

# Adaptive foraging behaviour increases vulnerability to climate change

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15

16 **Abstract:**

17 Adaptative foraging behavior should promote species coexistence and biodiversity under climate  
18 change as predators are expected to maximize their energy intake, according to principles of optimal  
19 foraging theory. We test these assumptions using a dataset comprising 22,185 stomach contents of  
20 fish species across functional groups, feeding strategies, and prey availability in the environment over  
21 12 years. Our results show that foraging shifts from trait-dependent prey selectivity to density  
22 dependence in warmer and more productive environments. This behavioral change leads to lower  
23 consumption efficiency as species shift away from their optimal trophic niche, undermining species  
24 persistence and biodiversity. By integrating this adaptive foraging behavior into dynamic models, our  
25 study reveals higher risk profiles for ecosystems under global warming.

26

27

28 **Main text:**

29

30 Ecosystems are experiencing abrupt changes in climatic conditions, making it ever more important to  
31 predict and understand how they will respond to future changes. Global warming will affect various  
32 levels of biological organization; from physiological processes occurring at the individual level<sup>1</sup> to  
33 patterns at macroecological scales<sup>2</sup>. Warming impacts will cascade through these different  
34 organizational levels, changing species composition<sup>3</sup> as well as community and food web structure<sup>4</sup>.  
35 By scaling up temperature effects from species physiology to food webs<sup>5</sup>, trophic interactions play a  
36 key role in the response of ecosystems to global warming<sup>6</sup>.

37 To assess the future of ecological communities, food web models that build on biological processes  
38 observed at the level of individual organisms can be used to translate mechanisms and predictions to  
39 the ecosystem level. For example, Allometric Trophic Networks<sup>7</sup> (ATN) quantify effects of body  
40 mass and temperature on the biological rates of consumers and resources to predict species biomass  
41 changes over time and across environmental conditions<sup>7-9</sup>. Thus, ATNs facilitate understanding of  
42 how physiological responses to warming translate into species coexistence and biodiversity<sup>10</sup>.

43 However, the ability of ATNs to derive sound predictions for large communities under changing  
44 environmental conditions has been challenged, stressing the need for more biological realism<sup>6,11</sup>.

45 Indeed, a strong limitation of these models is that species are characterized by a set of biological rates  
46 that respond to temperature, such as metabolic or attack rates. Therefore, species are limited to  
47 physiological responses to warming, whereas the behavioral component is largely ignored. However it  
48 is well established that species also respond to warming by changing their behavior<sup>12,13</sup>, and that this  
49 is a key variable in supporting species coexistence, which needs to be incorporated into food web  
50 models to improve their predictive power<sup>14-18</sup>.

51 Energetic demands increase with temperature, but species can offset this by adopting various  
52 strategies to increase their energy intake. Species can actively forage on more rewarding  
53 resources<sup>13,19</sup>, typically prey that are close to the maximum body mass that consumers can feed on<sup>20</sup>.  
54 Therefore, we expect that predators consume larger prey (trait-based selectivity) at higher  
55 temperatures, reducing predator-prey body mass ratios (H1). Alternatively, individuals under high

56 energetic stress may accept less rewarding (smaller, but more abundant) prey upon encounter (H2)  
57 leading to a lower trait-based selectivity, and a trophic niche driven more by neutral processes  
58 (random encounter probability). These two hypotheses would lead to contrasting effects on  
59 communities. Trait-based selectivity (H1) may increase the strength of interactions between predators  
60 and larger prey, depleting the latter's biomass. Alternatively, if neutral processes are driving  
61 selectivity (H2), predators will mostly forage on more abundant species, leading to a stronger control  
62 of their biomass, which could prevent competitive exclusion and therefore enhance species  
63 coexistence<sup>17,21</sup>. To test these hypotheses, we compiled a database of 22,185 stomach contents from 6  
64 demersal fish species and analyzed the response of these consumers behavior to changes in  
65 temperature and productivity. Subsequently, we addressed the consequences of these empirical  
66 relationships by integrating them into a population-dynamical model to predict how species  
67 coexistence changes with warming.

68

### 69 **Response of fish to temperature and productivity gradients**

70 We used our database to document how consumer foraging behavior responds to temperature and  
71 productivity. The six fish species considered belong to two functional groups differing in body shape  
72 and foraging behavior (flat, sit-and-wait predators versus fusiform, active hunters).

73 We used skewed normal distributions to fit the prey body mass distributions observed in fish  
74 stomachs (hereafter called the *realized distribution*) and in the environment (hereafter called the  
75 *environmental distribution*) (Fig. 1). The environmental distribution defines what is expected if  
76 neutral processes drive fish diets: it represents the expected body mass distribution of prey in fish  
77 stomachs if consumption were driven by density-based encounter rates only. However, these two  
78 distributions are usually not identical, because consumers actively select prey with specific body  
79 masses. We used the ratio of realized and environmental distributions to calculate fish selectivity with  
80 respect to these different prey body masses to obtain a *preference distribution* (Fig. 1), which  
81 describes consumer selectivity based on traits and consumer behavioral decisions (e.g. the optimal  
82 prey size that balances handling difficulties with energy gain). We first considered how the body mass  
83 distributions in consumer stomachs were changing with predator body mass and foraging strategy, as

84 well as environmental conditions (temperature and productivity) using a linear model to predict the  
85 median of the realized distribution. We selected the most parsimonious model based on AIC. In cases  
86 of a significant interaction between temperature and productivity (both continuous variables), we  
87 presented the effect of temperature at two different levels of productivity, corresponding to the two  
88 modes of the distribution of environmental productivity (SI I). As expected<sup>22</sup>, we observed that the  
89 median of prey body mass increased with predator body mass, with bigger predators consuming even  
90 bigger prey in higher productivity environments (Fig. 2(A,B), Table 1).

