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**Disentangling the nonlinear effects of habitat complexity
on functional responses**

RNDr. thesis

Mgr. Pavel Soukup

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Annotation

Habitat structural complexity modifies trophic interactions by providing refuges and altering predator and prey behavior. The quality and intensity of predator prey interactions can be described by functional responses, that is by the relationship between the number of preys consumed by a predator and initial prey density. We combine two complementary methods of functional response estimation to examine the effects of habitat complexity on the predation of *Aeshna cyanea* dragonfly larva on *Chaoborus obscuripes* glassworm larvae. We show that habitat complexity has nonlinear effects on functional response parameters (attack rate and handling time), despite the prevalence of stepwise responses reported in literature. Our results suggest that detailed understanding of habitat complexity effects on food webs requires complementary experimental approaches across a gradient of habitat complexity and should also consider predator and prey behavior.

Declaration [in Czech]

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Disentangling the nonlinear effects of habitat complexity on functional responses

Julien Mocq^{1,2}  | Pavel R. Soukup^{1,2}  | Joacim Näslund^{1,3}  | David S. Boukal^{1,2} 

¹Faculty of Science, Department of Ecosystem Biology & Soil and Water Research Infrastructure, University of South Bohemia, České Budějovice, Czech Republic

²Biology Centre, Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic

³Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

Correspondence

Julien Mocq
Email: julien.mocq@gmail.com

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Abstract

1. Structural complexity of habitats modifies trophic interactions by providing refuges and altering predator and prey behaviour. Nonlinear effects on trophic interaction strengths driven by these mechanisms may alter food web dynamics and community structure in response to habitat modifications. However, changes in functional response, the relationship between prey density and feeding rate, along habitat complexity (HC) gradients are little understood.
2. We quantified functional responses along a HC gradient from an entirely unstructured to highly structured habitat in a freshwater system, using dragonfly larvae (*Aeshna cyanea*) preying on *Chaoborus obscuripes* larvae. To disentangle mechanisms by which changes in HC affect functional responses, we used two different approaches—a population-level and a behavioural experiment—applied an information theoretic approach to identify plausible links between HC and functional response parameters, and compared our results to previous studies.
3. Functional response shape did not change, but we found strong evidence for nonlinear dependence of attack rate and handling time on HC in our study. Combined results from both experiments imply that attack rate increased stepwise between the unstructured and structured habitats in line with the threshold hypothesis, because the predators gained better access to the prey. Handling time was lowest at an intermediate HC level in the population-level experiment while the direct estimate of handling time did not vary with HC in the behavioural experiment. These differences point towards HC-driven changes in foraging activity and other predator and prey behaviour.
4. Most previous studies reported stepwise decrease in attack rate in line with the threshold hypothesis or no change with increasing HC. Moreover, changes in the handling time parameter with HC appear to be relatively common but not conforming to the threshold hypothesis. Overall, increased HC appears to, respectively, weaken and strengthen trophic links in 2D and 3D predator–prey interactions.
5. We conclude that detailed understanding of HC effects on food webs requires complementary experimental approaches across HC gradients that consider predator foraging strategies and predator and prey behaviour. Such studies can also help guide conservation efforts as addition of structural elements is frequently used for restoration of degraded aquatic habitats.

Julien Mocq and Pavel R. Soukup contributed equally to the manuscript.

KEYWORDS

Aeshna, attack rate, *Chaoborus*, dimensionality of predator–prey interactions, habitat domain, handling time, refuge, threshold hypothesis

1 | INTRODUCTION

Habitat structure is a ubiquitous environmental feature that underlies the diversity and composition of local communities (Newman et al., 2015; Thomaz et al., 2008). More structured habitats typically host more abundant and diverse communities (e.g. Heck & Wetstone, 1977; Jeffries, 1993; Newman et al., 2015), but see August, 1983; Reichstein et al., 2013). Habitat structure encompasses habitat heterogeneity, defined as the diversity of structural elements, and habitat complexity (hereafter 'HC'), defined as a multidimensional element consisting of qualitative and quantitative components, such as the type and density of macrophyte leaves in freshwaters or corals and macroalgae in the marine environment (Carvalho & Barros, 2017; Kovalenko et al., 2012).

Understanding the links between HC and community structure and functioning has important implications for conservation and management of habitats and ecosystems. Community responses to habitat alteration can be nonlinear (Tokeshi & Arakaki, 2012) and may include rapid deterioration or even catastrophic regime shifts (Scheffer et al., 2001). For example, marine macrofaunal community richness decreased strongly with decreasing HC of coral reefs, which contrasted with limited community-level responses above a

certain HC threshold (Newman et al., 2015). Such results suggest that community-level responses to HC could be reduced to the presence–absence scale, but the responses and underlying mechanisms across longer gradients of HC are incompletely understood (Tokeshi & Arakaki, 2012).

Changes in trophic interactions (Dean & Connell, 1987; Kovalenko et al., 2012), along with less diversified niches (Jeffries, 1993) and smaller amounts of total food and habitat area (Fontoura et al., 2019; Parker et al., 2001), drive community responses to habitat simplification. Trophic interactions determine the fluxes of energy and nutrients within food webs and their alterations can thus have cascading effects on the structure and stability of the underlying communities (Berlow et al., 2004). The 'threshold hypothesis' supported by numerous experiments posits that predation rates and anti-predator behaviour changes nonlinearly along HC gradients (Gotceitas & Colgan, 1989). Food web structure and dynamics may not respond to HC alterations outside a critical HC range, but even small changes in HC within that range could incur strong population- and community-level responses.

