

1 **Beyond ecological opportunity: prey diversity rather than abundance**
2 **shapes predator niche variation**

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21 hypothesis; predator-prey interactions; trophic niche.

22

23 **Abstract**

24 1. Ecological opportunity, i.e. the diversity of available resources, has a pivotal role in
25 shaping niche variation and trophic specialisation of animals. However, ecological
26 opportunity can be described with regard to both diversity and abundance of resources. It
27 is still relatively unexplored to what degree these two components contribute to niche
28 variation.

29 2. To address this, we utilise an extensive dataset on fish diet and benthic invertebrate
30 diversity and density from 73 sampling events in three Norwegian rivers in order to
31 explore realised trophic niches and the response of dietary niche variation along gradients
32 of resource diversity (potential trophic niches), resource density (as a proxy of resource
33 abundance) and fish density (as a proxy of inter- and intraspecific competition) in a
34 freshwater top predator (the brown trout, *Salmo trutta* L.).

35 3. Linear models indicated that individual and population niche variation increased with
36 increasing ecological opportunity in terms of prey diversity. However, no simple cause-
37 and-effect associations between niche indices and prey abundance were found. Our
38 multiple regression analyses indicated that the abundance of certain resources (e.g.
39 Chironomidae) can interact with prey diversity to determine individual and population
40 realised trophic niches. Niche variation (within-individual component and inter-
41 individual diet variation) decreased with increasing inter- and intraspecific competition.

42 4. This study extends prevailing trophic ecology theory by identifying diversity, rather
43 than density, of available prey resources as a primary driver of niche variation in fish of
44 temperate riverine systems with no extensive resource limitation. The study also shows
45 that ecological opportunity may mask the direction of the effect (compression or
46 expansion) of competition on niche variation when food resources are diverse.

47 5. Our study supports the view that broader trophic niche potentials promote broader
48 realised trophic niche variation of individuals, which lead to individual niche
49 diversification by opening access to alternatives resources, resulting in a concomitant rise
50 in the realised trophic niche width of the population.

51

52 **Introduction**

53 Ecologists have long emphasised the importance of ecological opportunity, i.e. the
54 availability of ecologically accessible resources that may be exploited (Stroud & Losos,
55 2016), in understanding niche variation and dietary specialisation of animals (Bolnick et
56 al., 2003; Araújo, Bolnick, & Layman, 2011). By definition, ecological opportunity has
57 typically been understood as the prey richness (i.e. species or resource diversity) available
58 for consumers, but it can also be considered as abundance or density of resources
59 (reviewed by Wellborn & Langerhans, 2015; but also see Stroud & Losos, 2016). In
60 addition, ecological opportunity can be extended towards the ecological niche concept
61 (Hutchinson, 1944; 1957), being key to distinguish realised (i.e. resource use by the model
62 species) and fundamental (resource availability) niches when attempting to identify niche
63 expansion and specialisation of animals (Dolédec, Chessel, & Gimaret-Carpentier, 2000;
64 Bolnick et al., 2003). Thus, consumers' specialisation can be decomposed into
65 fundamental (promoted by intrinsic traits such as morphology or behaviour) and realised
66 (promoted by intrinsic and/or extrinsic mechanisms such as prey patchiness and social
67 interactions) specialisation (Bolnick et al., 2003). Because prey resources are dynamically
68 affected by the focal species (Peterson et al., 2011), resource availability does not define
69 the fundamental trophic niche of model organisms *per se*, but rather reflects which prey
70 resources that are accessible and potentially can be utilised by the consumer species (i.e.
71 its ecological opportunity or *potential* trophic niche).

72 The niche variation hypothesis (NVH) suggests that populations tend to display niche
73 expansion when they are released from interspecific competition (Van Valen, 1965).
74 However, there are also other factors governing the magnitude of among-individual diet
75 variation in animals such as intraspecific competition, predation and ecological
76 opportunity (Araújo et al., 2011; Sjödin, Ripa, & Lundberg, 2018). Recent studies support

77 the view that resource competition promotes niche variation among individuals within a
78 population, including an important role of intraspecific competition for individual
79 specialisation (Svanbäck & Bolnick, 2007; Araújo et al., 2011; Tinker et al., 2012; Costa-
80 Pereira, Araújo, Souza, & Ingram, 2019; Mendes, Fernandes, Penha & Mateus, 2019).
81 There is also empirical support that fish species can display a generalist foraging
82 behaviour independent of density-dependent intraspecific competition (Sánchez-
83 Hernández & Cobo, 2013). However, intraspecific niche variation is expectedly also
84 influenced by ecological opportunity which may have an even stronger diversifying effect
85 on dietary niche width than the constraining effects of competition (Costa-Pereira et al.,
86 2019). Here, we empirically explore realised and potential trophic (diversity of available
87 prey resources) niches and test the response of niche variation at the individual and
88 population levels along gradients of resource diversity and density.

89 Theoretical and empirical work postulate that high ecological opportunity in terms of prey
90 diversity can promote higher intraspecific niche variation via both broader individual
91 niches and individual specialisation (e.g. Araújo et al., 2011; Araújo & Costa-Pereira,
92 2013; Costa-Pereira et al., 2019; Salvidio, Costa, & Crovetto, 2019; Rosa, Costa,
93 Salvidio, 2020) and population niche expansion of consumers (Sjödin et al., 2018),
94 whereas competing species may segregate in resource use by displaying different species-
95 level specialisation (Sánchez-Hernández, Gabler, & Amundsen, 2017a). Thus, population
96 niche expansion can suggestively occur in scenarios of high ecological opportunity in
97 terms of resource diversity by individual resource-specialisation (i.e. strict phenotypic
98 differentiation) (Sjödin et al., 2018). A growing number of studies indicate that trophic
99 niche breadth of both semi-aquatic (frog species) and terrestrial (lizards) consumers
100 expands along increases in diversity of available prey (Moreno-Rueda et al., 2018; Costa-
101 Pereira et al., 2019).

102 On the other hand, when addressing ecological opportunity in terms of abundance of
103 resources, individual variation in consumer's resource use has often been found to
104 increase with decreasing prey resource abundance leading to individual dietary
105 specialisation towards different prey types (Tinker, Bentall, & Estes, 2008; Svanbäck,
106 Rydberg, Leonardsson, & Englund, 2011). Therefore, it is thought that when preferred
107 resources are scarce, individuals expand their niche through the utilisation of previously
108 unutilised resources depending on the diversity of available resources (Araújo et al.,
109 2011), and thus it is reasonable to posit that this might only occur in high prey diversity
110 scenarios. In this sense, Rosa et al. (2020) observed differences in individual
111 specialisation of newts between two locations with similar prey abundance, concluding
112 that individual specialisation was promoted by high prey diversity.. Thus, it is possible
113 that the importance of prey abundance as a driver of consumer's niche variation depends
114 largely on prey diversity. Prey patchiness can also facilitate the understanding of niche
115 variation of animals as prey patchiness promotes realised specialisation and drives high
116 levels of individual specialisation (Bolnick et al., 2003; Araújo et al., 2011). However,
117 empirical studies addressing simultaneously the relative importance of the two different
118 facets of ecology opportunity (i.e. diversity and abundance) on individual and population
119 niches are still limited, especially on the basis of the ecological niche concept
120 (Hutchinson, 1944; 1957), remaining an important challenge for the understanding of the
121 mechanisms affecting niche variation.

122 To address this challenge, we here study the relative contribution of ecological
123 opportunity in terms of resource diversity and density (as a proxy of prey abundance) on
124 niche variation at both the individual and population levels using riverine brown trout
125 (*Salmo trutta* L.) and its prey as model system. Based on earlier studies (Tinker et al.,
126 2008; Araújo et al., 2011; Svanbäck et al., 2011; Araújo & Costa-Pereira, 2013; Salvidio

127 et al., 2019), niche variation both in terms of population niche width and individual
128 specialisation would be impacted by ecological opportunity; increasing with increasing
129 prey diversity and/or with decreasing prey density. However, we expected that prey
130 diversity, and not prey density, act as the true bottleneck in driving predator niche
131 variation because the diversity of available resources limits the baseline from where
132 individuals can segregate in prey categories (Figure 1). Our reasoning relies on the view
133 that scenarios with food resource limitation (low prey density) may promote niche
134 compression in consumer's population when prey diversity is low, and niche extension
135 when prey diversity is high. Thus, individuals can expand their niche to include
136 previously unutilised resources when preferred resources are scarce (Araújo et al., 2011),
137 but the magnitude of the expansion will greatly rely on the diversity of available resources
138 (Figure 1). Additionally, we explored whether fish density (as a proxy of inter- and
139 intraspecific competition) impacts niche variation, expecting that inter- and intraspecific
140 competition in line with NVH will play an important role for intraspecific niche variation
141 (Van Valen, 1965; Araújo et al., 2011). More specifically, we expect that higher consumer
142 densities (increasing both inter- and intraspecific competition) may lead individuals to
143 reduce their individual variation and specialise in resource use.

144

145 **Material and methods**

146 *Study systems*

147 We used a comprehensive dataset of fish diet composition and prey community structure
148 sampled in three Norwegian rivers [Beiarelva (67°00'07.1"N 14°37'29.9"E),
149 Klubbvasselva (65°41'53.3"N 13°11'52.3"E) and Litjvasselva (65°33'00.8"N
150 13°38'51.8"E)] (Figure 2). Brown trout and Atlantic salmon (*Salmo salar* Linnaeus, 1758)
151 are the dominant species in the fish communities of the studied rivers. Other fish species,

152 such as European eel (*Anguilla anguilla*, Linnaeus, 1758) and three-spine stickleback
153 (*Gasterosteus aculeatus* Linnaeus 1758), are also present in the river basins, but only
154 sporadically found at the current study sites. The study included 73 sampling events
155 between 1988 and 1992, implemented during the ice-free season (from April to October),
156 except in May, when high water-flow conditions due to spring flood made sampling
157 impossible. The study was replicated spatially across three (Beiarelva and Litjvasselva)
158 and five (Klubbvasselva) sampling stations. At each sampling event, fish and benthic
159 invertebrates were collected. Sampling protocols used in this study conform to the ethical
160 laws of the country (see Acknowledgements).

