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Title: Adaptive foraging behavior increases vulnerability to climate change

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Abstract:

Adaptative foraging behavior should promote species coexistence and biodiversity under climate change as predators are expected to maximize their energy intake, according to principles of optimal foraging theory. We test these assumptions using a dataset comprising 2,487 stomach contents of fish species across functional groups, feeding strategies, and prey availability in the environment over 12 years. Our results show that foraging shifts from trait-dependent prey selectivity to density dependence in warmer and more productive environments. This behavioral change leads to lower consumption efficiency as species shift away from their optimal trophic niche, undermining species persistence and biodiversity. By integrating this adaptive behavior into dynamic models, our study reveals that adaptive foraging yields higher risk profiles for ecosystems under global warming.

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Main text:

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

To assess the future of ecological communities, food web models that build on biological processes observed at the level of individual organisms can be used to translate mechanisms and predictions to the ecosystem level. For example, Allometric Trophic Networks[7] (ATN) quantify effects of body mass and temperature on the biological rates of consumers and resources to predict species biomass changes over time and across environmental conditions[7–9]. Thus, ATNs facilitate understanding of how physiological responses to warming translate into species coexistence and biodiversity[10]. However, the ability of ATNs to derive sound predictions for large communities under changing environmental conditions has been challenged, stressing the need for more biological realism[6,11]. Indeed, a strong limitation of these models is that species are characterized by a set of biological rates that respond to temperature, such as metabolic or attack rates. Therefore, species are limited to physiological responses to warming, whereas the behavioral component is largely ignored. However, it is well established that species also respond to warming by changing their behavior[12,13], which helps to support species coexistence, and thus needs to be incorporated into food web models to improve their predictive power[14–18].

Energetic demands increase with temperature, but species can offset this by adopting various strategies to increase their energy intake. Species can actively forage on more rewarding

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resources[13,19], typically prey that are close to the maximum body mass that consumers can feed on[20]. Therefore, we expect that predators consume larger prey individuals (trait-based selectivity) at higher temperatures, reducing predator-prey body mass ratios (H1). Alternatively, individuals under high energetic stress may be driven by their increased demand for food and accept less rewarding (smaller, but more abundant) prey upon random encounter (H2) leading to a lower trait-based selectivity, and a trophic niche driven more by neutral processes (random encounter probability). These two hypotheses would lead to contrasting effects on communities. Trait-based selectivity (H1) may increase the strength of interactions between predators and larger prey, depleting the latter's biomass. Alternatively, if neutral processes are driving selectivity (H2), predators will mostly forage on more abundant species, leading to a stronger control of their biomass, which could prevent competitive exclusion and therefore enhance species coexistence[17,21]. To test these hypotheses, we compiled a database of 22,185 stomach contents from six demersal fish species and analyzed their behavioral response to changes in temperature and productivity. Subsequently, we addressed the consequences of these empirical relationships by integrating them into a population-dynamical model to predict how species coexistence changes with warming.

Response of fish to temperature and productivity gradients

We used our database to document how consumer foraging behavior responds to temperature and productivity. The six fish species considered belong to two functional groups differing in body shape and foraging behavior (flat, sit-and-wait predators versus fusiform, active hunters). We used empirical means and standard deviations to describe the prey body mass distributions observed in fish stomachs (hereafter called the *realized distribution*) and in the environment (hereafter called the *environmental distribution*) (Fig. 1). The environmental distribution defines what is expected if neutral processes drive fish diets: it represents the expected body mass distribution of prey in fish stomachs if consumption was driven by density-based encounter rates only. However, the size distributions of prey in the environment and in consumer diets are usually not identical because consumers actively select prey individuals with specific body masses. We used the ratio of realized and environmental distributions to calculate fish selectivity with respect to these different prey body masses to obtain a

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preference distribution (Fig. 1), which describes consumer selectivity based on traits and consumer behavioral decisions. Traits define the fundamental trophic niche of a species (what a consumer can eat), while behavioral decisions define which parts of this fundamental niche the consumer will focus on. Therefore, a shift in behavior does not necessarily imply a shift in the identity of prey species, but can simply lead to a shift in the individual traits that are selected, within or across different species.

