *a priori* knowledge to maximise both genetic and functional
134 differentiations among populations (Fourtune *et al.* 2018; Raffard *et al.* 2019a) (Fig. S1).
135 Specifically, we sampled five populations mainly composed of small-bodied adults (mean
136 body mass ± standard error (SE) = 1.03 g ± 0.02) and five populations mainly composed of
137 large-bodied adults (mean body mass ± SE = 3.06 g ± 0.07) (Fig. S2a). These differences in
138 adult body mass are due to selective pressures from the local environment such as mean water
139 temperature; the higher the mean water temperature, the smallest the adult body mass due to
140 increased metabolic rate and an accelerated pace-of-life (Raffard *et al.* 2019a). These

141 populations also display unique genetic characteristic and can each be defined as unique
142 genetic entities (Fourtune *et al.* 2018; Prunier *et al.* 2019). Each population are geographically
143 distant, and they will hereafter be each considered as functionally and genetically unique
144 entity, and intraspecific richness will be manipulated by varying the number of populations in
145 independent mesocosms (see details below).

146 In September 2017, individuals were collected in each river by electrofishing a 200-m
147 section and visually selecting 30-50 individuals reflecting the size range of adults. Fish were
148 maintained at similar density in outdoor tanks for 3 weeks before the start of the experiment.
149 Fish were fed ad libitum with frozen Chironomidae during this period.

150

151 *Mesocosm experiment*

152 In October 2016, 24 outdoor mesocosms were filled with 900 L of water, and 3 cm of gravel.
153 Nutrients were added to the mesocosms using 10 mL of solution containing nitrogen and
154 phosphorus (ratio N:P:K = 3.3:1.1:5.8). Each mesocosm was then inoculated twice (October
155 2016 and May 2017) with 200 mL of a concentrated solution of phytoplankton and 200 mL of
156 concentrated solution of zooplankton collected from a unique lake nearby (Lamartine Lake,
157 France 43°30'21.5"N, 1°20'32.7"E). In May 2017, we introduced three adult pond-snails
158 (Lymnaeidae) and ten adult isopods (Asellidae) in each mesocosms. They were let uncovered
159 to allow natural colonization by other invertebrates and community assemblage until the start
160 of the experiment that occurred approximately 6 months later.

161 In October 2017, eight fish were weighted and introduced in each mesocosm, which
162 were assigned to one of four treatments according to a full-factorial design with *genotypic*
163 richness (two levels, *high* and *low* genotypic richness) and *functional* richness (two levels,
164 *high* and *low* functional richness) as the main factors. Genotypic richness was manipulated by

introducing individuals sourced from either two (*low genotypic richness*, four individuals from each population) or four (*high genotypic richness*, two individuals from each population) out of the ten populations. These two levels of genotypic richness were selected as it has previously been shown in a meta-analysis that the effect of intraspecific richness on ecosystem functioning increases linearly until four/six genotypes and then reaches a plateau beyond that (Raffard *et al.* 2019c). Since we aimed at testing the effect of richness while minimizing the effects of population identity, each replicate of each treatment of richness contained a different (unique) assemblage of populations. Functional richness consisted in manipulating the body mass of the individuals present in the mesocosms; hence, experimental populations contained individuals sourced either from large or small populations (i.e., one functional entity, *low functional richness*), or from both small and large populations (i.e., two functional entities, *high functional richness*, see Table S1 and Fig. S2 for details on the different experimental populations). It is noteworthy that populations containing only either small or large individuals were actually more functionally redundant than populations containing large and small individuals. Experimental populations hence varied simultaneously according to their genotypic and functional richness, leading to four treatments.

The experiment lasted 30 weeks (210 days) after fish were introduced. Mesocosms were checked daily for mortality, which was rarely observed over the course of the experiment. At the end of the experiment, we measured several ecological parameters to assess effects of genotypic and functional richness on population performance, community structure and ecosystem functioning:

- *Population performance*: All tanks were emptied and we recaptured all remaining fish to estimate mortality rate (1 - nb. survival fish/nb. introduced fish; mean per tank ± standard error (SE) = 0.22 ± 0.01). Fish were weighted to assess fish biomass production (biomass production = averaged final weight - averaged initial weight) of each experimental

population during the experiment. Since individuals with small initial body mass intrinsically displayed a higher growth rate than large individuals, a standardised biomass production index was calculated as the residuals of the relationship between biomass production and initial fish size.

- *Community structure*: Zooplankton community structure was quantified by filtering 5 L of water through a 200 µm sieve. Samples were conserved in a 70% ethanol solution and subsequently identified to the order or family levels, including Cyclopoida, Calanoida, Daphniidae, Chydoridae and Bosminidae. The diversity of zooplankton was calculated as the Simpson's diversity (*D-zoo*) representing the probability that two randomly chosen individuals belong to different clades. *D-zoo* was calculated as $1 - \frac{\sum N_i * (N_i - 1)}{N_{tot} * (N_{tot} - 1)}$, where N_{tot} was the total number of sampled individuals, and N_i the number of sampled individuals for each group (Simpson 1949; Lande 1996). Zooplankton abundance was quantified as the total number of individuals for all taxa pooled at the tank level.

Benthic invertebrates were collected from the mesh bags used to measure decomposition rates (*see below*), conserved in a 70% ethanol solution, and identified as Isopoda, Diptera, Gastropoda, Ephemeroptera, Plecoptera, Odonata, Copepoda, Cladocera, and Ostracoda. The diversity of benthic invertebrates was calculated as the Simpson's diversity (*D-inv*). The abundance of benthic invertebrates was quantified as the total number of individuals for all taxa pooled at the tank level.