161

162 *Fish sampling and stomach contents analysis*

163 We attempted to collect at least 20 brown trout for stomach contents analyses (SCA) in
164 each sampling event depending on fish abundance (sample size: 14-370 brown trout,
165 mean = 104.8 ± 10.4 SE). In order to avoid confounding effects of maturation and
166 migratory behaviour between migratory (i.e. anadromous) and resident individuals within
167 the populations (e.g. Klemetsen et al., 2003), we focused the current study on parr fish
168 (i.e. resident individuals mostly composed by juveniles). Accordingly, brown trout were
169 collected in their typical parr habitat (riffle stretches) of the rivers using portable backpack
170 electrofishing gear with pulsed direct current and a single anode of 30 cm diameter. Fish
171 sampling was conducted in an upstream direction from the riverbank to a water depth of
172 about 70 cm over a stream section of 100 m.

173 In total, the material for SCA included 8149 individuals (fish length range: 24-226 mm,
174 mean = 77.4 mm \pm 0.34 SE). Each individual was measured (fork length, mm) and
175 stomachs were removed for diet analysis. The stomachs were opened, and the percentage
176 of total fullness visually determined, ranging from empty (0%) to full (100%) (further

177 details in Amundsen & Sánchez-Hernández, 2019). Each prey item was then identified to
178 the lowest taxon possible (mostly family or order) under a binocular microscope
179 (magnification $\times 80$). The contribution of each prey category to the diet was estimated
180 based on their proportional abundance, and the diet composition at the individual and
181 population level was estimated using relative prey abundances (Amundsen, Gabler, &
182 Staldvik, 1996; Amundsen & Sánchez-Hernández, 2019).

183

184 *Fish density*

185 Because fish populations are commonly regulated through density-dependent
186 mechanisms (Henderson & Magurran, 2014), within and among-species fish density can
187 indicate levels of intra- and inter-specific competition, respectively (e.g. Sánchez-
188 Hernández & Cobo, 2013; Hasegawa, 2016). For some of the sampling events in
189 Beiarelva and Klubbvasselva ($n = 23$), fish densities were estimated through three-pass
190 removal electrofishing with 30 min intervals. Fish captured in each sampling pass were
191 removed and retained in oxygenated tanks before processing. Fish were identified to
192 species level, counted, and returned to the river (except for a sub-sample collected for
193 SCA; see above). Due to large river widths and depths, no nets were used to block the
194 upstream and downstream boundaries. The fish density was estimated as number of fish
195 per 100 m² using Zippin multiple-pass depletion method (Zippin, 1956; Bohlin, Hamrin,
196 Heggberget, Rasmussen, & Saltveit, 1989). This covariate (fish density) covered the
197 dominant species in these fish communities, including brown trout density (as a proxy of
198 intraspecific competition) and Atlantic salmon density (as a proxy of interspecific
199 competition).

200

201 *Ecological opportunity*

202 The ecological opportunity was defined by Stroud & Losos (2016) as “the availability of
203 ecologically accessible resources that may be evolutionarily exploited”, but it can also be
204 considered as abundance or density of resources (Wellborn & Langerhans, 2015). Thus,
205 ecological opportunity can be decomposed into two components, i.e. taking into account
206 abundance and/or diversity of niche availability. We estimated ecological opportunity
207 from the availability of benthic invertebrates, which are the prime food resource for
208 brown trout parr and juveniles (e.g. Sánchez-Hernández, Finstad, Arnekleiv, Kjærstad, &
209 Amundsen, 2019). It should be noted that benthic communities may reflect spatial
210 differences in the drift compositions among riverine systems as there is a positive
211 relationship between benthic and drift invertebrates (e.g. Sagar & Glova, 1992; Siler,
212 Wallace, & Eggert, 2001; Shearer, Stark, Hayes, & Young, 2003). Diptera (mainly
213 Chironomidae), Ephemeroptera, Plecoptera and Trichoptera are commonly the most
214 abundant drifting invertebrates over the ice-free season in Norwegian rivers (e.g.
215 Johansen, Elliott, & Klemetsen, 2000; Saltveit, Haug, & Brittain, 2001). The contribution
216 of surface prey (terrestrial arthropods and emerged aquatic insects) to the drift in
217 Norwegian rivers may also be noteworthy (Johansen et al., 2000). Unfortunately, no
218 information is available about drift patterns or magnitude of terrestrial subsidies into the
219 studied rivers and drifting invertebrates could therefore not be included in the analysis.
220 Since brown trout individuals were collected from riffles, we also sampled benthic
221 invertebrates from the same riffle habitats. Following protocols for quantitative sampling
222 in wadeable and hard-bottomed streams (Stark, Boothroyd, Harding, Maxted, &
223 Scarsbrook, 2001), five benthic invertebrate samples were collected using a 0.15 m²
224 Surber sampler (500 µm mesh size) at each sampling event. After collection, we fixed the
225 samples using 70% ethanol and stored them for later processing. In the laboratory, the
226 benthic invertebrates were sorted and identified to the same taxonomic level as for the

227 stomach contents. We partitioned ecological opportunity into two components: (i) prey
228 diversity, and (ii) prey density (number of individuals per m²). Because dietary indices
229 used in this study (see *Components of the trophic niche section* below) rely on prey
230 categories and their relative abundance, we also explored the importance of the absolute
231 abundance of the most represented prey categories. These prey categories included
232 Chironomidae, Ephemeroptera, Hydracarina, Oligochaeta, Plecoptera, Simuliidae and
233 Trichoptera (see Appendix 1), which includes primary dietary components of stream-
234 dwelling brown trout populations (i.e. Diptera, Ephemeroptera, Trichoptera and
235 Plecoptera) (Sánchez-Hernández et al., 2019). Thus, we covered total prey density and
236 absolute abundance of the most represented prey categories.

237 Prey diversity was calculated as taxon richness (i.e. number of taxa of benthic
238 invertebrates) and Shannon-Wiener's diversity index (hereafter "Shannon index"):

239

$$240 \text{ Shannon index } (H') = - \sum_{i=1}^s p_i \log_{10} p_i \quad \text{Eq. 1}$$

241

242 where p_i is the proportion of individuals found in species i and s is the number of species
243 in the benthic invertebrate samples (Shannon & Weaver, 1949). The use of these two
244 indices (taxon richness and Shannon index) enabled us to account for the structural
245 complexity of the benthic invertebrate community including only diversity (taxon
246 richness) and relative abundances (Shannon index).

247

248 *Realised and potential trophic niches*

249 Fundamental niche refers to the sum of all the environmental factors acting on the
250 organism, including both abiotic and biotic variables (Hutchinson, 1944; 1957), but here

251 we restrict our niche analyses to the diversity of available prey resources (i.e. ecological
252 opportunity) as a proxy of the potential trophic niche. The potential trophic niche consists
253 of all prey categories that the brown trout is able to consume (i.e., the availability of prey
254 resources in the environment). In contrast, the realised trophic niche is the variety of
255 organisms that actually are eaten. An exploration of the realised *versus* the potential
256 trophic niches of the model organism was carried out using the Outlying Mean Index
257 (OMI) (Dolédec et al., 2000) in the subniche package version 1.2 (Karasiewicz, Dolédec,
258 Lefebvre, 2017). This enabled us to disentangle how different the realised niches are from
259 the potential trophic niches, as well as to compare the species' realised trophic niches
260 along spatial scales (here among rivers).

261

262 *Diet selectivity*

263 We explored diet selectivity of brown trout by employing Chesson's selectivity index
264 (Chesson, 1983) and using data from all sampling events based on nine common prey
265 categories (Sánchez-Hernández et al., 2019): (i) benthic Crustacea, (ii) Mollusca, (iii)
266 Diptera larvae, (iv) Trichoptera larvae, (v) Coleoptera (both larvae and adults), (vi)
267 Heteroptera, (viii) Ephemeroptera nymphs, (viii) Plecoptera nymphs and (ix) other
268 benthic invertebrates (mostly Hydracarina, Oligochaeta, Turbellaria and Hirudinea). In
269 mathematical terms, Chesson's index (S) is based on proportional data:

270

$$271 \quad S = \frac{d_i/b_i}{\sum_{j=1}^m d_j/b_j}, i = 1, \dots, m, \quad \text{Eq. 2}$$

272

273 where d and b are the relative abundance of each prey category in the diet and in the
274 benthic invertebrate community, respectively (Chesson, 1983). This index varies from
275 zero (complete avoidance) to one (complete preference).