We first described how the body mass distributions in consumer stomachs were changing with predator body mass and foraging strategy, as well as environmental conditions (temperature and productivity) using a linear model to predict the median of the realized distribution. We selected the most parsimonious model based on AIC. As expected[22], we observed that the median of prey body mass in consumer guts increased with predator body mass in a similar way for the two different predator body shapes and foraging strategies(Fig. 2(**A**), Table 1). The body mass of consumed prey decreased with temperature, with a stronger effect in fusiform fish (Fig. 2(**B**), Table 1). These effects alone are insufficient to describe a change in fish behavior as the distribution of prey body masses in the environment also changes with environmental temperature and productivity (SI I). To disentangle the effect of prey availability (neutral processes) from the fish behavioral response, we estimated the preference distribution that depicts consumer selectivity independent of the environmental prey distribution and analyzed its response to test our two hypotheses. To do so, we built a Bayesian linear model with temperature, productivity, fish functional group, and consumer body mass as main effects, and interactive effects corresponding to our hypotheses: between temperature and productivity and between temperature and fish functional group (see Methods). Comparison of models with and without consumer fish functional group as a covariate with a “Leave One Out cross” validation approach[23] indicated that the behavioral responses to temperature and productivity were similar for fish species with different body shapes and foraging strategies. We therefore excluded this variable from the final model. Our results confirm the importance of species traits for structuring trophic interactions, as larger fish are foraging on larger prey (Fig. 3(**A**)). They also emphasize that ecosystem productivity alters the temperature-dependence of fish foraging behavior with a significant interaction between temperature and productivity (Fig 3(**B**), Table 2). The

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temperature effect was negative only in high productive environments (SI II), indicating that fish only adapted their feeding behavior to temperature by foraging on smaller prey in warmer conditions when resources were plentiful.

The energetic stress that warming imposes on individuals through increased metabolic rates should be mitigated by higher feeding rates at higher prey availability in more productive environments. Thus, because the effects of temperature and productivity should cancel each other out, we expected a stronger adaptive response at low productivity, where consumers must cope with maximum energetic stress. Surprisingly, we did not find a significant effect of temperature on preference for prey sizes in the least productive environments (Fig. 3(**B**), SI III). At very low productivity, fish are experiencing high energetic stress (regardless of temperature) because resource density is low and they cannot afford to miss a prey upon encountering it, even if it is much smaller than preferred. Under such stressful conditions, there may be no scope for predators to adapt their feeding behavior as temperature increases. In more productive environments, feeding behavior may be less constrained, increasing the adaptive capacity of the fish. Thus, high resource availability and the low energetic demands of a cool environment result in low energetic stress, allowing fish to select prey based on traits, whereas warming increases energetic stress because demands rise even though resource availability is the same, forcing fish to become less selective in their feeding behavior.

Therefore, our results support hypothesis 2 that fish become less selective for prey size as temperature increases in productive environments so they do not miss a foraging opportunity, which is consistent with what happens at any temperature when productivity is low. This density driven feeding behavior, which lowers trait-based selectivity, imposes several disadvantages on consumers. We observed a weak negative effect of temperature on the width of consumer trophic niches at high productivity levels (SI III), indicating that consumers miss out on larger and thus energetically more rewarding prey individuals, which can be critical to satisfy their energetic needs[24], while handling the more abundant smaller prey. This observation tends to mitigate our assumption that adaptive behavior leading to more neutral-driven consumption should increase species coexistence in the face of

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warming. Indeed, fish metabolic rates increase with warming over large temperature gradients[25] and do so faster than feeding rates, leading to the extinction of top predators due to starvation[26,27]. Combining this physiological starvation effect with our observed behavioral response indicates that consuming outside of the most efficient predator-prey body mass ratio should reduce energy flux through food webs, limiting the coexistence of consumer species[24,28]. The combination of direct and indirect effects of warming could thus increase the likelihood of extinction of top predators in food webs, which are usually considered key species for maintaining biodiversity and ecosystem functioning[29].

Consequences for species coexistence under global warming

Adaptive foraging in response to varying local conditions is often considered to foster species coexistence[17,18,30]. The general assumption behind this conclusion is that consumer species will adapt their foraging strategies in order to maximize their energetic gains[31]. However, our results, based on an allometric framework, suggest that consumers tend to depart from this optimal behavior under stressful conditions. We explored the consequences of this behavior using a population dynamic model, parameterized with species body masses and temperature, which predicts the temporal dynamics and coexistence of species in food webs (see Methods). We ran two versions of this model: one including adaptation of species diets to local temperature and productivity conditions as informed by our empirical results, and one without this adaptation, corresponding to the classical modelling approach. We simulated the dynamics for synthetic food webs of 50 species (30 consumers and 20 basal species) over a temperature gradient spanning from 0°C to 26°C to predict the number of extinctions at different temperatures. Overall, we observed that models incorporating adaptive foraging were more sensitive to warming, with more species extinctions over the temperature gradient (Fig. 4). These results were not affected by the functional response type, which are free parameters in our model (SI IV) but tended to weaken at very low levels of nutrient availability (i.e. productivity), consistently with our empirical results.