- *Ecosystem functioning*: Decomposition rate was measured by quantifying the mass loss of black poplar (*Populus nigra*, a dominant riparian tree in southern France) abscised leaves (Alp *et al.* 2016). On the 7th of March 2018 (19 weeks after the introduction of fish), 4 g of air-dried leaves were put in each mesocosm within a coarse mesh (1 x 1 cm) bag. At the end of the experiment, the remaining leaf material was removed from the mesocosms, rinsed with tap water, oven dried at 60°C for three days and weighed to the nearest 0.001 g to assess

215 the loss of biomass. The decomposition rate was calculated as $k = -\frac{ln\,(X)}{t}$ (Alp *et al.* 2016),
216 where X is the proportion of litter remaining and t is the elapsed time in days.

217 Pelagic algae stock was measured as the chlorophyll-a concentration (µg.L^{-1}) in the
218 water column using a multiparametric probe (OTT, Hydrolab DS5®). Five measurements
219 were taken in each mesocosm and averaged for subsequent analyses. Since phytoplankton are
220 the main primary producers in these mesocosms (Downing & Leibold 2002), pelagic algae
221 stock can be considered as a proxy for the biomass of primary producers.

222

223 *Statistical analyses*

224 Prior to analysis, the pelagic algae stock (i.e. the chlorophyll-a concentration), zooplankton
225 and benthic invertebrate abundances were log-transformed to reach normality of models'
226 residuals. After analyses of outliers, we removed one mesocosm from the final analyses that
227 displayed outliers for several of the measured variables. Analyses were hence run on 23
228 replicates.

229 We first assessed the ecological effects of genotypic and functional richness using
230 mixed effects linear models (LMMs). We ran one model for each ecological parameter as a
231 dependent variable, and the genotypic richness, functional richness, and the resulting two-
232 term interaction (that was removed when non-significant) as explanatory variables. Fish
233 mortality rate during the experiment was included as a fixed effect to control for a potential
234 effect of final density on ecological processes. To control for the disposition of the tanks
235 during the experiment, the position of tanks was added as a random term. To compare the
236 relative strength of a loss in genotypic and functional richness on ecological parameters we
237 calculated effect sizes. Hedges' g were computed as follow: $g = \frac{X_2 - X_1}{s_{pooled}}$, where X_1 and X_2 are
238 means of treatments (for each genotypic or functional richness treatment) measured for each

239 ecological parameters respectively, and s_{pooled} is the pooled standard deviation computed as

240 $s_{pooled} = \sqrt{\frac{(n_2-1)s_2^2+(n_1-1)s_1^2)}{n_1+n_2-2}}$, where n is sample size, and s^2 is variance (Nakagawa &

241 Cuthill 2007). An effect size was hence measured for each variable response (and each

242 treatment), and effect sizes were averaged. The absolute mean effect size for genotypic and

243 functional richness (g_G and g_S, respectively) were compared visually based on 95%

244 confidence intervals (CI).

245 Secondly, we ran confirmatory path-analysis (Shipley 2009) to assess the direct and

246 indirect links among intraspecific diversity (genotypic and functional richness), prey

247 (invertebrates and zooplankton) community structure and ecosystem functioning. We

248 expected that intraspecific diversity in European minnows affects directly invertebrate

249 community (both diversity and abundance), and indirectly ecosystem functions

250 (decomposition rate, algae stock) through trophic cascades. Specifically, we computed two

251 path analysis: one for the benthic food chain (fish-invertebrates-decomposition), and one for

252 the pelagic food chain (fish-zooplankton-algae stock) (Fig. S3). The fits of the structural

253 models were assessed using the *C* statistic, that follows a χ^2 distribution and whose associated

254 *p*-value indicates whether the models adequately fit the data or not. Finally, the structural

255 models were compared to null models that were actually models without the effects of

256 genotypic and functional richness on community parameters (see Fig. S3) using Akaike

257 Information Criteria (AIC, Cardon *et al.* 2011; Shipley 2013). This test allows assessing

258 whether the indirect effects of genotypic and functional richness lead to a better explanation

259 of the data, and whether trophic cascades were important or not.

260 All statistical analysis were run using R software (R Core Team 2013), LMM were

261 run using the R-package lme4 (Bates *et al.* 2014), and confirmatory path-analyses were run

262 using the R-package ggm (Marchetti *et al.* 2020).

263

264 **Results**

265 Both genotypic and functional richness of experimental populations significantly
266 affected several ecological processes (Table 1). At the population level, we found that the
267 interaction between genotypic and functional richness tended ($p = 0.057$) to alter fish biomass
268 production of experimental populations (Table 1, Fig. 2a). Specifically, the less diversified
269 experimental populations (low genotypic richness and low functional richness) displayed a
270 lower biomass production than all other treatments (Fig. 2a). At the community level, the
271 diversity of benthic invertebrates was significantly higher in the high genotypic richness
272 treatment (mean *D-inv* ± SE = 0.64 ± 0.04) than in the low genotypic richness treatment (*D-*
273 *inv* ± SE = 0.53 ± 0.03), and this pattern was repeatable across functional richness treatments
274 (Fig. 2d, Table 1). Irrespective of the genotypic richness treatment, mesocosms containing
275 fish populations with low functional richness had higher diversity of benthic invertebrates
276 than mesocosms containing fish populations with high functional diversity (Fig. 2d, Table 1).
277 At the opposite, the diversity of zooplankton (*D-zoo*) was affected by the interaction between
278 genotypic and functional richness (Fig. 2e, Table 1). Zooplankton diversity was strikingly
279 higher in populations with both high genotypic richness and high functional richness (Fig. 2e,
280 Table 1), suggesting that, in this case, the effect of genotypic richness depended on the
281 functional richness of experimental fish populations. Benthic invertebrates and zooplankton
282 abundances were consistently (i.e. across genotypic richness treatment) enhanced when
283 increasing functional richness (Fig. 2f, g, and Table 1). Genotypic richness of populations did
284 not affect benthic invertebrates and zooplankton abundances (Fig. 2f, g, and Table 1). A weak
285 but significant negative effect of functional richness on the pelagic algae stock was detected
286 (Table 1, Fig. 2c) and there was no significant effects genotypic and functional richness on
287 decomposition rate (Table 2). Overall, genotypic and functional richness induced ecological