91

92 The effect of temperature depended on environmental productivity: the body mass of consumed prey  
93 increased with temperature at low environmental productivity, but tended to decrease at higher  
94 productivity (Fig. 2(C,D), Table 1). Interestingly, the response of prey body mass was identical for  
95 the two different predator body shapes and foraging strategies.

96 These effects alone are insufficient to describe a change in fish behavior as the distribution of prey  
97 body mass also changes with environmental temperature and productivity (SI I). To disentangle the  
98 effect of prey availability (neutral processes) from the fish behavioral response, we estimated the  
99 preference distribution that depicts fish selectivity independent of the environmental prey distribution  
100 and analyzed its response in the same way as for the realized distribution (see Methods). Our results  
101 confirm the importance of species traits for structuring trophic interactions, as larger fish are foraging  
102 on larger prey (Fig. 3(A)). They also emphasize that ecosystem productivity alters the temperature-  
103 dependence of fish foraging behavior with a significant interaction between temperature and  
104 productivity (Fig 3(B), Table 2). The temperature effect was only significant above a productivity  
105 threshold of  $10^{2.52}$  g (SI II), indicating that fish only adapted their feeding behavior to temperature by  
106 foraging on smaller prey in warmer conditions when resources were plentiful. We did not detect any  
107 interaction between fish shape and other covariates, suggesting that the behavioral responses to  
108 temperature and productivity are similar for fish species with different body shape and foraging  
109 strategies.

110

111 The energetic stress that warming imposes on individuals through increased metabolic rates should be  
112 mitigated by higher feeding rates at higher prey availability in more productive environments. Thus,  
113 because the effects of temperature and productivity should cancel each other out, we expected a  
114 stronger adaptive response at low productivity, where consumers must cope with maximum energetic  
115 stress. Surprisingly, we did not find a significant effect of temperature on preference for prey sizes in  
116 the least productive environments (Fig. 3(B), SI II). One explanation for this may relate to the  
117 generally low productivity of the Baltic Sea during our study<sup>23</sup>. At very low productivity, fish are  
118 experiencing high energetic stress (regardless of temperature) because resource density is low and  
119 they cannot afford to miss a prey upon encountering it, even if it is much smaller than preferred.  
120 Under such stressful conditions, there may be no scope for predators to adapt their feeding behavior as  
121 temperature increases. In more productive environments, feeding behavior may be less constrained,  
122 increasing the adaptive capacity of the fish. Thus, high resource availability and the low energetic  
123 demands of a cool environment result in low energetic stress, allowing fish to select prey based on  
124 traits, whereas warming increases energetic stress because demands rise even though resource  
125 availability is the same, forcing fish to become less selective in their feeding behavior.  
126  
127 Therefore, our results support hypothesis 2 that fish become less selective for prey size as temperature  
128 increases in productive environments so they do not miss a foraging opportunity, which is consistent  
129 with what happens at any temperature when productivity is low. This density driven feeding behavior,  
130 which lowers trait-based selectivity, imposes several disadvantages on consumers. We observed a  
131 weak negative effect of temperature on the width of consumer trophic niches (SI III), indicating that  
132 consumers miss out on larger and thus energetically more rewarding resources, which can be critical  
133 to satisfying their energetic needs<sup>24</sup>, while handling the more abundant smaller prey. This observation  
134 tends to mitigate our assumption that adaptive behavior leading to more neutral-driven consumption  
135 should increase species coexistence in the face of warming. Indeed, metabolic rates increase with  
136 warming faster than feeding rates, leading to the extinction of top predators due to starvation<sup>25</sup>.  
137 Combining this physiological starvation effect with our observed behavioral response indicates that  
138 consuming outside of the most efficient predator-prey body mass ratio should reduce energy flux

139 through food webs, limiting the coexistence of consumer species<sup>24,26</sup>. The combination of direct and  
140 indirect effects of warming could thus increase the likelihood of extinction of top predators in food  
141 webs, which are usually considered key species for the maintenance of biodiversity and ecosystem  
142 functioning<sup>27</sup>.

143

#### 144 **Consequences for species coexistence under global warming**

145 Adaptive foraging in response to varying local conditions is often considered to foster species  
146 coexistence<sup>17,18,28</sup>. The general assumption behind this conclusion is that consumer species will adapt  
147 their foraging strategies in order to maximize their energetic gains<sup>29</sup>. However, our results, based on  
148 an allometric framework, suggest that consumers tend to depart from this optimal behavior under  
149 stressful conditions. We explored the consequences of this behavior using a population dynamic  
150 model, parameterized with species body masses and temperature, which predicts the temporal  
151 dynamics and coexistence of species in food webs (see Methods). We ran two versions of this model:  
152 one including adaptation of species diets to local temperature and productivity conditions as informed  
153 by our empirical results, and one without this adaptation, corresponding to the classical modelling  
154 approach. We simulated the dynamics for synthetic food webs of 50 species (30 consumers and 20  
155 basal species) over a temperature gradient spanning from 1°C to 25°C to predict the number of  
156 extinctions at different temperatures. Overall, we observed that models incorporating adaptive  
157 foraging were more sensitive to warming, with more species extinctions over the temperature gradient  
158 (Fig. 4). These results were not affected by nutrient availability (i.e. productivity) or the functional  
159 response type, which are free parameters in our model (SI IV).