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The effects of warming on the trait structure of communities and the distribution of trophic interactions[32] are well documented, but a framework for integrating changes in feeding behavior with a general modelling approach has been lacking. Our results stress the importance of accounting for foraging behavior to better understand and predict community responses to climate change, and challenge previous conclusions on this topic. Indeed, the discrepancies between the models with and without adaptive foraging suggest that the classical approach, which only accounts for changes in species physiology[6,10], may have overlooked a significant portion of species responses to warming. Importantly, our results show that, contrary to common expectation, behavioral adaptations in response to climatic stress reduce the likelihood of species coexistence and community biodiversity. The similarity in responses between the two feeding strategies of our consumer species (sit-and-wait and active foraging) indicates some generality of our results, but it is now important to investigate a wider range of species and ecosystem types. For instance, metabolic type has an important effect on the response of species to temperature[33] and endotherms could respond differently to ectotherms such as fish.

Generally, food web models incorporating foraging behavior are based on optimal foraging theory and thus miss a data-driven description of how the selectivity of consumer diets changes in a natural context. To address this, we developed a trait-based framework to document the response of foraging behavior to temperature, which can be incorporated into predictive models of food web structure and species coexistence. Our approach can be generalized to other ecological variables that affect food webs and foraging behavior, such as fear of predators[34] or habitat complexity[35]. Finally, the effects documented here come from data sampled at rather low levels of temperature and productivity. Therefore, it is crucial to extend our regression models to warmer and more productive ecosystems to assess whether very high levels of productivity could balance the energetic stress related to rising temperatures, limiting adaptive responses in eutrophic environments.

Conclusion

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It is generally assumed that consumers respond to environmental conditions by making choices that maximize their energy intake[18,36]. This assumption has been used to derive several predictions in ecology about community structure and species coexistence, and is often considered as a solution to May's paradox[37] of the mathematical infeasibility of complex communities despite empirical observations of ecosystem complexity. It is therefore usually assumed that behavior is a strong driver of community organization and supports species coexistence. We challenge this optimistic view of nature by demonstrating how consumer species can depart from their optimal behavior under stressful conditions, for instance when resources are scarce and they face energetic stress due to warming. Therefore, the ecological conclusions built into the assumptions that adaptive behavior favors coexistence do not necessarily hold in the context of global warming. Our mechanistic modelling demonstrates the consequences of this observation, with more species extinctions in response to warming when adaptive foraging is considered. This indicates that global warming may lead to a greater reduction in species coexistence than predicted by classical ecological models. Our findings also challenge the general paradigm that adaptive foraging should mitigate the consequences of global warming for natural ecosystems and call for a general data-driven theory-approach to forecasting biodiversity and functioning in future ecosystems.

Methods

The Kiel Bay database

Kiel Bay is located in the Baltic Sea, which is a marginal sea connected to the North Atlantic and considered the largest brackish sea in the world. It is a rather low productivity ecosystem with low biodiversity due to its glacial history and the strong salinity gradients that only a few species can tolerate[38,39]. The core of the Kiel Bay database comprises detailed dietary information based on stomach contents from 22,185 fish individuals of six species. These species were classified into two functional groups based on their body shape and habitat use: fusiform and benthopelagic species (*Gadus morhua*, *Merlangius merlangius*) versus flat and demersal species (*Limanda limanda*,

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Pleuronectes platessa, *Platichthys flesus*, and *Hippoglossoides platessoides*). This shape characteristic also corresponds to specific foraging behaviour[40].

The fish individuals were sampled using systematic and standardised bottom trawls. The trawls were carried out year-round between 1968 and 1978. The body lengths of fish were measured and rounded to the nearest integer (in cm). Species-specific regressions were used to estimate fish body masses. Stomach contents were identified to the highest taxonomic resolution possible and wet mass determined when possible. Hence, the database includes body size data for all fish (i.e. predators) but also for prey items from the stomach contents[41]. In addition, we were able to add independently-sampled abundance and body mass information on the benthic invertebrate (i.e. prey) fauna to the database. These data on prey abundances and body masses were sampled independently at the trawling locations using classical 0.1 m^2 van Veen grabs[42] (see [43] for detailed procedure). We have enriched the database with climatic (i.e. temperature) and oceanographic (i.e. salinity) data and geographical information on the distances between the sampling (trawling) sites. So far, the stomach content data have been published only partially and in German language[41] while parts of the invertebrate abundance data were treated and published separately[43]. The food web mainly consists of six demersal fish species and more than a dozen benthic invertebrate species from different groups (see Table SI V 2).