288 effects of similar intensity (mean $|g_G|$ = 0.356, CIs = 0.043-0.669, and mean $|g_S|$ = 0.564, CIs
289 = 0.247-0.882, see Fig. S4 for details).

290 Confirmatory path analyses revealed that effects of intraspecific diversity on
291 ecosystem functioning were primarily mediated by trophic cascades, through changes in
292 community structure (Fig. 3). First, genotypic and functional richness affected the diversity
293 and abundance of benthic invertebrates (Fig. 3), which subsequently and positively affected
294 the decomposition rate ($p < 0.001$, Fig. 4a, b and Table S2). Second, functional richness
295 positively affected abundance of zooplankton, leading to a decrease in pelagic algae stock (p
296 < 0.001, Fig. 4c, d, Table S2). Overall, the confirmatory path-analysis confirmed the key role
297 of intraspecific diversity for both food chains, and its indirect effects for ecosystem functions
298 (Fig. 3 and Table 2). Indeed, models including genotypic and functional richness reproduced
299 adequately the causal pathways (Table 2), and their AICs were better than that of the null
300 models for each ecosystem function (Table 2).

301

302 **Discussion**

303 The present study demonstrates that loosing intraspecific diversity in a secondary consumer
304 species has substantial top-down consequences for community structure and ecosystem
305 functioning in food webs. We showed that both losses in functional (mass) and genotypic
306 richness sustained these iBEFs, suggesting that differences in mass among individuals (an
307 important functional trait for food web dynamics, Woodward *et al.* 2005) did not capture the
308 entire functional space, and thus that genotypic richness encapsulates important and "cryptic"
309 (unmeasured) functional diversity. The loss of genotypes within consumer populations can
310 affect both the community structure and the abundance of lower trophic levels, as well as
311 ecosystem functions with a similar strength than the loss of functional entities (i.e. body

312 mass). Specifically, we found that diversity loss (genotypic and functional) within populations
313 indirectly affects primary producer biomass and organic matter recycling, two ecosystem
314 functions forming the bases of food chains. This suggests that intraspecific diversity is a key
315 but understudied facet of biodiversity as it indirectly sustains BEF relationships, even when
316 changes in intraspecific diversity occur at the top of the food chains.

317 Our study suggests that genotypic richness can support non-negligible cryptic
318 functional diversity. Cryptic functional traits, such as metabolic rates or behaviour, can induce
319 different energetic needs and ultimately affect individual diets (Brown *et al.*, 2004; Careau &
320 diversity, 2012; Rosenblatt & Schmitz, 2016). Hence, fish with different genotypes may share
321 obvious functional traits (such as body mass) but may subtly differ in other cryptic functional
322 traits, making them unique ecologically (Loreau 2001). Although such "ecological
323 dissimilarity-despite-morphological similarity" has rarely been demonstrated within species,
324 there is now ample evidence that cryptic species (species being morphologically and
325 phylogenetically similar) can actually be ecologically unique regarding their influence on
326 ecosystems (e.g. Fišer *et al.* 2015). Interestingly, this cryptic diversity can interact with
327 functional richness in various ways (i.e., additive, enhancing, or compensatory) depending on
328 the ecological parameter considered (i.e., benthic invertebrate diversity, zooplankton
329 diversity, and fish biomass production, respectively). For instance, we found that genotypic
330 richness can compensate for the loss of functional diversity for population performance (i.e.,
331 increase fish biomass production), with high genotypic richness maintaining high biomass
332 production even when the distribution of body mass in the population is limited. We speculate
333 that genotypic richness can increase niche variation among individuals, thereby limiting the
334 loss of biomass production when decreasing functional richness (Duffy *et al.* 2001). These
335 findings echo and extent studies at the interspecific level demonstrating that phylogenetic
336 diversity among species explains variance in ecosystem functions that is not explained either

337 by species or functional diversities, suggesting that phylogenetic diversity sustain unmeasured
338 functional differences among species (Cadotte *et al.* 2012; Mouquet *et al.* 2012; Le
339 Bagousse-Pinguet *et al.* 2019). We argue that iBEFs are sustained by differences in functional
340 traits among individuals that can be directly measured (e.g. mass) and/or indirectly captured
341 through quantification of the genetic pool of individuals composing populations.