160

161 The effects of warming on the trait structure of communities and the distribution of trophic  
162 interactions<sup>30</sup> are well documented, but a framework for integrating changes in feeding behavior with  
163 a general modelling approach has been lacking. Our results stress the importance of accounting for  
164 foraging behavior to better understand and predict community responses to climate change and  
165 challenge previous conclusions on this topic. Indeed, the discrepancies between the models with and  
166 without adaptive foraging suggest that the classical approach, which only accounts for changes in

167 species physiology<sup>6,10</sup>, may have overlooked a significant portion of species responses to warming.  
168 Importantly, our results show that, contrary to common expectation, behavioral adaptations in  
169 response to climatic stress reduce the likelihood of species coexistence and community biodiversity.  
170 The similarity in responses between the two feeding strategies of our consumer species (sit-and-wait  
171 and active foraging) indicates some generality of our results, but it is now important to investigate a  
172 wider range of species and ecosystem types. For instance, metabolic type has an important effect on  
173 the response of species to temperature<sup>31</sup> and endotherms could respond differently to ectotherms such  
174 as fish.

175 Generally, food web models incorporating foraging behavior are based on optimal foraging theory  
176 and thus miss a data-driven description of how the selectivity of consumer diets changes in a natural  
177 context. To address this, we developed a trait-based framework to document the response of foraging  
178 behavior to temperature, which can be incorporated into predictive models of food web structure and  
179 species coexistence. Our approach can be generalized to other ecological variables that affect food  
180 webs and foraging behavior, such as fear of predators<sup>32</sup> or habitat complexity<sup>33</sup>. Finally, the effects  
181 documented here come from data sampled at rather low levels of temperature and productivity.  
182 Therefore, it is crucial to extend our regression models to warmer and more productive ecosystems to  
183 assess whether very high levels of productivity could balance the energetic stress related to rising  
184 temperatures, limiting adaptive responses in eutrophic environments.

185

## 186 **Conclusion**

187 It is generally assumed that consumers respond to environmental conditions by making choices that  
188 maximize their energy intake<sup>18,34</sup>. This assumption has been used to derive several predictions in  
189 ecology about community structure and species coexistence, and is often considered as a solution to  
190 May's paradox<sup>35</sup> of the mathematical infeasibility of complex communities despite empirical  
191 observations of ecosystem complexity. It is therefore usually assumed that behavior is a strong driver  
192 of community organization and supports species coexistence. We challenge this optimistic view of  
193 nature by demonstrating how consumer species can depart from their optimal behavior under stressful  
194 conditions, for instance when resources are scarce and they face energetic stress due to warming.

195 Therefore, the ecological conclusions built into the assumptions that adaptive behavior favors  
196 coexistence do not necessarily hold in the context of global warming. Our mechanistic modelling  
197 demonstrates the consequences of this observation, with more species extinctions in response to  
198 warming when adaptive foraging is considered. This indicates that global warming may lead to a  
199 greater reduction in species coexistence than predicted by classical ecological models. Our findings  
200 also challenge the general paradigm that adaptive foraging should mitigate the consequences of global  
201 warming for natural ecosystems and call for a general data-driven theory-approach to forecasting  
202 biodiversity and functioning in future ecosystems.

203

## 204 **Methods**

205

### 206 *The Kiel Bay database*

207 The Kiel Bay is located in the Baltic Sea, which is a marginal sea connected to the North Atlantic and  
208 considered the largest brackish sea in the world. It is a rather low productivity ecosystem with low  
209 biodiversity due to its glacial history and the strong salinity gradients that only few species can  
210 tolerate<sup>23,36</sup>. The core of the Kiel Bay database comprises detailed diet information based on stomach  
211 contents from 22185 fish individuals of six species from the Kiel Bay. These species were classified  
212 into two functional groups based on their body shape and habitat use: fusiform and benthopelagic  
213 species (*Gadus morhua*, *Merlangius merlangius*) versus flat and demersal species (*Limanda limanda*,  
214 *Pleuronectes platessa*, *Platichthys flesus*, and *Hippoglossoides platessoides*). This shape characteristic  
215 also corresponds to specific foraging behaviour<sup>37</sup>.

216 The fish individuals were sampled using systematic and standardised bottom trawls. The trawls were  
217 carried out year-round between 1968 and 1978. The body lengths of fish were measured and rounded  
218 to the nearest integer (in cm). Species-specific regressions were used to estimate fish body masses.  
219 Stomach contents were identified to the highest taxonomic resolution possible and wet mass  
220 determined when possible. Hence, the database includes body size data for all fish (i.e. predators) but  
221 also for prey items from the stomach contents<sup>38</sup>. In addition, we were able to add independently-  
222 sampled abundance and body mass information on the benthic invertebrate (i.e. prey) fauna to the

223 database. These data on prey abundances and body masses were sampled independently at the  
224 trawling locations using classical 0.1 m<sup>2</sup> van Veen grabs<sup>39</sup>, see<sup>40</sup> for detailed procedure. We have  
225 enriched the database with climatic (i.e. temperature) and oceanographic (i.e. salinity) data and  
226 geographical information on the distances between the sampling (trawling) sites. So far, the stomach  
227 content data have been published only partially and in German language<sup>38</sup> while parts of the  
228 invertebrate abundance data were treated and published separately<sup>40</sup>. The food web mainly consists of  
229 six demersal fish species and more than a dozen benthic invertebrate species from different groups  
230 (see Table SI V 3).

231

### 232 *Filtering data*

233 To make comparisons between the distributions of prey observed in fish stomachs and the ones  
234 observed in the environment, we only used a subset of the database for which we were able to (i)  
235 associate information about a fish to information about its environment and (ii) have a body mass  
236 estimate of prey found in the stomach. We considered this association between fish and environment  
237 possible, when they were sampled in the same area and within less than 31 days. This first filter  
238 reduced the number of fish used in our analysis to 2,487.