Filtering data

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

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From this subset, we pooled all individuals from the same functional group occurring at the same place on the same date with the same body mass into a unique entity for statistical analysis, which we hereafter call "statistical fish". This choice is led by the allometric approach used in our analysis, where all individuals from the same species and with the same body mass are considered identical. This aggregation increases the quality of the estimation of the prey body mass distribution in stomachs at the cost of a lower statistical power for the analyses done on the shape of these distributions. For instance, with a high aggregation level, fewer data points are available to consider the effect of temperature on the average body mass of prey. This approach is therefore conservative as it reduces the probability of type 1 error. Lastly, we removed 26 statistical fish where less than 90% of the prey biomass found in the diet was also found in the environment. This resulted in a final dataset of 290 statistical fish, underpinned by 2,487 individuals. For our statistical analysis, we used fish body shape as a covariate instead of fish species, as models based on fish body shape were always found to be more parsimonious (based on AIC).

Fitting of gut content and environmental distributions

We used empirical means and standard deviations to describe all environmental distributions of $\log_{10}$ body masses and realised distributions of each predator identity. Taxon-specific characteristics of the prey, such as body toughness, could bias the dietary distributions towards prey containing shells or skeletons. We assumed that prey with hard body parts are more likely to be detected in stomach contents than species composed of soft tissues (due to their higher digestion time) and weighted their occurrence by a correction factor of 0.8[44]. Overall, the trends and effects observed when including this correction were similar to those observed without correction, thus suggesting an absence of systematic biases (SI V).

Determining allometric species' preferences

We assumed that a feeding event is defined by two independent probabilities: the probability for a consumer to encounter a prey of a certain body size x (defined by the environmental distribution $E(x)$)

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and the probability for a consumer to consume the prey when encountered (given by the preference distribution $P(x)$). Then, the realised distribution is proportional to their product

$$R(x) \sim E(x) \cdot P(x)$$

The preference distribution can therefore be expressed by the departure of the realised niche from the environmental distribution, or by filtering out the effect of species environmental availability from the realised distribution:

$$P(x) \sim \frac{R(x)}{E(x)}$$

Theoretically, it is possible to compute continuous distributions R and E from observed body masses r_i (i=1…n) and e_i (i=1…m), respectively, with e.g. kernel density estimation, and compute

$$P(x) = \frac{R(x)}{E(x)} / \int \frac{R(x)}{E(x)} dx$$

We chose, however, a more conservative approach that requires just a kernel density estimate for the environmental distribution $E(x)$: Moments of $P(x)$ can be computed as weighted moments of the observed realised body masses r_i with weights w_i=1/$E(r_i)$ as the inverse of environmental abundances. Thus, realised body masses that are highly abundant in the environment contribute less to the preference distribution, while those that are rare contribute more. Following[45] and assuming $W = \sum_i w_i$, the mean μ, variance σ^2 and skewness γ of the preference distribution $P(x)$ are:

$$\mu = \frac{1}{W} \sum_i w_i r_i,$$

$$\sigma^2 = \frac{1}{W} \sum_i w_i (r_i - \mu)^2$$

$$\gamma = \frac{1}{W\sigma^3} \sum_i w_i (r_i - \mu)^3$$

To assess changes in the distributions and how they depart from each other, we used variations in the point estimates (median and standard deviation).

Statistical analyses

To fit the parameters associated to the environmental and dietary (i.e. realised) distributions, we used an exploratory approach without a priori hypotheses, as the goal was to obtain a description of the

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different environmental conditions for fishes. To do so, we selected the most parsimonious models (based on AIC) within all the possible sub models deriving from the complete model with all covariates and their interactions. For the environmental distribution, the complete model was defined as a linear model including temperature and productivity (estimated from prey availability, grams log transformed) and their interactions as covariates. For the gut distribution, the complete model was defined as a linear model including temperature, productivity (log transformed), fish body shape and fish body mass (log transformed), as well as all possible interactions.

For the preference distributions, we used a Bayesian framework to explicitly test our hypotheses and started our analysis considering temperature, productivity, fish body shape, and fish body mass as covariates, as well as interactions between temperature and shape and temperature and productivity to answer to hypotheses H1 and H2. We first checked if fish body shape was an important predictor in our model using a "Leave-one-out" cross validation[23], and finally simplified our model by removing fish body shape from the covariates (see SI VI for a more comprehensive comparison of the different models).