342 Accordingly, we showed that genotypic and functional richness can affect
343 independently (i.e., additively) and consistently community structure, demonstrating that
344 multiple facets of intraspecific diversity can regulate lower trophic levels. First, genotypic
345 richness increased diversity benthic invertebrates. This effect was very robust, as it was
346 repeatable and consistent across functional richness treatments. Genotypic richness probably
347 enhanced resource partitioning, allowing individuals to forage on a more diverse array of
348 resources, regulating the abundance of each taxonomic group and leading to a higher diversity
349 (Duffy, 2002; Johnson *et al.*, 2006; Hughes et al. 2008). Second, functional richness led to
350 increased prey abundance that was repeatable across both communities of benthic
351 invertebrates and zooplankton. Previous studies at the inter- and intraspecific levels provide
352 non-consistent predictions, since an increase in consumer diversity can affect either positively
353 or negatively resource abundance (Sih *et al.* 1998; Griffin *et al.* 2013; Rudolf & Rasmussen
354 2013b; Antiqueira *et al.* 2018; Barnes *et al.* 2018). In our experiment, although functional
355 richness enhanced prey abundance, it also increased fish biomass production, suggesting that
356 functionally rich populations did not consume fewer resources than functionally poor
357 populations. On the opposite, flexible exploitation of resources might occur because European
358 minnows are omnivorous (Frost 1943; Collin & Fumagalli 2011), their diet probably included
359 some periphyton, decreasing the predation risk on animal resources. Because the top-down
360 control of intraspecific diversity on community structure is likely driven by trophic

361 mechanisms, quantifying individual diet and its temporal dynamic in such experiments would
362 allow making more accurate predictions regarding trophic niche partitioning.

363 Our results further revealed how changes in top consumers' genotypic and functional
364 richness percolate through the food web and alter ecosystem functions at the basis of the food
365 chains. Such trophic cascade induced by intraspecific diversity could be driven by a
366 "classical" (i.e. interspecific) BEF relationship between benthic invertebrate diversity and
367 decomposition rate (Hooper *et al.* 2005; Gessner *et al.* 2010). Specifically, fish genotypic
368 richness increased benthic invertebrate diversity that accelerated litter decomposition rate.
369 The higher decomposition rate of organic matter is likely produced by higher consumption
370 efficiency through trophic complementarity among clades of invertebrates in diverse
371 community (Gessner *et al.* 2010). Invertebrate community with a high diversity probably
372 harboured a high functional diversity (Cadotte *et al.* 2011), and focusing on the functional
373 type of invertebrates might allow a more precise understanding of this link. These results echo
374 those reported at the community level and those manipulating richness within primary
375 producer species (Downing & Leibold 2002; Crutsinger *et al.* 2006), while implying a
376 modification of top-down effects by intraspecific diversity in consumers. Biodiversity within
377 consumer species is largely impacted by anthropogenic activities (Miraldo *et al.* 2016),
378 involving the loss of non-measured functional diversity, which might further lead to
379 underestimated cascading impacts on ecosystem functioning.

380 In conclusion, we demonstrated that both genetic and functional richness within
381 consumer populations are important facets of biological diversity, inducing effects on prey
382 community structure and trophic cascades mediating ecosystem functions. These results are
383 consistent with previous synthetic works (Koricheva & Hayes 2018; Raffard *et al.* 2019c),
384 reinforcing the call for considering changes of intraspecific diversity in consumer species as
385 an important ecological predictor. Importantly, genotypic richness can sustain important

cryptic functional diversity, and future investigations should aim at developing a general framework from genes to ecosystems to better understand the global links existing among the multiple facets of biodiversity and ecosystem functioning, and ultimately ecosystem services.

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Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article.

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References

Abbott, J.M., Grosberg, R.K., Williams, S.L. & Stachowicz, J.J. (2017). Multiple dimensions of intraspecific diversity affect biomass of eelgrass and its associated community. *Ecology*, 98, 3152–3164.

Alp, M., Cucherousset, J., Buoro, M. & Lecerf, A. (2016). Phenological response of a key ecosystem function to biological invasion. *Ecol. Lett.*, 19, 519–527.

Antiqueira, P.A.P., Petchey, O.L. & Romero, G.Q. (2018). Warming and top predator loss drive ecosystem multifunctionality. *Ecol. Lett.*, 21, 72–82.

Barnes, A.D., Jochum, M., Lefcheck, J.S., Eisenhauer, N., Scherber, C., O'Connor, M.I., *et al.* (2018). Energy flux: the link between multitrophic biodiversity and ecosystem functioning. *Trends Ecol. Evol.*, 33, 186–197.

Baruah, G., Clements, C.F., Guillaume, F. & Ozgul, A. (2019). When do shifts in trait dynamics precede population declines? *Am. Nat.*, 193, 633–644.

Bates, D., Maechler, M, Bolker, B & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.

Bruno, J.F. & O'Connor, M.I. (2005). Cascading effects of predator diversity and omnivory in a marine food web. *Ecol. Lett.*, 8, 1048–1056.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.*, 48, 1079–1087.

Cadotte, M.W., Dinnage, R. & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93, S223–S233.

Cardinale, B.J., Srivastava, D.S., Emmett Duffy, J., Wright, J.P., Downing, A.L., Sankaran, M., *et al.* (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989–992.

Cardon, M., Loot, G., Grenouillet, G. & Blanchet, S. (2011). Host characteristics and environmental factors differentially drive the burden and pathogenicity of an ectoparasite: a multilevel causal analysis: Causalities in host-parasite interactions. *J. Anim. Ecol.*, 80, 657–667.

Careau, V. & Garland, T. (2012). Performance, Personality, and Energetics: Correlation, Causation, and Mechanism. *Physiol. Biochem. Zool.*, 85, 543–571.

Clements, C.F., Blanchard, J.L., Nash, K.L., Hindell, M.A. & Ozgul, A. (2017). Body size shifts and early warning signals precede the historic collapse of whale stocks. *Nat. Ecol. Evol.*, 1, 0188.

Clements, C.F. & Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. *Nat. Commun.*, 7, 10984.