276

277 *Components of the trophic niche*

278 We addressed dietary niche variation at the population and individual levels using the
279 RInSp package version 1.2.3 (Zaccarelli, Bolnick, & Mancinelli, 2013). The total niche
280 width of a population (TNW) can be partitioned into two components: (i) the within-
281 individual component (WIC, i.e. the variation in resource use within individuals) and (ii)
282 the between-individual component (BIC, i.e. the variance between individuals), so that
283 $TNW = WIC + BIC$ (Roughgarden, 1972; 1974; Bolnick et al., 2002):

284

285
$$TNW = - \sum_k q_k \ln(q_k) \quad \text{Eq. 3}$$

286

287
$$WIC = - \sum_i r_i \left(- \sum_k r_{ik} \ln(p_{ik}) \right) \quad \text{Eq. 4}$$

288

289
$$BIC = - \sum_k r_i \ln(r_i) - \sum_k q_k \left(- \sum_i t_{ik} \ln(t_{ik}) \right) \quad \text{Eq. 5}$$

290

291 where: r_i is the proportion of all resources used by individual i ; q_k is the proportion of the
292 k th resource category in the population's niche, and t_{ik} is the proportion of the
293 population's total use of resource k that was used by individual i (Zaccarelli et al., 2013).
294 The ratio WIC/TNW (inter-individual diet variation) quantifies how much smaller the
295 average individual niche is in comparison to the population niche (Araújo et al., 2011).
296 Values near 1 indicate low inter-individual diet variation (i.e. all individuals utilise the
297 full range of the population's niche), whereas values near 0 indicate decreasing inter-
298 individual overlap and hence a higher degree of individual specialisation (Bolnick et al.,

299 2002). To distinguish between more and less specialised individuals within the
300 populations, the proportional similarity (PS_i) index was calculated (Bolnick et al., 2002):

301

$$302 \quad PS_i = 1 - 0.5|P_{ij} - Q_j| = \sum(P_{ij}, Q_j) \quad \text{Eq. 6}$$

303

304 where P_{ij} is the proportion of resource category j in the diet of individual i , and Q_j the
305 proportion of resource category j in the diet of the population. This index compares each
306 individual's diet to that of the population, with values ranging between 0 and 1 ($0 < PS_i$
307 < 1). For individuals that specialise on a single or few prey types, PS_i values are low,
308 whereas for individuals that consume resources in a similar proportion to the population
309 as a whole, PS_i values approach 1 (Bolnick et al., 2002). Thus, niche variation includes
310 several indices that reflect the population and individual level (TNW, WIC, BIC,
311 WIC/TNW and PS_i).

312

313 *Statistics*

314 All analyses and visualization were carried out using R version 3.6.2 (R Core Team,
315 2019). A significance level of $P = 0.05$ was used for all analyses. The following
316 subsections show the methodological sequence in our analyses.

317

318 Normality checking and data transformation

319 Prior to modelling, data normality was tested. There were indications of non-normality in
320 some of the variables (Kolmogorov-Smirnov tests with Lilliefors correction), and WIC,
321 WIC/TNW, prey diversity (richness), total prey density and absolute abundance of the
322 most represented prey categories (i.e. densities of Chironomidae, Ephemeroptera,

323 Hydracarina, Oligochaeta, Plecoptera, Simuliidae and Trichoptera) were log-transformed
324 before the analysis (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

325

326 Linear models

327 We used linear models to explore simple cause-and-effect associations between the
328 response variable (prey selectivity and trophic niche components) and explanatory
329 variables. We first tested for relationship between prey selection (Chesson's index) as
330 response variable and the relative abundance of the same taxonomic group in the benthos
331 as predictor in order to explore whether brown trout populations select certain prey
332 categories irrespective of their relative availability (Sánchez-Hernández et al., 2019).
333 Secondly, in order to test how the various trophic niche components related to ecological
334 opportunity, we fitted a set of linear models with trophic niche components (TNW, WIC,
335 BIC, WIC/TNW or PS_i) as response variable, and prey diversity (taxon richness and
336 Shannon index) or prey density (total prey density, Chironomidae density, Ephemeroptera
337 density, Hydracarina density, Oligochaeta density, Plecoptera density, Simuliidae density
338 and Trichoptera density) as predictors.

339

340 Multiple regression models

341 We fitted a set of multiple regression models with the various trophic niche components
342 as response variable and prey diversity (taxon richness and Shannon index), prey density
343 (Chironomidae density, Ephemeroptera density, Hydracarina density, Oligochaeta
344 density, Plecoptera density, Simuliidae density and Trichoptera density) and mean fish
345 length (as a proxy of population size structure) as predictors. Spatial (sampling stations
346 and river) and size (fish length) effects were included as covariates in all multiple
347 regression models since ontogeny, population size structure and environmental

348 heterogeneity linked to geographic location play a key role in the trophic ecology of
349 brown trout (Sánchez-Hernández, Eloranta, Finstad, & Amundsen, 2017b; Sánchez-
350 Hernández et al., 2019), which calls for the need to control for them (i.e. controlling
351 variables) in the analyses.

352

353 Multiple regression models were also re-run for a subset of the data that included fish
354 densities (Atlantic salmon and brown trout; see section “Fish density”) in order to
355 disentangle the role of inter- and intraspecific competition on trophic niche components.
356 In this case, the full model consisted of trophic niche components as response variable,
357 12 predictor variables (taxon richness, Shannon index, fish length, intraspecific
358 competition, interspecific competition, Chironomidae density, Ephemeroptera density,
359 Hydracarina density, Oligochaeta density, Plecoptera density, Simuliidae density and
360 Trichoptera density) and the interaction term between intra- and interspecific
361 competition. These additional analyses allowed a better foundation for exploring the
362 drives of niche variation based on the integration of multiple factors in the modelling.

363

364 Nested design of models (both linear and multiple)

365 Since several stations were sampled within each river, there may be a dependency
366 between sampling stations due to a nested design. Hence, we started out with the above-
367 mentioned full structure of linear and multiple regression models incorporating sampling
368 stations nested within each river as a random factor. Sampling time (month) was entered
369 as GAM smoother terms in order to account for unobserved seasonal effects (generalised
370 additive mixed model fitted with the mgcv package version 1.8.28; Wood, 2017). We
371 tested for the inclusion of random terms into the models with a likelihood ratio test
372 according to Zuur et al. (2009). Except for linear models exploring TNW and BIC over

373 prey density, there was no indication of sampling stations nested within a river
374 contributing to the overall fit in any of the models (P -value > 0.05 , allowing us to accept
375 the null hypothesis that the models are similar). Hence, modelling (both linear and
376 multiple) was conducted without random terms, but including smoother terms for month
377 (generalised additive models).

378

379 Choosing the best model structure in multiple regression approaches

380 For the multiple regression approaches, we used Δ AIC based model selection (Burnham
381 & Anderson, 2002) to select the optimal fixed effects structure and rank candidate models
382 by model comparison using the MuMIn package version 1.40.0 (Bartoń, 2016). Models
383 with Δ AIC < 2 relative to best model were considered to have substantial support
384 (Burnham & Anderson, 2002). In all cases, there were several competing models within
385 the designated confidence set, and we conducted parameter estimation and explored
386 relative importance using model averaging (MuMIn package).

387

388 Bootstrapping replication

389 In order to generate robust interpretations overcoming possible problems with
390 heterogeneous data collection and unbalanced design, we applied bootstrapping
391 techniques with 999 replications in: i) the measure of the components of the trophic niche
392 (Zaccarelli et al., 2013), ii) the exploration of differences among rivers in subniche
393 position using the *rtest.discrimin* function (Chessel, Dufour, & Thioulouse, 2004), and
394 iii) the estimation of confidence intervals for the model coefficients (Wood, 2004;
395 Nakagawa & Cuthill, 2007) using the boot package version 1.3.22 (Canty & Ripley,
396 2019). In the case of models, we assumed that when observed and predicted

397 (bootstrapped) 95% confidence intervals were similar in data visualization, associations
398 between explanatory and response variables were reliable.

399

400 Model testing

401 Residuals of the final selected models were visually inspected for deviations from
402 normality and heteroscedasticity. Overall, no evidence for violation of model assumptions
403 were found in all cases except for four prey categories (Coleoptera, Crustacea, Mollusca
404 and Coleoptera) out of nine prey categories when modelling Chesson's selectivity index.

405

406 **Results**

407 *Ecological opportunity and diet selectivity*

408 Ephemeroptera was the most abundant taxon in the three river systems, representing
409 (mean \pm S.E.) 42.7% \pm 3.4 (Beiarelva), 34.5% \pm 4.1 (Klubbvasselva) and 30.9% \pm 7.8
410 (Litjvasselva) of the total number of individuals. Less numerous in the benthos, but still
411 abundant in all sampling events were Chironomidae (see Appendix 1). Regarding
412 stomach contents, Chironomidae (mean \pm S.E., 25.2% \pm 0.55 and 25.5% \pm 1.10 in
413 Beiarelva and Klubbvasselva, respectively) and Ephemeroptera (27.5% \pm 1.66 in
414 Litjvasselva) emerged as the primary dietary components of brown trout, with substantial
415 spatial variations within these taxon among rivers (see Appendix 2). Prey abundance and
416 seasonal effects had influence on diet selectivity (Appendix 3). The selection of the
417 dominant prey taxa (Trichoptera, Diptera, Ephemeroptera and Plecoptera) was negatively
418 linked to prey abundance (Figure 3), showing that brown trout preferred to consume prey
419 categories irrespective of their relative abundance in the environment.

420

421 *Realised and potential trophic niches*

422 Brown trout had broader realised trophic niches in Beiarelva (Figure 4a) and
423 Klubbvasselva (Figure 4b) than in Litjvasselva (Figure 4c); a pattern that was closely
424 linked to taxon richness (Beiarelva>Klubbvasselva>Litjvasselva) (Appendix 4). There
425 were differences in the realised trophic subniches among rivers ($P = 0.001$), with
426 Klubbvasselva having the broadest subniche (Figure 4d). Klubbvasselva and Litjvasselva
427 extended their subniches along the upper-left and bottom-left parts because of their higher
428 consumption on Planorbidae and Megaloptera, respectively (Figure 4e and Appendix 2).
429 Indeed, several prey categories (Ostracoda, Lymnaeidae, Planorbidae, Ceratopogonidae,
430 Simuliidae, Ephemeroptera, Plecoptera, Oligochaeta, surface prey and fish) were
431 responsible for the differences in the among-river comparisons (Table 1, see Appendix 2
432 for stomach contents).