Dynamic model

To simulate the population dynamics, we used a previously published model[46], based on the Yodzis and Innes framework[47]. The growth of consumer species B_i is determined by the balance between its energetic income (predation) and its energetic losses (predation metabolism)

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

where e_p = 0.545 and e_a = 0.906 represent the assimilation efficiency of a consumer foraging on plants and animals, respectively[48]. x_i defines the metabolic rate of species i, which scales allometrically with body mass:

$$x_i = x_0 m_i^{-0.25} e^{E_x \frac{T_0 - T}{k T_0 T}},$$

where $x_0 = 0.314$ is the scaling constant [46], E_x = -0.69 is the activation energy of metabolic rate (Binzer et al. 2015), k the Boltzmann constant, $T_0 = 293.15$ the reference temperature in Kelvin and T

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the temperature at which the simulation is performed. The trophic interactions are determined using a functional response F_{ij} that describes the feeding rate of consumer i over resource j:

$$F_{ij} = \frac{\omega_{ij} b_{ij} B_j^{1+q}}{1 + cB_i + \omega_{ij} \sum_k h_i b_{ik} B_k^{1+q}} \cdot \frac{1}{m_x}.$$

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

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

It corresponds to the product of encounter probabilities P_{ij} by the probability that an encounter leads to a realised predation event L_{ij}. As such, the parameters encode neutral processes (encounter probabilities) and trait-based selectivity, as the distribution L_{ij} represents the fundamental trophic niche of consumer i, i.e. the set of prey it can consume based on its traits. Both quantities are determined by species body masses. We assume that encounter probability is more likely for species with higher movement speeds of both consumer and resource species:

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

Since movement speed scales allometrically and based on feeding type[49], we drew β_i and β_j from normal distributions (carnivore: $\mu_\beta = 0.42$, $\sigma_\beta = 0.05$, omnivore: $\mu_\beta = 0.19$, $\sigma_\beta = 0.04$, herbivore: $\mu_\beta = 0.19$, $\sigma_\beta = 0.04$, primary producer: $\mu_\beta = 0$, $\sigma_\beta = 0$). Activation energy E_p is equal to -0.38, from [10]. L_{ij} is assumed to follow a Ricker curve[46], defined as:

$$L_{ij} = \left(\frac{m_i}{m_j R_{opt}} e^{1 - \frac{m_i}{m_j R_{opt}}} \right)^{\gamma},$$

where the optimal consumer-resource body mass ratio $R_{opt} = 71.68$ was calculated from the observed realised interactions in our dataset. We used a threshold $L_{ij} < 0.01$ under which values were set to 0, assuming that consumers do not consider prey which are too small or too large. The handling time h_{ij} of i on j is defined as:

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

where the scaling constant h_0 was set to 0.4 and the allometric coefficients for η_i and η_j where drawn from a normal distribution with mean and standard deviation of -0.48 and 0.03 for η_i and of -0.66 and 0.02 for η_j. E_h is equal to 0.26. The term w_{ij} informs on species selectivity[50], describing the foraging

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effort of a given consumer on part of its fundamental niche (described by the L_{ij}). For the models without behavioural expectations we used the classical parametrisation and defined it for every j as 1 over the number of prey of consumer i. When adaptive behaviour was included in the model, the value was determined by the predictions of our dataset: we used the moments (mean, standard deviation and skewness) of the different preference distributions to estimate parameters of a skewed normal distribution that we related to temperature, predator body mass, ecosystem productivity and the interaction between temperature and productivity using a linear model for parameters associated to location and shape and generalised linear model with a log link function for the scale parameter that is positive real.. To maintain the comparability with the model without adaptive behaviour, the w_{ij} values were transformed so that their sum was equal to 1 for each consumer. As for our experimental data, productivity was defined as the total biomass of prey available for each consumer. As this value can be highly variable during the simulations, especially in the transient dynamics, we rescaled this value between 0 and 6 to maintain it to a scale that is similar to the one from our dataset that we used to inform the skew normal distributions

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

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

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

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

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

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

Where $D = 0.25$ determines the nutrient turnover rate and $S_l = 5$ determines the maximal nutrient level. The loss of a specific nutrient N_l is limited by its relative content in plant species biomass (v_1=1, v_2=0.5). We ran our model on food webs of 50 species, composed of 30 consumers and 20 basal species. A link was drawn between two species i and j when $L_{ij} > 0$. For each temperature we ran 50 replicates of the two versions of the model (with and without adaptive behaviour) using an updated

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version of the ATNr package[51] and recorded the number of extinctions. We fitted a GAM model on this number of extinctions.