Collin, H. & Fumagalli, L. (2011). Evidence for morphological and adaptive genetic divergence between lake and stream habitats in European minnows (*Phoxinus phoxinus* , Cyprinidae). *Mol. Ecol.*, 20, 4490–4502.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313, 966–968.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. & Wilmers, C.C. (2009). Human predators outpace other agents of trait change in the wild. *Proc. Natl. Acad. Sci.*, 106, 952–954.

Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., *et al.* (2018). The ecological importance of intraspecific variation. *Nat. Ecol. Evol.*, 2, 57–64.

Downing, A.L. & Leibold, M.A. (2002). Ecosystem consequences of species richness and composition in pond food web. *Nature*, 416, 837–-841.

Duffy, J.E. (2002). Biodiversity and ecosystem function: the consumer connection. *Oikos*, 99, 201–219.

Duffy, J.E., Macdonald, K.S., Rhode, J.M. & Parker, J.D. (2001). Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology*, 82, 2417– 2434.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., *et al.* (2011). Trophic Downgrading of Planet Earth. *Science*, 333, 301–306.

Fišer, Ž., Altermatt, F., Zakšek, V., Knapič, T. & Fišer, C. (2015). Morphologically Cryptic Amphipod Species Are "Ecological Clones" at Regional but Not at Local Scale: A Case Study of Four Niphargus Species. *PLOS ONE*, 10, e0134384.

Fourtune, L., Prunier, J.G., Mathieu-Begne, E., Canto, N., Veyssiere, C., Loot, G., *et al.* (2018). Intraspecific genetic and phenotypic diversity: parallel processes and correlated patterns?

Fridley, J.D. & Grime, J.P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, 91, 2272–2283.

Frost, W.E. (1943). The natural history of the minnow, *Phoxinus phoxinus*. *J. Anim. Ecol.*, 12, 139.

Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., *et al.* (2010). Diversity meets decomposition. *Trends Ecol. Evol.*, 25, 372–380.

Griffin, J.N., Byrnes, J.E.K. & Cardinale, B.J. (2013). Effects of predator richness on prey suppression: a meta-analysis. *Ecology*, 94, 2180–2187.

Harmon, L.J., Matthews, B., Des Roches, S., Chase, J.M., Shurin, J.B. & Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, 458, 1167–1170.

Hauser, L., Adcock, G.J., Smith, P.J., Bernal Ramirez, J.H. & Carvalho, G.R. (2002). Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (Pagrus auratus). *Proc. Natl. Acad. Sci.*, 99, 11742–11747.

Hildrew, A.G., Raffaelli, D. & Edmonds-Browns, R. (2007). *Body size: the structure and function of aquatic ecosystems*. Cambridge University Press, Cambridge, UK.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.*, 11, 609–623.

Hughes, A.R. & Stachowicz, J.J. (2009). Ecological impacts of genotypic diversity in the clonal seagrass Zostera marina. *Ecology*, 90, 1412–1419.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., *et al.* (2017). Linking the influence and dependence of people on biodiversity across scales. *Nature*, 546, 65–72.

Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006). Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecol. Lett.*, 9, 24–34.

Keith, P., Persat, H., Feunteun, E. & Allardi, J. (2011). *Les poissons d'eau douce de France.* Muséum National d'Histoire Naturelle and Publications Biotope. Paris and Mèze.

Koricheva, J. & Hayes, D. (2018). The relative importance of plant intraspecific diversity in structuring arthropod communities: A meta-analysis. *Funct. Ecol.*, 32, 1704–1717.

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 76, 5.

Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M. & Maestre, F.T. (2019). Phylogenetic, functional, and taxonomic richness have both positive and

negative effects on ecosystem multifunctionality. *Proc. Natl. Acad. Sci.*, 116, 8419–8424.

Leigh, D.M., Hendry, A.P., Vázquez-Domínguez, E. & Friesen, V.L. (2019). Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. *Evol. Appl.*, eva.12810.

Loreau, M. (2001). Biodiversity and Ecosystem Functioning: Current Knowledge and Future Challenges. *Science*, 294, 804–808.

Marchetti, G.M., Drton, M. & Sadeghi, K. (2020). ggm: functions for graphical Markov models. Version 2.5.

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., *et al.* (2011). Toward an integration of evolutionary biology and ecosystem science. *Ecol. Lett.*, 14, 690–701.

Mimura, M., Yahara, T., Faith, D.P., Vázquez-Domínguez, E., Colautti, R.I., Araki, H., *et al.* (2016). Understanding and monitoring the consequences of human impacts on intraspecific variation. *Evol. Appl.*, 10, 121–139.

Miraldo, A., Li, S., Borregaard, M.K., Florez-Rodriguez, A., Gopalakrishnan, S., Rizvanovic, M., *et al.* (2016). An Anthropocene map of genetic diversity. *Science*, 353, 1532–1535.

Miró, A., Sabás, I. & Ventura, M. (2018). Large negative effect of non-native trout and minnows on Pyrenean lake amphibians. *Biol. Conserv.*, 218, 144–153.

Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J., *et al.* (2012). Ecophylogenetics: advances and perspectives. *Biol. Rev.*, 87, 769–785.

Naeem, S., Bunker, D.E., Hector, A., Loreau, M. & Perrings, C. (2009). *Biodiversity, Ecosystem Functioning, and Human Wellbeing*. Oxford University Press.

Nakagawa, S. & Cuthill, I.C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.*, 82, 591–605.

O'Connor, M.I. & Bruno, J.F. (2009). Predator richness has no effect in a diverse marine food web. *J. Anim. Ecol.*, 78, 732–740.

Palkovacs, E.P., Kinnison, M.T., Correa, C., Dalton, C.M. & Hendry, A.P. (2012). Fates beyond traits: ecological consequences of human-induced trait change. *Evol. Appl.*, 5, 183–191.