Functional responses (Holling, 1966) are central to studies linking trophic interaction strengths to food web dynamics and stability. Three parameters describe the most common functional response shapes (Figure 1): the Hill exponent characterizing the

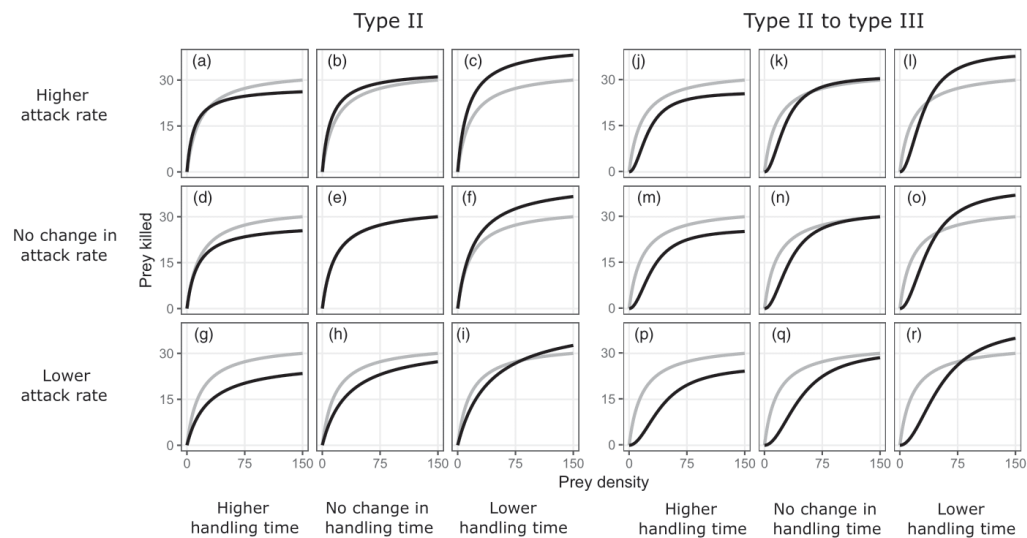


FIGURE 1 Possible responses (black lines) of a type II functional response (grey line) to changes in HC. These include no response (e), changes in handling time and/or attack rate without a shift to type III response (a–d, f–i), and changes from type II to type III (j–r). All curves based on the formula $y = (aN^b)/(1 + ahN^b)$, with baseline parameter values of attack rate (a–i: $a = 2$, j–r: $a = 0.028$) and handling time (a–i: $h = 0.03$, j–r: $h = 0.032$) altered by 50% (a) or 20% (h) according to the panel label. The Hill exponent was set to $b = 1$ for panels a–i and $b = 2$ for panels j–r

functional response shape, the attack rate corresponding to the slope of the functional response at low prey densities, and the handling time whose inverse determines the maximum impact of the predator at high prey densities (e.g. Barrios-O'Neill et al., 2015; Kalinkat, Schneider, et al., 2013). The shape and parameter values of functional response strongly influence the stability of consumer–resource interactions and population equilibria, and hence are of great importance in studies of population dynamics, community stability and effects of invasive species (Barrios-O'Neill et al., 2015; Boukal et al., 2007; Williams & Martinez, 2004).

HC can modify the shape and magnitude of functional responses by altering the attack rate, handling time or the Hill exponent (Figure 1). Using a modified Rosenzweig–MacArthur model as an example, some of these changes can destabilize predator–prey dynamics (Figure 1a–c) while others may have a stabilizing (Figure 1h–r) or either effect (Figure 1d,f,g,i) depending on the numerical values of model parameters (Boukal et al., 2007). The underlying proximate mechanisms include changes in predator or prey distribution in space, behavioural changes, movement interference and altered ability of predators to exploit prey driven by predator and prey habitat domains and relevant functional traits (Boukal, 2014; Gotceitas & Colgan, 1989; Klecka & Boukal, 2014).

Three broad types of such mechanisms have been recognized. First, impediments to predator movement or visual detection of the prey can decrease the attack rates (Figure 1g–i; Hauzy et al., 2010; Long et al., 2012; Manatunge et al., 2000). Second, HC can create perching sites for the predator (Klecka & Boukal, 2014) or compromise prey movement and visual range (Hauzy et al., 2010; Manatunge et al., 2000) and hence increase the attack rates (Figure 1a–c). Third, prey refuges in more complex habitats ('refuge effect'; Alexander et al., 2012; Lipcius & Hines, 1986) can change type II to type III functional response because some but not all prey can escape predation by using these refuges (Figure 1j–r). Interestingly, we lack mechanistic explanations for the surprisingly common observations of HC-dependent handling time with or without a concurrent change from type II to type III (Figure 1a,c,d,f,g,i,l,m,o,p,r; e.g. Kalinkat, Brose, et al., 2013; Lipcius & Hines, 1986; Wasserman et al., 2016). This parameter includes the predator's ability to process and digest captured prey that should be independent of HC but also other biological processes and activities (Jeschke, 2007; Li et al., 2018) that may vary with HC. For example, more frequent failed predation attempts or longer periods of predator inactivity increase handling times.

The impact of HC on functional responses is usually studied on the presence–absence scale or a scale with a structurally simple habitat and two levels of HC and rarely consider the HC as a gradient (Table S1). To date, only four studies included four HC levels (terrestrial: Hoddle, 2003; Kalinkat, Brose, et al., 2013; marine: Anderson, 2001; freshwater: Alexander et al., 2015), and one study used leaves of five terrestrial plant species differing in trichome density that we interpret as HC levels (Barbosa et al., 2019). These studies used different taxa and experimental set-ups and reached different conclusions on the effect of HC on functional responses. Changes in functional responses along more gradual gradients of HC

are thus poorly understood and we lack tests of the 'threshold hypothesis' in a dynamical setting. This hampers a robust understanding of the qualitative and quantitative effects of habitat alteration on trophic interactions and community structure.

To fill this gap, we carried out laboratory experiments to estimate the parameters of a functional response along a gradient of five HC levels ranging from an entirely unstructured to highly structured habitat. We used dragonfly *Aeshna cyanea* larvae feeding on phantom midge *Chaoborus obscuripes* larvae; both species frequently co-occur in nature. While the dragonfly larvae are climbers that hunt mainly visually with a sit-and-wait ambush strategy (Pritchard, 1965), *Chaoborus* larvae occupy the water column (Pastorok, 1981). The theory summarized above predicts two outcomes for this combination of predator and prey domains and predator foraging strategy: (a) increasing attack rates as the habitat transitions from simple to more complex because the predators gain better access to prey in the water column (Klecka & Boukal, 2014), followed by decreasing attack rates due to impeded access to the prey in highly structured habitat and (b) possible change from type II to type III functional response due to a 'refuge effect' in highly structured habitats.

2 | MATERIALS AND METHODS

We combined two complementary approaches to functional response estimation, with their own strengths and weaknesses, yet almost never used simultaneously, to obtain robust results: a population-level approach that estimates the parameters from prey mortality measured in feeding experiments conducted at multiple prey densities, and a behavioural approach in which the attack rates and handling times are estimated directly by observing the predation process (Hauzy et al., 2010; Hossie & Murray, 2010).