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

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Methodology: BG, BR, TB

Investigation: BG, BR

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Resources: GK, SK, EOG

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Supervision: UB

Writing – original draft: BG

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

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Tables

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

	Median of the realised distribution		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-1.24	-2.40 – -0.08	**0.036**
Predator body mass	0.65	0.08 – 1.23	**0.026**
Productivity	0.44	-0.01 – 0.90	0.054
Shape (fusiform)	0.09	-0.05 – 0.23	0.191
Temperature	-0.02	-0.03 – -0.01	**<0.001**
pred.BM:Productivity	-0.16	-0.39 – 0.06	0.153
shapefusiform:temperature	-0.02	-0.03 – -0.00	**0.032**
Observations	290		
R^2 / R^2 adjusted	0.286 / 0.271		

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

	Median of the preference distribution	
Predictors	*Estimates*	*CI (95%)*
Intercept	-1.06	-3.25 – 0.99
Predator body mass	0.55	0.40 – 0.70
Temperature	0.18	-0.03 – 0.39
Productivity	0.18	-0.53 – 0.92
temperature:productivity	-0.07	-0.14 – 0.00
Observations	290	
R^2 Bayes	0.279	

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Figures

Fig. 1:

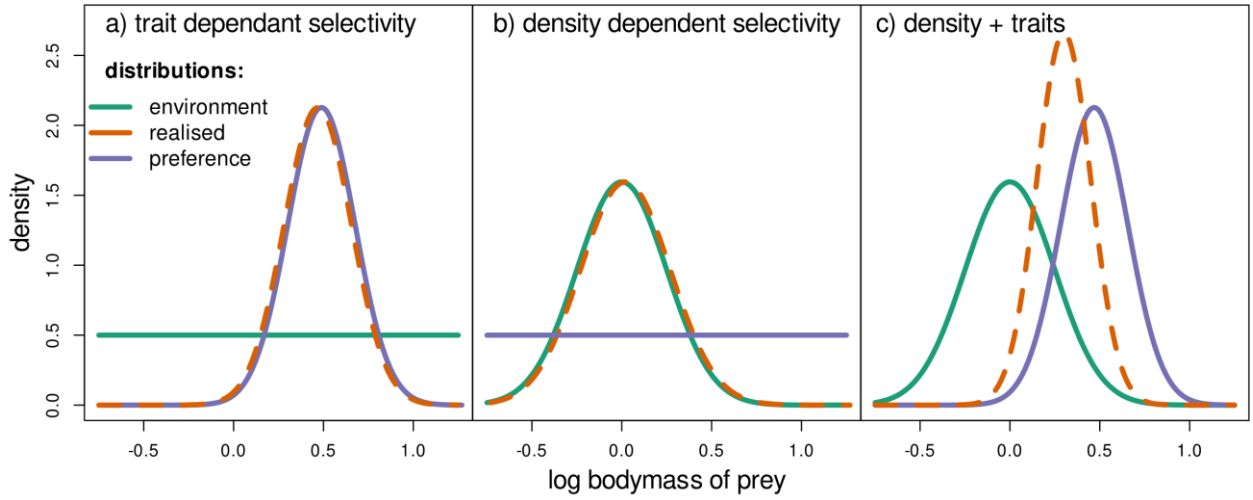

Fig. 1: Illustration of the different fish prey body mass distributions. The environmental distribution (green) represents the distribution of prey body mass in the ecosystem, the realized distribution (dashed red) represents the body mass of the prey in a consumer stomach, and the preference distribution (blue) represents the selectivity of a consumer for a specific prey body mass. a) All of the log prey body masses are equally represented in the environment, so the distribution of prey body masses observed in a consumer's gut represents the body masses on which it actively foraged (its preference distribution) and predation is driven by trait selectivity only (hypothesis 1). b) The body mass distribution of the prey observed in the gut and in the environment are equivalent, so the prey consumed by the predator were entirely driven by encounter probabilities (i.e. a neutral process), implying no active selectivity over specific prey size classes (hypothesis 2). Panels a) and b) represent extreme scenarios while real-world data are more likely to be described by two different distributions, as in c) where the body mass distribution of prey observed in the stomach and in the environment differs, so that the consumer specifically forages on some prey body masses that are represented by the preference distribution. High values in the preference distribution represent body masses that are over-represented in fish stomachs compared to what is available in the environment.