Palkovacs, E.P., Moritsch, M.M., Contolini, G.M. & Pelletier, F. (2018). Ecology of harvest-driven trait changes and implications for ecosystem management. *Front. Ecol. Environ.*, 16, 20–28.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, 37, 637–669.

Prunier, J.G., Chevalier, M., Raffard, A., Loot, G., Poulet, N. & Blanchet, S. (2019). *Contemporary loss of genetic diversity in wild fish populations reduces biomass stability over time* (preprint). Ecology.

R Core Team. (2013). R: a language and environment for statistical computing.

Raffard, A., Cucherousset, J., Prunier, J.G., Loot, G., Santoul, F. & Blanchet, S. (2019a). Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): The role of adaptive and nonadaptive processes. *Ecol. Evol.*, 9, 2833–2846.

Raffard, A., Cucherousset, J., Santoul, F., Di Gesu, L. & Blanchet, S. (2019b). Intraspecific variation alters ecosystem and next-generation performance as much as temperature. *bioRxiv*.

Raffard, A., Santoul, F., Blanchet, S. & Cucherousset, J. (2020). Linking intraspecific variability in trophic and functional niches along an environmental gradient. *Freshw. Biol.*, fwb.13508.

Raffard, A., Santoul, F., Cucherousset, J. & Blanchet, S. (2019c). The community and ecosystem consequences of intraspecific diversity: a meta-analysis. *Biol. Rev.*, 94, 648–661.

Rosenblatt, A.E. & Schmitz, O.J. (2016). Climate change, nutrition, and bottom-up and top-down food web processes. *Trends Ecol. Evol.*, 31, 965–975.

Rudolf, V.H.W. & Rasmussen, N.L. (2013a). Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology*, 94, 1046–1056.

Rudolf, V.H.W. & Rasmussen, N.L. (2013b). Population structure determines functional differences among species and ecosystem processes. *Nat. Commun.*, 4.

Rudolf, V.H.W., Rasmussen, N.L., Dibble, C.J. & Van Allen, B.G. (2014). Resolving the roles of body size and species identity in driving functional diversity. *Proc. R. Soc. B Biol. Sci.*, 281, 20133203.

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, 90, 363–368.

Shipley, B. (2013). The AIC model selection method applied to path analytic models compared using ad-separation test. *Ecology*, 94, 560–564.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., *et al.* (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, 5, 785–791.

Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.*, 13, 350–355.

Simpson, E.H. (1949). Measurement of diversity. *Nature*, 163, 688.

Vellend, M. (2005). Species diversity and genetic diversity: parallel processes and correlated patterns. *Am. Nat.*, 166, 199–215.

Vellend, M. & Geber, M.A. (2005). Connections between species diversity and genetic diversity. *Ecol. Lett.*, 8, 767–781.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J., Olesen, J., Valido, A., *et al.* (2005). Body size in ecological networks. *Trends Ecol. Evol.*, 20, 402–409.

592 **Figure captions**

593 **Fig. 1.** Predicted ecological effects of genotypic richness in relation with functional richness.
594 Functional richness is assumed to positively affect ecological functions, whereas genotypic
595 richness might have different effects depending on it support cryptic functional diversity.
596 First, if functional richness does capture the essential of the functional differences among
597 genotypes, then genotypic richness would have no ecological effects (a). Second, if genotypic
598 richness supports cryptic functional diversity, the effects could be (b) additive, (c) enhancing,
599 or (d) compensatory.

600

601 **Fig. 2.** Effects of genotypic and functional richness on populations biomass production index
602 (a), decomposition rate (b), algae stock (c), diversity of benthic invertebrates (e), diversity of
603 zooplankton (f), abundance of benthic invertebrates (g), and abundance of zooplankton (h).
604 Error bars represent ± 1 SE.

605

606 **Fig. 3.** Causal pathways between genotypic richness, functional richness, community
607 structure, and ecosystem functioning. Two models have been run separately on decomposition
608 rate (a), and pelagic algae stock (b). Only significant links are drawn, blue arrows represent
609 positive links, and yellow arrows negative links.

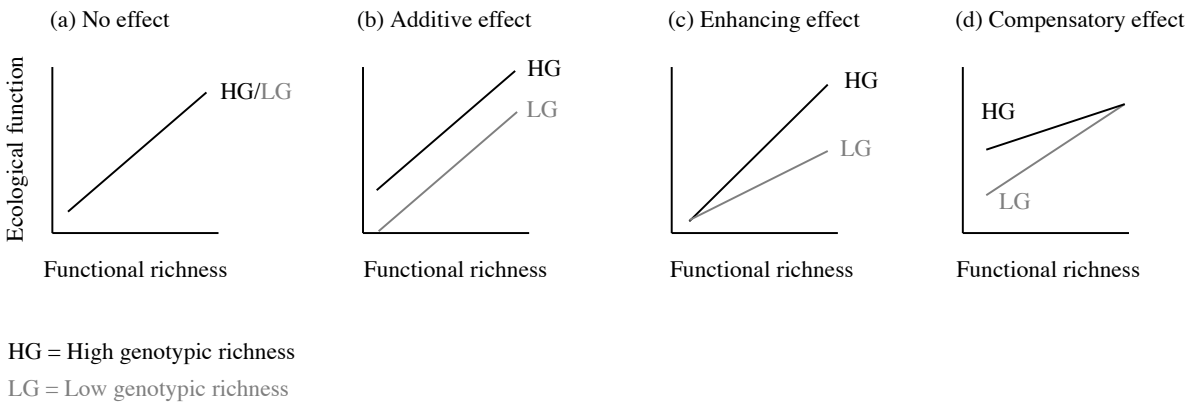
610

611 **Fig. 4.** Effects of the diversity (a) and the abundance (b) of benthic invertebrates on
612 decomposition rate; and effects of the diversity and the abundance of zooplankton on pelagic
613 algae stocks (c and d, respectively). Points are partial residuals extracted from models
614 described in the statistical analysis section (see also Table S2). Straight lines represent the

615 slope predicted by the models (see statistical analyses) when significant ($\alpha < 0.05$), and grey

616 shadows represent 95% CIs.