239 On this subset, we considered a unique statistical individual (hereafter called statistical fish) all  
240 individuals from the same functional group, occurring at the same place, on the same date with the  
241 same body mass. This choice is led by the allometric approach used in our analysis, where all  
242 individuals from the same species and with the same body mass are considered identical. This  
243 aggregation increases the quality of the estimation of the prey body mass distribution in stomachs at  
244 the cost of a lower statistical power for the analyses done on the shape of these distributions. For  
245 instance, with a high aggregation level, fewer data points are available to consider the effect of  
246 temperature on the average body mass of prey. This approach is therefore conservative as it reduces  
247 the probability of type 1 error. Lastly, we found that few fishes were mostly feeding on species that  
248 were not detected in the environment, suggesting that the information on the environment was not a  
249 good descriptor of available resources. When less than 90% of the prey biomass found in guts was  
250 explained by what was found in the environment, the fish were discarded (26 cases) Finally, we

251 obtained a final dataset of 290 statistical fish. For our statistical analysis we used fish shape as a  
 252 covariate instead of fish species. As some species were specific to some temperature or body mass  
 253 gradients, the species-specific slopes obtained would be meaningless. This question only holds for the  
 254 analysis about the fish stomach contents. For the analysis of preferences, fish shape or fish species  
 255 covariate were anyway removed by our AIC criterion.  
 256 Different factors affect prey retention time in consumers' guts. Temperature is certainly essential but  
 257 we assume that its impact was the same for all consumers introducing a constant bias with no effect  
 258 on the trends we observed. However, a more species-specific factor relating to species morphology,  
 259 like the presence of shells or skeletons, could impact our results. We thus compared two sets of  
 260 results, one for which we incorporated in the model a lower detection probability for species with hard  
 261 bodies (presented here), and one for which we did not (SI V). Overall, the trends and effects observed  
 262 when including this correction were similar to those observed without correction, thus suggesting an  
 263 absence of systematic biases.

264

265 *Fitting of gut content and environmental distributions*

266 We used a Bayesian approach to fit realised and environmental distributions. For the environment  
 267 distributions, we fitted skew normal distributions to the observed body masses  $y$ , with environment  $ID$   
 268 as a random effect. A skew normal distribution is defined by parameters for location  $\xi$ , scale  $\omega$  and  
 269 shape  $\alpha$ . Its probability density function reads

270 
$$p(y|\xi, \omega, \alpha) = \frac{1}{\omega\sqrt{2\pi}} \exp\left(\frac{-(y - \xi)^2}{2\omega^2}\right) \left(1 + \operatorname{erf}\left(\alpha \frac{y - \xi}{\omega\sqrt{2}}\right)\right)$$

271 where erf is the Gaussian error function<sup>41,42</sup>. For  $\alpha=0$ , this reduces to the non-skewed normal  
 272 distribution with mean  $\mu=\xi$  and standard deviation  $\sigma=\omega$ . For  $\alpha>0$  or  $\alpha<0$ , the distribution is positively  
 273 or negatively skewed, where skew  $\gamma(\alpha)$ , standard deviation  $\sigma(\omega,\alpha)$  and mean  $\mu(\xi,\omega,\alpha)$  are given as  
 274 functions of location, scale and shape parameters<sup>42</sup>.

275 The statistical model then is defined by an observed body mass  $y$  of a prey individual  $i$  in environment  
 276  $ID(i)$  being distributed as

277 
$$y_{i,ID} \text{ skewnormal}(\xi_{ID}, \omega_{ID}, \alpha_{ID})$$

278 ( $i=1, \dots, N, ID=1, \dots, M$ ). Using a hierarchical / partial pooling approach, we assume the individual  
279 parameters have a joint multivariate normal distribution

$$280 \quad (\xi_{ID}, \omega_{ID}, \alpha_{ID}) \text{ multivariatenormal} \left( (\xi, \omega, \alpha), \Sigma \right)$$

281 ( $ID=1, \dots, M$ ). The joint mean parameters  $\xi, \omega, \alpha$  and the 3x3 covariance matrix  $\Sigma$  are estimated during  
282 the model fitting approach. We used weakly informative priors for all model parameters. Samples  
283 from the posterior distribution were drawn using Hamiltonian Monte Carlo in Stan<sup>41</sup> and posterior  
284 medians were used as point estimates of  $(\xi_{ID}, \omega_{ID}, \alpha_{ID})$  for the subsequent analyses. The realised  
285 distributions were fitted analogously, using predator identity as a random effect. We however  
286 included here a correction factor to consider that the probability of detection of prey in guts relates to  
287 their body characteristic<sup>43</sup> (presence or absence of hard body parts like shells or skeleton). We  
288 assumed that prey with hard body parts are more likely to be detected in comparison to species  
289 composed of soft tissues only because of higher digestion time and corrected their biomass by  
290 multiplying it by 0.8. The results found without this correction were similar to the ones observed  
291 without (SI VI).