433

434 *Components of the trophic niche*

435 We found a positive relationship between: i) prey diversity (both Shannon index and
436 taxon richness) and TNW, ii) WIC and the Shannon index, and iii) BIC and taxon richness
437 (Figure 5 and summary table in Appendix 4). PS_i decreased with increasing Shannon
438 index and taxon richness (Figure 5). There was also consistent seasonal variation in some
439 trophic niche components (TNW, BIC and PS_i) (Appendix 4). There was in contrast little
440 support for any relationship between the trophic niche components and prey density, both
441 measured as absolute abundance of the most represented prey categories (Figure 5 and
442 Appendix 4) and total prey density (Appendix 4).

443 Multiple regression models (outputs from the model averaging are shown in the Appendix
444 5) showed the combined effect of prey diversity and absolute abundance of some key
445 prey categories (mainly Chironomidae, Oligochaeta and Ephemeroptera) on the
446 components of the trophic niche (Tables 2 and 3). With exception of WIC/TNW, the

447 model output supported the importance of prey diversity in combination with
448 Chironomidae density (TNW, BIC and PS_i) and Oligochaeta density (WIC) as a drivers
449 for the trophic niche components at both the population and individual levels according
450 to the best model configuration (Table 2) and the relative importance measure (Table 3).
451 Among the ecological opportunity measures, taxon richness emerged as the main driver
452 for PS_i , while TNW and BIC had similar support of taxon richness and Chironomidae
453 density and WIC from a combined effect of the Shannon index and Oligochaeta density
454 (Table 3). There was also consistent seasonal variation in the trophic niche components
455 (TNW, BIC and PS_i), as evident from the strong support of the GAM smoother variable
456 (month), which was included in all top-confidence sets of the model selection (Appendix
457 5 and Table 3). Most trophic niche components (TNW, WIC, BIC and WIC/TNW)
458 increased from April to July, but thereafter tended to decrease, whereas the opposite
459 pattern was observed for PS_i (Figure 6). Our best model configurations indicated a
460 positive effect of population size structure (i.e. mean fish length) on all the trophic niche
461 components (Table 2, also see all top-confidence sets in Appendix 5), which is also in
462 line with the relative importance measure (especially in WIC and WIC/TNW, Table 3).

463

464 *Components of the trophic niche (re-run including fish density)*

465 When the models were re-run for a subset of the data that included fish densities, the best
466 model configurations showed that inter- and intraspecific competition had little
467 importance compared to the other predictors (Table 4), with the exception of interspecific
468 competition having a negative effect on WIC and WIC/TNW (Appendix 6). Overall,
469 scenarios of higher inter- and intraspecific competition drove individuals to reduce their
470 individual variation (WIC) and specialise (WIC/TNW) in resource use according to the
471 models with substantial support ($\Delta AIC < 2$) (Appendix 6), but the competition effect

472 seemed to be masked by the stronger effect of ecological opportunity (both prey diversity
473 and Chironomidae density) and population size structure on the components of the trophic
474 niche (Table 4).

475

476 **Discussion**

477 This study brings novel insights to the understanding of individual and population niche
478 variation of animals and in particular of freshwater fish. Our multiple regression analyses
479 indicated that the abundance of certain resources (e.g. Chironomidae) can interact with
480 prey diversity to determine individual and population realised trophic niches. However,
481 we provided evidence that prey diversity, rather than density, is the major factor shaping
482 the trophic niche components of the studied predator as no simple cause-and-effect
483 associations between prey abundance and niche indices were found. We accept the view
484 that prey patchiness and broad potential trophic niches are fundamental to understand
485 niche extension or compression of animals (e.g. Tinker et al., 2008; Svanbäck et al., 2011;
486 Costa-Pereira et al., 2019), but diversity of available resources can have a stronger effect
487 on individual and population trophic realised niches than the constraining effects of
488 resource abundance (see Figure 1). We posit that scenarios with food resource limitation
489 (low prey density) may promote niche compression in consumer's population when prey
490 diversity is low, but rather lead to niche extension when prey diversity is high.

491

492 *Prey availability effects on niche variation*

493 We identified that niche variation increased with increasing prey diversity at the
494 population level via specialist individuals, supporting other studies concluding that
495 environments with high prey diversity can promote high intraspecific niche variation and
496 segregation in resource use by specialisation among competing consumers (Araújo et al.,

497 2011; Araújo & Costa-Pereira, 2013; Sánchez-Hernández et al., 2017a; Salvidio et al.,
498 2019; Rosa et al., 2020). Our study confirms that prey diversity *per se* can be more
499 important than prey density for dietary specialisation and niche variation both at the
500 population and individual levels. Generally, we identified that higher relative abundance
501 of available resources did not drive diet selectivity, which underlines that prey selection
502 patterns are complex and depend on the balance between diversity, density and
503 accessibility (i.e., patchiness) of available prey resources as well as intrinsic features of
504 the predator population (e.g. size-structured dominance hierarchies and personality traits
505 linked to boldness and experience of individuals; Reiriz, Nicieza, & Braña, 1998;
506 Harwood, Armstrong, Griffiths, & Metcalfe, 2002; Johnson, Coghlan & Harmon, 2007).
507 Although it is difficult to predict how predators respond to changes in prey availability,
508 we conclude that trophic niche utilisation and partitioning is better explained by prey
509 diversity. Our reasoning relies on the fact that increased prey diversity according to niche
510 theory should enhance the possibility of resource partitioning among individuals and
511 species (Sánchez-Hernández et al., 2017a and references therein). Feeding habits of
512 consumers, and thus niche variation, can be limited either by low prey abundance or high
513 consumer abundance (e.g. Araújo et al., 2011; Costa-Pereira, Tavares Camargo & Araújo,
514 2017). Some sampling events included high consumer densities (range: 0.01-0.47 and 0-
515 0.65 ind./m² for brown trout and Atlantic salmon, respectively) according to a previous
516 categorisation of salmonids densities (Table 3 in Sánchez-Hernández, Cobo, &
517 Amundsen, 2015). However, it is possible that prey densities were not low enough (range:
518 43.9-4351.7 ind./m²) to limit food consumption in comparison to other riverine systems
519 with substantially higher variation in benthic macroinvertebrate production (e.g. range:
520 7-12249 ind./m²; Miserendino, 2001). Thus, we accept the view that behavioural
521 diversification in feeding is primarily driven by prey diversity under scenarios with no

522 extensive food resource limitation, whereas prey density may become more important
523 when resource limitations are severe.

524 Our study supports recent conclusions that increased ecological opportunity promotes
525 population niche expansion through individual resource specialisation (i.e. strict
526 phenotypic or behavioural differentiation) of predators rather than a generalist feeding
527 strategy (Sjödín et al., 2018). These findings are consistent with a recent study in the
528 Alpine newt, *Ichthyosaura alpestris* (Laurenti, 1768), demonstrating that high ecological
529 opportunity in terms of prey diversity promotes higher individual specialisation (Salvidio
530 et al., 2019). Unlike Araujo et al. (2011) who concluded that individual niche width
531 (WIC) depends on the diversity of available resources, the individual's phenotypic traits
532 and resource abundance, our findings showed that individual niche width and
533 specialisation rely on prey diversity rather than prey abundance. Caution should however
534 be exercised regarding this conclusion as contradictory outcomes were found between
535 two indices measuring the degree of individual specialisation (PS_i and WIC/TNW). The
536 proportional similarity index (PS_i) showed a negative association with prey diversity
537 measured both by species richness and Shannon index, whereas the inter-individual diet
538 variation (WIC/TNW) in contrast suggested that individual specialisation decreased with
539 increasing prey diversity measured as Shannon index (Figure 5). A disadvantage of
540 WIC/TNW is that it assumes that resources are evenly distributed, maximised both by
541 many diet categories and an equal utilisation of each prey type, which in some cases may
542 bias the measurements and lead to inaccurate conclusions in respect to generalisation
543 versus specialisation (reviewed by Bolnick et al., 2002). Bolnick et al. (2002) also pointed
544 out that if resources are measured in a coarse-grained manner, which partly is the case in
545 the present study (see Appendices 1 and 2, i.e. mostly family level), the individuals may
546 falsely appear as generalised from the WIC/TNW ratio. WIC/TNW and PS_i could also be

547 overestimated with calculations based on single feeding events and more attention needs
548 to be paid in the future to multiple feeding events or diet-tracing techniques other than
549 stomach contents analysis, such as stable isotopes (Bearhop, Adams, Waldron, Fuller, &
550 Macleod, 2004; Sheppard et al., 2018), in order to enhance our understanding about niche
551 variation at the population and individual levels.

552 The view that variation in available prey types is a keystone in determining patterns of
553 individual niche variation is increasingly supported (e.g. Darimont, Paquet, & Reimchen,
554 2009; Robertson, McDonald, Delahayb, Kellyd, & Bearhop, 2015; Costa-Pereira et al.,
555 2019; Salvidio et al., 2019). For example, Yurkowski et al. (2016) observed an increasing
556 total niche width with increasing prey diversity in Arctic marine predators. Moreover,
557 Costa-Pereira et al. (2019) have recently provided empirical evidence that individual
558 niche breadth of tropical frog species increases with resource diversity. The present study
559 supports the previous findings demonstrating that trophic niche components increase with
560 enhanced ecological opportunity in terms of increased prey diversity. However, our study
561 also provides a novel empirical insight into the driving forces behind niche variation and
562 contributes to expanding prevailing trophic ecology theory by identifying diversity, rather
563 than density, of available prey resources as a primary driver of niche variation.