2.1 | Experiment 1

We first conducted a population-level experiment at five HC levels in a temperature-controlled room (mean \pm SD: 19.7 \pm 0.25°C, 18L:6D photoperiod) on 8–16 September 2016. Predators and prey were collected in small fishless forest ponds (49°4'59.078"N, 14°23'30.756"E) near České Budějovice, Czech Republic. *Chaoborus* larvae (4th instar, mean \pm SD wet mass 8.18 \pm 1.34 \times 10⁻³ g) were acclimated in 10-L plastic buckets and fed ad libitum with zooplankton (*Daphnia* sp.) for 1–2 days prior to the experiment. *Aeshna* larvae (wet mass 0.154 \pm 0.02 g, range 0.120–0.188 g) were acclimated individually in 150-ml plastic cups and fed ad libitum with *Tubifex* worms for 2–3 days prior to the experiment. Before the experiment, each *Aeshna* was weighted to the nearest 0.1 mg (ABT 120-SDM analytical balance; KERN & SOHN GmbH, Balingen, Germany) and starved for 24 hr.

Feeding trials were run in translucent plastic boxes (length \times width \times height = 16 cm \times 12 cm \times 12 cm) filled with 1.5 L (9 cm depth) of tap water continuously aerated for 24 hr. A 1-mm layer of fine quartz sand (grain size

–0.3 mm) was added to provide a bottom substrate. Arenas were separated by cardboard walls to prevent visual interference among predators. We placed $N_p = 0, 1, 2, 4$ or 8 plastic plant models in the arena to create a HC gradient. Each plant model consisted of four strips of green plastic mesh (18 cm long, 2 cm wide, 1.5 mm mesh size) tied to a small stone (2–3 cm diameter; Figure S1). Index of complexity of individual 'plants' I_{hv} equalled 9.4 ± 1.6 (mean \pm SD, $n = 8$)—measured as $I_{hv} = f_h/l_h + f_v/l_v$ with f_h and f_v the mean numbers of interstices intercepted per meter, respectively, along the horizontal and vertical axes, and l_h and l_v the mean lengths of interstices in meters, respectively, along the horizontal and vertical axes (Dibble et al., 1996).

We quantified the functional response at each HC level on a gradient of seven prey densities ($N_0 = 2, 4, 8, 16, 32, 64$ and 128 individuals). Prey were released into the arena 30 min before the experiment, after which the predator was added and allowed to forage for 8 hr. Afterwards, we noted the location of each predator, removed it and counted surviving and dead prey. All predators and prey were used only once. Arenas, sand and plastic plant models were used repeatedly but thoroughly rinsed with boiling water to eliminate chemical cues between subsequent trials.

We ran 8–10 replicates of predation trials for every combination of HC and prey density ($N_{tot} = 279$). Background prey mortality, assessed in 4–7 control replicates for each combination of HC and prey density, was low (proportion of dead individuals: mean \pm SD = 0.02 ± 0.05 , $n = 161$) and independent of HC and initial prey density (quasi-binomial GLM: HC, $p = 0.53$; prey density, $p = 0.48$). We thus ignored background prey mortality in the analyses.

2.2 | Experiment 2

In all, 18 *Aeshna* larvae (mean \pm SD wet mass 0.346 ± 0.048 g, range 0.275–0.475 g) and their prey (4th instar *Chaoborus*, mean \pm SD wet mass $9.45 \pm 1.69 \times 10^{-3}$ g) were collected from the same location as above in September 2017. Prior to the experiment, the animals were treated identically as in Experiment 1, including a 24-hr starvation period of the predators.

The experiment was run in thermal cabinets (Lovibond BSK ET 650; Tintometer GmbH, Dortmund, Germany) at 20°C (mean \pm SD = $20.3 \pm 0.2^\circ\text{C}$) and simulated daylight conditions. We used glass aquaria with nearly the same volume as in Experiment 1 (1.44 L, length \times width \times height = 15 cm \times 8 cm \times 15 cm, 12 cm water depth), allowing side video recording. Trials were run at three HC levels: none ($N_p = 0$ plant models per arena), low ($N_p = 1$) and high ($N_p = 4$). Each individual *Aeshna* was trialled in one level of HC at two prey densities (6 and 24 prey individuals, order of prey treatment randomized) over a 4-day period: each individual was starved during day 1, used in the first trial and subsequently fed *ad libitum* on day 2, starved on day 3, and trialled again on day 4. The set-up including the acclimation procedure was otherwise identical as in Experiment 1. We ran 36 trials in total (3 HC levels \times 2 prey densities \times 6 replicates per experimental conditions).

Prey were introduced into the arena 30 min before the predator. Its behaviour was recorded with PK-910H HD 1080p webcams (A4TECH; Taipei, Taiwan) at 30 frames per second for 50 min. Observations started after the introduced predator stopped swimming and settled onto a surface, indicating it has calmed and begun to search for prey. Its behaviour was then recorded for 40 min or until the handling of the last prey captured in the 40-min interval was completed. The camera was placed perpendicularly to the centre of the arena's wider side; two opposing cameras were used in the high complexity treatment to prevent unobserved predation events.

Four categories of predator behaviour were manually scored using BORIS v5.1.3 (Friard & Gamba, 2016): (a) substrate preference, defined as proportions of total time spent on the wall, bottom and on plant models, all rounded to the nearest second; (b) predator attack towards a prey, visible as a rapid extension of the mouthparts; (c) handling time, defined as time elapsed since prey capture to the last cleaning movement of the predator's mouthparts before its whole-body movement or another attack on prey and (d) duration of a foraging bout, defined as time interval from the start of the trial or the end of previous prey handling to the next successful attack or the end of the trial. We used the ratio between the number of successful and failed predator attacks to calculate the probability of successful prey capture and foraging bout durations to estimate attack rates (see below). Four events with zero handling time were excluded from the attack rate and handling time analysis, assuming that the predators were not hunting during prey handling.

2.3 | Data analyses

We used a model selection approach for the data from each experiment, and compared a suite of models covering all possibilities outlined in Figure 1 similar to Kalinkat, Brose, et al. (2013). We also compared the estimates of attack rate and handling time from the two experiments. We ran all analyses in R 3.6.2 (R Development Core Team, 2019).