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Fig. 2:

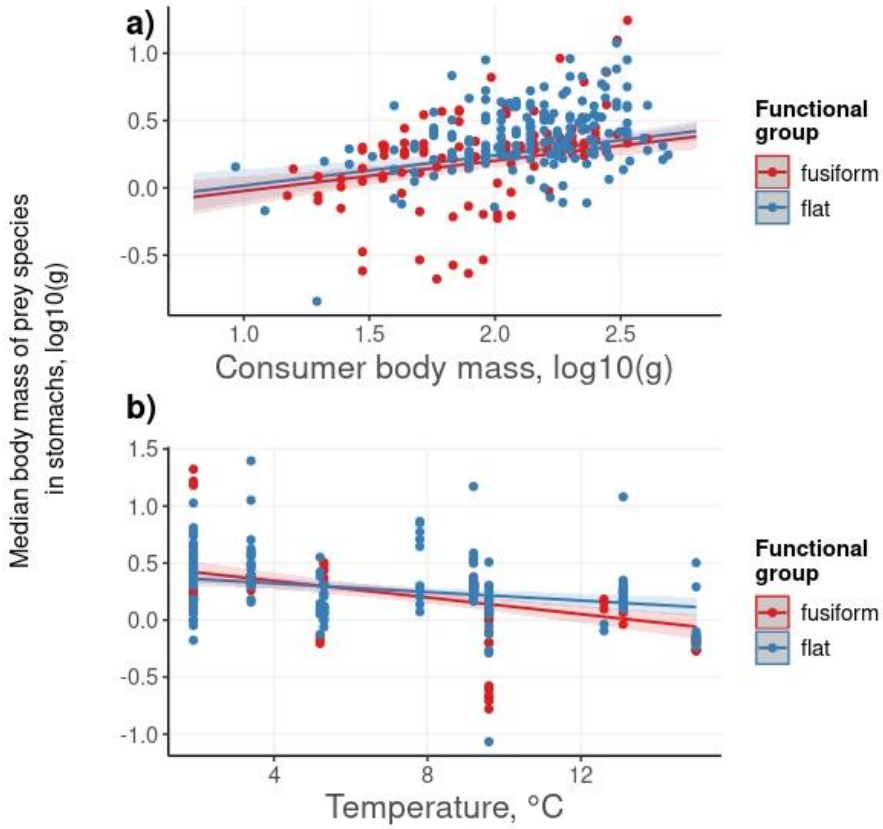

Fig. 2: Response of the median body mass of the realized prey body mass distribution. Response to predator body mass (a), and temperature (b) for the two fish functional groups. Points represent non-transformed data across all productivity levels and lines present model predictions. Regression lines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

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Fig. 3:

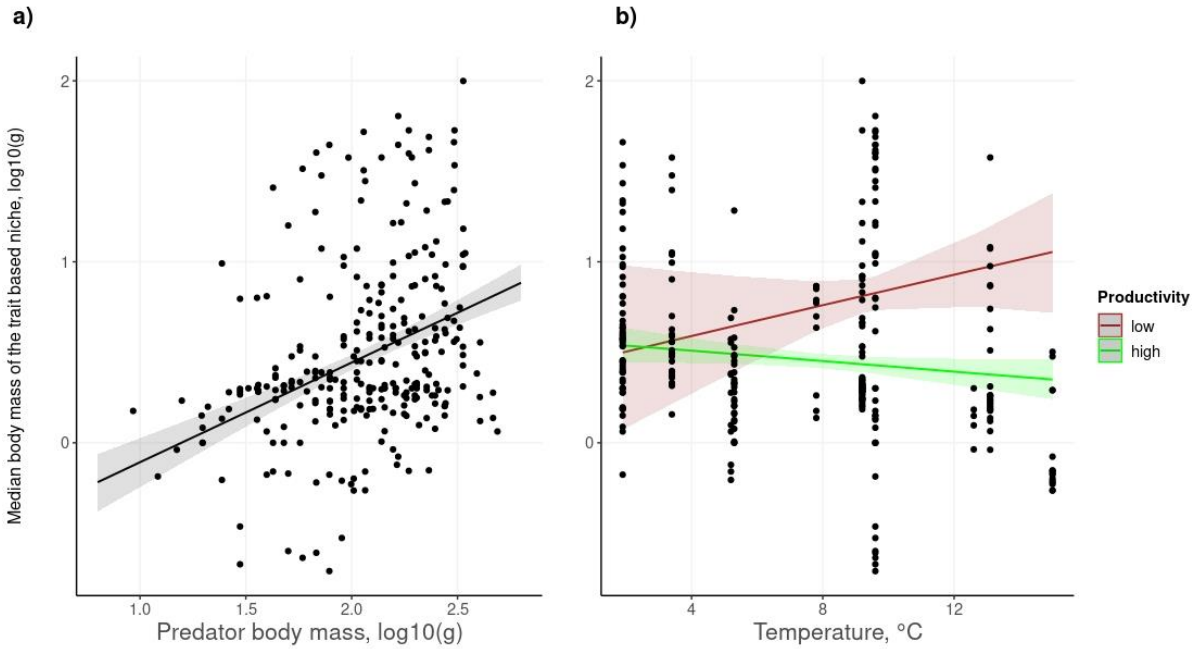

Fig. 3: Response of the median prey body mass of the preference distribution to (a) predator body mass and (b) temperature and productivity. Points represent non-transformed data across all productivity levels and lines represent model predictions. Regression lines represent model's prediction when all other covariates are considered. The shaded areas show the 95% confidence interval on the predicted values.