564

565 *Competition effects on niche variation*

566 Our findings suggest that higher inter- and intraspecific competition drive individuals to
567 reduce their niche variation (i.e. variation in resource use within individuals) and thereby
568 reduce niche diversification by among-individual differences in resource specialisation.
569 In line with the niche variation hypothesis (Van Valen, 1965), the direction of the effects
570 (compress or expand) of intra- and interspecific competition on niche variation can be
571 variable, chiefly depending on differences in rank-preference variation among individuals

572 and species (Araújo et al., 2011). Sheppard et al. (2018) observed that intragroup
573 competition promotes niche partitioning through individual specialisation within social
574 groups in a terrestrial mammal [banded mongooses *Mungos mungo* (Gmelin, 1788)]. Our
575 data suggest that higher consumer densities (i.e. both inter- and intraspecific competition)
576 drove individuals to reduce their individual niche width and specialise in resource use.
577 This support the findings of Svanbäck & Persson (2004), Tinker et al. (2012) and Mendes
578 et al. (2019), which suggested that increased intraspecific competition (i.e. population
579 density) promotes individual specialisation in perch (*Perca fluviatilis* L.), sea otters
580 [*Enhydra lutris* (Linnaeus, 1758)] and neotropical fish species [*Hoplerythrinus*
581 *unitaeniatus* (Spix & Agassiz, 1829)], respectively.

582 As pointed out earlier, the effect of competition on consumer diet variation may be
583 context dependent and driven by e.g. rank-preference variation among individuals/species
584 (Araújo et al., 2011). Indeed, Jones & Post (2016) have recently proposed that species
585 with large ecological top-down effects (i.e. predators) respond to increasing intraspecific
586 competition by niche compression at the population level, whereas other consumers may
587 respond with diversifying their niche. Although our results suggest that increased inter-
588 and intraspecific competition may reduce the variation in resource use within individuals,
589 we posit that prey diversity rather than competition acts as the main driver of niche
590 variation. Hence, in systems with no apparent resource limitation as in the current study,
591 variation in prey diversity may mask the direction of the effect of competition on niche
592 variation when food resources are diverse, advocating that the diversifying effects of
593 ecological opportunity have a stronger effect on dietary niche width than the constraining
594 effects of competition (Costa-Pereira et al., 2019).

595

596 *Conclusions*

597 Our study provides novel empirical insight to the driving forces behind niche variation
598 and reveals that diversity, rather than density, of available prey resources may be a
599 primary driver of niche variation in freshwater fish. Conclusions from the current study
600 should be contextualised in a scenario where the trophic niche components reflect a
601 population's realised trophic niche, while ecological opportunity in terms of prey
602 diversity reflects the potential trophic niche. Soberón & Arroyo-Peña (2017) empirically
603 tested in reptiles and amphibians that fundamental niches are wider than the realised
604 niches. Our study provides compelling evidence that differences in taxa richness among
605 riverine systems determined the degree to which the realised and potential trophic niches
606 differ. Thus, the current study supports the view that broader potential trophic niches
607 promote broader realised trophic niche variation of individuals, which lead to individual
608 niche diversification by opening access to alternatives resources while niche overlap
609 among individuals tends to decrease (Figure 1).

610

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622

623 **Data accessibility**

624 Data from the manuscript will be archived in the Figshare Digital Repository
625 (<https://figshare.com/>) on acceptance of the manuscript for publication.

626

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822 **Figure legends**

823 Figure 1. Conceptual view of the effect of ecological opportunity in terms of prey
824 diversity on components of the trophic niche (TNW = total niche width of a population
825 [yellow arrows], BIC = between-individual component [blue arrows], and WIC = within-
826 individual component [orange arrows]). This conceptual view illustrates that prey
827 diversity, and not prey density, act as the true bottleneck in driving predator niche
828 variation because the diversity of available resources limits the baseline from where
829 individuals can segregate in prey utilization. Arrows and boxes in red represent scenarios
830 under resource limitations (both low prey abundance and diversity), whereas the opposite
831 (high prey abundance and diversity) is presented in green. Dashed arrows show potential
832 predator-prey interactions under the two scenarios (red = resource limitations and green
833 = no resource limitations).

834

835 Figure 2. Map of Norway showing the location of the sampling sites used in this study
836 and annual mean temperatures (°C) according to Worldclim (Hijmans, Cameron, Parra,
837 Jones, & Jarvis, 2005) (A). Finer location of sampling sites in Beiarelva (B) and
838 Litjvasselva and Klubbvasselva (C).

839

840 Figure 3. Linear relationships between Chesson selectivity index of brown trout and the
841 relative contribution (%) of each prey type in the benthos (A-H) showing that prey
842 categories are consumed irrespective of their relative abundance in the environment. Note
843 that Chesson's index is based on proportional data, so no units are displayed. This index
844 varies from zero (complete avoidance) to one (complete preference). Fitted line (red line)
845 is shown in all models, whereas 95% confidence intervals (black lines) and bootstrapped
846 95% confidence intervals (dashed lines) only are shown for statistically significant

847 relationships. 95% confidence limits intervals were reliable in Diptera (C),
848 Ephemeroptera (F) and Plecoptera (G). Model outputs are available in Appendix 3.

849

850 Figure 4. OMI (Outlying Mean Index) analysis showing realised (prey used by brown
851 trout) and potential trophic niches (prey resources that are accessible and potentially can
852 be utilised by brown trout). The blue polygon represents the overall diversity of available
853 resources (potential trophic niches) and the orange polygon represents the realised trophic
854 niche (resource use) of brown trout for each river system (A, B and C). The part D shows
855 subniche (realised) positions according to riverine systems compared to the potential
856 trophic niche (blue polygon). The scatterplot (E) illustrates prey' niche positions in red
857 and canonical weights of available prey categories (potential trophic niches) in black of
858 the among-riverine comparison (D).

859

860 Figure 5. Linear relationships between trophic niche components and ecological
861 opportunity (Shannon index, taxon richness and prey density). Note panels about prey
862 density only included most relevant prey categories according to our best models (Table
863 1). TNW = total niche width of a population (A-C), WIC = within-individual component
864 (D-F), BIC = between-individual component (G-I), WIC/TNW = inter-individual diet
865 variation (J-L) and PS_i = individual specialisation (M-O). Fitted line (red line) is shown
866 in all models, but 95% confidence intervals (black lines) and bootstrapped 95%
867 confidence intervals (dashed lines) only are shown for statistically significant
868 relationships. 95% confidence limits intervals were reliable in all cases. Model outputs
869 are available in Appendix 4.

870

871 Figure 6. Violin plots showing the seasonal (month) variation of the components of
872 ecological opportunity (A-C) and trophic niche components (D-H). Statistically
873 significant seasonal effects were found only for total niche width of a population (TNW)
874 and individual specialisation (PS_i), see Table 2 for all model configurations. WIC =
875 within-individual component, BIC = between-individual component and WIC/TNW =
876 inter-individual diet variation. April = 4, June = 6, July = 7, August = 8, September = 9,
877 and October = 10. Seasonal variation of the absolute abundance of the most represented
878 prey categories (Chironomidae, Ephemeroptera, Hydracarina, Oligochaeta, Plecoptera,
879 Simuliidae and Trichoptera) is shown in the Appendix 4.

880

881 **Tables**

882 Table 1. OMI (Outlying Mean Index) analysis for prey categories showing the
 883 comparison between the utilised prey (realised trophic niche) and prey resources that are
 884 accessible and potentially can be utilised by the focal species (simulated potential trophic
 885 niche). Surface prey = unidentified terrestrial arthropods and emerged aquatic insects, L
 886 = larvae and N = nymph. The *P*-values were calculated with 999 permutations, see
 887 methods for further details. Statistically significant outcomes are marked in bold.

Prey category	Code	Outlying Mean Index (OMI)	Standard deviation of OMI	<i>P</i> -value
Ostracoda	Ost	10.8	2.784	0.029
Lymnaeidae	Lym	12.7	4.511	0.002
Planorbidae	Pla	57.0	3.685	0.002
Diptera (L)	Dip	7.3	1.915	0.062
Chironomidae (L)	Chi	0.1	0.399	0.312
Ceratopogonidae (L)	Cer	6.0	2.283	0.039
<i>Pericoma</i> sp. (L)	Psy	4.2	-0.211	0.396
Simuliidae (L)	Sim	1.7	5.223	0.001
Tipulidae (L)	Tip	1.2	0.200	0.311
Trichoptera (L)	Tri	0.1	0.905	0.176
Coleoptera	Col	1.5	-0.119	0.439
Hemiptera (Heteroptera)	Hem	3.5	-0.658	0.898
Ephemeroptera (N)	Eph	0.1	4.464	0.001
Plecoptera (N)	Ple	0.2	2.979	0.006
Hydracarina	Hyd	1.0	-0.073	0.461
Megaloptera (L)	Meg	46.4	1.183	0.133
Oligochaeta	Oli	1.4	3.322	0.007
Copepoda	Cop	17.5	1.607	0.082
Collembola	Coll	3.3	-0.451	0.511
Surface prey	Ins	0.5	3.977	0.001
Fish	Fis	5.2	2.669	0.019

888

889 Table 2. Summary table of the selected models according to ΔAIC values (see Appendix
890 5 for model selection table including models with $\Delta AIC < 2$ relative to best model)
891 explaining the niche variation at the individual and population levels of brown trout. Total
892 niche width of a population (TNW), within-individual component (WIC), between-
893 individual component (BIC), inter-individual diet variation (WIC/TNW), individual
894 specialisation (PS_i), and ecological opportunity [in terms of diversity (Shannon index and
895 taxon richness) and prey density]. Seasonal effects = s(Month). Edf = estimated degree
896 of freedom for smooth terms are shown. Bootstrapped 95% confidence intervals (CI) for
897 parametric coefficients. Statistically significant model fits are marked in bold.