Data from the population-level Experiment 1 were analysed with packages `BBMLE` (Bolker & R Development Core Team, 2017) and `EMDBOOK` (Bolker, 2016). We first distinguished between Type II and Type III functional response at each level of habitat complexity HC, expressed on a relative scale as $HC = N_p/8$. We used the logistic regression between the proportion of eaten prey N_e/N_0 and the initial prey density (Juliano, 2001):

$$\frac{N_e}{N_0} = \frac{\exp\left(P_0(HC) + P_1(HC)N_0 + P_2(HC)N_0^2 + P_3(HC)N_0^3\right)}{1 + \exp\left(P_0(HC) + P_1(HC)N_0 + P_2(HC)N_0^2 + P_3(HC)N_0^3\right)}, \quad (1)$$

where N_0 is the number of prey eaten and the HC-specific parameters $P_i(HC)$ are determined with the maximum likelihood method (Juliano, 2001). While $P_1(HC) < 0$ characterize a Type II functional response, $P_1(HC) > 0$ and $P_2(HC) < 0$ identify a Type III functional response for given HC. We have also attempted to fit models with a

variable Hill exponent, but these models did not converge (results not shown).

We found only Type II functional response at each level of HC and thus used Rogers equation to account for prey depletion (Rogers, 1972). To detect possible nonlinear effects of HC on attack rate a or handling time h , we considered 18 models of increasing complexity with HC-dependent parameters $a(\text{HC})$ and $h(\text{HC})$ (Table S2). Models (1)–(9) assumed that $a(\text{HC})$ and $h(\text{HC})$ are constant or scale linearly (i.e. $a(\text{HC}) = a_0 + a_1\text{HC}$ and/or $h(\text{HC}) = h_0 + h_1\text{HC}$) or as a second-order polynomial with HC (i.e. $a(\text{HC}) = a_0 + a_1\text{HC} + a_2\text{HC}^2$ and/or $h(\text{HC}) = h_0 + h_1\text{HC} + h_2\text{HC}^2$). Models (10)–(12) described a stepwise change in the attack rate (i.e. $a(0) = a_{v0}$ and $a(\text{HC}) = a_{v1}$ for $\text{HC} > 0$) combined with a constant, linear or unimodal dependence of handling time on HC. Models (13)–(15) further generalized models (10)–(12) using a linear relationship $a(\text{HC}) = a_{v1} + a_v\text{HC}$ for $\text{HC} > 0$ with a maximum attack rate at $N_p = 1$ for negative a_v values. Finally, models (16)–(18) assumed that the attack rate or handling time vary freely across HC levels, that is, $a(\text{HC}) = a_{vj}$ or $h(\text{HC}) = h_{vj}$ for j artificial ‘plants’ ($j = 0, 1, 2, 4$ and 8). Model (1) corresponds to no effect of HC on the functional response, models (10)–(12) correspond to a qualitative, presence-absence driven effect of HC on attack rate, models (13)–(15) correspond to an initial increase in attack rate followed by a possibly decelerating or negative effect of HC on attack rate in more complex habitats and model (18) with HC-specific parameters is closest to the approach taken in many previous studies (Tables S1 and S2).

Prey consumption increased with predator size W even within the relatively narrow preselected size range. We accounted for this effect in models (1)–(18) by incorporating allometric scaling of handling time and attack rate as $a(\text{HC}, W) = a(\text{HC})W^b$ and $h(\text{C}, W) = h(\text{HC})W^c$, where b and c are the respective allometric exponents (Weterings et al., 2015), yielding a modified Rogers equation:

$$N_e = N_0 \left(1 - \exp \left(a(\text{HC}) W^b (N_e h(\text{HC}) W^c - T) \right) \right), \quad (2)$$

where the number of eaten prey N_e depends on initial prey density N_0 , duration of experiment T and the parameters outlined above. We used Lambert-W function to solve the equation (Bolker, 2008). Each model was fitted by maximum likelihood estimation (Bolker, 2008) and all 18 models ranked by their Bayesian information criterion (BIC) values (Brewer et al., 2016). We considered models with $\Delta\text{BIC} \leq 2$ as plausible alternatives to the most parsimonious model (Burnham & Anderson, 2002).

We characterize the magnitude of the HC effect in each functional response parameter r ($r = a$ or h) of each plausible model by calculating the largest relative change $\Delta r = \min_{\text{HC}} (\ln(r(\text{HC})/r(0)))$ if $r(\text{HC}) \leq r(0)$ or $\Delta r = \max_{\text{HC}} (\ln(r(\text{HC})/r(0)))$ if $r(\text{HC}) \geq r(0)$ across the four increased HC levels. We used the same approach to extract data from previous studies (Table S1). We also fitted the log-transformed $\log_{10}(N_e + 1)$ data as advised by Uszko et al. (2020) with nonlinear least squares regression to verify that our results are robust; the maximum-likelihood method was unable to produce parameter estimates for these data. We do not report parameter values estimated from the log-transformed data as they lack direct interpretation and cannot be compared to previous studies.

We then used the data from Experiment 2 to analyse the effects of HC and prey density on the microhabitat use (i.e. proportions of time spent on the wall, bottom and artificial plants when present), probability of a successful attack, number of eaten prey, handling time and attack rate of the predators. In each analysis, we constructed a set of candidate models and used BIC to identify the most parsimonious and plausible models as in Experiment 1. Candidate models for all four response variables covered all possible combinations of HC and prey density as fixed-effect predictors, including their statistical interactions (Table S3). Prey density was included as a linear covariate and HC as a linear (HC , scaled as $\text{HC} = N_p/4$), quadratic ($\text{HC} + \text{HC}^2$, scaled as $\text{HC} = N_p/4$) or binary (HC_{bin} , set to 0 if $\text{HC} = 0$ and to 1 if $\text{HC} = 1$ or 4) covariate. This yielded 11 candidate models for all analyses except the effect of artificial plants on microhabitat use (5 candidate models due to plant absence at $\text{HC} = 0$). We used scaled initial prey density ($N_0/24$) in the analyses of microhabitat use, probability of prey capture, number of eaten prey and handling time, and scaled prey density at the time of attack ($N_t/24$) in the analysis of attack rate to account for possible effects of prey depletion.

Data on microhabitat use, handling time, probability of prey capture and number of eaten prey from Experiment 2 were fitted with linear mixed models (LMMs) and generalized linear mixed models (GLMMs) using the `lme4` package (Bates et al., 2015) with a random replicate effect nested within predator identity to account for variation among individual replicates and predators. Data on microhabitat use and the probability of a successful attack were analysed using binomial GLMMs with logit link function. Data on handling time were analysed using a LMM with a log-transformed response, and the number of eaten prey was analysed using a Poisson GLMM with a log link function. Preliminary inspection of the data showed that the number of eaten prey did not change but handling time decreased with predator weight W . To facilitate comparison of both experiments, we included $\ln(W^c)$ as an offset in the analyses of handling time from Experiment 2, using the mean value of c estimated by Equation 1 in all 18 functional response models weighted by the BIC model weights reflecting their relative parsimony (see Table S2). DHARMA package version 0.2.7 (Hartig, 2020) was used to validate model residuals and test for the lack of over- and underdispersion and for influential outliers in the most parsimonious models. Table S5 was generated in `sjPlot` version 2.8.2 (Lüdtke, 2021).