292

### 293 *Determining allometric species' preferences*

294 The preference distributions of each statistical fish were estimated as the departure of the realised  
295 niche from the environmental distribution. We removed the effect of species environmental  
296 availability from the realised to define the preference distribution as:

$$297 \quad P = \frac{R}{E},$$

298 where  $P, R$  and  $E$  represent the preference, realised and environmental distributions, respectively. By  
299 doing so, we assumed that a feeding event is defined by two independent probabilities: the probability  
300 for a consumer to encounter a prey (defined by the  $R$  distribution) and of the probability for a  
301 consumer to consume the prey when encountered (given by the preference distribution). To assess  
302 changes in the distributions and how they depart from each other, we used variations in the point  
303 estimates (median and standard deviation). This limited the amount of information used in our study.  
304 Quantifying the neutral versus trait-based processes would benefit from the comparison between the

305 environmental and realised distributions using metrics like the Kullback-Leibler divergence. With  
 306 such an approach, one could argue that the more divergent the distributions are, the more predation  
 307 events are driven by traits. However, this would be limited by the impossibility of disentangling the  
 308 part of the divergences explained by changes in the environmental distribution and what relates to a  
 309 change in fish behaviour. However, we believe that a more controlled approach in micro- or  
 310 mesocosms where the body mass distribution of prey species available could be standardised could  
 311 elegantly solve this issue.

312

### 313 *Dynamic model*

314 To simulate the population dynamics, we used a previously published model <sup>44</sup>, based on the Yodzis  
 315 and Innes framework <sup>45</sup>. The growth of consumer species  $B_i$  is determined by the balance between its  
 316 energetic income (predation) and its energetic losses (predation metabolism)

317

$$318 \frac{dB_i}{dt} = e_p B_i \sum_j F_{ij} + e_A B_i \sum_j F_{ij} - \sum_j B_i F_{ji} - x_i B_i,$$

319 where  $e_p = 0.545$  and  $e_a = 0.906$  represent the assimilation efficiency of a consumer foraging on plants  
 320 and animals, respectively <sup>46</sup>.  $x_i$  defines the metabolic rate of species  $i$ , which scales allometrically with  
 321 body mass:

$$322 x_i = x_0 m_i^{-0.25} e^{\frac{E_x(T_0 - T)}{kT_0T}},$$

323 where  $x_0 = 0.314$  is the scaling constant <sup>44</sup>,  $E_x = -0.69$  is the activation energy of metabolic rate  
 324 (Binzer et al. 2015),  $k$  the Boltzmann constant,  $T_0 = 293.15$  the reference temperature in Kelvin and  $T$   
 325 the temperature at which the simulation is performed. The trophic interactions are determined using a  
 326 functional response  $F_{ij}$  that describes the feeding rate of consumer  $i$  over resource  $j$ :

$$327 F_{ij} = \frac{\omega_{ij} b_{ij} B_j^{1+q}}{1 + c B_i + \omega_{ij} \sum_k h_{ik} b_{ik} B_k^{1+q}} \cdot \frac{1}{m_x}.$$

328

329  $b_{ij}$  represent the species-specific capture and is determined by predator and prey body masses:

$$330 b_{ij} = P_{ij} L_{xz}.$$

331 It corresponds to the product of encounter probabilities  $P_{ij}$  by the probability that an encounter leads  
 332 to a realised predation event  $L_{ij}$ . Both quantities are determined by species body masses. We assume  
 333 that encounter probability is more likely for species with higher movement speeds of both consumer  
 334 and resource species:

$$335 \quad P_{ij} = p_0 m_i^{\beta_i} m_j^{\beta_j} e^{E_p \frac{T_0 - T}{kT_0 T}}.$$

336 Since movement speed scales allometrically and based on feeding type<sup>47</sup>, we drew  $\beta_x$  and  $\beta_z$  from  
 337 according normal distributions (carnivore:  $\mu_\beta = 0.42$ ,  $\sigma_\beta = 0.05$ , omnivore:  $\mu_\beta = 0.19$ ,  $\sigma_\beta = 0.04$ ,  
 338 herbivore:  $\mu_\beta = 0.19$ ,  $\sigma_\beta = 0.04$ , primary producer:  $\mu_\beta = 0$ ,  $\sigma_\beta = 0$ ). Activation energy  $E_p$  is equal to -  
 339 0.38 (Binzer et al. 2015).  $L_{ij}$  is assumed to follow a Ricker curve (Schneider et al. 2016), defined as:

$$340 \quad L_{xz} = \left( \frac{m_x}{m_z R_{opt}} e^{1 - \frac{m_x}{m_z R_{opt}}} \right)^Y,$$

341 where the optimal consumer-resource body mass ratio  $R_{opt} = 47.9$  was calculated from the observed  
 342 realised interactions in our dataset. We used a threshold  $L_{ij} < 0.01$  under which values were set to 0,  
 343 assuming that too small or too large prey are not considered by consumers. The handling time  $h_{ij}$  of  $i$   
 344 on  $j$  is defined as:

$$345 \quad h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j} e^{E_h \frac{T_0 - T}{kT_0 T}},$$

346 where the scaling constant  $h_0$  was set to 0.4 and the allometric coefficients for  $\eta_i$  and  $\eta_j$  were drawn  
 347 from a normal distribution with mean and standard deviation of -0.48 and 0.03 for  $\eta_i$  and of -0.66 and  
 348 0.02 for  $\eta_j$ .  $E_h$  is equal to 0.26. The term  $w_{ij}$  informs on species selectivity<sup>48</sup>. For the models without  
 349 behavioural expectations we used the classical parametrisation and defined it for every  $j$  as 1 over the  
 350 number of prey of consumer  $i$ . When adaptive behaviour was included in the model, the value was  
 351 determined by the predictions of the skewed normal distribution we fitted on our dataset. These were  
 352 informed by the consumer and resource body masses, at given levels of productivity and temperature.  
 353 To maintain the comparability with the model without adaptive behaviour, the  $w_{ij}$  values were  
 354 normalised to 1 for each consumer. As for our experimental data, productivity was defined as the total  
 355 biomass of prey available for each consumer. As this value can be highly variable during the  
 356 simulations, especially in the transient dynamics, we rescaled this value between 0 and 4 to maintain