		<i>Dependent variable (components of the trophic niche of brown trout)</i>				
		TNW	WIC	BIC	WIC/TNW	PS_i
<u>Parametric coefficients</u>						
Constant (Intercept)	Estimate	1.040	0.015	1.013	0.050	0.401
	<i>t</i> -value	5.513 (<i>P</i><0.001)	0.523 (<i>P</i> =0.603)	5.579 (<i>P</i><0.001)	3.157 (<i>P</i>=0.002)	9.212 (<i>P</i><0.001)
	CI	0.756, 1.337	-0.0492, 0.0743	0.689, 1.282	0.0248, 0.0853	0.3203, 0.4890
Fish length (mm)	Estimate	0.002	0.0004	—	0.0003	-0.0004
	<i>t</i> -value	1.439 (<i>P</i> =0.155)	1.452 (<i>P</i> =0.151)	—	1.661 (<i>P</i> =0.101)	-1.527 (<i>P</i> =0.131)
	CI	-0.0014, 0.0047	-0.0001, 0.0010	—	0.0000, 0.0006	-0.0010, 0.0002
Richness	Estimate	0.338	—	0.361	—	-0.070
	<i>t</i> -value	3.553 (<i>P</i><0.001)	—	4.003 (<i>P</i><0.001)	—	-3.183 (<i>P</i>=0.002)
	CI	0.1828, 0.5454	—	0.2077, 0.5302	—	-0.1256, -0.0254
Shannon	Estimate	—	0.043	—	—	—
	<i>t</i> -value	—	2.821 (<i>P</i>=0.006)	—	—	—
	CI	—	0.0122, 0.0814	—	—	—
Chironomidae density (ind/m ²)	Estimate	-0.048	—	-0.039	—	0.006
	<i>t</i> -value	-2.775 (<i>P</i>=0.007)	—	-2.775 (<i>P</i>=0.021)	—	1.592 (<i>P</i> =0.116)
	CI	-0.0795, -0.0078	—	-0.0760, -0.0012	—	-0.0034, 0.0142
Ephemeroptera density (ind/m ²)	Estimate	—	—	—	-0.003	—
	<i>t</i> -value	—	—	—	-1.291 (<i>P</i> =0.201)	—
	CI	—	—	—	-0.0074, 0.0010	—
Oligochaeta density (ind/m ²)	Estimate	—	-0.010	—	-0.005	—
	<i>t</i> -value	—	-3.320 (<i>P</i>=0.001)	—	-2.485 (<i>P</i>=0.015)	—
	CI	—	-0.0175, -0.0023	—	-0.0094, 0.0000	—
<u>Smooth terms</u>						
Seasonal effects	Edf	1.617	—	1.557	—	1.761
	<i>F</i> -value	1.617 (<i>P</i>=0.044)	—	4.208 (<i>P</i> =0.057)	—	5.589 (<i>P</i>=0.014)
Observations		73	73	73	73	73
Adjusted R ²		0.31	0.20	0.30	0.10	0.31
GCV		0.030	0.002	0.029	0.001	0.002
Deviance explained		35.3	23	33.7	14	35.3

898

899 Table 3. Relative variable importance of the best models according to model averaging
900 ($\Delta AIC < 2$) (see Appendix 5 for model selection table including models with $\Delta AIC < 2$
901 relative to best model) showing the most influential variables responsible of niche
902 variation at the individual and population levels. Total niche width of a population
903 (TNW), within-individual component (WIC), between-individual component (BIC),
904 inter-individual diet variation (WIC/TNW), individual specialisation (PS_i). n = number
905 of containing models. The relative variable importance ranges from 0 to 1, and thus 1
906 indicates that a variable was included in all models with substantial support. The most
907 important variables in each model are marked in bold.
908

	TNW		WIC		BIC		WIC/TNW		PS_i	
	Importance	Models (n)	Importance	Models (n)	Importance	Models (n)	Importance	Models (n)	Importance	Models (n)
<u>Predictor variables</u>										
Shannon	0.06	2	1.00	11	0.15	2	0.34	7	0.09	3
Richness	1.00	21			1.00	11	0.13	3	1.00	29
Fish length (mm)			0.92	10	0.20	2	0.92	20	0.64	19
Chironomidae density (ind/m ²)	1.00	21	0.07	1	1.00	11	0.07	2	0.40	11
Plecoptera density (ind/m ²)	<u>0.57</u>	12	0.16	2	0.28	3	0.05	1	0.33	<u>9</u>
Ephemeroptera density (ind/m ²)	<u>0.15</u>	4	0.07	1	0.07	1	0.42	10	0.12	<u>5</u>
Trichoptera density (ind/m ²)	<u>0.07</u>	2	0.23	2	0.07	1	0.14	3	0.05	2
Simuliidae density	<u>0.03</u>	1	0.07	1	0.07	1	0.07	2	0.19	<u>6</u>
Hydracarina density (ind/m ²)	<u>0.17</u>	4	0.07	1	0.08	1	0.11	3	0.07	3
Oligochaeta density (ind/m ²)	<u>0.29</u>	6	1.00	11	0.07	1	0.96	21	0.05	2
<u>Smooth terms</u>										
Seasonal effects	1.00	21	0.07	1	1.00	11	0.03	1	1.00	29

909

910 Table 4. Relative variable importance of the best models for the subset of data that
 911 included fish density according to model averaging ($\Delta AIC < 2$) (see Appendix 6 for
 912 model selection table including models with $\Delta AIC < 2$ relative to best model) showing
 913 the most influential variables responsible of niche variation at the individual and
 914 population levels. Total niche width of a population (TNW), within-individual component
 915 (WIC), between-individual component (BIC), inter-individual diet variation
 916 (WIC/TNW), individual specialisation (PS_i). n = number of containing models. The
 917 relative variable importance ranges from 0 to 1, and thus 1 indicates that a variable was
 918 included in all models with substantial support. The most important variables in each
 919 model are marked in bold.
 920

	TNW		WIC		BIC		WIC/TNW		PS_i	
	Importance	Models (n)	Importance	Models (n)	Importance	Models (n)	Importance	Models (n)	Importance	Models (n)
<u>Predictor variables</u>										
Shannon	0.07	1	0.87	16	0.10	2	0.43	17	0.04	<u>1</u>
Richness	0.85	10	0.04	1	0.95	17	0.09	5	0.39	6
Fish length (mm)	1.00	12	1.00	19	1.00	18	0.83	34	1.00	16
Intraspecific competition (ind/m ²)	0.06	1	0.27	5	0.09	2	0.27	12	0.05	<u>1</u>
Interspecific competition (ind/m ²)	0.09	1	0.87	16	0.11	2	0.83	34	0.14	3
Chironomidae density (ind/m ²)	1.00	12	0.04	1	1.00	18	0.04	2	1.00	16
Plecoptera density (ind/m ²)	0.06	1	0.60	11	0.09	2	0.80	33	0.05	<u>1</u>
Ephemeroptera density (ind/m ²)	0.07	1	0.09	2	0.09	2	0.16	8	0.05	<u>1</u>
Trichoptera density (ind/m ²)	<u>0.12</u>	1	0.04	1	0.45	8	0.29	13	0.21	<u>3</u>
Simuliidae density	0.07	1	0.11	2	0.04	1	0.02	1	0.12	<u>2</u>
Hydracarina density (ind/m ²)	<u>0.14</u>	2	0.16	3	0.09	2	0.21	9	0.87	14
Oligochaeta density (ind/m ²)	<u>0.07</u>	1	0.14	14	0.10	2	0.77	31	0.10	2
<u>Best model</u>	TNW ~ Richness + Length + Chironomidae density		WIC ~ Shannon + Interspecific competition + Length + Plecoptera density + Oligochaeta density		BIC ~ Richness + Length + Chironomidae density		WIC/TNW ~ Shannon + Interspecific competition + Length + Plecoptera density + Oligochaeta density		PS_i ~ Length + Chironomidae density + Hydracarina density	