We used survival analysis for the right-censored attack rate data from Experiment 2. Duration of foraging bouts used to estimate the attack rates did not visibly vary with predator weight unlike in Experiment 1, presumably due to smaller size range in Experiment 2. We thus did not correct for predator body size in this analysis. Data were first fitted with parametric frailty models to account for repeated measures within trials (`PARFM` package version 2.7.5; (Munda et al., 2012)) and then re-fitted with a parametric survival model (`FLEXSURV` package version 0.7.1; Jackson, 2016) with the same covariates as the most parsimonious parametric frailty model to obtain the treatment-specific, size-corrected attack rate estimates (see Text S2 for details).

3 | RESULTS

3.1 | Experiment 1: Population-level estimates

We only found support for type II functional responses (all $P_1(\text{HC}) \leq 9.56$, Table S4). The estimated attack rate exponents b were systematically positive (weighted mean \pm SD = 1.68 ± 0.42 , range 1.05–2.51) and handling time exponents c systematically negative (weighted mean \pm SD = -1.13 ± 0.17 , range -1.37 to -1.00), suggesting a consistent effect of varying body sizes of the individual predators across the models and HC levels.

Our analysis identified three plausible models for the dependence of attack rate a and handling time h on HC with untransformed data (Table 1; Table S1). The most parsimonious model (6) included a constant attack rate and a concave-up dependence of handling time on HC with a minimum corresponding to ~30% reduction at intermediate HC levels ($N_p \sim 4$, $\Delta h = -0.35$). Other plausible models (10) and (12) included a stepwise, up to twofold increase in attack rate (model (10): $\Delta a = 0.67$, model (12): $\Delta a = 0.41$) with the transition from a structurally simple ($\text{HC} = 0$) to more complex habitats ($\text{HC} > 0$), and a constant or unimodal dependence of handling time on HC (Figure 2). Functional responses based on the three plausible models were all similar and their fit to the data overlapped with the functional response based on separate fitting of the data for each HC level with model (18), especially for $N_p = 2$ and 8 (Figure 3; Figure S2). Analysis based on log-transformed data ranked these three models in the same order but gave less support to models (10) and (12). Models (1–4) assuming constant values or a linear dependence of attack rate and handling time on HC were not supported by the data (Table 1; Table S1). The predators almost always sat on the artificial plants at the end of the feeding trial (98.2% of the replicates with $N_p > 0$). In the absence of the plants, they mostly sat on the wall (80% of the replicates).

3.2 | Experiment 2: Estimates derived from behavioural data

Our model selection approach revealed only 1–2 plausible models for each of the five response variables. Based on these models, predator microhabitat use varied with HC but not with prey density

(Tables S3 and S5). We observed the same shift in microhabitat use from walls to artificial plants as perching sites when the plants were present (Figure 4a) as in Experiment 1. As HC increased, the proportion of time spent by the predators on artificial plants increased while proportions of time spent on the walls and on the bottom decreased.

Prey handling times in Experiment 2 (mean \pm SD = 39.9 ± 23.3 s, range 5.6–144.2 s, $n = 115$) were independent of HC (Tables S3

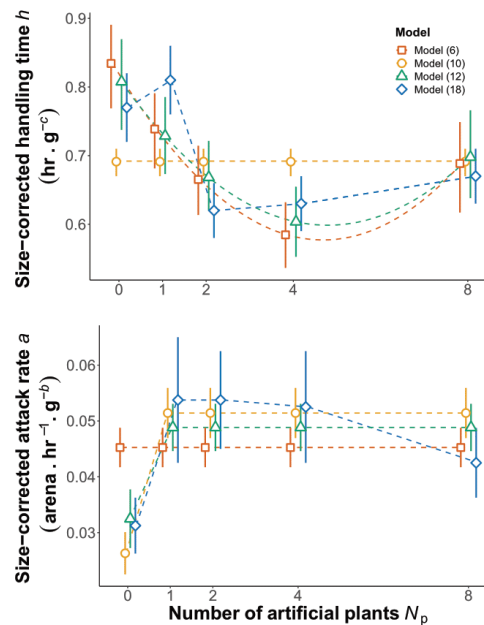
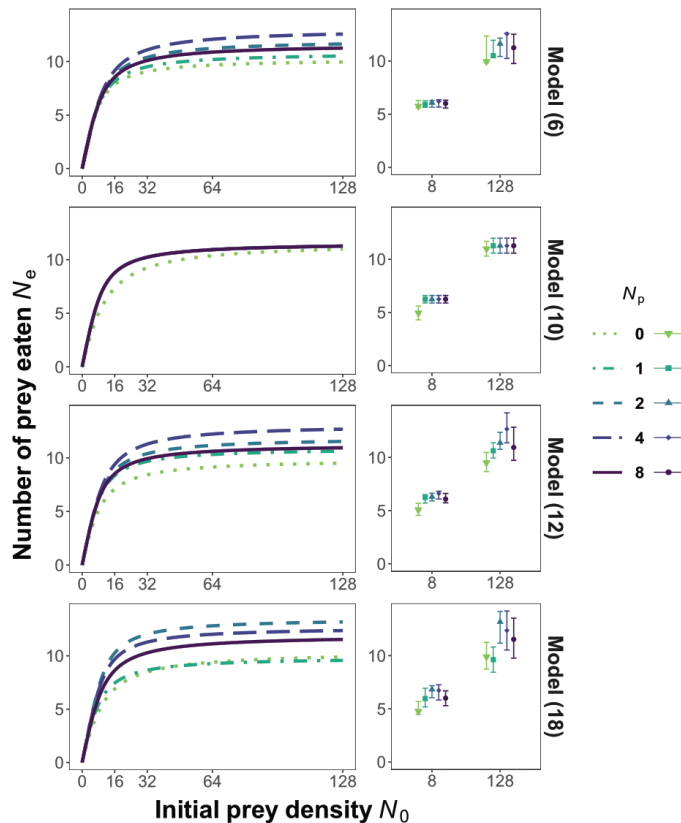