617



HG = High genotypic richness

LG = Low genotypic richness

Fig. 1.

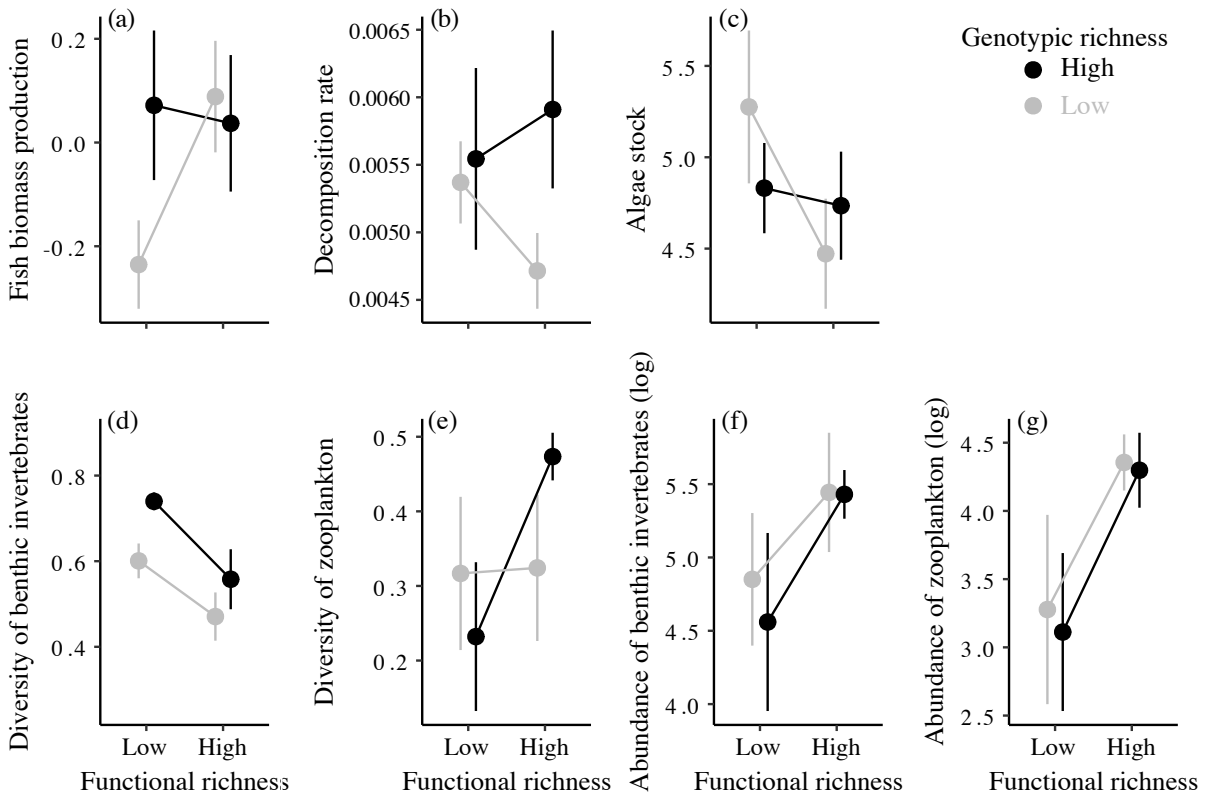

(a)
Fish biomass production
0.2
0.0
-0.2
(b)
Decomposition rate
0.0065
0.0060
0.0055
0.0050
0.0045
(c)
Algae stock
5.5
5.0
4.5
Genotypic richness
High
Low
(d)
Diversity of benthic invertebrates
0.8
0.6
0.4
Low
High
Functional richness
(e)
Diversity of zooplankton
0.5
0.4
0.3
0.2
Low
High
Functional richness
(f)
Abundance of benthic invertebrates (log)
5.5
5.0
4.5
4.0
Low
High
Functional richness
(g)
Abundance of zooplankton (log)
4.5
4.0
3.5
3.0
2.5
Low
High
Functional richness

Fig. 2.