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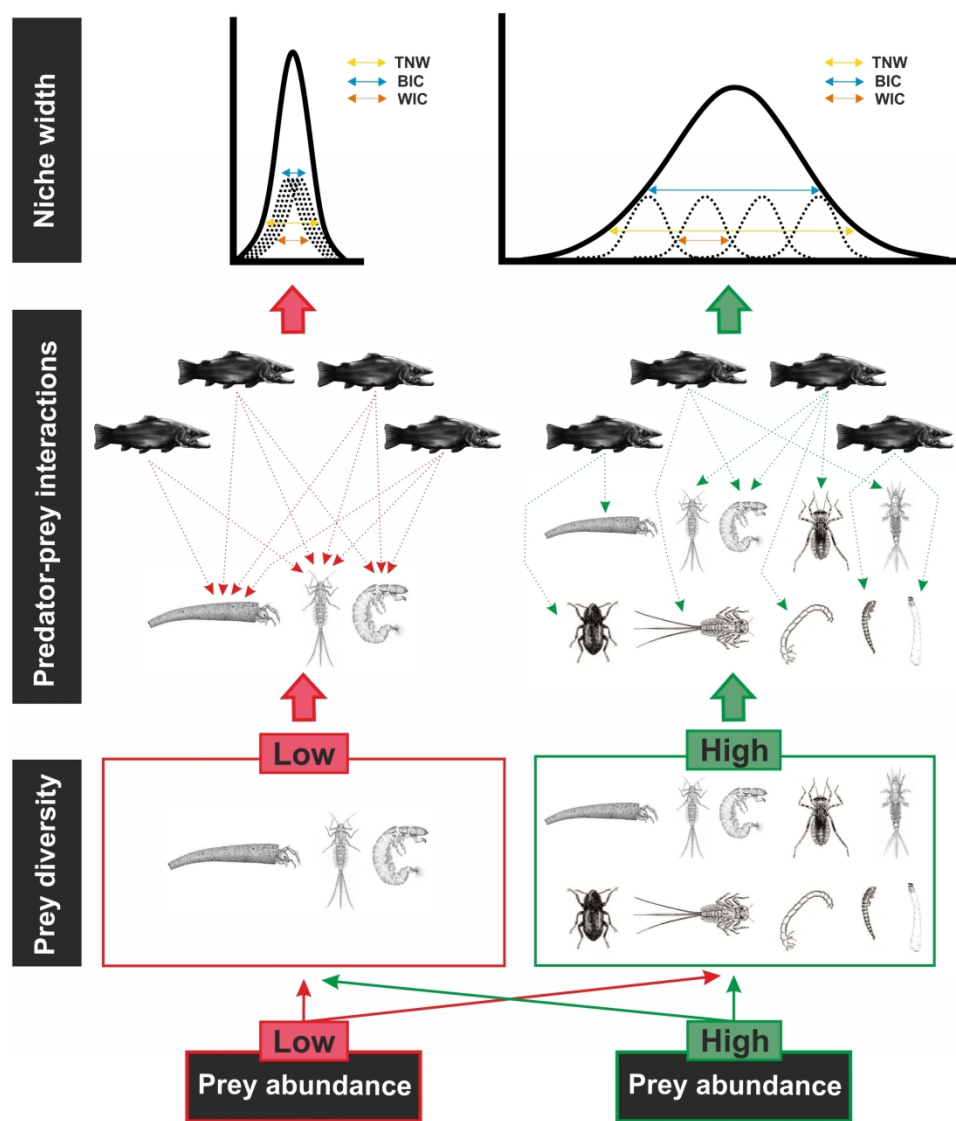
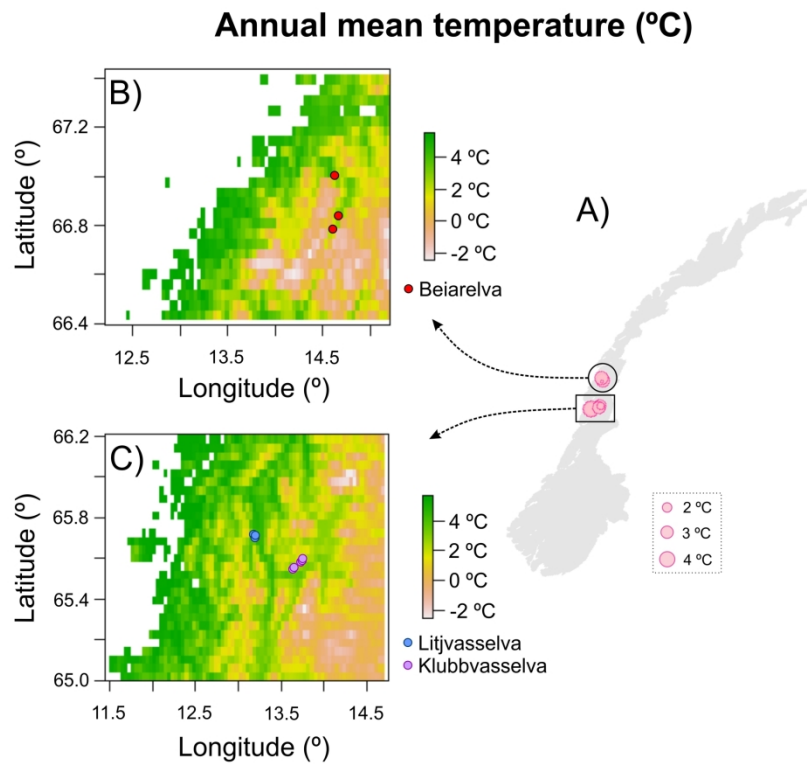


Figure 1. Conceptual view of the effect of ecological opportunity in terms of prey diversity on components of the trophic niche [TNW = total niche width of a population (yellow arrows), BIC = between-individual component (blue arrows), and WIC = within-individual component (orange arrows)]. This conceptual view illustrates that prey diversity, and not prey density, act as the true bottleneck in driving predator niche variation because the diversity of available resources limits the baseline from where individuals can segregate in prey utilization. Arrows and boxes in red represent scenarios under resource limitations (both low prey abundance and diversity), whereas the opposite (high prey abundance and diversity) is presented in green. Dashed arrows show potential predator-prey interactions under the two scenarios (red = resource limitations and green = no resource limitations).

203x236mm (300 x 300 DPI)



34 Figure 2. Map of Norway showing the location of the sampling sites used in this study and annual mean
35 temperatures (°C) according to Worldclim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) (A). Finer
36 location of sampling sites in Beiarelva (B) and Litjvasselva and Klubbvasselva (C).

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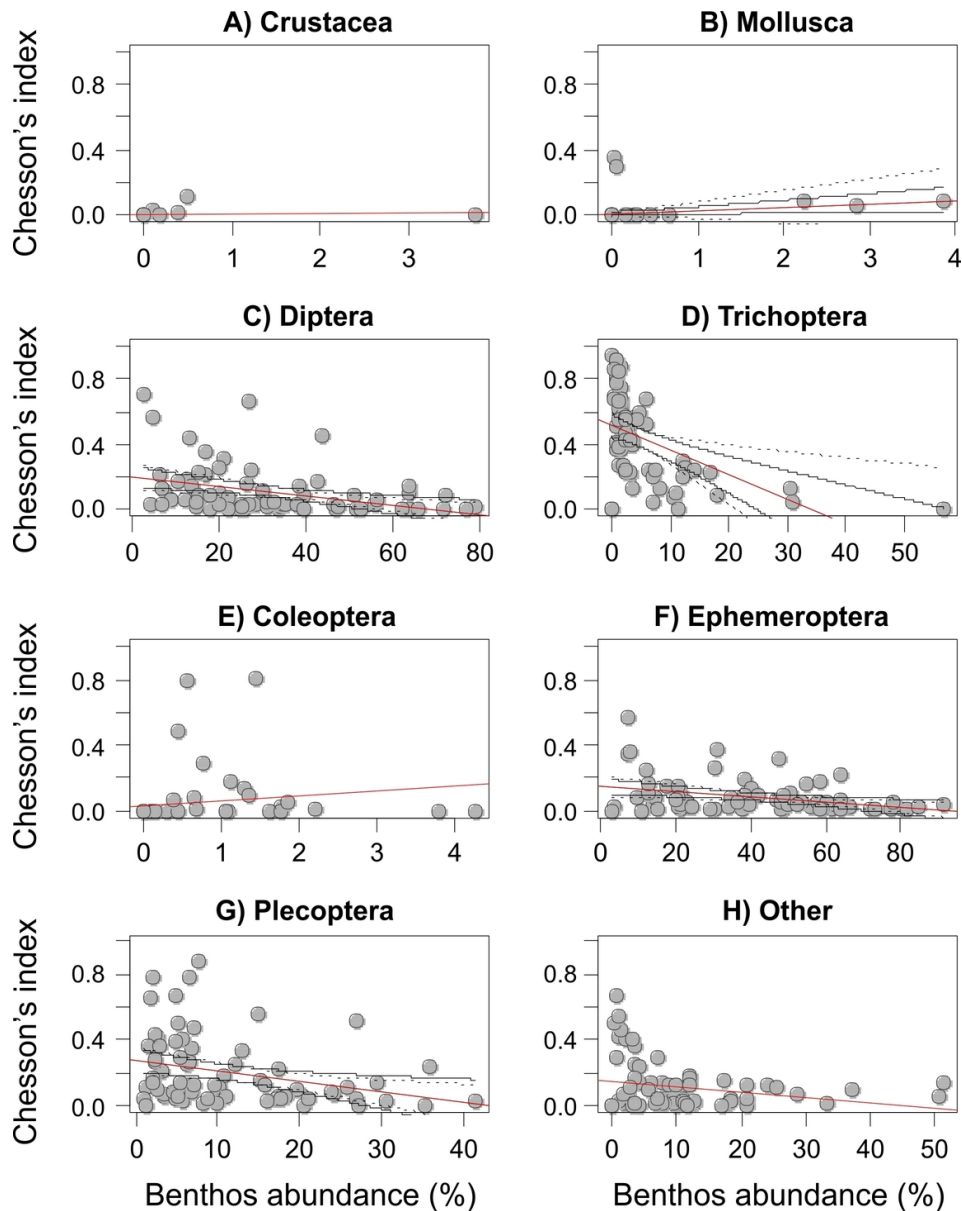


Figure 3. Linear relationships between Chesson selectivity index of brown trout and the relative contribution (%) of each prey type in the benthos (A-H) showing that prey categories are consumed irrespective of their relative abundance in the environment. Note that Chesson's index is based on proportional data, so no units are displayed. This index varies from zero (complete avoidance) to one (complete preference). Fitted line (red line) is shown in all models, whereas 95% confidence intervals (black lines) and bootstrapped 95% confidence intervals (dashed lines) only are shown for statistically significant relationships. 95% confidence limits intervals were reliable in Diptera (C), Ephemeroptera (F) and Plecoptera (G). Model outputs are available in Appendix 3.