FIGURE 2 Dependence of size-corrected attack rate a and handling time h from Equation 2 on HC (N_p , number of artificial plants) in the most parsimonious model (6) and plausible models (10) and (12). Model (18) estimating a and h separately for each HC level illustrated for comparison. Estimates shown as mean \pm 95% confidence interval. See Table S2 for the respective values of the allometric exponents for attack rate (b) and handling time (c)

TABLE 1 Summary of plausible models of the effect of HC on attack rate a and handling time h from the analyses using untransformed and log-transformed data. $\text{Ln}(L)$ = log-likelihood; ΔBIC = difference of the BIC value from that of the most parsimonious model; W_{BIC} = model weight based on BIC value. See Section 2 for details

Model	Model structure	Untransformed data					Log-transformed data			
		df	$\text{Ln}(L)$	ΔBIC	W_{BIC}	Rank	$\text{Ln}(L)$	ΔBIC	W_{BIC}	Rank
(6)	constant a quadratic h	6	-568.1	0	0.359	1	189.3	0	0.710	1
(12)	stepwise a quadratic h	7	-565.8	1.0	0.220	2	189.8	4.7	0.069	2
(10)	stepwise a constant h	5	-571.9	2.0	0.135	3	184	5.1	0.056	3

FIGURE 3 Dependence of the functional response of *Aeshna* feeding on *Chaoborus* on HC gradient, fitted with the three parsimonious models (6), (10) and (12) and with the most complex model (18). Left column: mean prey consumption, right column: means with 95% bootstrapped confidence intervals at $N_0 = 8$ and 128; see Table 1 and Table S2 for details. Note that model (10) yields identical functional response curves for $N_p = 1-8$



and S5). With predator size fixed to the mean mass in Experiment 1, the predicted size-corrected handling times based on Experiment 2 (mean = 88.0 s, 95% CI = 76.0–101.8 s) were much lower than the minimum handling time estimates from Experiment 1 (model (6), $N_p = 4$: mean = 2,104 s, 95% CI = 1,931–2,278 s, Figure 2) and this relationship remained unchanged across a wide range of plausible size-scaling exponents of handling time (Figure S3).

The most parsimonious models further showed that the probability of a successful attack increased sharply with HC, especially at the low prey density (Tables S3 and S5, Figure 4b). Number of eaten prey and attack rate increased with prey density and were higher in structurally complex environments, but did not differ between trials with 1 and 4 artificial plants (number of eaten prey: Tables S3 and S6 and Figure 4c; attack rates: Table S3 and Text S2) while the numbers of prey attacks were highest at low HC ($N_p = 1$) and lowest at no HC ($N_p = 0$, details not shown; compare Figure 4b,c). The estimated size-corrected attack rates in the absence of artificial plants ($N_c = 6$ ind. arena⁻¹: $a = 0.15$ arena.hr⁻¹, 95% CI = 0.07–0.30 arena.hr⁻¹; $N_c = 24$ ind.arena⁻¹: $a = 0.37$ arena.hr⁻¹, 95% CI = 0.18–0.74 arena.hr⁻¹) were comparable to those from Experiment 1 but became significantly

higher than in Experiment 1 when artificial plants were present ($N_c = 6$ ind.arena⁻¹: $a = 1.16$ arena.hr⁻¹, 95% CI = 0.86–1.55 arena.hr⁻¹; $N_c = 24$ ind.arena⁻¹: $a = 2.91$ arena.hr⁻¹, 95% CI = 2.20–3.80 arena.hr⁻¹).

4 | DISCUSSION

The diversity of observed effects of HC on functional responses (Figure 1, Text S1 and Table S1) points towards the importance of predator and prey functional traits and other habitat characteristics in determining how gradual changes in HC alter predator-prey interactions and population dynamics. Their synthesis is currently hampered by the relative paucity of suitable data and lack of standardized methods to assess the dependence of functional responses on HC.

Our study systematically explored quantitative changes in functional response along a HC gradient. We used a model selection approach, which enables a direct comparison of different relationships between HC and functional response parameters (Long et al., 2012;

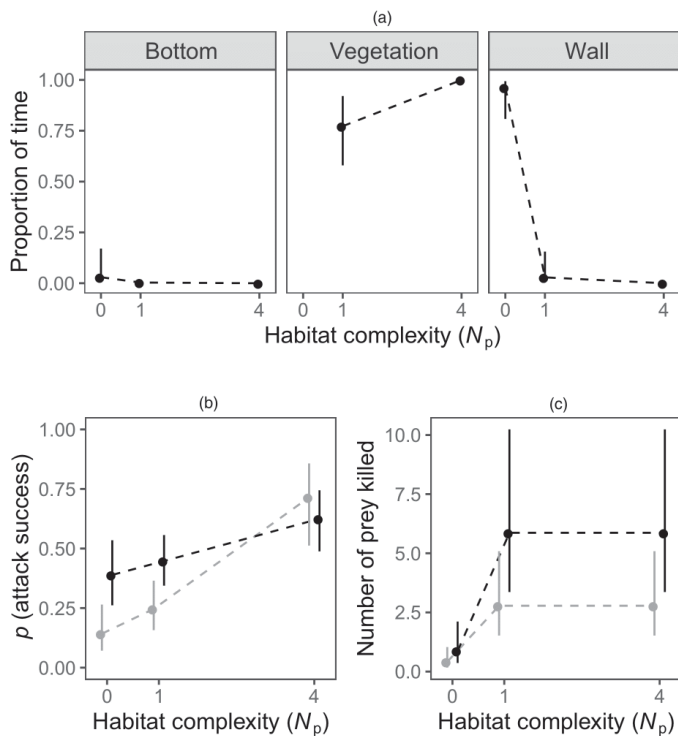


FIGURE 4 Predicted effects of HC (N_p , number of artificial plants) on (a) predator microhabitat use, (b) probability of a successful attack and (c) number of successful attacks in Experiment 2 based on the most parsimonious models. In panels (b) and (c), the initial prey density N_0 is 6 (grey) and 24 (black) ind.arena⁻¹. Circles = mean predicted values; error bars = 95% CIs based on fixed effects

Rall et al., 2012) and provides a general framework to test the relevance of various underlying mechanisms. We demonstrated that HC can have substantially nonlinear effects on functional responses, and the combination of the population-level and behavioural approaches allowed us to identify possible underlying mechanisms. While some effects observed in our experiment and previous studies are in line with the 'threshold hypothesis' (Gotceitas & Colgan, 1989), we also identified more complex relationships between HC and functional response parameters driven by changes in predator behaviour and foraging performance.