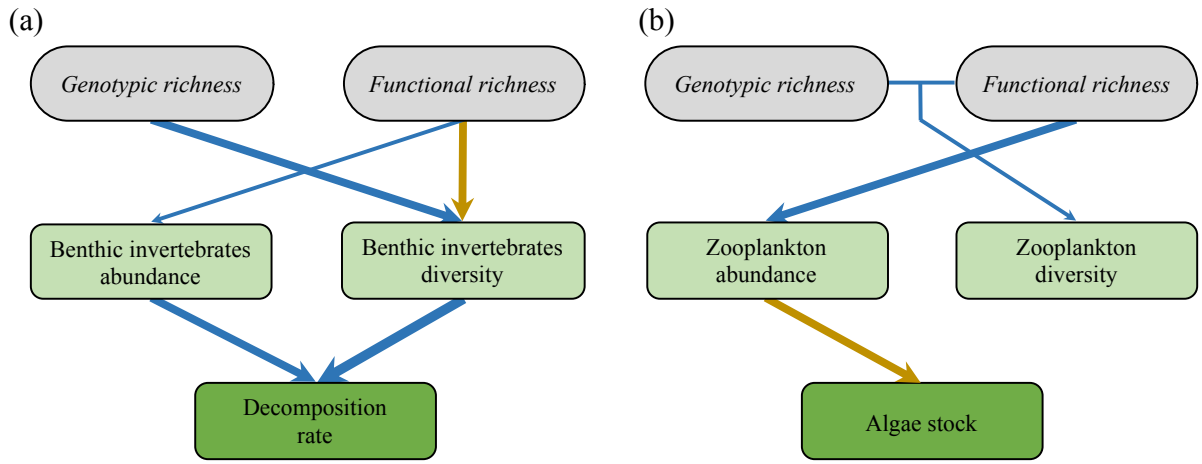

(a)
Genotypic richness
Functional richness
Benthic invertebrates abundance
Benthic invertebrates diversity
Decomposition rate
(b)
Genotypic richness
Functional richness
Zooplankton abundance
Zooplankton diversity
Algae stock

Fig. 3

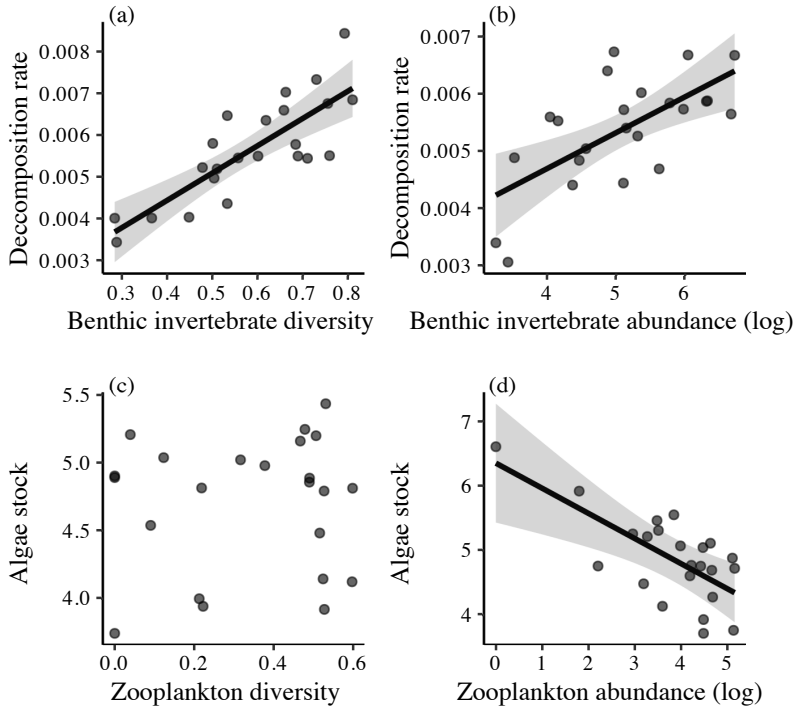

(a)
Deccomposition rate
0.008
0.007
0.006
0.005
0.004
0.003
0.3 0.4 0.5 0.6 0.7 0.8
Benthic invertebrate diversity
(b)
Decomposition rate
0.007
0.006
0.005
0.004
0.003
4 5 6
Benthic invertebrate abundance (log)
(c)
Algae stock
5.5
5.0
4.5
4.0
0.0 0.2 0.4 0.6
Zooplankton diversity
(d)
Algae stock
7
6
5
4
0 1 2 3 4 5
Zooplankton abundance (log)

Fig. 4.

630 **Table 1.** Results of the mixed effect linear models quantifying the relationships between
631 genotypic richness, functional richness and ecological parameters. Significant -and near
632 significant- *p*-values are displayed in bold. Interaction terms were removed from the model
633 when not significant.

634

Response	Effect	*p*-value	χ^2, d.f.
Fish biomass production	Genotypic richness	0.301	(1.071, 1)
	Functional richness	0.634	(0.227, 1)
	Genotypic richness* Functional richness	**0.057**	(3.621, 1)
	Mortality	**0.023**	(5.196, 1)
Benthic invertebrates diversity	**Genotypic richness**	**0.007**	(7.152, 1)
	Functional richness	**0.002**	(9.484, 1)
	Mortality	0.212	(1.551, 1)
Zooplankton diversity	**Genotypic richness**	**0.052**	(3.756, 1)
	Functional richness	**0.004**	(8.163, 1)
	Genotypic richness* Functional richness	**0.038**	(4.287, 1)
	Mortality	0.851	(0.035, 1)
Benthic invertebrates abundance	Genotypic richness	0.300	(1.072, 1)
	Functional richness	**0.031**	(4.667, 1)
	Mortality	0.238	(1.392, 1)
Zooplankton abundance	Genotypic richness	0.885	(0.021, 1)
	Functional richness	**0.004**	(8.154, 1)
	Mortality	0.220	(1.503, 1)
Decomposition rate	Genotypic richness	0.140	(2.169, 1)
	Functional richness	0.690	(0.158, 1)
	Mortality	0.893	(0.018, 1)
Pelagic algae stock	Genotypic richness	0.834	(0.044, 1)
	Functional richness	**0.053**	(3.742, 1)
	Mortality	0.412	(0.673, 1)

635
636

637 **Table 2.** Model fits of the two confirmatory path-analyses to explain decomposition rate and
638 algae stock. The full models included the effect of genotypic and functional richness on
639 community components while the null model did not.
640

Variable	*C*	df	*p*-value	AIC full model	AIC null model
Decomposition rate	8.555	6	0.200	32.555	75.043
Algae stock	6.745	10	0.749	52.745	64.679

641