97x123mm (300 x 300 DPI)

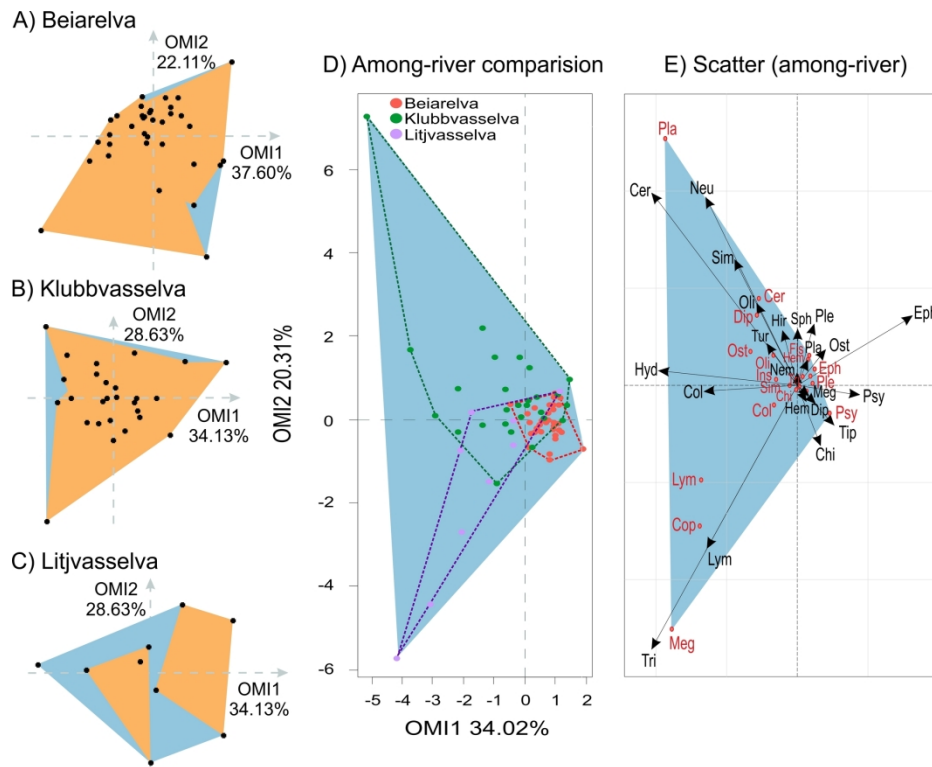


Figure 4. OMI (Outlying Mean Index) analysis showing realised (prey used by brown trout) and potential trophic niches (prey resources that are accessible and potentially can be utilised by brown trout). The blue polygon represents the overall diversity of available resources (potential trophic niches) and the orange polygon represents the realised trophic niche (resource use) of brown trout for each river system (A, B and C). The part D shows subniche (realised) positions according to riverine systems compared to the potential trophic niche (blue polygon). The scatterplot (E) illustrates prey' niche positions in red and canonical weights of available prey categories (potential trophic niches) in black of the among-riverine comparison (D).

217x165mm (300 x 300 DPI)

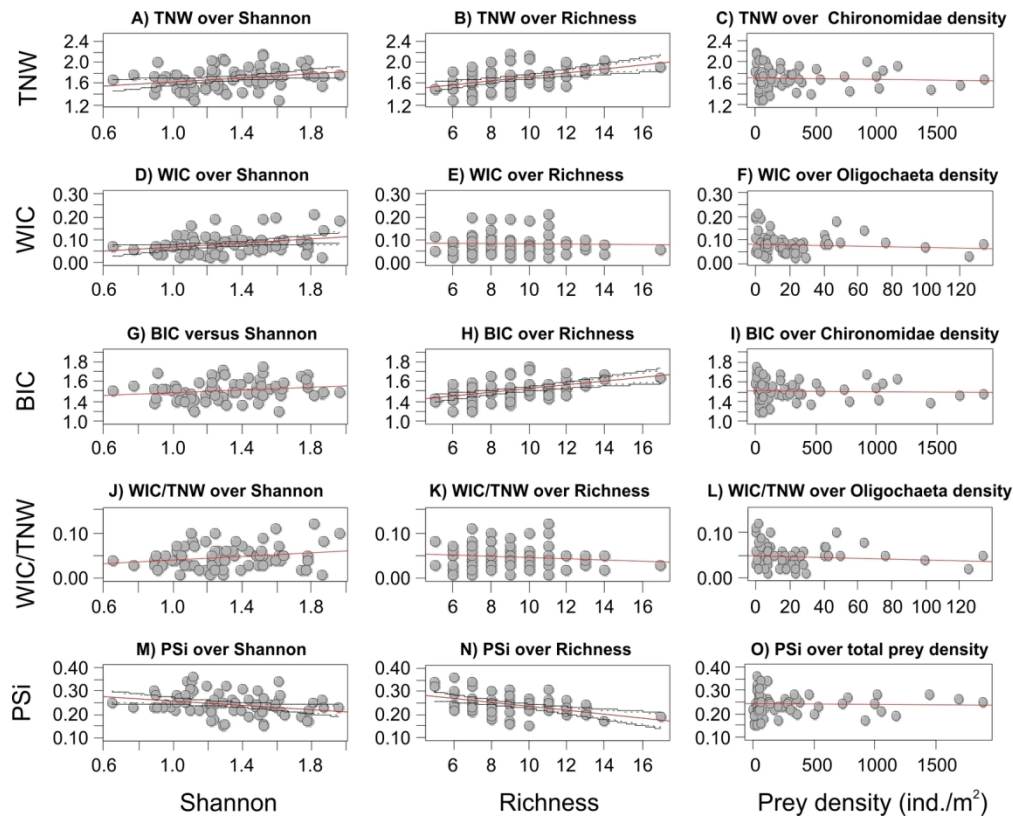


Figure 5. Linear relationships between trophic niche components and ecological opportunity (Shannon index, taxon richness and prey density). Note panels about prey density only included most relevant prey categories according to our best models (Table 1). TNW = total niche width of a population (A-C), WIC = within-individual component (D-F), BIC = between-individual component (G-I), WIC/TNW = inter-individual diet variation (J-L) and PSi = individual specialisation (M-O). Fitted line (red line) is shown in all models, but 95% confidence intervals (black lines) and bootstrapped 95% confidence intervals (dashed lines) only are shown for statistically significant relationships. 95% confidence limits intervals were reliable in all cases. Model outputs are available in Appendix 4.

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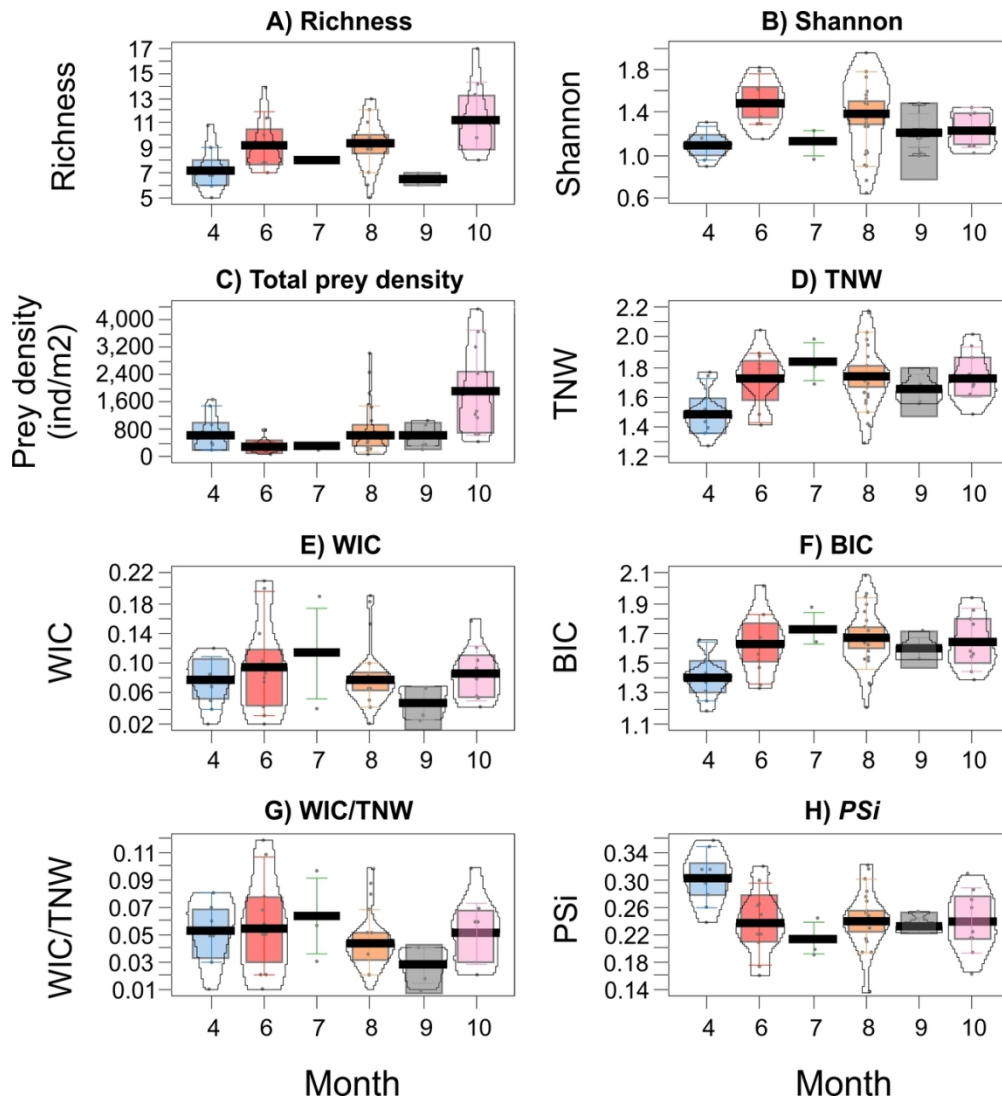


Figure 6. Violin plots showing the seasonal (month) variation of the components of ecological opportunity (A-C) and trophic niche components (D-H). Statistically significant seasonal effects were found only for total niche width of a population (TNW) and individual specialisation (PSi), see Table 2 for all model configurations. WIC = within-individual component, BIC = between-individual component and WIC/TNW = inter-individual diet variation. April = 4, June = 6, July = 7, August = 8, September = 9, and October = 10.

Seasonal variation of the absolute abundance of the most represented prey categories (Chironomidae, Ephemeroptera, Hydracarina, Oligochaeta, Plecoptera, Simuliidae and Trichoptera) is shown in the Appendix 4.

111x121mm (300 x 300 DPI)