357 it to a scale that is similar to the one from our dataset that we used to inform the skew normal  
358 distributions

359 The biomass dynamic of the basal species  $i$  is defined as:

$$360 \frac{dB_i}{dt} = r_i G_i B_i - \sum_j B_j F_{ji} - x_i B_i,$$

361 where  $r_i = m_i^{-0.25}$  defines the species growth rate.  $G_i$  is the species-specific growth factor,  
362 determined by the concentration of two nutrients  $N_1$  and  $N_2$ :

$$363 G_i = \min\left(\frac{N_1}{K_{i1} + N_1}, \frac{N_2}{K_{i2} + N_2}\right),$$

364 Where  $K_{il}$  determines the half saturation density of plant  $i$  nutrient uptake rate. It is determined  
365 randomly from a uniform distribution in  $[0.1, 0.2]$ . The dynamic of the nutrient concentrations is  
366 defined by:

$$367 \frac{dN_l}{dt} = D(S_l - N_l) - v_l \sum_i r_i G_i P_i,$$

368 Where  $D = 0.25$  determines the nutrients turnover rate and  $S_l = 5$  determines the maximal nutrient  
369 level. The loss of a specific nutrient  $l$  is limited by its relative content in the plant species' biomass  
370 ( $v_1=1, v_2=0.5$ ).

371 We ran our model on food webs of 50 species, composed of 30 consumers and 20 basal species. A  
372 link was drawn between two species  $i$  and  $j$  when  $L_{ij} > 0$ . For each temperature we ran 50 replicates of  
373 the two model's versions (with and without adaptive behaviour) and recorded the number of  
374 extinctions. We fitted a GAM model on this number of extinctions

375

376 **Code availability:** Code can be made available to editors and reviewers on request. Should the  
377 manuscript be accepted, code will be made publicly available and associated to a DOI.

378

379

380 **References:**  
381

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494 Resources: GK, SK, EOG

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496 Supervision: UB

497 Writing – original draft: BG

498 Writing – review & editing: BG, BR, GK, TB, MJ, SK, EOG, UB

499

500 **Competing interest:** Authors declare that they have no competing interests

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506 **Tables**

507

508 Table 1: response of the realized distribution to predator body mass and environmental gradients

<i>Predictors</i>	<b>Median of the realised distribution</b>		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	-2.63	-3.68 – -1.57	<b>&lt;0.001</b>
Predator body mass	-0.13	-0.50 – 0.25	0.509
Productivity	0.91	0.51 – 1.31	<b>&lt;0.001</b>
Shape (fusiform)	-0.08	-0.12 – -0.03	<b>0.001</b>
Temperature	0.33	0.25 – 0.41	<b>&lt;0.001</b>
pred. BM:Productivity	0.16	0.01 – 0.30	<b>0.034</b>
Productivity:Temperature	-0.13	-0.16 – -0.10	<b>&lt;0.001</b>
Observations	223		
R <sup>2</sup> / R <sup>2</sup> adjusted	0.449 / 0.434		

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510 Table 2: response of the preference distribution to predator body mass and environmental gradients

<i>Predictors</i>	<b>Median of the preference distribution</b>		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	-2.283	-4.395 – -0.170	<b>0.034</b>
Predator body mass	0.525	0.363 – 0.686	<b>&lt;0.001</b>
Productivity	0.788	0.009 – 1.566	<b>0.047</b>
shapefusiform	-0.102	-0.216 – 0.013	0.083
Temperature	0.240	0.033 – 0.446	<b>0.023</b>
Productivity:Temperature	-0.103	-0.180 – -0.025	<b>0.010</b>
Observations	223		
R <sup>2</sup> / R <sup>2</sup> adjusted	0.258 / 0.241		

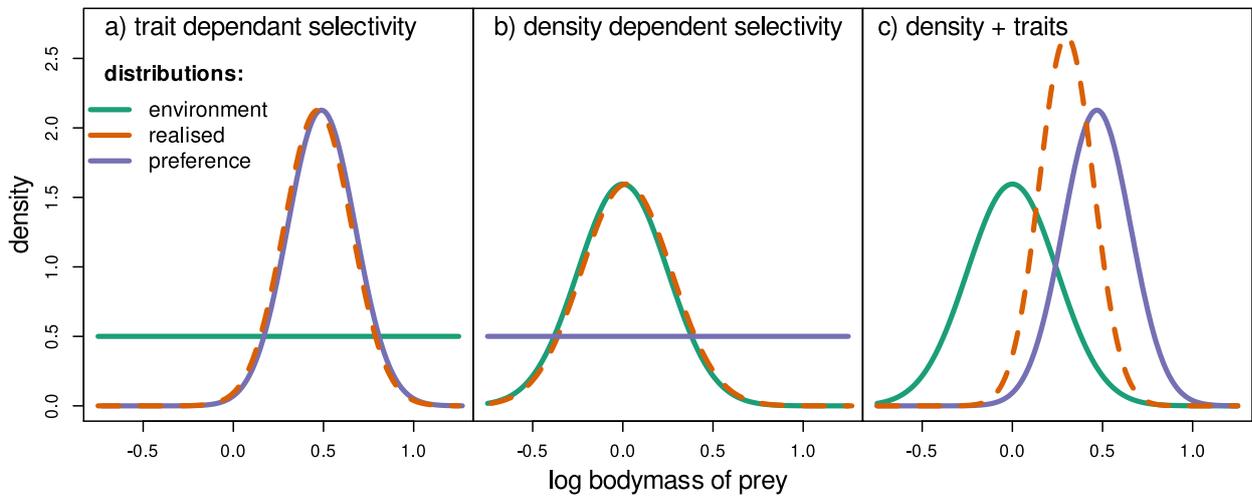
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512 **Figures**