4.1 | Dependence of functional response shape on HC

We observed only type II functional responses across all HC levels. Categorical functional responses, used also in our study, may not detect subtle changes in functional response curvature driven, for example, by prey refuge use in more complex environments or by increased presence of movement obstacles that hinder predators (Barrios-O'Neill et al., 2015; Hauzy et al., 2010). However, only the 'pelagic' prey in our experiment likely perceived the added HC only as obstacles. Type II functional responses are common in aeshnid larvae (Johansson & Johansson, 1992; Van Buskirk et al., 2011); only

Hossie and Murray (2010) observed a shift from type II to type III in *Anax* larvae when HC generated by sufficient amount of leaf litter provided refuge for the tadpole prey.

Changes in the functional response shape along a HC gradient (Figure 1j-l) were detected or suspected in only 10 out of 40 tested predator-prey pairs in previous studies with relevant data (Table S1), thereby suggesting that increased HC may not stabilize predator-prey and food web dynamics through the prey refuge effect as often as previously thought. This should however be confirmed by long-term experiments under more natural conditions as most studies reported in Table S1 used more or less artificial laboratory settings.

4.2 | Dependence of attack rate on HC

We expected to observe maximum attack rates at intermediate HC levels, at which the benefits of improved access to the prey (Klecka & Boukal, 2014) in less used part of the arenas (Uiterwaal et al., 2019) would dominate over costs of limited prey detection and movement hindrance (Gotceitas & Colgan, 1989). While the population-level data were congruent with this expectation, the most parsimonious models identified no change or a stepwise increase of attack rate between none and low HC (i.e. zero and one artificial plant). Behavioural data also followed the latter threshold pattern. Observed differences

in size-corrected attack rates in our two experiments are consistent with experimental duration. The population-level experiment ran longer, which typically leads to lower and potentially more realistic estimates of attack rate due to more time spent on foraging-unrelated activities, for example, due to satiation (Li et al., 2018).

HC-specific differences in the attack rate estimates from both experiments thus imply that *Aeshna* larvae forage more efficiently in the presence of artificial plants. Although the relationship between macrophyte density and attack rate of aeshnid larvae would likely be more gradual in natural habitats with larger volumes, our results lend further support to the 'threshold hypothesis' (Gotceitas & Colgan, 1989) and to the possibility of nonlinear responses of freshwater communities to habitat alterations driven by changes in trophic interactions (Soukup et al., in prep.).

More generally, current theory posits that higher HC should modify predator search efficiency and encounter rates (Gotceitas & Colgan, 1989; Hauzy et al., 2010; Hossie & Murray, 2010). Half of the previous studies confirm this theory, with 3 out of 32 predator-prey pairs with relevant data showing an increase as in our study, 13 pairs exhibiting a decrease, and 16 pairs showing no significant change in attack rates with HC, sometimes possibly due to few replicates. Magnitude of the effect across studies was usually comparable to or smaller than our result (increase in a with HC: $\Delta a = 0.14$ – 1.67 , mean = 0.77 ; decrease: $\Delta a = -2.20$ to -0.45 , mean = -1.15 ; no change: $\Delta a = -2.14$ to 2.49 , mean = -0.10 ; Figure 5). Like us, most studies including three or more HC levels found a stepwise change in attack rate in line with the 'threshold hypothesis' (8 out of 15 predator-prey pairs; e.g. Barrios-O'Neill et al., 2015; Wasserman et al., 2016). Other results suggest HC-independent attack rates

(e.g. Barbosa et al., 2019; Hoddle, 2003) or a monotone relationship (Alexander et al., 2012; Table S1).

Results from our behavioural experiment provide further insights into the mechanisms by which HC can modulate foraging behaviour of predators. In the structurally simple environment, *Aeshna* larvae attacked least often and had the lowest foraging success, resulting in the lowest attack rates and prey mortality. The increasing probability of a successful attack was leveraged by fewer attacks in high HC relative to low HC, most likely as the predator's hunger level decreased (Jeschke et al., 2002). This leads to constant prey mortality and attack rates across all positive HC levels.

The relationship between HC and attack rate may further be context-dependent and, for example, vary with temperature (Wasserman et al., 2016) or the choice of the functional response formula (Barrios-O'Neill et al., 2015). Encounter rates also depend on the dimensionality of predator-prey interactions and predator-prey encounter mode (Barrios-O'Neill et al., 2016, 2019; Pawar et al., 2012). Data from our experiment and previous studies imply that attack rates decrease and increase in more complex habitats when the interactions occur in 2D and 3D, respectively (Figure 5). This suggests that HC tends to impede predators in 2D predator-prey interactions irrespective of the encounter mode. More data, especially from 3D contexts in terrestrial and marine environments, could help disentangle the relative importance of these putative drivers on changes in functional responses along HC gradients.

4.3 | Dependence of handling time on HC

Current evidence of possible links between HC and the maximum feeding capacity of predators, characterized by the handling time parameter of functional responses, is equivocal. We found strongest support for a concave-up response with the shortest handling times at intermediate levels of HC in the population-level experiment. This contrasted with HC-independent estimates of handling time, defined as the time needed to subdue and process the prey, in our and most other behavioural studies (4 out of 5 predator-prey pairs; e.g. Hauzy et al., 2010; Hossie & Murray, 2010; Table S1). We conclude that HC may directly interfere with handling behaviour only in special cases such as wading birds probing the mud for hiding molluscs (de Fouw et al., 2016).