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Fig. 4:

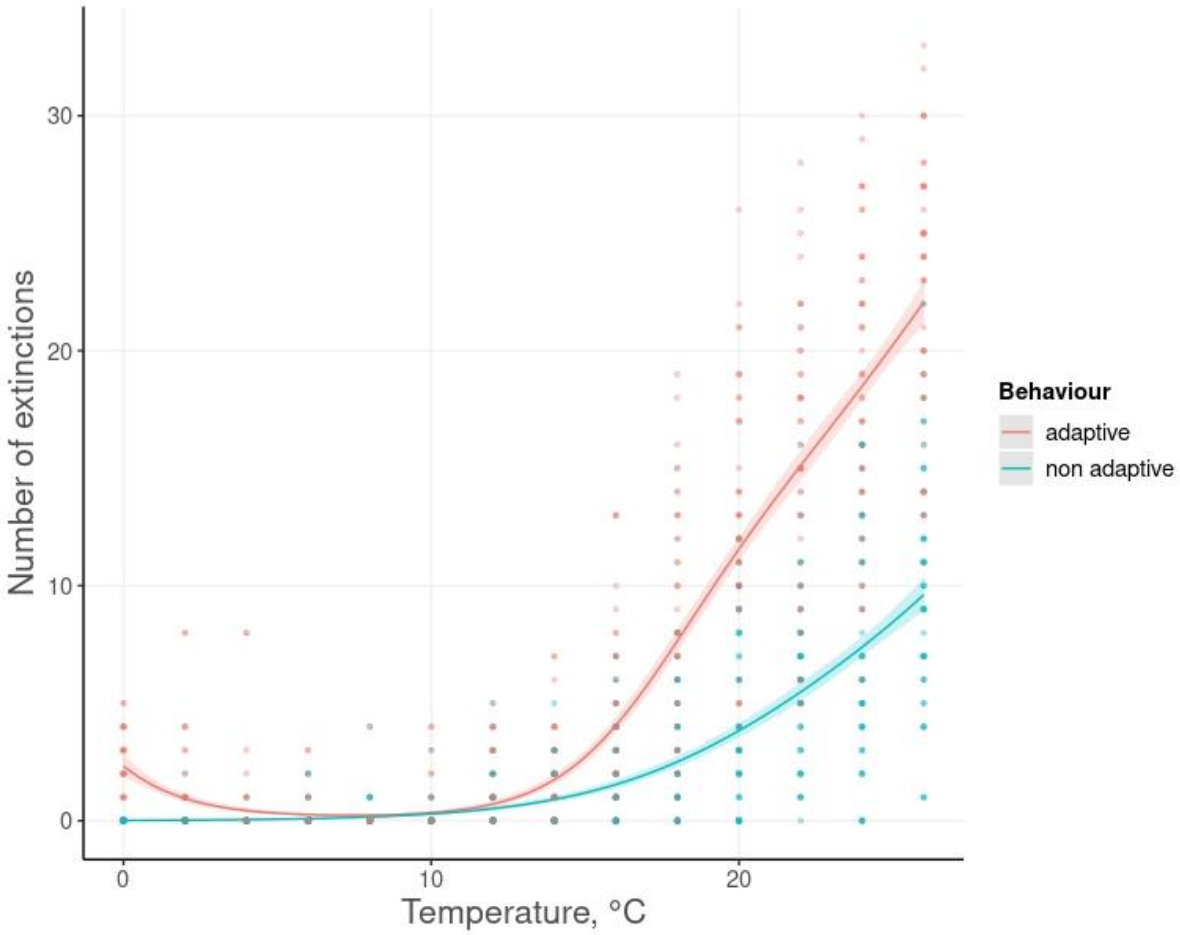

Fig. 4: Number of species extinctions predicted by the model at different temperatures. The blue line represents the model output with adaptation of species diets to local temperature and productivity conditions considered, whilst the red line shows extinctions without allowing for this adaptation. The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