513

514 **Fig. 1:**

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517 Fig. 1: Presentation of the different distributions of fish prey body mass. The environmental distribution (green)

518 represents the distribution of prey body mass in the ecosystem, the realized distribution (dashed red) represents

519 the body mass of the prey in a consumer stomach, and the preference distribution (blue) represents the

520 selectivity of a consumer for a specific prey body mass. a) All of the log prey body masses are equally

521 represented in the environment so the distribution of prey body masses observed in a consumer's gut represents

522 the body masses on which it actively foraged (its preference distribution) and predation is driven by trait

523 selectivity only (hypothesis 1). b) The body mass distribution of the prey observed in the gut and in the

524 environment are equivalent, so the prey consumed by the predator were entirely driven by encounter

525 probabilities (i.e. a neutral process), implying no active selectivity over specific prey size classes (hypothesis 2).

526 Panels a) and b) represent extreme scenarios while real-world data are more likely to be described by two

527 different distributions, as in c) where the body mass distribution of prey observed in the stomach and in the

528 environment differs, so that the consumer specifically forages on some prey body masses that are represented by

529 the preference distribution. High values in the preference distribution represent body masses that are over-

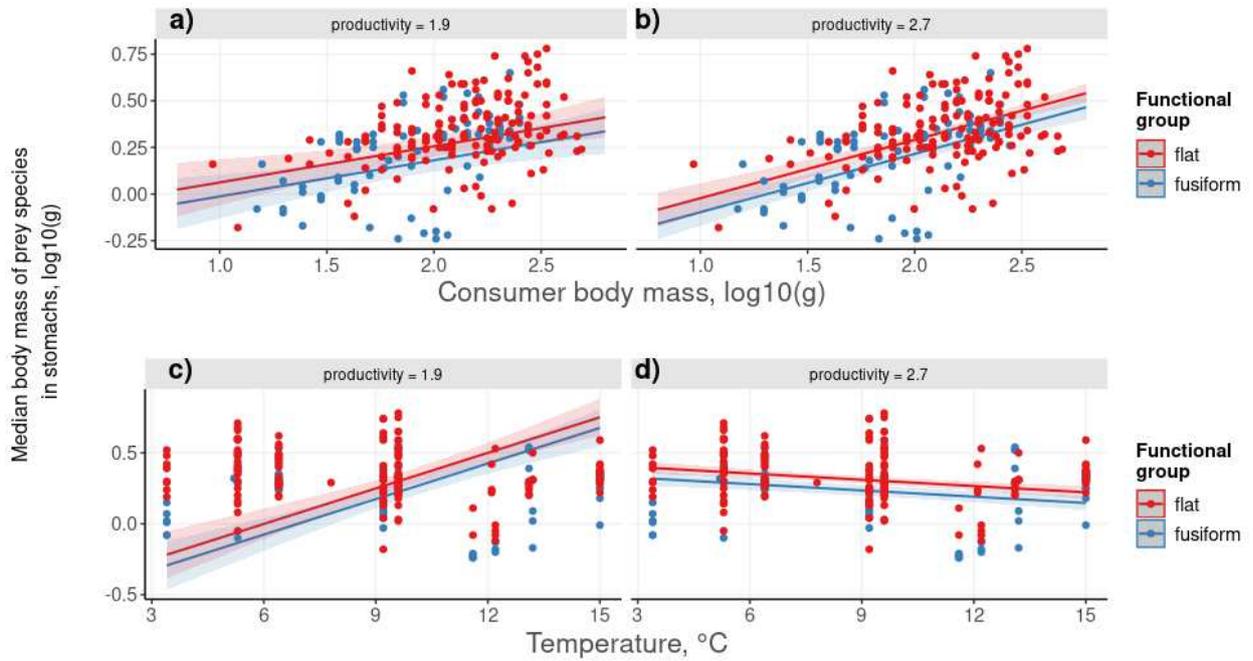
530 represented in fish stomachs compared to what is available in the environment.