Population-level studies (Table S1) usually reported no change (22 out of 34 predator-prey pairs with relevant data) or longer handling times (8 predator-prey pairs) in more complex environments. Magnitude of the effect was mostly comparable to or larger than in our study (increase of h with HC: $\Delta h = 0.11$ – 2.53 , mean = 0.83 ; decrease: $\Delta h = -1.08$ to -0.16 , mean = -0.51 ; no change: $\Delta h = -0.63$ to 0.69 , mean = 0.002 ; Figure 5). Among the studies including three or more HC levels, c. half of them found constant handling time (9 out of 16 predator-prey pairs; e.g. Hauzy et al., 2010). The remaining ones reported a concave-down relationship with the longest handling time at intermediate levels of HC (Hoddle, 2003), stepwise or monotone decline (Kalinkat, Brose, et al., 2013; Wasserman et al., 2016), or stepwise

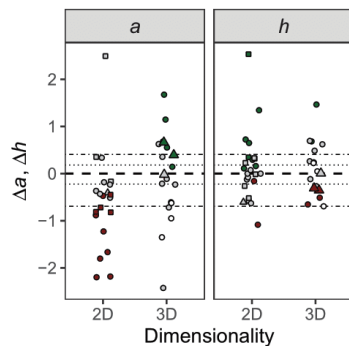


FIGURE 5 Magnitudes of the HC effect on attack rate a (Δa) and on handling time h (Δh) found in previous population-level experiments (circles, squares and small triangles; data in Table S1) and in the three plausible models of our data (large triangles). Predator-prey encounter mode: circles = active mobile, squares = active static, triangles = sit-and-pursue; symbol fill: white = effect was not tested, grey = no significant change, red = decline and green = increase with increasing HC. Dotted horizontal lines show $\pm 20\%$ change (as in h in Figure 1) and the dash-dotted lines are $\pm 50\%$ change (as in a in Figure 1). See Text S1 and Table S1 for details

or monotone increase with HC (Alexander et al., 2012; Cuthbert et al., 2020; Long et al., 2012; Table S1). As with the attack rate, some of the results depended on the experimental or modelling context (Barrios-O'Neill et al., 2015; Wasserman et al., 2016). Interestingly, handling times tend to, respectively, decrease and increase in more complex habitats for trophic interactions in 3D and 2D (Figure 5).

Given that digestion should be independent of HC, the reported variation of the handling time parameter of the functional response could stem from HC-driven changes in foraging activity and other predator and prey behaviour (Jeschke, 2007; Li et al., 2018). Our study implies that the relative importance of the mechanisms affecting maximum foraging rates varies with HC such that the largest positive or negative effect on handling time typically occurs at the transition from a structurally simple to more complex habitat. In our study, *Aeshna* larvae attacked the prey more often and were more successful in the structurally complex environments, thereby supporting the 'threshold hypothesis' (Gotceitas & Colgan, 1989). This pattern was likely driven by increased access to the prey in the water column and improved perching of the predators, which increased their strike accuracy. These mechanisms may also explain the stepwise decrease in handling time found in one experiment by Wasserman et al. (2016).

On the other hand, highly complex habitats can increase the time predators spend to orientate to and pursuit prey (Anderson, 1984), which may lead to the commonly observed increases in handling time parameter with HC as discussed above. In our experiment, *Chaoborus* larvae likely aggregated in pockets of free space created by the convoluted 'leaves' of the artificial plants at the highest HC level, and spatial aggregation of the prey is known to affect functional responses (Uiterwaal et al., 2019). *Chaoborus* larvae can also detect and avoid predators (Berendonk & O'Brien, 1996), which could have forced *Aeshna* to relocate and prolong pursuit. Taken together, these mechanisms could generate a nonlinear, unimodal dependence of handling time on HC as in our population-level experiment.

Another reason for the commonly reported HC-dependent handling times in the population-level experiments could be the non-independency of attack rate and handling time estimates and the ability of different parameter combinations to fit the same functional response curve (Uszko et al., 2020). We thus recommend using additional evidence to inform the population-level models and resolve the inherent uncertainty in parameter estimates and in the identification of (most) parsimonious models of the population-level data. In our study, results from Experiment 2 align best with models (10) and (12) from Experiment 1 assuming a stepwise increase in attack rate and a constant or varying handling time. Model (10) assuming constant handling time, despite its lower BIC ranking, may thus appropriately describe the changes in functional response along a HC gradient in our data.

4.3.1 | Implications for predator–prey dynamics, habitat restoration and regime shifts

In sum, our results and some of the previous studies show that functional responses can change nonlinearly along HC gradients. This

will have important implications for predator–prey and community dynamics (Barrios-O'Neill et al., 2015; Williams & Martinez, 2004). Current evidence suggests that the functional response shape is usually independent of HC (but see Barrios-O'Neill et al., 2015), which means that predator–prey and community responses to HC alterations will be mostly driven by changes in attack rates and handling time. The combination of a stepwise increase in attack rate and a concave-up dependence of handling time (Figure 1a) found in our Experiment 1 has not been reported before. Together with this result, the reported changes cover all scenarios defined in Figure 1a–i and include cases that can both stabilize and destabilize predator–prey dynamics (Table S1). Observed relative changes of attack rate or handling time due to HC alteration vary substantially across studies; their magnitude would determine the strength of this (de)stabilizing effect. Overall, increased HC appears to, respectively, weaken and strengthen trophic links in 2D and 3D predator–prey interactions.

Human-driven changes in HC are a pervasive issue in aquatic ecology (Kovalenko et al., 2012). These changes can have negative or positive effects on the biota, such as the removal of coarse wood debris from rivers or management practices aiming to restore or conserve elements of complexity in degraded rivers (Foote et al., 2020). Other examples include shallow lake eutrophication and the loss of submerged macrophytes versus re-oligotrophication aiming to restore the original lake status (Perrow et al., 1999), and coral- or oyster-based reef flattening versus creation of artificial reefs in marine habitats (Newman et al., 2015). Nonlinear changes in functional responses may amplify or dampen other mechanisms by which these changes in HC alter local communities, especially if the communities are relatively simple and the changes of HC affect trophic interactions of top predators or other keystone species (Kalinkat, Brose, et al., 2013).

Future studies of trophic interactions across HC gradients should thus go beyond the commonly used presence–absence binary scale, combine different experimental approaches to disentangle the underlying mechanisms and involve multiple predator–prey pairs to investigate how gradual changes in HC alter food web dynamics and community structure.

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AUTHORS' CONTRIBUTIONS

J.M., P.R.S. and D.S.B. designed the experiment 1; P.R.S., J.N. and D.S.B. designed the experiment 2; J.M. and P.R.S. conducted the experiments; J.M., P.R.S. and D.S.B. analysed the data with additional input from J.N.; J.M. and P.R.S. wrote the first draft and all authors contributed significantly to revisions.

DATA AVAILABILITY STATEMENT

All experimental data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.931zcrjrr> (Mocq et al., 2021).

ORCID

Julien Mocq  <https://orcid.org/0000-0003-4492-8815>
 Pavel R. Soukup  <https://orcid.org/0000-0001-8864-9530>
 Joacim Näslund  <https://orcid.org/0000-0003-1091-2225>
 David S. Boukal  <https://orcid.org/0000-0001-8181-7458>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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