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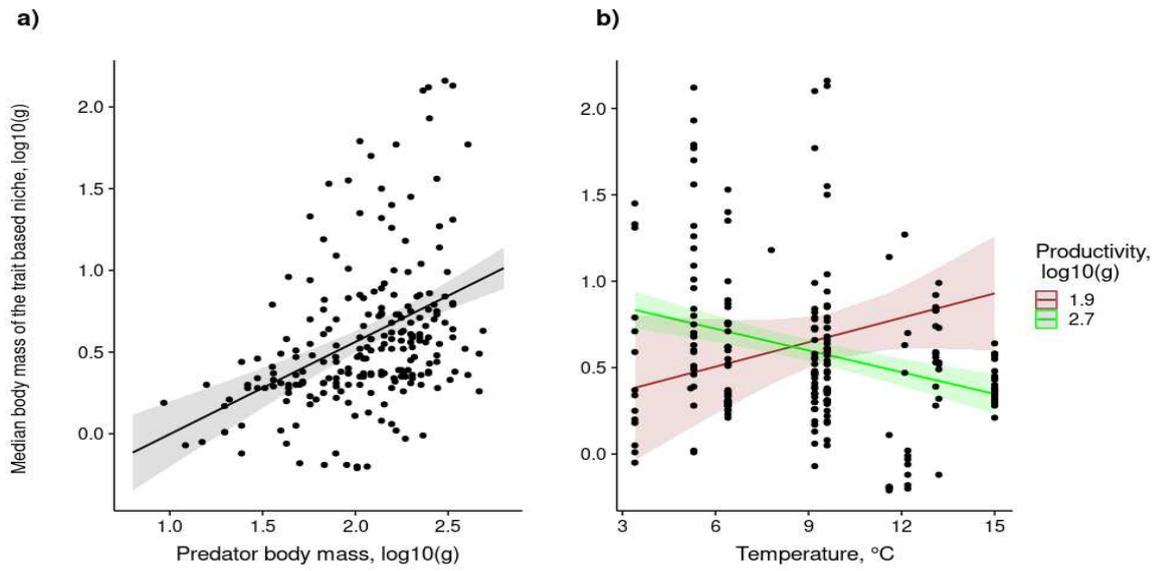
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534 **Fig. 2:**  
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538 Fig. 2: Response of the median body mass of the realized prey body mass distribution. Response to predator  
539 body mass (a, b), and temperature (c, d) at different productivity levels (g) for the two fish functional groups.  
540 Points represent non-transformed data across all productivity levels and lines present model predictions.  
541 Regression lines represent model's prediction when all other covariates are considered. The shaded areas show  
542 the 95% confidence interval on the predicted values.  
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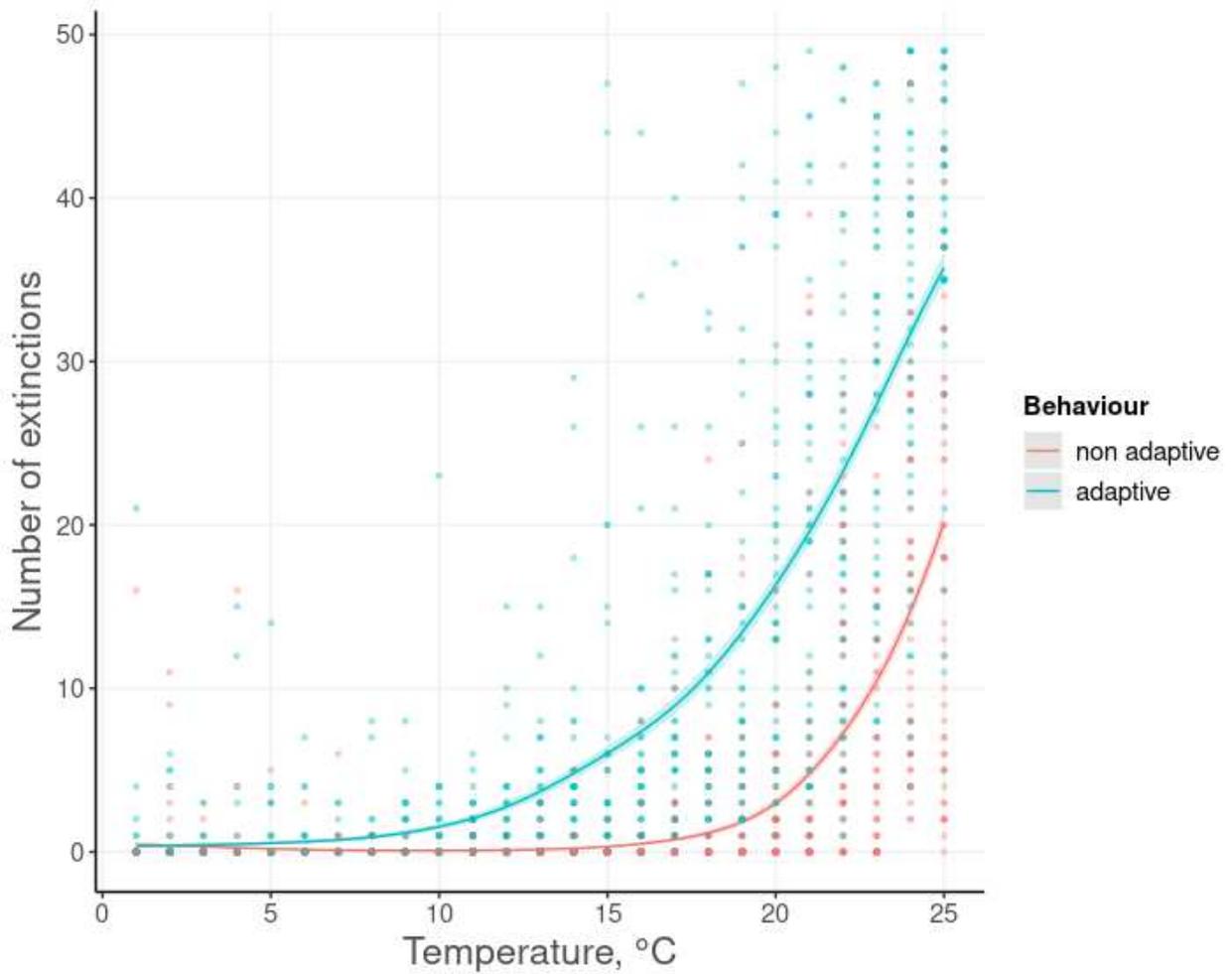
545 **Fig. 3:**  
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Fig. 3: Response of the median prey body mass of the preference distribution to (a) predator body mass and (b) temperature and productivity. Points represent non-transformed data across all productivity levels and lines represent model predictions. Regression lines represent model's prediction when all other covariates are considered. The shaded areas show the 95% confidence interval on the predicted values.

556 **Fig. 4:**  
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Fig. 4: Number of species extinctions predicted by the model at different temperatures. The blue line represents the model output with adaptation of species diets to local temperature and productivity conditions considered, whilst the red line shows extinctions without allowing for this adaptation. The shaded areas show the 95% confidence interval on the predicted values. Predictions were estimated using a GAM (REML method) with a binomial link function.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [KielbaynatureSI.pdf](#)